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This is a taxonomic revision of the corticolous and lignicolous taxa of the genera *Bacidia* and *Bacidina* (Lecanoraceae, Lecanorales, lichenized Ascomycotina) in the continental United States and Canada. Twenty-seven species of *Bacidia* (one of which is divided into two subspecies) and twelve species of *Bacidina* are recognized. The morphology, secondary chemistry, ecology, and phytogeography of these species are discussed, and a key is provided. Apothecium pigmentation, thallus composition, presence of crystals in the proper exciple, hymenium height, thickness of paraphyses, spore shape and size, in *Bacidina* sometimes also conidial type and tholus structure, have proved to be the most important characters to distinguish between species. Circumscriptions of *Bacidia* and *Bacidina* are attempted. Tholus structure, cell structure of the proper exciple, presence of goniocysts, presence of crystals in the thallus cortex, and size of conidiogenous cells are the most valuable characters in the delimitation of these genera. Nine new taxa are described: *Bacidia diffracta*, *B. helicospora*, *B. salmonea*, *Bacidina aenea*, *Bn. californica*, *Bn. crystallifera*, *Bn. ramea*, *Bn. squamellosa*, and *Bn. varia*. Twelve new combinations are introduced: *Bacidia campalea*, *Bacidia laurocerasi* subsp. *idahoensis*, *Bacidina assulata*, *Bn. egenuloidea*, *Byssoloma meadii*, *Fellhanera floridana*, *Herteliana alaskensis*, *Lecania stigmatella*, *L. subfuscula*, *Pachyphiale gyalizella*, *Ropalospora phaeoplaca*, and *Ophioparma rubricosa*. In addition to the newly described species, 12 species of *Bacidia* and four species of *Bacidina* are correctly reported from the study area for the first time. The genera *Psorella* and *Toniniopsis* are reduced into synonymy with *Bacidia*.

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Contents

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Introduction

When De Notaris described *Bacidia* in 1846, he included only *B. rosella* (Pers.) De Not. and the species presently known as *Pachyphiale carneola* (Ach.) Arnold (De Notaris 1846). In the following years, the genus was variously treated. Numerous species were described as new or combined into *Bacidia* by Arnold, Lettau, and Vainio. Other authors, for example Nylander, did not accept the genus at all. *Bacidia* was typified with *B. rosella* by Fink (1910). It was with Zahlbruckner's *Catalogus lichenum universalis* that *Bacidia* received its first consistent and comprehensive treatment (Zahlbruckner 1921-1940). In Zahlbruckner's taxonomy, *Bacidia*, with a some exceptions, comprised all crustose lichens with a chlorococcoid photobiont, biatorine or lecideine apothecia, and spores with three or more transverse but no longitudinal septa. Altogether, he referred 647 accepted species and a large number of additional synonyms to *Bacidia*. Similarly, he referred species with non-septate spores to *Lecidea*, species with one-septate species to *Catillaria*, and species with muriform spores to *Lopadium*. These genera included 1486, 304, and 110 accepted species, respectively. *Lecidea*, *Catillaria*, *Bacidia*, together with *Toninia*, *Rhizocarpon*, and a number of small genera, constituted the family Lecideaceae in the sense of Zahlbruckner.

Zahlbruckner's *Catalogus* has been the most influential work of 20th century lichenology, despite the fact that it was soon realized that the system presented was highly artificial. For example, Santesson (1952) remarked that Zahlbruckner's system "has become dominating in a way strongly detrimental to the development of a more natural lichen classification". Regarding *Bacidia*, he noted that the delimitation was probably unnatural.

Even in our enlightened time, the ghost of Zahlbruckner haunts lichenology. Practically every contemporary lichen flora, to some extent, still uses a more or less Zahlbrucknerian concept of *Lecidea*, *Catillaria*, and *Bacidia*. This is, of course, not done in the belief that this system is natural, but for practical reasons and since detailed knowledge of many species is still wanting.

Since the publication of *Catalogus lichenum universalis* a large number of species have been transferred to other genera, which are not seldom distantly related to *Bacidia* s. str. as typified by *B. rosella* (Fig. 1). Particular attention has been paid to the foliicolous members of *Bacidia* sensu Zahlbruckner, many of which have been referred to genera in the families Pilocarpaceae and Ectolechiaceae, e.g., *Fellhanera*, *Badimia*, *Calopadia*, *Loflammia*, *Sporopodium*, and *Tapellaria* (Hafellner 1984, Vězda 1986, Lücking 1992, Malcolm & Vězda 1994; see also compilation by Farkas & Sipman 1993). The number of species referrable to *Bacidia* in the strict sense is unknown, but I would roughly estimate it to 60-90 species worldwide. A vast majority of them has probably already been described. Most are probably corticolous, but some inhabit various other substrata.

Bacidina is one of the segregate genera from *Bacidia* sensu Zahlbruckner, but contrary to many other such genera, *Bacidina* is closely related to *Bacidia* s. str. The history of this genus is a short one. It was first recognized as the "*Bacidia phacodes*-Gruppe" by Vězda (1983) and was later formally described as *Bacidina* by Vězda (1991). *Bacidina* is, however, antedated by *Woessia* and *Lichingoldia*, both described in the same publication (Hawksworth & Poelt 1986). Until now, 17 species (including one which I consider to be a synonym) have been formally referred to *Bacidina* (Vězda 1991, Lumbsch & Vězda 1992, Farkas & Vězda 1993, Vězda 1994, Wirth 1994). Six new species and two combinations in this genus are added here. *Woessia* and *Lichingoldia*, on the other hand, have (with one exception) not at all been used in taxonomic or floristic literature following their publication. The reason why these names did not receive any attention is that the authors obviously were not aware of describing the *Bacidia phacodes* group, and nor was it their intention to do so. An attempt to introduce the use of *Woessia* was recently published by Sérusiaux (1995). In my opinion, a reestablishment of *Woessia* would be a clear violation of the spirit of the present International Code of Botanical Nomenclature (Greuter et al. 1994). Thus, it is suggested that *Bacidina* be conserved against *Woessia* and *Lichingoldia*. Pending the final solution of this matter, the use of *Bacidina* is retained here.

Contrary to most species of *Bacidia*, those of *Bacidina* are often very inconspicuous. They are small, "scurfy", often sparingly or not at all fertile, and hence they are likely to escape attention. On a worldwide basis, almost half of the presently known species are foliicolous. Several species are exclusively corticolous, but some can be found on practically every substratum where competition from other lichens is low, including such odd ones as brick, rusty iron, and leather. The 24 presently known species in *Bacidina* probably constitute only a small part of the true number. Many species remain to be discovered.

Objectives

The objectives of this study are to provide (1) a taxonomic revision of the North American corticolous and lignicolous taxa belonging in the genera *Bacidia* (in the strict sense) and *Bacidina*, and (2) a preliminary hypothesis on the circumscription of these genera, based mainly on the North American taxa studied.

At a critical point in my work during early 1994, I was choosing between delimiting my work the way

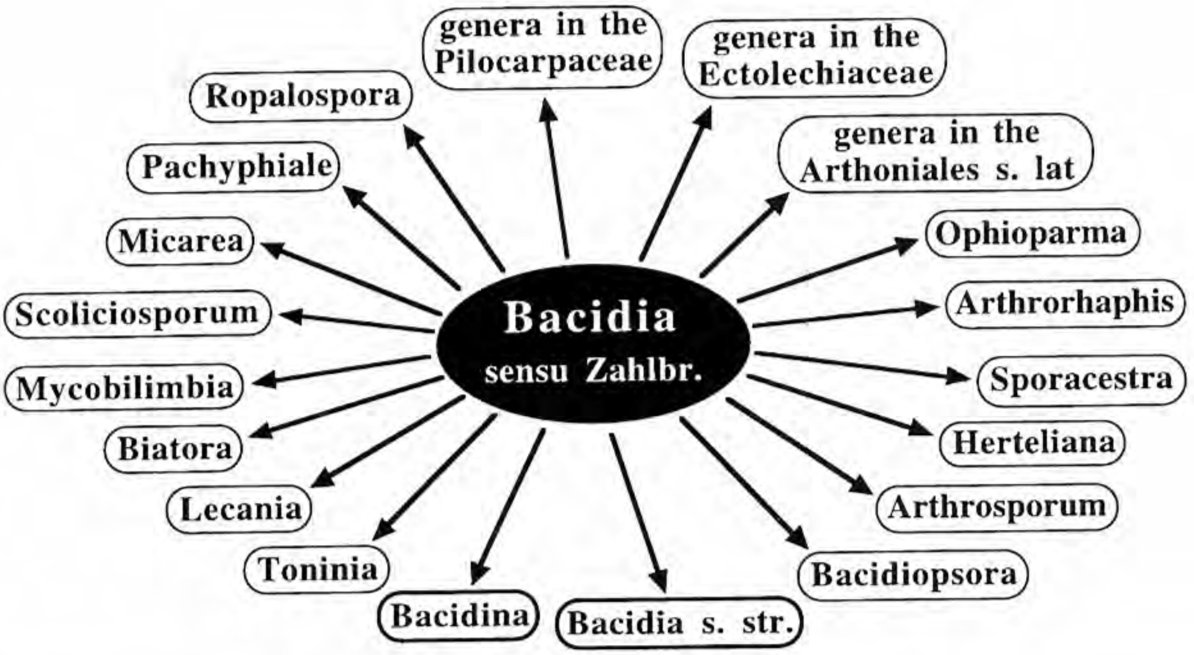


Fig. 1. Transfers of species from *Bacidia* sensu Zahlbruckner to other genera made after the publication of *Catalogus lichenum universalis* (Zahlbruckner 1921-1940), including those suggested in this study. – The circumscription of the Ectolechiaceae by Vězda (1986) is probably artificial, being based mainly on the presence of campylidia. The presence of this structure has been shown to appear in widely different families and thus to be polyphyletic in origin (Sérusiaux 1986, Aptroot & Sipman 1993, Lücking 1995, Sérusiaux 1995). Lücking et al. (1994) doubt the distinctness of the family Ectolechiaceae to Pilocarpaceae.

done here or treating all North American species of *Bacidia* (but not *Bacidina*) irrespective of substratum choice. Treating all North American *Bacidia* and *Bacidina* was out of the question, due to the time limits set on the work. My choice fell on the present delimitation, for the simple reason that it would be impossible to delimit *Bacidia* properly without also studying members of *Bacidina*.

Material and methods

Study area

The study area includes the continental United States and Canada. This area is henceforth referred to as "North America", although I am aware that other ways of delimiting this continent have been suggested.

Material

All North American species of *Bacidia* and *Bacidina* found on tree-bark or lignum have been treated in their entirety, i.e., specimens from all substrata have been included if at least one specimen of the species is corticolous or lignicolous.

Slightly more than 2000 specimens were examined, including material from the following herbaria (abbreviated according to Holmgren et al. 1990): BG, CANL, COLO, FH, FLAS, H, LD, MICH, MIN, MSC, MU, NY, OSC, S, SFSU, TSB, UBC, UPS, US, WIS, WTU, WWB, and the private herbaria of Charis Bratt, Willa Noble, and Shirley Tucker. My own material, comprising about 300 specimens, is deposited in LD. In the course of finding type material for names that might be applicable to North American species (well over 200 names), I have seen material from numerous other herbaria.

Field work

Field work was carried out in California, Oregon, Washington, and British Columbia in March-May 1989, in Minnesota, Michigan, Ontario, Quebec, New Brunswick, Nova Scotia, Maine, Delaware, and Maryland in September-October 1989, in Louisiana, Mississippi, and Florida in October-November 1993, and in California and Arizona in March-April 1995. From the last journey, only some ecological results have been included in this work, whereas the majority of the collections still await revision. Twenty-three out of 28 taxa of

Bacidia and 8 out of 12 taxa of *Bacidina* have been studied in the field in North America. Two additional species occurring in North America have been studied in Sweden but not in North America.

Morphology and anatomy

Characteristics of the thallus and apothecia were examined from hand-cut sections or squash preparations mounted in deionized water, except paraphyses, which were measured in a 10 % aqueous solution of KOH. Characters were studied under an ordinary light microscope, a polarized light microscope, and/or an interference contrast light microscope, depending on what was most suitable. Lactophenol-cottonblue (LCB) was used to enhance the contrast when studying excipular or cortical structures. When studying excipular structures, a 0.2 % aqueous solution of sodium hypochlorite (a commercial solution diluted about 20 times) was sometimes used to bleach pigments and improve the optical clarity of the gelatinous cell walls. Higher concentrations of hypochlorite should be avoided, since the cell walls may swell and rupture, and thus alter the appearance of the cell structure.

The following standard reagents were used to study the colour reactions of pigments and solubility of crystals: a 10 % aqueous solution of KOH (abbreviated K), a commercial 4.4 % aqueous solution of sodium hypochlorite (abbreviated C), and a 50 % solution of HNO_3 (abbreviated N).

Routine investigations of the structure of the ascus apex were carried out on gently squashed hand-cut sections stained with a 0.3 % aqueous solution of iodine, following pretreatment with K. I decided to use this method after having performed a small pilot study on a small number specimens of a few randomly chosen species. Asci of these specimens were stained according to the method mentioned, with the same iodine solution but without pretreatment with K, as well as with a 0.3 % solution of iodine in which lactic acid was substituted for water, with and without pretreatment with K. All four methods were shown to give the same result, but the method finally chosen was the one which gave the optically clearest preparations combined with a low number of ruptured asci. The "lactic-iodine", which has lately been used by several authors, including myself, in this case resulted in a high proportion of ruptured asci, probably since the solution is very viscous and more force is needed when squashing the preparations. Particular care was always taken not to study asci with ruptured walls, since such asci often show "freak" structures.

The number of specimens from which measurements of quantitative characters have been extracted (N; see below) is c. 20 or higher in common species. In uncommon species, I have used as many collections as possible, provided they have been reasonably large. It was attempted to use specimens from various parts of the distribution range. I have refrained from using more than one specimen from a single locality. Otherwise, there is a risk of a single genotype becoming over-represented in the measurements.

Measurement accounts

Measurements are generally given as "(minimum value observed -) lowest specimen arithmetic mean observed - arithmetic mean of all observations - highest specimen arithmetic mean observed (- maximum value observed) (s, N, n)", where s is the standard deviation of all observations, N the number of specimens studied, and n the number of observations per specimen. The total number of observations is thus N × n. When N= 1 or n= 1, the lowest and highest specimen arithmetic means are not meaningful, and have consequently been left out. The unit of the standard deviation is always the same as the character itself, but has generally been left out of the description in order to make them easier to read. All characters were shown to be about normally distributed before using the arithmetic mean and standard deviation as measures of distribution center and dispersal.

In some cases, where detailed measurements were difficult to obtain and/or of little use, the standard form "minimum value observed - maximum value observed" was employed.

There are a number of reasons for using this particular method of presenting measurements. Basically, I feel that making a large number of measurements and then preparing descriptions using only the minimum and maximum values observed is a huge waste of useful information. Fortunately, it has become increasingly common to see measurements (particularly of spores) that are presented as the arithmetic mean ± 1 or 1.5 standard deviations. This method is commendable, but I think such figures are slightly difficult to use in practical determination work, particularly if similar species have overlapping measures. The advantage of the method used here is that different information can be extracted depending on the needs of the user. The disadvantage is that the descriptions become long and difficult to read. I think, however, that the advantages outweigh the disadvantages. If one wishes to compare species with each other or compare the variation between different distribution areas of a single species, one can use the arithmetic mean and the standard deviation. The remaining figures can be used for ordinary determinations. If the aim is to see whether a single measurements of, i.e., spore length lies within the variation of a particular species, one is confined to the minimum and maximum values (the values within brackets). If, instead, one uses an average of n measurements (often 5 or 10, rarely 20), the same comparison should be made using the lowest and highest specimen arithmetic mean (the values flanking the mean). The range of variation of the latter measure is invariably smaller than the range from the minimum to the maximum value. Thus, it is often worth the effort to use an average of n measurement instead of single measurements. It definitely results in more reliable determinations.

Measurements, both in the dissecting microscope and in the light microscope, were usually at first made with one scale division as the unit. Later on, when preparing the description, the unit "scale divisions" was multiplied with the appropriate factor to obtain the measurements in µm or mm. This has caused some of the measurements in the descriptions to appear rather odd. For example, the reader will notice that the figure 1.6 µm appears rather often in the descriptions (often for the width of the paraphyses). This is explained by the fact that 1.6 µm exactly corresponds to two scale divisions when using the 100× lens in my light microscope!

Chemistry

Secondary metabolites were investigated using high performance thin layer chromatography (HPTLC) according to the method described by Arup et al. (1993). *Bacidia friesiana*, *B. igniarii*, and *Bacidina assulata* were excepted due to sparsity of material, otherwise all species were studied. Between one and 11 specimens per species were studied, in all 110 specimens.

Distribution

In the discussion on phytogeography and in the distribution maps, I have consistently ignored literature records, since they are not reliable.

Numerical and statistical methods

Phytogeography

The similarity in composition of *Bacidia* species between twelve phytogeographic regions (nine North American and three European) was studied. The 27 North American and four additional European species of *Bacidia* were scored as present (1) or absent (0) in each of the twelve regions. The similarity in species composition between each pair of the regions were then calculated using the simple matching dichotomy (S4) coefficient. The resulting similarity matrix was used in a single linkage cluster analysis. The calculations were performed with the SYSTAT 5.2.1 statistical package (Wilkinson 1992). Details of the methods used as well as definitions of the twelve phytogeographic regions are found in the chapter *Phytogeography*.

Taxonomy

The distinctness of *Bacidia polychroa* vis-à-vis *B. diffracta*, *B. laurocerasi* subsp. *laurocerasi* vis-à-vis subsp. *idahoensis*, and western vis-à-vis eastern populations of *B. heterochroa* were investigated using two statistical methods, one-way analysis of variance (one-way ANOVA) and chi-square, and two numerical methods, canonical variate analysis (CVA) and principal components analysis (PCA), the latter based on a Pearson correlation matrix among the original characters. In the PCAs, the combination of characters giving the best separation was chosen. All calculations were performed with the SYSTAT 5.2.1 statistical package (Wilkinson 1992), except the ANOVAs of *Bacidia laurocerasi* s. lat., which were performed with SuperANOVA (Abacus Concepts 1989).

The CVA, also known as canonical discriminant analysis or simply discriminant analysis, and the PCA are similar in producing a number of orthogonal, linear axes (called canonical variates or principal components) composed of the original characters, i.e., a kind of composite characters (Dunn & Everitt 1982). A PCA arranges the axes in order of decreasing amount of total variance explained, each maximizing the amount of variance. In a CVA, on the other hand, each axis maximizes the separation between a number of pre-defined groups along each of the axes.

The measurements used in the data analyses are basically the same as the ones used to prepare the descriptions of the species, the only exceptions being that I have included eight specimens of European *B. laurocerasi* in one of the analyses and that I have excluded specimens from which I have been unable to extract a full set of measurements of all the characters used (hence the slight discrepancies between the species descriptions and the tables in the chapter *Numerical and statistical treatment*). When more than one measurement of a character was made on a specimen (i.e., when $n > 1$), the arithmetic mean of the n measurements was used in the subsequent analyses. Prior to the analyses, the distribution of the measurements of each character was studied. No distribution was found to be skew enough to violate the assumptions of the methods used. Thus, no transformations were found to be necessary, nor did I have to exclude any characters for this reason. Methodological details of the individual analyses are presented in the chapter *Numerical and statistical treatment*.

Nomenclature

The abbreviation of authors follows Brummitt & Powell (1992). Names that have been lectotypified, neotypified, or suggested for conservation with a conserved type in this work have been marked with an asterisc in the index (see p. 145).

Taxonomic concepts

A taxonomic species concept has been used (Cronquist 1988: 71). In my opinion, species boundaries are marked by correlated discontinuities in the variation of two or more independent characters, i.e., by the absence (or at least extreme rareness) of certain combinations of character states. A genus is a monophyletic assemblage of species. It is an abstraction without characters of its own; it is defined by the species included in it. Since genera have no independent existence in nature, their boundaries (and hence their size) are somewhat arbitrary. In my opinion, genera should be operational to other than the specialist(s) on the genus/genera concerned.

The North American Bacidia and Bacidina - an outline

To my present knowledge, 27 species of *Bacidia* (one of which is divided into two subspecies) and 12 species of *Bacidina* occur on bark and lignum in the continental United States and Canada. Apart from the nine species described here as new, 16 are reported (correctly) for the first time from this area: *Bacidia absistens*, *B. aggregatula*, *B. auerswaldii*, *B. biatorina*, *B. campalea*, *B. friesiana* (previous reports erroneous), *B. heterochroa*, *B. igniarii* (previous reports erroneous), *B. insularis*, *B. mutabilis*, *B. reagens*, *B. russeola*, *Bacidina arnoldiana* (previous reports erroneous), *Bn. assulata* (previous reports erroneous), *Bn. chloroticula*, and *Bn. egenula* (previous reports erroneous).

Among the corticolous and lignicolous species treated here only three have so far been collected in North America on soil or rock as well, viz. *Bacidia suffusa*, *Bacidina egenula*, and *Bn. egenuloidea*. A number of exclusively terricolous, saxicolous, or foliicolous species have been reported for North America, however. In *Bacidia*, one marine saxicolous species, *B. scopulicola* (Nyl.) A. L. Sm., and three terricolous/muscicolous species, *B. bagliettoana* (A. Massal & De Not.) Jatta, *B. herbarum* (Stizenb.) Arnold, and *B. illudens* (Nyl.) Lynge, have been reported. My preliminary findings show that these determinations are correct. Two additional species of *Bacidina*, *Bn. apiahica* (Müll. Arg.) Zahlbr. and *Bn. inundata* (Fr.) Vězda, have been reported for North America. *Bn. apiahica* is a foliicolous species found in the Gulf States. It has been reported to be corticolous on twigs on occasions (Santesson 1952), but I know of no such finds from this area. North American collections of *Bn. inundata* are exclusively saxicolous, but in Europe it is sometimes found on the bark of roots and tree bases near water. The saxicolous, terricolous, and muscicolous species of *Bacidia* and *Bacidina* are still rather poorly known, and further species should be expected.

Morphology and anatomy

Thallus

Growth form

The thalli of all treated species of *Bacidia* and *Bacidina* are lichenized, and crustose or (in *Bacidina squamellosa*) finely squamulose. In many species, the thallus is more or less continuous, often more or less rimose. Only seldom it is areolate or entirely without cracks. A number of species possess a discontinuous thallus, consisting of discrete to contiguous areoles. In several species with a normally continuous thallus, young parts of the same thallus or less well-developed specimens may be more or less discontinuous.

In seven species of *Bacidia*, *B. auerswaldii*, *B. biatorina*, *B. diffracta*, *B. hostheleoides*, *B. rubella*, *B. schweinitzii*, and *B. subincompta*, the thallus is commonly or exclusively granular. The granules are homologous to areoles, but contrary to normal areoles the granules are not necessarily attached to the substratum by their lower surface. Instead, they may form obliquely upwards from old areoles (which may or may not be attached to the substratum), thus causing the thallus to become several granule layers thick.

Bacidina squamellosa is the only species in the two genera that has a squamulose thallus. These squamules are small, deeply incised, and vary from prostrate to ascending. When prostrate, the squamules are virtually inseparable from effigurate areoles, which indicates that the squamulose habit is easily derived from a crustose one (or vice versa).

Prothallus

All species of *Bacidina* treated here lack a prothallus, whereas it is present in many species of *Bacidia*. It is usually endosubstratal, very thin, pale grey to white, and present as a diffuse zone along the edge of the thallus and sometimes also between discrete areoles. In six species (*B. aggregatula*, *B. campalea*, *B. helicospora*, *B. heterochroa*, *B. mutabilis*, and *B. russeola*), on the other hand, the prothallus forms a narrow, episubstratal, black

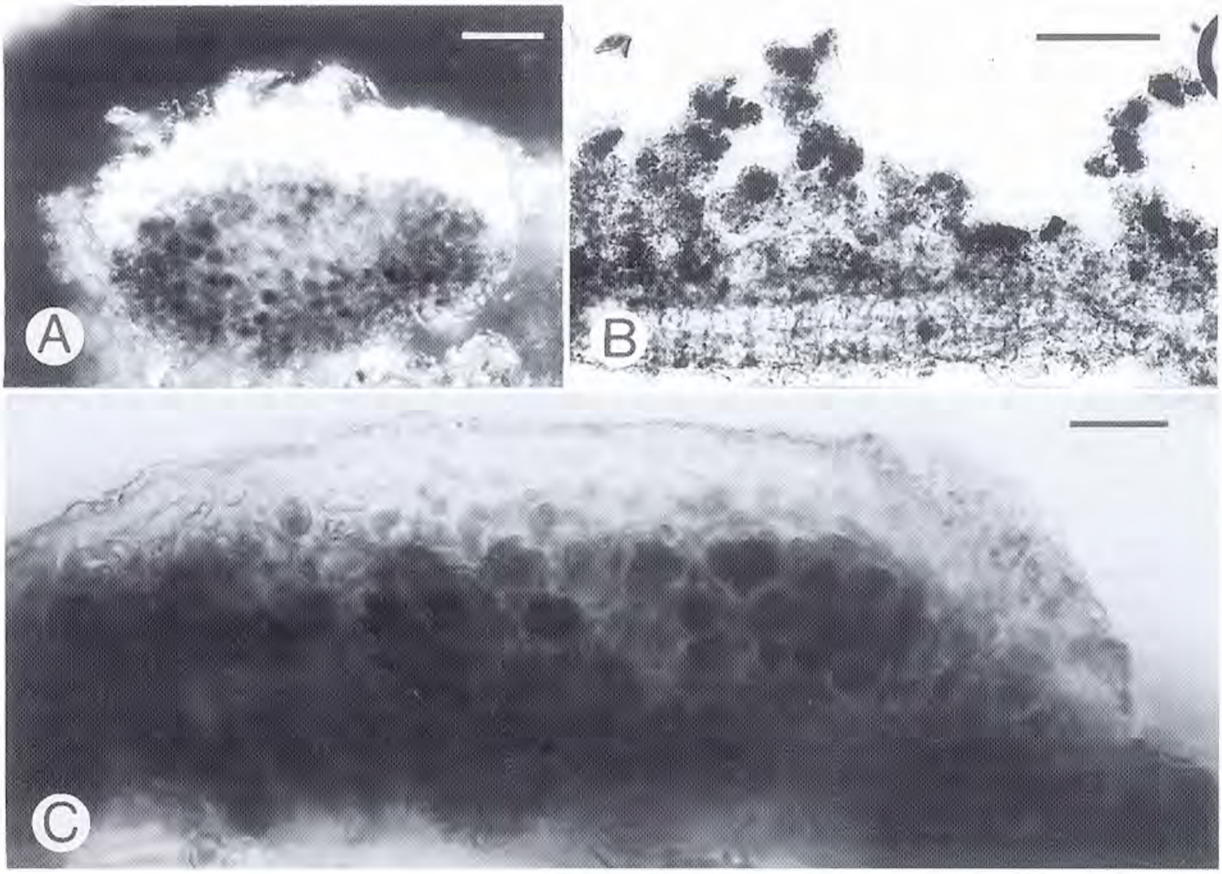


Fig. 2. Thallus, transverse sections stained with LCB, viewed in interference contrast. – *A. Bacidia rubella* (Ekman L960, LD), transverse section of thallus granule showing brilliant white crystals in cortex of upper side. Bar = 30 µm. – B. *Bacidina varia* (Ekman L1191, LD), section through thallus producing goniocysts in chains that become almost coralloid or isidia-like. Bar = 100 µm. – C. *Bacidina californica* (Ekman L632, LD), transverse section showing algal layer (dark), stainable layer (grey), and epinecral layer (pale). Bar = 10 µm.

line along the edge of the thallus, often where the specimen meets other lichens. Remarkably, the latter kind of prothallus is present in five out of eight species that are mainly distributed south of the study area, whereas it is present in only one out of 18 species endemic to North America or mainly distributed in temperate areas of the northern hemisphere (difference in proportion tested by Yates' corrected chi-square; $p= 0.006$). This is particularly interesting, since there is no reason to believe that the southern species are more closely related to each other than to other species of *Bacidia*. Thus, it appears that the black, episubstratal prothallus is polyphyletic in origin and that its evolution has somehow been favoured by a tropical or subtropical climate.

Surface

The surface of many species is furnished with variously shaped, coarse, irregular projections. I have used a rather arbitrary, five-graded scale to describe the surface, arranged here by increasing height of the projections: (1) Smooth, with no projections, (2) wrinkled, (3) warted, (4) tuberculate, and (5) subsquamulose. It should be noted that I use the term "warted" for a surface with rather high, often very irregular projections that are more or less unequal in size and direction. This means that I do not refer to a regularly papillose surface, nor should it be translated to the anglisized latin word "verrucose", which is often used to describe the shape of an entire areole.

Most species of *Bacidia* and *Bacidina* have a wrinkled or warted thallus surface. A smooth thallus may occasionally be present in a number of species, but no species has an invariably smooth thallus. Likewise, a tuberculate to subsquamulose thallus may be present in some individuals of a few species, although rarely and never invariably within a species. Subsquamulose individuals, like the term implies, have projections high and large enough as to give the thallus an almost squamulose appearance.

In some species, the surface structure is more or less strongly affected by the presence of goniocysts; see *Vegetative dispersal* below.

Pseudocyphellae are not present in any species of *Bacidia* or *Bacidina*, nor is a crystal layer on the surface of the thallus. Crystals may be present in the cortex, however (see below).

Cortex

An upper cortex is present in all species of *Bacidia* and most species of *Bacidina*. Basically, it consists of two layers (Fig. 2C) similar to the upper cortex of *Toninia* as described by Timdal (1991). Accordingly, I am retaining his terminology: the lower layer is comprised of living hyphae that are anticlinally, irregularly, or rarely (in some granular forms of *Bacidia subincompta* and in *Bacidina ramea*) more or less periclinally arranged, the lumina of which are easily discernable and deeply stainable with lactic cotton blue (LCB). This is termed the *stainable layer* by Timdal. The upper layer, termed the *epinecral layer*, consists mainly of periclinally arranged, mostly dead hyphae with lumina that are difficult to discern and not stainable in LCB (apart from a few living cell lumina). In all species of *Bacidia*, the epinecral layer contains minute crystals (visible at least between two polarizing filters) that are soluble in KOH but insoluble in HNO_3 and H_2SO_4 (Fig. 2A). These crystals may be absent from some poorly developed individuals of some species, e.g., *B. vermifera*. Conversely, the crystals may be very abundant not only in the epinecral layer but also in the stainable layer in a few species, e.g., *B. suffusa*. In *Bacidina*, on the other hand, crystals are never present in the upper cortex (Fig. 2B, C). Dead photobiont cells can be found in both of the cortex layers in all species.

A lower surface which is not attached to the substratum and different in anatomy from the upper, corticate one is found in two species of *Bacidia* with granular thallus, *B. rubella* and *B. diffracta*. The lower surface consists of a few layers of periclinally arranged, living hyphae that are deeply stainable in LCB. In both the species mentioned, an upper cortex of normal compositon is present.

Although most species of *Bacidia* and *Bacidina* conform to the pattern described above, there are several interesting variations and deviations. The most important ones concern a group of species of *Bacidia* with granular thallus, namely *B. auerswaldii*, *B. biatorina*, and some forms of *B. subincompta* among the North American species, and also the European *B. caesiovirens* S. Ekman & Holien (not treated here). In these species, the entire surface of the thallus granules (i.e., also the upper one) is identical in anatomy to the lower, ecorticate surface of *B. diffracta* and *B. rubella* (Fig. 2A). Possibly, they are not only identical in anatomy, but even truely homologous. *B. auerswaldii*, *B. biatorina*, *B. subincompta*, and *B. caesiovirens* prefer humid environments. Perhaps the lack of a crystal inspersed epinecral layer has been an advantage in such environments, possibly since gaseous exchange is facilitated and the risk of prolonged desiccation is minimal.

In *Bacidina squamellosa*, the only known species in the genus with a squamulose thallus, the upper as well as lower surface of the squamules is very similar in anatomy to the species discussed above, i.e., it is ecorticate and instead comprised of a layer of periclinally arranged, living hyphae stainable in LCB.

Whereas an epinecral layer is lacking in some species, the stainable layer is lacking in some forms of a few other species, namely *B. schweinitzii*, *B. suffusa*, and some non-granular specimens of *B. subincompta*. The epinecral layer is well-developed in these species, however.

The distinct stratification present in many species is disrupted by the presence of goniocysts in several species of *Bacidina*. Goniocysts are discussed below under *Vegetative dispersal*.

Photobiont layer

The photobiont of all species is green, unicellular, up to c. 15 µm in diameter, and almost certainly belongs in the Chlorococcales. In *Bacidina arnoldiana*, the photobiont has been shown to belong to *Chlorella saccharophila* (Krüger) Mig. var. *ellipsoidea* (Gerneck) Fott & Nováková (Tschermak-Woess 1988a, as *Woessia fusarioides*). Tschermak-Woess (1988b) lists no additional determination (to genus or species) of the photobiont of any species presently referred to *Bacidia* s. str or *Bacidina*. It has been outside the scope of this study to identify the photobiont.

The photobiont layer is commonly continuous and generally does not exceed 50 µm in thickness. In some specimens of *Bacidia heterochroa* and in several species of *Bacidina* with goniocysts, I have observed a discontinuous photobiont layer with colonies of algae separated by more or less wide strands of loosely interwoven fungal hyphae.

Medulla

A medulla is not developed in most species of *Bacidia*.

Only in species with a thick thallus a medulla is sometimes present, e.g., in *Bacidia schweinitzii* and *B. suffusa*. A medulla in the strict sense, i.e., a fungal layer between the algal layer and the surface of the substratum, is lacking in all species of *Bacidina* (but see below under *Vegetative dispersal*).

Attachment

The thallus is attached to the substratum by sparse hyphae extending from the lower surface. The hyphae penetrate into the surface of the phorophyte, usually only to a depth of about 10-100 µm. In one extreme case, I have observed hyphae of *Bacidia rubella* penetrating c. 400 µm into the substrate.

Vegetative dispersal

Isidia are absent from all studied species of *Bacidia* and *Bacidina*, and soredia are absent from *Bacidia*. The thallus structure of several species of *Bacidina* is complicated. In nine out of twelve North American species, the thallus is sometimes at least in part composed of loosely to firmly aggregated granules (Fig. 2B). When firmly aggregated, the granules may form isidia-like or coralline structures. The thallus granules found in *Bacidina* have been referred to as goniocysts by Vězda (1980, 1990), Sérusiaux (1985), and Lücking (1992). See Tab. 1 for an account of the occurrence of goniocysts in the species of *Bacidina* treated here.

The function of the so-called goniocysts appears to vary between and even within the species. In *Bn. arnoldiana*, *Bn. egenula*, and *Bn. egenuloidea*, the goniocysts constantly form the main part of the thallus. Even so, one cannot rule out the possibility that the goniocysts may function as vegetative dispersal units as well. In other species, the thallus is not entirely composed of goniocysts. Instead, the goniocysts are more or less loosely aggregated in distinct or diffuse spots on the thallus. In these cases, it is obvious that the goniocysts function as vegetative dispersal units. *Bn. varia* (Fig. 2B) and *Bn.* sp #1 often form large, goniocystate thalli without apothecia, which implies that in such cases the goniocysts are the main method of dispersal. Furthermore, as in many species with both soralia and apothecia, the number of apothecia in a specimen is more or less inversely proportional to the quantity of goniocysts. This indicates that the lichen, due to environmental influence and/or genetic predisposal, can use either ascospores or goniocysts/soredia as the principal mean of dispersal.

The presence of goniocysts strongly affects the general appearance as well as the anatomy of the thallus. In most species of *Bacidina*, the goniocysts usually form finely granular, pale (sometimes yellowish) green masses on the surface of the thallus. Specialized goniocystangia, as described by Sérusiaux (1985) for *Bacidina mirabilis* (Vězda) Vězda and four species of foliicolous *Opegrapha*, are not present in any *Bacidina* treated here. Goniocystate parts of a thallus generally acquire a completely disrupted algal layer (Fig. 2B). The algae may become more or less "clumped", i.e., form colonies within the fungal tissue, or they may form a very interrupted layer. In any case, there is a marked concentration of algae near the surface of the thallus, and a considerable amount of the thallus forms a kind of medulla. The mitotic activity of both the alga and the fungus is obviously very high near the thallus surface. Goniocysts are formed by the enwrapment of the algal cells by the fungus. In *Bn. chloroticula*, I have observed that the goniocysts are originally formed from one single algal cell, but I have not established whether or not this holds true for the other eight species with goniocysts. Once formed, the goniocysts may bud off more or less immediately, or they may remain to form more or less coherent aggregations of isidia-like or coralline structure.

There is no modern, satisfactory definition of a goniocyst. The use of the term goniocyst, the anatomy of various structures named goniocysts, and the possible distinction between a goniocyst and a soredium was discussed in detail by Sérusiaux (1985). Although not explicit, it is clear from the context of his paper that Sérusiaux favours the definition of a goniocyst used by Vězda (1980) with some changes and amendments: the formation of a goniocyst is initiated by the capture of one single algal cell by the fungal hyphae. The hyphae quickly enclose the algal cell, all future divisions of which must take place within the structure. In comparing the goniocystate *Bacidina mirabilis* (Vězda) Vězda with available data on sorediate species of Parmeliaceae, he remarks that "the algal divisions are responsible for the formation of soredia", whereas the formation of the goniocyst is an initiative of the fungus. However, as also pointed out by Sérusiaux, the question of how to distinguish between a soredium and a goniocyst anatomically awaits a final solution.

In my opinion, the anatomical/ontogenetical definition of a goniogyst has some shortcomings. Firstly, one has to decide whether a goniocyst and a soredium should be defined by function or by anatomy/ontogeny. I believe it would be a logical flaw assuming that there must necessarily be a difference in anatomy between a soredium and a goniocyst. There are no data showing that soredia consistently arise from more than one algal cell, which would be the logical assumption if goniocysts are to be distinguishable on the basis of this character. And why draw the line between the formation from one and two algal cells? I fail to see the principal difference; such a line appears to me as arbitrary. Soredia and goniocysts obviously do not differ in being enclosed by fungal hyphae. When it comes to the mycobiont or the photobiont taking the initiative in the formation of the structure, I doubt that it is possible to draw such a clear line, considering that we are dealing with symbiotic organisms, in which many processes must be coordinated. One should also bear in mind that soredia and, most likely, also goniocysts have evolved several times. Consequently, there is little reason to believe that soredia or goniocysts of widely differing groups are similar in all traits, or not even homologous.

The functional view of a goniocyst advocated by Hawksworth et al. (1983) and Coppins (1983) appears to me as more attractive. In this definition, both goniocysts and soredia consist of clusters of algal cells (the number of which they originate from being irrelevant) surrounded by fungal hyphae. The difference lies in the function: Goniocysts are the main component of the thallus, and do not normally serve in the propagation of the lichen. Soredia, on the other hand, primarily function as vegetative dispersal units. A consequence of this definition is that the two concepts become overlapping, which in my opinion is logical. The function of a "thallus granule" can, in some species, be to serve in the propagation *as well as* to be the component of which the thallus is built. If the latter definition is used, then several of the North American species of *Bacidina* may be termed sorediate.

Nevertheless, as a provisional measure, I have chosen to retain the term goniocyst for the "thallus granules" formed by the *Bacidina*, as long as there is no general agreement on the definition of the terms involved.

In the granular species of *Bacidia* discussed previously, the granules are homologous with normal areoles, and should not be confused with the goniocysts of *Bacidina*. Anyway, it is likely that the granules of the *Bacidia* species can function as vegetative propagules.

Apothecia

Morphology and ontogeny

The apothecia are biatorine or lecideine in all North American species of *Bacidia* and *Bacidina* except *Bn. ramea*. In *Bn. ramea*, the apothecia are zeorine, possessing a proper exciple that is as well-developed as in other species of *Bacidina*, as well as a thin thalline margin that soon becomes excluded (Fig. 43E). The thalline margin, however, is usually easily observed in sections, even in old apothecia.

The apothecia of *Bacidia* and *Bacidina* are usually sessile on the thallus or slightly constricted below. When young, the disc is plane or slightly concave, and the margin is distinct, level with the disc or, more commonly, slightly raised. The disc becomes increasingly convex with age in many species, and simultaneously, the margin becomes increasingly suppressed, finally to be entirely excluded. In a number of species, however, the disc often or always remains (almost) flat and the margin distinct: *Bacidia absistens* (often), *B. auerswaldii*, *B. biatorina*, *B. campalea*, *B. circumspecta* (often), *B. helicospora*, *B. heterochroa*, *B. igniarii*, *B. insularis*, *B. mutabilis*, *B. reagens* (often), *B. russeola*, *B. vermifera*, *Bacidina chloroticula*, and *Bn. egenuloidea*.

A white pruina occurs occasionally or invariably in eight species of *Bacidia*, namely *B. aggregatula* (sometimes), *B. diffracta* (always), *B. insularis* (sometimes), *B. mutabilis* (always?), *B. polychroa* (sometimes), *B. rubella* (sometimes), *B. schweinitzii* (rarely), and *B. suffusa* (always). The pruina may vary from thin to thick, and it is variable within the same species whether the pruina occurs on the edge of the apothecium, the disc, or both. It is not uncommon that only young apothecia are pruinose. In *Bacidina*, none of the species is pruinose. I define a pruina as a layer of crystals external to the tissues. It should not be confused with an internal crystal layer, which is present between the paraphyses or in the proper exciple of several species (see below).

I have not made detailed ontogenetic studies of the apothecia. The essential features of the apothecial ontogeny of *Bacidia* and *Bacidina*, however, appear to agree with the ones described for *Lecidella elaeochroma* (Ach.) M. Choisy by Letrouit-Galinou (1967, 1968). This type of apothecial ontogeny was later referred to as a variant of the *Xanthoria*-type (Letrouit-Galinou & Bellemère 1989).

Proper exciple

The proper exciple of *Bacidia* and *Bacidina* is well-developed, annular, and composed of distinctly or indistinctly radiating hyphae (Fig. 3B-C, 4A-B). The anatomy of the proper exciple provides some of the best characters to separate these two genera, and also to separate both of them from other genera.

The excipular hyphae of *Bacidia* are, at least in the outer part, distinctly radiating. In some species, the innermost part of the proper exciple forms a more or less distinct layer with an intricate texture. The presence or absence of such a layer varies between closely allied taxa. For example, such a layer is present in *Bacidia igniarii*, but absent from the closely related *B. circumspecta*.

The hyphae of the radiating part of the proper exciple are abundantly furcate but sparingly or not at all anastomosed (Fig. 3B-C). The cell lumina in the interior of the proper exciple are usually more or less narrowly cylindrical and distinctly constricted near the septa (Fig. 3D),

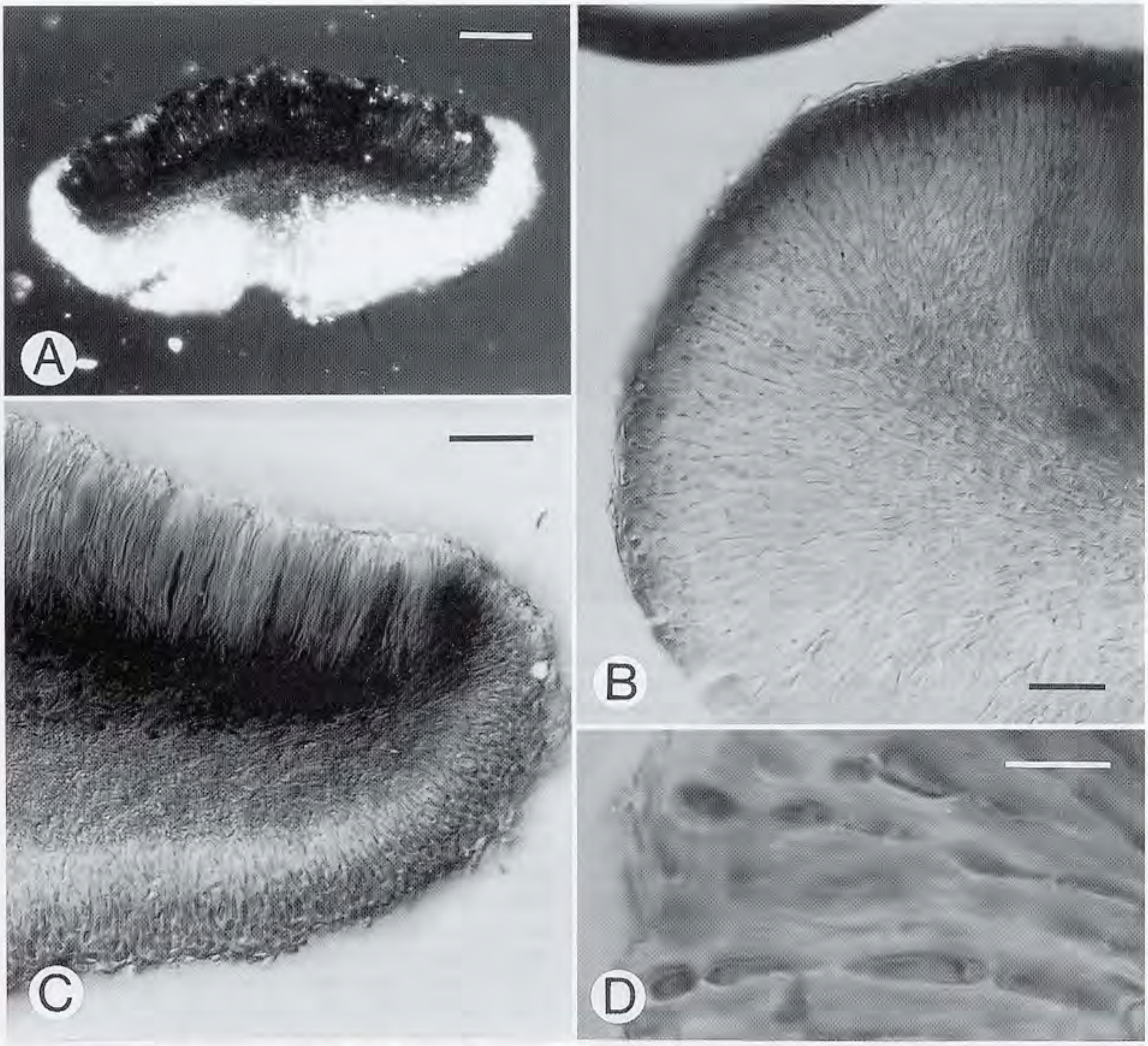


Fig. 3. Sections of apothecia in *Bacidia*, unstained (A) or stained with LCB (B-D), viewed between two polarizing filters (A) or in interference contrast (B-D). – A. *Bacidia campalea* (Ekman L1177, LD), crystals in proper exciple. Bar = 100 µm. – B. *Bacidia laurocerasi* subsp. *laurocerasi* (Ekman L1070, LD), very narrow excipular cell lumina. Bar = 20 µm. – C. *Bacidia suffusa* (Wetmore 60307, MIN), layer of enlarged cell lumina along rim of proper exciple. Bar = 30 µm. – D. *Bacidia rubella* (Ekman L950, LD), detail of lateral part of proper exciple showing constrictions of cell lumina at septa. Bar = 10 µm.

except in very narrow lumina. They are usually 8-25 µm long, 1-3 µm wide, and 5-11 times as long as wide. The walls are gelatinized and thick, and the boundaries between adjacent hyphae cannot be discerned. The distance between two adjacent cell lumina in the interior of the proper exciple practically always exceeds the width of a cell lumen, but more commonly this distance is 2-5 times the width of a lumen.

In many species of *Bacidia*, the outermost cells of the excipular hyphae, along the rim of the proper exciple, differ in shape and size from the inner ones in being wider, often globose or widely ellipsoid. Often, only the terminal cells are enlarged, but in some species the outermost 2-4(-11) cells are more or less enlarged. These wide, outer cell lumina can either form a distinctly delimited layer along the rim of the proper exciple, or the lumina may enlarge gradually towards the rim. Only four species regularly possess a distinct layer of enlarged cells along the rim of the proper exciple thicker than two cell layers, namely *B. absistens*, *B. campalea*, *B. russeola*, and *B. suffusa* (Fig. 3C).

Crystals can be found in 14 out of the 27 species of

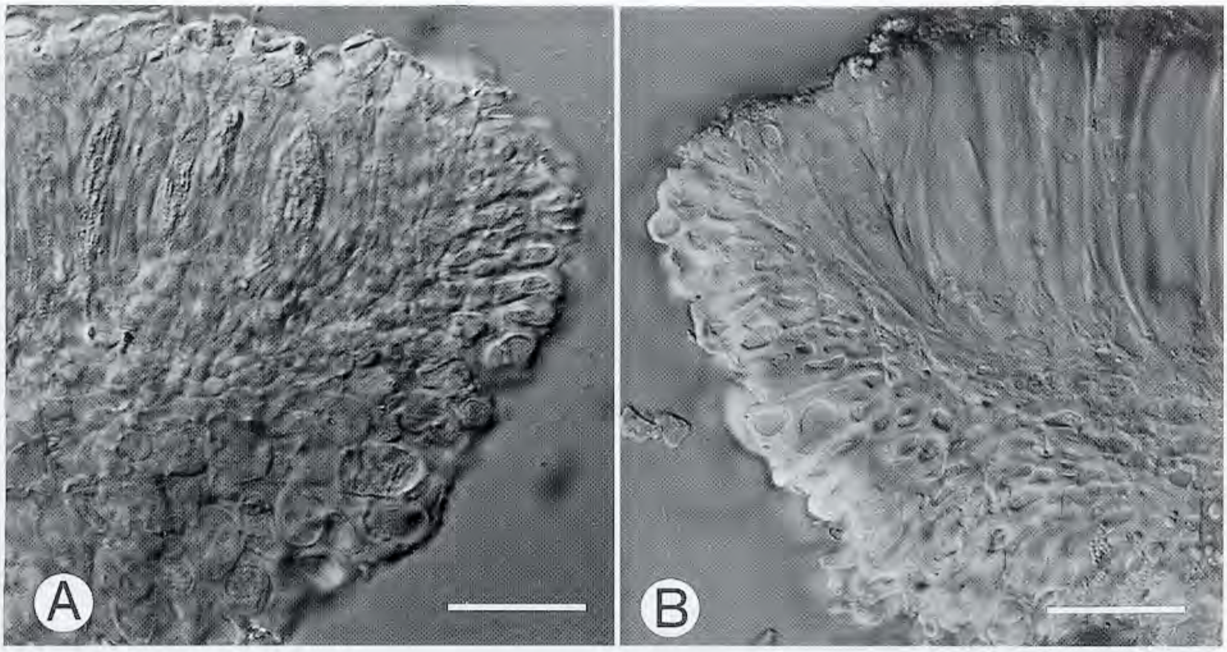


Fig. 4. Sections of apothecia in *Bacidina*, unstained but treated with a diluted hypochlorite solution, viewed in interference contrast.– A. *Bacidina chloroticula* (Wong 2709A, CANL), excipular hyphae that are indistinctly radiating and possess ellipsoid cell lumina. Bar = 20 µm. – B. *Bacidina varia* (Ekman L1135 LD), fairly distinctly radiating excipular hyphae with broadly cylindrical to ellipsoid lumina that become gradually larger towards rim of proper exciple. Bar = 20 µm.

Bacidia (Fig. 3A), and they constitute a good character for separating some species. They are often minute, up to 1 µm wide, but can in some species be much larger, up to 10 µm. Only in a few species the crystals are more or less evenly dispersed in part of the proper exciple. More commonly, the crystals are aggregated in clusters. Characteristically, the clusters are elongated and radiating, i.e., arranged in the direction of the excipular hyphae. Oil droplets are never present in any of the species of *Bacidia* or *Bacidina*.

The proper exciple of *Bacidina* is different from that in *Bacidia* (Fig. 4A-B). In some species, the excipular hyphae are distinctly radiating, in others not. A distinction between two layers, like in some *Bacidia*, is never found in *Bacidina*. The hyphae of the proper exciple are sparingly to abundantly furcate, and usually abundantly anastomosed (sparingly to moderately so in *Bn. aenea* and *Bn. chloroticula*). The cell lumina in the interior of the proper exciple are very variable, but all species contain a fair amount of short and wide cell lumina (almost globose, ± ellipsoid, rectangular, or irregular) with a width exceeding 2.5 µm and a length/width ratio less than 4.0. In *Bn. californica*, *Bn. chloroticula* (Fig. 4A), and *Bn. ramea*, the cell lumina are homogeneously globose to ellipsoid throughout the proper exciple, but the remainder of the species contain a mixture of such lumina and longer and narrower ones. Commonly, they are spatially separated. In *Bn. arnoldiana*, *Bn. egenula*, *Bn. egenuloidea*, and *Bn. squamellosa*, the cell lumina are distinctly wider in the lower, older part of the proper exciple than in the upper, younger part. In *Bn. varia* (Fig. 4B), the reverse is true, i.e., the upper lumina are often wider than the lower ones. In this species, there is also a clear tendency for the hyphae to expand gradually towards the rim. The proper exciple of *Bn. aenea*, *Bn. crystallifera*, and *Bn.* sp. #1 also contain hyphae with cell lumina that gradually expand towards the rim, but in these species there is no difference between the upper and the lower part of the proper exciple. Finally, the proper exciple of *Bn. assulata* is composed of an apparently fairly unorganized mixture of hyphae with wide and narrow lumina, although there appears to be a tendency for the upper hyphae to be slightly narrower than the lower ones.

The cell lumina of the excipular hyphae found in the species of *Bacidina* are, like in *Bacidia*, usually constricted at the septa, very narrow hyphae excepted. The walls are gelatinized, but unlike *Bacidia*, they are thin. The distance between two adjacent cell lumina is usually less than the width of a cell lumen. Furthermore, the species of *Bacidina* lack enlarged terminal cells of the excipular hyphae. Crystals are found in only one species, *Bn. crystallifera*, the proper exciple of which always contains evenly dispersed crystals up to 1 µm wide.

The proper exciple of most *Bacidia* and several *Bacidina* is more or less pigmented; see *Pigmentation*..

Hypothecium

A distinct hypothecium of different texture than the proper exciple is present in all studied species of *Bacidia* and *Bacidina* (Fig. 3A, C). The hyphae are irregularly oriented and their cell lumina are very variable in size and shape. The hypothecium is often pigmented (see *Pigmentation*). Crystals and oil droplets are never present in the hypothecium.

Subhymenium

A very thin subhymenium is always present betwen the hymenium and the hypothecium. It is always amyloid (contrary to the hypothecium) and often intermediate in pigmentation between the hypothecium and the hymenium.

Hymenium

The hymenium is amyloid, 40-130 µm high in *Bacidia* and 40-80 µm high in *Bacidina*. In all species of *Bacidia* and most of *Bacidina*, the paraphyses constitute the major part of the tissues, but in two species of *Bacidia*, namely *Bn. chloroticula* and *Bn. varia*, the asci are dominating. The hymenium is often pigmented (see *Pigmentation*), either in a distinct layer in the upper part of the hymenium or in a diffuse zone with upwards and gradually increasing colour intensity. In the descriptions, I have avoided the term "epithecium" for the pigmented zone. By definition, this term refers to the layer above the asci (cf. Hawksworth et al. 1983), but in many species of *Bacidia* and *Bacidina* the pigmentation is not restricted to this layer.

A layer of minute crystals between the apices of the paraphyses is present in some species, namely *Bacidia aggregatula*, *B. rosella*, and *Bacidina crystallifera*. Oil droplets, however, are never present in any species.

Paraphyses

The paraphyses are unbranched or branched in the upper part. In *Bacidia*, they are 0.5-2.4 µm wide and in *Bacidina* 0.8-2.0 µm wide in mid-hymenium. The width of the apices varies considerably between and within species. It is sometimes a good character for separating species. In many species, the majority of the apices are more or less swollen, often taking a more or less clavate shape. In *Bacidia campalea*, *B. helicospora*, *B. hostheleoides*, *B. medialis*, *B. mutabilis*, *B. russeola*, *B. suffusa*, and *Bacidina aenea*, on the other hand, the paraphyses are consistently uniformly thick throughout, or only slightly thickened or even slightly tapering at the apices.

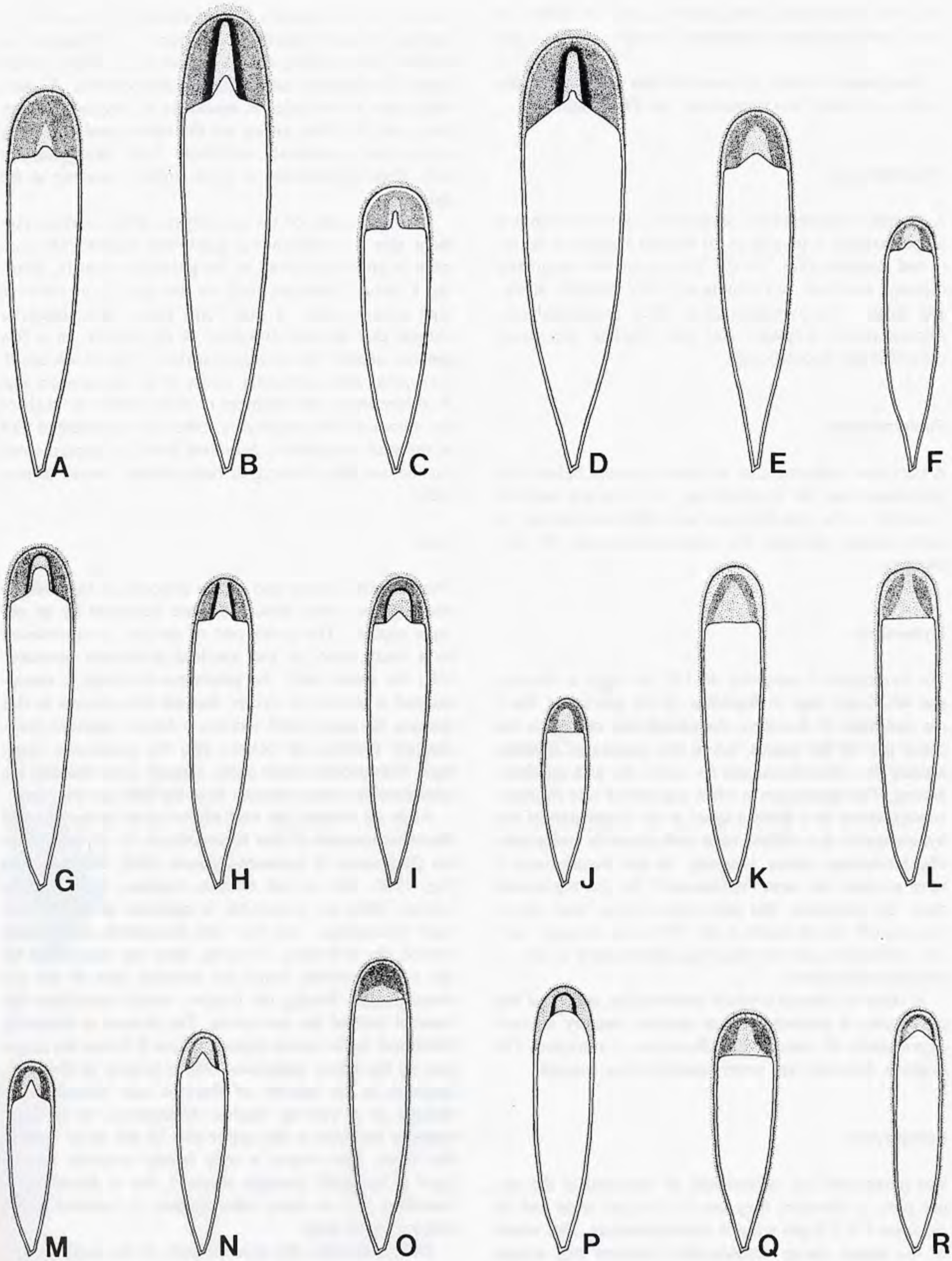
The upper part of the paraphyses often secretes pigment into the surrounding gelatinous matrix. The pigment is either dissolved in the gelatinous matrix, forming a distinct external hood on the apices, or, when in high concentration, it may form fairly large, irregular clumps that are not dissolved in the matrix. In a few species, namely *Bacidia auerswaldii*, *B. heterochroa*, *B. vermifera*, and occasional forms of *B. laurocerasi* and *B. subincompta*, the pigment remains within the wall of the apices of the paraphyses. Often, the pigmented part of the wall is distinctly delimited from the unpigmented part below, thus forming distinct internal "caps" of pigment.

Asci

The asci are clavate and firmly attached to the ascogenous hyphae, from which they are delimited by an oblique septum. The upper part of the asci is surrounded by a fuzzy, more or less amyloid gelatinous envelope. Like the ascus itself, the gelatinous envelope is unpigmented in all species except *Bacidia helicospora*. In this species, the ascus wall secretes a brown pigment (Laurocerasi Brown; see below) into the gelatinous envelope. This process starts early, already when the asci are immature and much smaller than the fully grown ones.

As in all lichens, the wall of the ascus in *Bacidia* and *Bacidina* consists of four layers, the a-, b-, c-, and d-layers (Bellemère & Letrouit-Galinou 1988: 167; see also Fig. 15B). The a- and b-layers together form the exoascus. They are impossible to separate in an ordinary light microscope, and they are henceforth collectively termed the a+b-layer. Inwards, they are succeeded by the c-layer, which forms the external part of the endoascus, and, finally, the d-layer, which constitutes the internal part of the endoascus. The d-layer is distinctly thickened in the apical region, where it forms the major part of the apical apparatus. The a+b-layer is distinctly amyloid in all species of *Bacidia* and *Bacidina*, although to a varying degree. Commonly, it is more strongly amyloid in the upper part of the ascus than in the lower. The c-layer is only faintly amyloid. The d-layer is basically strongly amyloid, but in *Bacidia* and *Bacidina*, like in many other lichens, it contains a less amyloid axial body.

Within *Bacidia*, the apical region of the ascus is fair-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Tab. 1. Goniocysts in North American corticolous and lignicolous *Bacidina*. Statements refer to North American material only (but see notes). Notes: – 1. This statement should be interpreted with caution, since only 1-2 North American specimens have been investigated. – 2. Far from all European specimens have goniocysts. – 3. In Europe, many (but far from all) specimens are entirely dissolved into goniocysts.

	Goniocysts present	All specimens with goniocysts	Distribution of goniocysts	Aggregation of goniocysts	Average diam. of goniocysts (μm)
Bn. aenea	yes	yes[1]	small spots	loose	24
Bn. arnoldiana	yes	yes	almost entire thallus	firm	32
Bn. assulata	yes	yes[1, 2]	rather small spots	loose	22
Bn. californica	yes	no	small to rather large spots	loose	30
Bn. chloroticula	yes	no	rather large spots[3]	loose to rather firm	35
Bn. crystallifera	no				
Bn. egenula	yes	yes[1]	entire thallus	firm	49
Bn. egenuloidea	yes	yes[1]	entire thallus	firm	46
Bn. ramea	no				
Bn. squamellosa	no				
Bn. varia	yes	no	small spots to entire thallus	rather loose	28
Bn. sp #1	yes	yes[1]	rather small spots	loose	14

ly homogeneous. It contains a conical, high or low, ocular chamber and a more or less conical, blunt or pointed axial body that never reaches all through the d-layer (Fig. 5A-D). In some species, the axial body is surrounded by a distinct or fuzzy zone that is very strongly amyloid, more so than the remainder of the d-layer. The width of the axial body never exceeds one third of the entire width of the d-layer. The c-layer is constantly narrow.

Within *Bacidina*, on the other hand, there is more extensive variation in the composition of the ascus (Fig. 5E-R). A distinct, high or low, more or less conical, blunt or pointed ocular chamber is often found in *Bn. aenea*, *Bn. arnoldiana*, *Bn. assulata*, *Bn. californica*, *Bn. egenula*, *Bn. egenuloidea*, sometimes also in *Bn. varia* and in *Bn.* sp. #1. In *Bn. chloroticula*, *Bn. crystallifera*, *Bn. ramea*, and *Bn. squamellosa*, on the other hand, an ocular chamber is lacking. An axial body is present in all species. It is usually more or less conical or cylindrical, and constitutes one third or more of the entire width of the d-layer. In *Bn. ramea*, the axial body is extreme, taking a cushion-like, very wide and low shape. In *Bacidina californica* and *Bn. crystallifera*, the axial body vertically extends through the entire d-layer in some, but not all, asci. This is variable even within the same specimen. A distinct, strongly amyloid zone surrounding the axial body can be found in *Bn. assulata*, *Bn. californica*, and (sometimes) *Bn. varia*. In the last species, however, most asci lack this zone. The faintly amyloid c-layer is, like in *Bacidia*, narrow in most species. A few species deviate, however, in possessing a distinctly widened c-layer, namely *Bn. crystallifera*, *Bn. egenuloidea*, *Bn. squamellosa*, and *Bn.* sp. #1. Particularly in *Bn. squamellosa*, the c-layer is extremely well developed relative to the d-layer, resulting in an ascus apex with an appearance unlike any other lichen that I know of.

All the ascus appearances are variations on one and the same theme: an ocular chamber that may or may not be present, and a distinct axial body that is basically conical but varies in height and width. There is a striking difference in variation pattern between the two genera, however. Whereas *Bacidia* exhibits rather little variation in ascus apex structure, *Bacidina*, despite the smaller number of species, is much more variable. An attempt to explain this difference in variation pattern must necessarily be highly speculative. There are two principal explanations:

1. Contrary to *Bacidia*, the ascus apex of several species of *Bacidina* has lost its function in the dispersal of the spores. Hence, it is not subjected to any selective pressure. Through drift, various deviating ascus apices have evolved.

2. The ascus apex of several species of *Bacidina* is highly specialized with respect to the mechanism of spore dispersal, which may in its turn be an adaptation to, e.g., certain climatic or chemical conditions (the reason for the specialization is actually unimportant to the

Fig. 5. Amyloid reaction of asci. The immature spore content has been omitted from the figures. – A. *Bacidia arceutina*. – B. *B. heterochroa*. – C. *B. medialis*. – D. *B. rubella*. – E. *Bacidina aenea*. – F. *Bn. arnoldiana*. – G. *Bn. assulata*. – H-I. *Bn. californica*. – J. *Bn. chloroticula*. – K-L. *Bn. crystallifera*. – M. *Bn. egenula*. – N. *Bn. egenuloidea*. – O. *Bn. ramea*. – P. *Bn. squamellosa*. – Q. *Bn. varia*. – R. *Bn.* sp. #1. – Drawings by Ulf Arup.

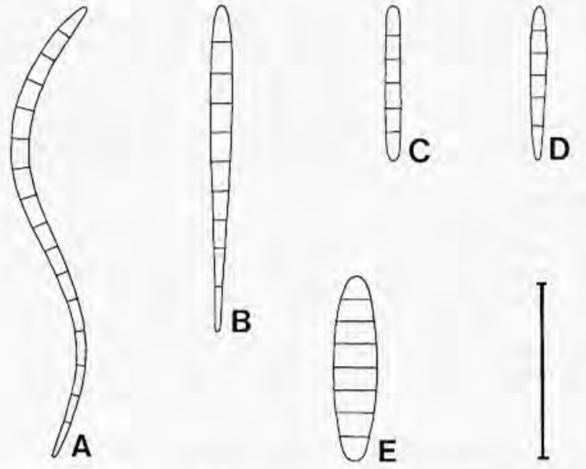


Fig. 6. Spore types. Bar = 25 µm. – A. Sigmoid, acicular spore in *Bacidia laurocerasi* subsp. *laurocerasi*. – B. Straight, acicular spore in *Bacidia heterochroa*. – C. Bacilliform spore in *Bacidia circumspecta*. – D. Clavate (intermediate between bacilliform and acicular) spore in *Bacidia circumspecta*. – E. Fusiform spore with blunt ends in *Bacidia auerswaldii*. – Drawings by Ulf Arup.

line of argument). Thus, it is (or has been) exposed to a strong selective pressure.

The most likely reason for the ascus apex to loose its importance in the dispersal would be that vegetative dispersal has taken over as the mean method of propagation. At first, this may seem as an attractive hypothesis for what has taken place in *Bacidina*, since several species, contrary to *Bacidia*, produce goniocysts. However, if one makes the plausible assumption that an ascus apex similar to that in *Bacidia* is the original, plesiomorphic character state in *Bacidina*, then four species stand out as particularly derived from this state, namely *Bn. crystallifera*, *Bn. egenuloidea*, *Bn. ramea*, and *Bn. squamellosa*. This group embraces all three North American species of *Bacidina* that *never* produce goniocysts (Tab. 1), i.e., the species that are entirely dependent on spore dispersal for their propagation! It should be noted, that the probability of randomly picking four out of twelve species that includes all three species dependent on spore dispersal is 1.8 %. Consequently, the second hypothesis appears less contradictory. The three North American species are not the only ones not producing vegetative propagules. Among the European species, at least *Bacidina phacodes* (the type species of the genus) and *Bn. inundata* never reproduce vegetatively. The reason why *Bn. egenuloidea* possesses a highly derived ascus apex even though it reproduces vegetatively may be that the ascus apex originally evolved in a non-goniocystate ancestor of this species.

The use of the ascus apex structure as a regular component in taxonomic revisions of lichens is still fairly new, covering only about a decade. Many genera are still insufficiently studied in this respect. It was with the work of Hafellner (1984) that the importance of this characeter set in lichen taxonomy was first clearly pointed out. In my opinion, this was the greatest achievement of this work, whereas the material studied was far too small to support many of the rather far-reaching taxonomical conclusions.

As often is the case when a new character is introduced in taxonomic work, it is given an *a priori* weight to the taxonomy, which is hence strongly influenced by this single character. This is exactly what has happened in lichen taxonomy over the last decade. Furthermore, the study of the ascus apex has not seldom been restricted to generic type species or "representative species", methods based on the, in my opinion, dangerous assumption that the ascus apex is invariable within genera or at least species groups within genera. It is commonly seen in the literature, that asci are referred to "ascus types" (e.g., *Bacidia*-type, *Biatora*-type, or *Lecanora*-type). There is an apparent risk that important taxonomic information is lost when an observed ascus is squeezed into any of a limited number of "ascus types" that, moreover, have never been properly defined.

In my opinion, the ascus apex characters should be treated like any other character. Its variation within species, genera, and families should be studied together with all other characters used. It is then the pattern of covariation in the characters studied that, *a posteriori*, determines the value of the ascus apex, or any other character for that matter. This reasoning may seem self-evident, but there are, unfortunately, many examples of how ascus apex characters have *not* been treated this way. In *Bacidia* and *Bacidina*, the ascus apex, *even though* variable within the latter genus, has proven to be of utmost importance to circumscribe the genera, but also to characterize some of the species of *Bacidina*.

Spores

The spores of all *Bacidia* and *Bacidina* treated here are long and narrow, colourless, rather thick-walled, and lack perispore and ornamentation. In *Bacidia*, they are 11-108 µm long, 1.2-7.8 µm wide, and 3-66 times as long as wide, whereas they are 16-60 µm long, 0.9-3.3 µm wide, and 9-56 times as long as wide in *Bacidina*. Although often highly variable within a species or even a single specimen, the spore size is an important character to distinguish between some species (Fig. 6, Tab. 2).

The spores are usually eight per ascus, or sometimes reduced to seven or six. They may or may not be more or less coiled in the ascus. This is, however, variable within the same species, not rarely even within the same

Tab. 2. The presence of various spore shapes in *Bacidia* and *Bacidina*, and the length (μm), width (μm), length/width ratio, and number of septa per spore. The values presented are not the endpoints of the variation, but the interval within which an average of 10 (or in some cases 20, denoted here with an "*") measurements per individual varies. A single value indicates that spores, due to availability of material, have been meaured in one specimen only, and that hence only one average value is obtainable.

	Acicular	Clavate	Bacilliform	Fusiform	Length	Width	Ratio	Septa
Bacidia								
absistens	+	.	.	.	45-74	2.3-4.1	17.5-24.5	6.8-14.3
aggregatula	+	.	.	.	44-57	2.5-2.6	17.1-22.1	4.7-7.5
arceutina	+	.	.	.	47-64	1.5-2.2	25.3-36.4	5.0-10.7
auerswaldii	.	.	.	+	23-31	6.5-7.0	3.6-4.4	5.7-6.4
biatorina	+	.	.	.	49*	2.5*	19.5*	10.1*
campalea	+	.	.	.	52-55	3.2-3.5	15.3-17.1	6.6-8.0
circumspecta	.	+	+	.	12-37	1.7-3.2	6.0-15.8	3.0-6.8
diffracta	+	.	.	.	37-54	2.6-3.2	12.4-19.3	4.1-7.8
friesiana	+	.	.	.	34*	3.1*	10.8*	7.2*
helicospora	+	.	.	.	50-64	2.6-3.1	18.0-22.9	7.8-14.8
heterochroa	+	.	.	.	36-67	3.1-4.0	11.7-18.9	4.5-13.6
hostheleoides	.	.	+	+	19*	3.6*	5.4*	3.1*
igniarii	.	+	+	.	15*	2.6*	5.9*	3.0*
insularis	+	.	.	+	30-55	3.5-4.7	6.4-14.1	6.6-10.3
laurocerasi subsp. *la.*	+	.	.	.	57-87	2.5-3.5	18.3-31.5	11.9-22.2
laurocerasi subsp. *id.*	+	.	.	.	69-96	2.8-3.2	23.9-30.4	17.5-23.0
medialis	.	.	+	+	20-26	2.0-3.4	6.7-10.7	3.0-4.2
mutabilis	+	.	.	.	42-47*	3.3-3.4*	12.7-14.4*	5.9-6.3*
polychroa	+	.	.	.	38-57	2.3-4.0	11.4-21.6	3.1-11.9
reagens	+	.	+	.	29-59	1.8-2.6	15.8-22.8	3.5-12.5
rosella	+	.	.	.	46-47	2.0-2.2	20.8-23.5	5.6-8.7
rubella	+	.	.	.	44-63	2.4-3.2	15.7-24.4	3.2-8.7
russeola	+	.	.	.	53-58	2.9-3.1	17.8-20.1	6.6-7.3
salmonea	+	.	.	.	48-61	1.6-1.8	30.2-36.5	6.8-9.4
schweinitzii	+	.	.	.	44-73	2.5-3.2	15.5-30.6	4.3-13.6
subincompta	+	+	+	+	23-50	2.1-5.1	4.6-19.2	3.0-9.7
suffusa	+	.	.	.	48-69	2.7-3.6	14.4-21.9	6.3-12.6
vermifera	.	+	+	.	16-27	2.3-2.9	6.3-11.2	3.0-4.3
Bacidina								
aenea	+	+	.	.	35*	2.2*	16.3*	5.1*
arnoldiana	+	.	.	.	39-42	1.2-1.6	28.0-33.8	1.5-6.4
assulata	+	.	.	.	39	2.3	17.2	7.0
californica	+	.	.	.	35-46	1.9-2.8	16.7-19.7	3.6-7.5
chloroticula	+	.	.	.	24-28	1.0-1.2	23.3-24.5	0.6-1.8
crystallifera	+	.	.	.	40-52	1.4-1.7	26.5-33.4	4.6-6.7
egenula	+	.	.	.	21-25	1.4-1.6	15.1-15.5	1.1-2.8
egenuloidea	+	.	.	.	25-34	1.1-1.9	18.3-22.6	0.5-2.4
ramea	+	.	.	.	31-49	1.6-2.2	18.5-28.5	3.2-5.4
squamellosa	+	.	.	.	45-48	1.3-1.4	33.9-38.5	3.2-4.4
varia	+	+	.	.	23-41	1.7-2.4	10.0-23.5	3.0-6.6
sp. #1	+	.	.	.	37	1.4	27.9	3.4

specimen.

The spores are acicular in many species, i.e., they possess one narrow, tapering, more or less acute end, one thick and blunt end, and a length/width ratio exceeding about 10. In a few species, namely, *Bacidia circumspecta*, *B. hostheleoides*, *B. igniarii*, *B. medialis*, *B. vermifera*, and *Bacidina varia*, the spores are often either bacilliform (i.e., evenly wide with blunt ends) or intermediate in shape between acicular and bacilliform (referred to here as "clavate"). *B. reagens*, *B. subincompta*, and *Bn. aenea* often produce acicular spores, but occasionally also long-bacilliform ones. In *B. auerswaldii*, the spores are invariably fusiform with blunt ends, in *B. hostheleoides*, *B. medialis*, *B. insularis*, and *B. subincompta* occasionally so. The narrow, tapering end of an acicular or clavate spore is always directed towards the proximal end of the ascus, and the wider, blunt end towards the distal end. The various spore

Fig. 7. *Bacidia helicospora* (Chester 4413, US), squash preparation in KOH. Released package of eight helically arranged and strongly conglutinated spores.

shapes present in the species treated here are presented in Fig. 6 and Tab. 2.

The spores are straight, curved, or more or less "sigmoid". The latter term has commonly been used to describe the spores in *Bacidia*, but it is actually a misnomer. It implies that the spores are S-shaped in one plane, but they are actually shaped like a shallow spiral. I have, however, chosen to retain this term anyway. Sigmoid spores are mainly found in species with acicular spores (Fig. 6A). The most extremely sigmoid spores are found in *B. helicospora* and *B. vermifera*. In the former species, the spores are also strongly conglutinated (Fig. 7) and can often only be separated using KOH and vigorous squashing. In all other species, the spores are easily separated at maturity.

In most species of *Bacidia* and *Bacidina*, the spores are generally more than three-septate when mature. The maximum number of septa is commonly, depending on the species, between seven and fifteen. In *Bacidia laurocerasi* subsp. *idahoensis*, however, I have encountered spores with up to 28 septa. In some species, on the other hand, a majority of the spores never acquire more than three septa (*Bacidia circumspecta*, *B. hostheleoides*, *B. igniarii*, *B. medialis*, *B. vermifera*, and *Bacidina varia*). In a few species of *Bacidina* (*Bn. arnoldiana*, *Bn. chloroticula*, *Bn. egenula*, and *Bn. egenuloidea*), mature spores with fewer than three septa are often found.

Tab. 3. The total number of spores with odd and even number of septa, the proportion of odd- to even-septate spores, and the significance level of the chi-square values obtained from the goodness-of-fit test for species of *Bacidia* and *Bacidina*. The null hypothesis tested was that the number of odd- and even-septate spores are randomly distributed, i. e. that both the number of odd- and even-septate spores= (Odd+ Even)/2. Only species in which at least 30 spores have been studied *and* in which the majority of the mature spores possess more than three septa have been included in the test. The significance levels are denoted * for 0.01<p≤0.05, ** for 0.001<p≤0.01, *** for p≤0.001, and ns (not significant) for p>0.05.

	Odd	Even	Odd/even	Sign. level of χ^2
Bacidia				
absistens	51	19	2.7	***
aggregatula	32	8	4.0	***
arceutina	126	34	3.7	***
auerswaldii	26	4	6.5	***
campalea	23	7	3.3	**
diffracta	95	35	2.7	***
helicospora	40	10	4.0	***
heterochroa	128	72	1.8	***
insularis	46	4	11.5	***
laurocerasi subsp. *idahoensis*	58	32	1.8	**
laurocerasi subsp. *laurocerasi*	115	95	1.2	ns
polychroa	152	68	2.2	***
reagens	36	4	9.0	***
rosella	22	8	2.8	*
rubella	129	61	2.1	***
salmonea	25	5	5.0	***
schweinitzii	186	84	2.2	***
subincompta	133	37	3.6	***
suffusa	164	46	3.6	***
Bacidina				
californica	48	12	4.0	***
crystallifera	38	2	19.0	***
ramea	74	16	4.6	***

Tab. 4. Conidial types in the North American corticolous and lignicolous species of *Bacidia* and *Bacidina*. These are defined in the text, and are only briefly characterized here: 1 = filiform (a = curved; b = straight; c = multiseptate contrary to a, b, and d; d = strongly conglutinated, bundle-forming contrary to a-c); 2 = oblong, ellipsoid, fusiform, or bacilliform; 3 = falcate; 4 = acicular. An "s" denotes a conidial type that occurs singly in a pycnidium, whereas an "m" denotes a conidial type that occur mixed with a second conidial type in the same pycnidium. Information within brackets refer to information based on European collections (Sw. = Sweden, Ge. = Germany). The number of conidial types in a species and the number of species with a particular conidial type refers to North American material, but within brackets the total number (including the information based on European collections) is given.

	No. of conidial types	1a	1b	1c	1d	2	3	4
Bacidia								
absistens	1	s	.	.	.	.	.	.
aggregatula	1	s	.	.	.	.	.	.
arceutina	1	s	.	.	.	.	.	.
auerswaldii	0	.	.	.	.	.	.	.
biatorina	1	s	.	.	.	.	.	.
campalea	0	.	.	.	.	.	.	.
circumspecta	3	s	.	.	.	s	s	.
diffracta	1	s	.	.	.	.	.	.
friesiana	0	.	.	.	.	.	.	.
helicospora	0	.	.	.	.	.	.	.
heterochroa	1	s	.	.	.	.	.	.
hostheleoides	2	m	.	.	.	m	.	.
igniarii	0 (1)	.	.	.	.	(s, Sw.)	.	.
insularis	1	s	.	.	.	.	.	.
laurocerasi	1	s	.	.	.	.	.	.
medialis	1	.	s	.	.	.	.	.
mutabilis	0	.	.	.	.	.	.	.
polychroa	1	s	.	.	.	.	.	.
reagens	0	.	.	.	.	.	.	.
rosella	1 (2)	(s, Sw.)	.	s	.	.	.	.
rubella	1	s	.	.	.	.	.	.
russeola	0	.	.	.	.	.	.	.
salmonea	1	s	.	.	.	.	.	.
schweinitzii	1	s	.	.	.	.	.	.
subincompta	1	s	.	.	.	.	.	.
suffusa	1	s	.	.	.	.	.	.
vermifera	2	.	s	.	.	s	.	.
Bacidina								
aenea	0	.	.	.	.	.	.	.
arnoldiana	1	s	.	.	.	.	.	.
assulata	1	s	.	.	.	.	.	.
californica	2	s	.	.	.	s	.	.
chloroticula	1	s	.	.	.	.	.	.
crystallifera	0	.	.	.	.	.	.	.
egenula	1 (2)	s (m, Ge.)	.	.	.	.	.	(m, Ge.)
egenuloidea	3	s	.	.	m	.	.	m
ramea	1	s	.	.	.	.	.	.
squamellosa	1	.	.	s	.	.	.	.
varia	1	.	.	s	.	.	.	.
sp. #1	1	.	.	s	.	.	.	.
No. of species		23 (24)	2	4	1	4 (5)	1	1 (2)

The number of spores with an odd number of septa are often significantly higher than the number of spores with an even number of septa in several species (Tab. 3). This shows that the septation of the spores in *Bacidia* and *Bacidina* is not random. The most reasonable explanation to this pattern is that, after the formation of the first, median septum, the subsequent septa arise more or less synchronously in pairs. The synchroniza-

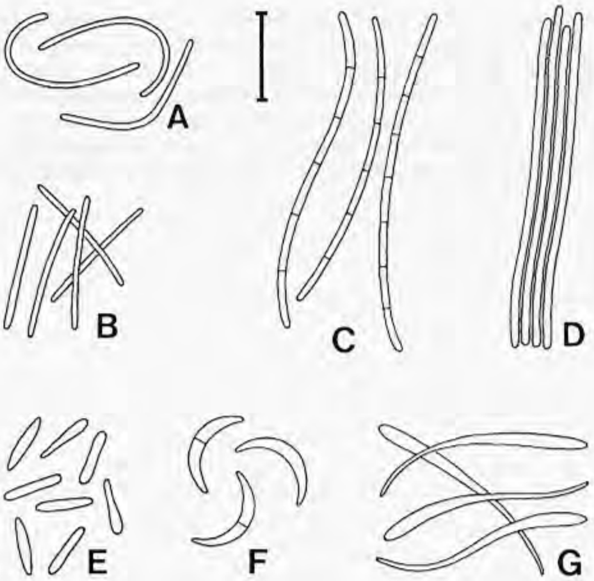


Fig. 8. Conidial types. Bar = 10 µm. – A. Type 1a in *Bacidia schweinitzii*. – B. Type 1b in *Bacidia medialis*. – C. Type 1c in *Bacidina varia*. – D. Type 1d in *Bacidina egenuloidea*. – E. Type 2 in *Bacidia circumspecta*. – F. Type 3 in *Bacidia circumspecta*. – G. Type 4 in *Bacidina egenuloidea*. – Drawings by Ulf Arup.

tion cannot be entirely perfect, however, otherwise even-septate spores would be virtually non-existent.

All spore measurements in *Bacidia* and *Bacidina* should be performed on mature spores that have been released from the asci. In practice, the absolute length of the spores is impossible to measure, and consequently, I have chosen here to define the length of a spore as the distance between the two ends, irrespective of the curvature. This means that the absolute length is slightly underestimated in most species, since the spores are often slightly curved or sigmoid. Only in *Bacidia helicospora* and *B. vermifera*, both with strongly sigmoid spores, is the underestimation severe. The width of the spores should be measured at the widest part of the spores, i.e., in acicular spores, near the wide, blunt end.

Pycnidia

Pycnidia have been found in North American specimens of 19 out of the 27 species of *Bacidia* and 10 out of the 12 species of *Bacidina*. In most species, they are small and inconspicuous, and only present in some specimens and in in a low number. Thus, they are often difficult to find, and they may have been overlooked in some of the 10 species in which they have not yet been found. In some species of *Bacidina*, on the other hand, they are fairly abundant and thus easy to find.

The pycnidia are more or less immersed in the thallus or, rarely, in the prothallus. Only in *Bacidia circumspecta* and *B. igniarii* are they sometimes sessile. They are generally 40-175 µm wide in *Bacidia* and 60-200 µm in *Bacidina*, but in *Bacidia circumspecta* they are sometimes up to 300 µm wide. In most cases, they are very similar in pigmentation to the apothecia, except in some species of *Bacidina*, which have unpigmented pycnidia even though the apothecia are pigmented. The pycnidia are unilocular and globose, ampulliform, or slightly flattened in shape.

Conidiogenous cells

The inside of the pycnidial cavity is lined by conidiogenous cells that produce conidia terminally and lack distinct conidiophores (or the conidiophores can be said to form the pycnidial wall). The conidiogenous cells are 7-15 × 1.0-2.5 µm, cylindrical or slightly tapering in *Bacidia*, 4-8 × 1.0-1.5 µm and cylindrical in *Bacidina*.

Conidia

Within the North American *Bacidia* and *Bacidina*, I have encountered altogether seven types of conidia, as classified by size, shape, curvature, septation, and conglutination (Fig. 8). Among the 29 species found with pycnidia in North American material, 24 possess one single conidial type. Three species, *Bacidia hostheleoides*, *B. vermifera*, and *Bacidina californica* possess two different conidial types. In *B. hostheleoides*, both conidial types occur mixed in the same pycnidium. Two species, *Bacidia circumspecta* and *Bacidina egenuloidea*, possess as many as three different conidial types. In the latter species, two of the three conidial types occur mixed in the same pycnidia. Few other lichens are known to produce pycnidia containing a mixture of two conidial types. To my knowledge, they have so far been reported from *Lecania cyrtellina* (Nyl.) Sandst. and *L. cyrtella* (Ach.) Th. Fr. (Ekman 1994, but by then already known from the former species by Brian Coppins), and from *Lecanora schistina* (Nyl.) Arnold (Etayo & Diederich 1993) and *Opegrapha vulgata* (Ach.) Ach. (Coppins pers. comm.)

The following conidial types have been found in the North American *Bacidia* and *Bacidina*. The presence of the various types in each of the species is presented in Tab. 4. All conidial types are borne singly on the conidiogenous cells, except type 2, which is formed repeatedly.

1. Filiform, more or less curved or not, 0-11-septate, conglutinated or not. The filiform conidia divides into four types:

Tab. 5. Pigments present in the apothecia of the North American corticolous and lignicolous species of *Bacidia* and *Bacidina*. The pigments are described in the text. A "+" refers to a pigment that is always or nearly always present, whereas a "±" denotes a pigment that may or may not be present (including rarely occurring pigments). Unidentified pigments are pigments that occur in so small amounts as to be impossible to identify with any of the named pigments. It is likely that the unidentified pigments are synonymous with Rubella Orange.

	Bacidia Green	Laurocerasi Brown	Rubella Orange	Schweinitzii Red	Arceutina Yellow	Bacidia Brown	Thalloidima Green	Arnoldiana Brown	unid. pigments
Bacidia									
absistens	+	±	±	.	.	.	.	.	.
aggregatula	±	.	+	+	.	.	.	.	.
arceutina	.	.	.	.	+	.	.	.	.
auerswaldii	.	+	+	.	.	.	.	.	.
biatorina	.	+	+	.	.	.	.	.	.
campalea	.	+	+	.	.	.	.	.	.
circumspecta	+	+	±	.	.	.	.	.	.
diffracta	.	.	+	.	.	+	.	.	.
friesiana	+	+	.	.	.	.	.	.	.
helicospora	.	+	+	.	.	.	.	.	.
heterochroa	.	+	+	.	.	.	.	.	.
hostheleoides	.	.	+	.	.	.	.	.	.
igniarii	+	+	.	.	.	.	.	.	.
insularis	+	+	+	.	.	.	.	.	.
laurocerasi	.	+	+	.	.	.	.	.	.
medialis	.	.	±	.	.	.	.	.	.
mutabilis	.	.	±	.	.	.	.	.	.
polychroa	.	.	+	.	.	+	.	.	.
reagens	.	+	+	.	.	.	+	.	.
rosella	.	.	±?	.	.	.	.	.	.
rubella	.	.	+	.	.	.	.	.	.
russeola	.	+	+	.	.	.	.	.	.
salmonea	.	.	±	.	.	.	.	.	.
schweinitzii	±	.	+	±	.	.	.	.	.
subincompta	+	+	.	.	.	.	.	.	.
suffusa	.	+	+	.	.	.	.	.	.
vermifera	.	+	.	.	.	.	.	.	.
Bacidina									
aenea	.	.	.	.	+	.	.	.	.
arnoldiana	.	.	.	.	.	.	.	+	.
assulata	.	.	+	.	.	.	.	.	.
californica	.	.	.	.	.	.	.	±	.
chloroticula	.	.	.	.	.	.	.	.	±
crystallifera	.	.	.	.	.	.	.	.	±
egenula	+	+	+	.	.	.	.	±	.
egenuloidea	.	+	+	.	.	.	.	.	.
ramea	.	±	±	.	.	.	.	.	.
squamellosa	.	.	.	.	.	.	.	.	.
varia	.	±	±	.	.	.	.	.	.
sp. #1	.	.	.	.	.	.	.	.	±

a) More or less curved, non-septate (rarely 1-septate), not conglutinated, 5-43 × c. 0.5-0.8(-1.0) µm (Fig. 8A). This is by far the commonest conidial type in both *Bacidia* and *Bacidina*.

b) Straight, non-septate, not conglutinated, 6-17 × 0.5-1.0 µm (Fig. 8B).

c) More or less curved, sometimes straight (variable within the same species), 3-11-septate, not conglutinated, 14-58 × 0.6-1.6 µm (Fig. 8C).

d) Straight to sigmoid, 0-1-septate, strongly conglutinated and hence forming thick bundles, 35-49 × 0.8-1.2 µm (Fig. 8D).

2. Oblong, ellipsoid, fusiform, or bacilliform, 0-1(-2)-septate, 3-12 × 1.2-2.0 µm (Fig. 8E).

3. Falcate (i.e., curved, thickest at the middle and tapering towards the ends), 0-1-septate, 6-25 × 1.2-1.6 µm (Fig. 8F).

4. Acicular (distinctly thicker at the proximal end

Tab. 6. A summary of the pigments found in North American *Bacidia* and *Bacidina*: their colours and reactions with K, C, and N. A minus sign denotes the absence of a reaction.

Pigment	Colour in pure water	Reaction with		
		K	C	N
Bacidia Green I	Green to blue-green	-	-	Purple
Bacidia Green II	Purplish (dirty)	Green	-	Purple
Laurocerasi Brown	Reddish brown (grey, grey-brown)	Purplish	-	Orange to red
Rubella Orange	Orange to orange-brown (yellow)	± intensifying	-	± intensifying
Schweinitzii Red	Dark red to red-black	- (intensifying?)	-	- (intensifying?)
Arceutina Yellow	Yellow to yellow brown	-	-	-
Bacidia Brown	Brown to red-brown	Purple-red	-	-
Thalloidima Green	Green-grey to dirty grey	Purple to violet	Violet	Red
Arnoldiana Brown	Brown	Green-brown	-	-

than the distal end), 0-7-septate, 16-45 × 1.0-1.6 µm (Fig. 8G).

The length of the conidia varies considerably within a pycnidium, between pycnidia on the same thallus, and between specimens. In some species, the length has been found to be rather invariable within a pycnidium but highly variable between specimens (difference in length up to about 100 %). Finding pycnidia is often a difficult and time-consuming task, and consequently, only a few pycnidia have been studied in most species. The length values of the conidia accounted for in the descriptions should thus be interpreted conservatively. The width of the conidia, on the other hand, appears to be much less variable.

The conidia provide important characters to separate *Bacidia* and *Bacidina* from other, related genera. All species so far found with pycnidia (with the exception of *Bacidia igniarii*, which is anyway obviously closely related to *B. circumspecta*) at least sometimes produce filiform conidia (type 1). The distribution of the conidial types within the two genera indicates that closely related species are likely to produce similar conidia. For example, *Bacidina egenula* and *Bn. egenuloidea* both produce the peculiar type 4 conidia. *Bn. varia* and *Bn.* sp. #1 both produce type 1c conidia, and *Bacidia circumspecta*, *B. igniarii*, and *B. vermifera* all produce type 2 conidia. A few cases, however, indicate that the conidial type produced is perhaps not always such a conservative character as one might believe. In *Bacidia rosella*, the North American specimens differ from the European ones in the type of conidia produced. There are no additional distinct differences between them, other than that the North American specimens appear more poorly developed. Furthermore, the spectacular variation in the conidia exhibited by *Bacidia circumspecta* appears to lack any correlation with other characters or with geographic origin.

Pigmentation

The acetone-insoluble pigments found in the apothecia provide the single most important character set to distinguish between species within both *Bacidia* and *Bacidina*. They should be studied in transmitted light on microtome sections or thin handcut sections mounted in water. The colour caused by these pigment, as seen in transmitted light, is determined by their concentration, distribution, and by the texture of the tissue in which they are located. Furthermore, mixtures of two or three pigments in the same tissue are fairly common. In reflected light, as for example when studying the surface of an apothecium in a dissecting microscope, the colour of the pigments is often perceived in a different way. For example, both brown and green pigments may give a completely black colour to the apothecia in reflected light, and yellow, orange, and brown pigments may give very similar brown hues. Thus, it is important to study the pigments in transmitted light and not in reflected light.

There may be much variation within a species in the concentration of various pigments and to some extent also their distribution within the apothecium. The types of pigments present, however, are relatively invariable. Most species contain one or two pigments, but as many as three may be present, even in the same apothecium (but then in different parts of the apothecium). In several species, occasional pigment deficient specimens occur that may be difficult to determine. Other patterns appear to be a normal part of the variation within a species. In *Bacidia schweinitzii*, for example, there is almost a dimorphism. Most of the variation within the species can be classified into one morph dominated by a green pigment (with bluish or black apothecia) and one morph with a brown-orange pigment (with orange to brown apothecia). There are intermediates, however, and a few specimens possess apothecia of both colour morphs. The species of *Bacidina* are, on average, less pigmented than *Bacidia*. Among the species treated here, *Bn. californica*, *Bn. chloroticula*, *Bn. crystallifera*, *Bn. ramea*, *Bn. squamellosa*, *Bn. varia*, and *Bn.* sp. #1 are commonly pigment deficient. Some of these species (*Bn. californica*, *Bn. ramea*, and *Bn. varia*), however, display an extreme variation in the amount of pigment present, and they include forms with even dark brown apothecia! It should be noted that entirely pigment deficient apothecia are not pure white, but usually pale pink or sometimes pale yellow or pale greyish. Obviously, the texture of the tissues in themselves contribute slightly to the colour of the apothecia.

An attempt is made here to classify the pigments found in the species studied. I am aware that such a classification is a rather blunt instrument. It is possible, in some cases even likely, that what is classified here as one single pigment may in reality be comprised of two or more chemical substances. If chemical analyses of the pigments found in the apothecia of *Bacidia* and *Bacidina* would be possible, the conditions for taxonomic work in these genera would be greatly enhanced. For the sake of making the descriptions and discussions simpler, the pigments discussed below have been named. Some of them already have more or less established names originally provided by Bachman (1890). I have retained these names (although in an anglicized version), and given new, provisional names to others. The presence of the pigments in the apothecia in each of the species treated is accounted for in Tab. 5. The colours and reactions with K, C, and N have been summarized in Tab. 6. It should be noted that most, if not all, pigments occur in other lichen genera than *Bacidia* and *Bacidina*. "Intensifying" reactions with K and N mentioned below refer to reactions where the shade of colour remains unchanged but the colour intensity increases. A case could be made for regarding such reactions as negative.

(1) *Bacidia Green* (including both the "Bacidiagrün" and the "Lecideagrün" of Bachmann). Usually green (sometimes dirty) to blue-green, in more or less acidic conditions purplish. Reacts K- (or actually a purification of the green) or when purplish K+ green, and C-, N+ purple, with or without a precipitate of small blue crystals. Usually found in the proper exciple and in the upper part of the hymenium, rarely in other parts of the apothecia. Occurs in eight species of *Bacidia* and one species of *Bacidina*. – I have chosen to treat the "Bacidiagrün" and the "Lecideagrün" of Bachmann (1890) collectively. According to Bachmann, "Bacidiagrün" is supposed to precipitate small blue granules in nitric acid, whereas "Lecideagrün" is not. I have found much variation between specimens of the same species in their tendency to precipitate blue crystals, without seeing any other differences in colour or reactions with K, C, or N. Not seldom, the amount of blue crystals formed varies even between sections from the same apothecium studied in one and the same slide. Blue crystals appear to be more abundantly formed in sections that are thick and/or have a high concentration of pigment. On the other hand, I have encountered specimens with very high amounts of green pigment in the hymenium that do not produce a single blue crystal in nitric acid. This implies that there is some other factor than amount and concentration of pigment that controls the precipitation of blue crystals. Perhaps, Bacidia Green consists of a mixture of similar substances occurring in different proportions in different specimens. It may also be that the ability to precipitate blue crystals is dependent on the texture of the tissues or the presence of quite different substances that can function as condensation nuclei for the crystals.

In most species, Bacidia Green takes the normal, green hue without any reaction with K (Bacidia Green I in Tab. 5). In *B. absistens*, on the other hand, many European and a few North American specimens have a purplish upper part of hymenium, which reacts K+ green (Bacidia Green II in Tab. 5). The reactions of Bacidia Green are pH-dependent and reversible, and the purplish colour of *B. absistens* shifts towards green already in very diluted KOH solutions. It is possible that the colour of the hymenium in *B. absistens* is affected by the pH of the substratum and the water trickling over the specimen. There are, however, a few Swedish and Norwegian specimens that possess a green hymenium even though they are from acid habitats, which indicates that the lichen, to some extent, has the ability to regulate the pH in its tissues.

(2) *Laurocerasi Brown*. Usually more or less brown (often reddish), in low concentration grey-brown or even almost grey. Reacts K+ purplish, C-, and N+ orange to red. Usually found in the proper exciple and in the upper part of the hymenium, sometimes in the hypothecium. Occurs in 16 species of *Bacidia* and four species of *Bacidina*.

(3) *Rubella Orange*. Yellow in low concentrations, orange to orange-brown in higher concentrations. Reacts K+ intensifying (in low amounts sometimes K-), C-, and N+ intensifying (in low amounts N-). Found in all apothecial tissues. Occurs in 20 (21?) species of *Bacidia* and five species of *Bacidina*. – This is the commonest pigment in *Bacidia* and *Bacidina*. In *Bacidia mutabilis*, which normally contains Rubella Orange as the single pigment, I have once observed entirely colourless apothecial sections of a shade form react distinctly K+ yellow. This implies that Rubella Orange is actually a group of substances, at least one of which is colourless before treatment with K.

4. *Schweinitzii Red*. Red, but often in such high concentrations as to appear red-black. Reacts K- (or K+ intensifying?), C-, and N- (or N+ intensifying?). Occurs in

the hypothecium and proper exciple of two species of *Bacidia*.

5. *Arceutina Yellow*. Yellow or brown-yellow, in high concentration brown with only a slight yellowish hue. Reacts K-, C-, and N-. Occurs in the proper exciple, hypothecium, and upper part of the hymenium in one species of *Bacidia* and one species of *Bacidina*.

6. *Bacidia Brown* ("Bacidiabraun"). Pure brown to red-brown. Reacts K+ purple-red, C-, and N-. Occurs in the proper exciple, hypothecium, and upper part of the hymenium in two species of *Bacidia*.

7. *Thalloidima Green* ("Thalloidimagrün"). Green-grey to dirty grey. Reacts K+ purple to violet, C+ violet, and N+ red. Occurs in the proper exciple and upper part of the hymenium in one species of *Bacidia*.

8. *Arnoldiana Brown*. Brown. Reacts K+ green-brown, C-, N-. Possibly synonymous with the "Sphaeromphalebraun" of Bachmann. Found in the proper exciple, hypothecium, and upper part of the hymenium. Occurs in three species of *Bacidina*.

When two or three pigments are present in the same apothecium, their distribution within the apothecium sometimes overlap. Such mixtures make the individual pigments difficult to identify. Fortunately, the pigments do not usually overlap completely. Furthermore, the distribution and relative concentration of the pigments often vary between different apothecia, which also facilitates identification. If nothing else helps, the pigments may be slowly bleached using a dilute hypochlorite solution (c. 0.2 %). The pigments are variously resistant to bleaching, and during the few minutes it takes for all of the pigments to become completely bleached, their presence and distribution can be studied. For example, when the sometimes almost black proper exciple of *Bacidia circumspecta* is bleached, the brown pigment (Laurocerasi Brown) quickly fades, revealing the presence of a green pigment (Bacidia Green), which is much more resistant to bleaching.

As mentioned earlier, the apothecia of pigment deficient specimens are pale pink, pale yellowish, or pale grey. After a few years in a herbarium, however, pigment deficient apothecia start to darken, and old herbarium specimens may become nearly medium-orange. On the other hand, the few old collections with originally pale grey apothecia (concerns *Bacidina chloroticula*) seen by me appear not to have been affected by aging. The darkening of pigment deficient apothecia due to aging is probably caused by an alteration of the tissue structure, not by the formation of a pigment.

The pycnidial wall, when pigmented, always possesses the same pigments as the apothecia. Species with three pigments in the apothecia, however, usually only have two of these pigments in the pycnidia, at least as far as can be detected.

Chemistry

Eleven of the 25 investigated species of *Bacidia* and none of the eleven investigated species of *Bacidina* were found to produce secondary metabolites in concentrations detectable with HPTLC. *Bacidia friesiana*, *B. igniarii*, and *Bacidina assulata* were not investigated due to sparsity of material. Among the eleven species of *Bacidia* found to contain secondary metabolites, seven produced atranorin (occasionally or invariably) as the only substance. Zeorin appears to be a regularly occurring substance in two species, and a rare substance in one additional species. The chemical patterns found in the species investigated is shown in Fig. 9.

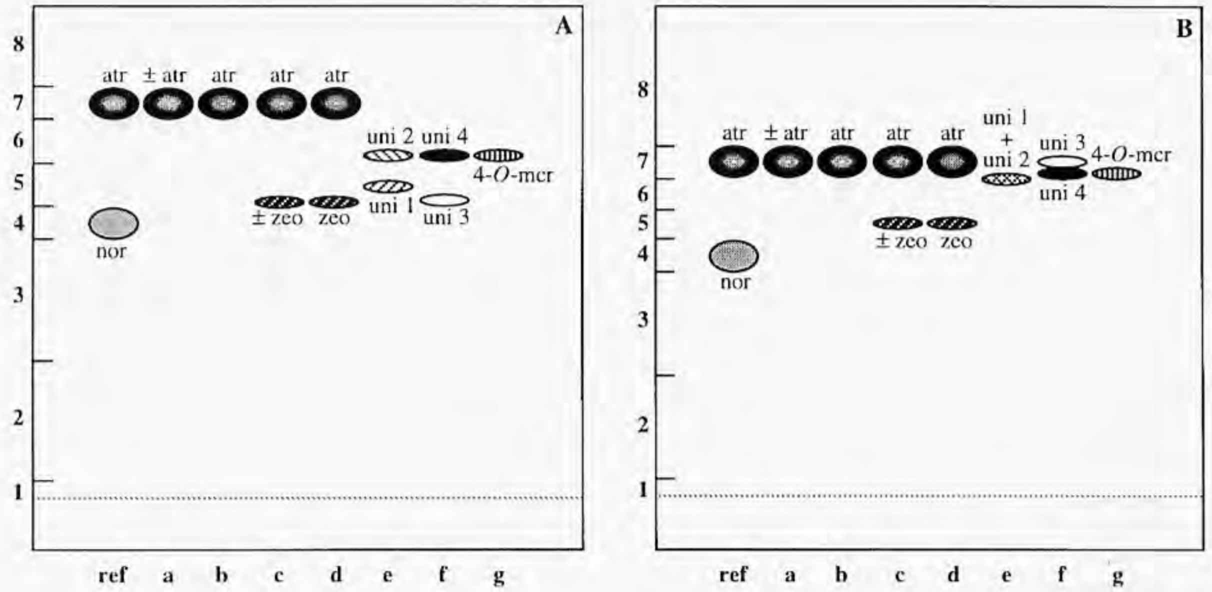
Bacidia heterochroa is the only species treated that exhibits a geographically correlated chemical pattern within the study area. In this species, all specimens from California and Oregon were void of secondary metabolites, whereas the ones from the Southeast were found to contain atranorin. The chemical difference between these population groups is correlated with a number of morphological and anatomical characters. This case is treated in the chapter *Numerical and statistical treatment* and under the species in the chapter *Taxonomy*.

Only one species, *Bacidia absistens*, was found to have a complex secondary chemistry. Tønsberg et al. (1995) reported 4-*O*-methylcryptochlorophaeic acid, a rare *meta*-depside in the orcinol series, as the only major secondary product in a number of specimens from Norway and Sweden. I investigated three specimens from California, Washington, and British Columbia. They were found to produce four orcinol *meta*-depsides in two different combinations. None of these substances is identical to 4-*O*-methylcryptochlorophaeic acid, nor is any of them identical to merochlorophaeic acid, sekikaic acid, or homosekikaic acid. The identity of the four substances remains unknown, but there is no doubt that they are orcinol *meta*-depsides. This group of substances produces characteristic, narrow spots that intensify to a deep purple hue during the first few days after having been exposed to sulphuric acid and heat. Further investigations of the chemistry of *Bacidia absistens* are required. More, large collections of *Bacidia absistens* are needed, since very few of the presently available North American ones are large enough to allow chemical investigations.

Ecology

Substratum

Since the ecology has been used to circumscribe the content of this work, all species are, by definition, corticolous or lignicolous. Most species are exclusively corticolous. *Bacidia circumspecta*, *B. laurocerasi* subsp.



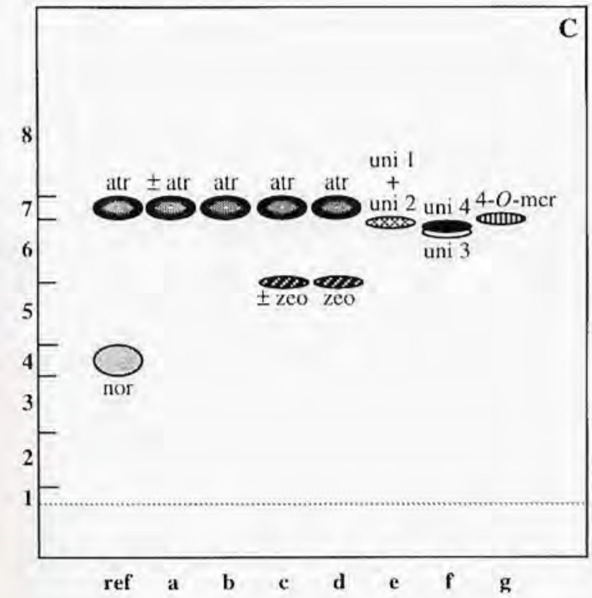


Fig. 9. Chromatograms in the solvent systems A, B, and C obtained by high performance thin layer chromatography (HPTLC). The figures 1-8 on the left side of the chromatograms represent Rf classes according to Culberson & Kristinsson (1970). The distance between the dotted line (where the acetone extract is applied) and the upper edge (where the solvent front stops) is 45 mm. Abbreviations of substances: nor = norstictic acid, atr = atranorin, zeo = zeorin, uni 1-4 = four unidentified *meta*-depsides in the orcinol series, and 4-*O*-mcr = 4-*O*-methylcryptochlorophaeic acid. A "±" means that the substance is only occasionally present. The standard reference with norstictic acid and atranorin is abbreviated "ref". The following chemical patterns have been found in the species investigated: a in *Bacidia aggregatula*, *B. polychroa*, and *B. schweinitzii*, b in *B. rubella*, *B. russeola*, *B. suffusa*, and *B. heterochroa* from the southeastern U. S., c in *B. diffracta*, d in *B. campalea* and *B. mutabilis*, e in two specimens of *Bacidia absistens* from California and British Columbia (Ca., Ekman L656, LD, and BC., 1908, ?Macoun, CANL), f in one specimen of *Bacidia absistens* from Washington (Foster 2888, MIN), and g (for comparison) in Norwegian and Swedish specimens of the same species. Secondary substances are absent from all other species investigated. Note that uni 1 and uni 2 can be separated only in solvent system A. I am uncertain whether the relative order between uni 3 and uni 4 in solvent system B is really correct. My preliminary conclusion is based on the difference in intensity of the spots. Unfortunately, there are no colour differences. Uni 3 and uni 4, like all other orcinol *meta*-depsides involved, have the same, deep purple hue.

idahoensis, *B. polychroa*, *B. subincompta*, and *Bacidina arnoldiana* are predominantly corticolous, but have been collected on lignum a few times. *B. suffusa*, being predominantly corticolous as well, has occasionally been collected on rock. Among the remaining species, *Bacidina chloroticula* has been collected once on bark and once on lignum, *Bn. egenula* once on bark and once on rock, and finally *Bn. egenuloidea* once on lignum and rock. *Bn. egenuloidea*, which is so far known only from the type locality, is the only species treated here that has never been collected on bark. Some of the species can be expected on additional subtrates. For exam-

Tab. 7. The minimum number of phorophytes, lignicolous and saxicolous occurences, and important phorophytes for the North covering at least 10 % of the total number of collections with known substrate of that particular species. The number of collections

	Min. no. of phorophytes	lignicolous	saxicolous	*Abies*	*Acer*	*Aesculus*	*Alnus*	*Annona*	*Artemisia*	*Carpinus*	*Carya*	*Celtis*	*Cephalanthus*	*Conocarpus*	*Cupressus*
Bacidia															
absistens	4	·	·	·	●	·	●	·	·	·	·	·	·	·	·
aggregatula	4	·	·	·	●	·	·	·	·	·	·	·	·	●	·
arceutina	16	·	·	·	●	·	●	·	·	·	·	·	·	·	·
auerswaldii	3	·	·	·	●	·	·	·	·	·	·	·	·	·	·
biatorina	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
campalea	4	·	·	·	●	·	·	●	·	·	·	·	·	·	·
circumspecta	16	●	·	·	·	·	·	·	·	·	·	·	·	·	·
diffracta	8	·	·	·	·	·	·	·	·	·	·	·	·	·	·
friesiana	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
helicospora	2	·	·	·	·	·	·	·	·	●	·	·	·	·	·
heterochroa	40	·	·	·	·	·	·	·	·	·	●	·	·	·	·
hostheleoides	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
igniarii	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
insularis	2	·	·	·	·	·	·	·	●	·	·	·	·	·	·
laurocerasi subsp. *la.*	15	·	·	●	·	·	·	·	·	·	·	·	·	·	·
laurocerasi subsp. *id.*	12	●	·	●	●	·	·	·	·	·	·	·	·	·	·
medialis	10	·	·	·	·	·	·	·	·	·	·	·	·	·	·
mutabilis	2	·	·	·	·	·	·	·	·	·	·	·	·	●	·
polychroa	21	●	·	·	·	·	·	·	·	·	·	·	·	·	·
reagens	3	·	·	·	●	·	·	·	·	·	·	·	·	·	·
rosella	2	·	·	·	●	·	·	·	·	·	·	·	·	·	·
rubella	14	·	·	·	●	·	·	·	·	·	·	·	·	·	·
russeola	1	·	·	·	·	·	·	·	·	·	·	●	·	·	·
salmonea	2	·	·	·	●	·	·	·	·	·	·	·	·	·	·
schweinitzii	54	·	·	·	·	·	·	·	·	·	·	·	·	·	·
subincompta	10	●	·	·	·	·	·	·	·	·	·	·	·	·	·
suffusa	16	·	●	·	●	·	·	·	·	·	·	·	·	·	·
vermifera	5	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Bacidina															
aenea	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
arnoldiana	2	●	·	·	·	·	●	·	·	·	·	·	·	·	·
assulata	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
californica	3	·	·	·	·	●	·	·	·	·	·	·	·	·	●
chloroticula	1	●	·	·	·	·	·	·	·	·	·	·	·	·	·
crystallifera	4	·	·	·	·	·	·	·	·	·	·	·	·	·	·
egenula	1	·	●	·	·	·	·	·	·	·	·	·	·	·	·
egenuloidea	0	●	●	·	·	·	·	·	·	·	·	·	·	·	·
ramea	10	·	·	·	●	·	·	·	·	·	·	·	·	·	·
squamellosa	3	·	·	·	·	·	·	·	·	·	·	·	●	·	·
varia	9	·	·	·	·	·	·	·	·	·	·	·	●	·	·
sp. # 1	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·

American corticolous and lignicolous species of *Bacidia* and *Bacidina*. As "important" have been counted a phorophyte genus with unknown phorophytes is large in many species. All species except *Bacidina egenuloidea* are known to inhabit tree-bark.

Eugenia	*Fagus*	*Fraxinus*	*Krugiodendron*	*Laguncularia*	*Liquidambar*	*Lithocarpus*	*Nyssa*	*Picea*	*Piscidia*	*Planera*	*Populus*	*Quercus*	*Rhizophora*	*Rhus* s. lat.	*Sabal*	*Salix*	*Sambucus*	*Thuja*	*Ulmus*	*Umbellularia*	*Vitis*	*Wisteria*
·	·	·	·	·	·	·	·	·	·	·	●	·	·	·	·	·	·	·	·	●	·	·
·	·	·	·	●	·	·	·	·	·	·	·	·	●	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	●	·	·	·	·	·	·	●	·	·	·	·
·	·	·	·	·	·	●	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	●	·	·	·	·	·	·	●	·	·	·	·	·	·
·	·	●	·	·	·	·	·	·	·	·	●	●	·	·	·	·	·	●	·	·	·	·
·	●	●	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	●	●	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	●	·	·	·	·	·	·
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ple, *Bacidia arceutina*, *B. polychroa*, *B. rubella*, *Bacidina arnoldiana*, *Bn. chloroticula*, and *Bn. egenula* have been collected on rock in western Europe. *Bn. chloroticula* is known to inhabit various anthropogenic substrata as well.

The corticolous finds have been made on a variety of trees, shrubs, and vines. *Bacidia* has been collected on altogether at least 128 and *Bacidina* on at least 27 phorophyte species. This is an underestimation, however, since about 30 % of the collections lack any information on the substratum. An additional 20 % of the collections have information only on the genus to which the phorophyte belongs. These have been included in the figures mentioned above only when there is no other phorophyte determined to species that belongs to the same genus (and thus must constitute a phorophyte species different from all other although not determined to species).

The number of phorophytes known to be inhabited by *Bacidia* and *Bacidina* is, of course, to some degree dependent on the number of collections available. Examining the "common" species of *Bacidia* and *Bacidina*, i.e., those known from more than ten localities, shows that they have been collected on a minimum number of phorophytes ranging from 9 to 54. Most species, however, inhabit a smaller number of preferred phorophytes, on which the bulk of the collections have been made (Tab. 7).

The ecological demands of several species of *Bacidia* and *Bacidina* overlap, with the result that some phorophytes are more species-rich than others. The phorophytes richest in *Bacidia* are *Populus tremuloides* (10 species), *Acer macrophyllum* (8), *Thuja occidentalis* (8), *Ulmus americana* (8), *Acer saccharum* (7), *Fraxinus nigra* (7), *Populus trichocarpa* (7), *Fagus grandifolia* (5), and *Liquidambar styraciflua* (5). The phorophytes so far known to be the richest in *Bacidina* are *Fraxinus caroliniana* (3 species), *Vitis rotundifolia* (3), *Alnus rubra* (2), *Cephalanthus occidentalis* (2), *Fagus grandifolia* (2), *Sambucus canadensis* (2), and *Umbellularia californica* (2). Considering that the species of *Bacidina* are extremely overlooked, this list will probably soon have to be updated. It should also be noted that regionally, other phorophytes than the ones mentioned may be the most important. However, the most species-rich phorophytes mentioned altogether house 20 out of 27 species of *Bacidia* and 9 out of 12 species of *Bacidina*.

Habitat

The habitats of *Bacidia* and *Bacidina* cover a range of woodland from sea level to an altitude of about 3000 meters (*Bacidia subincompta* in the Rocky Mountains of Colorado and Arizona). Many species favour localities that combine high air humidity with a fair amount of sunlight, such as light forests or forest edges in swamps, river and creek valleys, and hill and mountain slopes close to the sea or near lakes or swamps. Only a few species thrive in deep shade, viz. *Bacidia helicospora*, *B. schweinitzii*, and *Bacidina squamellosa*, although at least the two last are also found under lighter conditions. Similarly, only a few species have been found on solitary trees, namely *Bacidia rubella* and *B. subincompta*. *Bacidia insularis* deviates markedly from all other species in not preferring woodland, but chaparral or scrub close to the sea. Contrary to the European situation, no species is regularly found on dust-enriched tree trunks (in avenues, in churchyards, on way-side trees etc.). In Europe, *B. friesiana*, *B. laurocerasi*, *B. rosella*, and, particularly, *B. rubella* are often found under such conditions. On the whole, the lichen flora of dust-enriched tree-trunks appears to be much poorer in species and individuals than the corresponding European flora.

Many woodland species favour oldgrowths, and are particularly abundant on the rough bark of old trees. A number of species, however, have been found on young substrata with little competition from other lichens and thus appear to be fast colonizers, viz. *Bacidia absistens*, *B. arceutina*, *B. heterochroa*, *Bacidina chloroticula*, *Bn. crystallifera*, *Bn. egenula*, *Bn. egenuloidea*, *Bn. ramea*, and *Bn. varia*. Apparently, the proportion of fast colonizers is distinctly higher in *Bacidina* than in *Bacidia*. The behaviour of *Bacidia absistens* in North America is remarkable. It is encountered on young trunks or branches, sometimes even the thinnest branches in the uppermost part of the crown of the trees. In western Europe, on the other hand, it appears to be restricted to large tree-trunks in old woodlands. Possibly, the North American populations have had to adapt to a colonizing way of life, since the trunks of its favourite phorophytes are often completely covered with bryophytes.

It is not uncommon to find one, two, or even three species of *Bacidia* and *Bacidina* in a single locality. A higher number is unusual, however. The richest locality known to me is the Burden Research Plantation, East Baton Rouge Parish in Louisiana, which hosts three species of *Bacidia* and four species of *Bacidina*.

Phytogeography

Many of the species of *Bacidia* and *Bacidina* exhibit distinctive distribution patterns on the North American continent. Most of these are previously well-known from other lichens, bryophytes, and vascular plants. The causal relations behind these patterns have been discussed elsewhere and are generally not repeated here

Tab. 8. The number of taxa, number of endemic taxa, and geographic connections in the phytogeographic elements represented among the corticolous and lignicolous species of *Bacidia* (28 taxa, 27 species) and *Bacidina* (12 species) in North America. Continents on which the North American species are known have been marked, but this list is almost certainly incomplete. Only collections seen by me or reasonably reliable reports have been included. Continents are abbreviated Eu = Europe, As = Asia, SA = South America, Af = Africa, and Au = Australia.

Element	No. of taxa	No. of endemics	Species known also from				
Subelement	(*Bacidia, Bacidina*)	(*Bacidia, Bacidina*)	Eu	As	SA	Af	Au
Boreal	2, 0	0, 0	+				
Temperate							
Pan-North American	1, 0	0, 0	+				
East temperate + Appalachian	6, 0	2, 0	+	+			
Oceanic	1, 1	0, 0	+				
North Pacific coast	4, 1	2, 1	+				
Appalachian + North Pacific coast	1, 0	0, 0	+				
Coastal Plain	1, 0	1, 0					
Tropical							
South Pacific coast + Coastal Plain	2, 0	0, 0	+	+	+	+	+
Coastal Plain	6, 4	0, 0-4		+	+	+	
South Pacific coast	1, 1	0, 1			+		
Unclassified	3, 5	0, 0-2	+				
Total	28, 12	5, 2-8	+	+	+	+	+

(Braun 1955, Imshaug & Brodo 1966, Schofield 1969, Gowan 1983).

It is important to note that no species treated here has a distribution limited by the availability of suitable phorophytes. Instead, the distributions are limited by various other ecological, climatic and historic factors. The classification of the distribution patterns used here has been adapted from Brodo (1968), Brodo & Gowan (1983), Brodo & Hawksworth (1977), Gowan (1983), Gowan & Brodo (1988), and Hale (1961). Representatives of the arctic and maritime elements do not occur among the North American *Bacidia* and *Bacidina*. The species-richness and the endemism have been summarized in Tab. 8.

Fairly reliable hypotheses about distributional patterns can be made for 24 of the 27 species of *Bacidia* and 7 of the 12 species of *Bacidina*. The remaining 8 species are too poorly known to permit credible interpretations, although educated guesses can be made in most cases: *Bacidia biatorina* (north Pacific coast subelement?), *B. friesiana* (ditto?), *B. igniarii* (boreal?), *Bacidina assulata* (Ozarkian or, as in Europe, continental?), *Bn. chloroticula* (?), *Bn. crystallifera* (Coastal Plain subelement of the temperate element?), *Bn. egenula* (eastern temperate subelement?), and *Bn. egenuloidea* (?).

Examples other than species of *Bacidia* and *Bacidina* have been included in the account only when the (sub)element has not been previously suggested. This concerns the Californian element and the southern Pacific coast-Coastal Plain subelement of the tropical element.

The boreal element

Bacidia subincompta and probably also *B. vermifera* belong to the boreal element. They constitute 7 % of the taxa of *Bacidia*. Both species occur in Europe as well. As pointed out by Brodo & Hawksworth (1977), the boreal element is difficult to interpret on a North American scale due to the effects of glaciations and subsequent recolonizations. Both species, however, are coniferous forest species, mainly confined to *Populus tremuloides*. Brodo & Gowan (1983) distinguished between a northern and a southern boreal distribution type. *B. subincompta* exhibits a more or less typical southern boreal distribution type. With hesitation, I have placed *Bacidia vermifera* in the boreal element although it is not present in the true boreal zone. Instead, it occupies similar habitats in the Rocky Mountains and in the Cascades, and can be said to have a "western montane" distribution type. Possibly, it was displaced southwards during the glaciatons, and has not (yet) reinvaded the northern territories.

The temperate element

The temperate element is the largest one, constituting 50 % of the *Bacidia* and 17 % of the *Bacidina*. The endemism is 36 % in *Bacidia* and 50 % in *Bacidina*. The latter figure, however, is probably strongly distorted by the fact that that several species of *Bacidina* have been excluded from the analysis. The temperate element can be divided into a large number of subelements, seven or eight of which are represented among the *Bacidia* and *Bacidina*.

The Pan-North American subelement

Only one species, *Bacidia circumspecta*, can be said to belong to the Pan-North American subelement, although it appears that this species avoids much of the southeastern coastal plain, the Great Plains, and high altitudes in most of the Rocky Mountains. *Bacidia circumspecta* is widespread in Europe. The endemism among lichens with this distribution type is low or nonexistent (Brodo & Hawksworth 1977).

The eastern temperate and Appalachian subelements

One species, *Bacidia schweinitzii*, clearly belongs to the eastern temperate subelement, whereas *Bacidia laurocerasi* subsp. *laurocerasi* belongs to the Appalachian subelement with a Great Lakes-Appalachian distribution type. Probably, *Bacidia rosella* also belongs to the latter subelement. Three species, viz. *Bacidia diffracta*, *B. polychroa*, and *B. suffusa*, have distribution types intermediate betweeen these subelements. All three occur over much of the eastern temperate region, but they have a clear preference for the Great Lakes-Appalachian-Ozark Plateau regions. Possibly, the intermediate distribution type, and perhaps also the eastern temperate type have been derived from an original Appalachian distribution type following the glaciations. Among the species discussed here, *Bacidia schweinitzii* and *B. laurocerasi* are known from eastern Asia, *B. laurocerasi* subsp. *laurocerasi* and *B. polychroa* from Europe, whereas *B. diffracta* and *B. suffusa* are endemic. The former of the endemics is closely related to *B. polychroa*, whereas the latter is much closer related to the tropical species *B. campalea*, *B. fusconigrescens* (Nyl.) Zahlbr. and *B. millegrana* (Taylor) Zahlbr. than to any temperate (Asian, North American, or European) species that I know of.

The oceanic subelement

Two species, *Bacidia arceutina* and *Bacidina arnoldiana*, can be referred to the oceanic subelement. *Bacidia arceutina* is bicoastal with very few finds on the east coast (none of which have been confirmed in recent time), whereas *Bacidina arnoldiana* is known from humid areas of the Pacific Northwest and the southern Appalachian Mountains. Neither of these species is endemic.

The northern Pacific coast subelement

The northern Pacific coast subelement consists of five species with similar ecological demands as the oceanic subelement, viz. *Bacidia absistens*, *B. auerswaldii*, *B. laurocerasi* subsp. *idahoensis*, *B. salmonea*, and *Bacidina ramea*. They are mainly restricted to the coastline and low elevations of the western slopes of the Coast Range and the Cascades from central California to British Columbia. *Bacidia auerswaldii* and *B. laurocerasi* subsp. *idahoensis* also occur in areas with fairly high precipitation on the western slope of the mountain ranges closest to the east of the Cascades in Idaho, Montana, and British Columbia. *Bacidina ramea* occurs along the coast to southern California, but has been referred to this distribution type, since it appears rather poorly developed in the southern localities, and since the northern localities are very rich in well-developed individuals. In other words, the localities in southern California appear to be a southerly extension of a mainly northern distribution.

Bacidia absistens and *B. auerswaldii* are known from Europe, whereas the remainder of the taxa are endemic. Thus, the endemism (60 %) in this subelement is the highest of all.

This subelement corresponds to the "lowland to western montane (humid forests)" plus parts of the "coastal lowland" distribution type of Brodo & Hawksworth (1977). The connections of this subelement has been discussed by Jørgensen (1983).

The Appalachian-north Pacific coast subelement

A single species, *Bacidia rubella*, belongs to the Appalachian-north Pacific coast subelement. The bulk of the localities are situated in the Great Lakes-Appalachian regions, but there are a few outliers between the Coast Range and the Cascades in the northern Pacific region. *Bacidia rubella* is known from Europe as well.

The Coastal Plain subelement

Bacidia helicospora, being a North American endemic, is the only representative belonging to the Coastal Plain subelement of the Temperate element. It is found mainly in the Coastal Plain and at low elevations in the valleys of Mississippi and Tennessee Rivers, but contrary to the species referred to the Coastal Plain subelement of the Tropical element, it avoids the entire Florida Peninsula. Furthermore, *B. helicospora* is likely to have originated in the Appalachian region, since its closest living relative appears to be *B. laurocerasi*, a temperate species.

The tropical element

The tropical element is the second largest one, comprising 32 % of the *Bacidia* and 42 % of the *Bacidina*. The endemism is probably low, although the newly described species of *Bacidina* belonging to this element have not yet been reported south of the U. S. All species documented to occur outside the U. S. and Canada are found in the neotropics, however, and some are probably even pantropical species. The tropical element can be divided into two subelements.

The southern Pacific coast-Coastal Plain subelement

The southern Pacific coast-Coastal Plain subelement includes *Bacidia heterochroa* and probably also *B. reagens*. The former is a "weedy", mainly pantropical species that extends into subtropical and even into temperate areas of the world. The latter is a very inconspicuous and overlooked species, which has so far not been collected in the strictly tropical region of South America. It is known from southern subtropical Brazil and humid forests of Louisiana, Georgia and southern California.

To my knowledge, only a few other lichens have a similar distribution type, for example *Teloschistes flavicans* (Sw.) Norman and *T. exilis* (Michx.) Vain. (Rudolph 1955).

The Coastal Plain subelement

This subelement consists of tropical species with their northern distribution limit in the Florida Peninsula or the immediate coast of the Gulf of Mexico, but not much further inland. This subelement may very well be divisible into a number of distribution types, but I refrain from doing so in a formal way due to the still rather poor knowledge of the distribution of several species, particularly in peninsular Florida. It may suffice to call attention to the fact that a number of species, namely *Bacidia aggregatula*, *B. campalea*, *B. hostheleoides*, *B. mutabilis*, and *Bacidina aenea*, appear to be restricted to the southern tip of the Florida peninsula north to a west-easterly line across Tampa Bay, which is also the northern limit for the red mangrove, *Rhizophora mangle*. Other species occur further north and west, namely *Bacidia medialis*, *Bacidina squamellosa*, *Bn. varia*, and *Bn.* sp. #1. *Bacidia russeola* has been encountered only in the Brownsville area of southernmost Texas. This species is widespread on Cuba, and may be expected in southern Florida as well.

Several additional species of *Bacidia* are found south of the study area, some of which may turn up on the Florida Peninsula or the southernmost tip of Texas. Two distinct species, *Bacidia combinans* (Nyl.) Zahlbr. and *B. horista* (Nyl.) Zahlbr. occur as close as on Cuba. Furthermore, at least *B. cuyabensis* Malme, *B. millegrana* (Tayl.) Zahlbr., and *B. testacea* Malme appear to be common and widespread in the neotropics (K. Kalb in litt.).

The Californian element

A Californian element among the lichens has apparently never been ventured. It was suggested for bryophytes by Schofield (1969), and I believe that such an element can be discerned among the lichens as well. This element is basically subtropical, and includes species mainly restricted to the southern, "Mediterranean" area of coastal southern California north to about San Francisco. The connections lie mainly with the Mediterranean region of Europe and with western South America (Kärnefelt 1980, Jørgensen 1983). Among the species treated here, two can be referred to the Californian element, viz. *Bacidia insularis* and *Bacidina californica*. The former is known also from the Galapagos Islands, whereas the latter appears to be endemic. There are further examples of species belonging to this element in *Lecanora* (Brodo 1984) and *Pertusaria* (Dibben 1980).

Similarites between regions

Methods

Nine North American regions were compared regarding species composition of *Bacidia*. Only the genus *Bacidia* was included in the investigation, since the distribution pattern of several species of *Bacidina* are too poorly known. To make possible a comparison with extra-North American conditions, three northwest European regions were also included. The regions were defined in the following way (abbreviations used in the cluster diagram):

Tab. 9. The binary matrix on which the cluster analysis of nine North American and three European regions was based. The species of *Bacidia* are coded 1 for regions where it is present and 0 for regions from which it is absent. A species has been coded as present even if it is now considered extinct from the region (concerns BRIS and SSWE). The abbreviations of the regions (NPAC etc.) are explained in the text.

	NPAC	SPAC	MONT	BORE	GLNA	OZAR	SAPP	COPL	FLPE	BRIS	SSWE	NSWE
absistens	1	1	0	0	0	0	0	0	0	1	1	0
aggregatula	0	0	0	0	0	0	0	0	1	0	0	0
arceutina	1	1	0	0	1	0	0	0	0	1	1	0
auerswaldii	1	0	0	0	0	0	0	0	0	1	1	0
biatorina	1	0	0	0	0	0	0	0	0	1	1	0
caesiovirens	0	0	0	0	0	0	0	0	0	1	0	0
campalea	0	0	0	0	0	0	0	0	1	0	0	0
circumspecta	1	1	1	1	1	1	0	1	0	1	1	1
diffracta	0	0	0	0	1	1	1	1	0	0	0	0
fraxinea	0	0	0	0	0	0	0	0	0	0	1	0
friesiana	1	0	0	0	0	0	0	0	0	1	1	0
helicospora	0	0	0	0	0	0	1	1	0	0	0	0
heterochroa	1	1	0	0	0	0	0	1	1	0	0	0
hostheleoides	0	0	0	0	0	0	0	0	1	0	0	0
igniarii	0	0	0	1	0	0	0	0	0	1	1	1
incompta	0	0	0	0	0	0	0	0	0	1	1	0
insularis	0	1	0	0	0	0	0	0	0	0	0	0
laurocerasi	1	0	0	0	1	0	0	0	0	1	1	0
medialis	0	0	0	0	0	0	0	1	1	0	0	0
mutabilis	0	0	0	0	0	0	0	0	1	0	0	0
polychroa	0	0	0	0	1	1	1	1	1	1	1	0
reagens	0	1	0	0	0	0	0	1	0	0	0	0
rosella	0	0	0	1	1	0	0	0	0	0	1	0
rubella	1	0	0	1	1	0	1	0	0	1	1	1
russeola	0	0	0	0	0	0	0	1	0	0	0	0
salmonea	1	0	0	0	0	0	0	0	0	0	0	0
schweinitzii	0	0	0	0	1	1	1	1	0	0	0	0
subcircumspecta	0	0	0	0	0	0	0	0	0	1	0	0
subincompta	1	0	1	1	1	0	0	0	0	1	1	1
suffusa	0	0	0	0	1	1	1	1	0	0	0	0
vermifera	0	0	1	1	0	0	0	0	0	1	1	1

(1) NPAC: Northern Pacific coast region, including the coast and the Coast Range from central California (north of Marin Co.) to southern British Columbia, plus low elevations (up to c. 1000 m) on the western slopes of the Cascades and the Rocky Mountains.

(2) SPAC: Southern Pacific region, including the coast and the Coast Range in southern California north to (and including) Marin Co.

(3) MONT: High elevations in the Rocky Mountains, the Cascades and the Sierra Nevada of western United States.

(4) BORE: All of Canada and Alaska except the areas belonging to 1 or 5.

(5) GLNA: The Great Lakes and the northern Appalachian region, including the Great Lakes, the area immediately north of the lakes, eastwards to the coast of New Brunswick and Nova Scotia, southwards along the coast to New York and along the Appalachian Mountains south to the level of Washington D. C., plus the area south of the Great Lakes, south to, but not including, the Appalachian Mountains and the Ozark Plateau.

(6) OZAR: The Ozark Plateau.

(7) SAPP: The southern Appalachian mountains, i.e., the part of the Appalachian mountain range not included in 5.

(8) COPL: The Coastal Plain from Texas to New York (except southern peninsular Florida), plus the valleys of Mississippi and Tennessee Rivers north to southern Illinois.

(9) FLPE: The Florida Peninsula south of a west-easterly line across Tampa.

(10) BRIS: The British Isles.

(11) SSWE: Southern Sweden south of the northern distribution limit of *Quercus* (limes norrlandicus).

(12) NSWE: Northern Sweden north of *limes norrlandicus*.

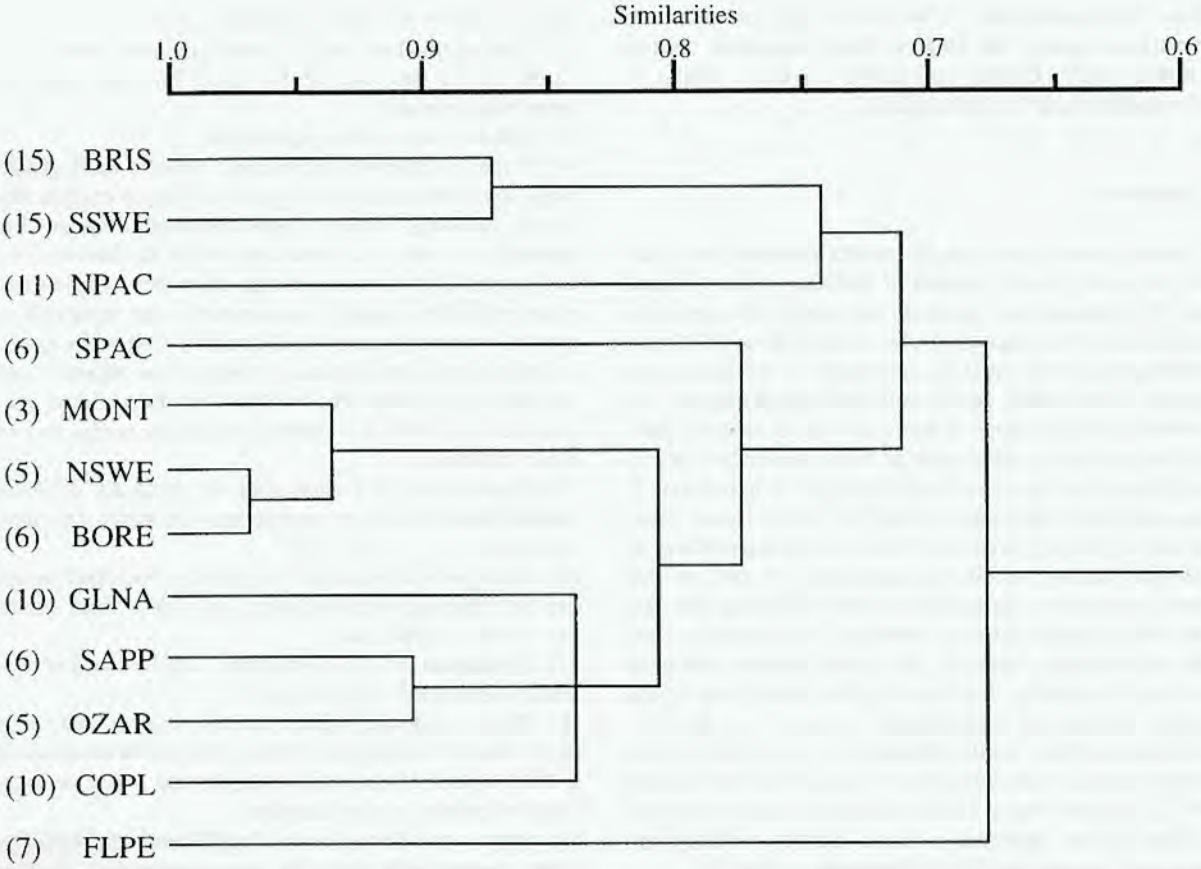


Fig. 10. Single linkage cluster analysis of nine North American and three European regions regarding species composition of the *Bacidia* flora. The simple matching dichotomy (S4) coefficient was used to calculate similarities between each pair of regions, using the binary matrix in Tab. 9. Distances between clusters are Euclidean. The abbreviations and delimitations of the regions (NPAC etc.) are explained in the text. The number of species of *Bacidia* presently known from each region is presented within brackets.

The choice of the three extra-North American regions was based on knowledge. The *Bacidia* flora of these regions is fairly well-known, the British Isles through the work of Coppins (in Purvis et al. 1992) and Sweden through my own studies. Four species occur in the European regions but not in North America: *Bacidia caesiovirens* S. Ekman & Holien (Ekman & Holien 1995), *B. fraxinea* Lönnr. (Ekman & Nordin 1993), *Bacidia incompta* (Borrer ex Hook.) Anzi, and *B. subcircumspecta* Coppins (regarding the two latter, see Coppins et al. 1992 and Coppins in Purvis et al. 1992). Note that *Bacidia igniarii* has recently been reported for the British Isles (Purvis et al. 1993). The 27 North American species and 4 additional European species were scored as present (1) or absent (0) in each of the twelve regions (Tab. 9). The similarity in species composition between each pair of the regions was then calculated using the simple matching dichotomy (S4) coefficient. The S4 coefficient measures similarity as the proportion of common presences plus common absences, i.e., $(n_{00}+n_{11})/(n_{00}+n_{01}+n_{10}+n_{11})$, where n_{00} is the number of species absent from both regions, n_{11} the number of species present in both regions, and n_{01} and n_{10} the number of species present in only one the two regions. Finally, the resulting similarity matrix was used in a single linkage cluster analysis.

Results

The cluster diagram is shown in Fig. 10. MONT, BORE, and NSWE are the regions that are most similar to each other. SAPP and OZAR are also fairly similar, as are BRIS and SSWE. FLPE is very different from all other regions. NPAC is more similar to BRIS and SSWE than to any other North American region. Apart from FLPE and NPAC, SPAC is the most deviant North American region. The eastern North American regions GLNA, SAPP, OZAR, and COPL are more similar to one another than to other regions.

Discussion

Generalizations based on the results obtained here cannot be made. Similar studies of floristic similarity based on other genera are required, and ideally the entire lichen flora of the regions involved should be used. Nevertheless, the result must be applicable to the species on which it was based, and it calls for an explanation. The northern Pacific region is more similar to nemoral parts of Europe than to other areas of North America concerning the species composition of *Bacidia*. A hypothesis to explain this observation is that the West Coast, compared to other regions, has offered better possibilities of survival during periods of glaciation for species that were once more widespread over the continent. The reason why northern Sweden, northern North America, and the mountainous parts of the United States appear so similar is probably that these regions house part of the same, widespread circumboreal element. It is not surprising that the Florida Peninsula is so different from other regions, considering that a majority of the species are of tropical origin. Had a neotropical region been included in this analysis, it would almost certainly had come out next to the Florida Peninsula in Fig. 10.

Taxonomic delimitations above the species level

I have attempted to characterize *Bacidia* s. str and *Bacidina*, to outline the differences between these genera, and to delimit them from other genera. This work is presented here as a preliminary hypothesis based mainly on North American species. I have, however, tested it on a number of species from other parts of the world, mainly Europe and South America, and so far it has proved successful.

Characterization of Bacidia and Bacidina

Depending on what other genus *Bacidia* is compared with, a particular set of characters can be used to separate them. In the following characterization of *Bacidia*, I have included the minimum amount of characters necessary to convincingly separate this genus from *Bacidina* and from the genera treated in the section *Related genera and species groups*:

(1) Lichenized with green, chlorococcoid algae.
(2) Thallus crustose, never dissolving into goniocysts. Upper cortex two-layered, the upper layer an epinecral layer with crystals.
(3) Biatorine or lecideine apothecia.
(4) Proper exciple well-developed, without thick gelatinous layer along the rim. Hyphae of proper exciple distinctly radiating, more or less abundantly furcate but sparingly or not at all anastomosed. Cell lumina long and narrow (but lumina near rim of proper exciple often enlarged), often distinctly constricted at the septa (not in species with very narrow cell lumina). Cell walls heavily gelatinized, the distance between two adjacent cell lumina (1-)2-5 times the width of a lumen. Some species deviate from this pattern in one or rarely two of these features.
(5) Hypothecium not chondroid, of distinctly different texture than the proper exciple and distinctly delimited from this.
(6) Paraphyses unbranched or sparsely branched in upper part, sparingly anastomosed, not with a thick, gelatinized wall in upper part.
(7) Hymenium and subhymenium amyloid, often distinctly pigmented in upper part.
(8) Tholus amyloid, with a narrow c-layer, with a ± high, blunt or pointed axial body, the width of which is a third or less of the entire d-layer, and a low or high, blunt or pointed ocular chamber.
(9) Spores acicular, clavate, bacilliform, or fusiform, when mature with three or more transversal, distinct septa. They are colourless, rather thick-walled, and lack perispore or ornamentation.
(10) Pycnidia with cylindrical conidiogenous cells (7-15 µm long) that produce conidia terminally. Conidia usually filiform and curved, either formed singly or repeatedly from the conidiogenous cells.
(11) Sometimes producing atranorin, rarely zeorin or 4-*O*-methylcryptochlorophaeic acid or unidentified orcinol *meta*-depsides.

Bacidina is circumscribed here as to include species with the features mentioned below. The set of characters has been chosen on the same grounds as for *Bacidia*.

(1) Lichenized with green, chlorococcoid algae.
(2) Thallus crustose, often partly or entirely dissolving into goniocysts. Upper cortex two-layered, the outer layer an epinecral layer without crystals.
(3) Biatorine, lecideine, or exceptionally zeorine (with a thin thalline margin) apothecia.
(4) Proper exciple well-developed, without thick gelatinous layer along the rim. Hyphae of proper exciple indistinctly or distinctly radiating, more or less abundantly furcate but sparingly or not at all anastomosed. Cell lu-

Tab. 10. Observed differences between the genera *Bacidia* and *Bacidina*, as understood in this work.

	Bacidia	*Bacidina*
Thallus cortex	With minute crystals	Without crystals
Thallus structure	Never dissolved into goniocysts	Often dissolved into goniocysts
Apothecia	Usually strongly pigmented, not seldom in distinct layers	Often weakly and diffusely pigmented
Proper exciple inside rim	Composed of thick-walled hyphae with narrowly cylindrical cell lumina	Composed of rather thin-walled hyphae, most of which have cell lumina that are broadly ellipsoid, almost globose, or irregular
Axial body	≤1/3 of the entire width of the d-layer, vertically not reaching through this	>1/3 of the entire width of the d-layer, in some species vertically reaching all through this
Terminal cell of conidiophores	7-15 µm long	4-8 µm long
Secondary chemistry	Often atranorin, rarely other substances	None

mina varying from narrowly cylindrical to almost globose, but at least partly short and wide (even inside the rim), ± ellipsoid, globose, or irregular (width > 2.5 µm, length > 4 times the width, often distinctly constricted near septa. Walls gelatinized, the distance between two adjacent lumina usually less than the width of a lumen.

(5) Hypothecium not chondroid, of distinctly different texture than the proper exciple and distinctly delimited from this.

(6) Paraphyses unbranched or more or less branched in upper part, not anastomosed, without a thick, gelatinized wall in upper part.

(7) Hymenium and subhymenium amyloid, sometimes pigmented in a ± diffuse layer in upper part

(8) Tholus amyloid, with a narrow or wide c-layer, with a high or low, blunt axial body (sometimes penetrating through the entire d-layer), the width of which is more than a third of the entire d-layer; ocular chamber absent or present, low or high, blunt or pointed.

(9) Spores acicular, when mature with three or more transversal, distinct or indistinct septa. They are colourless, rather thick-walled, and lack perispore or ornamentation.

(10) Pycnidia with cylindrical conidiogenous cells (4-8 µm long) that produce single conidia terminally. Conidia usually filiform and curved.

(11) Contains no lichen substances.

The relationship between Bacidia and Bacidina

In my opinion, *Bacidia* and *Bacidina* are closely related to each other, about as closely as *Bacidia* and *Toninia*. *Bacidia*, *Bacidina*, *Toninia*, and *Arthrosporum* probably together form a monophyletic group. Unfortunately, the differences between *Bacidia* and *Bacidina* have often been oversimplified and exaggerated. For example, *Bacidina* has repeatedly been stated to have a "paraplectenchymatic" proper exciple contrary to a "prosoplectenchymatic" one in *Bacidia*. Some species of *Bacidina* have an entirely "paraplectenchymatic" proper exciple, but several species have a mixture of narrow and wide cell lumina. On the other hand, some species of *Bacidia* have enlarged cell lumina along the rim of the proper exciple. Thus, the real difference between *Bacidia* and *Bacidina* appears to be that *Bacidina* has at least some wide cell lumina in the inner of the proper exciple, whereas *Bacidia* does not. Furthermore, it has been stated that *Bacidia* has "*Bacidia* type" asci and *Bacidina* "*Lecanora* type" asci. As I have indicated earlier, I object to such a statement, since there are no generally accepted definitions of these "ascus types", but also because such a terminology can make even minor differences sound fundamental. As far as I can understand, the tholus structure in *Bacidia* and *Bacidina* is essentially the same, but the width of the axial body relative to the d-layer is larger in the latter genus. The characters that can be used to separate *Bacidia* from *Bacidina* (including the ones discussed here) are summarized in Tab. 10.

Related genera and species groups

This section concerns a number of genera and species groups that are related to *or* have recently been thought to be related to *Bacidia* and *Bacidina*. I have included all genera accepted in the "Bacidiaceae" by Eriksson & Hawksworth (1993) and some additonal genera believed to be relevant to the discussion (*Auriculora*, *Bapalmuia*, *Eschatogonia*, *Megalaria*, *Myrionora*, *Physcidia*, *Scoliciosporum*, *Sporacestra*, *Toninia*, and *Tylothallia*). Furthermore, three species groups, mainly consisting of species that I exclude from *Bacidia* and *Bacidina*, are treated. They are all more or less closely related to *Bacidia* and *Bacidina*, and may constitute undescribed genera or parts of already described genera. The list of related species groups could easily have been made longer, but I have restricted the discussion to groups that are well-characterized and relatively rich in species. It should be noted that in a brief discussion by Hertel & Rambold (1995), *Compsocladium*, *Eschatogonia*, *Physcidia*, and *Japewia* were thought not to be members of the Lecanoraceae (incl. Bacidiaceae). I admit to have treated the genera below very inconsistently. The amount of information included is more or less correlated with my knowledge and interest in the particular genus. *Toniniopsis* Frey and *Psorella* Müll. Arg. are considered here to be synonyms of *Bacidia* and are treated as such under this genus in the *Taxonomy* chapter.

Adelolecia Hertel & Hafellner

Hafellner 1984: 260.

Type: *A. pilati* (Hepp) Hertel & Hafellner (holotype).

Adelolecia consists of two known species, *A. pilati* and *A. kolaensis* (Nyl.) Hertel & Rambold (Hertel & Rambold 1995). The genus differs from *Bacidia* and *Bacidina* mainly in having more richly branched paraphyses and 0-1-septate, ellipsoid spores.

Arthrosporum A. Massal.

Massalongo 1853a: 127.

Type: *A. populorum* A. Massal (holotype)

The genus *Arthrosporum* was re-established by Hafellner (1984) to accomodate the single known species, *A. populorum* A. Massal., previously known as *Bacidia populorum* (A. Massal.) Trevis. or *Bacidia acclinis* (Flot.) Zahlbr. *Arthrosporum* differs from *Bacidia* by possessing a proper exciple built up of fairly thin-walled hyphae with lumina (laterally, just inside the rim) that are more or less rectangular (up to 12 µm long, generally 1-2 times as long as wide) and not constricted at the septa. Furthermore, the genus differs from *Bacidina* in having a narrower axial body, and in having more regularly rectangular cell lumina without constrictions at the septa inside the rim.

Although distinct from *Bacidia* and *Bacidina*, *Arthrosporum* appears to be very close to *Toninia*. As also pointed out by Timdal (1991), *Arthrosporum* differs from *Toninia* only in the corticolous habit and in the polysporous asci. There is a distinct possibility that *Arthrosporum* should be included in *Toninia*, considering that ecology hardly is a reason to separate genera and that there are several other examples of octosporous species that are closely related to species with polysporous asci (in, e.g., *Candelariella*, *Caloplaca*, *Lecania*, and *Lecanora*).

Auriculora Kalb

Kalb 1988: 2.

Type: *A. byssomorpha* (Nyl.) Kalb (holotype).

The genus *Auriculora* was established by Kalb (1988) for the single species, *A. byssomorpha*. It was stated to have "asci similes typo Lecanoraceae" and was placed in the Lecanoraceae by Eriksson & Hawksworth (1989, 1991b) for this reason. Later studies by Henssen & Titze (1990) led Eriksson & Hawksworth (1991a, 1993) to put the genus among the Lecanorales incertae sedis. Sérusiaux (1993), however, considered the asci to be of "*Bacidia*-type" and referred *Auriculora* to "Bacidiaceae" with a query.

Auriculora byssomorpha has ear-like portions of old decaying hymenia attached to the edge of the younger hymenia. According to Hensse & Titze (1990), this peculiar appearance is caused by the formation of new hymenia below the old ones, which disintegrate. My own observations of the tholus show that it is not at all similar to the ones found in *Bacidia*. Instead, it possesses a wide axial body reaching all through the d-layer, and is thus rather similar to the tholus appearance found in *Scoliciosporum umbrinum* (Ach.) Arnold (see Hafellner 1984: 340). Furthermore, *Auriculora* differs from *Bacidia* and *Bacidina* in having a non-amyloid hymenial gel.

Bacidiopsora Kalb

Kalb 1988: 4.

Type: *B. squamulosula* (Nyl.) Kalb (holotype).

This genus was introduced to accomodate a single species, which was previously known as *Bacidia squamulosula* (Nyl.) Zahlbr. Studies by Klaus Kalb, however, have shown that there are a number of additional species belonging to this genus (Kalb & Elix 1995). *Bacidiopsora squamulosula* has a thallus consisting of squamules that are tightly adpressed to a black hypothallus, a colour which is caused by a bluish pigment that reacts N+ purple with a precipitate of blue crystals. The apothecia are formed on the hypothallus, not on the areoles. The anatomy of the spores, paraphyses, and proper exciple agrees with *Bacidia*. Also the pigmentation is similar to some species of *Bacidia*: The rim and the upper part of the proper exciple is dark red-brown to black-brown (K+ purplish; Laurocerasi Brown), whereas the inner part is pale orange (K+ intensifying; Rubella Orange). The hypothecium is brown-orange (K+ intensifying; Rubella Orange), and the hymenium is colourless except for the epithecium, which contains a mixture of a green (K+ emerald green, N+ purple with a precipitate of blue crystals; Bacidia Green) and a brown-orange pigment (K- or + intensifying; Rubella Orange). According to Kalb & Elix (1995), *Bacidiopsora* differs from *Bacidia* also in containing homosekikaic and hyperhomosekikaic acids in the thallus. Although obviously close to *Bacidia*, I consider *Bacidiopsora* to be a different genus.

Bapalmuia Sérus.

Sérusiaux 1993: 449.

Type: *B. palmularis* (Müll. Arg.) Sérusiaux (holotype).

Although *Bapalmuia* was not definitely stated to be closely related to *Bacidia*, these genera were compared by Sérusiaux (1993). He found the tholus to contain no structures or occasionally only a slightly darker cap directly above the spore-mass. My own observations on *B. palmularis* confirm that most asci fit this description, but some were found to contain a narrow, tubular structure that widens and extends through the entire d-layer. Obviously, this structure is visible for only a very short transient period during the ontogeny of the tholus. The appearance of the tholus, the structure of the proper exciple, and the conidial type together indicate that *Bapalmuia* is best accomodated in the Pilocarpaceae.

Biatora Fr.: Fr.

E. M. Fries 1817: 7, non Ach. 1809.

Type: *B. vernalis* (L.) Fr. (lectotype selected by Clements & Shear 1931: 319).

The European species of *Biatora* have recently been given a monographic treatment by Printzen (1995). The genus appears to be widely distributed in temperate and arctic parts of the world. *Biatora* differs from *Bacidia* in having a proper exciple of moderately branched and non-anastomosed hyphae that run almost parallel to each other. The cell lumina are narrowly cylindrical, evenly thick, and do not widen markedly near the rim of the proper exciple. The walls are moderately thick (as in *Bacidina*, but thinner than in *Bacidia*). Furthermore, *Biatora* differs by possessing a chondroid hypothecium, milky-white in a dry condition, that is fairly water-resistent (most marked in the large species), an often weak and diffuse pigmentation of the apothecia, 0-3-septate and more or less ellipsoid spores, and ampulliform conidiogenous cells. Contrary to the statement by Hafellner (1984: 268), *Bacidia* and *Biatora* do not differ consistently in the composition of the tholus.

Catinaria Vain.

Vainio 1922: 143.

Type: *C. atropurpurea* (Schaer.) Vězda & Poelt (conserved type proposed by Jørgensen & Santesson 1993).

The genus *Catinaria*, a name which should be restricted to *C. atropurpurea* and its relatives, includes species with generally 1-septate spores (although one undescribed species with 3-septate spores is mentioned by Coppins in Purvis et al. 1992) and a proper exciple made up of densely packed, rather thin-walled, richly branched but not anastomosed hyphae with cell lumina that are 1-1.5 µm wide and not or only slightly widened near the rim.

The protologue of *Catinaria* included two elements, *C. montana* (Nyl.) Vain. and *C. grossa* (Nyl.) Vain. (Vainio 1922). Hafellner (1984) lectotypified the genus with *C. montana* (fig. 18 on p. 273 in this work is probably *Catinaria atropurpurea*) and transferred *C. grossa* to the newly described *Megalaria*. Jørgensen & Santesson (1993) proposed to conserve *Catinaria* against *Biatorina* A. Massal., and also to conserve *Catinaria* with *C. atropurpurea* (Schaer.) Vězda & Poelt as type instead of *C. montana* on the plea that *C. montana* is a poorly known species. I have studied a syntype of *C. montana* (H-NYL 16823), originally described as *Lecidea vernalis* var. *montana* Nyl., and found it to be a member of the "*Lecidea*" *hypnorum* group, which includes *L. hypnorum* Lib., *L. sanguineoatra* auct., *L. ahlesii* (Körb.) Nyl., and *L. berengeriana* (A. Massal.) Nyl. The type of *C. montana* is muscicolous, and like *L. hypnorum*, it has asci similar to those of *Porpidia*, dark violet (K+ blue-green) crystals in the hymenium, and spores with a finely warted perispore. It differs from *L. hypnorum* mainly in having consistently two-celled spores, a much thicker proper exciple (laterally exceeding 100 µm), and a higher hymenium (c. 100 µm). Thus, *Catinaria* is the oldest generic name for *Lecidea hypnorum* and its relatives, a group worthy of recognition at genus level. *Catinaria* has never been used in this sense, and this a further strong reason why *Catinaria* should be conserved with *C. atropurpurea* as the conserved type species

Cliostomum Fr.

E. M. Fries 1825: 116.

Type: *C. corrugatum* (Ach.) Fr. (lectotype selected by Timdal 1991).

Presently, seven species are recognized in *Cliostomum*, *C. corrugatum* (Ach.: Fr.) Fr., *C. griffithii* (Sm.) Coppins, *C. leprosum* (Räsänen) Holien & Tønsberg (Tønsberg 1992), *C. vitellinum* Gowan (Gowan 1990), *C. flavidulum* Hafellner & Kalb (Kalb & Hafellner 1992), *C. spermogoniatum* (Zahlbr.) Kantvilas & Elix, and *C. vezdae* Kantvilas & Elix (Kantvilas & Elix 1995). *C. luteolum* Gowan was considered a synonym of *C. leprosum* by Tønsberg (1992). The boundaries of *Cliostomum* are still poorly studied, and the genus will almost certainly "grow" in the future. For example, "*Bacidia*" *pallens* probably belongs here (see *Excluded or not examined species*).

Cliostomum can be separated from *Bacidia* and *Bacidina* on account of the wide and irregularly shaped cell lumina in the proper exciple, the often crystal-inspersed epithecium and proper exciple, the 1-3-septate bacilliform spores, the branched conidiophores bearing subglobose to ellipsoid to short-bacilliform conidia. Two of the species contain usnic acid in the thallus and/or the apothecia. Black and widely gaping pycnidia are characteristic of some species. *Cliostomum* is closely related to *Biatora*, but the latter genus differs in having sparsely branched, ampulliform (not cylindrical) conidiogenous cells and in having cylindrical, almost parallel and distinctly radiating excipular hyphae.

Compsocladium I. M. Lamb

Lamb 1956: 157.

Type: *C. archboldianum* I. M. Lamb (holotype, not seen).

According to Lamb (1956), this monotypic genus, described from Irian Jaya (formerly Dutch New Guinea), differs markedly from both *Bacidia* and *Bacidina* by possessing a fruticulose, richly branched, homoiomerous thallus (forming small peltate hemispherical tufts) containing a mixture of cyanobacteria and chlorococcoid algae, an apothecial margin of thalline origin (although not containing algae), richly branched and anastomosed paraphyses, and in having the thallus inspersed with yellowish granules that dissolve with C into a rose-red solution (substance not identified). The asci and the spores of *Compsocladium*, however, are strikingly similar to *Bacidia* and *Bacidina*.

Echidnocymbium Brusse

Brusse 1987a: 173.

Type: *E. speciosum* Brusse (holotype, not seen).

Echidnocymbium, comprising only the type species, differs from *Bacidia* and *Bacidina* in having lecanorine apothecia, more abundantly branched paraphyses, non-septate ellipsoid spores, black and large pycnidia that are superficial on the thallus, needle-like conidia, and in containing stictic acid. The genus was, in my opinion, referred to the "Biatoraceae" on very dubious grounds.

Eschatogonia Trevis.

Trevisan 1853: 5.

Type: *E. prolifera* (Mont.) R. Sant., treated as *E. montagnei* by Trevisan, a superfluous nomenclatural synonym (holotype).

According to Brako (1989) and Kalb & Elix (1995), this genus comprises a few tropical species that differ from *Bacidia* and *Bacidina* in being squamulose, in having a lower cortex with a distinct outer layer of uniformly arranged cells, and in containing didymic acid and related substances.

Herteliana P. James

Hawksworth et al. 1980: 106.

Type: *H. taylorii* (Salwey) P. James (holotype).

Herteliana comprises two species, the type species, *H. taylorii* (Salwey) P. James, and *H. alaskensis* (Nyl.) S. Ekman (see *Excluded or not examined species*). It differs from *Bacidia* and *Bacidina* in having a root-like hypothecium extending into the thalline medulla, non- or

3-septate spores, and a "paraplectenchymatic" proper exciple which is not distinctly delimited from the hypothecium and composed of densely packed hyphae with broadly rectangular to ellipsoid cell lumina.

Japewia Tønsberg

Tønsberg 1990: 205.

Type: *J. tornoensis* (Nyl.) Tønsberg (holotype).

Three species were referred to *Japewia* by Tønsberg (1990). It was placed in the Bacidiaceae by Eriksson & Hawksworth (1991a) "on the basis of ascus structure". Its placement near *Bacidia* is questionable, however. *Japewia* is probably closely related to *Mycoblastus* Norman. *Japewia* can be separated from *Bacidia* and *Bacidina* on account of the more abundantly anastomosed paraphyses with apices surrounded by a gel coat, very wide asci, and large, thick-walled, non-septate, sometimes abortive spores that often possess a gelatinous perispore.

Lecania A. Massal.

Massalongo 1853b: 12.

Type: *L. fuscella* (Schaer.) A. Massal. (holotype)

Traditionally, *Lecania* has been restricted to species with a lecanorine apothecial margin. Such a delimitation of this genus is artificial, however. When several characters are taken into consideration, it becomes clear that *Lecania* includes a variation from typically lecanorine species like *L. fuscella* and *L. cyrtella*, to intermediate ones with a poorly developed thalline margin (*L. cyrtellina*, *L. hutchinsiae*), and finally to a number of species with a biatorine margin. Four species with a biatorine apothecial margin should be referred to *Lecania* (all formerly placed in *Bacidia*), viz. *L. naegelii* (Hepp) Diederich & P. Boom, *L. cuprea* (A. Massal.) P. Boom & Coppins, *L. subfuscula* (Nyl.) S. Ekman, and *L. stigmatella* (Tuck.) S. Ekman. The first two species were transferred from *Bacidia* to *Lecania* by van den Boom (1992) and van den Boom et al. (1994), unfortunately without any discussion on the grounds for this. Future investigations of *Lecidea* s. lat. and *Catillaria* s. lat. may show that several species should be included in *Lecania*. The European saxicolous species of *Lecania* in the traditional sense have been treated by Mayrhofer (1988).

In its revised circumscription, *Lecania* includes species with the following features: (1) lichenized, crustose thallus (or fruticulose, if *Thamnolecania* is included, see below), with or without goniocysts (often termed blastidia in *Lecania* terminology, but I fail to see the difference), (2) lecanorine to biatorine apothecia with a proper exciple consisting of few to many hyphae, (3) fairly abundantly furcate but non-anastomosed excipular hyphae, the cell lumina of which are narrowly cylindrical (1-1.5 µm wide) in the interior of the proper exciple but gradually become thicker towards the rim (up to 5 µm wide), thus giving each hypha a characteristically club-shaped appearance, (4) yellowish, brown, and blue-green pigments in the apothecia that are often markedly unevenly distributed in the upper part of the hymenium, thus giving the apothecial disc a characteristically "dotted" appearance in a wet condition (not seen in pigment deficient specimens), (5) paraphyses that are easily separated in K and gradually thicken in the upper part, the terminal cell being up to 5 µm, (6) 0-3-, rarely up to 5-septate, ellipsoid, fusiform or bacilliform, rather thick-walled spores that are often slightly curved but lack perispore and ornamentation, (7) a tholus with a fairly low and blunt, more or less conical ocular chamber, and a fairly high, conical axial body that is often but not always (often lacking in *L. cuprea*) surrounded by a heavily amyloid zone that is darker than the remainder of the d-layer, (8) strongly curved (or sometimes sigmoid in *L. fuscella*), 0.5-0.8 µm wide, 0-1-septate microconidia and more or less curved, 1.0-2.0 µm wide, 0-1-septate (5-7-septate in *L. naegelii*) macroconidia.

Megalaria Hafellner

Hafellner 1984: 302.

Type: *M. grossa* (Nyl.) Hafellner (holotype).

Megalaria is presently comprised of six accepted species (Ekman & Tønsberg 1996), but the number will probably increase in the future. It is distinguished from *Bacidia* and *Bacidina* mainly on account of the one-septate, thick-walled, ellipsoid to subglobose spores, the indistinct ocular chamber, and (when applicable) the short, ellipsoid, oblong, or ampulliform conidia.

Mycobilimbia Rehm

Rehm 1889 (1887-1895): 327.

Type: *M. obscurata* (Sommerf.) Rehm (lectotype selected by Clements & Shear 1931: 315).

Mycobilimbia is closely related to and very similar to *Biatora*, but was separated from this genus by Printzen (1995) on the basis of a different apothecial ontogeny. Four species, *M. tetramera* (syn. *M. obscurata* auct.), *Catillaria sphaeroides*, *Bacidia epixanthoides*, and *Bacidia carneoalbida*, were tentatively included. This delimitation is quite different from the one suggested by Hafellner (1989). The typification of *M. obscurata* is complicated; see note by Timdal (1991: 26).

Myrionora R. C. Harris

Harris et al. 1988: 27.

Type: *M. albidula* (Willey) R. C. Harris (holotype, not seen).

This monotypic genus appears doubtfully distinct from *Scoliciosporum*, differing from *Scoliciosporum curvatum* Sérus. mainly in having straight spores, the number of which exceeds 30 per ascus (Harris et al. 1988, Sérusiaux 1993). Polyspory is known in *S. curvatum* Sérus. and straight spores are found in *S. chlorococcum* (Graewe ex Stenh.) Vězda and *S. gallurae* Vězda & Poelt. A similar variation in the number of spores per ascus is found in *Candelariella* and *Ropalospora*. For the distinction from *Bacidia* and *Bacidina*, see *Scoliciosporum*.

Phyllopsora Müll. Arg.

Müller 1894: 11.

Type: *P. breviuscula* (Nyl.) Müll. Arg. (lectotype selected by Clements & Shear 1931: 319, not seen).

Phyllopsora is a medium-sized genus with a world-wide tropical and subtropical distribution. According to Brako (1989, 1991) and Swinscow & Krog (1981), *Phyllopsora* differs from *Bacidia* and *Bacidina* mainly in having a usually squamulose, sometimes isidiate thallus with a well-developed cortex lacking an epinecral layer, a web- or mat-forming prothallus, a hypothecium and a proper exciple of the same texture (the texture of the hypothecium being very similar to the texture of the cortex), 0-1-septate spores, and in lacking a distinct subhymenium. Swinscow and Krog (1981) discussed four species, *Phyllopsora thaleriza* (Stirt.) Gotth. Schneid., *P. compaginata* (Müll. Arg.) Gotth. Schneid., *P. stylophora* (Malme) Gotth. Schneid., and *Bacidia laciniosa* Swinscow & Krog, that they understood as intermediate between *Bacidia* and *Phyllopsora*. Brako (1991) synonymized *P. compaginta* with *P. thaleriza* and excluded this species and *P. stylophora* from *Phyllopsora* to two undescribed genera in Bacidiaceae and Lecanoraceae, respectively.

Physcidia Tuck.

Tuckerman 1862: 399.

Type: *P. wrightii* (Tuck.) Tuck. (lectotype selected by Clements & Shear 1931: 322, not seen).

Kalb & Elix (1995) include seven species in the genus *Physcidia*, which can be separated from *Bacidia* and *Bacidina* on the basis of the squamulose or foliose thallus that often produces isidia, the distinct upper cortex lacking an epinecral layer, the thin-walled, 1-3-septate spores, and the different secondary chemistry.

Rolfidium Moberg

Moberg 1986: 305.

Type: *R. peltatum* Moberg (holotype, not seen).

Two species have been referred to *Rolfidium*, namely the type species *R. peltatum* Moberg and *R. coccocarpioides* (Nyl.) Timdal (Timdal 1991). According to Moberg (1986), this genus differs from *Bacidia* and *Bacidina* in forming small, indistinctly lobate, foliose thalli with rhizines, in having ellipsoid, 1-septate spores, and large pycnidia containing sparsely branched conidiophores and filiform, more or less straight conidia.

Schadonia Körb.

Körber 1859: 93.

Type: *S. alpina* Körb. (holotype).

Schadonia, comprising only two species (Poelt & Vězda 1981), differs from *Bacidia* and *Bacidina* in having more abundantly branched and anastomosed paraphyses, and asci with 2-8, large and muriform spores.

Schistoplaca Brusse

Brusse 1987b: 245.

Type: *S. alvearialis* Brusse (holotype).

Two species were referred to *Schistoplaca* by Brusse

(1987b). The genus was reduced into synonymy with *Lecanora* by Lumbsch & Feige (1994).

Scoliciosporum A. Massal.

Massalongo 1852: 104.

Type: *S. holomelaenum* (Flörke) A. Massal., a younger synonym of *S. umbrinum* (Ach.) Arnold (lectotype selected by Vězda 1978: 414).

Scoliciosporum, to which altogether nine species have been referred (Vězda 1978, Vězda & Poelt in Nimis & Poelt 1987, Sérusiaux 1993), is distinguished from *Bacidia* and *Bacidina* on account of the poorly developed proper exciple consisting of paraphysis-like hyphae, the abundantly branched and anastomosed paraphyses, the wide axial body reaching through the entire d-layer of the tholus, and (Coppins 1983: 97) the presence of some deviating paraphyses terminating in swollen apices that are surrounded by a darkly pigmented cap. It should be noted that the tholus of *S. chlorococcum* (Graewe ex Stenh.) Vězda, contrary to *S. umbrinum* (depicted by Hafellner 1984: 340) has a rather distinct, heavily amyloid zone surrounding the axial body.

Solenopsora A. Massal.

Massalongo 1855: 20.

Type: *S. requienii* A. Massal. (holotype, not seen).

The delimitation of this genus is still poorly investigated. The core of *Solenopsora* appears to be distinguished from *Bacidia* and *Bacidina* on account of the placodioid or squamulose thallus, the lecanorine apothecia, the 1-septate spores, the lack of both an ocular chamber and an axial body in the ascus, the branched conidiophores, and the short-bacilliform conidia (Poelt 1969, Hertel & Rambold 1988, Purvis & James in Purvis et al. 1992).

Speerschneidera Trevis.

Trevisan 1861: 52.

Type: *S. euploca* (Tuck.) Trevis. (holotype, not seen).

The monotypic genus *Speerschneidera* differs from *Bacidia* and *Bacidina* in being foliose, and in having a thick cortex of periclinally arranged hyphae, paraphyses with a distinct cap of pigment in the distal part of the swollen terminal cell, generally 1-septate spores, unbranched conidiophores producing conidia both terminally and laterally, and short-cylindrical conidia (Hafellner & Egan 1981).

Sporacestra A. Massal.

Massalongo 1860: 264.

Type: *Biatora prasina* Tuck. & Mont., nom. illeg., non (Fr.) Trevisan 1856 (holotype).

Sporacestra is the oldest generic name for *Psorella pertexta* (Nyl.) Müll. Arg., *P. microphyllina* (Tuck ex Nyl.) Zahlbr. and *P. cognata* (Nyl.) Zahlbr., a group which was tentatively proposed as a genus different from *Bacidia* and *Phyllopsora* by Brako (1989). In fact, the only species included in *Sporacestra* by Massalongo, *Biatora prasina* Tuck. & Mont. (a nomen illegitimum), is synonymous with *Psorella pertexta*, a fact which has been overlooked up until now. A legitimate nomen novum, *Biatora prasinata* Tuck., was made later (Tuckerman 1888), on which Coppins (1983) based the combination *Bacidia prasinata* (Tuck.) Coppins.

Sporacestra differs from *Bacidia* and *Bacidina* in having a finely squamulose thallus, excipular hyphae that often protrude from the lower side of the apothecium (anchorage hyphae?), paraphyses with an apical swelling due to a thickened gelatinous wall without a corresponding widening of the cell lumen (similar to the paraphyses of *Squamacidia*, see Brako 1989: 7, fig. 3D), and thin-walled spores with indistinct septa. According to Brako (1989), this species group is separated from *Phyllopsora* on account of the different tissue types in the hypothecium and the proper exciple, the less gelatinized paraphyses, and the longer and septate spores. Due to an observed variation in the ontogeny of the tholus and a suspicion that several species presently included in *Bacidia* should be included in the *Psorella pertexta* group, Brako (1989) at the time refrained from treating this group as a separate genus. With the possible exception of *Bacidia augustinii* (Tuck.) Zahlbr., none of the North American species belong here. Furthermore, I have seen the types of nearly all South and Central American *Bacidia* s. lat. with long and septate spores, but no species is close to *Psorella pertexta*. Thus, judging from the neotropical species, it seems unlikely that *Sporacestra*, if accepted as a genus, is much richer in species than originally thought by Brako.

Squamacidia Brako

Brako 1989: 6.

Type: *S. janeirensis* (Müll. Arg.) Brako (holotype).

According to Brako (1989), the monotypic genus *Squamacidia* differs from *Bacidia* and *Bacidina* by possessing a squamulose and isidiate thallus with a cortex lacking an epinecral layer, 1-3-septate spores with thin walls, rod-shaped conidia sometimes produced in groups of 2-3 terminally on the conidiogenous cells, and in having a different secondary chemistry. Furthermore, my own observations show that *Squamacidia* is separated from *Bacidia* and *Bacidina* also in having a quite different proper exciple, which is composed of hyphae with narrow cell lumina with gelatinous walls, the borders of which remain distinct and can be easily seen in a light microscope. Furthermore, the terminal cells along the rim of the proper exciple are not the least swollen.

Squamarina Poelt

Poelt 1958: 524.

Type: *S. gypsacea* (Sm.) Poelt (holotype).

Squamarina, comprising almost 20 species (Poelt 1958, Poelt 1975, Vänskä 1985, Haugan & Timdal 1992), is distinguished from *Bacidia* and *Bacidina* on the basis of the squamulose or almost foliose thallus, lecanorine apothecia, and non-septate spores. According to Hertel & Rambold 1988: 301), the tholus of *S. gypsacea* contains a tubular structure similar to that found in Porpidiaceae or Psoraceae sensu Hafellner (1984). These findings were confirmed for sect. *Squamarina* by Haugan & Timdal (1992), whereas sect. *Petroplaca* was found to have a tholus resembling the one seen in *Lecanora muralis*. *Squamarina* was listed in Bacidiaceae with a query by Eriksson & Hawksworth (1993). Its placement near *Bacidia* appears very doubtful.

Tephromela M. Choisy

Choisy 1929: 522.

Type: *T. atra* (Huds.) Hafellner (holotype).

About 20 species have so far been referred to the genus *Tephromela* (Hertel & Rambold 1985, Poelt & Grube 1993, Rambold 1993, Haugan & Timdal 1994). *Tephromela* differs from *Bacidia* and *Bacidina* in having thick-walled paraphyses, non-septate ellipsoid spores, branched conidiophores producing conidia laterally, bacilliform conidia, and a different chemistry. The dark purplish hymenium and the lecanorine apothecia generally associated with the most well-known species, *T. atra* (Huds.) Hafellner, are typical of only a portion of the genus.

Thamnolecania (Vain.) Gyeln.

Gyelnik 1933: 8.

Type: *T. brialmontii* (Vain.) Gyeln. (lectotype selected by Dodge 1948: 181, not seen).

Gyelnik (1933) recognized two species, and Dodge (1948) described two more species in *Thamnolecania*. All are fruticulose and more or less Antarctic in distribution. Hafellner (1984) questioned the distinctness of *Thamnolecania*, since it apparently differs from *Lecania* only in the growth form of the thallus.

Tibellia Vězda & Hafellner

Hafellner & Vězda 1992: 186.

Type: *T. dimerelloides* Vězda & Hafellner (holotype, not seen).

According to Hafellner & Vězda (1992), this monotypic genus differs from *Bacidia* and *Bacidina* in forming large, byssoid thalli comprised of thick hyphae. Furthermore, the terminal part of the excipular hyphae are ungelatinized, the hymenium is unpigmented, the paraphyses lack terminal swelling, and the spores are ellipsoid and 1-septate.

Toninia A. Massal.

Massalongo 1852: 107.

Type: *T. cinereovirens* (Schaer.) A. Massal. (lectotype, selected by Fink 1910).

Toninia was given a detailed monographic treatment and a new circumscription by Timdal (1991). For a long time, the delimitation adopted by Fries (1874) has been used. In his sense, *Toninia* included all squamulose species of the Lecideaceae having septate spores. The new and improved delimitation provided by Timdal (1991) is mostly concerned with the anatomy of the paraphyses and asci. Timdal recognized 48 species in *Toninia*.

Toninia is obviously very closely related to *Bacidia*. They share features in the paraphyses, asci, spores, and pigmentation. In particular, group 3 of Timdal (1991: 28), containing *T. aromatica* and its relatives, is very similar to *Bacidia circumspecta*, *B. igniarii*, *B. illudens*, *B. subincompta*, and *B. schweinitzii*. The members of these groups share a similar apothecium pigmentation, and bacilliform or acicular, 3- or more-septate spores are present within both groups. However, *Toninia* appears distinct from *Bacidia*, and I have so far found no corticolous species traditionally treated in *Bacidia* to belong in *Toninia*.

Toninia can be separated from *Bacidia* on account of the anatomy of the proper exciple. Contrary to *Bacidia*, the proper exciple of *Toninia* is made up of hyphae that are not furcate, but more or less abundantly anastomosed. The lumina are shorter and wider relative to those of *Bacidia*, usually 5-15 (exceptionally 20) µm long and 1.5-5 µm wide (lumina near rim of proper exciple excepted), commonly 2-5 times as long as wide (exceptionally up to 8 or down to 0.75 times as long as wide), hardly ever constricted near septa (*T. coelestina* excepted). The walls are gelatinized but, compared to *Bacidia*, thinner, the distance between two adjacent cell lumina being about the same as the width of a cell lumen (sometimes shorter, sometimes up to twice the width of a luminum).

A number of additional differences between *Toninia* and *Bacidia* were accounted for in the comparison by Timdal (1991), in which he used the type species of *Bacidia*, *B. rosella*, as a "model species". Once more species of *Bacidia* are taken into consideration, it becomes clear that the listed differences cannot be used to separate the genera. It is clear, however, that Timdal was well aware of the dangers with using type species as models.

Toninia differs from *Bacidina* mainly in having a narrower axial body, and in having more regularly rectangular cell lumina without constrictions at the septa inside the rim. Furthermore, compared to *Toninia*, the species of *Bacidina* usually contain lower amounts of pigment in the apothecia, sometimes no pigments at all.

Tylothallia P. James & H. Kilias

Kilias 1981: 409.

Type: *T. biformigera* (Leight.) P. James & H. Kilias (holotype).

Two species, *T. biformigera* (Leight.) P. James & H. Kilias and *T. pahiensis* (Zahlbr.) Hertel & H. Kilias, have been referred to this genus (Kilias 1981, Hertel 1983). They differ from *Bacidia* and *Bacidina* in having abundantly branched and anastomosed paraphyses, consistently 1-septate spores, a different chemistry, and (Timdal 1991) smaller conidia.

Waynea Moberg

Moberg 1990: 249.

Type: *W. californica* Moberg (holotype).

Three species have so far been referred to *Waynea*, viz. *W. californica* Moberg (Moberg 1990, 1991), *W. stoechadiana* (Abbassi Maaf & C. Roux) C. Roux & P. Clerc (Roux & Clerc 1991, Roux & Giralt 1991), and *W. adscendens* V. J. Rico (Rico 1991, Bricaud & Roux 1993). The taxonomy has been summarized by Roux et al. (1995). *Waynea* differs from *Bacidia* and *Bacidina* by possessing a squamulose thallus with lip-, cup, or helmet-shaped soralia, a distinct proso- or paraplectenchymatic upper cortex, rather short, bacilliform to fusiform, 3-septate spores, and cylindrical excipular cell lumina. *Waynea* shows an interesting western North American-Mediterranean disjunction.

The Bacidia beckhausii group

Three species belong to this group: *Bacidia beckhausii* Körb., *B. hemipolia* (Th. Fr.) Malme, and *B. verecundula* (Th. Fr.) H. Magn. The last is a poorly known species that has been collected only once, in northern Norway. The report from Northwest Territories, Canada, is erroneous and refers to an undescribed species in the *Bacidia sabuletorum* group (see below).

The *Bacidia beckhausii* group differs from *Bacidia* and *Bacidina* in having a more poorly developed proper exciple, a tholus with a blunt and indistinct ocular chamber or no ocular chamber at all, an axial body that reaches all through the d-layer and has sides that are parallel or upwards slightly convergent, a rather distinct zone surrounding the axial body that is more heavily amyloid than the remainder of the tholus, and spores that are bacilliform to fusiform and usually three-septate.

The *B. beckhausii* group shares the poorly developed proper exciple and the general appearance of the tholus with *Scoliciosporum*, and together with the *Bacidia lutescens* group it appears to form a link between *Bacidia*/*Bacidina* and *Scoliciosporum*. Contrary to *Scoliciosporum*, however, the excipular hyphae of the *B. beckhausii* group do not resemble paraphyses, and the axial body is distinctly narrower. The *B. beckhausii* group is very closely related to the *B. lutescens* group, and it seems probable that they together should form a genus that is yet to be described. These groups differ mainly in the amount of pigment in the apothecia and the presence of oil droplets in the hypothecium and proper exciple. *B. hemipolia*, however, exhibits a continuous variation in the pigmentation of the apothecia (not seldom on the same thallus) from darkly pigmented to entirely pigment deficient. Despite the close relationship between the *B. beckhausii* and the *B. lutescens* groups, I have chosen to treat them separately in order not to loose any information. *B. beckhausii* itself was treated as a *Micarea* by Poelt & Vězda

(1977) but it was excluded from that genus by Coppins (1983).

The Bacidia lutescens group

The *Bacidia lutescens* group is comprised of *Bacidia lutescens* Malme, *B. americana* (Fée) Zahlbr., *B. fuscula* (Nyl.) Zahlbr., *Scoliciosporum pruinosum* (P. James) Vězda (also known as *Bacidia pruinosa* P. James), and one or two apparently undescribed species from southeastern United States. Once the tropical members of *Bacidia* s. lat. have been studied in more detail, this group may prove to be much larger.

The *B. lutescens* group is separated from *Bacidia*, *Bacidina*, and *Scoliciosporum* in much the same way as the *B. beckhausii* group. In addition, all members of the *B. lutescens* group have minute KOH-soluble crystals in the proper exciple and oil droplets in the hypothecium and sometimes also in the proper exciple. The oil droplets are usually abundant but may sometimes be sparse. Furthermore, the apothecia are mostly weakly and diffusely pigmented in the upper part of the hymenium and along the rim of the proper exciple. Like in the *B. beckhausii* group, the axial body is usually surrounded by a thin zone that is more heavily pigmented than the remainder of the tholus. This zone is lacking only in *Scoliciosporum pruinosum*. For a discussion on the relationship with the *B. beckhausii* group, see above.

The Bacidia sabuletorum group

This group consists of *Bacidia sabuletorum* (Schreb.) Lettau (including *B. accedens* (Arnold) Lettau), *B. accedens* sensu R. C. Harris (1977), non (Arnold) Lettau, *B. microcarpa* (Th. Fr.) Lettau, *Toninia lobulata* (Sommerf.) Lynge, and an undescribed parasymbiontic or parasitic species on *Lecanora* cf. *impudens* Degel. from Northwest Territories, Canada.

The *Bacidia sabuletorum* group is closely related to *Biatora* and *Mycobilimbia* and differs from these genera mainly in having a more heavily pigmented hypothecium, stouter paraphyses, more thick-walled asci, an oily yellowish content in the mature spores, a green pigment in the upper part of the hymenium, and in having a proper exciple, the rim of which is covered by a rather thick gelatinous layer that swells markedly (and finally almost dissolves) in KOH or dilute hypochlorite solutions. Furthermore, *B. sabuletorum* and *T. lobulata* have a warted perispore (although sometimes overlooked, since it is easily detached from the spores). Apart from the pigmentation of the hypothecium, all these characters also separate the *Bacidia sabuletorum* group from *Bacidia* and *Bacidina*.

The *Bacidia sabuletorum* group almost certainly represents a separate genus. It was included in *Mycobilimbia* by Hafellner (1984, 1989), but I am convinced that it is not congeneric with the taxon usually treated as the type of *Mycobilimbia*, *M. obscurata* auct. (= *M. tetramera*).

Family

Hafellner (1984) referred *Bacidia* to Bacidiaceae. At that time, *Bacidina* was not described, and none of the species later referred to this genus was investigated by Hafellner. Eriksson & Hawksworth (1993) treated *Bacidia* in the Bacidiaceae, but their concept of this family was much wider than Hafellner's. *Bacidina* was referred to Lecanoraceae by these authors, an action which was based on the statement "Asci tholis generi *Lecanora* instructi" in the diagnosis of this genus by Vězda (1991).

In the light of the variation observed within *Bacidia* and *Bacidina*, I endorse the theory of Hertel & Rambold (1995), that the Bacidiaceae and the Lecanoraceae, more or less in the sense of Eriksson & Hawksworth (1993) should be united into one family, Lecanoraceae. *Bacidia*, *Bacidina*, as well as *Toninia* (treated in the Catillariaceae by Eriksson & Hawksworth) should be referred to this family. This should be viewed upon as a tentative hypothesis, however. Contemporary lichenology should be careful not to flatter itself by thinking that a final ascomycete system, which reflects true phylogenetic relationships, has been achieved. There are times when I wonder if future taxonomists will not look at our present-day ascomycete system in much the same way as we are now looking upon the system by Zahlbruckner (1921-1940)!

Numerical and statistical treatment

During my studies of *Bacidia* and *Bacidina*, I have come across some taxonomically complicated cases in need of scrutiny. In these cases, I have chosen to use various numerical and statistical methods to throw some light on the problems. Such methods are powerful tools to summarize the numerical information available from measurements, and can thus provide important arguments in favour of or against certain taxonomic solutions. Naturally, they do not supply any direct evidence. The result of a statistical or numerical analysis is always open to interpretation, as are the results of any other method used by taxonomists.

Three cases with a sufficient number of measurements are treated here. Among the North American *Bacidia* and *Bacidina*, there are certainly further cases that would benefit from a numerical and statistical analysis. For example, the variation within the present concept of

Tab. 11. Descriptive statistics and the significance of the F-values obtained from the one-way ANOVAs comparing *B. diffracta* (granular thallus) and *B. polychroa* (continuous thallus). Extreme morphs from Sanford, Florida, have been excluded. The abbreviations of the characters are explained in the text. The standard deviation is abbreviated "s. d." The input values used for APWID, HYM, and PARWID are means of five measurements per specimen, for SPLEN, SPWID, and SEPTA means of 10 measurements per specimen, and for APHGT and EXCIP a single measurement per specimen. Thus, the values of all but the two latter characters correspond to the minimum and maximum mean values in the species descriptions. Significance levels of F are denoted ** for $0.001<p\leq0.01$, *** for $p\leq0.001$, and ns (not significant) for $p>0.05$.

Character	*Bacidia polychroa* (N= 22)			*Bacidia diffracta* (N= 13)			Significance of F
	mean	s. d.	min-max	mean	s. d.	min-max	
APWID/mm	0.7	0.1	0.6-0.8	0.8	0.1	0.5-0.9	ns
APHGT/µm	273	51	176-359	465	95	344-688	***
EXCIP/µm	63	13	45-95	64	14	52-103	ns
HYM/µm	77	10	63-95	82	6	70-90	ns
PARWID/µm	2.4	0.3	1.7-3.0	2.0	0.3	1.6-2.6	**
SPLEN/µm	48	5	38-57	45	5	37-54	ns
SPWID/µm	2.7	0.4	2.3-4.0	2.9	0.2	2.6-3.3	ns
SEPTA	6.3	2.0	3.1-11.9	6.2	1.0	4.1-7.8	ns

Bacidia circumspecta (potential correlations between conidial types and other characters), the relationship between this species and *B. igniarii*, and the relationship between *B. hostheleoides* and *B. medialis* would have gained from a closer investigation. In these cases, however, the measurements available from North American material are too few in number. With the exception of European *Bacidia laurocerasi*, the study of extra-North American material has not been within the scope of the present study.

Bacidia polychroa and B. diffracta

Background

In the eastern United States and Canada there are two very similar taxa, both with ± brown apothecia dominated by a K+ purple-red pigment (Bacidia Brown). There is an obvious difference between them in thallus structure. One, which corresponds to *B. polychroa*, has a continuous, smooth or warted, ± rimose thallus. The other one, named here as *B. diffracta*, has a finely granular thallus. In addition, there is an apparent, but not completely discontinuous, difference in apothecium height. The pattern is further complicated by the existence of a very extreme morph collected a few times in a single locality in the Sanford area of Florida. It has very wide and very high apothecia, and, above all, a thallus that is not readily classified as granular or continuous. In fact, it is partly smooth with almost no cracks at all, and partly granular. The question is, are *B. polychroa* and *B. diffracta* distinct species or just extreme appearances in a continuously varying species?

Methods

Twenty-two specimens of the continuous morph (*Bacidia polychroa*) and 13 specimens of the granular morph (*B. diffracta*) were used (the same ones used to prepare the descriptions of these species). In addition, two specimens of the Florida morph from the same locality were studied. Eight characters were measured on these specimens:

1. Apothecium width (APWID).
2. Apothecium height (APHGT).
3. Width of proper exciple lateral to the hymenium (EXCIP).
4. Hymenium thickness (HYM).
5. Width of paraphysis apices (PARWID).
6. Spore length (SPLEN).
7. Spore width (SPWID).
8. Number of spore septa (SEPTA).

The difference between the continuous (*B. polychroa*) and the granular morph (*B. diffracta*), excluding the Florida specimens mentioned above, was investigated with one-way ANOVAs performed on each of these characters. The distinctness of the granular, the continuous, and the Florida morphs was investigated with a CVA.

Results

Descriptive statistics and the significance of F in the ANOVAs are presented in Tab. 11. The continuous and the granular morph differ significantly in apothecium height and width of the paraphysis apices. None of the

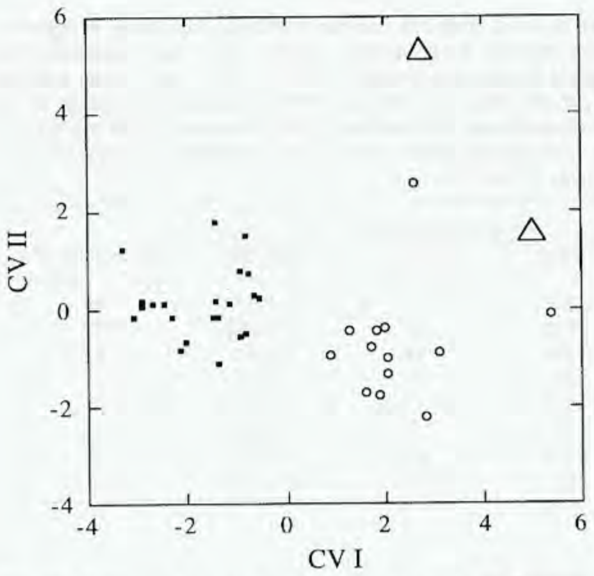


Fig. 11. Canonical variates plot of 22 specimens of *Bacidia polychroa* (squares), 13 specimens of *B. diffracta* (circles), and two specimens of a deviant population from Sanford, Florida (triangles).

characters studied separate the morphs entirely discontinuously.

The canonical variates plot is presented in Fig. 11, and the canonical loadings in Tab. 12. The continuous morph forms a distinct swarm, whereas the granular morph consists of a fairly distinct swarm with a few outliers. The two Floridan specimens from the same locality are rather different from each other, but are only slightly more extreme than the two outliers of the granular group (from Minnesota and Massachusetts, respectively). The discrimination along the first canonical variate is perfectly discontinuous, which shows that there is a discontinuity in the correlation between the original characters. The first canonical variate is composed largely by APHGT, but all other characters except SEPTA contribute markedly. The contribution to the second variate is dominated by EXCIP, but all characters except PARWID contribute clearly.

Tab. 12. Loadings for the eight characters on the first and second canonical variates (× 100) in a CVA performed to investigate the distinctness of *Bacidia polychroa*, *B. diffracta*, and a deviant population from Sanford, Florida. The sign shows whether the character makes a positive or negative contribution to the canonical variate.

	Canonical variate	
Character	I	II
APWID	21	37
APHGT	72	25
EXCIP	20	84
HYM	21	16
PARWID	-31	-3
SPLEN	-10	31
SPWID	16	17
SEPTA	1	15

The linear function defining the axes can be extracted using the canonical correlation coefficients. The first axis, CV I, is defined by the function

$$f\ (APWID,\ APHGT,\ EXCIP,\ HYM,\ PARWID,\ SPLEN,\ SPWID,\ SEPTA) = 0.0155 \times APHGT + 0.00434 \times HYM + 0.00538 \times EXCIP + 0.0180 \infty SEPTA - 4.05 \times APWID - 2.00 \times PARWID - 0.127 \times SPLEN - 0.343 \times SPBRD + 7.90,$$

where APWID is in mm, SEPTA is unitless, and the remaining variables are in µm. Note that the input values for APWID, HYM, and PARWID are means of five measurements per specimen, for SPLEN, SPWID, and SEPTA means of ten measurements per specimen, and for APHGT and EXCIP a single measurement per specimen.

Conclusions

Apart from thallus structure, it is clear that the continuous, *Bacidia polychroa*, and the granular morph, *B. diffracta*, are separated by a discontinuity in the correlation among a number of characters. I conclude that they should be recognized as distinct species. The position of the Florida population is slightly more uncertain. Since there is rather conspicuous variation within the Florida population, and since it is only slightly more extreme than the extremest of clear *B. diffracta*, I draw the tentative conclusion that it is best included in *B. diffracta*. More material is needed, however, since a recognition of the Florida population at an infraspecific taxonomic level may prove to be the best solution. Unfortunately, my own attempts to find this morph in the field have been unsuccessful.

Since the discrimination along the first axis is perfect, the value of the function defining this axis can be used for identification purposes. This may be useful in case there are difficulties classifying the thallus of an unidentified specimen as granular or continuous. For *B. polychroa* $f < 0$, and for *B. diffracta* $f > 0$.

Bacidia laurocerasi

Background

Bacidia laurocerasi s. lat. has a disjunct distribution in North America. It occurs in the coastal lowland and in

Tab. 13. Descriptive statistics of quantitative characters in *Bacidia laurocerasi* from western and eastern North America, and from Europe (represented by specimens from Sweden, Germany, Switzerland, and Great Britain). The abbreviations of the characters are explained in the text. The standard deviation is abbreviated "s. d." The input values used for APWID, HYM, and PAR are means of five measurements per specimen, for SPLEN, SPWID, and SEPTA means of 10 measurements per specimen, and for EXCIP a single measurement per specimen. Thus, the values given for all but the latter character correspond to the minimum and maximum specimen means in the subspecies descriptions.

	Western North America (N= 9)			Eastern North America (N= 21)			Europe (N= 8)		
Character	mean	s. d.	min-max	mean	s. d.	min-max	mean	s. d.	min-max
APWID/mm	0.8	0.1	0.7-0.9	0.7	0.1	0.5-0.9	0.7	0.1	0.6-0.8
EXCIP/µm	86	13	69-103	78	19	54-138	81	12	69-108
HYM/µm	108	10	94-125	91	7	81-105	103	5	98-113
PARWID/µm	1.9	0.4	1.1-2.4	2.1	0.4	1.1-2.7	2.4	0.5	1.8-3.2
SPLEN/µm	81	9	69-96	70	6	57-87	70	9	56-84
SPWID/µm	3.0	0.1	2.8-3.2	2.7	0.2	2.5-3.5	3.1	0.4	2.7-3.7
SEPTA	20	2	17-23	15	3	11-22	14	2	11-17

the montane region of Oregon, Washington, and British Columbia, but also in the Great Lakes and northern Appalachian region of northeastern United States and southeastern Canada. When studying material, I soon became aware of slight differences in thallus structure, apothecium colour, and spore septation between collections from the two distribution areas. Therefore, I decided to examine this case closer. I also included a small number of European specimens in the study in order to see which one of the two potential North American taxa is morphologically closest to the European population.

Methods

Eight specimens from Europe (Sweden, Germany, Switzerland, and Great Britain) deposited in LD and UPS, nine specimens from western North America, and 21 specimens from eastern North America were used. The North American specimens were also used to prepare the description of the species. Nine characters were scored or measured:

1. Thallus structure (THALL) was scored 0 if the thallus had few cracks or no cracks at all, 1 if the thallus was distinctly cracked.
2. Colour of apothecial margin in upper part (MARG) was scored 0 if it was ± brown to black in most apothecia, 1 if it was ± brown-red.
3. Apothecium width (APWID).
4. Width of proper exciple lateral to the hymenium (EXCIP).
5. Hymenium thickness (HYM).
6. Width of paraphysis apices (PARWID).
7. Spore length (SPLEN).
8. Spore width (SPWID).
9. Number of spore septa (SEPTA).

Pairwise comparisons of the three distribution groups were made. For the qualitative variables THALL and MARG, I used Yates' corrected chi-square, but I made the test more conservative by dividing the ordinary significance cut-off values by three (i.e., the number of comparisons made) in order to compensate for the multiple comparisons. The remainder of the characters are quantitative and were studied with one-way ANOVAs using the Scheffé's S procedure for post-hoc multiple mean comparisons.

All characters except EXCIP were used in a PCA performed to investigate the distinctness of the three distribution groups.

Results

Descriptive statistics of the quantitative variables and the distribution of the qualitative variables are presented in Tab. 13 and 14, respectively. The result of the pairwise comparisons of the distribution groups is shown in Fig. 12. There are significant differences between all three groups, but obviously all characters are overlapping. The western populations differ significantly from both of the other groups in having a different thallus structure, apothecial margin colour, spore length, and spore septation. The eastern group differs significantly from the other groups in having a different hymenium height and spore width. The European group does not differ significantly from both of the other groups in any character.

The PCA plot, in which the specimens have been plotted against the first three principal components, is shown in Fig. 13. The component loadings and the amount of variance explained is given in Tab. 15. Although occupying different spaces in the PCA plot, all three swarms overlap. The overlap between the eastern

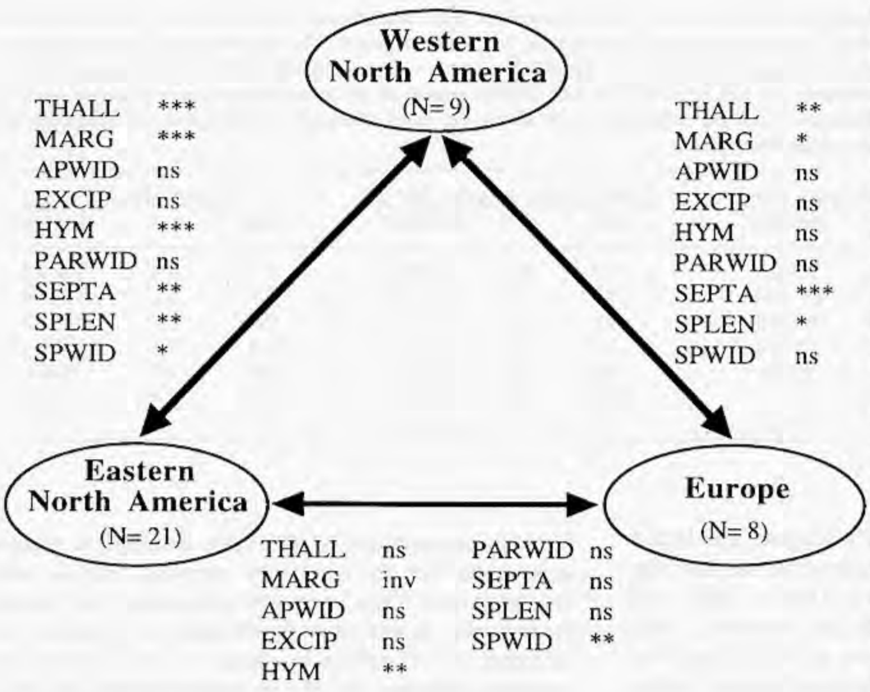


Fig. 12. A comparison of *Bacidia laurocerasi* from western North America, eastern North America, and Europe. The abbreviations of the characters are explained in the text. The qualitative characters THALL and MARG were compared with Yates' corrected chi-square. The ordinary significance levels were divided by three to compensate for the multiple comparisons. Thus, * denotes $0.0033< p\leq0.017$, ** $0.00033<p \leq0.0033$, *** $p\leq0.00033$, and ns $p> 0.017$. MARG is invariable (abbreviated "inv" in the figure) within both the European and the eastern group, and hence the difference could not be tested. The remaining characters are quantitative and were examined with one-way ANOVAs, using the Scheffé's S procedure for post-hoc multiple mean comparisons. The significance levels are denoted * for $0.01< p \leq0.05$, ** for $0.001< p \leq0.01$, *** for $p\leq0.001$, and ns (not significant) for $p> 0.05$.

and European groups is larger than the overlap between the western and any of the two other groups.

Conclusions

Since there are obvious differences between the western North American group on the one hand, and the eastern North American and the European group on the other, I beleive that it is justified to recognize the former taxonomically. Since all characters are overlapping, I find the subspecies level to be the most appropriate one. There is a name already available for this taxon at the species level, *Bacidia idahoensis* H. Magn. This name is combined here to the subspecies level under *B. laurocerasi*.

Tab. 14. Distribution of two qualitative characters (given as number of specimens) in *Bacidia laurocerasi* from western and eastern North America, and from Europe (represented by specimens from Sweden, Germany, Switzerland, and Great Britain). The abbreviations of the characters are explained in the text.

	Western North America (N= 9)	Eastern North America (N= 21)	Europe (N= 8)
THALL			
cracks few or lacking	1	20	8
densely cracked	8	1	0
MARG			
brown to black	2	21	8
brown-red	7	0	0

The relationship between the European and the eastern North American groups is more difficult to evaluate. Despite the low number of specimens studied of the European group, they differ significantly in two characters, and there is a clear separation in the PCA. It should be noted, however, that all characters are widely overlapping, that the significant differences are few, that the overlap in the PCA is large, and that European *B. laurocerasi* is still insufficiently studied. This leads me to the conclusion that presently, the best arrangement is to include both the eastern North American and the European representatives in the concept of subsp. *laurocerasi*. This conclusion must be considered as tentative, however.

The reason why I have included so few specimen of European *B. laurocerasi* is that it has been considered peripheral to my work. Naturally, further studies of the European group and its relationships with other parts of the world are necessary. Furthermore, when European *B. laurocerasi* has been studied in more detail, it may prove to contain a significant amount of geographically correlated variation.

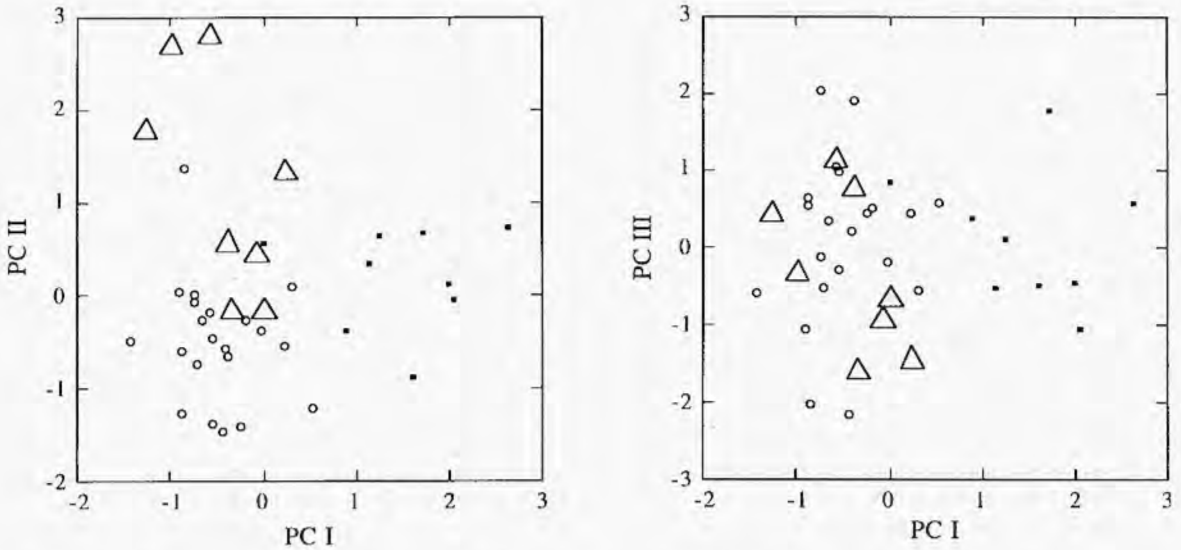


Fig. 13. Principal components plots of 38 specimens of *Bacidia laurocerasi* s. lat from western North America (squares), eastern North America (circles), and Europe (triangles). The first three components (PC I-III) account for 77 % of the total variance.

Bacidia heterochroa

Background

In North America, *Bacidia heterochroa* occurs within two different areas: along the coast in California and Oregon, and in the Gulf States (with a few outliers along the coast north to North Carolina). It would be incorrect to assume that this is a disjunct distribution, however. *Bacidia heterochroa* is mainly a tropical species, and it is apparently fairly common in the neotropics. Thus, there is a distinct possibility that the North American occurrences are northerly extensions of one, continuous distribution. This, however, is yet to be proven.

The eastern populations of *Bacidia heterochroa* were found to consistently produce atranorin, whereas the western ones contain no detectable amounts of any secondary substance. Thus, a search for additional differences in morphology was carried out.

Methods

Fifteen specimens representing the eastern population group and eight specimens representing the western population group were used in this study (the same ones later used to prepare the description of the species). Eight characters were measured:

1. Apothecium width (APWID).
2. Apothecium height (APHGT).
3. Width of proper exciple lateral to the hymenium (EXCIP).
4. Hymenium thickness (HYM).
5. Width of paraphysis apices (PARWID).
6. Spore length (SPLEN).
7. Spore width (SPWID).
8. Number of spore septa (SEPTA).

Tab. 15. Loadings for the five characters on the first three principal components (× 100) in a PCA performed to investigate the differences between population groups of *Bacidia laurocerasi* with different geographic origins (western and eastern North America, and Europe). The sign denotes whether the character makes a positive or negative contribution to the principal component. The variance explained (in %) by each component is given.

	Principal component		
Character	I	II	III
THALL	85	3	4
MARG	83	3	1
APWID	20	-22	91
HYM	71	36	0
PARWID	-44	60	56
SPLEN	86	-13	-5
SPWID	26	88	-14
SEPTA	80	-14	14
Variance explained	45	17	15

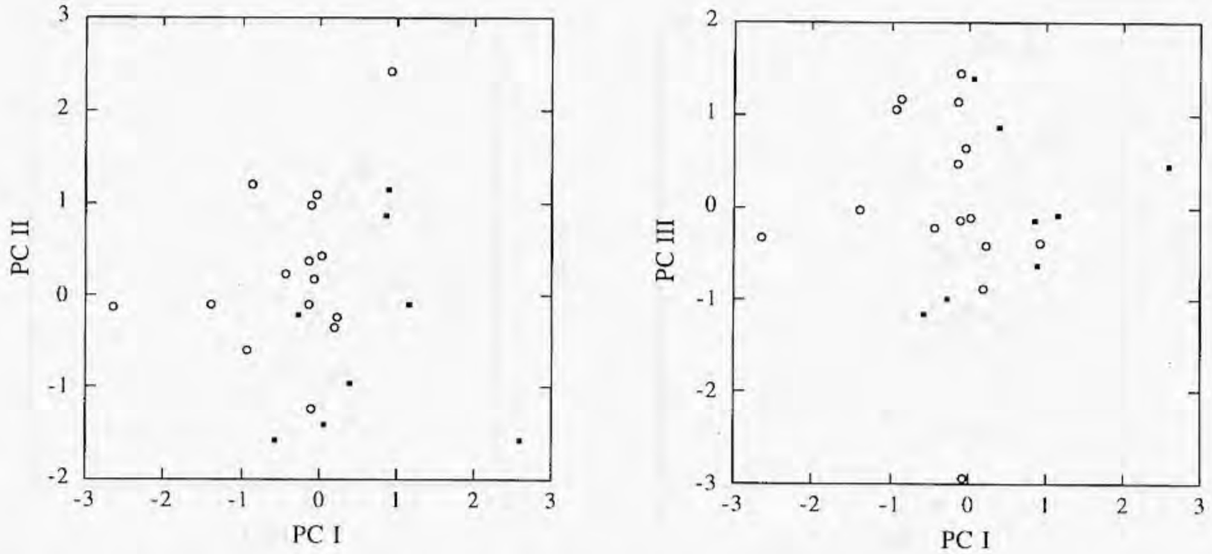


Fig. 14. Principal components plots of 23 specimens of *Bacidia heterochroa* from western (squares) and southeastern United States (circles). The first three components account for 90 % of the total variance.

One-way ANOVAs were performed on each of these characters. APHGT, HYM, SEPTA, SPLEN, and SPWID were used in a PCA in order to study the distinctness of the two population groups.

Results

Descriptive statistics and the significance of F in the ANOVAs are presented in Tab. 16. The western and eastern population groups differ significantly (i.e., $p < 0.05$) in apothecium height, spore width, and spore septation. None of the characters studied separate the groups discontinuously.

The PCA plots, in which the specimens have been plotted against the first three principal components, are shown in Fig. 14. The component loadings and the amount of variance explained is given in Tab. 17. In the PCA plots, the western and the eastern populations are separated, although not discontinuously. They are mainly separated by the first principal component, to which all of the included characters contribute markedly.

Tab. 16. Descriptive statistics and the significance of the F-values obtained from the one-way ANOVAs comparing western and eastern populations of *Bacidia heterochroa*. The abbreviations of the characters are explained in the text. The standard deviation is abbreviated "s. d." Note that the input values used for APWID, HYM, and PAR are means of five measurements per specimen, for SPLEN, SPWID, and SEPTA means of 10 measurements per specimen, and for APHGT and EXCIP a single measurement per specimen. Thus, the values of all but the two latter characters correspond to the minimum and maximum mean values in the species descriptions. Significance levels of F are denoted * for $0.01 < p \leq 0.05$ and ** for $0.001 < p \leq 0.01$, and ns (not significant) for $p > 0.05$.

	Western North America (N= 8)			Southeastern North America (N= 15)			
Character	mean	s. d.	min-max	mean	s. d.	min-max	Significance of F
APWID/mm	0.7	0.1	0.6-0.8	0.7	0.1	0.5-0.8	ns
APHGT/µm	278	36	231-329	226	45	168-329	**
EXCIP/µm	63	14	52-95	69	17	46-120	ns
HYM/µm	92	9	78-109	91	9	76-110	ns
PARWID/µm	2.4	0.3	2.0-3.0	2.5	0.3	1.9-3.0	ns
SPLEN/µm	53	7	43-67	49	5	36-55	ns
SPWID/µm	3.5	0.3	3.1-4.0	3.3	0.2	3.0-3.6	*
SEPTA	10.7	2.2	7.0-13.1	8.6	2.0	4.1-12.0	*

Conclusions

It is obvious that the western and eastern groups, in addition to chemistry, differ slightly in a few morphological traits, and that these differences are correlated. Although there are differences, the morphological variation is completely continuous. Normally, I would argue that a number of morphological differences in addition to a discontinuous chemical pattern would suffice for taxonomic recognition at some level. In this case, however, one should remember that the species is mainly distributed outside the study area, and that the differences are fairly small. As long as the chemistry and morphology of tropical representatives have not been studied, no well-founded taxonomic conclusion can be drawn. In particular, Central American *B. heterochroa* should be studied carefully. It is important to establish whether or not the western North American distribution area is really continuous with the remainder of the species.

Tab. 17. Loadings for the five characters on the first three principal components (× 100) in a PCA performed to investigate the difference between the western and the eastern populations groups of *Bacidia heterochroa*. The sign denotes whether the character makes a positive or negative contribution to the principal component. The variance explained (in %) by each component is given.

	Principal component		
Character	I	II	III
APHGT	62	-32	-65
HYM	64	55	-40
SPLEN	88	12	30
SPWID	44	-83	10
SEPTA	84	13	41
Variance explained	50	23	17

Taxonomy

A guide to the use of the key and the descriptions

The aim of this section is to gather most information needed to correctly understand the structure and the content of the keys and the descriptions. Some of the content below is repeated from the chapters *Material and Methods* and *Morphology and anatomy*, although in an abridged version.

Nomenclature. The synonymy has been kept short. I have not necessarily treated *all* combinations based on a certain epithet, usually only those thought to be important to the nomenclature. Generally, only the basionym and the name in *Bacidia*/*Bacidina* have been listed, but in case the basionym is below species level, the earliest combination at the species level has been added. A few exceptions from these rules have been made in nomenclaturally problematic cases. Unless otherwise explicitly stated, types have been seen by me.

The source of the descriptions. The descriptions are based exclusively on material from the continental United States and Canada. In some cases, however, variation in European or South American material is discussed, but such observations have never been included in the descriptions.

Characterizations. The characterizations contain the minimum amount of information needed to identify the species. The information included is not necessarily consistent, since species are variously difficult to identify and to distinguish from other, confusingly similar species.

Measurement accounts. Measurements are generally given as "(minimum value observed -) lowest specimen mean observed - arithmetic mean of all observations - highest specimen mean observed (- maximum value observed)". The standard deviation of all observations is denoted "s". "N" is the number of specimens studied, and "n" is the number of observations per specimen, the total number of observations thus being N × n. In some characters, only one measurement per specimen has been made (n= 1), and hence, specimen means are identical to the maximum and minimum values observed. In some species, only one specimen has been available for measurements (N= 1), with the result that specimen means are identical to the mean of all observations. In cases like these, measurements are accounted for in basically the same way, but the specimen means have been omitted: "(minimum value observed -) mean of all observations (- maximum value observed)". Paraphysis width in mid-hymenium and pycnidial and conidial sizes are accounted for in the form "minimum value observed - maximum value observed". Since specimen means are much less variable than single measurements, they have also been used in the key, although in a simplified manner. "Spores (average of 10 or more) 1.0-1.4 µm wide" is such an example (step 27). In the three species that key out under this alternative, a single measurement of spore width may vary from 0.9 to 1.9 µm, whereas, as can be seen, an average of ten measurements is much less variable.

In a few cases, particularly when N is low, the minimum/maximum value observed may be equal to the lowest/highest specimen arithmetic mean. This happens when all the n observations are equal to the maximum/minimum value. This is an unlikely event but nevertheless it occurs. In other cases, the value provided for the arithmetic mean of all observations is the same as the lowest or highest specimen mean observed, even when N> 1. These cases are always due to rounding; the arithmetic mean of all observations is never exactly equal to the highest or lowest specimen arithmetic mean when N> 1.

Preparations. Observations on apothecial anatomy should be made on hand-cut sections mounted in pure water. One or a few median sections should be kept in a separate preparation. This preparation is used to study all apothecial characters except pigment reactions, crystal solubility, and paraphysis width. The reamaining sections should be distributed among at least two additional preparations, which are primarily used to study pigment reactions with K, N, and sometimes also C (in which case a fourth preparation is needed). Never attempt to use more than one reagent on a single preparation! Note that reactions with K are stable, whereas reactions with N and C will soon fade. Once the reaction with K has been observed, this preparation is squashed and the paraphyses subsequently measured. The squashing is necessary to properly separate the paraphyses from each other. All measures of paraphyses in the keys and descriptions refer to squash preparations in K! Since the paraphyses may swell slightly in K, it is advisable not to measure them in pure water.

Apothecia. Only apothecia old enough to expose a distinct hymenium should be measured. Thus, it is possible to obtain a lower limit to the variation of the apothecium diameter. In apothecia that are not perfectly circular, the "diameter" should be interpreted as the maximum length.

Proper exciple. The width of the proper exciple is understood here as the lateral thickness of the proper exciple adjacent to the hymenium (Fig. 15A). It should be measured at about half the height of the hymenium, in the direction (tangent) of the surface of the hymenium near the proper exciple.

An artificial subdivision of the proper exciple has been used in order to describe the pigmentation, presence of crystals etc. (Fig. 15A): (1) *Rim*. The outermost few cell layers. (2) *Lateral interior*. The part inside the rim, but still lateral to the hymenium and the hypothecium. (3) *Medullary part*. The remainder of the proper exciple inside the rim, i.e., the oldest parts that are constricted below the hypothecium.

Crystals. Crystals in the proper exciple and in the upper part of the hymenium can usually easily be seen at high magnification in an ordinary light microscope. Should there be some hesitation, use two polarizing filters, one above and one below the preparation. Angle them as to minimize the amount of light that passes through the preparation, and the crystals will appear as brilliant white against a dark background.

Hymenium. The thickness of the hymenium is measured as the distance from the basal septum of the ascus to the upper surface of the apothecium.

Tholus. Routine investigations of the structure of the ascus apex are best carried out on gently squashed hand-cut sections stained with a 0.3 % aqueous solution of iodine, following pretreatment with K. Be sure not to study the tholus of asci with a ruptured wall. The denomination of the layers of the tholus follows Bellemère & Letrouit-Galinou (1988). The a+b-layer forms the exoascus, the c-layer the external part of the endoascus, and the d-layer the internal part of the endoascus (Fig. 15B). In *Bacidia* and *Bacidina*, the a+b-layer is strongly amyloid and the c-layer only slightly amyloid. The d-layer is basically strongly amyloid, but in most cases it contains a much less amyloid axial body.

Spores. Only spores that have been released from the ascus should be studied. Spore length should be measured as the distance between the ends of the spore, irrespective of curvature. The width should be measured at the widest part of the spore.

Conidia. Length and width of conidia should be measured the same way as spores.

Pigmentation. How the colour of a pigments is perceived is to some degree dependent on the thickness of the section used. The colours as described here refer to fairly thin, hand-cut sections (c. 30-60 µm thick). Several pigments react with K, C, or N. The strength of the reaction is proportionate to the concentration of the pigment. Thus, it is an advantage to select the darkest apothecium possible for study. Pigmentation should be studied in transmitted light in a light microscope with an (almost) maximally opened aperture. Closing the aperture will increase the contrast between tissues with different properties, which results in a blurring of the pigmentation. Preferrably, the source of light should be of near day-light quality.

Specimen citation. All specimens used in this study are cited, although in a very abridged form. The following information has been included, to the extent available from the labels: county (comté), parish, or equivalent division (parts of Canada), followed by year of collection, collector, collection number, and herbarium. On many labels, county/parish has not been specified. In that case, the name of a village, town, city, lake, mountain, or equivalent used on the label has been cited. The only exception from this rule are the Minnesota localities of Fink, which are generally not given with counties. On the labels of the Fink collections in MIN, however, county information has been added by Clifford Wetmore, and I have chosen to use this information here. Fink's Minnesota collecting sites have been discussed by Wetmore (1978).

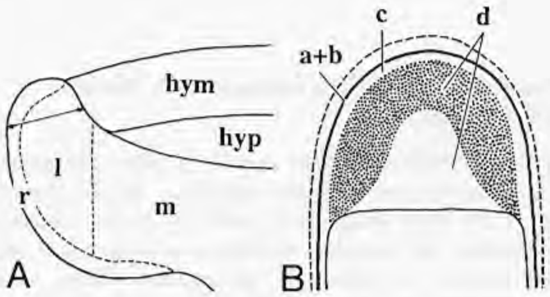


Fig. 15. Terminology used for the divisions of apothecia and asci. – A. Schematic median section through an apothecium showing the hymenium (abbreviated "hym"), hypothecium ("hyp"), and the artificial subdivision of the proper exciple used to describe the presence of pigments and crystals: rim ("r"), lateral interior ("l"), and medullary part ("m"). The double arrow indicates how the width of the proper exciple should be measured. – B. Ascus apex showing the layers of the tholus according to Bellemère & Letrouit-Galinou 1988 (a+b, c, d).

Mixed collections are fairly common. All admixtures determined and registered by me have been listed. I admit, however, to having been inconsistent. There are many collections with small admixtures of poorly developed specimens of *Bacidia* and *Bacidina* that I have not bothered to study. In the collection lists, specimens that occur as admixtures in collections of other species are preceded by a "+". The name of the species under which the collection is filed is preceded by "filed with".

Distribution maps. A single symbol on a distribution map may represent one or more nearby localities.

Colour photos. Colour photos of hand-cut apothecial sections of all species with distinct internal pigmentation are provided (Figs 40A-43E), as are habitus photos of the nine newly described species (Fig. 43F-44F).

Keys

Key to taxa that can be confused with Bacidia and Bacidina

This key contains species, species groups, and genera that are easily confused with *Bacidia* s. str. and *Bacidina*. It has been designed to work for North American conditions, and includes corticolous or lignicolous taxa that possess a crustose or squamulose thallus, disc-shaped, biatorine (or appearing so), lecideine, or zeorine (then with a well-developed proper exciple) apothecia, and spores with three or more transverse septa but no longitudinal ones. This key is presented as a service to the reader, since it is often as difficult to determine whether or not a specimen belongs in *Bacidia*/*Bacidina*, as it is to determine the species. I have chosen to include several genera that are very distantly related to *Bacidia* and *Bacidina*. For example, species of *Bactrospora* and *Loxospora* are commonly mistaken for *Bacidia*! Some of the taxa included are treated in *Excluded or not examined species*.

Apart from my own observations, I have used the following sources of information to construct this key: Coppins (1983), Timdal (1984), Egea & Torrente (1993), Lücking et al. (1994), Printzen (1995), Roux et al. (1995), and Staiger & Kalb (1995).

1. Photobiont *Trentepohlia* 2
1. Photobiont a green member of the Chlorococcales 5

2. Apothecia pale yellowish to dark brown; disc concave with a distinctly raised margin 3
2. Apothecia black (although sometimes pruinose); disc plane to convex 4

3. Most or all asci with more than 8 spores ... *Pachyphiale*
3. Asci with 8 spores .... *Gyalecta*

4. Asci difficult to separate from ascogenous hyphae when squashed in K. Spores not fragmenting .... *Lecanactis*
4. Asci easily separated from ascogenous hyphae whem squashed in K. Spores fragmenting in some species .... *Bactrospora*

5. Thallus squamulose 6
5. Thallus crustose, or if squamulose with pale pink apothecia 9

6. Squamules very small, almost granular, usually not exceeding 0.2 mm in width. Apothecia orange-brown. Not sorediate .... "*Psorella*" *pertexta*
6. At least some squamules exceeding 0.5 mm in width. Apothecia brown to black. Some species sorediate 7

7. Thallus of grey, placoid squamules that are adpressed to a black, episubstratal, felty prothallus. Not sorediate .... "*Bacidia*" *augustinii*
7. Prothallus indistinct or lacking. Often sorediate 8

8. Thallus with a para- or prosoplectenchymatic cortex, without epinecral layer. Apothecia greyish, bluish, or brownish to almost black, with algal cells below hypothecium .... *Waynea californica*
8. Thallus with a stainable layer and an epinecral layer. Apothecia either brown or black, without algal cells below hypothecium .... *Hypocenomyce*

9. Apothecia bright red, K+ blue ... *Ophioparma rubricosa*
9. Apothecia differently pigmented, not K+ blue 10

10. Asci polysporous, clavate with a ± pronounced swelling at the apex. A+b-layer of tholus thickened terminally .... *Ropalospora chlorantha* (and *R. viridis*, when fertile)
10. Asci with 1-16 spores (usually 8), without pronounced swelling at the apex. A+b-layer of tholus not thickened terminally 11

11. Apothecia with poorly developed proper exciple, immarginate. Paraphyses and excipular hyphae similar, abundantly branched and anastomosed. Photobiont usually "micareoid", i.e., fungal hyphae penetrating algal cells by intracellular haustoria .... *Micarea*
11. Apothecia with ± well-developed proper exciple, visible as a distinct margin at least in young apothecia. Paraphyses and excipular hyphae often not similar. Photobiont not "micareoid" 12

12. Asci 1-4-spored. Spores with walls c. 2 µm thick .... *Megalospora*
12. Asci with 8-16 spores. Spore wall thinner 13

13. Thallus PD+ yellow to orange, K+ vividly yellow (with thamnolic acid) .... *Loxospora*
13. Thallus often PD- and K- to K+ faintly yellow (without thamnolic acid) 14

14. Tholus without axial body but with a strongly amyloid, towards the tip slightly widened tubular structure. Proper exciple paraplectenchymatic or byssoid (but sometimes encrusted with crystals) 15
14. Tholus with ± conical, cylindrical, or lens-shaped axial body that is sometimes surrounded by a strongly amyloid zone. Proper exciple proso- or paraplectenchymatic 16

15. Proper exciple ± byssoid, at least in outer part .... *Byssoloma*
15. Proper exciple "normal", i.e., composed of hyphae with ± gelatinized walls .... *Fellhanera*

16. Tholus with a ± cylindrical axial body that reaches all through the d-layer (see, e.g., Hafellner 1984: 340) 17

16. Tholus with a ± conical (or rarely lens-shaped) axial body that usually does not reach all through the d-layer, at least not in all asci (see, e.g., Hafellner 1984: 261-268) 20

17. Paraphyses abundantly branched, some terminating in swollen apices that are provided with darkly pigmented caps. Apothecia often shiny ...... *Scoliciosporum*

17. Paraphyses moderately or not at all branched; apices sometimes pigmented but not with distinct caps. Apothecia matt 18

18. Hypothecium brown. Spores with both ends pointed ...... "*Bacidia*" *jacobi*

18. Hypothecium colourless or yellowish. Spores with at least one blunt end 19

19. Apothecia in transection, if at all, faintly and diffusely pigmented. At least some oil droplets present in hypothecium ...... The "*Bacidia*" *lutescens* group

19. Apothecia in transection usually at least partly distinctly pigmented (± greenish). Without oil droplets ...... The "*Bacidia*" *beckhausii group*

20. Spores 3-septate, bean-shaped. Upper part of hymenium green to blue-green ...... *Arthrosporum populorum*

20. Without this combination of characters 21

21. Rim of proper exciple covered by a rather thick gelatinous layer that swells markedly (and finally almost dissolves) in K or a dilute hypochlorite solution. Spores with warted perispore in some species ...... The "*Bacidia*" *sabuletorum* group

21. Rim without such gelatinous layer. Spores without warted perispore 22

22. Excipular hyphae of mature apothecia moderately branched, running closely parallel to each other; cell lumina narrowly cylindrical, evenly thick, not markedly widened near rim of proper exciple 23

22. Proper exciple different 24

23. Apothecia when very young almost globose, with a distinct core of young, immature asci and ascogenous hyphae surrounded by a distinctly delimited proper exciple ...... *Mycobilimbia*

23. Apothecia when very young moderately convex. Immature asci and ascogenous hyphae dispersed in the sterile tissue, not forming a distinct core distinctly delimited from the proper exciple ...... *Biatora*

24. Apothecia pale yellow to yolk-yellow, soon becoming convex. Spores 1-3-septate. Epithecium inspersed with crystals 25

24. Without this combination of characters 26

25. Apothecia pale yellow. Spores consistently 3-septate ...... "*Bacidia*" *pallens*

25. Apothecia yolk-yellow. Spores predominantly 1-septate, but occasionally up to 3-septate ...... *Cliostomum vitellinum*

26. Spores often with more than 5 septa. Apothecia not with "dotted" pigmentation in a wet condition. Excipular hyphae usually not club-shaped, with narrowly cylindrical to almost globose cell lumina ...... *Bacidia* and *Bacidina*, continue below

26. Spores with up to 5 septa. Epithecial pigmentation unevenly distributed, apothecial disc thus appearing "dotted" in a wet condition. Excipular hyphae club-shaped, i.e., narrowly cylindrical in interior of proper exciple but gradually becoming thicker towards rim 27

27. Length of spores not exceeding 6 times the width ...... *Lecania naegelii*

27. Length of spores exceeding 7 times the width ...... *Lecania stigmatella*

Key to corticolous and lignicolous species of Bacidia and Bacidina

1. Upper part of hymenium green, blue-green, or green-grey, N+ red to purple (sometimes with a precipitate of blue crystals) 2

1. Upper part of hymenium colourless to yellow to orange to brown to dirty purplish, reaction with N variable 11

2. Upper part of hymenium grey to grey-green, C+ violet ...... 19. *B. reagens*

2. Upper part of hymenium green to blue-green, C- 3

3. Proper exciple laterally with ± evenly dispersed, minute crystals (mostly less than 1 µm) ...... 1. *B. absistens*

3. Proper exciple without crystals or with radiating clusters of ± coarse crystals (mostly 1-7 µm) 4

4. Hypothecium colourless or very pale yellowish/brownish 5

4. Hypothecium orange to brown 7

5. Spores acicular. Apothecial margin finally excluded ...... 9. *B. friesiana*

5. Spores bacilliform or clavate. Apothecial margin usually persistent 6

6. Young apothecia low and flat. Proper exciple mainly consisting of regularly radiating hyphae .... 7. *B. circumspecta*
6. Young apothecia barrel-shaped. Proper exciple below hypothecium forming a thick cushion of irregularly intertwined and richly branched hyphae .... 13. *B. igniarii*

7. Hypothecium brown, downwards gradually merging into the dark brown-red to red-black proper exciple .... 24. *B. schweinitzii*
7. Hypothecium brown in a ± distinct zone, in the lower part usually changing to colourless or yellowish (not gradually merging into a dark proper exciple) 8

8. Spores acicular, narrower than 2 µm. At least lower part of proper exciple with ± ellipsoid cell lumina. Hypothecium K- or K+ greenish brown ... 34. *Bn. egenula*
8. Spores bacilliform, fusiform, clavate, or acicular, width always exceeding 1.5 µm and usually also 2.0 µm. Cell lumina in proper exciple (outermost cell layers excepted) cylindrical. Hypothecium K- or K+ purplish 9

9. Proper exciple, at least rim, dominated by a green to blue-green pigment (K-) .... 14. *B. insularis*
9. Proper exciple usually dominated by a brown, K+ purplish pigment. Some ± pigment deficient specimens dominated by a green to blue-green pigment, but then in low concentration and only in upper part of proper exciple 10

10. Hypothecium colourless or pale orange to brown-orange, K-. Spores (average of 10) 1.7-3.2 µm wide, never with more than 7 septa. Apothecial margin usually persistent .... 7. *B. circumspecta*
10. Hypothecium pale to dark (often reddish) brown, K+ purplish. Spores (average of 10) 2.1-5.1 µm wide, with 3-13 septa. Apothecial margin finally excluded .... 25. *B. subincompta*

11. Spores bacilliform or fusiform, straight or only slightly curved, not coiled in the ascus, length/width ratio (average of 10 or more spores) never exceeding 11 (often much less) 12
11. Spores usually acicular, straight to curved to sigmoid, often coiled in the ascus when immature, length/width ratio (average of 10 or more spores) exceeding 10. *If* length/width ratio not exceeding c. 10 and spores bacilliform to clavate, then spores coiled in ascus, distinctly curved or sigmoid 14

12. Spores fusiform with blunt ends, width exceeding 5.5 µm. Western .... 4. *B. auerswaldii*
12. Spores bacilliform, width never exceeding 5.0 µm. Southeastern 13

13. Thallus often dissolved into goniocysts. Proper exciple at least in outer portion with wide, ellipsoid to globose cell lumina .... 38. *Bn. varia*
13. Thallus never dissolved into goniocysts. Proper exciple of ± cylindrical cell lumina 14

14. Apothecia usually pink. Cell lumina wider in lower (old) part of proper exciple than in upper (young) part .... 16. *B. medialis*
14. Apothecia usually brown-orange to ± purple-brown. Cell lumina in lower part of proper exciple narrower than or as wide as lumina in upper part .... 12. *B. hostheleoides*

15. Upper part of hymenium dirty purplish, K+ pure green, N+ pure purple (often with a precipitate of blue crystals). Proper exciple inspersed with minute crystals (< 1 µm) .... 1. *Bacidia absistens*
15. Upper part of hymenium colourless to yellow to orange to brown; reactions with K and N variable but not K+ pure green and N+ pure purple. Proper exciple with or without minute crystals 16

16. Hypothecium and/or proper exciple immediately below hypothecium dark (brown-orange, orange-brown, red-brown, dark brown, or red-black) 17
16. Hypothecium and proper exciple below hypothecium pale (colourless, pale yellowish, pale orange, or pale brown) 21

17. Hypothecium K+ green-brown. Thallus with c. 20-50 µm wide goniocysts .... 29. *Bn. arnoldiana*
17. Hypothecium K-, K+ intensifying, or K+ purple-red. Thallus smooth or granular, granules then mostly exceeding 50 µm 18

18. At least young apothecia with abundant, ± evenly dispersed minute crystals in the epithecium and rim of proper exciple (use polarizing filters!) .... 2. *B. aggregatula*

18. Apothecia without crystals or with radiating clusters of crystals in the proper exciple 19

19. Brown pigment in apothecia K+ intensifying .... 24. *B. schweinitzii*
19. Brown pigment in apothecia K+ purple-red 20

20. Thallus smooth, wrinkled, or warted.. 18. *B. polychroa*
20. Thallus finely granular .... 8. *B. diffracta*

21. Apothecia (when fresh) pink, pale yellow, pale grey, or almost white (N.B.! As herbarium specimens age, pale apothecia often darken to near medium-orange).. 22

21. Apothecia at least partly brown-yellow or ± orange to red-brown to black 33

22. Epithecium and/or proper exciple with crystals 23
22. Epithecium and proper exciple without crystals 27

23. Proper exciple with coarse crystals (≤8 µm diam.) in lower part and (usually) minute crystals (≤1.5 µm diam.) in upper part; rim usually with stronger pigmentation in lower part than in upper. Margin distinctly paler than disc, usually pinkish or pale brownish. Extreme South .... 6. *B. campalea*
23. Proper exciple either with clusters of coarse crystals or with ± evenly dispersed minute crystals; rim with stronger pigmentation in upper part than in lower. At least upper part of margin (closest to hymenium) usually concolorous with disc or only slightly darker or paler 24

24. Proper exciple along the rim with a distinct, 4-6 cell layers thick zone of enlarged cells .... 26. *B. suffusa*
24. Proper exciple along the rim without or with a 1-2 cell layers thick zone of enlarged cells 25

25. At least margin of young apothecia with a thick white pruina. Margin persistent .... 17. *B. mutabilis*
25. Apothecia without or with thin pruina. Margin finally excluded 26

26. Width of apothecia seldom exceeding 0.3 mm. Spores (average of 10) up to 1.7 µm wide. Ocular chamber lacking. Southeastern .... 33. *Bn. crystallifera*
26. Width of apothecia usually exceeding 0.5 mm. Spores (average of 10) at least 2.0 µm wide. Ocular chamber narrow and high. Great Lakes and northwards .... 20. *B. rosella*

27. Spores (average of 10 or more) 1.0-1.4 µm wide 28
27. Spores (average of 10 or more) 1.6-2.8 µm wide 30

28. Apothecia with pale yellow or pale grey disc. Margin paler than disc, persistent. .... 32. *Bn. chloroticula*
28. Apothecia with ± pink disc. Margin concolorous with disc, finally excluded. Southeastern 29

29. Thallus partly dissolving into finely granular goniocysts (granules c. 20 µm or less) .... 39. *Bn. sp. #1*
29. Thallus of small, deeply incised squamules, the lobes of which are 20-30 µm wide; not dissolving into goniocysts .... 37. *Bn. squamellosa*

30. Hymenium (average of 5 measurements in one apothecium) 75-88 µm high .... 23. *B. salmonea*
30. Hymenium (average of 5 measurements in one apothecium) 42-73 µm high 31

31. Most young apothecia with a thin thalline margin (visible at least in section), which is soon suppressed by the proper exciple. Axial body lens-shaped .. 36. *Bn. ramea*
31. Apothecia without thalline margin. Axial body ± conical 32

32. Hymenium (average of 5) 57-73 µm high. Paraphyses fairly abundant in relation to number of asci. Conidia bacilliform or filiform, the latter non-septate. California .... 31. *Bn. californica*
32. Hymenium (average of 5) 42-61 µm high. Paraphyses rather few in relation to number of asci. Conidia filiform, usually 3-11-septate. Southeastern .... 38. *Bn. varia*

33. Disk of at least some young (not seldom all) apothecia brown-yellow or yellow-brown, without tinge of red. Rim of proper exciple K-, in upper part brown-yellow, yellow-brown, or almost pure brown, downwards usually gradually changing to pale yellow or colourless 34
33. Apothecial disk at least partly orange to reddish brown to black. Rim of proper exciple at least in part ± orange to pure brown to red-brown to purple-brown (when ± brown K+ green-brown or K+ purplish) 35

34. Thallus not dissolving into goniocysts. Proper exciple (the outermost cell layer excepted) of cells with ± narrowly cylindrical lumina. Bicoastal ...... 3. *B. arceutina*
34. Thallus partly dissolving into finely granular goniocysts. Proper exciple partly of cells with ± ellipsoid lumina. Florida .... 28. *Bn. aenea*

35. Thallus entirely consisting of rather large granules (average of 20 granules exceeding 70 µm) 36
35. Thallus either not at all granular, or partly or entirely dissolving into finely granular goniocysts (average of 20 granules less than 60 µm) 37

36. Apothecia in section ± yellowish to pale orange throughout, K+ intensifying but never K+ purplish. Upper cortex with crystals .... 21. *B. rubella*
36. Apothecia in section with at least upper part of proper exciple and part of the hymenium ± red-brown, K+ purplish. Cortex without crystals .... 5. *B. biatorina*

37. Outermost 4-8 cell layers of proper exciple with enlarged cell lumina that are distinct from the inner, narrower ones, or cell lumina gradually but distinctly enlarging towards the rim (if in doubt due to obscuring pigments, use a diluted hypochlorite solution to bleach them) 38
37. Outermost 1-2 cell layers of proper exciple with enlarged cell lumina that are distinct from the inner, narrower ones, or entirely without enlarged cell lumina along rim 39

38. Apothecia variously coloured (but usually not brown-orange to red-brown). At least some apothecia with white pruina, particularly on the edge. Proper exciple with a distinct, 4-6 cell layers thick zone of cells with enlarged lumina along the rim. Eastern .... 26. *B. suffusa*

38. Apothecia brown-orange to red-brown, without pruina. Proper exciple with cell lumina gradually enlarging towards edge, or with a ± distinct, 6-8 cell layers thick zone of cells with enlarged lumina along the rim. Extreme South .... 22. *B. russeola*

39. Orange to brown pigment of the apothecia K+ green-brown .... 31. *Bn. californica*

39. Apothecium pigments K-, K+ intensifying, or K+ purplish 40

40. Upper part of hymenium and at least upper part of proper exciple with a ± distinct, dark brown, K+ purplish, continuous layer of pigment 41

40. Upper part of hymenium diffusely and usually weakly pigmented, pale orange to ± brown, never with a distinct and continuous layer of a brown, K+ purplish pigment 45

41. Spores (average of 10) 16–27 µm long, usually strongly curved or sigmoid .... 27. *B. vermifera*

41. Spores (average of 10) exceeding 35 µm, straight or ± curved to sigmoid 42

42. Epithecial pigment forming ± distinct grey-brown "caps" over the apices of the paraphyses (best seen by squashing strongly pigmented part of apothecium in K) .... 11. *B. heterochroa*

42. Most of the epithecial pigment dissolved in the gelatinous matrix or as irregular granules between the apices of the paraphyses 43

43. Spores strongly conglutinated, ± helically twisted, often released in packages of 8. Hymenial pigment concentrated to the gelatinous matrix surrounding the ascus apices. Southeastern .... 10. *B. helicospora*

43. Spores not conglutinated, although sometimes coiled prior to the release. Hymenial pigment evenly distributed in upper part. Western and Great Lakes-northern Appalachian 44

44. Thallus usually rather thick, grey-green, finely areolate. Margin of at least young apothecia paler than disc, usually ± carmine red .... 15a. *B. laurocerasi* subsp. *idahoensis*

44. Thallus usually thin, ± grey, rarely areolate. Margin of apothecia ± concolorous with disc, ± brown to black. Great Lakes-northern Appalachian .... 15b. *B. laurocerasi* subsp. *laurocerasi*

45. At least some young apothecia with thick white pruina on the edge. Spores > 3 µm wide .... 17. *B. mutabilis*

45. Apothecia without pruina. Spores < 3 µm wide 46

46. Hymenium (average of 5) at least 75 µm high. Most spores at least 30 times longer than wide. Proper exciple (outermost 1-2 cell layers excepted) with narrowly cylindrical cell lumina only. .... 23. *B. salmonea*

46. Hymenium (average of 5) 70 µm or lower. Most spores less than 25 times as long as wide. Proper exciple even in inner part with at least some broadly cylindrical, irregular, or almost globose lumina 47

47. Thallus thin, entirely dissolved into granular goniocysts 35-57 µm wide (average of 10) .... 35. *Bn. egenuloidea*

47. Thallus usually not at all or only partly dissolved into granular goniocysts. *If* entirely dissolved, then goniocysts less than 30 µm wide (average of 10) 48

48. Young apothecia often with a thin thalline margin (visible at least in section). Axial body lens-shaped. Western .... 36. *Bn. ramea*

48. Apothecia without thalline margin. Axial body conical to subcylindrical. Central and southeastern U. S. 49

49. Hymenium c. 70 µm high. Pigmented parts of apothecia K+ intensifying. Conidia curved, non-septate .... 30. *Bn. assulata*

49. Hymenium rarely exceeding 60 µm. Pigmented parts of apothecia K+ purplish or K+ intensifying. Conidia curved or sigmoid, usually 3-11-septate .. 38. *Bn. varia*

Bacidia De Not.

G. Bot. ital. 2: 189 (1846). – Type: *B. rosella* (Pers.) De Not. (lectotype selected by Fink 1910: 87).

Psorella Müll. Arg., Bull. Herb. Boissier 2, appendix 1: 11 (1894). – Type: *P. pannaroidea* (C. Knight) Müll. Arg. (lectotype selected by Clements & Shear 1931: 319).

Toniniopsis Frey, Ber. schweiz. bot. Ges. 35: 73 (1926). – Type: *T. obscura* Frey (holotype).

Bacidiomyces Cif. & Tomas., Atti Ist. bot. Univ. Lab. crittogam. Pavia, ser. 5, 10: 39 & 65 (1953). – Type: *B. rubella* (Hoffm.) Cif. & Tomas.

Lichenized species. Thallus crustose, episubstratal, often continuous, without cracks or rimose to areolate to granular, smooth to wrinkled to warted to subsquamulose, sometimes discontinuous and of discrete to contiguous areoles. Prothallus lacking or present, then either thin, ± endosubstratal, white to grey, between discrete areoles or bordering the thallus, or distinct, dark brown to black, bordering the thallus. Soredia and isidia absent. Goniocysts absent. Upper cortex of one inner layer of anticlinal or irregular hyphae stainable in LCB and an outer epinecral layer (one or the other may be missing), both usually with minute crystals soluble in K but insoluble in N and H_2SO_4. Photobiont layer ± continuous, photobiont chlorococcoid. Medulla absent or (in thick areoles) present, rather thin, composed of loosely interwoven hyphae, without crystals. Lower cortex absent.

Apothecia ± sessile, biatorine or lecideine, when mature 0.1-2.0 mm wide, pale pink or pale yellow to orange to brown to brown-violet to red-brown to purple-brown to reddish or bluish black or pure black; pruina absent or present, white. Disc plane or slightly concave when young, often soon becoming ± convex. Margin usually slightly raised above disc in young apothecia, later level with the disc, often becoming excluded in old and convex apothecia.

Proper exciple without thick gelatinous layer along rim, without oil droplets, sometimes with crystals (c. 0.5-10 µm) that are either evenly dispersed or form radiating clusters; composed of radiating, more or less abundantly furcate but sparingly or not at all anastomosed hyphae. Cell lumina usually narrowly cylindrical, usually 8-25 µm long and 1-3 µm wide (lumina near rim of proper exciple excepted), usually 5-11 times as long as wide, often distinctly constricted near septa (not in species with very narrow lumina). Walls thick and gelatinized, the distance between two adjacent cell lumina at least the same as the width of a lumen, often twice the distance, and sometimes even up to five times the width of a lumen. Cell lumina along the rim of the proper exciple often ± enlarged in relation to the inner lumina, forming a distinct zone, although sometimes gradually enlarging towards the rim of the proper exciple. Hypothecium colourless to yellowish to brown-orange to dark brown, without crystals or oil droplets, not chondroid. Hymenium 40-130 µm high, amyloid, usually colourless in lower part and pigmented in a distinct or diffuse layer in the upper part, sometimes with a layer of crystals in the upper part, without oil droplets. Paraphyses unbranched or ± branched in upper part, often also ± anastomosed; apices not at all swollen to ± clavate, often surrounded by pigment or sometimes containing pigment in the wall, never with a thick and gelatinized wall. Asci clavate, surrounded by a thin, amyloid gelatinous sheet; tholus amyloid, with a narrow c-layer, with a ± high, blunt or pointed axial body, the width of which is a third or less of the entire d-layer, and a low or high, blunt or pointed ocular chamber. Spores eight per ascus, acicular, clavate, bacilliform, or fusiform, with 3-28 septa, straight, curved, or sigmoid, straight or coiled in ascus (often variable even within the same apothecium), colourless, rather thick-walled, without perispore or ornamentation, 11-108 µm long and 1.2-7.8 µm wide, 3-66 times as long as wide, usually easily separated from each other at maturity.

Pycnidia usually ± immersed in thallus or prothallus (rarely sessile), usually concolorous with apothecia, unilocular. Conidiogenous cells lining the pycnidial cavity, cylindrical or slightly tapering, 7-15 × 1.0-2.5 µm, producing conidia apically, lacking distinct conidiophores. Conidia of five different types (one to three types in one species; usually only one type, rarely two types mixed in the same pycnidium): (1) filiform, ± curved, non-septate, 5-32 × 0.5-0.8(-1.0) µm, (2) falcate, 0-1-septate, 6-25 × 1.2-1.6 µm, (3) oblong to ellipsoid to fusiform to bacilliform, 0-1(-2)-septate, 3-12 × 1.2-2.0 µm, (4) filiform, straight, non-septate, 6-17 × 0.5-1.0 µm, and (5) filiform, slightly curved, distinctly 5-9-septate, 27-35 × 1.2-1.6 µm.

Chemistry: No lichen substances or sometimes atranorin, zeorin, and rarely *meta*-depsides in the orcinol series in the thallus. Thallus K- or K+ yellow, C-, KC- or KC+ yellow, PD-, UV-.

Discussion. The generic description above is based on my observations on the North American species and must be viewed upon as tentative as long as *Bacidia* has not been studied worldwide.

The type of *Psorella pannaroidea* (syntype in WELT!), the type species of *Psorella*, fits well within the concept of *Bacidia* s. str. used here. Already Brako (1989) remarked that *Psorella* should probably be synonymized with *Bacidia*. *Toniniopsis obscura* (type specimens in BERN!) is a younger taxonomic synonym of *Bacidia illudens* (Nyl.) Lynge, a species of *Bacidia* s. str.

1. Bacidia absistens (Nyl.) Arnold

Flora, Jena 53: 472 (1870). - *Lecidea absistens* Nyl., Flora, Jena 52: 295 (1869). – Type: France, "Brest.", 1868, Crouan (H-NYL 17737b, lectotype selected here).

Illustrations. Figs 16 (map), 40A.

Characterization. Apothecia blue-black to black, although sometimes ± pigment deficient. Proper exciple laterally with brown and green pigmentation, with evenly dispersed, minute crystals. Hypothecium colourless to brown. Upper part of hymenium greenish, rarely dirty purplish. Spores acicular, 40-90 × 1.9-5.0 µm, with 3-15 septa.

Thallus indeterminate, thin to rather thick, usually discontinuous, of discrete or contiguous, convex, often slightly effigurate areoles that are sometimes warted or subsquamulose; sometimes continuous, ± cracked, warted, pale grey, yellow-grey, ± green-grey, or grey-green.

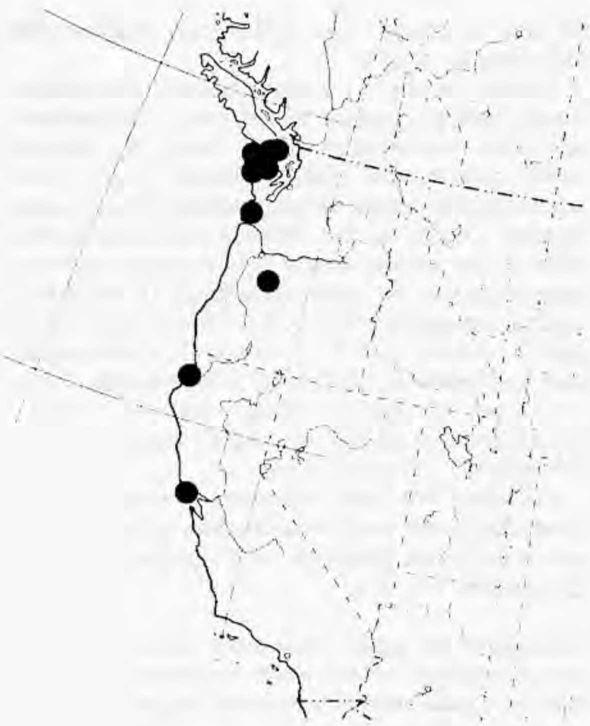


Fig. 16. Known North American distribution of *Bacidia absistens*.

Areoles when discrete (61-)88-137-174(-242) µm large (s= 45, N= 6, n= 10). Prothallus lacking or sometimes present between discrete areoles, then thin, endophloeodal, pale grey.

Apothecia (0.3-)0.3-0.7-0.9(-1.4) mm diam. (s= 0.2, N= 6, n= 10), plane or moderately convex, remaining so or sometimes becoming markedly convex, epruinose. Disc usually blue-black to pure black, sometimes grey-brown, purple-brown, red-brown, or brownish pink, sometimes mottled with different colours. Margin concolorous with or paler than disc, ± grey, ± blue-grey, brownish pink, grey-brown, red-brown, purple-brown, dark brown, or black, sometimes mottled with different colours and when ± darkly pigmented often paler in the lower part (to pale yellow-brown), raised above disc in young apothecia, soon level with the disc, persistent or later excluded.

Proper exciple laterally (43-)62(-74) µm wide (s= 11, N= 8, n= 1), at least in the inner part with crystals that are usually less than 1 µm large, sometimes up to 2 µm, usually abundant and evenly dispersed but sometimes few and inconspicuous (visible at least in polarized light). Rim ± blue-green, green-brown, or ± brown in uppermost part, downwards ± brown (seldom blue-green), then fading to colourless, with cell lumina gradually enlarging towards the edge, or along the edge with a ± distinct, 2-11 cell layers thick zone of enlarged cells with lumina that are up to 20 × 6 µm. Lateral interior ± brown, downwards fading to colourless. Medullary part colourless. Hypothecium colourless, pale yellow, or ± brown. Hymenium (68-)74-86-112(-116) µm thick (s= 13, N= 8, n= 5), lower part colourless or pale purplish brown, uppermost part ± green, blue-green, or green-blue, rarely dirty purplish or yellow-brown, usually ± distinctly delimited. Paraphyses 1.2-1.6 µm wide in mid-hymenium; apices usually ± clavate, sometimes weakly or not at all swollen, (1.2-)1.8-2.4-3.3(-4.9) µm wide (s= 0.8, N= 7, n= 10), without internal pigment. Spores acicular, straight, curved, or sigmoid, not coiled in ascus, (40-)45-58-74(-90) µm long (s= 13, N= 7, n= 10), (1.9-)2.3-3.0-4.1(-5.0) µm wide (s= 0.6, N= 7, n= 10), (14.3-)17.5-20.0-24.5(-34.0) times as long as wide (s= 3.9, N= 7, n=10), with (3-)6.8-11.4-14.3(-15) septa (s= 3.4, N= 7, n= 10).

Pycnidia almost entirely immersed in thallus, uppermost part of wall concolorous with apothecia, 50-100 µm diam. Conidia filiform, curved, non-septate, 7-32 × c. 0.5 µm.

Chemistry: Different combinations of at least three unidentified *meta*-depsides in the orcinol-series. Apparently, none of these substances is 4-*O*-methylcryptochlorophaeic acid, which was reported from Scandinavian specimens of this species (Tønsberg et al. 1995).

Pigments: Green parts of hymenium and proper exciple K-, N+ purple, with or without a precipitate of small blue crystals. Proper exciple and sometimes hypothecium (brown parts) K+ purplish, N+ brown-orange to orange-red. – Bacidia Green in hymenium and proper exciple. Laurocerasi Brown in proper exciple, pycnidial wall, and sometimes hypothecium. Rubella Orange sometimes in hypothecium, rarely in proper exciple and hymenium.

Ecology. On trunks and branches of *Acer macrophyllum*, *Alnus rubra*, *Populus trichocarpa*, and *Umbellularia californica* in shady and humid habitats.

Distribution. Along the coast from central California to southern British Columbia.– Europe.

Discussion. *Bacidia absistens* is similar to *B. friesiana*, *B. insularis*, and *B. subincompta*. All three species differ from *B. absistens* in lacking small, evenly dispersed crystals in the interior of the proper exciple. In addition, *B. friesiana* has shorter spores, a lower hymenium, and a pigment deficient inner part of the proper exciple. *B. insularis* has a proper exciple dominated by Bacidia Green even in the lower parts, spores that are generally fusiform, thinner paraphyses, and paraphysis apices that often have distinct caps of Bacidia Green. *B. subincompta* has a proper exciple which is heavily pigmented even in the lower parts (downwards changing to colourless in *B. absistens*).

One collection of *Bacidia absistens* (Foster 2888, MIN) contains orange-brown apothecia in addition to the normally pigmented, blue-black ones. In the orange-brown apothecia, the pigments Bacidia Green and Laurocerasi Brown have been replaced by Rubella Orange, which sometimes occurs in small amounts in the hypothecium of normally pigmented apothecia. In addition to Rubella Orange, small amounts of Laurocerasi Brown are produced in the proper exciple. I have never encountered any specimen with orange-brown apothecia only. In case such forms are found, they can easily be mistaken for several other species with normally ± brown pigmented apothecia. However, the presence of minute, evenly dispersed crystals in the proper exciple, and enlarged cells along the edge of the proper exciple is unique to *B. absistens*.

Collections examined. CANADA. *Vancouver Island*. Colquitz River, 1908, probably collected by Macoun (CANL). Jordan River, 1966, Brodo 7897B (CANL). – U. S. A. *California*. Humboldt Co., 1989, Ekman L656 (LD). Marin Co., 1978, Hewlett 1096 (SFSU). *Oregon*. Breitenbush, 1930, Anderson 519 (NY). *Washington*. Clallam Co., Foster 2764 (MIN), 1989, Ekman L730 (LD). Jefferson Co., 1989, Ekman L725 (LD). Pacific Co., 1989, Ekman L717 (LD). Port Angeles, 1914, Foster 2888 (MIN).

2. Bacidia aggregatula Malme

Ark. Bot. 27A (5): 34 (1935). – Type: Brazil, "Matto Grosso, Guia pr. Cuyabá, in silva clara ripae fluminis Coxipó Guassú", 1894, Malme 2685b (S, lectotype selected here; UPS isolectotype).

Illustrations. Figs 17 (map), 40B.

Characterization. Apothecium colour very variable even within the same specimen, pink to red-brown. Proper exciple in the interior brown to red-black, in the rim with a layer of evenly dispersed, minute crystals. Hypothecium colourless to red-black, pigmentation merging into the proper exciple. Upper part of hymenium pale orange, with a layer of minute crystals. Spores acicular, 37-66 × 2.1-3.3 µm, with 3-9 septa.

Thallus determinate, very thin to rather thick, usually continuous, without cracks or ± cracked, wrinkled, pale grey, pale yellow-grey, ± green-grey, or grey-green. Prothallus bordering the individual, narrow, black where it meets other lichens, otherwise pale grey or lacking.

Apothecia (0.5-)0.7-0.8-1.1(-1.7) mm diam. (s= 0.3, N= 4, n= 10), plane when young, later becoming convex, epruinose or with a very thin pale pruina on disc and margin. Disc very variable in colour (even within the same specimen), pink, pale grey, pale brown to grey-brown to grey-black (the latter colour in young apothecia only), or pale brown-yellow to yellow-brown to orange-brown to dark red-brown; although very variable rarely mottled with different colours. Margin in upper part concolorous with or slightly paler or darker than disc, pink, pale grey to grey, pale brown to brown, pale brown-grey to dark grey-brown, pale brown-orange to orange-brown to red-brown, or pale brown-yellow to yellow-brown; lower part concolorous with upper part or (particularly in pale apothecia) darker, dark brown or dark grey-brown; raised above disc in young apothecia, soon level with the disc, later becoming excluded.

Fig. 17. Known North American distribution of *Bacidia aggregatula* (dots) and *B. campalea* (triangles).

Proper exciple laterally (50-)63(-69) µm wide (s= 9, N= 4, n=1), along the rim with a layer of minute crystals (at least in the upper part) that are up to c. 1 µm large, usually abundant and evenly dispersed but sometimes few and inconspicuous (visible at least in polarized light). Rim colourless to brown-orange, along the edge without or with a single layer of enlarged cells with lumina that are up to 11 × 6 µm. Lateral interior brown-orange to red-black, sometimes with dirty green spots near the rim. Medullary part pale brown-orange to red-black, often darker in the lower part than in the upper part. Hypothecium colourless, pale brown, or pale brown-orange to dark brown-red, downwards usually darkening and merging into the colour of the exciple. Hymenium (74-)80-84-89(-93) µm thick (s= 5, N= 4, n= 5), lower part colourless, uppermost part ± pale orange, with a thin layer of minute crystals. Paraphyses 0.5-1.2 µm wide in mid-hymenium; apices usually ± clavate, sometimes weakly or not at all swollen, (0.8-)1.7-2.2-2.4(-3.2) µm wide (s= 0.6, N= 4, n= 10), without internal pigment. Spores acicular, straight, or slightly curved or sigmoid, straight or only slightly coiled in ascus, (37-)44-

53-57(-66) µm long (s= 8, N= 4, n= 10), (2.1-)2.5-2.6-2.6(-3.3) µm wide (s= 0.2, N= 4, n= 10), (11.1-)17.1-20.5-22.1(-26.5) times as long as wide (s= 3.7, N= 4, n= 10), with (3-)4.7-6.4-7.5(-9) septa (s= 1.7, N= 4, n= 10).

Pycnidia ± immersed in thallus, uppermost part of wall dark brown (even when apothecia are pale), 75-125 µm diam. Conidia filiform, curved, non-septate, 15-24 × c. 0.5 µm.

Chemistry: Trace amounts of atranorin or no lichen substances at all.

Pigments: Dark parts of proper exciple and lower part of hypothecium K-, N-. Upper part of hymenium and ± orange or brown parts of proper exciple K+ intensifying, N+ intensifying. Greenish parts of proper exciple K-, N+ purple. Crystals in proper exciple and epithecium partly soluble in K but insoluble in N. – Schweinitzii Red in proper exciple, hypothecium and pycnidial wall. Rubella Orange in proper exciple, hypothecium and hymenium. Bacidia Green sometimes in small amounts in proper exciple.

Ecology. At West Lake, Dade Co., *B. aggregatula* grew abundantly together with *B. heterochroa* and *B. mutabilis* on *Conocarpus erectus*, *Laguncularia racemosa*, and *Rhizophora mangle* in a mangrove swamp. In Corkscrew Swamp, Collier Co., *B. aggregatula* occurred sparingly on *Acer rubrum* in a swamp dominated by old *Taxodium distichum*. At two additional localities, where I did not observe *B. aggregatula* myself, it was found on an unidentified tree in a "swamp forest" and on cultivated hardwoods in a botanical garden.

Distribution. Known from only four localities in Collier, Dade, and Sarasota Counties in southern Florida. – Previously known only from the Brazilian type collection.

Discussion. *Bacidia aggregatula* is obviously closely related to *B. schweinitzii* and the neotropical species *B. horista* (Nyl.) Zahlbr. and *B. combinans* (Nyl.) Zahlbr. All four species have a darkly pigmented proper exciple dominated by Schweinitzii Red, and Bacidia Green is often or always present in the hymenium or proper exciple of all species except *B. combinans*. *B. schweinitzii* is separated from *B. aggregatula* by the thicker paraphyses, by the absence of minute crystals in the epithecium and proper exciple, and by the pigmentation: *B. schweinitzii* is usually dominated by either Schweinitzii Red in the proper exciple and Bacidia Green in the upper part of the hymenium, or by Rubella Orange in both the proper exciple and the upper part of the hymenium. In *B. aggregatula*, on the other hand, neither Rubella Orange nor Bacidia Green are ever dominant pigments. *B. horista* differs from *B. aggregatula* in lacking crystals in the proper exciple and apothecium, and in having shorter and wider, more or less fusiform spores, the length of which rarely exceeds 10 times the width. *B. combinans*, although very similar to the other species in pigmentation, is easily separated by the short (up to c. 20 µm long), bacilliform, usually 4-celled spores and the lack of Bacidia Green in the apothecia.

Collections examined. U. S. A. *Florida*. Collier Co., 1993, Ekman L1025 (LD). Dade Co., 1993, Ekman L1186, 1187, 1188 (LD), 1982, Tucker 25229 (herb. Tucker). Sarasota Co., 1981, Thor 2189 (S).

3. Bacidia arceutina (Ach.) Arnold

Verh. zool.-bot. Ges. Wien 19: 624 (1869). - *Lecidea luteola* var. *arceutina* Ach., Method. Lich. 61 (1803). - *Lecidea arceutina* (Ach.) Gray, Nat. Arrang. Brit. Plants 1: 472 (1821). – Type: Sweden (H-ACH 347E, lectotype selected here).

Illustrations. Figs 5A, 18 (map), 40C.

Characterization. At least young apothecia ± yellowish, without orange or red hues. Proper exciple distinctly brown-yellow to yellow-brown in the rim, otherwise pale. Hypothecium ± yellowish. Upper part of hymenium brown-yellow to yellow-brown. Spores acicular, 35-71 × 1.2-2.8 µm, with 3-15 septa.

Thallus indeterminate or determinate, thin, continuous, smooth or wrinkled, rarely warted or almost granular, ± cracked or areolate, rarely discontinuous and of discrete or contiguous, thin areoles; usually pale grey but sometimes chalky white, pale yellow-grey or pale green-grey. Prothallus sometimes present between discrete areoles, endosubstratal, thin, light grey.

Apothecia (0.3-)0.4-0.5-0.8(-1.1) mm diam. (s= 0.1, N= 16, n= 5), ± plane when young, later becoming convex, epruinose. Disc pale brown, yellow-brown, grey-brown, or brown to brown-black, rarely pale beige, red-brown, or purplish brown to purplish black, at least when young with a yellowish hue. Margin in upper part concolorous with disc or slightly darker, in lower part usually paler than disc and upper part of margin, pale beige to brown, distinct, raised above disc in young apothecia, soon level with the disc, and finally excluded in old and convex apothecia.

Proper exciple laterally (29-)50(-72) µm wide (s= 12, N= 16, n= 1), without crystals or rarely with diffuse clusters of minute crystals (less than 1 µm in diam.). Rim pigmented in a distinct zone, brown-yellow to dark yellow-brown to almost pure brown in upper part, downwards usually gradually changing to pale yellow or colourless, along the edge with a single row of enlarged

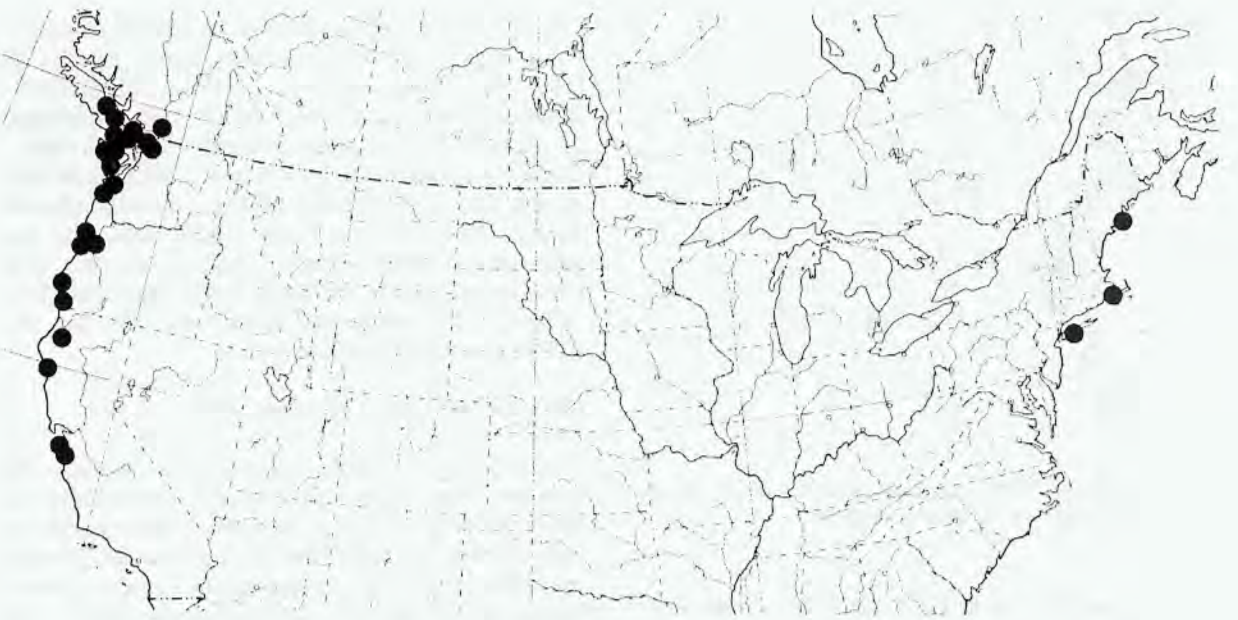


Fig. 18. Known North American distribution of *Bacidia arceutina*.

cells with lumina that are up to 9 × 8 µm. Lateral interior paler than rim, colourless, except upper part close to hymenium, which is often pale yellow to brown-yellow. Medullary part usually paler than hypothecium and concolorous with lateral interior, colourless to pale yellow. Hypothecium usually ± yellowish, only rarely entirely colourless. Hymenium (56-)63-78-93(-99) µm thick (s= 8, N= 16, n= 5), lower part colourless, uppermost part brown-yellow to dark yellow-brown to almost pure brown in a thin distinct layer. Paraphyses 1.0-1.6 µm wide in mid-hymenium; apices ± clavate or not at all swollen, (1.0-)1.8-2.2-2.7(-3.2) µm wide (s= 0.5, N= 16, n= 5), without internal pigment. Spores acicular, usually ± sigmoid, but sometimes straight or curved, sometimes coiled in ascus, (35-)47-54-64(-71) µm long (s= 7, N= 16, n= 10), (1.2-)1.5-1.8-2.2(-2.8) µm wide (s= 0.3, N= 16, n= 10), (18.3-)25.3-30.2-36.4(-46.0) times as long as wide (s= 5.5, N= 16, n= 10), with (3-) 5.0-7.0-10.7(-15) septa (s= 2.1, N= 16, n= 10).

Pycnidia immersed in thallus (only ostiole visible), colourless, 75-100 µm diam. Conidia filiform, curved, non-septate, 9-17 × 0.6-0.8 µm.

Chemistry: No lichen substances detected.

Pigments: Apothecia K-, N-. – Arceutina Yellow in proper exciple, hypothecium, and hymenium.

Ecology. In hardwood or mixed forests or forest fringes, where it grows directly on the bark of hardwoods and shrubs, rarely over bryophytes. It can be found on trunks, but more often it is found on thin, smooth-barked branches of trees and shrubs. It favours *Acer macrophyllum*, *Alnus rubra*, and *Populus trichocarpa*, but has occasionally been found on *Amelanchier alnifolia*, *Arbutus menziesii*, *Corylus cordata*, *Fraxinus latifolia*, *Ilex opaca*, *Juniperus virginiana*, *Lonicera* sp., *Oemleria cerasiformis*, *Prunus ilicifolia*, *Quercus velutina*, *Ribes bracteosum*, *Salix* sp., *Thuja occidentalis*, and *Umbellularia californica*.

Distribution. Coastal Maine, Massachusetts, and New York, and along the West Coast from central California to southern British Columbia. – Europe.

Discussion. *Bacidia arceutina* is a characteristic species that is only likely to be confused with *B. salmonea* (see that species) and *B. laurocerasi*. *B. laurocerasi* differs from *B. arceutina* in having a ± brown, K+ purplish, N+ orange pigment in the proper exciple and the upper part of the hymenium, and in having shorter and narrower spores with fewer septa.

Collections examined. CANADA. *British Columbia*. 1912, Macoun (CANL). Hope, 1969, Brodo 15641, Krog & James (CANL). Vancouver Island, Comox, 1893, Macoun (CANL, NY, US, WIS). Vancouver Island, Sidney, 1912, 1913, Macoun (FH), 1916, Macoun 308, 326 (UBC). Vancouver Island, Qualicum Beach, 1989, Ekman L756, L757, L758, L759 (LD). Vancouver Island, Victoria, 1893, Macoun (NY), 1989, Ekman L771, L774 (LD). Vancouver Island, Jordan River,

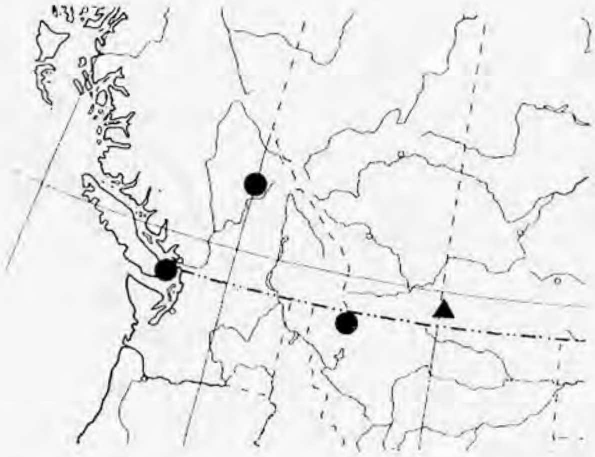


Fig. 19. Known North American distribution of *Bacidia auerswaldii* (dots) and *B. igniarii* (triangle).

1966, Brodo 7897a (CANL, COLO, WIS), + Vancouver Island, Mount Douglas Park, 1989, Ekman L779 (filed with *Bn. ramea*, LD). Mayne Island, 1980, Noble 7277 (herb. Noble). Salt Spring Island, 1989, Ekman L782, L784, L787, L789 (LD). – U. S. A. *California*. Humboldt Co., 1989, Ekman L659 (LD). Mendocino Co., 1989, Ekman L651 (LD), + 1982, Thiers 45648 (filed with *B. heterochroa*, SFSU). San Mateo Co., 1967, Jordan 818 (SFSU). Santa Cruz Mountains, 1885, probably collected by Herre (FH). *Maine*. Rockport, 1921, Merrill (FH). South Thomaston, 1910, Merrill (FH). *Massachusetts*. Dartmouth, 1888, Willey (US). Fairhaven, 1887, Willey (US). New Bedford, Willey (FH, US). *New York*. Suffolk Co., 1961, Brodo 3209 (MSC). *Oregon*. Benton Co., 1972, Pike 2777, 3117 (OSC), 1989, Ekman L638, L682, L683, L684, L686, L689, L696, L697, L702, L703 (LD), + 1989, Ekman L688, L691, L692, L701, L704 (filed with *Bn. ramea*, LD). Curry Co., 1989, Ekman L670, L674, L675 (LD), + 1989, Ekman L673 (filed with *B. salmonea*, LD). Lincoln Co., 1972, Denison (OSC), 1952, Weber S1140 (COLO). *Washington*. Clallam Co., 1989, Ekman L731 (LD), 1969, Brodo 15335 (CANL). Gray's Harbor Co., 1989, Ekman L718, L719 (LD). Pacific Co., 1989, Ekman L715, L716 (LD). Skagit Co., 1989, Ekman L734, L738 (LD). Whatcom Co., 1914, Herre (FH), 1980, 1982, Ryan (WWB), 1982, Rhoades (WWB), 1989, Ekman L740, L741, L742, L745, L749, L 750 (LD). + Jefferson Co., 1989, Ekman L727 (filed with *B. salmonea*, LD).

4. Bacidia auerswaldii (Hepp ex Stizenb.) Mig.

Kryptogamen-Flora 4 (2): 267 (1931). - *Bilimbia effusa* Auersw. ex Rabenh., Rabenhorst: Lich. Eur. exs. 32 (1855). - *Lecidea effusa* (Auersw. ex Rabenh.) Stizenb., Nova Acta Acad. Caesar. Leop. Carol. 34 (2): 23 (1867), nom. illeg., non (Pers. ex Hoffm.) Mudd 1861. - *Bacidia effusa* (Auersw. ex Rabenh.) Lettau, Hedwigia 52: 132 (1912), nom. illeg., non (Sm.) Trevisan 1856. - *Lecidea auerswaldii* Hepp ex Stizenb., Ber. Tät. St Gall. naturw. Ges. 1880/81: 416 (1882). - *Bacidia effusella* Zahlbr., Cat. Lich. Univ. 4: 110 (1926), nom. illeg. (superfluous). – Type: Germany, "Leipzig, an einer alten Ulme im Rosenthale, die Rinde mehre Ellen weit überziehend", 1855, Auerswald, Rabenhorst: Lich. Eur. exs. 32 (W, lectotype selected here).

Illustrations. Figs 6E, 19 (map), 40D.

Characterization. Thallus finely granular; granules 36-145 µm diam. Apothecia normally purple-brown to black, but often ± pigment deficient. Proper exciple laterally orange to black-brown. Hypothecium (almost) colourless. Upper part of hymenium orange to black-brown. Spores fusiform with blunt ends, 19-33 × 5.6-7.8 µm, with 3-9 septa.

Thallus indeterminate, thin, of discrete or contiguous, ± globose or irregular, often slightly flattened granules, pale grey, pale yellowish grey, pale green to green, or ± grey-green to brown-green. Granules (36-)63-72-82(-145) µm diam. (s= 22, N= 3, n= 10), without crystals in the cortex. Prothallus sometimes present between discrete granules, very thin, endophloeodal, pale grey.

Apothecia (0.3-)0.4-0.5-0.6(-1.1) mm diam. (s= 0.2, N= 2, n= 10), at first plane, remaining so or becoming moderately convex, epruinose. Disc brown-orange, orange-brown to red-brown to purple-brown to black, in some apothecia mottled with different colours. Margin in upper part concolorous with or slightly darker than disc, in lower part commonly distinctly paler, pale pink to orange-brown, distinct, raised above disc in young apothecia, later level with the disc, persistent.

Proper exciple laterally (43-)59(-74) µm wide (s= 15, N= 3, n= 1), without crystals. Rim pale orange to brown-orange to red-brown to black-brown in upper part, downwards gradually changing to colourless, along the edge with a single layer of enlarged cells with lumina that are up to 9 × 5 µm. Lateral interior ± concolorous with or slightly paler than rim. Medullary part colourless. Hypothecium colourless or very pale yellowish. Hymenium (74-)80-95-110(-114) µm thick (s= 13, N= 3, n= 5), colourless in lower part, pale orange to orange-brown to red-brown to black-brown in a distinct or diffuse layer in the upper part. Paraphyses 1.0-1.6 µm wide in mid-hymenium; apices ± clavate, (1.6-)2.6-3.0-3.2(-5.7) µm wide (s= 0.8, N= 3, n= 10), without internal pigment or wall with ± brown or grey-brown pigment. Spores fusiform with blunt ends, straight, not coiled in ascus, (19-)23-28-31(-33) µm long (s= 4, N= 3, n= 10), (5.6-)6.5-6.8-7.0(-7.8) µm wide (s= 0.6, N= 3, n= 10), (2.9-)3.6-4.1-4.4(-5.1) times as long as wide (s= 0.6, N= 3, n= 10), with (3-)5.7-6.1-6.4(-9) septa (s= 1.6, N= 3, n= 10).

Pycnidia not seen.

Chemistry: No lichen substances detected.

Pigments: Upper part of hymenium and proper exciple partly K+ intensifying and N+ intensifying, partly K+ purplish and N+ orange-red, or entirely K+ purplish and N+ orange-red. Hypothecium K+ intensifying, N+ intensifying. – Laurocerasi Brown and Rubella Orange in hymenium and proper exciple. Rubella Orange in hypothecium (small quantities).

Ecology. There is no uniform picture of the ecology of *B. auerswaldii*, since the habitats of the three finds are very different among themselves. One find was made on a large *Acer macrophyllum* on a roadside, where it occurred together with *Anisomeridum nyssaegenum*, *Bacidia circumspecta*, and *Strangospora ochrophora*. Another locality is on a *Populus trichocarpa* in a humid forest dominated by *Picea engelmannii*, *Thuja plicata*, and *Betula papyrifera*. No other lichens were present in the immediate vicinity, but "*Bacidia*" *carneoalbida* occurred abundantly lower down on the same trunk. In the third locality, *B. auerswaldii* was, according to the label, found on a *Thuja plicata* in a gorge with a creek at the bottom. In this collection, *B. auerswaldii* is accompanied by "*Bacidia*" *beckhausii* and *Biatoridium delitescens*.

Distribution. Known from one locality in northwestern Montana and two in British Columbia (one on Saltspring Island in the Strait of Georgia and one in Wells Gray Provincial Park). – Europe.

Discussion. *Bacidia auerswaldii* is easily recognized by the very wide, fusiform and blunt-ended spores. Under the microscope, it can hardly be confused with any other species. In its overall habit, it resembles *B. biatorina* and *B. rubella*.

The affinities of *B. auerswaldii* are clearly with *Bacidia* in the strictest sense, despite the shape of the spores. It is probably closely related to *B. biatorina*, with which it shares a similar apothecium pigmentation and the granular thallus.

Collections examined. CANADA. *British Columbia*. Saltspring Island, 1989, Ekman L788 (LD). Wells Gray Provincial Park, 1989, Ekman L796 (LD). – U. S. A. *Montana*. Flathead Co., 1991, McCune 19222 (LD, OSC).

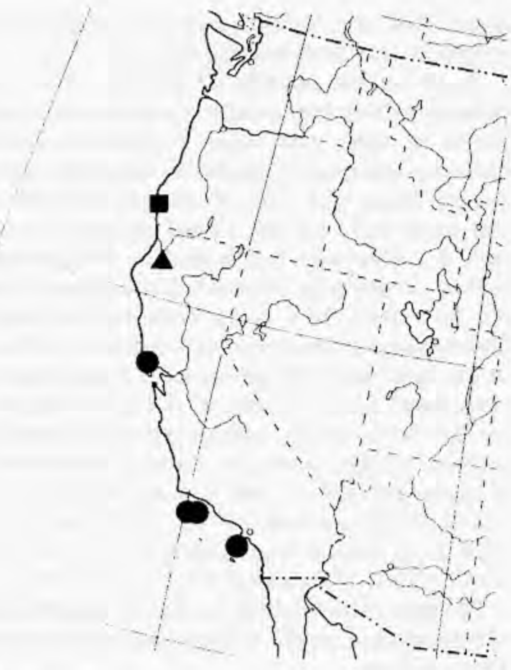


Fig. 20. Known North American distribution of *Bacidia biatorina* (triangle), *B. friesiana* (square), and *B. insularis* (dots).

5. Bacidia biatorina (Körb.) Vain.

Acta Soc. Fauna Flora fenn. 53 (1): 178 (1922). - *Rhaphiospora atrosanguinea* var. *biatorina* Körb., Parerga Lich., fasc. 3: 238 (1861). – Type: Germany, "Würtemberg", Kemmler (L-910205-1689, lectotype selected here).

Illustrations. Figs 20 (map), 40E.

Characterization. Thallus granular, without crystals in the cortex; granules 48-121 µm diam. Apothecia orange-brown to dark purplish brown. Proper exciple laterally orange-brown to dark red-brown. Hypothecium (almost) colourless. Upper part of hymenium brown-orange to red-brown, the latter pigment K+ purplish. Spores acicular, 42-57 × 2.1-2.9 µm, with 3-15 septa.

Thallus indeterminate, thin to rather thick, of discrete or contiguous, globose or irregular, often slightly flattened granules, green-grey. Granules (48-)85(-121) µm diam. (s= 16, N= 1, n= 20), without crystals in the cortex. Prothallus lacking.

Apothecia (0.4-)0.6(-0.9) mm diam. (s= 0.1, N= 1, n= 10), remaining plane, epruinose. Disc orange-brown to dark purplish brown, in many apothecia mottled with different hues. Margin concolorous with or slightly darker than disc, distinct, raised above disc in young apothecia, later level with the disc, persistent.

Proper exciple laterally 52 µm wide (N= 1, n= 1), without crystals. Rim usually orange-brown to dark red-brown in upper part (rarely colourless), downwards gradually changing to colourless, along the edge with a 1-2 cell layers thick zone of enlarged cells with lumina that are up to 12 × 6 µm. Lateral interior ± concolorous with rim. Medullary part colourless. Hypothecium colourless or very pale yellowish. Hymenium (83-)84(-87) µm thick (s=2, N=1, n=5), colourless in lower part, brown-orange to red-brown in a distinct or diffuse layer in the upper part. Paraphyses 0.8-1.6 µm wide in mid-hymenium; apices ± clavate, (1.6-)2.6(-4.0) µm wide (s= 0.8, N= 1, n= 20), without internal pigment. Spores acicular, straight, curved, or sigmoid, sometimes coiled in ascus, (42-)49(-57) µm long (s= 4, N= 1, n= 20), (2.1-)2.5(-2.9) µm wide (s= 0.2, N= 1, n= 20), (16.5-) 19.5(-23.0) times as long as wide (s= 1.8, N= 1, n= 20), with (3-)10.1(-15) septa (s= 3.6, N= 1, n= 20).

Pycnidia half-immersed in thallus, pale orange, 50-130 µm diam. Conidia filiform, curved, non-septate, 9-16 × c. 0.5 µm.

Chemistry: No lichen substances detected.

Pigments: Upper part of hymenium and proper exciple K+ intensifying and N+ intensifying, or K+ purplish and N+ orange-red to red. Hypothecium and inner parts of proper exciple K+ intensifying, N+ intensifying. – Laurocerasi Brown in hymenium, proper exciple, and pycnidial wall. Rubella Orange in hypothecium (very small quantities), hymenium, proper exciple, and pycnidial wall.

Ecology. In bark crevices of an old *Lithocarpus densiflorus* in a fairly open forest (dominated by *Quercus garryana* and *Pseudotsuga menziesii*) in a valley.

Distribution. Presently known from only one locality in the intermontane region of northern California. – Europe.

Discussion. *B. rubella* is very similar to *B. biatorina* in habit, but differs in having larger thallus granules with crystals in the cortex, and in always lacking the brownish, K+ purplish and N+ orange-red to red pigment, which is present in most or all of the apothecia of *B. biatorina*.

European specimens of *B. biatorina* usually have a yellowish or brownish green thallus and darker, purple-brown to black-brown apothecia with evenly coloured disks. However, the green-grey thallus and the partly brown-orange apothecia present in the Californian specimen are sometimes found also in European specimens. Furthermore, the Californian specimen appears to deviate from European *B. biatorina* in having a thinner apothecial margin.

Collections examined. U. S. A. *California*. Trinity Co., 1989, Ekman L661 (LD).

6. Bacidia campalea (Tuck.) S. Ekman & Kalb, comb. nov.

Lecanora campalea Tuck., Amer. Journ. Sci. Arts, ser. 2, 28: 205 (1859). - *Haematomma campaleum* (Tuck.) Zahlbr., Cat. Lich Univ. 5: 758 (1928). – Type: Cuba, 1857, Wright (FH-TUCK, lectotype selected here).

Lecidea subluteola Nyl., Flora, Jena 52: 122 (1869). - *Bacidia subluteola* (Nyl.) Zahlbr., Sber. Akad. Wiss. Wien 111 (1): 395 (1902). – Type: Brazil, 1867, Glaziou (H-NYL 17052b, lectotype selected here).

Bacidia variegata Zahlbr., Denksch. Akad. Wiss., Wien 83: 129 (1909). – Type: Brazil, "Prov. Sao Paulo. Prope Rio Grande ad Sao Paulo Railway, 800 m. s. m.", 1901, Schiffner (W, lectotype selected here).

Bacidia vergarensis Räsänen, Revta sudam. Bot. 7: 13 (1942). – Type: Uruguay, "Tr. y Tres, Vergara, corticola", 1932, Herter (H, lectotype selected here).

Illustrations. Figs 3A, 17 (map), 40F.

Characterization. Apothecia with pink to brown to almost black disc; margin paler. Proper exciple colourless to brown-orange to dark brown, in lower part with large clusters of crystals and in upper part with evenly dispersed, minute crystals; with cell lumina gradually enlarging towards the edge, or along the edge with a 6-8 cell layers thick zone of enlarged cell lumina. Hypothecium brown-orange to brown. Upper part of hymenium orange-brown to red-brown. Spores acicular, 41-71 × 2.5-3.7 µm, with 3-11 septa.

Thallus determinate, ± thin, continuous, ± cracked, wrinkled, or sometimes partly discontinuous and of discrete or contiguous, convex areoles; pale bluish grey. Prothallus sometimes bordering the thallus, narrow and black; sometimes present also between discrete areoles, thin, endophloeodal or epiphloeodal, pale grey.

Apothecia (0.5-)0.6-0.7-0.7(-0.9) mm diam. (s= 0.1, N= 3, n= 10), plane or moderately convex, when young or medium-aged usually slightly pruinose on disc and margin. Disc pink, pale orange, dirty brown, dark brown, purple-brown, dark brown-violet, purple-black, or brown-black. Margin paler than disc, ± pink, brown-pink, pale pink-brown, ± grey-violet, or pale to dark brown, lower part concolorous with or darker than upper part, raised above disc in young apothecia, soon level with the disc, persistent.

Proper exciple laterally (52-)60(-68) µm wide (s= 8, N= 3, n= 1), in lower part with large clusters of crystals (single crystals up to 8 µm in diam.) and at least in upper part usually with abundant and evenly dispersed minute crystals that are up to 1.5 µm in diam. Rim colourless or ± brown-orange to dark brown, often heavier pigmented in lower part than in upper part, with cell lumina gradually enlarging towards the edge, or along the edge with a ± distinct, 6-8 cell layers thick zone of enlarged cells with lumina that are up to 12 × 6 µm. Lateral interior colourless, or brown-orange close to the hymenium. Medullary part colourless to pale yellow. Hypothecium brown-orange to brown. Hymenium (78-)84-98-105(-112) µm thick (s= 11, N= 3, n= 5), lower part colourless, uppermost part diffusely and unevenly orange-brown to red-brown, with a thin layer of crystals above the apices of the paraphyses. Paraphyses 0.5-1.0 µm wide in mid-hymenium; apices not at all swollen or narrowly clavate, (0.8-)1.3-1.3-1.4(-2.0) µm wide (s= 0.3, N= 3, n= 10), without internal pigment. Spores acicular, straight or slightly curved, straight or slightly coiled in ascus, (41-)52-53-55(-71) µm long (s= 6, N= 3, n= 10), (2.5-)3.2-3.3-3.5(-3.7) µm wide (s= 0.3, N= 3, n= 10), (12.3-)15.3-16.0-17.1(-22.8) times as long as wide (s= 2.3, N= 3, n= 10), with (3-)6.6-7.5-8.0(-11) septa (s= 1.5, N= 3, n= 10).

Pycnidia not seen.

Chemistry: Atranorin and zeorin.

Pigments: Pigmented parts of apothecia mainly K+ intensifying, N-, but in parts K+ purplish, N+ orange-red. – Rubella Orange in proper exciple, hypothecium, and hymenium. Laurocerasi Brown in hypothecium and hymenium (small quantities).

Ecology. Both localities are swamp fringes along roads, where *B. campalea* is growing on the illuminated trees closest to the road. It has been found on *Acer rubrum*, *Annona glabra*, *Piscidia piscipula*, and *Salix caroliniana*.

Distribution. Presently known from only two localities in Collier County in southernmost Florida. – Probably widespread in the neotropics, and extending into subtropical areas on both sides of the tropical belt.

Discussion. *B. campalea* is closely related to *B. suffusa*, *B. fusconigrescens* (Nyl.) Zahlbr., and *B. millegrana* (Taylor) Zahlbr. *B. suffusa* can be separated from *B. campalea* by the lack of a bluish tinge of the thallus, the lack of minute crystals in the proper exciple (although clusters of large crystals may be present), the narrower zone of enlarged cells along the edge of the proper exciple, and by the thicker paraphysis apices. *B. fusconigrescens*, which is presently known only from tropical America and Asia, differs in having a proper exciple with abundant minute crystals but no clusters of large crystals, in having a thin but distinct, pigmented zone along the edge of the proper exciple, in having a K+ purplish pigment (Laurocerasi Brown) dominating the upper part of the hymenium, and in having wider paraphysis apices (min-max 1.6-2.8 µm). *B. millegrana*, which probably is a pantropical species, differs in having a distinctly yellowish thallus with bullate areoles, a very distinct, two cell layers thick zone of enlarged cells along the edge of the proper exciple, and in lacking crystals in the proper exciple. *B. russeola* is rather similar to *B. campalea*, and both species share the very wide zone of enlarged cells along the edge of the proper exciple. *B. russeola* is, however, easily separated by the differently coloured apothecia, the lack of minute crystals in the proper exciple, and (usually) by the presence of a K+ purplish pigment in the proper exciple and hymenium. Furthermore, *B. heterochroa* may occasionally be mistaken for *B. campalea*. The former can be separated by the distinct, brown cap of pigment in the wall of the paraphysis apices and by the complete lack of a very wide zone of enlarged cells along the edge of the proper exciple.

The types of *Bacidia subluteola* (Nyl.) Zahlbr., *B. variegata* Zahlbr., and *B. vergarensis* Räsänen are typical, well-developed specimens of *B. campalea*, and they are hence reduced here into synonymy.

Collections examined. U. S. A. *Florida*. Collier Co., 1985, Thor 4645 (S), 1993, Ekman L1176, L1177, L1178, L1179, L1180, L1202 (LD).

7. Bacidia circumspecta (Nyl. ex Vain.) Malme

Bot. Notiser 1895: 140 (1895). - *Lecidea bacillifera* f. *circumspecta* Nyl., nom. nudum, Norrlin & Nyl: Herb. Lich. Fenn. 185 (1875). - *Lecidea bacillifera* var. *circumspecta* Nyl. ex Vain., Meddn Soc. Fauna Flora fenn. 10: 22 (1883). - *Lecidea circumspecta* (Nyl. ex Vain.) Hedl., Bih. K. svenska VetenskAkad. Handl. 18, 3 (3): 71 (1892). – Type: Finland, "Tavastia australis, Lammi, Evo, supra corticem salicis", 1874, Norrlin, Norrlin & Nyl: Herb. Lich. Fenn. 185 (H, lectotype selected here).

Illustrations. Figs 6C-D, 8E-F, 21 (map), 40G.

Characterization. Apothecia usually black, flat. Proper exciple with green and brown (sometimes almost black) pigmentation, mainly consisting of distinctly radiating hyphae. Hypothecium colourless to brown-orange. Upper part of hymenium greenish, sometimes also with some purplish brown pigmentation. Spores bacilliform to clavate, 11-45 × 1.6-3.7 µm, with 3-7 septa.

Thallus indeterminate, thin to rather thick, either discontinuous, of discrete or partly contiguous, convex, sometimes subsquamulose areoles, or continuous, wart-

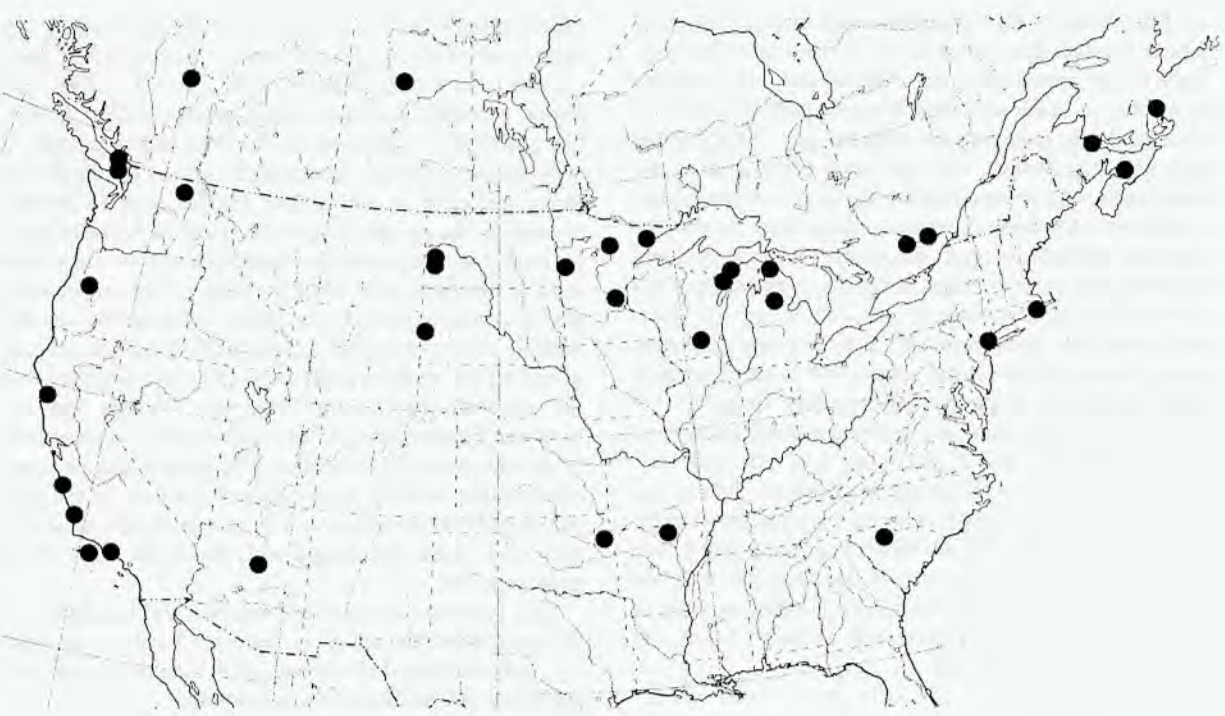


Fig. 21. Known North American distribution of *Bacidia circumspecta*.

ed or sometimes smooth, ± rimose or without cracks; light grey to grey to yellow-grey to green-grey to grey-green to green-brown to grey-brown. Prothallus lacking or present between discrete areoles, white, thin, endosubstratal.

Apothecia (0.2-)0.3-0.4-0.7(-0.8) mm diam. (s= 0.1, N= 16, n= 5), ± plane, remaining so or becoming moderately convex or rarely markedly convex, epruinose, low and flat, 2.1-4.0 times as wide as high. Disc usually pure black, seldom partially or entirely blue-black, blue-grey or dirty yellow. Margin concolorous with, or rarely slightly paler or darker than disc, often glossy, distinct, raised above disc in young apothecia, later level with the disc, persistent or only rarely excluded.

Proper exciple laterally (19-)46(-69) µm wide (s= 13, N= 16, n= 1), without crystals, almost entirely formed by regularly radiating hyphae with 0.8-3.5 µm wide lumina (except for the innermost part of the exciple, flanking the hypothecium, which consists of a few, 0.8-3.0 µm wide, sparsely branched hyphae that are not clearly directed towards the rim). Rim grey-green to blue-green to ± brown to black, rarely colourless or pale green, in upper part, downwards usually gradually changing to colourless or ± brown, along the edge with a single cell layer of enlarged cells with lumina that are up to 8 × 7 µm. Lateral interior usually paler than rim, or sometimes concolorous with or (predominantly in lower part of the exciple) darker than rim. Medullary part usually paler than hypothecium and lateral interior, colourless or rarely pale brown or brown-orange. Hypothecium colourless or sometimes pale yellow to brown-orange, rarely pale to medium brown. Hymenium (43-)47-61-73(-78) µm thick (s= 9, N= 16, n= 5), lower part colourless except for occasional vertical streaks with green to blue-green pigment, upper part dirty green to blue-green or partly purplish brown, indistinctly or distinctly delimited. Paraphyses 0.8-1.6 µm wide in mid-hymenium; apices ± clavate or a few only slightly or not at all swollen, (1.2-) 1.7-3.1-4.1(-6.5) µm wide (s= 1.0, N= 16, n= 5), without internal pigment but with an external cap of green or brown pigment. Spores bacilliform to clavate, straight or slightly curved, not coiled in ascus, (11-)12-24-37(-45) µm long (s= 7, N= 16, n= 10), (1.6-)1.7-2.4-3.2(-3.7) µm wide (s= 0.4, N= 16, n= 10), (5.0-) 6.0-10.2-15.8(-20.0) times as long as wide (s= 3.4, N= 16, n= 10), with (3-)3.0-3.9-6.8(-7) septa (s= 1.4, N= 16, n= 10).

Pycnidia common but not present in all specimens, sessile or half-immersed in thallus, uppermost part of wall concolorous with apothecia, 75-300 µm diam. Conidia of three types (never more than one type in a thallus): (1) oblong to fusiform to bacilliform, 0-1-

septate, 7-12 × 1.2-1.9 µm, (2) filiform, curved, nonseptate, 8-19 × 0.5-0.8(-1.0) µm, and (3) falcate, 0-1-septate, 6-25 × 1.2-1.6 µm.

Chemistry: No lichen substances detected.

Pigments: Upper part of hymenium K- and N+ purple (with or without a precipitate of blue crystals), or partly K+ purplish, N+ orange-red. Proper exciple K+ purplish, N+ purplish. Hypothecium K+ intensifying or very rarely K+ purplish. – Bacidia Green in hymenium, proper exciple, and pycnidial wall. Laurocerasi Brown in proper exciple, paraphysis apices, pycnidial wall, and very rarely hypothecium. Rubella Orange occasionally in hypothecium.

Ecology. *Bacidia circumspecta* is found in a wide variety of habitats, from exposed and dry to to shady and humid ones. It has been collected on *Acer grandidentata*, *A. macrophyllum*, *Betula alleghaniensis*, *Fraxinus* spp., *Malacothamnus fasciculatus*, *Picea glauca*, *Platanus occidentalis*, *Populus grandidentata*, *P. tremuloides*, *Quercus agrifolia*, *Q. garryana*, *Q. macrocarpa*, *Q. rubra*, *Thuja occidentalis*, *T. plicata*, *Ulmus americana*, and rarely on lignum (stumps, fenceposts).

Distribution. Probably more or less Panamerican, but apparently avoiding northern Canada, the extreme Southeast, and high altitudes in the Rocky Mountains and the Appalachians. – Europe.

Discussion. *Bacidia circumspecta* is similar to *B. igniarii*, *B. reagens*, *B. schweinitzii*, and *B. subincompta*. The distinction of *B. igniarii* from *B. circumspecta* is discussed under the former species. *B. subincompta* can be separated by the longer spores, the K+ purplish hypothecium, the margin that becomes excluded in old apothecia, and (often) on the distinctly granular thallus. In *B. schweinitzii*, the hypothecium is brown, and the spores acicular. *B. reagens* has a K+ purple to violet and C+ violet upper hymenium.

The main part of North American *B. circumspecta* agrees completely with European representatives. The range of variation in hymenium height, spore size, spore shape, apothecium pigmentation, and conidial appearance, however, is much larger in North America than in Europe. In European material, I have not observed forms with a brown or brown-orange hypothecium, clavate spores, or conidial types other than the oblong to fusiform to bacilliform. Since the different conidial types never seem to occur on the same thallus, and not even at the same locality, I have considered the possibility that North American *B. circumspecta* in the present sense should be split into two or more species. The variation in conidial type, however, is apparently not correlated with any other character, and thus I interpret *B. circumspecta* as one single, variable species.

Part of the North American variation within *B. circumspecta* approaches *B. subcircumspecta* Coppins, described from Scotland (Coppins et al. 1992). *B. subcircumspecta* was separated from *B. circumspecta* by the filiform, curved conidia (instead of oblong conidia), the dominance of a purplish pigment (Laurocerasi Brown?) in the hymenium (instead of Bacidia Green), the lower hymenium (30-35 µm instead of 45-55 µm), the different habitat requirement (hard lignum instead of tree-trunks). Some North American specimens of *B. circumspecta* combine curved conidia with having an abundance of purplish brown paraphysis apices (mixed with green ones), although the exact combination of characters in *B. subcircumspecta* is not found. Furthermore, some North American specimens are lignicolous. The distinction between *B. subcircumspecta* and the most extreme of North American *B. circumspecta* is fairly subtle, however, and had *B. subcircumspecta* occurred in North America, I am sure it would have been perceived as the extreme end of a continuous variation within *B. circumspecta*. Nevertheless, I think it is correct to treat *B. subcircumspecta* as a separate species. It is so far known only from Scotland, where it is sympatric with *B. circumspecta* from which it remains morphologically and ecologically distinct. Possibly, *B. subcircumspecta* has evolved through a founder effect following the long-distance dispersal of an ancestor of *B. circumspecta* with an extreme character combination from eastern North America to the British Isles.

Collections examined. CANADA. *British Columbia*. Gabriola Island, 1974, Noble 3008 (herb. Noble). Vancouver Island, William Head, 1975, Noble 4594B (herb. Noble), 1989, Ekman L766 (LD). Vancouver Island, Mount Douglas, 1991, M. Ryan (herb. M. Ryan). Wells Gray Prov. Park, 1994, McCune 21862 OSC). *New Brunswick*. Kent Co., 1978, Egger 683b (CANL). *Nova Scotia*. Victoria Co., 1989, Ekman L1069 (LD). Hants Co., 1989, Ekman L1037 (LD). *Ontario*. Renfrew Co., 1985, Wong 3809 (CANL). *Quebec*. Gatineau Co., 1989, Ekman L1025 (LD). *Saskatchewan*. Prince Albert Nat. Park, 1969, Jesberger 1150 WIS). – U. S. A. *Arizona*. Coconino Co., 1974, Brodo 20306a (CANL). *Arkansas*. Izard Co., 1988, Harris 21649a, 21653a (NY). *California*. Santa Monica Range, 1894, 1903, Hasse (US). Mendocino Co., 1989, Ekman L790 (LD). Monterey Co., 1989, Ekman L1219 (LD). San Luis Obispo Co., 1900, Barker (NY). Santa Barbara Co., 1989, Ekman L633, L634 (LD). *Massachusetts*. New Bedford (FH). *Michigan*. Cheboygan Co., 1974, Harris (NY). Delta Co., 1976, Harris 11946a (CANL, MICH), 1969, Harris 4034 (MIN, MSC). Menominee Co., 1965, Harris 752b (MSC). Roscommon Co., 1974, Wang 635 (MSC). *Minnesota*. Anoka Co., 1980, Trana 10096 (MIN). Itasca Co., 1977, Trana 2973 (MIN). Lake Co., 1989, Ekman L944 (LD). Otter Tail Co., 1900, Fink 3 (MIN). *New*

Fig. 22. Known world distribution of *Bacidia diffracta*.

York. Bronx Co., 1988, Buck (NY). *North Dakota*. Billings Co., 1982, Wetmore 45454a (MIN). McKenzie Co., 1982, Wetmore 44658 (MIN). *Oklahoma*. Cherokee Co., 1988, Harris 21362 (NY). *Oregon*. Linn Co., 1970, Pike 1368 (OSC). *South Carolina*. Chester, Green (NY). *South Dakota*. + Lawrence Co., 1960, Anderson (filed with *B. vermifera*, COLO). *Washington*. Republic, 1913, Foster (FH). *Wisconsin*. Dane Co., 1976, Thomson 18823 (CANL, MIN).

8. Bacidia diffracta S. Ekman, sp. nov.

Type: Canada, Nova Scotia, Queens Co., Kejimkujik Nat. Park, E side of Kejimkujik Lake, c. 700 m SE of the N end of Peter Point, on *Fagus grandifolia*, alt c. 100 m, 1989, Ekman L1050 (LD, holotype; CANL, isotype).

A simili *Bacidia polychroa* differt thallo granuloso, apotheciis altioribus (proportione altitudinis hymenii cum ea apothecii minori), apicibus paraphysorum angustioribus.

Etymology. *Diffractus*, broken in pieces.

Illustrations. Figs 22 (map), 40H, 43F.

Characterization. Thallus granular; granules 36-97 µm diam. Apothecia brown-orange to red-brown to dark purplish brown, at least some pruinose. Proper exciple ± brown-orange to orange-brown. Hypothecium darker than proper exciple. Upper part of hymenium colourless to orange-brown. Most pigmented parts K+ purple-red. Spores acicular, 32-69 × 1.9-4.1 µm, with 3-11 septa.

Thallus indeterminate, thin to rather thick, continuous or ± discontinuous, finely granular, pale grey, pale greenish grey, yellowish grey, greenish grey, greyish green, or grey. Granules (36-)56-67-82(-97) µm diam. (s= 16, N= 13, n=5), ± globose or irregular in shape.

Prothallus lacking or present between discrete granules, endosubstratal, white to pale grey.

Apothecia (0.5-)0.5-0.8-0.9(-1.1) mm diam. (s= 0.2, N= 13, n= 5), ± plane when young, later becoming convex, with thin to thick white pruina on edge and/or disc of at least some apothecia apothecia (mainly young and medium-aged ones). Disc brown-orange to dark orange-brown, brown, or red-brown to dark purplish brown, often darkening as the apothecia age. Margin concolorous with disc, level with or raised above disc in young apothecia, later level with the disc, and finally excluded in old and convex apothecia.

Proper exciple laterally (52-)64(-103) µm wide (s= 14, N= 13, n= 1), usually with radiating clusters of minute crystals (up to 1 µm). Rim pale brown-orange to orange-brown, without a layer of enlarged cells along the edge. Lateral interior usually ± concolorous with rim or sometimes paler. Medullary part concolorous with lateral interior part or paler, almost colourless to pale brownish orange or pale orange. Hypothecium pale brown-orange to brown-orange to orange brown, darker than exciple (pigmentation distinctly or indistinctly delimited). Hymenium (68-)70-82-91(-97) µm thick (s= 7, N= 13, n= 5), constituting (12-)19(-24) % of the entire height of the apothecium (s= 3, N= 13, n= 1), without distinct epithecium, colourless to pale brown-orange to pale brown in lower part, upper part concolorous or slightly darker, pale brown-orange to orange-brown, often with darker pigmented, pale brown-orange to orange-brown vertical streaks. Paraphyses 1.2-1.6 µm wide in mid-hymenium; apices ± clavate or not at all swollen, (1.2-) 1.6-2.0-2.6(-3.1) µm wide (s= 0.5, N= 13, n= 5), without internal pigment. Spores acicular, straight, curved, or sigmoid, sometimes coiled in ascus, (32-) 37-45-54(-69) µm long (s= 7.4, N= 13, n= 10), (1.9-) 2.6-2.9-3.2(-4.1) µm wide (s= 0.4, N= 13, n= 10), (8.7-)12.4-15.8-19.3(-26.5) times as long as wide (s= 3.5, N= 13, n= 10), with (3-)4.1-6.2-7.8(-11) septa (s= 1.7, N= 13, n= 10).

Pycnidia ± immersed in thallus or prothallus, pale orange-brown to brown-orange above, 150 µm diam. Conidia curved, non-septate, 10-15 × 0.5-0.6 µm.

Chemistry: Atranorin (sometimes only as a trace), rarely with a trace of zeorin.

Pigments: Brown parts of apothecia K+ purple-red, N-. – Bacidia Brown and Rubella Orange in hymenium, hypothecium, proper exciple, and pycnidial wall.

Ecology. On tree trunks, preferrably old ones with coarse bark, in shady and humid habitats. Known phorophytes include *Acer saccharum*, *Fagus grandifolia*, *Fraxinus* spp., *Liquidambar styraciflua*, *Populus tremuloides*, *Quercus alba*, *Thuja occidentalis*, and *Ulmus americana*.

Distribution. More or less eastern, but with a preference for the Great Lakes, Appalachian, and Ozark Plateau regions. – Endemic.

Discussion. *Bacidia diffracta* is similar to *B. rubella* and *B. polychroa*. *B. rubella* can be separated from *B. diffracta* on account of the coarser thallus granules and the lack of a K+ purple-red pigment (Bacidia Brown) in the apothecia. *B. polychroa* is obviously the closest relative of *B. diffracta*. They can be readily separated by the structure of the thallus: *B. diffracta* is finely granular, whereas *B. polychroa* has an entire, ± wrinkled or warted thallus. Apart from this diagnostic difference, there are statistically significant differences in apothecium height, proportion of hymenium to apothecium height, and in paraphysis width. This case is treated in more detail in the chapter *Numerical and statistical treatment*.

Four collections from Florida (all probably from the same locality) deviate in having extremely high and wide apothecia, and in having a thallus that is partly smooth. They are tentatively referred to *B. diffracta*, and a recognition at infraspecific level may be justified. See also the chapter *Numerical and statistical treatment*. The deviating collections have not been included in the description above. They are specified in the collection list below.

Additional specimens examined. CANADA. *Nova Scotia*. Queens Co., 1989, Ekman L1051, L1056, L1057 (LD). *Ontario*. Hastings Co.,1989, Buck 17544 (NY). Renfrew Co., 1985, Wong 3817 (CANL). Thunder Bay District, 4 km SE of Dorion, 1985, Garton 23215 (CANL). – U. S. A. *Arkansas*. Newton Co., 1979, Brodo 23480 (CANL). Stone Co., 1988, Harris 21592 (NY). *Florida* (deviating specimens, see discussion). Monroe, 1908, Rapp 25-XV (FH), 1908, Rapp (US). Sanford, 1908, Rapp XV.6. (FH), 1924, Rapp 47 (FH). *Illinois*. Athens, 1878, Hall (MIN). *Louisiana*. Sabine Par., 1970, Tucker 8883 (herb. Tucker). *Iowa*. + Fayette Co., 1894, Fink (filed with *B. rubella*, NY). *Kentucky*. + Jessamine Co., 1951, Prescott 87 (filed with *B. polychroa*, US). *Massachusetts*. Acushnet, 1895, 1896, Willey (US). Middlesex Co., Tuckerman (NY). New Bedford, Willey (MIN, US), 1890's, Willey (US). *Michigan*. Cheboygan Co., 1977, Brodo 22475 (CANL). Gogebic Co., 1989, Ekman L986 (LD). *Minnesota*. Clearwater Co., 1975, Buck B402 (CANL). Itasca Co., 1977, Trana 3034 (MIN, NY), 1977, Trana 3132 (MIN). Mahnomen Co., 1976, Wetmore 26401 (COLO, MIN), 1976, Wetmore 26437 (MIN). Pennington Co., 1900, Fink 783 (MIN). + Polk Co., 1976, Wetmore 26468 (filed with *B. rubella*, MIN). Roseau Co., 1901, Fink 264 (MIN). St. Louis Co., 1978, Wetmore 31786, 33709 (MIN), + 1979, Wetmore 39573 (filed with *B. rubella*, NY). *Mis-*

souri. + Oregon Co., 1988, Harris 21713a (filed with *B. polychroa*, NY). *North Carolina*. + Swain Co., 1976, Harris 11009 (filed with *B. polychroa*, NY). *Pennsylvania*. Bushkill Falls, 1937 (NY) Pike Co., 1940, Thomson 2150 (UPS). *Tennessee*. Carter Co., 1985, Harris 18334 (NY). *Vermont*. Monkton, 1879, Farlow (NY).

9. Bacidia friesiana (Hepp) Körb.

Parerga Lich., fasc 2: 133 (1860). - *Biatora friesiana* Hepp, Flechten Europas 288 (1857). – Type: Switzerland, probably near Zürich, Hepp (BM-22207b, lectotype selected here).

Illustrations. Figs 20 (map), 41A.

Characterization. Apothecia green-blue to almost black, or partly or entirely yellowish. Proper exciple ± grey-green in the rim, otherwise pale, without crystals. Hypothecium (almost) colourless. Upper part of hymenium colourless to blue-green. Spores acicular, 31-38 × 2.5-3.7 µm, with 7-9 septa.

Thallus indeterminate, very thin, discontinuous, of discrete or contiguous, almost granular areoles, pale grey to pale brown-grey. Areoles when ± discrete (24-)53(-85) large (s= 17, N= 1, n= 20). Prothallus often present between discrete areoles, very thin, endophloeodal, pale grey.

Apothecia (0.1-)0.2(-0.2) mm diam. (s= 0.04, N= 1, n= 20), at first plane, later becoming convex, epruinose. Disc green-blue, grey-blue, blue-black, or pale dirty brown-yellow, often mottled with different colours. Margin concolorous with or paler than disc, blue-grey, brown-grey, green-blue, grey-blue, blue-black, or pale dirty brown-yellow, like the disc often mottled with different colours, raised above disc in young apothecia, soon level with the disc, finally excluded.

Proper exciple laterally 53 µm wide (N= 1, n= 1), without crystals. Rim grey-green, downwards fading to pale grey-green, along the edge without or with a single cell layer of enlarged cells with lumina that are up to 4 × 4 µm. Lateral interior colourless. Medullary part colourless to pale blue-green. Hypothecium colourless to pale blue-green. Hymenium (38-)47(-55) µm thick (s= 6, N= 1, n= 7), lower part colourless to pale blue-green, uppermost part colourless to blue-green. Paraphyses c. 1.5 µm wide in mid-hymenium; apices usually ± clavate, sometimes weakly or not at all swollen, (1.6-)2.3(-3.2) µm wide (s= 0.5, N= 1, n= 20), without internal pigment. Spores acicular, straight, curved, or sigmoid, not coiled in ascus, (31-)34(-38) µm long (s= 2, N= 1, n= 20), (2.5-)3.1(-3.7) µm wide (s= 0.3, N= 1, n= 20), (8.3-)10.8(-13.5) times as long as wide (s= 1.3, N= 1, n= 20), with (7-)7.2(-9) septa (s= 0.6, N= 1, n= 20).

Pycnidia not seen.

Chemistry: Not investigated due to sparsity of material.

Pigments: Upper part of hymenium and proper exciple mainly K- and N+ purple (without a precipitate of small blue crystals). Proper exciple partly K+ purplish, N+ orange-red.– Bacidia Green in hymenium, rim of proper exciple, and sometimes also in small amounts in the hypothecium and the medullary part of the proper exciple. Laurocerasi Brown in the rim of the proper exciple, and sometimes in small amounts in the upper part of the hymenium.

Ecology. On branches of a *Salix* sp, which formed a scrub in an otherwise open, boggy area along a river, near its outlet in the sea.

Distribution. Known from only one locality on the coast of southwestern Oregon. Previous records from North America are erroneous. They are based on an undescribed species of *Scoliciosporum* from the coast of British Columbia. – Europe.

Discussion. *Bacidia absistens* is similar to *B. friesiana*, but differs in having crystals in the inner of the proper exciple, longer spores, a thicker hymenium, and in having a brown pigment (Laurocerasi Brown) in the lateral interior of the proper exciple.

Collections examined. U. S. A. *Oregon*. Curry Co., 1989, Ekman L1218 (LD).

10. Bacidia helicospora S. Ekman, sp. nov.

Type: U. S. A., "Tennessee, Henderson Co., on hardwoods in mixed pine-hardwood forest (*Cornus*, *Liquidambar*, *Pinus echinata*) along road to Greener Cemetary, 1 mi. S of US 40, 8 mi. E of intersection with State 32, near Natchez Trace State Park", 1973, Tucker 11128b (herb. S. Tucker, holotype).

A simili *Bacidia laurocerasi* differt sporis firme conglutinatis et inter se contortis, pigmentoque epithecii in matricem gelatinosam circa ascos contracto. Etiam *B. heterochroae* similis quae pigmentum cinereo-fuscum in apicibus paraphysorum et sporas non conglutinatas habet.

Etymology. *Helico*-, spirally twisted, and *sporus*, spore.

Illustrations. Figs 7, 23 (map), 41B, 43G.

Characterization. Apothecia purple-brown to black. Proper exciple red-brown to black-brown in the rim, otherwise colourless to orange-brown. Hypothecium ± pale yellow to pale orange-brown. Upper part of hymenium ± brown, pigment accumulated around the upper part of the asci. Spores acicular, helical and tightly coiled, 33-81 × 2.1-3.7 µm, with 7-19 septa.

Thallus indeterminate or determinate, thin, usually continuous, smooth, wrinkled, or rarely warted, without cracks or ± cracked, rarely discontinuous, of ± discrete, thin areoles, light grey to greenish or yellowish grey. Prothallus sometimes present as a thin, black line along the edge of the thallus.

Apothecia (0.4-)0.4-0.6-0.7(-1.0) mm diam. (s= 0.1, N= 7, n= 5), plane or slightly convex, epruinose. Disc purple-brown to purplish black or pure black, sometimes mottled with orange-brown or beige (particularly in young apothecia). Margin concolorous with disc or darker, purple-brown to black, in the lower part sometimes paler, ± brownish, distinct, raised above disc in young apothecia, soon level with the disc, persistent.

Proper exciple laterally (43-)59(-70) µm wide (s= 10, N= 7, n= 1), without crystals. Rim red-brown to black-brown in a thin distinct zone, only rarely downwards gradually changing to pale brown, along the edge with a 1-2 cell layers thick zone of enlarged cells with lumina up to 8 × 5 µm. Lateral interior paler than rim, colourless to yellowish to brown-orange to orange-brown or partly mottled with red-brown. Medullary part concolorous with or paler than hypothecium and lateral interior, colorless to pale orange-brown. Hypothecium very pale yellow to pale orange-brown. Hymenium (74-)76-90-103(-105) µm thick (s= 9, N= 7, n= 5), lower part colourless except for the brown-pigmented gelatinous matrix surrounding the young asci, uppermost part brown to black-brown, unevenly pigmented due to the accumulation of pigment to the upper part of the asci. Paraphyses 0.8-1.6 µm wide in mid-hymenium; apices usually not at all or only slightly swollen, but sometimes narrowly clavate, (1.0-)1.3-1.6-1.8(-2.8) µm wide (s= 0.4, N= 8, n= 5), diffusely surrounded by brown pigment, mainly near ascus apices. Spores acicular, helical, strongly conglutinated and coiled in packages of 8, often very difficult to separate even when squashed in K, (33-)50-56-64(-81) µm long (s= 9, N= 20, n= 5), (2.1-)2.6-2.8-3.1(-3.7) µm wide (s= 0.3, N= 5, n= 10), (11.7-)18.0-20.6-22.9(-28.3) times as long as wide (s= 3.7, N= 5, n= 10), with (7-)7.8-12.8-14.8(-19) septa (s= 3.0, N= 5, n= 10).

Pycnidia not seen.

Chemistry: No lichen substances detected.

Pigments: Upper part of hymenium and rim of proper exciple K+ purplish, N+ orange-red to red. Hypothecium and inner parts of proper exciple K+ slightly intensifying, N-. – Laurocerasi Brown in hymenium and rim of proper exciple. Rubella Orange in hypothecium and inner part of proper exciple.

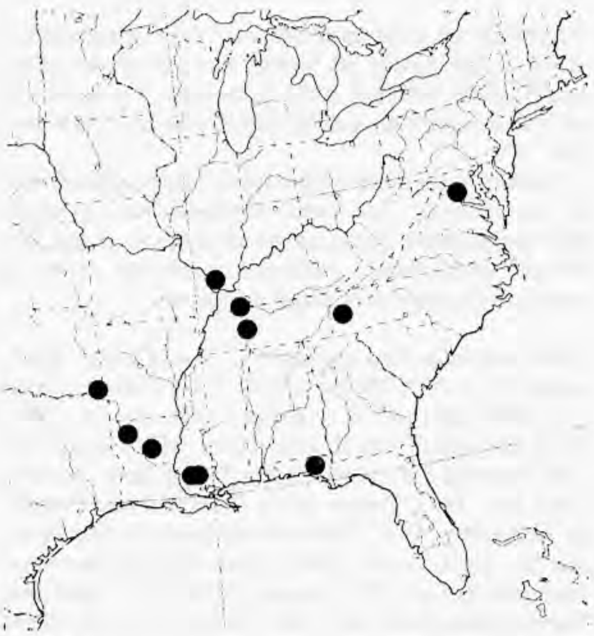


Fig. 23. Known world distribution of *Bacidia helicospora*.

Ecology. On tree trunks, preferrably in shady and humid habitats. Unfortunately, the labels of the majority of the specimens lack phorophyte data. Known phorophytes, however, include *Carpinus caroliniana* and *Liquidambar styraciflua*.

Distribution. Known from Maryland, South Carolina, Tennessee, the Florida Panhandle, Louisiana, southeastern Oklahoma, and southern Illinois. All localities except one are situated at low elevations (all below 180, most of them even below 100 m) in the Coastal Plain or in the valleys of Mississippi and Tennessee Rivers. A single find was made at about 400 m above sea level in the valley of Little Tennessee River near the south border of Great Smoky Mountain National Park. – Endemic.

Discussion. *Bacidia helicospora* is very similar in habit and pigmentation to *B. laurocerasi*, and the spores of the latter may even be helically arranged in young asci. However, the spores of *B. laurocerasi* are easily separated at maturity, and they are never released in packages like in *B. helicospora*. The upper part of the hymenium of *B. laurocerasi* is evenly pigmented, whereas the epithecial pigmentation of *B. helicospora* is concentrated to the gelatinous matrix surrounding the asci and the paraphyses adjacent to the asci. Very young apothecia of *B. helicospora* yet lacking asci are sometimes almost pigment deficient in the hymenium. The apothecia of *B. helicospora* are usually flatter than in *B. laurocerasi*.

Bacidia helicospora is also likely to be confused with *B. heterochroa*. The latter however, has distinctly brown-pigmented apices of the paraphyses, spores that are not conglutinated (although sometimes coiled in young asci), and wider paraphysis apices.

Additional collections examined. U. S. A. *Florida*. Washington Co., 1993, Ekman L1140 (LD). *Illinois*. Union Co., 1878, Earle (NY). *Kentucky*. + Calloway Co., 1975, Buck B34 (filed with *B. schweinitzii*, MIN). *Louisiana*. East Feliciana Par., 1969, Tucker 7833B (herb. Tucker). Grant Par., 1973, Tucker 11315 & Jones (herb. Tucker). St. Helena Par., 1972, Tucker 10149 (herb. Tucker). Webster Par., 1973, Tucker 11440B (herb. Tucker). *Maryland*. Montgomery Co., 1933, Leonard 2202 (US). *Oklahoma*. Beavers Bend State Park, 1946, Chester 4413 (US). *South Carolina*. Ravenel 143 (US). *Tennessee*. Blount Co., 1956, Sierk & Sharp 32 (US).

11. Bacidia heterochroa (Müll. Arg.) Zahlbr.

Cat. Lich. Univ. 4: 204 (1926). - *Patellaria heterochroa* Müll. Arg., Flora, Jena 63: 280 (1880). – Type: Argentina, "Buenos Ayres, auf *Excaecaria biglandulosa*", 1880, Schnyder (G, lectotype selected here).

Patellaria subpellucida Müll. Arg., Flora, Jena 64: 522 (1881). - *Bacidia subpellucida* (Müll. Arg.) Darb., Wiss. Ergebn. schwedish. Südpolarexpedit. 4 (11): 49 (1912). – Type: Argentina, "Insula de Becreo in Argentinium", 1881, Schnyder (G, lectotype selected here).

Patellaria atlantica Müll. Arg., Bot. Jb. 5: 137 (1884). - *Bacidia atlantica* (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 4: 178 (1926). – Type: Atlantic Islands, "Ascension, in ramulis", 1883, Naumann 42 (G, lectotype selected here).

Bacidia alutacea sensu Malme, Ark. Bot. 27A (5): 17 (1935), non (Krempelh.) Zahlbr.

Nomenclature. The name *Bacidia alutacea* was used for this species by Malme (1935), and his use has been followed by some authors. The type of that name, however, is a quite different species of *Bacidia* s. str. *Bacidia heterochroa* is the only species of *Bacidia* I know of, which has been collected in all continents of the world. Thus, there is a risk that an older name will be found.

Illustrations. Figs 5B, 6B, 24 (map), 41C.

Characterization. Apothecia usually mainly purple-brown to black but often mottled with various pink, orange, brown, or violet hues. Proper exciple brown or red-brown in the rim, otherwise colourless to orange-brown. Hypothecium colourless or pale yellow. Upper part of hymenium ± brown; pigment forming distinct caps over the apices of the paraphyses. Spores acicular, 32-73 × 2.5-4.3 µm, with 3-15 septa.

Thallus indeterminate or determinate, very thin to rather thick, usually continuous, usually wrinkled but sometimes smooth or warted, without cracks, ± cracked, or areolate, rarely discontinuous, of ± discrete, thin areoles, light grey to grey to yellow-grey to green-grey to blue-grey, rarely grey-green or greyish yellow. Prothallus often present as a thin, black line bordering the thallus.

Apothecia (0.5-)0.5-0.7-0.8(-1.1) mm diam. (s= 0.1, N= 23, n= 5), plane or moderately convex, remaining so or rarely becoming markedly convex, epruinose or rarely thinly pruinose on the edge of a few young apothecia. Disc purple-brown to purplish black to pure black, often mottled with pale pink, pale orange, pale brown-violet, brownish pink, pink-brown, brown-purple, or greyish violet. Margin in upper part often concolorous with disc, sometimes paler than disc (i.e., like the lower part of the margin), or rarely darker than disc, lower part concolorous with or paler than disc, commonly ± brown or ± pink; distinct, raised above disc in young apothecia, soon level with the disc, persistent or only rarely excluded.

Proper exciple laterally (46-)67(-120) µm wide (s= 16, N= 23, n= 1), without crystals or rarely with radiating clusters of crystals that are up to 4 µm in diam. Rim pigmented in a distinct zone, ± brown or red-brown in upper part, downwards usually gradually changing to pale yellow or colourless, along the edge with a single layer of enlarged cells with lumina that are up to 9 × 6 µm. Lateral interior paler than rim, colourless, pale yellow, brown-orange, or orange-brown. Medullary part usually concolorous with or paler than hypothecium and lateral interior, colourless to pale yellow. Hypothecium colourless or pale yellow. Hymenium (74-)76-91-110(-115) µm thick (s= 9, N= 23, n= 5), lower part colourless except for occasional vertical streaks with brown pigment, uppermost part ± brown, red-brown, grey-brown, or black-brown, usually ± distinctly delimited. Paraphyses 0.8-1.6 µm wide in mid-hymenium; apices ± clavate or not at all swollen, (1.2-)1.9-2.6-3.0(-4.0) µm wide (s= 0.6, N= 23, n= 5), with grey-brown pigment in the wall forming a distinct "cap". Spores acicular, straight, slightly curved, or sometimes ± sigmoid, sometimes coiled in ascus, (32-)36-50-67(-73) µm long (s= 8, N= 23, n= 10), (2.5-)3.1-3.4-4.0(-4.3) µm wide (s= 0.4, N= 23, n= 10), (9.3-)11.7-15.1-18.9(-23.9) times as long as

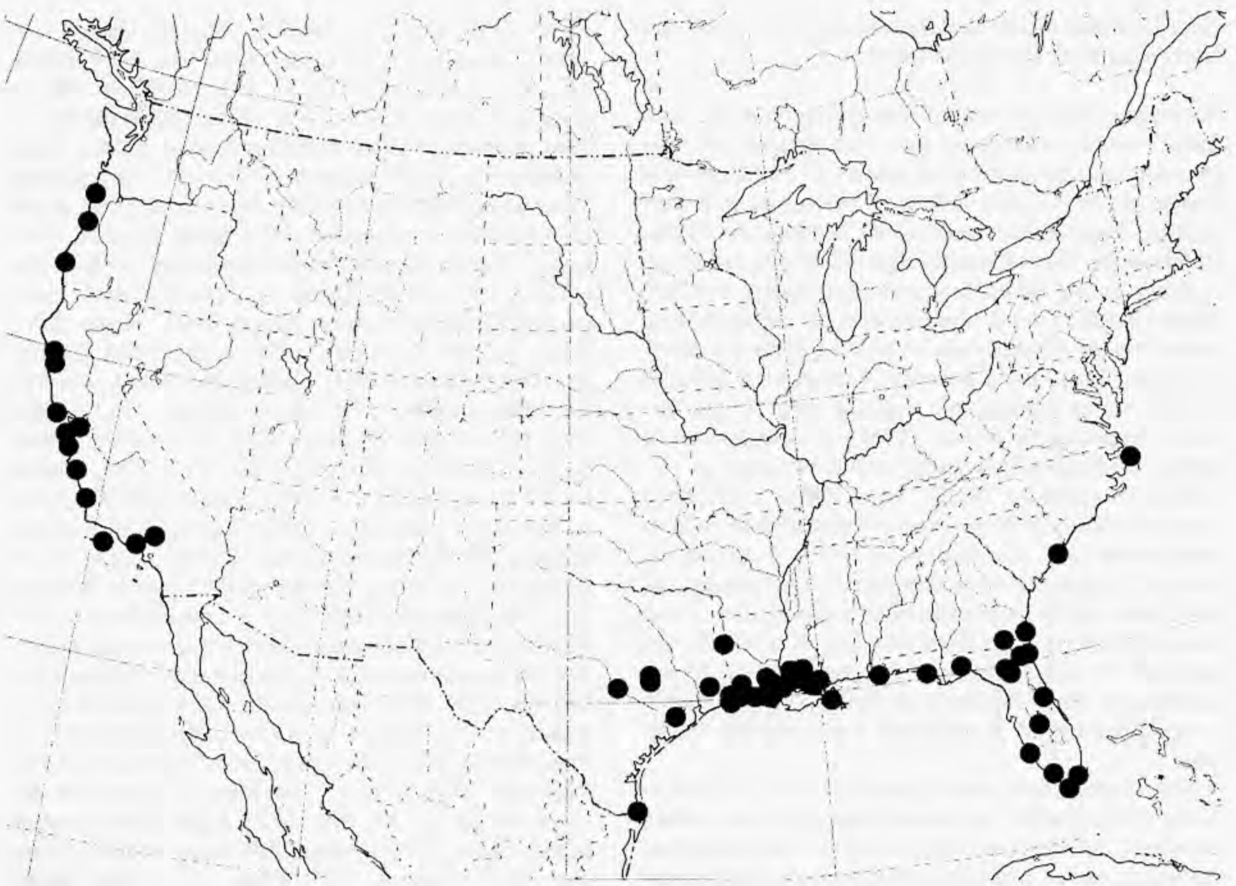


Fig. 24. Known North American distribution of *Bacidia heterochroa*.

wide (s= 2.8, N= 23, n= 10), with (3-)4.5-9.6-13.6(-15) septa (s= 3.1, N= 23, n= 10).

Pycnidia partly or entirely immersed in thallus, uppermost part of wall concolorous with apothecia, 40-100 µm diam. Conidia filiform, curved, non-septate, 5-18 × 0.8-1.0 µm.

Chemistry: Western specimens contain no lichen substances, whereas eastern ones contain atranorin (although sometimes only in trace amounts).

Pigments: Upper part of hymenium and rim of proper exciple K+ purplish, N+ orange-red to red. Hypothecium and inner parts of proper exciple K+ slightly intensifying, N-. – Laurocerasi Brown in hymenium (as caps on paraphysis apices), rim of proper exciple, and pycnidial wall. Rubella Orange in hypothecium and inner part of proper exciple.

Ecology. This species has a very wide ecological amplitude. It has been found on trunks and branches of a wide variety of trees and shrubs in forests ranging from shady and humid to sun-lit and dry. Occasionally, it has been found in planted tree-stands. Known phorophytes include (in the Southeast:) *Carya illinoensis*, *Salix* spp., *Avicennia germinans*, *Cephalanthus occidentalis*, *Cornus foemina*, *Datura* sp., *Cornus foemina*, *Diospyros virginiana*, *Liquidambar styraciflua*, *Myrsine floridana*, *Morus rubra*, *Lysiloma latisiliquum*, *Sambucus canadensis*, *Piscidia piscipula*, *Planera aquatica*, *Quercus* spp., *Rhizophora mangle*, *Althaea* sp., *Celtis laevigata*, *Sapium sebiferum*, *Azalea* sp., *Forestiera acuminata*, *Lagerstroemia indica*, *Nyssa* sp., *Populus deltoides*, *Wisteria sinensis*, *Vitis rotundifolia*, *Juniperus ashei*, *J. silicicola*, (in the West:) *Acer macrophyllum*, *Ceanothus divaricatus*, *Cupressus macrocarpa*, *Pinus ponderosa*, *Prunus ilicifolia*, *Quercus agrifolia*, *Q. lobata*, *Rhus diversiloba*, *Salix* spp., *Sambucus coerulea*, and *Umbellularia californica*.

Distribution. In the west known from California and Oregon, and in the southeast from Texas, Louisiana, Alabama, Florida, Georgia, South Carolina, and North Carolina. – Probably one of the most widespread species of *Bacidia*. I have seen specimens from tropical and subtropical areas around the world.

Discussion. *Bacidia heterochroa* is likely to be confused with *B. helicospora* (see that species), *B. laurocerasi*, and the neotropical species *B. megapotamica* Malme. *B. laurocerasi* differs in having none or few pigment caps in the wall of the paraphyses apices, more-septate, more distinctly sigmoid spores, and in only rarely having the apothecium disks mottled with different colours. Like *B. heterochroa*, *B. megapotamica* forms distinct pigment caps in the wall of the paraphyses apices. These caps, however, consist of a different greyish brown pigment not reacting with K. Furthermore, according to Malme (1935), *B. megapotamica* differs in having shorter spores with fewer septa.

Bacidia eckfeldtii (Müll. Arg.) Zahlbr., described from the vicinity of Monterey in northeastern Mexico, is very similar to *B. heterochroa*. It differs in having the hymenial pigment evenly distributed (not forming distinct caps), and in having distinctly sigmoid spores with more septa (11-17). In these respects, *B. eckfeldtii* approaches *B. laurocerasi*, but the pigmentation of the apothecia is more similar to *B. heterochroa*. The only known specimen of *B. eckfeldtii* was collected on lignum.

The western and eastern populations of *B. heterochroa* differ slightly but consistently in the secondary chemistry. Furthermore, the numerical and statistical analysis revealed additonal differences in morphological characters. These differences, however, are slight and overlapping. I have not been able to detect any other discontinuous difference between these groups of populations other than the chemistry. Further detailed analyses of the variation patterns, also including material from Central and South America, is needed before a final conclusion can be drawn as to the taxonomic status of the eastern and western population groups.

The types of *Bacidia subpellucida* (Müll. Arg.) Darb. and *B. atlantica* (Müll. Arg.) Zahlbr. are typical specimens of *B. heterochroa* and are thus reduced here into synonymy

Collections examined. U. S. A. *Alabama*. Baldwin Co., 1925, Evans 435, 441, 458 (NY, US). *California*. Contra Costa Co., 1930, Herre (US). Marin Co., 1925, Parks 2883 (COLO). + 1925, Parks 2883 (filed with *Bn. californica*, COLO), + 1939, Koch 565a (filed with *B. insularis*, COLO), 1969, Wennekens 77 (SFSU), 1977, Calhoun 125 (SFSU), 1989, Ekman L640, L642, L644 (LD), + 1989, Ekman L645 (filed with *Bn. californica*, LD). Mendocino Co., 1973, Thiers 30885 (SFSU), 1982, Thiers 45648 (SFSU), 1989, Ekman L650 (LD). + Monterey Co., 1966, Weber & Santesson (filed with *Bn. californica* in Weber: Lich. Exs. Boulder 182, COLO, MIN, SGSC, UBC, US, WTU). San Luis Obispo Co., 1989, Ekman L624 (LD). San Mateo Co., 1967, Jordan 636, 665, 818, 826 (SFSU), 1974, Brodo 20413, Thiers, Sigal & Toren (CANL), 1978, Thiers 39236 (SFSU), + 1967, Jordan 818 (filed with *B. arceutina*, SFSU). Santa Barbara Co., 1989, Ekman L637 (LD). San Gabriel Mountains, 1902, Hasse (NY). Santa Cruz, 1888, possibly collected by Anderson (NY). Santa Monica, 1897, Hasse 536 (NY). Santa Monica Mountains, 1906, Hasse (COLO, US), + 1909, Hasse 2122 (filed with *Bn. ramea*, MIN). Santa Monica Range, 1902, Hasse (NY), Hasse 536 (NY). *Florida*. 1878, Austin (US). Calkins 76 (NY), Calkins 89 (FH), Calkins 91 (COLO). Alachua Co., 1982, Griffin 96, 137 (herb. Tucker), 1982, Griffin 137a (FLAS, herb. Tucker, MIN, NY), 1993, Ekman L1141, L1142, L1143 (LD). Bay Co., 1993, Ekman L1217 (LD). Collier Co., 1993, Ekman L1174, L1203, L1204 (LD). Dade Co., 1982, Tucker 25228 (herb. Tucker), 1993, Ekman L1182, L1183, L1184 (LD). Highlands Co., 1965, Wetmore 13905 (MIN). Wakulla Co., 1993, Ekman L1209 (LD). + Caloosa River, 1878, Austin (in type specimen of *Biatora caloosensis* Tuck.= *Bacidia hostheleoides*, FH). Fort George, Calkins (COLO, FH, MIN, NY). Jacksonville, 1886, Eckfeldt (US), Calkins (COLO, NY, US), 1889, Calkins (MIN). Sanford, Rapp (FH), 1909, 1912, 1913, Rapp (FH), 1914, Rapp (FH, MIN, US), + 1914, Rapp 22 (filed with *Bn. varia* and *Bn.* sp. #1, FH), 1929, Rapp (UPS). Sanibel Island, Hume (NY). Upsala, 1909, Rapp 32 (FH). *Georgia*. 1877, Ravenel (US). Glynn Co., 1969, Brodo 16455 (CANL). Ware Co., 1989, Wetmore 64692 (MIN). *Louisiana*. 1895, Langlois (FH). Allen Par., 1986, Tucker 27294 (herb. Tucker). Calcasieu Par., 1991, Lievens 5030a (herb. Tucker). Cameron Par., 1967, Tucker 6794 (herb. Tucker), 1991, Lievens 4876c (herb. Tucker). East Baton Rouge Par., 1968, Tucker 7296b (herb. Tucker), 1969, Tucker 7943 (COLO, herb. Tucker, US), 1969, Tucker 7943b (herb. Tucker), 1970, Tucker 8988 (herb. Tucker), 1971, Tucker 9044b (herb. Tucker), 1971, Tucker 9969 (herb. Tucker, MIN), 1974, Tucker 11698b (CANL), 1977, Tucker 16833 (MIN). Evangeline Par., 1969, Tucker 8384 (herb. Tucker). Iberia Par., 1984, Tucker 26637 (herb. Tucker). + Iberville Par., 1974, Tucker 13391 (filed with *B. schweinitzii*, herb. Tucker). Jefferson Par., 1970, Johnson 45 (herb. Tucker). + Livingston Par., 1968, Tucker 7351 (filed with *B. schweinitzii*, herb. Tucker). Plaquemine Par., 1884, Langlois 589, 593, s. n. (US), 1884, Langlois 599 (US), 1886, Langlois 598 (US), 1885, Langlois 186 (US), 1884-85, Langlois 184 (US). + Sabine Par., 1967, Wetmore 17563, 17587 (filed with *B. schweinitzii*, MIN). + St. Helena Par., 1972, Tucker 10149 (filed with *B. helicospora*, herb. Tucker). St. Martin Par., 1889, Langlois 590 (US). St. Tammany Par., 1982, Tucker 24442a (herb. Tucker). Tangipahoa Par., 1975, Tucker

15149 (NY), 1976, Tucker 15285 (herb. Tucker). Vermilion Par., 1991, Lievens 4869b (herb. Tucker). + West Feliciana Par., 1978, Tucker 18127 (filed with *B. schweinitzii*, herb. Tucker). Banker's, 1894, Langlois (US). Bayou Silan, 1898, Langlois (US). Bayou Tortue, 1893, Langlois (US). Bois Charmant, 1893, Langlois (US). Bois Lobbé, 1891, Langlois (US), + 1893, Langlois 868 (filed with *B. schweinitzii*, US). Breaux Bridge, 1893, Langlois 867 (US). Charenton, 1889, Langlois 591 (US). Grand Coteau, 1894, Langlois (filed with *B. schweinitzii*, US). John Durand's, 1894, Langlois (US). Opelousas, 1889, Langlois 617 (US). Petite Prairie, 1884, Langlois 5-97 (US). Pointe-à-la-Hache, 1884, Langlois 183, 588, s. n. (US). St. Leo, 1893, Langlois (US). St. Martinsville, 1893, Langlois 866 (US), 1895, Langlois (CANL, NY, US), 1895, Langlois 475 (NY). *North Carolina*. Dare Co., 1959, Schallert L510 (WTU). *Oregon*. + Curry Co., 1989, Ekman L673 (filed with *B. salmonea*, LD). + Lincoln Co., 1989, Ekman L680, L681 (filed with *B. salmonea*, LD). Tillamook Co., 1989, Ekman L709 (LD), + 1989, Ekman L711 (filed *B. salmonea*, LD). *South Carolina*. + Ravenel (filed with *B. schweinitzii*, US). Charleston Co., 1988, Wetmore 61553 (MIN). *Texas*. Burleson Co., 1976, Tucker 15714 (herb. Tucker). Cameron Par., 1990, Lievens 4573b (herb. Tucker). Fort Bend Co., 1991, Lievens 5344 (herb. Tucker). + Hardin Co., 1975, Tucker 14027 (filed with *B. schweinitzii*, herb. Tucker). Robertson Co., 1976, Tucker 15797 (herb. Tucker). Travis Co., 1989, Lievens 3594c, Lynch, Kramer & Kramer (herb. Tucker).

12. Bacidia hostheleoides (Nyl.) Zahlbr.

Cat. Lich. Univ. 4: 205 (1926). - *Lecidea hostheleoides* Nyl., Acta Soc. Sci. fenn. 7: 458 (1863). – Type: Venezuela, "Nova Granata, Villeta, alt. 1200 m", 1860, Lindig 2668 (PC, lectotype selected here; H, isolectotype).

Patellaria rufescens Müll. Arg., Flora, Jena 67: 467 (1884). - *Bacidia rufescens* (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 4: 239 (1926). – Type: Mexico, "Orizaba", 1853, Müller (G, lectotype selected by Awasthi & Mathur 1987 as "holotype").

Biatora caloosensis Tuck., Synopsis North. Am. Lich. 2: 41 (1888). - *Bacidia caloosensis* (Tuck.) Zahlbr., Cat. Lich. Univ. 4: 184 (1926). – Type: U. S. A., Florida, "Caloosa River", 1878, Austin (FH-TUCK, lectotype selected here, excluding specimen d'; US, isolectotype)

Lecidea subpar Nyl., Labuan et Singapore 39 (1891). - *Bacidia subpar* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 243 (1926). – Type: Cuba, Tuckerman: Wright Lich. Cub. 114 (H-NYL 17370, lectotype selected here).

Bacidia vexans Zahlbr., Denkschr. Akad. Wiss., Wien 83: 128 (1909). – Type: Brazil, "Sao Paulo. Prope Fazenda Bella Vista in districtu urbis S. Cruz ad flumen Rio Pardo, ca 500 m s m, corticola", 1901, Wettstein & Schiffner (W, lectotype selected here).

Fig. 25. Known North American distribution of *Bacidia hostheleoides* (dot) and *B. mutabilis* (triangle).

Bacidia rissoensis Malme, Ark. Bot. 27A (5): 32 (1935). – Type: Paraguay, "Colonia Risso", 1893, Malme 1813 (LD, syntype).

Bacidia medialis f. *majuscula* Malme, Ark. Bot. 27A (5): 32 (1935). – Type: Brazil, "Coxipó Mirim pr. Cuyabá", 1894, Malme 2346 (S, lectotype selected here).

Illustrations. Fig. 25 (map).

Characterization. Thallus greyish. Apothecia brown-orange. Proper exciple very pale orange; lumina in lower part narrower than or as wide as lumina in upper part. Hypothecium very pale orange. Upper part of hymenium very pale orange. Spores bacilliform, fusiform, or almost clavate, (almost) straight, 16-25 · 2.9-5.0 µm, with 3-5 septa. – Neotropical specimens usually have brown-orange to ± purple-brown, seldom ± pink apothecia, a colourless to ± orange or partly ± red-brown proper exciple, and a colourless to ± red-brown upper part of the hymenium

Thallus indeterminate, thin to thick, mainly continuous, ± cracked and wrinkled, or granular to subsquamulose, partly discontinuous, of discrete to contiguous granules, pale grey to pale green-grey. Granules (31-)57(-80) µm wide (s= 15, N= 1, n= 20). Prothallus lacking.

Apothecia (0.5-)0.6(-0.8) mm diam. (s= 0.08, N= 1, n= 20), at first plane, later becoming convex, epruinose. Disc brown-orange. Margin concolorous with disc, raised above disc in young apothecia, later level with the disc, finally excluded.

Proper exciple laterally 40 µm wide (N= 1, n= 1), without crystals; lumina inside rim in upper part 1.2-2.8

µm wide, in lower part 1.0-1.5 µm wide. Rim very pale orange, without distinct zone of enlarged cells along the edge (lumina gradually expanding towards edge or not at all expanded). Lateral interior concolorous with rim. Medullary part colourless. Hypothecium very pale orange. Hymenium (57-)60(-62) µm thick (s= 2, N= 1, n= 5), colourless in lower part, diffusely and very pale orange in upper part. Paraphyses 1.0-1.6 µm wide in mid-hymenium; apices only slightly or not at all swollen, (1.2-)1.8(-2.4) µm wide (s= 0.4, N= 1, n= 20), without internal pigment. Spores bacilliform, fusiform, or almost clavate, straight or slightly curved, not coiled in ascus, (16-)19(-25) µm long (s= 3, N= 1, n= 20), (2.9-)3.6(-5.0) µm wide (s= 0.4, N= 1, n= 20), (3.8-)5.4(-8.7) times as long as wide (s= 1.2, N= 1, n= 20), with (3-)3.1(-5) septa (s= 0.4, N= 1, n= 20).

Pycnidia half-immersed in thallus, pale orange, 50-100 µm diam., containing a mixture of two types of conidia: (1) filiform, curved, non-septate, 10-14 × 0.5 µm, and (2) short-fusiform to ellipsoid to oblong, non-septate, 6-9 × 1.6-2.0 µm.

Chemistry: No lichen substances detected.

Apothecial and pycnidial pigments: All parts of apothecia and pycnidia K-. – Small amounts of Rubella Orange in proper exciple, hypothecium, hymenium, and pycnidial wall.

Ecology. On the bark of an unidentified hardwood.

Distribution. Collected once in southwestern Florida (the type specimen of *Biatora caloosensis* Tuck.). – Widely distributed in the neotropics.

Discussion. Judging from neotropical material, *Bacidia hostheleoides* is a very variable species in thallus formation and apothecium pigmentation. The thallus ranges from almost smooth to granular, and the apothecia vary from pink to dark purple-brown. In these respects, the variation much parallels that of *B. medialis*, which is obviously a very close relative. There is, however, a difference in that apothecia of *B. medialis* are usually ± pinkish, whereas they are usually brown-orange to ± purple-brown in *B. hostheleoides*. There is also a difference in thallus colour: *B. medialis* is commonly ± deep grey-green, whereas *B. hostheleoides* usually is pale grey to pale green-grey. The entire variation from pink to purple-brown apothecia and pale grey to dark grey-green thallus, however, occurs in both species. The only constant difference between the two species appears to be the anatomy of the proper exciple. In *B. hostheleoides*, the lumina in the lower part of the proper exciple are as narrow or usually narrower than the ones in the upper part of the proper exciple. In *B. medialis*, on the other hand, the lower part of the proper exciple to a large extent consists of hyphae with lumina that are ± ellipsoid and distinctly wider than the lumina of the upper part of the proper exciple. Possibly, there is also a difference between the species in the length-width ratio of the spores, but this requires confirmation.

Apart from *B. medialis*, *B. hostheleoides* can be confused with *Bacidina varia* and an unidentified (possibly undescribed) species of *Catillaria* sensu Zahlbr. *B. hostheleoides* is distinguished from these species in much the same way as *B. medialis* (see this species).

Bacidia hostheleoides is a poorly understood species, which has had the unfortunate destiny of being described several times. The types of *Bacidia rufescens* (Müll. Arg.) Zahlbr., *B. caloosensis* (Tuck.) Zahlbr., *B. subpar* (Nyl.) Zahlbr., *B. vexans* Zahlbr., *B. rissoensis* Malme, and *B. medialis* f. *majuscula* Malme all represent typical specimens of *B. hostheleoides*. In North American literature, this species has mostly been known under the name *B. caloosensis*.

Collections examined. U. S. A. *Florida*. Caloosa River, 1878, Austin (FH, US).

13. Bacidia igniarii (Nyl.) Oksner

Flor. Lish. Ukraini 2: 166 (1968). - *Lecidea igniarii* Nyl., Flora, Jena 50: 328 (1867). – Type: Finland, "Ad Polyp. igniarium in Tavastia", 1863, Norrlin (H-NYL 17232, lectotype selected here).

Bacidia abbrevians Th Fr., Lich. Scand. 2: 362 (1874). – Type: Not designated; isosyntype in LD studied.

Illustrations. Figs 19 (map), 41D.

Characterization. Apothecia black, high and barrel-shaped to inversely cone-shaped. Proper exciple with green and brown pigmentation, strongly developed below hypothecium, to the greater part consisting of intricately intertwined hyphae. Hypothecium pale. Upper part of hymenium blue-green. Spores bacilliform to clavate, 12-19 × 2.5-2.9 µm, with 3 septa.

Thallus indeterminate, rather thin, discontinuous, of discrete or contiguous, convex, sometimes subsquamulose areoles, light brown-grey. Hypothallus not visible.

Apothecia (0.2-)0.3(-0.4) mm diam. (s= 0.05, N= 1, n= 10), ± plane, remaining so or becoming slightly convex, high and barrel-shaped when young, later becoming inversely cone-shaped, 1.7 times a wide a high. Disc pure black. Margin black in upper part, downwards gradually changing to light yellow-brown, distinct, raised above disc in young apothecia, later level with the disc, persistent.

Proper exciple laterally 35 µm wide (N= 1, n= 1), without crystals, strongly developed below hypothecium; outermost part formed by radiating hyphae (the lumina of which are ± cylindrical, 0.8-2.5 µm wide), inner (major) part of narrow, intricately intertwined and richly branched hyphae (lumina 0.5-1 µm wide). Rim dark brown-green in uppermost part, downwards gradually changing to dirty brown, pale brown and then colourless, along the edge without or with a single cell layer thick zone of cells with enlarged lumina. Lateral interior usually paler than rim, pale brown in upper part, downwards gradually changing to colourless. Medullary part colourless. Hypothecium very pale brown. Hymenium (42-)46(-47) µm thick (s= 2, N= 1, n= 5), lower part colourless, upper part ± blue-green. Paraphyses 1.2-2.0 µm wide in mid-hymenium; apices ± clavate, (2.0-)2.8(-4.0) µm wide (s= 0.5, N= 1, n= 20), many with an external hood of green pigment. Spores bacilliform to clavate, slightly curved (banana-shaped) or (a few) straight, (12-)15(-19) µm long (s= 2, N= 1, n= 20), (2.5-)2.6(-2.9) µm wide (s= 0.2, N= 1, n= 20), (4.3-)5.9(-7.0) times as long as wide (s= 0.7, N= 1, n= 20), with 3 septa.

Pycnidia not seen in North American specimens.

Chemistry: Not examined due to sparsity of material.

Pigments: Upper part of hymenium and uppermost part of proper exciple K- or partly K+ purplish, and N+ purple with a precipitate of blue crystals. Proper exciple and hypothecium K+ purplish, N+ orange-red. – Bacidia Green in hymenium and uppermost part of exciple. Laurocerasi Brown in proper exciple, hymenium (small amounts), and hypothecium (small amounts).

Ecology. *Bacidia igniarii* was collected on a trunk of *Populus tremuloides* 1.3 m above the ground.

Distribution. Known from only one single North American locality in southwesternmost Saskatchewan. – Europe.

Discussion. All previous reports of *B. igniarii* from North America have turned out to be erroneous, being based on short-spored forms of *B. circumspecta*. *B. igniarii* is similar to *B. circumspecta*, *B. schweinitzii*, *B. reagens*, and *B. subincompta*. The three last species all have longer spores than *B. igniarii*. Furthermore, *B. schweinitzii* has an orange-brown to red-black proper exciple that merges into the hypothecium, *B. reagens* a C+ violet upper hymenium, and *B. subincompta* a brown K+ purplish hypothecium. *B. circumspecta* is the species that is the most similar to *B. igniarii*. Although *B. igniarii* in most floras is keyed out as having shorter spores than *B. circumspecta*, this is not the critical character for separating these species. Although there are probably differences in average spore length and average number of spore septa, the only diagnostic character positively separating the two species is the anatomy of the proper exciple. In *B. circumspecta*, the apothecia are low and flat. The main part of the proper exciple is formed by regularly radiating hyphae. Only a small portion of the innermost part of the exciple, flanking the hypothecium, consists of hyphae that are not clearly directed towards the rim. In *B. igniarii* on the other hand, the young apothecia are high and barrel-shaped with almost vertical sides. As they age, the apothecia remain high, but become more or less inversely cone-shaped. This appearance is caused by a strongly developed exciple below the hypothecium. The outermost part of the proper exciple is formed by regularly radiating hyphae, but the inner dominating part consists of intricately intertwined and richly branched hyphae.

Pycnidia have not been observed in the North American specimen. In Swedish specimens, however, they are often present. They are black and sessile, 75-100 µm in diameter. The conidia are bacilliform, straight, 0-1-septate, and 5-12 × 1.2-1.5 µm, i.e., similar to type 1 of *B. circumspecta* (see that species).

Like in the North American specimen of *B. igniarii*, 3-septate spores are dominating also in North European specimens. In some Swedish specimens, however, I have observed 5-septate spores mixed with the 3-septate ones.

Collections examined. CANADA. *Saskatchewan*. Cypress Hills, 1964, Jonescu (WIS).

14. Bacidia insularis Zahlbr.

Annls mycol. 29: 82 (1931). - Type: Ecuador, "Insulae Galapagos: Charles Island, Postoffice Bay, ad cortices laeves", Herre, Zahlbruckner in Kneiff & Hartmann: Krypt. exs. Vindobon. 3155 (W, lectotype selected here; LD, isotype)

Illustrations. Figs 20 (map), 41E.

Characterization. Apothecia black, often pruinose. Proper exciple laterally blue-green with only some brown pigmentation, otherwise colourless to blue-green. Hypothecium ± brownish and sometimes also partly blue-green. Upper part of hymenium blue-green. Paraphyses 0.8-1.2 µm wide in mid-hymenium. Spores fusiform to acicular, 26-77 × 3.1-5.3 µm, with 3-15 septa.

Thallus indeterminate or determinate, thin to rather thick, usually continuous, warted to subsquamulose or sometimes almost granular, ± cracked, rarely discontinuous, of ± discrete, thin to rather thick, convex and warted areoles, light grey, green-grey, brown-grey, or grey-green. Prothallus sometimes present between discrete areoles, thin, light grey.

Apothecia (0.4-)0.5-0.7-1.0(-1.7) mm diam. (s= 0.2, N= 5, n= 10), plane or slightly convex, epruinose or with white pruina on edge of young to medium-aged apothecia. Disc black. Margin black, distinct, raised above disc in young apothecia, later level with the disc, persistent.

Proper exciple laterally (57-)67(-83) µm wide (s= 11, N= 5, n= 1), without crystals or with radiating clusters of crystals that are up to 3 µm wide. Rim dark blue-green to almost black (often in a distinct zone) in upper part, downwards changing to pale blue-green, along the edge with a ± distinct, 1-3 cell layers thick zone of enlarged cells that are up to 10 × 5 µm. Lateral interior paler than rim, colourless to blue-green, sometimes mixed with some brown. Medullary part colourless. Hypothecium ± pale brown, dirty brown, green-brown, or sometimes blue-green in upper part and pure brown in lower part. Hymenium (74-)82-90-96(-99) µm thick (s= 7, N= 5, n= 5), lower part colourless, uppermost part dark blue-green to almost black in a distinct layer. Paraphyses 0.8-1.2 µm wide in mid-hymenium; apices ± clavate, (1.6-)2.6-2.9-3.5(-4.9) µm wide (s= 0.8, N= 5, n= 10), unpigmented or with an external cap of blue-green pigment. Spores fusiform or sometimes acicular, (26-)30-40-55(-77) µm long (s= 12, N= 5, n= 10), (3.1-)3.5-4.2-4.7(-5.3) µm wide (s= 0.6, N= 5, n= 10), (5.3-)6.4-10.0-14.1(-20.7) times as long as wide (s= 4.1, N= 5, n= 10), with (3-)6.6-7.8-10.3(-15) septa (s= 2.2, N= 5, n= 10).

Pycnidia ± immersed in thallus, uppermost part of wall concolorous with apothecia, 100-150 µm diam. Conidia filiform, curved, non-septate, 7-14 × c. 0.5 µm.

Chemistry: No lichen substances detected.

Pigments: Upper part of hymenium and proper exciple K-, N+ purple with a precipitate of blue crystals. Hypothecium K+ slightly intensifying or K+ purplish, and N+ intensifying, N+ orange-red, or N+ purplish to purple with a precipitate of blue crystals. – Bacidia Green in hymenium, hypothecium (small amounts) and proper exciple. Laurocerasi Brown and Rubella Orange in hypothecium.

Ecology. On branches and twigs of shrubs in ± exposed or slightly shady habitats, e.g., in *Artemisia* chaparral. Known phorophytes include *Artemisia californica* and *Rhus laurina*.

Distribution. Known from the southern and central parts of coastal California. – *Bacidia insularis* was described on a single collection made by Herre in the Galapagos Islands, until now the only known locality. Future investigations may well show that this species is rather widespread in coastal areas of Central and South America.

Discussion. *Bacidia insularis* is similar to *B. circumspecta* and *B. subincompta*. Both these species differ from *B. insularis* in usually having the proper exciple dominated by a brown pigment (Laurocerasi Brown). Furthermore, *B. circumspecta* has narrower spores with fewer septa, and usually a colourless hypothecium that never contains Bacidia Green. *B. subincompta* also differs in having wider paraphyses. Although similar to the species mentioned, there is a possibility that *B. insularis* is more closely related to other species with a zone of enlarged cells along the edge of the proper exciple, i.e., *B. campalea*, *B. russeola*, and *B. suffusa*.

The type collection differs from the Californian collections in a having more abundant white pruina on the margins of the apothecia, a wider zone of enlarged cells along the rim of the proper exciple (3-5 cell layers), and larger conidia (13-22 × c. 0.8 µm, non-septate or 1-septate). In my opinion, these differences do not justify a separation of the Californian populations as a separate species. *B. insularis* is a poorly known species, and as more collections become available, it may turn out that the variation is continuous.

Collections examined. U. S. A. *California*. Catalina Island, 1911, Hasse (FH), 1912, Hasse (MIN), 1915, Hasse (Plitt: Lich. exs. ex herb. Hasse rel. 52, COLO). Santa Barbara Co., 1994, Nimis & Tretiach (TSB, 3 coll.). Marin Co., 1939, Koch 565a (COLO).

15. Bacidia laurocerasi (Delise ex Duby) Zahlbr.

Cat. Lich. Univ. 4: 213 (1926). - *Patellaria laurocerasi* Delise ex Duby, Botanicon Gallicum 2: 653 (1830). – Type: Not seen.

Biatora atrogrisea Delise ex Hepp, Flechten Europas 26 (1853). - *Bacidia atrogrisea* (Delise ex Hepp) Körb., Parerg. Lich. 133 (1861). – Type: Switzerland, "Zürich, an der Rinde junger Tannen und Nussbäume", Hepp, Hepp: Flecht. Eur. 26 (LD, syntype).

Lecidea endoleucula Nyl., Lich. Japon. 68 (1890). - *Bacidia endoleucula* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 194 (1926). – Type: Japan, "Itjigome", 1879, Almquist (H-NYL 17734, syntype).

Lecidea invertens Nyl., Acta Soc. Sci. fenn. 26 (10): 33 (1900). - *Bacidia invertens* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 252 (1926). – Type: Japan, "Nagasaki", 1879, Almquist (H-NYL 17281, lectotype selected here).

Bacidia subacerina Vain., Acta Soc. Fauna Flora fenn. 53 (1): 174 (1922). – Type: Not designated; isosyntypes in LD studied.

Bacidia endoleuca auct.

Nomenclature. I have not been able to trace any original material of *Patellaria laurocerasi* Delise ex Duby. Further efforts to find such material should be made, particularly in PC and STR, before a neotypification is made.

I refrain from lectotypifying *Lecidea endoleucula* Nyl., since the only syntype seen is very small and scrappy. Further efforts to trace original material should be made before a lectotypification is made.

Characterization. Apothecia usually with purple-brown to purple-black disc; margin in upper part concolorous with disc or ± red, in lower part often distinctly paler. Proper exciple usually dark red-brown to black-brown in rim, otherwise colourless to red-brown. Hypothecium ± yellowish. Upper part of hymenium usually ± dark brown; pigmentation evenly distributed in the gelatinous matrix surrounding the paraphyses (neither forming caps over the apices of the paraphyses, nor accumulated around the ascus apices). Spores acicular, 50-108 × 1.9-3.7 µm, with 7-28 septa.

Thallus indeterminate, thin to rather thick, either discontinuous, of discrete or contiguous, flat or convex areoles, or continuous, smooth to wrinkled to warted, sometimes subsquamulose or (when overgrowing bryophytes) forming a thin, varnish-like crust; without cracks, ± cracked, or sometimes areolate, almost white to pale grey to grey to yellowish grey, or grey-green. Prothallus present between discrete areoles, thin, white, endophloeodal.

Apothecia (0.4-)0.5-0.8-0.9(-1.3) mm diam. (s= 0.2, N= 30, n= 5), ± plane when young, later becoming convex, epruinose. Disc ± purple-brown to purple-black, rarely red-brown, brown-black, or pure black. Margin glossy, upper part concolorous with disc or ± red, lower part concolorous with upper part or, more often, paler, pale brown-yellow to dark purplish brown; raised above disc in young apothecia, later level with the disc, finally excluded in old and convex apothecia.

Proper exciple laterally (54-)80(-138) µm wide (s= 17, N= 30, n= 1), without crystals. Rim usually dark red-brown to black-brown, sometimes yellow-brown to red-brown to purple-brown, often pigmented in a distinct zone, downwards often gradually changing to almost colourless, along the edge with a single layer of cells with enlarged lumina that are up to 9 × 6 µm. Lateral interior usually paler than rim, colourless, pale brown, brown-yellow to yellow-brown, or pale brown-red to red-brown. Medullary part colourless to pale brown to brown-yellow. Hypothecium very pale yellow to brown-yellow. Hymenium (71-)81-96-125 (-131) µm thick (s= 12, N= 30, n= 5), lower part colourless to pale yellowish, upper part ± dark (often reddish) brown (rarely yellow-brown to orange-brown) in a distinct zone. Paraphyses 1.0-1.6 µm wide in mid-hymenium; apices ± clavate or not at all swollen, (1.2-) 1.5-2.1-2.7(-5.0) µm wide (s= 0.7, N= 30, n= 5), without internal pigment or sometimes a few with pale grey-brown wall. Spores acicular, slightly curved to sigmoid, sometimes coiled in ascus, (50-)57-74-96(-108) µm long (s= 11, N= 30, n= 10), (1.9-)2.5-2.8-3.5(-3.7) µm wide (s= 0.4, N= 30, n= 10), (14.7-) 18.3-26.4-31.5(-40.0) times as long as wide (s= 4.5, N= 30, n= 10), with (7-)11.9-17.1- 23.0(-28) septa (s= 4.0, N= 30, n= 10).

Pycnidia ± immersed in thallus, upper part concolorous with apothecia, c. 100-120 µm diam. Conidia filiform, curved, non-septate, 9-17 × c. 0.8 µm.

Chemistry: No lichen substances detected.

Pigments: Brown parts K+ purplish, N+ orange-red, ± yellowish parts K+ intensifying, N+ intensifying. – Laurocerasi Brown in hymenium, proper exciple, and pycnidial wall. Rubella Orange in hymenium (usually low amounts), hypothecium, and proper exciple.

Ecology. On trunks and branches of hardwoods and conifers, mainly in shady and humid habitats, but sometimes also in semi-open and rather dry forests. *B. laurocerasi* is the only North American species of *Bacidia* that occurs regularly on conifers other than *Thuja occidentalis*.

Discussion. Bacidia laurocerasi is likely to be confused with *B. helicospora* and *B. heterochroa* (see these species).

The western and eastern groups of populations are distinguished above all by the apothecium coloration, thallus appearance, hymenium thickness, spore length, and spore septation. Practically all specimens can be determined to subspecies on a combination of these characters, without knowledge of the geographic origin. The differences are rather vague, however, and the variation overlaps in each single character. Hence, I believe it is best to to regard them as geographically separated subspecies of one and the same species. The eastern group of populations is referred to here as subsp. *laurocerasi*, since it agrees fairly well with the western European populations. For further details, see the chapter *Numerical and statistical treatment*.

The type material of *Bacidia atrogrisea* (Delise ex Hepp) Körb. is typical *Bacidia laurocerasi* subsp. *laurocerasi*. The position of the Japanese *B. endoleucula* (Nyl.) Zahlbr. and *B. invertens* (Nyl.) Zahlbr. is slightly more problematic. The types of these names agree well with typical *B. laurocerasi* in most characters except for the smaller and slightly flatter apothecia. They are, in my opinion, best included in *B. laurocerasi*. Future investigations may prove them to belong in a separate subspecies, or to be nothing but poorly developed specimens of *Bacidia laurocerasi* subsp. *laurocerasi*. I am certain, however, that *Bacidia endoleucula* and *B. in-*

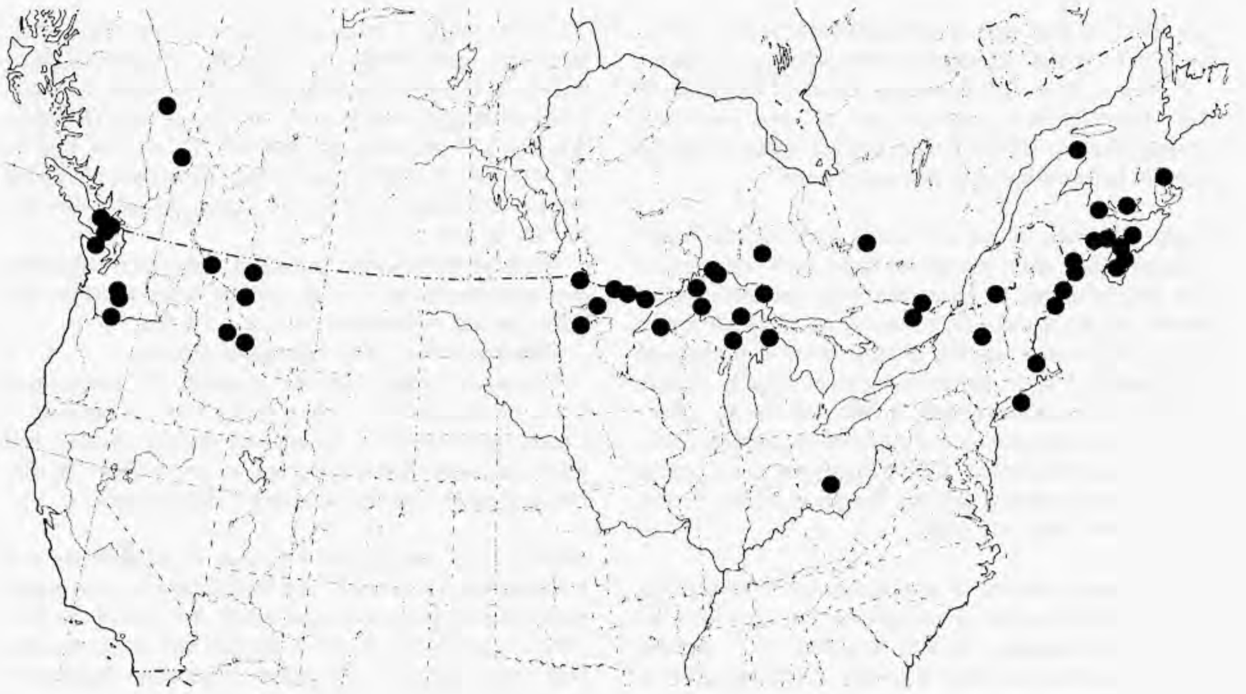


Fig. 26. Known North American distribution of *Bacidia laurocerasi*. - Western (Washington, British Columbia, Idaho, and Montana): known world distribution of subsp. *idahoensis*. - Eastern: known North American distribution of subsp. *laurocerasi*.

vertens have nothing to do with *B. laurocerasi* subsp. *idahoensis*.

Some authors distinguish between *Bacidia laurocerasi* and *B. subacerina* Vain. They are then mainly separated by apothecium shape. The former is stated to have broadly adnate apothecia that fairly soon become convex, and the latter cup-shaped apothecia that remain plane for a longer time. Additional characters have also been used, usually very vague and widely overlapping. In my opinion, the variation observed in North American as well as European material does not justify a taxonomic recognition of *B. subacerina* at the species level. The variation is continuous, and both the supposedly discriminating character states can sometimes be found in a single specimen. Should future investigations of European *B. laurocerasi* show that further subspecies ought to be recognized (see discussion in the chapter *Numerical and statistical treatment*), then the epithet *subacerina* may reappear at this taxonomic level.

15a. subsp. laurocerasi

Illustrations. Figs 3B, 6A, 26 (map), 41F.

Thallus usually thin, almost white to grey, or yellowish grey, very rarely grey-green, without cracks or ± cracked, rarely areolate. Apothecial margin in upper part ± concolorous with disc, only very rarely with a reddish hue. Hymenium (71-)81-91-106(-118) µm thick (s= 9, N= 21, n= 5). Spores (50-)57-70-87(-99) µm long (s= 10, N= 21, n= 10), (1.9-)2.5-2.7-3.5(-3.7) µm wide (s= 0.4, N= 21, n= 10), with (7-)11.9-15.9-22.2(-28) septa (s= 3.6, N= 21, n= 10).

Ecology. Known phorophytes include *Abies balsamea*, *Acer rubrum*, *Acer saccharum*, *Fraxinus* spp., *Juniperus virginiana*, *Picea* spp., *Populus* spp., *Quercus rubra*, and *Thuja occidentalis*.

Distribution. The Great Lakes and northern Appalachian regions. – East Asia (?), Europe.

Collections examined. CANADA. *New Brunswick*. Albert Co., 1980, Gowan 2049, 3188, 4009 (CANL). Charlotte Co., 1989, Ekman L1085, L1086, L1088, L1092 (LD). Kent Co., 1978, Egger 147a (CANL). King's Co., 1970, Ireland 13476 (CANL). *Nova Scotia*. Victoria Co., 1989, Ekman L1070, L1071 (LD). Hants Co., 1989, Ekman L1039 (LD). Kings Co., 1989, Ekman L1041 (LD). Lunenburg Co., 1972, Brodo 18954

& Argus (CANL). Queens Co., 1989, Ekman L1058 (LD). *Ontario*. Algoma District, Nagamisis Prov. Park, 1968, Brodo 13883 (CANL). Renfrew Co., 1986, Wong 4035 (CANL). Thunder Bay District, Rainbow Falls Prov. Park, 1965, Brodo 6636 (CANL, COLO). Lake Superior Prov. Park, 1989, Ekman L1000 (LD). Slate Islands, 1976, Wetmore 25256, 25637 (MIN). *Prince Edward Island*. Brackly Point, 1888, Macoun 2824 (CANL). *Quebec*. Comté Abitibi-Ouest, 1970, Brodo 16938, Gaudreau, Cloutier & Miron (CANL). Compton Co., 1963, Brodo 498 (CANL). Comté Gaspé-Est, 1972, Savage 16 (CANL). Comté Gatineau, 1977, Brodo 21225 (CANL). – U. S. A. *Maine*. 1922, Plitt (US). Eastport, 1877, Farlow (FH). Mount Desert Island, 1891, White (NY). Rockport, 1911, Merrill (FH). Salisbury Cove, 1922, Plitt (US). South Thomaston, 1912, Merrill (FH), 1912, Merrill, Merrill: Lich. exs. 260 (COLO, FH). South West Harbor, 1907, Sevivey (FH). *Massachusetts*. Wellesley, 1903, Cummings (FH). *Michigan*. Alger Co., 1987, Wetmore 59566 (MIN). Delta Co., 1976, Harris 11785b (CANL, MIN), 1976, Harris 12010 (UBC). Emmet Co., 1974, Buck (NY). Keweenaw Co., 1947, Thomson, 2914 (MIN), 1983, Wetmore 49271 (MIN). *Minnesota*. Becker Co., 1974, Wetmore 23768a (MIN). Clearwater Co., 1963, Hale 23463, 23482 (US), 1972, Wetmore 20400, 20513 (MIN), 1972, Wetmore 20820 (CANL, MIN), 1976, Wetmore 26163 (MIN). Hubbard Co., 1974, Wetmore 23141 (CANL, MIN, US). Koochiching Co., Hale 22212, 22215 (US), 1978, Wetmore 33463 (MIN), 1979, Wetmore 37301, 37881 (MIN), 1978, Wetmore 33428 (CANL, MIN). Lake Co., 1977, Wetmore 26602, 26651b (MIN), 1989, Ekman L943 (LD). Roseau Co., 1901, Fink 303 (MIN), 1901, Fink 324 (US). St. Louis Co., 1973, Wetmore 21697 (MIN), 1978, Wetmore 31294, 31412, 31716, 32364, 32787, 33695, 33930, 34062, 34141, 34287, 34539 (MIN), 1978, Wetmore 35414 (COLO, MIN), 1979, Wetmore 38856, 38964, 40082 (MIN), 1979, Wetmore 39845 (MIN, NY). *New York*. Suffolk Co., 1910 Latham (FH), 1920, Latham 950 (US), Latham (FH). Warren Co., 1982, Harris 16310 (NY). *Ohio*. Georgesville, 1894, Bogue, Merrill: Lich. exs. 226 (COLO, US). *Wisconsin*. Bayfield Co., 1987, Wetmore 61007 (MIN).

15b. subsp. idahoensis (H. Magn.) S. Ekman, comb. et stat. nova

Bacidia idahoensis H. Magn., Acta Horti gothoburg. 19: 45 (1952). – Type: U. S. A., "Idaho, Idaho Co., one half mile up Rackliff Ridge Trail from Rackliff Creek Public Camp Ground, along the Selway River, Nez Perce National Forest, 3100 ft, on *Amelanchier* bark", 1949, Cooke & Cooke 25174 (UPS, holotype).

Nomenclature. The date on the label of the holotype is given as "14 May 1949", but in the protologue it is erroneously cited as "May 15, 1940" There are two facts pointing towards the label bearing the correct date and the protologue an incorrect date. Firstly, Stevenson (1971) mentions that most of the material collected jointly by Dr. Cooke and Mrs Cooke was collected after 1942. Secondly, in the same work, two labels are depicted, one dated June 16, 1939 with the collection number 13257, and one dated November 5, 1949 with the collection number 26271. Provided that the Cookes numbered their collections sequentially, the type specimen of *Bacidia idahoensis* (numbered 25174) must be collected much closer to November 1949 than to June 1939. That the specimen in question really is the holotype, and not some other specimen irrelevant to the typification of the name, is further supported by the fact that in the protologue, the holotype specimen of *Bacidia idahoensis* is stated to occur as an "admixture in *Pertusaria* sp. (conf. *multipuncta*, without spores)". On the label, "*Pertusaria* cfr. *multipuncta*" is mentioned, and this lichen dominates the collection.

Illustrations. Fig. 26 (map).

Thallus rather thick, grey-green, finely areolate. Apothecial margin paler than disc (particularly conspicuous in young apothecia), with an (orange to) dark carmine red to red-brown hue. Hymenium (90-)94-108-125(-131) µm thick (s= 11, N= 9, n= 5). Spores (52-)69-81-96(-108) µm long (s= 11, N= 9, n= 10), (2.5-)2.8-3.1-3.2(-3.7) µm wide (s= 0.3, N= 9, n= 10), with (9-)17.5-19.8-23.0(-28) septa (s= 3.5, N= 9, n= 10).

Ecology. Known phorophytes include *Abies* spp., *Acer glabrum*, *A. macrophyllum*, *Alnus rubra*, *Amelanchier* sp., *Betula papyrifera*, *Cornus nuttallii*, *Pseudotsuga menziesii*, *Quercus garryana*, *Salix* sp., *Taxus brevifolia*, and *Thuja plicata*.

Distribution. Western coastal lowland and western montane region of Oregon, Washington, British Columbia, Idaho, and Montana. The single known locality in Oregon is unspecified and has not been marked on the map. – Endemic.

Additional collections examined. CANADA. *British Columbia*. Vancouver Island, Old Baldy Mountain, 1975, Noble 4399 (herb. Noble). Vancouver Island, NW of Nanoose, 1989, Ekman L755 (LD). Vancouver Island, Thetis Lake, 1989, Ekman L773 (LD). Vancouver Island, Victoria, 1977, Noble 6459c (herb. Noble). Van-

Fig. 27. Known North American distribution of *Bacidia medialis*.

couver Island, Mount Douglas Park, 1991, Ryan (herb. M. Ryan, LD). Prevost Island, 1974, Noble 1221b (herb. Noble). Purden Lake Prov. Park, 1976, Crane & Noble 5953 (CANL, herb. Noble). Wells Gray Provincial Park, 1989, Ekman L800 (LD). – U. S. A. *Idaho*. Priest Lake, 1966, Thiers 17346 (SFSU). *Montana*. Flathead Co., 1983, DeBolt 372 (OSC). Lake Co., 1977, McCune 8928 (OSC), 1989, McCune 17596, 17624, 17627, 17630, 17640, 17642 (OSC). Ravalli Co., 1981, McCune 11435 (OSC). *Oregon*. Cusick (US). *Washington*. Clallam Co., 1989, Ekman L729, L732 (LD). Klickitat Co., 1882, Suksdorf (WTU), 1884, Suksdorf 297 (WTU), 1885, Suksdorf 310 (COLO). Lewis Co., 1989, Thor 8376 (S). Pierce Co., 1994, Tønsberg 20212 (BG).

16. Bacidia medialis (Tuck. ex Nyl.) de Lesd.

Bryologist 24: 68 (1921). - *Lecidea medialis* Tuck. ex Nyl., Annals Sci. nat., 4, 19: 346 (1863). – Type: Nicaragua, Wright (H-NYL 17372 specimen c, lectotype selected here).

Biatora molybditis Tuck., Synops. North Amer. Lich. 2: 34 (1888). - *Bacidia molybditis* (Tuck.) Zahlbr., Cat. Lich. Univ. 4: 126 (1926). – Type: U. S. A., "Florida", 1877, Smith 10 (FH-TUCK, lectotype selected here).

Patellaria rosellina Müll. Arg., Revue mycol. 10: 4 (1888). - *Bacidia rosellina* (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 4: 238 (1926). – Type: Uruguay, "Montevideo", 1887, Arechavaleta (G, lectotype selected here).

Illustrations. Figs 5C, 8B, 27 (map).

Characterization. Thallus usually greenish or brownish. Apothecia usually pale pinkish or yellowish, seldom pale orange to red-brown. Proper exciple colourless to pale brown-orange; lumina wider in lower part than in upper part. Hypothecium colourless to pale brown-orange. Upper part of hymenium colourless to pale brown-orange. Spores bacilliform, fusiform, or almost clavate, (almost) straight, 16-40 × 1.9-3.7 µm, with 3-7 septa.

Thallus indeterminate, thin to rather thick, usually continuous, ± cracked to areolate, wrinkled to warted, sometimes subsquamulose or partly tuberculate to granular, rarely discontinuous, of discrete to contiguous, thin, convex areoles; usually grey-green to green-brown, rarely ± grey. Prothallus lacking or present between discrete areoles and along the edge of the thallus, thin, endophloeodal, pale grey.

Apothecia (0.3-)0.3-0.5-0.7(-0.9) mm diam. (s= 0.6, N= 9, n= 10), at first plane, later becoming convex, epruinose. Disc usually pale pink, pale yellow-pink, or pale yellow, sometimes pale orange to brown-orange to orange-brown to red-brown. Margin concolorous with disc, level with or raised above disc in young apothecia, later level with the disc, rather persistent but usually finally excluded.

Proper exciple laterally (40-)48(-63) µm wide (s= 7, N= 9, n= 1), without crystals, lumina inside rim in upper part 1.2-3.2 µm wide, in lower part 1.5-5.0 µm wide. Rim colourless to pale brown-orange, without distinct zone of enlarged cells along the edge (lumina gradually expanding towards edge or not at all expanded). Lateral interior usually concolorous with rim (sometimes darker or slightly paler), colourless to pale brown-orange, rarely brown-orange. Medullary part colourless to pale brown-orange. Hypothecium colourless to pale brown-orange, rarely brown-orange. Hymenium (45-)47-60-68(-74) µm thick (s= 7, N= 9, n= 5), colourless or partly and diffusely pale yellowish to pale brown-orange. Paraphyses 1.0-1.6 µm wide in mid-hymenium; apices only slightly or not at all swollen, some occasionally ± clavate, (1.0-)1.5-1.7-2.1(-3.2) µm wide (s= 0.4, N= 9, n= 10), without internal pigment. Spores bacilliform, fusiform, or almost clavate, straight or slightly curved, not coiled in ascus, (16-)20-23-26(-40) µm long (s= 3, N= 9, n= 10), (1.9-)2.0-2.8-3.4(-3.7) µm wide (s= 0.5, N= 9, n= 10), (4.8-)6.7-8.2-10.7(-16) times as long as wide (s= 1.9, N= 9, n= 10), with (3-)3.0-3.2-4.2(-7) septa (s= 0.8, N= 9, n= 10).

Pycnidia almost entirely immersed in thallus, colourless, c. 75 µm diam. Conidia filiform, straight or slightly curved, non-septate, 13-17 × 0.8-1.0 µm.

Chemistry: No lichen substances detected.

Pigments: Pigmented parts of apothecia K+ intensifying, N-. – Without pigments or with Rubella Orange in proper exciple, hypothecium, and hymenium.

Ecology. On the bark of hardwoods and shrubs in humid or dry, open or more or less shady forests and forest edges. A few finds are in planted tree-stands. Known phorophytes include *Cedrela odonta*, *Eugenia* spp., *Ilex* sp., *Krugiodendron ferreum*, *Mastichodendron foetidissimum*, *Rhizophora mangle*, *Salix caroliniana*, *Sambucus canadensis*, *Ulmus americana*, and *Ximenia americana*.

Distribution. Florida, southernmost Louisiana, and one unspecified locality in Texas (not on the map). – Probably pantropical.

Discussion. *Bacidia medialis* is closely related to, and easily confused with *B. hostheleoides* (see that species). *B. medialis* is superficially similar to *Bacidina varia*, which can be separated on the basis of the longer and narrower, usually more-septate spores that are never distinctly bacilliform, and on the anatomy of the proper exciple. From Florida and Louisiana, I have seen several specimens of a species of *Catillaria* sensu Zahlbr., which superficially is very similar to *Bacidia medialis*. It is separated from *B. medialis* by the shorter, constantly 2-celled spores and the lack of an ocular chamber in the tholus. I have not come across any published name for this species. It does not belong in *Catillaria* s. str., but may be related to *Lecania naegelii* and *Lecania stigmatella*.

In North American literature, *Bacidia medialis* has mostly been known as *Bacidia molybditis* (Tuck.) Zahlbr. The types of the latter name and *Bacidia rosellina* (Müll. Arg.) Zahlbr. agree completely with *B. medialis*, however. *Bacidia granulifera* (Müll. Arg.) Zahlbr., described from Costa Rica, is apparently very close to (and perhaps conspecific with) *B. medialis*. It differs from *B. medialis* mainly in having consistently 7-septate spores and a slightly higher hymenium (c. 80 µm).

Collections examined. U. S. A. *Florida*. 1877, Smith 10 (FH). Collier Co., 1993, Ekman L1175 (LD). Dade Co., 1985, Thor 4641 (S). Monroe Co., 1993, Ekman L1193, L1194, L1195, L1196, L1197, L1198, L1201 (LD). Polk Co., 1993, Ekman L1167 (LD). Miami, 1924, ex herb. Plitt (US), 1914, Nuttall (US), 1982, Tucker 25230 (herb. Tucker). Sanford, 1914, Rapp 51 (MIN).

17. Bacidia mutabilis Malme

Ark. Bot. 27A (5): 24 (1935). – Type: Brazil, "Matto Grosso, Cuyabá", 1893, Malme (S, lectotype selected here).

Illustrations. Fig. 25 (map).

Characterization. Apothecia pink, with thick white pruina. Proper exciple (almost) colourless, with large clusters of crystals, along the edge with a single cell layer of enlarged cell lumina. Hypothecium (almost) colourless. Upper part of hymenium colourless. Spores acicular, 33-57 × 2.9-3.7 µm, with 3-9 septa. – Neotropical specimens usually have pale orange to purplish black apothecia, a pale yellow, brown-orange, or partly red-brown rim of the proper exciple, which is concolorous with the upper part of the hymenium.

Thallus determinate, thin, continuous, ± cracked, wrinkled, pale green-grey. Prothallus lacking or present, bordering the thallus, narrow, black.

Apothecia (0.4-)0.5-0.5-0.6(-0.6) mm diam. (s= 0.06, N= 2, n= 10), plane or moderately convex, with thick white pruina, particularly on the margin. Disc pink. Margin pale pink, raised above disc in young apothecia, soon level with the disc, persistent.

Proper exciple laterally (77-)82(-86) µm wide (s= 6, N= 2, n= 1), with abundant large clusters of crystals (single crystals up to 9 µm diam.). Rim colourless, along the edge with a single layer of enlarged cells that are up to 5 × 3 µm. Lateral interior colourless. Medullary part colourless or very pale yellow. Hypothecium colourless or very pale yellow. Hymenium (56-)65-68-71(-74) µm thick (s=6, N=2, n=5), colourless, uppermost part with thick layer of crystals. Paraphyses 0.8-1.6 µm wide in mid-hymenium; apices not at all swollen, slightly tapering, or narrowly clavate, (1.0-) 1.4-1.6-1.7(-2.8) µm wide (s= 0.5, N= 2, n= 20), without internal pigment. Spores acicular, straight, curved, or sigmoid, ± straight in ascus, (33-)42-44-47(-57) µm long (s= 6, N= 2, n= 20), (2.9-)3.3-3.3-3.4(-3.7) µm wide (s= 0.3, N= 2, n= 20), (9.3-)12.7-13.6-14.4(-18.4) times as long as wide (s= 2.3, N= 2, n= 20), with (3-) 5.9-6.2-6.3(-9) septa (s= 1.4, N= 2, n=20).

Pycnidia not seen.

Chemistry: Atranorin and zeorin.

Pigments: Hypothecium and proper exciple K+ pale yellow, N-. – Sometimes Rubella Orange in hypothecium and medullary part of proper exciple. Unknown, K+ yellow substance in proper exciple. This substance is probably not atranorin, since the secondary metabolites in *Bacidia* are generally restricted to the thallus.

Ecology. *Bacidia mutabilis* was collected on the branches of *Rhizophora mangle* and *Conocarpus erectus* in a dense mangrove stand.

Distribution. Presently known from only two specimens collected at West Lake in Everglades National Park, southernmost Florida. – Previously known from a number of localities in Brazil and Paraguay.

Discussion. Although a rather nondescript species, *B. mutabilis* can be recognized by a combination of characters: dominance of Rubella Orange in the apothecia, a thin or absent zone of enlarged cell lumina along the edge of the proper exciple, presence of crystals in the proper exciple, and presence of a thick white pruina in at least some young apothecia. The Florida specimens of *B. mutabilis*, however, deviate from South American specimens in being very poorly pigmented and in having more crystals in the proper exciple. These differences may be entirely due to habitat modification. The locality in Florida is very shady and humid, whereas Malme (1935) reported it from light forests.

In typical South American *B. mutabilis*, the colour of the apothecia is very variable, even within the same thallus. They vary from pale orange to brown-orange to purple-brown to purplish black (disc and margin ± concolorous except lower part of margin, which may be paler). The upper part of the hymenium and the edge of the proper exciple is pale yellow to brown-orange (Rubella Orange), sometimes partly red-brown (Laurocerasi Brown). The remainder of the apothecial tissues is colourless to very pale yellow. Along the rim of the proper exciple, there is a 1-2 cell layers thick zone of cells with enlarged lumina. Crystals are abundant in the proper exciple, but they do not obscure the tissues as in the Florida specimens.

Bacidia mutabilis can be confused with, above all, *B. rosella* and *B. suffusa*. *B. rosella* can be separated by the thicker apices of the paraphyses and by the absence of a pruina in the strict sense (although it has a layer of crystals between the paraphyses and in the proper exciple). *B. suffusa* has a wider zone of enlarged cell lumina along the edge of the proper exciple, a thicker thallus lacking prothallus, and generally larger apothecia.

Collections examined. U. S. A. *Florida*. Dade Co., 1993, Ekman L1193, L1194 (LD).

18. Bacidia polychroa (Th. Fr.) Körb.

Parerga Lich., fasc. 2: 131 (1860). - *Biatora polychroa* Th. Fr., Öfvers. K. VetenskAkad Förh. 12 (1): 17 (1855). – Type: Ukraine, "Ucrania in Acere campestri", probably collected near Charkow, Czerniajev (UPS, lectotype selected here).

Verrucaria fuscorubella Hoffm., Deutschl. Flora 2: 175 (1796), nom. inval. - *Lecidea luteola* var. *fuscorubella* Ach., Meth. Lich. 61 (1803). - *Secoliga fuscorubella* (Ach.) Stizenb., Nova Acta Acad. Caesar. Leop. Carol. 30 (3): 53 (1863). - *Bacidia fuscorubella* (Ach.) Bausch, Verh. naturw. Ver. Karlsruhe 4: 107 (1869). – Type: Germany, "Germania" (H-ACH 345A, lectotype selected here).

Lecidea subspadicea Nyl., Sert. Lich. Trop. Labuan et Singapore 39 (1891), nom. illeg. (homonym of the 1-2 months older *Lecidea subspadicea* (Müll. Arg.) Stizenb.). - *Bacidia subspadicella* Zahlbr., Cat. Lich. Univ. 4: 244 (1926). – Type: U. S. A., "Jacksonville, Florida", 1888, Eckfeldt (H-NYL 17119, lectotype selected here).

Nomenclature. *Verrucaria fuscorubella* was not accepted by the author in the original publication (Hoffmann 1796), and the name is consequently invalid (Art. 34.1). In the preface, Hoffmann states that taxa within brackets or lacking a number (as, e.g., *Verrucaria fuscorubella*) are doubtful ("Varietates autem, subspecies, atque etiam tales species, quales ut veras statuere adhuic dubitavi, aut uncis ( ) inclusas in adnotationibus, aut numero carentes speciei proxime confini adpositas reperies").

The type collection of *Lecidea subspadicea* Nyl. contains a mixture of typical *Bacidia polychroa* (dominating) and *B. suffusa*. It is clear, however, that Nylander referred to *B. polychroa*, since the K-reaction of the hypothecium and the proper exciple is mentioned in the diagnosis.

Illustrations. Figs 28 (map), 41G.

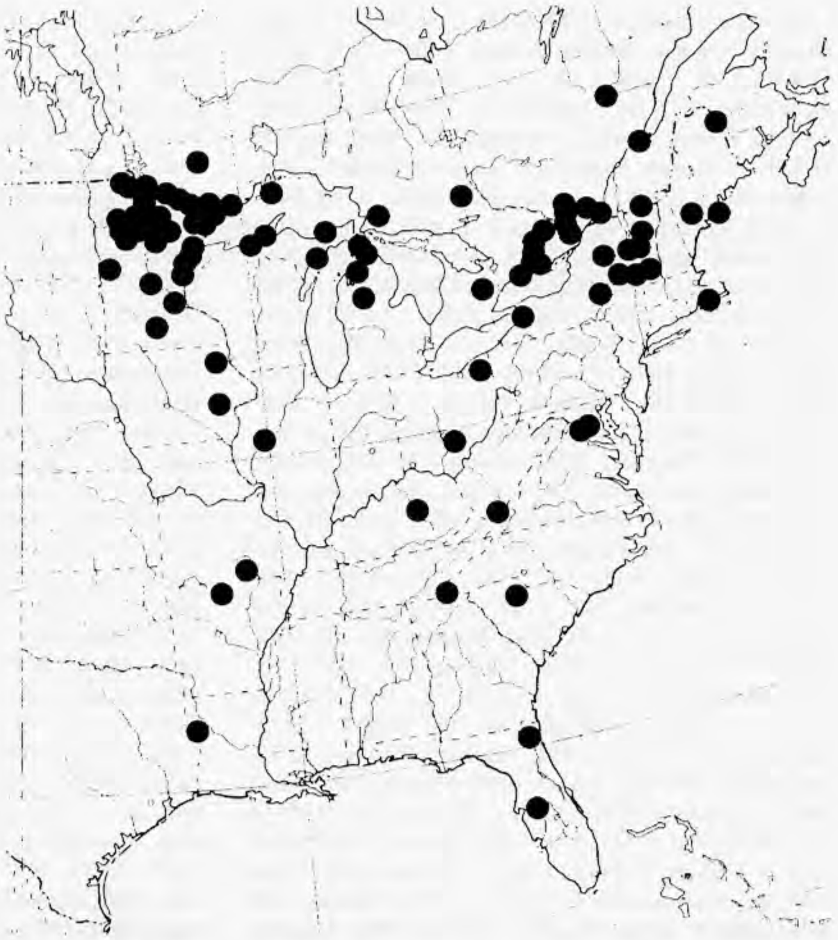
Characterization. Thallus cracked to areolate. Apothecia brown-orange to red-brown to dark purplish brown, sometimes pruinose. Proper exciple usually ± brown-orange to orange-brown. Hypothecium darker than proper exciple. Upper part of hymenium colourless to orange-brown. Most pigmented parts K+ purple-red. Spores acicular, 31-74 × 1.9-5.0 µm, with 2-15 septa.

Thallus indeterminate, thin to thick, either continuous, finely wrinkled to warted, ± cracked or sometimes areolate, or discontinuous, of thin, discrete to contiguous, convex areoles, almost white to grey or yellowish grey.

Apothecia (0.4-)0.6-0.7-0.8(-1.2) mm diam. (s= 0.1, N= 22, n= 5), ± plane when young, later becoming convex, epruinose or with thin to thick white pruina on edge and disc of young to medium-aged apothecia. Disc brown-orange to medium brown to red-brown to purplish brown, rarely orange or dark purple-brown, often darkening as the apothecia age. Margin concolorous with disc or slightly darker, thick and raised above disc in young apothecia, later level with the disc, and finally excluded in old and convex apothecia.

Proper exciple laterally (45-)63(-95) µm wide (s= 13, N= 22, n= 1), without crystals or with radiating clusters of minute crystals (up to 1 µm). Rim ± brown-orange or ± orange-brown, sometimes pale yellowish, pale yellowish brown, or pale to dark brown, along the edge without or with a single cell layer thick zone of cells with enlarged lumina that are up to 9 × 5 µm. Lateral interior usually ± concolorous with rim (sometimes paler or darker). Medullary part concolorous with lateral interior part or slightly paler. Hypothecium ± brown-orange, ± orange-brown, red-brown, or dark brown, darker than proper exciple

Fig. 28. Known North American distribution of *Bacidia polychroa*.



(pigmentation distinctly or indistinctly delimited). Hymenium (56-)63-77-94(-102) µm thick (s= 10, N= 22, n= 5), constituting (19-)29(-39) % of the entire height of the apothecium (s= 6, N= 22, n= 1), in lower part colourless or very pale brown-orange to pale brown, upper part concolorous or (rarely) with fairly distinct brown-orange pigmentation. Paraphyses 1.0-1.6 µm wide in mid-hymenium; apices ± clavate or not at all swollen, (1.2-)1.7-2.3-3.0(-3.7) µm wide (s= 0.5, N= 22, n= 5), without internal pigment. Spores acicular, straight, curved, or sigmoid, sometimes coiled in young asci, (31-)38-48-57(-74) µm long (s= 7.4, N= 22, n= 10), (1.9-)2.3-2.7-4.0(-5.0) µm wide (s= 0.5, N= 22, n= 10), (7.3-)11.4-18.2-21.6(-30.0) times as long as wide (s= 3.8, N= 22, n= 10), with (2-)3.1-6.3-11.9(-15) septa (s= 2.4, N= 22, n= 10).

Pycnidia ± immersed in thallus, pale brown or pale orange-brown above, 100-170 µm diam. Conidia filiform, curved, non-septate, 10-17 × 0.6-0.8 µm.

Chemistry: Atranorin (usually only trace amounts) or no lichen substances at all.

Pigments: Most parts of apothecia K+ purple-red, N-. – Bacidia Brown and Rubella Orange in hymenium, hypothecium, proper exciple, and pycnidial wall.

Ecology. Mainly on the coarse bark of old trees in shady or semi-open, usually humid habitats. It prefers *Fraxinus* spp. and *Thuja occidentalis*, but has also been found on *Acer saccharum*, *Alnus* sp., *Carya* spp., *Celtis occidentalis*, *Fagus grandifolia*, *Juglans cinerea*, *Liriodendron tulipifera*, *Ostrya virginiana*, *Platanus occidentalis*, *Populus* spp., *Quercus* sp., *Salix* sp, *Taxodium distichum*, *Tilia americana*, and *Ulmus americana*.

Distribution. Eastern temperate region with a preference for the Great Lakes, Appalachians, and the Ozark Plateau. – Europe.

Discussion. *Bacidia polychroa* is similar to *B. diffracta* and *B. rubella*. *B. rubella* can be separated by the granular thallus and the lack of a K+ purple-red pigment (Bacidia Brown) in the apothecia. For details on the separation of *B. polychroa* and *B. diffracta*, see the latter species and the chapter *Numerical and statistical chapter*.

Collections examined. CANADA. Calkins 101 (MIN). *Ontario*. Algoma District, Aubrey Falls, 1965, Brodo 7208 (CANL). Carleton Co., 1978, Brodo 22774 & Egger (CANL, COLO). Dufferin Co., 1984, Wong 3596, Krug & Warren (CANL). Hastings Co., 1893, Macoun 189 (NY). Kenora District, 51 mi E of Dryden, 1969, Brodo 14872 (CANL). Lanark Co., 1986, Wong 3976 (CANL). Lennox & Addington Co., 1972, Wong 855b, Shchepanek & Ley (CANL). Northumberland Co., 1979, Wong 3194 (CANL). Ottawa-Carleton Co., 1989, Ekman L1018, L1019, L1020, L1021, L1022 (LD). Renfrew Co., 1985, Brodo 25212 (CANL), 1986, Wong 4094 (CANL). Belleville, 1868, 1882 (CANL), + 1882, Macoun 2805 (filed with *B. suffusa*, CANL). + Belleville and Ottawa, 1881, Macoun 63 (filed with *B. suffusa*, US). Britannia, 1902, Macoun (CANL). Carp, 1907, Macoun (CANL, FH). Central Ontario Junction, 1893, Macoun 189 (CANL). Emo, 1901, Fink 708, 712 (MIN). Hull, 1900, Macoun 390 (CANL). Lake Timagami, 1936, Cain (COLO, US), 1945, Cain (SFSU). Ottawa, 1884, Macoun 2791, 2795, 2799 (CANL), 1884, Macoun 61 (CANL, US), 1891, Macoun 68, 102, 273-74, 275-76 (CANL), 1891, Macoun 102, 339 (US), 1891, Macoun 190 (CANL, COLO, US), 1892, Macoun 571/2779 (CANL), 1893, Macoun 191 (CANL), 1893, Macoun 191 (COLO), 1898, Macoun 340 (US), 1905, Macoun 191 (CANL, US), + 1884, Macoun 2804 (filed with *B. suffusa*, CANL), + 1891, Macoun 273-74 (filed with *B. suffusa*, CANL), + 1892, Macoun 2807 (filed with *B. suffusa*, CANL), + 1897, Macoun 2801 (filed with *Bn. chloroticula*, CANL), + 1900, Macoun 221 (filed with *B. suffusa*, CANL, COLO), 1905, Macoun 191 (filed with *B. suffusa*, CANL). Seymour, 1893, Macoun 2786 (CANL). Victoria Park, 1902 (CANL). *Quebec*. Argenteuil Co., 1984, Brodo 25017b & Brodo (CANL). Gatineau Co., 1983, Brodo 24967a, Gowan & Selva (CANL, NY), 1989, Ekman L1028, L1029 (LD). Aylmer, 1891, Macoun 281 (CANL), 1907, probably collected by Macoun (CANL). Hull, 1891, Macoun 68/2781 (CANL), 1902, probably collected by Macoun (CANL), 1907, 1911, probably collected by Macoun (CANL). Lac St-Jean-0., Ile de la Traverse, 1984, Lutzoni 840718-L167 (2/2) (CANL). Lake Memphremagog, Willey (US). Montmorency Falls, 1905, Macoun (FH). Montmorency, 1905, Macoun (CANL). Montmorency River, 1904, Macoun 68/3805 (CANL), 1905, Macoun 69/3804 (CANL), without year and collector but probably collected by Macoun (CANL). Montreal, 1966, DeSloover & LeBlance 257 (CANL). – U. S. A. *Arkansas*. Izard Co., 1988, Harris 21653 (NY). *Florida*. Polk Co., 1917, Jennings 5758 (US), 1916, 1917, Jennings (COLO). Jacksonville, 1888, Eckfeldt (type specimen of *Lecidea subspadicea* Nyl., H-NYL). *Illinois*. Calkins 114 (NY). Canton, unknown collector (NY), 1888, Wolf (NY), Wolf 17, s. n. (US). *Iowa*. Fayette Co., 1894, Fink (CANL, MIN, NY, US), + 1894, Fink (filed with *B. suffusa*, US). Johnson Co., 1898, Shimek (MIN). Iowa City, Shimek (MIN). *Kentucky*. Jessamine Co., 1951, Prescott 87 (US). *Louisiana*. Sabine Par., 1970, Tucker 8883 (US), + 1967, Wetmore 17587 (filed with *B. schweinitzii*, MIN), + 1970, Tucker 8883 (filed with *B. diffracta*, herb. Tucker), + 1970, Tucker 8883 (filed with *B. suffusa*, COLO). *Maine*. Aroostook Co., 1893, Cummings, Cummings: Decades N. Am. Lich. 208 (NY, US), 1893, Cummings & Teller, Cummings: Decades N. Am. Lich. 228 (NY, US). Oxford Co., 1929, Parlin (NY). Camden, 1905, Merrill 536 (FH). South Thomaston, 1909, Merrill (FH). Warren, 1910, Merrill (FH). *Maryland*. Montgomery Co., 1907, Fink 20 (US). Takoma Park, 1896, Williams, Cummings: Decades N. Am. Lich. 258 (FH, NY, US), 1896, Williams, Cummings et al.: Lich. Boreali-Am. 195 (COLO). *Massachusetts*. New Bedford, Willey (FH, US), 1886, Willey (US), + Willey (filed with *B. diffracta*, MIN). *Michigan*. Alger Co., 1987, Wetmore 58909, 59114 (MIN). Charlevoix Co., 1979, Tan 79-322 (CANL). Cheboygan Co., 1958, Shetler M323 (US), 1974, Buck (NY). Delta Co., 1976, Harris 11979 (CANL), + 1977, Brodo 22475 (filed with *B. diffracta*, CANL). Gogebic Co., 1975, Harris 10049 (MIN), 1989, Ekman L965, L968, L969, L972, L980 (LD). Keweenaw Co., 1983, Wetmore 48343 (CANL, MIN), + 1983, Wetmore 48690 (filed with *B. rubella*, MIN), + 1984, Wetmore 51516 (filed with *B. rubella*, MIN). Mackinac Co., 1977, Harris 12353 (NY), 1977, Harris 12566a (UBC). Missaukee Co., 1962, Awasthi (COLO). Ontonagon Co., 1989, Ekman L990, L993, L998 (LD). *Minnesota*. Aitkin Co., 1985, Wetmore 53635, 53654 (MIN). Becker Co., 1974, Wetmore 23854 (MIN). Beltrami Co., 1900, Fink 681 (MIN), 1977, Trana 3697 (MIN). Blue Earth Co., 1899, Fink 35 (MIN), + 1899, Gardner 77 (filed with *B. suffusa*, NY). + Cass Co., 1976, Trana 1115 (MIN). Clearwater Co., 1972, Wetmore 20355 (MIN), 1974, Wetmore 22822, 23125 (MIN), 1976, Wetmore 26020, 26068, 26096, 26145, 26202 (MIN), 1978, Wetmore 35844, 36338 (MIN), 1980, Wetmore 41655, 41679 (MIN). Cook Co., 1986, Wetmore 57067 (MIN). Hennepin-Ramsey Co., 1896, Fink 107 (MIN). Hubbard Co., 1974, Wetmore 23258 (CANL, MIN). Itasca Co., 1985, Wetmore 53619 (MIN), 1977, Trana 2998 (MIN, WWB), 1977, Trana 3007, 3013, 3057a, 3211b (MIN). Koochiching Co., 1901, Fink 892, 981 (MIN), Hale 22139 (US), 1978, Wetmore 33473, 33495, 33499, 36579, 36612 (MIN), 1978, Wetmore 33480 (CANL, MIN), 1979, Wetmore 37337, 37407, 37414, 37446, 37557 (MIN), 1979, Wetmore 37922 (MIN, NY). Lake Co., 1897, Fink 816, 861, 872 (MIN), 1986, Trana 13733, 13993, 14191 (MIN), 1989, Ekman L931, L941, L951 (LD). Lake of the Woods Co., 1896, MacMillan 7 (MIN), 1901, Fink 72, 78, 80, 407 (MIN). Mahnomen

Co., 1976, Wetmore 26441 (CANL, MIN). Otter Tail Co., 1900, Fink 72, 172 (MIN). Pennington Co., 1900, Fink 868 (MIN). Pine Co., 1983, Schuster 450, 552, 859, 1364, 1534, 1946 (MIN). Roseau Co., 1901, Fink 221, 274, 301 (MIN). St. Louis Co., 1901, Fink 1516, 1770 (MIN), 1902, Fink 5463 (MIN), 1973, Wetmore 21685 (MIN), 1977, Wetmore 27534, 27967, 30791, 30860, 30867 (MIN), 1978, Wetmore 31338a, 31348, 31372, 31449, 31782, 31783, 31792, 32472, 32693, 33047, 33140, 33144, 33269, 33925, 34214, 34431, 34448, 34668, 34768, 34850, 34913 (MIN), 1978, Wetmore 34610 (CANL, MIN), 1978, Wetmore 34715 (NY), 1978, Wetmore 32480, 33378 (COLO, MIN), 1979, Wetmore 38263, 38605, 39156, 39737, 39830, 40265, 40269 (MIN), 1986, Trana 13331, 13493 (MIN), 1986, Wetmore 57599 (MIN, NY). Collegeville, 1910, Hansen 1 (MIN). Minneapolis, 1896, Fink 101 (US). Red Lake, 1900, Fink 892 (CANL, MIN). Snowbank Lake, 1897, Fink 861 (US). St. Cloud, 1897, Morgan (US). *Missouri*. Oregon Co., 1988, Harris 21713a (NY). *New York*. + Buffalo, Wilson (filed with *B. suffusa*, US). East Galway, 1893, Burt (FH), + 1893, Burt (filed with *B. suffusa*, FH). Newcomb, 1936, Lowe 6007 (NY). Richfield Springs, Willey (US). Shushan, Plitt 28 (US). Warrensburg, 1933, Lowe 3649a (NY). *North Carolina*. Swain Co., 1976, Harris 11009 (NY), 1987, Harris 20975 (NY). *Ohio*. 1897, Bogue (NY). Bogue 874 (NY). Orwell, 1891, Bogue, Merrill: Lich. exs. 171 (COLO, US). Sugar Grove, 1893, Bogue 419 (NY). *South Carolina*. Lamoille Co., 1985, Harris 18256 (NY). Chester, 1882, Green (US), 1883, Eckfeldt 48, 102 (CANL). *Vermont*. Brandon, 1920, Dutton 989 (COLO), 1921, Merrill 1189 (WIS). Jamaica, 1906, Dobbin (NY). Leicester, 1915, Merrill 864 (US). *West Virginia*. Mercer Co., 1963, Brodo B-4596, 4610 & Brodo (CANL).

19. Bacidia reagens Malme

Ark. Bot. 27A (5): 20 (1935). – Type: Brazil, "Rio Grande do Sul: Santo Angelo pr. Cachoeira", 1893, Malme 970 (S, lectotype selected here).

Illustrations. Figs 29 (map), 41H.

Characterization. Apothecia usually grey-brown to black-brown. Proper exciple with some green-grey to dirty green and some orange pigmentation. Hypothecium very pale yellowish to brown-orange. Upper part of hymenium dominated by a green-grey to dirty green pigment (same as in proper exciple), which reacts C+ violet. Spores acicular (rarely long-bacilliform), 22-69 × 1.6-2.9 µm, with 3-15 septa.

Thallus indeterminate, ± thin, either discontinuous, of discrete or contiguous, convex, often almost granular or slightly effigurate areoles that are sometimes warted or subsquamulose, or continuous, ± cracked to areolate, wrinkled or warted, grey-green or grey-brown. Prothallus sometimes present between discrete areoles, thin, endophloeodal, pale grey.

Apothecia (0.3-)0.4-0.4-0.5(-0.7) mm diam. (s= 0.09, N= 4, n= 10), plane or moderately convex, remaining so or sometimes becoming markedly convex, epruinose. Disc usually grey-brown to dark purplish brown to black-brown, seldom pink, pale orange, blue-grey, or yellow-brown, sometimes mottled with different colours. Margin concolorous with disc or slightly darker, sometimes paler in lower part (to pale grey) than in upper part, level with or raised above disc in young apothecia, soon level with the disc, persistent.

Proper exciple laterally (26-)44(-60) µm wide (s= 17, N= 4, n= 1), without crystals. Rim grey-brown to green-grey to dirty green in upper part, downwards often changing to colourless to pale orange, with cell lumina gradually slightly enlarging towards the edge (wider in lower part than in upper part). Lateral interior colourless to pale orange to grey-brown; if grey-brown then downwards usually changing to colourless or pale orange. Medullary part colourless to brown-orange. Hypothecium very pale yellowish to brown-orange, rarely colourless. Hymenium (53-)57-65-82(-84) µm thick (s= 11, N= 4, n= 5), lower part colourless, upper part green-grey or dirty green, sometimes with grey-brown spots. Paraphyses 1.0-1.2 µm wide in mid-hymenium; apices ± clavate or only slightly swollen, sometimes not thickened or even slightly tapering, (0.8-)1.3-2.3-2.9(-4.4) µm wide (s= 0.8, N= 4, n= 10), without internal pigment but sometimes with a distinct external hood of greenish or brownish pigment. Spores acicular or occasionally long-bacilliform, straight or slightly curved, occasionally sigmoid, not coiled in ascus, (22-)29-37-59(-69) µm long (s= 14, N= 4, n= 10), (1.6-)1.8-2.0-2.6(-2.9) µm wide (s= 0.4, N= 4, n= 10), (11.2-)15.8-17.8-22.8(-28.0) times as long as wide (s= 3.8, N= 4, n= 10), with (3-)3.5-6.8-12.5(-15) septa (s= 4.0, N= 4, n= 10).

Pycnidia not seen.

Chemistry: No lichen substances detected.

Pigments: Edge, inner upper part of proper exciple (sometimes), and upper part of hymenium K+ purple to violet, C+ violet, N+ red. Hypothecium and most of the inner part of proper exciple K+ intensifying, C-, N-. – Thalloidima Green in proper exciple and upper part of hymenium. Laurocerasi Brown in upper part of hymenium. Rubella Orange in proper exciple and hypothecium.

Fig. 29. Known North American distribution of *Bacidia reagens* (squares), *B. rosella* (triangles), and *B. russeola* (star). Known world distribution of *Bacidia salmonea* (dots).

Ecology. On the bark of hardwoods in shady and humid localities. Known phorophytes include *Acer macrophyllum*, *Nyssa sylvatica*, and *Quercus agrifolia.*

Distribution. Known from a few localities in coastal southern California and from one locality each in southern Louisiana and southernmost Georgia. – *Bacidia reagens* has previously been reported only from the type collection and one additional collection, both from Rio Grande do Sul in southern Brazil (Malme 1935). It is an inconspicuous species likely to escape attention. Thus, it is uncertain whether it is widely distributed in the neotropics with some outliers in the subtropical areas of the U. S. and southern South America, or restricted to subtropical areas north and south of the neotropics.

Discussion. Bacidia reagens is superficially similar to *Bacidia absistens*, *B. subincompta*, *B. circumspecta*, and *B. igniarii.* Unlike these species, *B. reagens* contains Thalloidima Green in the apothecia, which reacts C+ violet.

I know of only one additional species of *Bacidia* s. str. that contains Thalloidima Green in the apothecia, namely *B. violascens* K. Kalb & Vězda, described from Hawaii (Kalb & Vězda 1980). It is very similar to *B. reagens* in pigmentation but differs in the shorter and wider, fusiform spores that are usually only 3-4 times as long as wide.

Collections examined. U. S. A. *California.* Monterey Co., 1989, Ekman L627, L628, L801 (LD). Santa Barbara Co., 1989, Ekman L619, L620 (LD). *Georgia.*

Ware Co., 1989, Wetmore 65677 (MIN). *Louisiana*. East Baton Rouge Par., 1972, Tucker 10007 (herb. Tucker).

20. Bacidia rosella (Pers.) De Not.

G. Bot. ital. 2, 1 (1): 190 (1846). - *Lichen rosellus* Pers., Annaln Bot. 7: 25 (1794). – Type: Germany, "Schwerin (Mecklenburg), an Buchen und von da auf Eichen übersiedelnd", Wüstnei, Rabenhorst: Lich. Eur. exs. 30 (UPS, neotype selected here)

Nomenclature. I have been unable to trace any original material of *Lichen rosellus* Pers., which was described from the vicinity of Göttingen in Germany. The neotype, a well-developed collection from Schwerin in northern Germany, has been distributed as Rabenhorst: Lich. Eur. exs. 30. According to Lynge (1915) and Sayre (1969), this exsiccate is found also in B, FH, NY, STR, and W. The isotypes in these herbaria have not been studied by me.

Illustrations. Fig. 29 (map).

Characterization. Apothecia ± pink. Proper exciple colourless, with evenly dispersed, minute crystals. Hypothecium (almost) colourless. Hymenium colourless, inspersed with crystals in upper part. Spores acicular, 36-62 × 1.6-2.5 µm, with 3-11 septa.

Thallus indeterminate, thin, usually continuous, warted, slightly cracked or without cracks, or sometimes partially discontinuous, of discrete, warted areoles, light grey. Prothallus lacking or present between discrete areoles, light grey.

Apothecia (0.4-)0.5-0.5-0.5(-0.6) mm diam (s= 0.1, N= 2, n= 10), at first plane, later becoming markedly convex, epruinose (but with a granular inspersed epithecium). Disc pale pink or pale yellowish pink. Margin concolorous with or slightly paler than disc, distinct, slightly raised above disc in young apothecia, soon level with the disc, and finally excluded.

Proper exciple laterally (48-)63(-72) µm wide (s= 13, N= 3, n= 1), with evenly dispersed, minute crystals (less than 1 µm in diam) that are abundant in the upper part but more sparse in the lower part, colourless in all parts. Rim along the edge with a single cell layer of enlarged cells with lumina that are up to 9 × 6 µm. Hypothecium colourless or very pale yellowish. Hymenium (71-)76-80-85(-87) µm thick (s= 5, N= 2, n= 5), colourless, inspersed with crystals between the paraphyses apices in the upper 10-15 µm; crystals less than 1 µm. Paraphyses 0.8-1.2 µm wide in mid-hymenium; apices ± clavate, (1.6-)2.2-2.3-2.5(-3.2) µm wide (s= 0.4, N= 2, n= 10), without pigment. Spores acicular, curved or sigmoid, coiled in young asci, (36-)46-46-47(-62) µm long (s= 6, N= 3, n= 10), (1.6-)2.0-2.1-2.2(-2.5) µm wide (s= 0.3, N= 3, n= 10), (16.5-)20.8-21.8-23.5(-30.0) times as long as wide (s= 3.8, N= 3, n= 10), with (3-)5.6-7.4-8.7(-11) septa (s= 2.5, N= 3, n= 10).

Pycnidia half-immersed in thallus, colourless, 100-175 µm diam. Conidia filiform, slightly curved, distinctly 5-9-septate, 27-35 × 1.2-1.6 µm.

Chemistry: No lichen substances detected.

Pigments: All parts of apothecia without reactions in K, C, or N. – Sometimes small amounts of Rubella Orange (?) in hypothecium.

Ecology. The localities on Isle Royale are mixed conifer-hardwood forests situated on more or less dry ridges, where *B. rosella* occurs on *Populus tremuloides*. On Slate Island, it was found on *Acer spicatum* in a conifer forest along the shore of a stream. The Moose Factory locality is a mixed *Abies balsamea-Populus balsamifera* stand at the edge of a stream, where *B. rosella* was collected on the trunk of a fallen *Populus balsamifera*.

Distribution. Presently known only from the vicinity of Moose Factory close to James Bay in northern Ontario, and from Isle Royale and Slate Islands in the northern part of Lake Superior (Michigan and Ontario, respectively). – Europe.

Discussion. Most North American specimens previously referred to *B. rosella* are misidentified specimens of *B. polychroa*, *B. rubella*, and *B. suffusa*. Of these species, only the last can sometimes be truly similar to *B. rosella*. In particular, forms of *B. suffusa* with a light grey thallus and pigment deficient apothecia are easily mistaken for *B. rosella*. In such cases, *B. suffusa* can be separated from *B. rosella* by the 4-6 cell layers thick zone of enlarged cell lumina along the edge of the proper exciple, the presence of radiating clusters of rather large crystals in the proper exciple (not evenly distributed minute crystals as in *B. rosella*), and the absence of a layer of crystals in the epithecium (although pruina my be present on the surface of the apothecia). There are two further species of *Bacidia* that are similar to *B. rosella*, namely *B. mutabilis* and *B. salmonea* (see these species). In addition, *B. rosella* has some superficial resemblance with *Bacidina crystallifera* (q.v.).

North American specimens deviate slightly from European in appearing more poorly developed: The thallus is thinner, the apothecia are smaller and the apothecial margin is proportionately thinner. Furthermore, European *B. rosella* has different conidia. The shape is similar to North American specimens, but they are much thinner (0.5-0.8 µm) and shorter (10-17 µm), and, above all, non-septate. This means that in this character, European *B. rosella* is more similar to most other species of *Ba-*

cidia than to North American *B. rosella*. A case could be made for recognizing North American *B. rosella* taxonomically. Given the overall anatomical similarities and the very small number of known North American specimens, I refrain from doing so at the moment.

Collections examined. CANADA. *Ontario*. Thunder Bay District, 1977, Wetmore 29024 (MIN). + Cochrane District, 1969, Brodo 14717c (filed with *B. subincompta*, CANL) – U. S. A. *Michigan*. Keweenaw Co., 1980, Wetmore 41319B (MIN), 1983, Wetmore 49341 (MIN).

21. Bacidia rubella (Hoffm.) A. Massal., nom. cons. prop.

Ricerch. Auton. Lich. 118 (1852). - *Lichen rubellus* Ehrh., Plant. Crypt. Linn. 196 (1791), nom. nudum. - *Verrucaria rubella* Hoffm., Deutschl. Flora 2: 174 (1796). - *Bacidia rubella* (Hoffm.) A. Massal., Ricerch. Auton. Lich. 118 (1852). – Type: Germany, Hannover, Ehrhart: Plant. Crypt. Linn. 196 (GOET, lectotype selected here). - Proposed conserved type: Sweden, "Gotland Prov., Atlingbo par., Lilla Atlings forest meadow, c. 1.6 km ESE Atlingbo church. 57°28'N 18°22'E. On *Ulmus minor*", 1990, Nordin, Sundin & Thor, Moberg: Lichenes selecti exsiccati upsaliensis 107 (UPS, isotypes in several herbaria, see Moberg 1991).

?*Lichen lutereus* J. F. Gmel., Systema Naturae, ed. 13, tom 2, pars 2: 1359 (1792). - *Lichen luteolus* Schrad., Spicil. Flor. German. 85 (1794), nom. illeg., non J. F. Gmel. 1792 (p. 1368). (superfluous younger homonym). - *Lecidea luteola* (Schrad.) Ach., Meth. Lich. 60 (1803), nom. illeg. (superfluous; including the types of both *Lichen lutereus* Gmelin and *Verrucaria rubella* Hoffm.). - *Biatora luteola* (Schrad.) Fr., K. svenska VetenskAkad. Handl. 1822: 272 (1822), nom. illeg. (superfluous). - *Bacidia luteola* (Schrad.) Mudd, Manual Brit. Lich. 183 (1861), nom. illeg. (superfluous). – Type: Not seen.

?*Lichen corticalis* Rutstr., Spicil. Plant. Cryptog. Suec. 7 (1794). – Type: Not seen, probably lost.

Nomenclature. The oldest name, the present type of which is conspecific with *B. rubella* is *Lichen vernalis* L., better known as *Biatora vernalis* (L.) Fr. (Jørgensen et al. 1994a). Fortunately, this name has been proposed to be conserved with a conserved type agreeing with its present usage (Jørgensen et al. 1994b). *Lichen vernalis* L. is the type species of *Biatora* Fr.: Fr., and unless conserved, the generic name *Biatora* will take precedence over *Bacidia*, and *Biatora vernalis* will take precedence over *Bacidia rubella*.

The types of *Lichen lutereus* and *Lichen corticalis* have not been studied. *Lichen lutereus* is, next to *Lichen vernalis* L., the oldest name for *Bacidia rubella*, provided that the type of *Lichen lutereus* J. F. Gmel. turns out to fall within the present concept of the species. In the protologue of *Lichen lutereus*, Gmelin (1792) referred to Schrader. It is unlikely that Gmelin ever saw any material of this species; he probably relied on information provided by Schrader. Later, Schrader (1794) made *Lichen luteolus*, which is superfluous since he included (by direct reference) *Lichen lutereus* J. F. Gmel. Unfortunately, Schrader erroneously cited *Lichen lutereus* as "*Lichen luteolus*", but from the phrase description ("cinereus, tuberculis, sparsis, lutescentibus") and the reference to a page and the number of the species ("Gmel. Syst. Nat. II p. 1359 n. 50"), it is clear that he referred to *Lichen lutereus*. This has caused some confusion, since Gmelin's treatment included also a "genuine" *Lichen luteolus* J. F. Gmel. (1792: 1368, no. 161). Thus, *Lichen luteolus* Schrad. is not only a superfluous synonym of *Lichen lutereus* J. F. Gmel., but a younger homonym of *Lichen luteolus* J. F. Gmel. All subsequent combinations based on *Lichen luteolus* Schrad. (including the much used *Bacidia luteola*), by direct or indirect reference, includes the type of *Lichen lutereus* and are thus nomenclaturally superfluous. If any original material of *Lichen lutereus* Schrad. can be traced and it turns out to belong to *Bacidia rubella* in the present sense, then *Bacidia luterea* would be the correct name for this species. This name has never been in use, however. To minimize the number of disadvantageous nomenclatural changes, I suggest that *Lichen lutereus* J. F. Gmel. be rejected, provided that future investigations prove the type of this name to agree with *B. rubella* auct. It should be noted that *Lichen lutereus* or a combinatioon based on this name has never been in use for *Bacidia rubella* auct.

According to Zahlbruckner (1926), also *Lichen corticalis* Rutstr. is likely to belong to *Bacidia rubella*. If *Lichen lutereus* J. F. Gmel. turns out to be taxonomically different from *Bacidia rubella*, *Lichen corticalis* may be the oldest name. Rutström's herbarium is probably lost, however, and the description (Rutström 1794: 7) is very vague ("leprosus, crusta farinosa, viridicinerea, tuberculis subsessilibus, depressiusculis, ferrugineis"). Thus, the identity of *Lichen corticalis* will most likely remain an unsolved problem.

In the protologue of *Verrucaria rubella*, Hoffmann (1796) included Ehrhart's Plant. Crypt. Linn. 196 and, indicated by the star to the lower left of the figure preceeding the species name, some unspecified material from the area of Göttingen (from the preface: "Asterisci signum, ubi antepositum est speciebus, eas denotat,

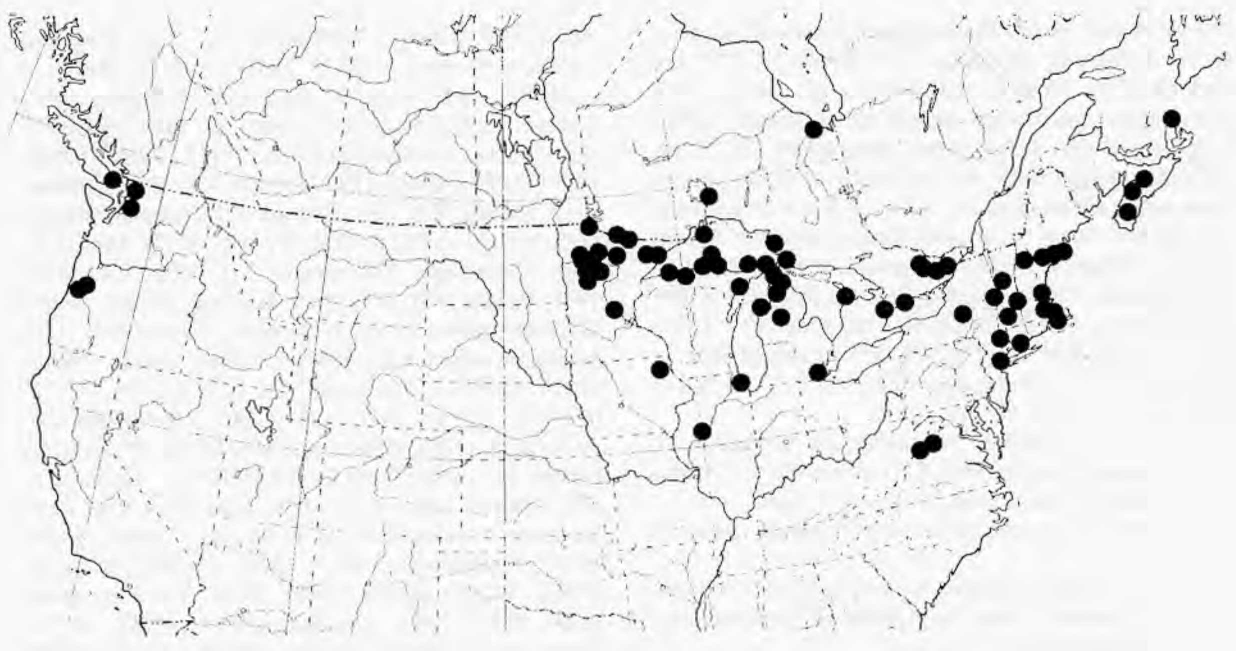


Fig. 30. Known North American distribution of *Bacidia rubella*.

quae circa Göttingen, atque in montibus Hercyniis inveniuntur."). I have, however, been unable to trace any original material other than Ehrhart's exsiccate. The specimen in GOET, which is likely to have been available to Hoffmann, contains a very well-developed and abundantly fertile thallus of what is presently known as *Bacidia fraxinea* Lönnr. (Lönnroth 1858; see also Ekman & Nordin 1993). This specimen is selected here as the lectotype of *B. rubella*. Unless conserved with a new type, however, the name *Bacidia rubella* will take precedence over *B. fraxinea*, a species which is much rarer and has a much more restricted distribution than *B. rubella* auct. In addition, the name *B. rubella* for *B. rubella* auct. will have to be replaced. Although earlier the name *B. luteola* has been used for this taxon, *B. rubella* has been widely used for at least the last few decades. I suggest that *Verrucaria rubella* Hoffm. be conserved with a conserved type in order to preserve its present usage, which also has the desirable effect of retaining the name *Bacidia fraxinea* Lönnr. As a conserved type, I suggest a collection distributed by R. Moberg in the exsiccate *Lichenes selecti exsiccati upsaliensis*.

Illustrations. Figs 2A, 3D, 5D, 30 (map), 42A.

Characterization. Thallus granular; granules 73-290 µm diam. Apothecia usually brown-orange to orange-brown. Proper exciple, hypothecium, and hymenium colourless to pale yellowish to orange, K+ intensifying. Spores acicular, 31-104 × 2.1-4.3 µm, with 3-13 septa.

Thallus indeterminate, thin to thick, continuous or discontinuous, coarsely granular, pale grey, greenish or yellowish grey, or greyish green, turning yellow or brownish in the herbarium. Granules (73-)92-139-218(-290) µm diam. (s= 47, N= 19, n= 5), globose or usually ± flattened, almost squamulose and slightly incised. Prothallus lacking or present, endosubstratal, white to pale grey.

Apothecia (0.6-)0.7-0.9-1.2(-2.0) mm diam. (s= 0.2, N= 19, n= 5), ± plane when young, later becoming convex, without or with thin to rather thick white pruina on edge and/or disc of young and medium-aged apothecia. Disc usually brown-orange to orange-brown, sometimes pale orange, pink-orange, orange, pale orange-brown, or brown-red. Margin concolorous with disc or slightly paler, level with or raised above disc in young apothecia, later level with the disc, and finally excluded.

Proper exciple laterally (59-)79(-103) µm wide (s= 12, N= 19, n= 1), without crystals or sometimes with radiating clusters of minute crystals (up to 1 µm). Rim almost colourless or pale yellowish to orange. Lateral interior usually ± concolorous with rim or sometimes slightly paler, along the edge without or with a single cell layer thick zone of cells with enlarged lumina that are up to 6 × 6 µm. Medullary part concolorous with lateral interior part or slightly paler. Hypothecium almost colourless or pale yellowish to orange, concolorous with or slightly darker than exciple (pigmentation indistinctly delimited). Hymenium (67-)69-86-97(-109) µm thick (s= 8, N= 19, n= 5), colourless or pale yellowish to pale orange, concolorous throughout or slightly darker in upper part than in lower part. Paraphyses 1.0-1.5 µm wide in mid-hymenium; apices usually ± clavate, sometimes not at all swollen, (1.2-)2.2-2.8-3.5(-4.3) µm wide (s= 0.6, N= 19, n= 5), without internal pigment. Spores acicular, straight to curved to sigmoid, sometimes coiled in young asci, (31-)44-52-63(-104) µm long (s= 8, N= 19, n= 10), (2.1-)2.4-2.7-3.2(-4.3) µm wide (s= 0.3, N= 19, n= 10), (9.7-)15.7-19.5-24.4(-33.6) times as long as wide (s= 3.5, N= 19, n= 10), with (3-)3.2-7.1- 8.7(-13) septa (s= 2.0, N= 19, n= 10).

Pycnidia ± immersed in thallus or prothallus, ± brown-orange in upper part, 85-125 µm diam. Conidia filiform, curved, non-septate, 10-19 × c. 0.5 µm.

Chemistry: Atranorin (sometimes as trace amounts only).

Pigments: Pigmented parts K+ intensifying, N+ intensifying. – Rubella Orange in hymenium, hypothecium, proper exciple, and pycnidial wall.

Ecology. In the West, *B. rubella* is mainly found on *Quercus garryana* and *Populus trichocarpa*, and in the East mainly on *Fraxinus* spp., *Thuja occidentalis*, and *Ulmus* spp. Other phorophytes known to accomodate *B. rubella* are *Acer* spp., *Fagus grandifolia*, *Juniperus virginiana*, *Ostrya virginiana*, *Picea glauca*, *Populus balsamifera*, *P. tremuloides*, other species of *Quercus*, and *Tilia americana*.

Distribution. The Great Lakes and Appalachian regions, and scattered localities along the West Coast. – Europe.

Discussion. *Bacidia rubella* is similar to *B. biatorina*, *B. diffracta*, and *B. polychroa* (see these species).

Collections examined. CANADA. *British Columbia*. Vancouver Island, Mount Douglas, 1991, Ryan (herb. M. Ryan). *Nova Scotia*. Victoria Co., 1989, Ekman L1063, L1073 (LD). Hants Co., 1989, Ekman L1038 (LD). Kings Co., 1989, Ekman L1040 (LD). Queens Co., 1989, Ekman L1053, L1054 (LD). *Ontario*. Algoma District, 19 km E of Hwy 17 on Hwy 556, 1977, Malachowski 7144a (MSC), 1979, Tan 79-633 (UBC). Bruce Co., 1976, Wong 2130 (CANL). Cochrane District, Moose Factory, 1969, Brodo 14685 (CANL). Lanark Co., 1968, Shchepanek 203a (CANL). + Northumberland Co., 1979, Wong 3194 (filed with *B. polychroa*, CANL). Ottawa-Carleton Co., 1989, Ekman L1023 (LD). Renfrew Co., 1972, Ireland 15886 (CANL), 1985, Brodo 25250 (CANL). Thunder Bay District, Lake Nipigon, 1976, Imshaug 59271 (MSC). York Co., 1948, Cain (COLO, US). Lake Superior Prov. Park, 1989, Ekman L1005, L1008, L1009 (LD). – U. S. A. *Connecticut*. New Haven Co., 1873, Hall (FH, US). *Illinois*. + Cook Co, 1897, Calkins (filed with *B. suffusa*, NY). Canton, Wolf (US). *Iowa*. Fayette Co., 1894, Fink (NY, US). *Maine*. Androscoggin Co., 1932, Parlin 10552, 10577 (US). Auburn, 1897, Merrill (NY, US). Gardiner, 1912, Merrill (FH, US). Warren, 1913, Merrill, Merrill: Lich. exs. 30 (COLO, MIN, NY, US, WIS). *Massachusetts*. Cambridge, Tuckerman (FH, US). Lanesboro, 1911, Riddle (FH, US). New Bedford, Willey (MIN). Waltham, Mann (US). Weymouth, Willey (FH, US). *Michigan*. Alger Co., 1987, Wetmore 58854, 58856, 58924 (MIN). Charlevoix Co., 1979, Tan 79-319 (CANL), 1979, Tan 79-624 (UBC). Cheboygan Co., 1974, Buck (NY). Delta Co., 1969, Harris 4119 (MIN). Emmet Co., 1983, Ford L-138 (MICH). Gogebic Co., 1989, Ekman L981, L985 (LD). Keweenaw Co., 1959, Wetmore 4214 (MIN), 1972, Wetmore 20841 (MIN), 1976, Malachowski 4615 (MSC), 1980, Wetmore 41169, 41220, 41588 (MIN), 1983, Wetmore 46663 (MIN, NY), 1983, Wetmore 46895, 47295, 47587, 47643, 47935, 48184, 48265, 48690, 48730, 49100, 49237 (MIN), + 1983, Wetmore 49341 (filed with *B. rosella*, MIN), 1984, Wetmore 51516, 52116, 52540, 52842, 53162a (MIN). Leelanau Co., 1987, Wetmore 58370 (MIN). Luce Co., 1979, Tan 79-268 (CANL). Mackinac Co., 1977, Harris 12352 (CANL), + 1977, Harris 12353 (filed with *B. polychroa*, NY). Marquette Co., 1976, Malachowski 3683a (MSC). Missoukee Co., 1962, Awasthi (COLO). Ontonagon Co., 1989, Ekman L989, L992 (LD). Mc Cargo Cone, 1930, Lowe 322, 344 (NY). *Minnesota*. Beltrami Co.,1977, Trana 3683, 3685 (MIN), + 1900, Fink 596 (filed with *B. subincompta*, MIN). Cass Co., 1976, Trana 1111b, 1112 (MIN). Clearwater Co., 1972, Trana 307 (MIN), 1972, Wetmore 20616 (CANL, MIN), 1972, Wetmore 20667 (MIN), 1975, Buck B372a (NY), 1976, Wetmore 26030, 26217 (MIN). Hubbard Co., 1957, Anderson (COLO). Itasca Co., 1977, Trana 3046 (MIN). Koochiching Co., 1901, Fink 1151 (MIN). Lake Co., 1989, Ekman L930, L946, L949, L950, L956, L960, L962, L964 (LD). Lake of the Woods Co., 1901, Fink 494 (MIN). Mahnomen Co., 1976, Wetmore 26402 (MIN). + Pennington Co., 1900, Fink 783 (filed with *B. diffracta*, MIN). Polk Co., 1976, Wetmore 26468 (CANL, MIN). Roseau Co., 1901, Fink 197 (MIN). St. Louis Co., 1901, Fink 1475, 1450 (MIN), 1978, Wetmore 31766 (CANL, MIN), 1978, Wetmore 31334 (MIN), 1978, Wetmore 34219 (MIN), 1979, Wetmore 39573 (MIN, NY). St. Cloud, 1897, Morgan (US). *New Hampshire*. Jefferson, 1895, Willey (US). Stratham, 1884, Cummings (NY). *New Jersey*. Closter, 1867 (CANL). *New York*. Washington Co., 1914, Baumham (FH, US). Poughkeepsie, Gerard (NY). Richfield Springs, 1884, Willey (US). *Oregon*. Benton Co., 1989, Ekman L693

(LD). Linn Co., 1972, Rossman 610 (NY). *Vermont*. Chittenden Co., 1890, Pringle (COLO). + Brandon, 1921, Merrill 1189 (filed with *B. polychroa*, WIS). Brattleboro, Frost (MIN). *Virginia*. Highland Co., 1975, Harris 9941 (MIN). + Madison Co., 1966, Wetmore 15391 (filed with *B. schweinitzii*, MIN). *Washington*. Skagit Co., 1989, Ekman L733, L735, L736 (LD). Snohomish Co., 1994, Tønsberg 21678, 21688 (BG). *Wisconsin*. Ashland Co., 1987, Wetmore 60581 (MIN).

22. Bacidia russeola (Kremp.) Zahlbr.

Cat. Lich. Univ. 4: 239 (1926). - *Lecidea russeola* Kremp., Flora, Jena 61: 518 (1878). – Type: Argentina, 1872-74, Lorentz & Hieronymus (M, lectotype selected here).

Patellaria phaeoloma Müll. Arg., Flora, Jena 67: 690 (1884). - *Bacidia phaeoloma* (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 4: 232 (1926). – Type: Cuba, 1878, Gray, Tuckerman: Wright Lich. Cub. 220 (G, lectotype selected here).

Biatora suturalis Eckfeldt, Bull. Torrey bot. Club 21: 394 (1894). - *Bacidia suturalis* (Eckfeldt) Zahlbr., Cat. Lich. Univ. 4: 245 (1926). – Type: Mexico, "San Luis Potosi", 1888, Pringle 183 (PH, lectotype selected here).

Patellaria subacerina Müll. Arg., Flora, Jena 69: 308 (1886). - *Bacidia subacerinoides* Zahlbr., Cat. Lich. Univ. 4: 242 (1926) (N.B.! The existence of *Bacidia subacerina* Vain. 1922 necessitated a nomen novum). – Type: Jamaica, "Gordon-Town. Comm. Joshua 1885" (G, lectotype selected here).

Bacidia papantlensis Vain., Dansk Botan. Arkiv 4 (11): 20 (1926). – Type: Mexico, "Papantla", 1841, Liebmann 7379 (TUR-V, syntype).

Bacidia subtestacea Malme, Ark. Bot. 27A (5): 23 (1935). - Type: Paraguay, "Asuncion, Villa Morra", 1893, Malme 1561 (S, lectotype selected here).

Bacidia parvula Malme, Ark. Bot. 27A (5): 33 (1935). – Type: Paraguay, "Colonia Riso. In cortice Piperis, in silva clara", 1893, Malme, bark pieces a and d (S, lectotype selected here).

Nomenclature. The original material of *Bacidia parvula* Malme, a single collection in S, is heterogenous. Two of the four bark pieces (marked "a" and "d") agree well with the diagnosis, whereas the other two (marked "b" and "c") represent a different species of *Bacidia* s. str. with pale greenish epithecium and short, 3-septate, bacilliform spores.

Illustrations. Figs 29 (map), 42B.

Characterization. Apothecia with brown-orange to red-brown disc; margin paler. Proper exciple very pale yellow to orange-brown, rim sometimes slightly darker (to red-brown), never with evenly dispersed, minute crystals (but sometimes with large clusters), with cell lumina gradually enlarging towards the edge, or along the edge with a ± distinct, 6-8 cell layers thick zone of enlarged cell lumina. Hypothecium very pale yellow to pale orange. Upper part of hymenium pale brown-orange to ± red-brown. Parts of proper exciple and hymenium usually K+ purplish. Spores acicular, 41-67 · 2.5-3.7 µm, with 5-9 septa.

Thallus determinate, rather thin to rather thick, continuous, ± cracked, wrinkled to warted, pale grey or pale green-grey. Prothallus lacking or present, bordering the thallus, narrow, black or brown.

Apothecia (0.5-)0.5-0.6-0.6(-0.9) mm diam. (s= 0.1, N= 2, n= 10), plane or moderately convex, epruinose. Disc brown-orange to brown-red to red-brown, or occasionally purple-brown to purplish black. Margin paler than disc, pale brown-orange, pale orange-brown, pale to dark red-brown, ± brown-red, or purple-brown, lower part paler than upper part; raised above disc in young apothecia, soon level with the disc, persistent.

Proper exciple laterally (43-)48(-52) µm wide (s= 6, N= 2, n= 1), without crystals or with radiating clusters of crystals that are up to 7 µm. Rim ± brown-orange or red-brown in upper part, downwards gradually changing to colourless, with cell lumina gradually enlarging towards the edge, or along the edge with a ± distinct, 6-8 cell layers thick zone of enlarged cells with lumina that are up to 14 × 5 µm. Lateral interior ± concolorous with rim, ± orange-brown in upper part, downwards gradually changing to colourless. Medullary part very pale yellow/orange. Hypothecium very pale yellow to pale orange. Hymenium (69-)75-79-83(-87) µm thick (s= 6, N= 2, n= 5), lower part colourless, uppermost part pale brown-orange to orange-brown, sometimes with spots of red-brown. Paraphyses 0.8-1.6 µm wide in mid-hymenium; apices weakly or not at all swollen, sometimes even slightly tapering, (0.8-)1.6-1.6-1.7(-2.8) µm wide (s= 0.5, N= 2, n= 10), without internal pigment. Spores acicular, straight, curved, or sigmoid, straight or slightly coiled in ascus, (41-)53-56-58(-67) µm long (s= 6, N= 2, n= 10), (2.5-)2.9-3.0-3.1(-3.7) µm wide (s= 0.4, N= 2, n= 10), (14.3-)17.8-18.9-20.1(-27.0) times as long as wide (s= 3.6, N= 2, n= 10), with (5-)6.6-7.0-7.3(-9) septa (s= 0.9, N= 2, n= 10).

Pycnidia not seen.

Chemistry: Trace amounts of atranorin.

Pigments: Edge of proper exciple and upper part of hymenium K+ purplish, N+ orange, other parts K+ intensifying, N- or N+ intensifying. – Laurocerasi Brown in proper exciple and hymenium. Rubella Orange in hypothecium, proper exciple, and upper part of hymenium.

Ecology. Very little is known about the ecology of this species, except that one of the three specimens was collected on *Celtis laevigata*. In Brazil and Paraguay, this species occurs in open forests (Malme 1935).

Distribution. Collected twice near Brownsville, Texas, with a 56-year interval, and once in an unspecified locality in Texas (not on the map). – Widely distributed in the neotropics. There are several finds of this species from Cuba, and it may well occur in southern Florida as well.

Discussion. Neotropical *B. russeola* displays some variation in apothecium pigmentation. Most specimens have Laurocerasi Brown in the hymenium and react K+ purplish, whereas some are almost or entirely deficient of this pigment, and thus do not react with K. Such specimens were named *Bacidia subtestacea* by Malme (1935). The specimens from Texas, however, are very similar to mainstream *B. russeola* from Central and South America. They are as well-developed as such specimens, and the pigment Laurocerasi Brown is present.

Among the North American species, *Bacidia russeola* is likely to be confused only with *B. campalea* (see that species) and brown-fruited morphs of *B. schweinitzii*. Such specimens of *B. schweinitzii* differ from *B. russeola* in having a ± brown hypothecium and proper exciple. Furthermore, *B. schweinitzii* often has a granular thallus.

The types of *B. phaeoloma* (Müll. Arg.) Zahlbr., *B. suturalis* (Eckfeldt) Zahlbr., *B. subacerinoides* Zahlbr., and *B. papantlensis* Vain. all are typical specimens of *B. russeola* with Laurocerasi Brown in the hymenium. *B. parvula* Malme, as lectotypified here, is a poorly developed specimen of *B. russeola* with mostly young apothecia.

Bacidia chapadensis Malme, described from Brazil by Malme (1935), is very similar to *B. russeola* in overall habit, but differs in having slightly longer and wider, 9-17-septate spores and a distinct, 2-3 cell layers thick zone of enlarged cells along the edge of the proper exciple. This species is known only from the type collection.

Collections examined. U. S. A. *Texas*. Higginson (US). Brownsville, 1888, Pringle 59 (COLO), 1944, Runyon 3883b (US).

23. Bacidia salmonea S. Ekman, sp. nov.

Type: Canada, British Columbia, Vancouver Island, Port Alberni, Roger Creek City Park, just E of the Gertrude St.-Pemberton St. intersection, open parkland, on *Acer macrophyllum*, alt. 10 m, 1989, Ekman L753 (LD, holotype).

A simili *Bacidia rosella* differt apotheciis obscurioribus, conidiis non septatis; strato crystallifera epithecii caret. Etiam *B. arceutinae* similis a qua differt conidiis subrectis et apotheciis pigmento fulvo carentibus.

Etymology. *Salmoneus*, salmon-pink.

Illustrations. Figs 29 (map), 42C, 43H.

Characterization. Apothecia ± pinkish or pale orange. Proper exciple colourless, pale yellowish or pale brown-orange, without crystals, along the edge with a 1(-2) cell layers thick zone of enlarged cell lumina. Hypothecium yellowish or pale brown-orange. Upper part of hymenium colourless or very pale brown-orange, without crystals. Spores acicular, 41-82 × 1.2-2.1 µm, with 3-15 septa. Conidia only slightly curved.

Thallus indeterminate, thin, either discontinuous, of discrete or contiguous, convex, sometimes almost granular areoles, or continuous, ± cracked, wrinkled to warted, pale green-grey to green-grey. Prothallus often present between discrete areoles and sometimes also bordering the thallus, very thin, endophloeodal, pale grey.

Apothecia (0.3-)0.4-0.5-0.5(-0.7) mm diam. (s= 0.1, N= 4, n= 10), at first plane, later becoming markedly convex, epruinose. Disc ± pink, orange-pink, brown-pink, pale orange, or sometimes pink-brown. Margin concolorous with disc, raised above disc in young apothecia, soon level with the disc, finally excluded.

Proper exciple laterally (55-)69(-91) µm wide (s= 16, N= 4, n= 1), without crystals. Rim colourless, along the edge with a 1(-2) cell layers thick zone of enlarged cells that are up to 11 × 6 µm. Lateral interior colourless or very pale yellowish to pale brown-orange, rarely brown-orange. Medullary part colourless to pale brown-orange. Hypothecium very pale yellowish to pale brown-orange, sometimes with heavier pigmented, brown-orange spots. Hymenium (72-)75-81-88(-93) µm thick (s= 6, N= 4, n= 5), lower part colourless except for occasional vertical streaks of very pale brown-orange pigment, uppermost part colourless or very pale brown-orange in a diffuse layer. Paraphyses 1.0-1.2 µm wide in mid-hymenium; apices ± clavate or only weakly swollen, (1.6-)1.9-2.1-2.3(-4.0) µm wide (s= 0.5, N= 4, n= 10), without internal pigment. Spores acicular, usually sigmoid, sometimes straight or curved, coiled in ascus, (41-)48-56-61(-82) µm long (s= 9, N= 3, n= 10), (1.2-)1.6-1.7-1.8(-2.1) µm wide (s= 0.3, N= 3, n= 10), (24.1-)30.2-33.6-36.5(-66.0) times as long as wide (s= 8.5, N= 3, n= 10), with (3-)6.8-7.8-9.4(-15) septa (s= 2.5, N= 3, n= 10).

Pycnidia half-immersed in thallus, uppermost part of wall concolorous with apothecia, c. 100 µm diam. Conidia filiform or slightly thicker at the middle, slightly curved, non-septate, 11-14 × 0.5-0.8 µm.

Chemistry: No lichen substances detected.

Pigments: Pigmented parts of apothecia K+ intensifying and N-. – Usually small amounts of Rubella Orange in hymenium, hypothecium, proper exciple, and pycnidial wall.

Ecology. Preferably on young trunks, branches and twigs, rarely on old trunks in humid, shady to fairly open forests and forest edges. All finds are on *Acer macrophyllum* and *Populus trichocarpa*.

Distribution. Along the coast from southern Oregon to southern British Columbia. – Probably endemic.

Discussion. *Bacidia salmonea* is similar to *B. arceutina*, *B. rosella* and several species of *Bacidina* with pale apothecia. *B. arceutina* can be separated by the presence of a brown-yellow pigment in the apothecia, the unpigmented and entirely immersed pycnidia, and the strongly curved conidia. *B. rosella* differs in having a crystal layer in the epithecium, in usually being less pigmented than *B. salmonea*, and in having septate conidia. All species of *Bacidina* can be separated from *B. salmonea* by the structure of the proper exciple.

Additional collections examined. CANADA. *British Columbia*. Vancouver Island, Port Alberni, 1977, Noble 6161 (herb. Noble). – U. S. A. *Oregon*. Curry Co., 1989, Ekman L673 (LD). Lincoln Co., 1989, Ekman L 679, L680, L681 (LD). Tillamook Co., 1989, Ekman L710, L711, L714 (LD). *Washington*. Jefferson Co., 1989, Ekman L726, L727 (LD). Whatcom Co., 1989, Ekman, L743, L744, L746, L747, L748 (LD).

24. Bacidia schweinitzii (Fr. ex E. Michener) A. Schneid.

Guide Study Lich. 110 (1898). - *Biatora schweinitzii* Fr. ex E. Michener in Darlington, Flora Cestrica ed. 3: 447 (1853). - *Biatora rubella* var. *schweinitzii* (Fr. ex E. Michener) Tuck., Genera Lich. 166 (1872). – Type: U. S. A., Pennsylvania, "Chester Co. On trunks.", Michener's Lichens, book 5, pg. 7, specimen marked "126" (BPI, lectotype selected here).

?*Patellaria granulosa* Michx., Flora Bor.-Americ. ed. 2: 320 (1803). – Type: Not seen.

Lecidea abducens Nyl., Lich. Japon. 68 (1890). - *Bacidia abducens* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 166 (1926). – Type: Japan, "Fusijama, 6000 ped.", 1879, Almquist (H-NYL 17580, syntype).

Lecidea abductans Nyl., Lich. Japon. 68 (1890). - *Bacidia abductans* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 166 (1926). – Type: Florida, "on *Nyssa*", Calkins 33 (H-NYL 17581, lectotype selected here).

Bacidia melanocardia Zahlbr., Hedwigia 74: 201 (1934). – Type: China, "Muli: Mountain of Djago", Rock (W, lectotype selected here).

Bacidia nigra Zahlbr., Hedwigia 74: 200 (1934). – Type: China, "Lidjiang snowrange, in the forests of Ndaza Ko, 11300-12000'", 1931, Rock (W, lectotype selected here).

Nomenclature. *Bacidia granulosa* Darb., Wiss. Ergebn. Schwedisch. Südpolar-Expedit. 4 (11): 6 (1912), which is not conspecific with *Bacidia schweinitzii*, blocks the use of *Patellaria granulosa* Michx. in *Bacidia*. I have not seen the type of the latter name, but according to Müller (1878) it is synonymous with *Bacidia schweinitzii*.

The events associated with the description of *Biatora schweinitzii* are a complicated matter. In the protologue, it is mentioned as "B. Schweinitzii, Fr. MS." No indication is given as to why it is named after Lewis David von Schweinitz or why the name is ascribed to Elias Fries. The second time the name appeared was in Tuckerman's exsiccate Lichenes Americae Septentrionalis no. 136 (published in 1854). Here, it is cited as "Biatora Schweinitzii, Fr. hb., Tuckerm. in Darlingt. Fl. Cestr. edit. tert. p. 447." Tuckerman (1872) treated it as *Biatora rubella* var. *schweinitzii* but "*Biat. schweinitzii* Fr. *herb*. Tuck. *exs* n. 136" is cited. Later on, Tuckerman (1888) changed his mind and again decided to treat the taxon as a species and (like in the exsiccate) ascribe the protologue in Darlington's *Flora Cestrica* to Fries and himself: "Fr. herb Tuckerm. in Darlingt. Fl. Cestr., edit 3, p. 447, & in Lich. exs. n. 136". In FH-TUCK, there is a specimen collected by Schweinitz at Salem, North Carolina, and marked "dedit mihi Fries" (= sent to me by Fries) by Tuckerman. What appears to have taken place is that Schweinitz, during his time as a resident of Salem, North Carolina (1821-35), sent a sample of a lichen to Fries, who provisionally named it *Biatora schweinitzii*. Fries then passed the material on to Tuckerman, who saved it for his own herbarium. There is no duplicate material preserved in UPS. Ezra Michener, having discovered the same species in Chester Co., Pennsylvania, was probably informed by Tuckerman about the existence of the name *Biatora schweinitzii*, and used it in his account of the lichens in Darlington's *Flora Cestrica* (Darlington 1853). Probably mostly by coincidence, Michener was the first to provide a valid description of *Biatora schweinitzii* (the protologue was almost certainly written by Michener's hand). The mate-

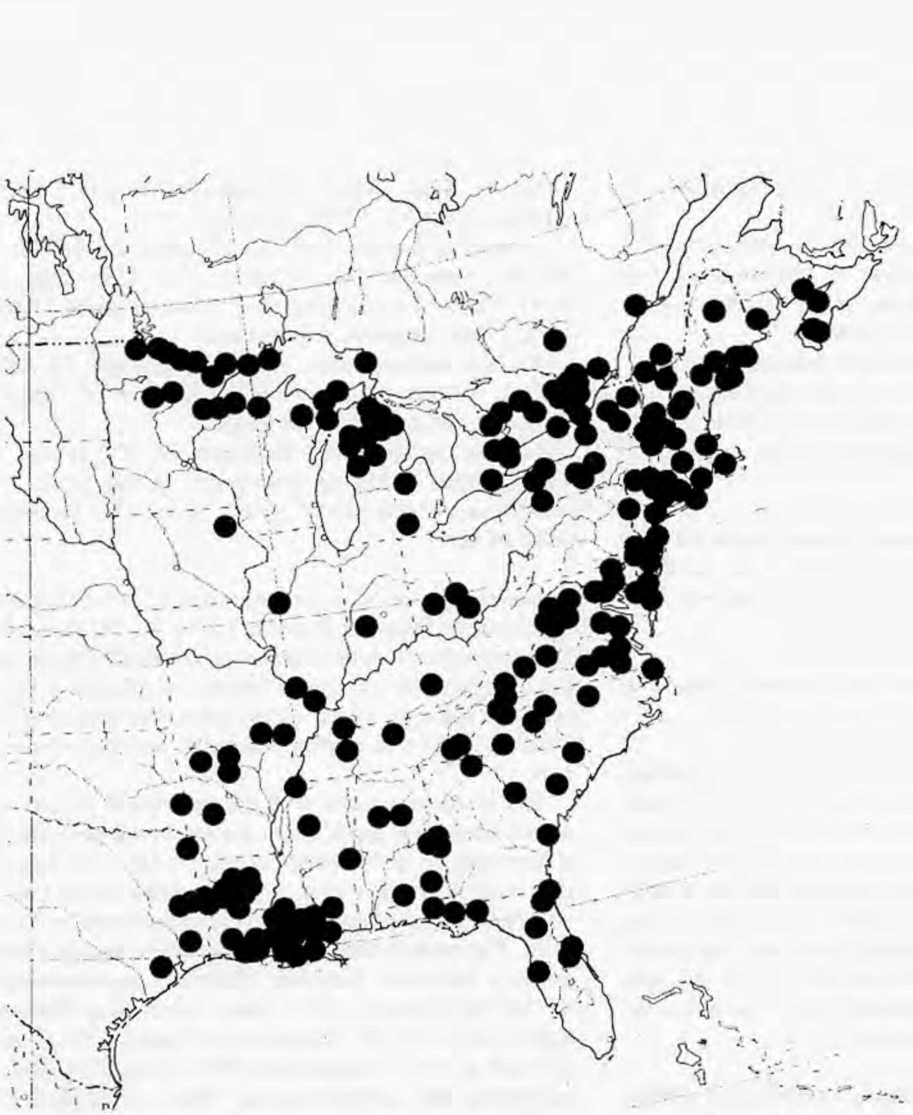


Fig. 31. Known North American distribution of *Bacidia schweinitzii*.

rial distributed by Tuckerman in his exsiccate soon thereafter was collected "ad truncos (praesertim Betula excelsae, Fagique) in montibus Novae Angliae", and has nothing to do with the material sent to him by Fries.

Although the collection sent to Fries by Schweinitz was the first one to bear the name *Biatora schweinitzii*, it was almost certainly not seen by Michener. Instead, Michener's diagnosis was based on his own material, which consists of four collections now preserved in BPI. One of these, a well-developed and typical specimen, is here chosen as the lectotype.

Harris (1977) treated *Biatora rubella* var. *schweinitzii* in Tuckerman (1872) as a different name with a different type than *Biatora schweinitzii* Fr. ex Michener in Darl. The fact that Tuckerman (1872) cited his exsiccate when he made *Biatora rubella* var. *schweinitzii*, and that Darlington's *Flora Cestrica* in its turn is cited in the exsiccate, makes it fairly certain that Tuckerman merely made a new combinations based on the same epithet.

I refrain from lectotypifying *Lecidea abducens* Nyl., since the only syntype studied is very poor. I have been unable to trace any of Almquist's material of this species in S.

Illustrations. Figs 8A, 31 (map), 42D-E.

Characterization. Thallus granular or ± rimose. Apothecia usually orange-brown to dark purple-brown to black. Proper exciple at least in inner part orange-brown to red-black, merging into the pigmentation of the hypothecium, without minute, evenly dispersed crystals (although sometimes with a few clusters). Hypothecium pale orange-brown to dark brown. Upper part of hymenium either ± greenish or pale orange-brown. Spores acicular, 32-88 × 1.9-4.3 µm, with 3-15 septa.

Thallus indeterminate, thin to thick, either discontinuous, of discrete granules or low, convex areoles, or continuous, granular or not, then without cracks or ± rimose to areolate, smooth to wrinkled to warted to tuberculate or sometimes subsquamulose; grey to green-grey to grey-green to brown-green. Granules ± globose, cylindrical, or flattened, (48-)53-94-121(-145) µm (s= 27, N= 27, n= 5). Prothallus lacking or sometimes present between discrete areoles/granules, thin, endosubstratal, white to pale grey.

Apothecia (0.5-)0.6-0.9-1.4(-1.8) mm diam. (s= 0.3, N= 27, n= 5), ± plane when young, later becoming convex, usually epruinose, rarely with thin white pruina on margin of young to medium-aged apothecia. Disc in most cases either orange-brown or dark purple-brown to purple-black to blue-black to pure black, rarely pink to greyish pink, bluish or purplish grey, pale brown, grey-brown, or greyish blue. Margin usually concolorous with or paler than disc, rarely slightly darker than disc, rather thick, level with or raised above disc in young apothecia, later level with the disc, and finally excluded.

Proper exciple laterally (52-)87(-138) µm wide (s= 25, N= 27, n= 1), sometimes with radiating clusters of up to 7 µm wide crystals. Rim almost colourless or pale yellow to orange-brown to dark brown to dark red-brown, often bluish or greenish near the hymenium, cell lumina gradually slightly enlarging towards the edge, near the edge up to 11 × 4 µm. Lateral interior usually darker than rim, pale yellow/brown to orange-brown to dark red-brown to brown-black to red-black. Medullary part darker than or sometimes concolorous with lateral interior part, orange-brown to dark brown-red to red-black. Hypothecium pale orange-brown to orange-brown to dark brown, downwards gradually merging into the colouration of the proper exciple. Hymenium (66-)69-92-110(-118) µm thick (s= 11, N= 27, n= 5), lower part colourless except for occasional vertical streaks with blue-green pigment, upper part either blue-green (rarely pale blue-green or dark green) or pale orange-brown, indistinctly or distinctly delimited. Paraphyses 1.2-2.0 µm wide in mid-hymenium; apices ± clavate or not at all swollen, (1.2-)1.6-1.9-2.7(-4.0) µm wide (s= 0.5, N= 27, n= 5), without internal pigment. Spores acicular, straight to curved to sigmoid, (32-)44-56-73(-88) µm long (s= 9, N= 27, n= 10), (1.9-)2.5-2.8-3.2(-4.3) µm wide (s= 0.4, N= 27, n= 10), (10.3-)15.5-20.2-30.6(-46.7) times as long as wide (s= 4.6, N= 27, n= 10), with (3-)4.3-7.9-13.6(-15) septa (s= 2.8, N= 27, n= 10).

Pycnidia ± immersed in thallus or prothallus, uppermost part of wall concolorous with apothecia, 75-175 µm diam. Conidia filiform, curved, non-septate, 9-20 × c. 0.7-0.8 µm.

Chemistry: Usually no lichen substances, but sometimes with atranorin.

Pigments: Yellowish to orange-brown parts K+ intensifying, N- or N+ intensifying. Dark reddish brown to red-black parts K-, N-. Green parts K-, N+ purple with a precipitate of dark blue crystals (in apothecia with ± blue-green hymenium). – Bacidia Green often in hymenium, uppermost part of proper exciple, and pycnidial wall. Rubella Orange in hypothecium, proper exciple, pycnidial wall, and sometimes in hymenium. Schweinitzii Red often in hypothecium, proper exciple, and pycnidial wall.

Ecology. On the trunks of trees, sometimes branches of trees, shrubs, and vines, mainly in shady and humid localities, but sometimes also in more or less open habitats such as forest edges and solitary trees. The commonest phorophytes are *Acer* spp., *Fagus grandifolia*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Quercus* spp., and *Thuja occidentalis*, but it has also been found on *Aesculus* sp., *Betula* spp., *Carpinus caroliniana*, *Carya* spp., *Celtis laevigata*, *Cephalanthus occidentalis*, *Chionanthus virginicus*, *Cornus* spp., *Crataegus* sp., *Euonymus americanus*, *Fraxinus* spp., *Hamamelis virginiana*, *Ilex* sp., *Juglans* spp., *Juniperus virginiana*, *Magnolia* spp., *Morus rubra*, *Nyssa* spp., *Ostrya virginiana*, *Picea* sp., *Platanus occidentalis*, *Populus tremuloides*, *Salix* spp., *Sapium sebiferum*, *Sas- safras albidum*, *Taxodium distichum*, *Tecoma stans*, *Tilia americana*, *Ulmus americana*, and *Vitis rotundifolia*.

Distribution. The eastern temperate region of eastern North America, where it is the by far commonest species of *Bacidia*. – Previously thought to be a North American endemic, but it has turned out that it occurs in eastern Asia (at least China and Japan) as well, from where it has been described under at least three different names (see synonymy).

Discussion. *Bacidia schweinitzii* is similar to *B. aggregatula*, *B. circumspecta*, *B. igniarii*, *B. russeola*, and *B. subincompta*. For distinguishing characters, see these species.

Bacidia schweinitzii is the most variable species of *Bacidia* in North America. There is a large variation in thallus structure, from granular to almost smooth, which much parallels the variation seen in *B. subincompta*. There is also extensive variation in the pigmentation of the apothecia. Most apothecia are either black with a blue-green upper hymenium and more or less red-black hypothecium and proper exciple, or brown with brown upper hymenium and more or less brown hypothecium and proper exciple. Intermediate apothecia are sometimes found, and in some cases I have observed brown as well as black apothecia mixed on the same thallus. In most thalli, however, all apothecia are either brown or black. Although all combinations of apothecium pigmentation and thallus structure occur within all parts of the distribution range, there is a clear tendency that individuals with brown apothecia and/or non-granular thallus are more common in the South than in the North. An explanation for this may be that only a part of the variation within the species has been involved in the recolonization of the North after the latest glaciation(s).

The Japanese *Bacidia abducens* (Nyl.) Zahlbr., and the Chinese *B. melanocardia* Zahlbr. and *B. nigra* Zahlbr. should be included in *B. schweinitzii*. All three have a ± continuous, non-granular thallus with black apothecia containing Bacidia Green in the hymenium. Morphs with granular thallus or lacking Bacidia Green in the hymenium are so far not known outside North America. The type of *Bacidia abductans* (Nyl.) Zahlbr. from Florida is a typical specimen of *B. schweinitzii* with black apothecia containing Bacidia Green in the hymenium and a partly smooth, partly granular thallus.

Additional collections examined. CANADA. Lac Trumblant, 1922, Plitt (US). *New Brunswick*. Albert Co., 1980, Gowan 3051 (CANL), 1981, Gowan 4362, 4989, 5066 & Brodo (CANL), 1989, Ekman L1079 (LD). Charlotte Co., 1989, Ekman L1089, L1090, L1094 (LD). *Nova Scotia*. Kings Co., 1972, Brodo 18908 (CANL), 1989, Ekman L1042 (LD). Queens Co., 1989, Ekman L1045, L1046, L1047, L1055 (LD). *Ontario*. Brant Co., 1944, Cain (CANL). Dufferin Co., 1984, Wong 3595, Krug & Warren (CANL), Lake Superior Prov. Park, 1989, Ekman L996, L997, L999, L1007, L1010, L1011, L1012, L1013, L1015, L1016, L1017 (LD). Frontenac Co., 1941, Cain (CANL, COLO, NY, US). Hastings Co., 1989, Buck 17530, 17539 (NY). Lanark Co., 1986, Wong 3975 (CANL). Muskoka District, Univ. of Toronto Forest, 1964, Denison 487 (CANL). Peel Co., 1946, Cain (CANL, OSC, SFSU, UBC). Renfrew Co., 1973, Brodo 20571b (CANL), 1975, Wong 1832, Ireland, White & Dugal (CANL), 1985, Brodo 25255 (CANL), 1985, Wong 3805, 3810 (CANL). Simcoe Co., 1964, Denison 489 (CANL), 1967, Krug 223, 224a (CANL). York Co., 1941, Cain (CANL, NY), 1946, Cain (COLO), 1953, Cain (CANL). Algonquin Prov. Park, 1900, Macoun (CANL), 1972, Dickson 91 (CANL). Belleville, 1868 (CANL), 1892, probably collected by Macoun (CANL). Belleville and Ottawa, 1881, Macoun 63 (CANL). Carleton Place, 1900, Macoun (CANL). Carp, 1907 (CANL). Emo, 1901, Fink 842 (MIN). Kingston, 1864, Drummond (FH). Britannia, 1904, Macoun 173 (CANL), 1904, probably collected by Macoun (CANL). Ottawa, 1891, Macoun, 83, 484, 512 (CANL), 1892, Macoun 2815, 2821 (CANL), 1892, Macoun 342 (US), 1895, Macoun (US), 1902, Macoun 192 (CANL, COLO, US). *Quebec*. Argenteuil Co., 1984, Brodo 25017a (CANL). Brome Co., 1965, Denison 29 (CANL). Gatineau Co., 1968, Brodo 13340 (CANL), 1969, Brodo 16331 (CANL), 1971, Hanes (CANL), 1973, Brodo 19134 (CANL), 1989, Ekman L1024, L1026, L1027, L1030 (LD). Pontiac Co., 1969, Brodo 14849 (CANL). Comté Portneuf, 1975, Brodo 20678b (CANL). Sherbrooke Co., 1972, Kantrud (CANL). Hairy Lake, 1902, unknown collector (CANL). Chelsea, 1907, Macoun 51 (CANL). – U. S. A. *Alabama*. Lee Co. 1893, 1897, Earle & Baker (MIN, NY, US). Pike Co., 1964, Johnson (NY). Randolph Co., 1987, Bowers & Haynes 12561b-1 (herb. Tucker). Talladega Co, 1900, Pollard & Maxon 239 (US). Tuscaloosa Co., 1987, Bowers & White 13103 (herb. Tucker). Brooklyn, 1860, Beaumont 72309 (FH). Dadeville, 1900, Pollard and Maxon 130 (US). *Arkansas*. Newton Co., 1979, Ryan (WWB), 1979, Brodo 23491 (CANL), 1988, Harris 21511 (NY). Stone Co., 1988, Harris 21618 (NY), + 1988, Harris 21592 (filed with *B. diffracta*, NY), + 1993, Tønsberg 19258 (filed with *B. suffusa*, BG). Van Buren Co., 1993, Tønsberg 19227, 19236 (BG). Malvern, 1899, Russell 23 (US). *Connecticut*. Fairfield Co., 1926, Evans 852 (FH, US). Litchfield Co., 1949, Hale 140 (US). New Haven Co., 1925, Musch 342 (FH, US). New London Co., 1925, Nichols & Musch 576 (FH, US). *D. C.* Lehnert (US). *Delaware*. Sussex Co., 1966, Brodo 9540 & Brassard (CANL, COLO), 1966, Brodo 9563 & Brassard (CANL), 1989, Ekman L1047, L1101, L1102, L1104 (LD). Wilmington, 1890, Commons 42 (NY). *Florida*. Calkins (FH, US). 1886-87, Calkins (MIN). Alachua Co., 1915, Nelson (FH, US), 1993, Ekman L1145, L1146, L1147 (LD). Holmes Co., 1993, Ekman L1138 (LD). Leon Co., 1990, Tucker 29736, 29737, 29739B, 29771, 30169 (herb. Tucker), 1991, Tucker 30318 (herb. Tucker). Liberty Co., 1993, Ekman L1214, L1216 (LD). Nassau Co., 1987, Harris 21153 (NY). Orange Co., 1993, Ekman L1165 (LD). Wakulla Co., 1993, Ekman L1211, L1212 (LD). Jacksonville, 1888, 1889, 1890, 1892, Calkins (CANL, FH, NY, US). Sanford, 1911, 1912, 1914, 1915, Rapp (FH, US). Six Mile Creek, Calkins (COLO, NY). *Georgia*. Chatman Co., 1974, Tucker 12224a (herb. Tucker). Rabun Co., 1981, Brodo 23888 (CANL). Towns Co., 1976, Harris 11210 (NY). White Co., 1976, Harris 11148, 11168 (NY). Savannah, 1917-18, Hervey 78, 89 (FH, US). Illinois. Union Co., 1968, Skorepa 4122 (US). Canton (NY). *Indiana*. Owen Co., 1988, Harris 21824 (NY). Putnam Co., 1893, Underwood 13 (NY), 1970, Brodo 17084 (CANL). *Iowa*. Fayette Co., 1894, Fink (MIN). *Kentucky*. Calloway Co., 1975, Buck B34 (MIN). Madison Co., 1941, Allen 44, 208, 515 (US). Rockcastel Co., 1927, Fink (CANL). *Louisiana*. Acadia Par., 1894, Langlois 1020 (NY). Allen Par., 1986, Tucker 27296b (herb. Tucker). + Ascension Par., 1981, Tucker 21473 (filed with *B. suffusa*, herb. Tucker). Assumption Par., 1981, Tucker 21638c (herb. Tucker). Caldwell Par., 1984, Tucker 26355 (herb. Tucker). East Baton Rouge Par., 1971, Tucker 9087 (herb. Tucker), 1974, Tucker 11835 (CANL, COLO, MIN, UBC), 1974, Tucker 11835a, 11836b, 11987 (herb. Tucker), 1974, Tucker 12571 (herb. Tucker, CANL, MIN), 1975, Tucker 13991 (herb. Tucker), 1976, Tucker 15636, 16204 (herb. Tucker), 1977, Tucker 16834 (CANL), 1977, Tucker 16834a (herb. Tucker), 1977, Tucker 16834b (MIN, NY), 1977, Tucker 17250 (COLO, NY), 1978, Tucker 17598, 18049 (herb. Tucker), 1978, Schwarzwalder (MIN), 1980, Tucker 20887 (herb. Tucker), 1986, Tucker 27237c (herb. Tucker), 1987, Tucker 28129 (herb. Tucker), 1991, Tucker 30557 (herb. Tucker), 1993, Ekman L1117, L1118, L1126, L1129 (LD). East Feliciana Par., 1968, Tucker 7715b, 7718 (herb. Tucker), 1969, Tucker 7833, 7833a, 7859a (herb. Tucker), 1969, Tucker 7859 (MIN), + 1969, Tucker 7833b (filed with *B. helicospora*, herb. Tucker), 1976, Tucker 15555, 15556, 15557 (herb. Tucker), 1978, Tucker 17367, 18104 (herb. Tucker), 1979, Tucker 18401 (CANL, COLO, herb. Tucker, MIN), 1979, Tucker 18511 (herb. Tucker, NY), 1984, Tucker 26294 (herb. Tucker). + Grant Par., 1973, Tucker 11315 & Jones (filed with *B. helicospora*, herb. Tucker). Iberville Par., 1974, Tucker 13334b, 13391 (herb. Tucker). Jackson Par., 1972, Tucker 10886 (herb. Tucker). Lafourche Par., 1980, Tucker 21240b (herb. Tucker), 1980, Givens (herb. Tucker). Lincoln Par., 1984, Tucker 26039, 26049, 26050 (herb. Tucker). Livingston Par., 1968, Tucker 7612, 7638a (herb. Tucker), 1968, Tucker 7351 (COLO, herb. Tucker). Natchitoches Par., 1976, Brodo 21091 (CANL), 1976, Harris 11435, 11468 (NY), 1976, Tucker 16090, 16123 (herb. Tucker), 1978, Tucker 17612, 17614, 17877 (herb. Tucker), 1980, Wussow (herb. Tucker), 1989, Tucker 29230 (herb. Tucker). Orleans Par., 1982, Pruski 2330 (herb. Tucker). Ouachita Par., 1973, Tucker 11359, Thomas & Jones, Tucker 11424, Thomas & Jones (herb. Tucker). Rapides, 1981, Tucker 21905 (herb. Tucker). Sabine Par., 1967, Wetmore 17563, 17587, 17593 (MIN), 1970, Tucker 8879 (CANL, herb. Tucker), + 1970, Tucker 8883 (filed with *B. diffracta*, CANL, herb. Tucker). St. Helena Par., 1972, Tucker 10072 (herb. Tucker), + 1972, Tucker 10149 (filed with *B. helicospora*, herb. Tucker), 1973, Tucker 11073, 11083 (herb. Tucker), 1974, Tucker 11876, 11885 (herb. Tucker), 1986, Tucker 27950 (herb. Tucker). St. Tammany Par., 1993, Ekman L1134 (LD), Tangipahoa Par., 1993, Ekman L1127 (LD), 1974, Tucker 12649 (herb. Tucker), 1985, Tucker 27175 (herb. Tucker). Washington Par., 1980, Tucker 21006 (herb. Tucker), 1982, Tucker 24528 (herb. Tucker). West Feliciana, 1972, Tucker 10049 (herb. Tucker), 1978, Tucker 18127 (herb. Tucker), 1982, Tucker 25590 (herb. Tucker), 1987, Tucker 28154 (herb. Tucker), 1988, Tucker 29199 (herb. Tucker), 1989, Tucker 29177 (herb. Tucker). Bayou Millieu, 1894, Langlois (US). Bayou Tortue, 1893, 1895, Langlois (US). Bois Lobbé, 1893, Langlois 868 (US). Chenal, 1894, Langlois (US). Covington, 1894, Langlois (US). Duchamps, 1894, Langlois (US). Grand Coteau, 1894, Langlois (US). Near St. Martinville, 1895, Langlois 295 (NY). Opelousas, 1889, Langlois 587 (US). *Maine*. Hancock Co., 1983, Sullivan 1213, 1567 (MIN), 1983, Wetmore 46178 (MIN), 1984, Sullivan 3390, 3853 (MIN). Oxford Co., 1929, Parlin 9231 (NY). Brunswick, 1911, Merrill (FH, US), 1911, Merrill, Merrill: Lich. exs. 214 (COLO, FH, US). Camden, 1905, Merrill (FH, US). Oakland, 1897, Merrill (NY). Orland, 1897, Merrill (NY). Rockland, 1909, Merrill (FH, US). Rockport, 1913, Merrill (FH, US), 1921, Merrill (FH, US). Togue Pond Camps (near Mt. Katahdin), 1939, Degelius (MIN, US). Union, 1921, Merrill (FH, US). *Maryland*. 1911, Plitt (US). 1930, Plitt 12994 (US). Plitt 669 (US). Anne Arundel Co., 1906, Plitt 69, 69a, 177d (US), 1908, Plitt 298 (US), 1916, Plitt (US). Baltimore Co., 1905, Plitt 63 (US), 1906, Plitt 69b, 117e (US), 1907, Plitt 117c (US), 1909, Plitt 234, 234a, 323, s. n. (US), 1910, Plitt 234b, s. n. (US), 1911, Plitt (US). Montgomery Co., 1933, Leonard 2192 (US). Prince Georges Co., 1963, Weber (COLO). Worcester Co., 1989, Ekman L1105 (LD). Benfield, 1906, Plitt 117, 117a (US). Bladensburg, 1941, Leonard 19151 (US). Landsdown, 1908, Plitt 425 (FH, US). Sharptown, 1915, Otis (US). Takoma Park, 1896, Williams, Cummings et al.: Lich. Boreali.-Am. 169 (COLO), 1896, Williams, Cummings: Decades N. Am. Lich. 247 (NY). *Massachusetts*. Amherst, 1910, Riddle (FH, US). New Bedford, 1880's, Willey (FH, US), 1881, Willey (US), 1884, Willey (US), Willey (FH, MIN, US). Concord (FH, US). Fairhaven, 1883, Willey (US). *Michigan*. Alger Co., 1987, Wetmore 58932, 59100, 59141, 59294, 59359, 59582, 59839, 59899 (MIN). Antrim Co., 1953, Ogden 5305 (CANL, COLO, MIN, US). Cheboygan Co., 1957, Sierk 533 (US), 1945, Wagner 556 (NY), 1974, Buck (NY), 1979, Tan 79-348 (UBC). Delta Co., 1976, Harris 11704 (CANL). Dickinson Co., 1971, Harris 7595 (MIN). Emmet Co., 1969, Hale 3653 (US), 1979, Tan 79-112 (UBC). Gogebic Co., 1975, Harris 10012 (MIN), 1989, Ekman L975, L982 (LD). Jackson Co., 1979, Harris 13083 (NY). Keweenaw Co., 1983, Wetmore 48656 (MIN), 1984, Wetmore 51862 (CANL, MIN), 1984, Wetmore 52988 (MIN, NY), 1984, Wetmore 53035 (MIN). Lake Co., 1968, Harris 3866a (MIN). Leelanau Co., 1957, Sharp 682 (COLO, US). Leelanau Co., 1987, Wetmore 58138 (MIN). Mackinac Co., 1977, Harris 12498 (UBC). Missaukee Co., 1962, Awasthi (COLO). Presque Isle Co., 1979, Tan 79-254 (CANL). Montmorency Co., 1967, Wells 169 (SFSU). Antrim, 1933, Lowe 1586 (NY, US). Benzie Co., 1987, Wetmore 57965 (MIN). Lake Huron, Bois Blanc Island, 1945, Wagner 469 (NY). Reeses Bog, Burt Township, 1967, Thiers (SFSU). *Minnesota*. Aitkin Co., 1985, Wetmore 53651 (MIN). Cass Co., 1975, Buck B520 (CANL), 1975, Buck B535 (MIN), 1976, Trana 1134 (WWB), 1976, Trana 1130 (MIN), 1976, Wetmore 25929, 25930, 25933, 25954 (MIN). Cook Co., 1897, Fink 493 (MIN), 1902 Fink, Hibbard Photo 5253 (MIN). Koochiching Co., 1901, Fink 1017 (MIN). Lake Co., 1897, Fink 963 (MIN). Lake of the Woods Co., 1901, Fink 116, 460 (MIN). St. Louis Co., 1901, Fink 1498, 1574, s. n. (MIN), + 1901, Fink 1475 (filed with *B. rubella*, MIN), 1977, Wetmore 27547, 28065 (MIN), 1977, Wetmore 27583 (CANL, MIN), 1978, Wetmore 32478 (COLO, MIN), 1978, Wetmore 35510 (CANL, MIN, NY), 1978, Wetmore 34198, 34959 (MIN), 1979, Wetmore 39554 (MIN). Duluth, 1900, Kimball 2 (US). *Mississippi*. Amite Co., 1991, Tucker 30600, 30601 (herb. Tucker). DeSoto Co., 1939, Johnson & Andrews 2053, 2072, 2076 (NY), 1952, Johnson 1016 (NY). Franklin Co., 1976, Harris 11537 (NY). Grenada Co., 1939, Johnson & Andrews 2968 (NY). Hancock Co., 1993, Ekman L1136 (LD). Kemper Co., 1939, Johnson & Andrews 2930 (NY). Lamar Co., 1980, Tucker 21074 (herb. Tucker). Sharkey Co., 1978, Johnson 7016, 7036, 7037, 7040, 7043, 7045, 7059, 7097, 7099a, 7121, 7161, 7163, 7165, 7203, 7204, 7211, 7222, 7231, 7232, 7233, 7284, 7285, s. n. (NY). *Missouri*. Oregon Co., 1988, Harris 21701 (NY). Neelyville, Butler, 1899, Russell 147 (US). Perryville, 1886, Demetrio 108 (NY). *New Hampshire*. Brighthollow-Canaan, 1947, Hutchinson (NY). Plymouth, 1897, Cummings, Cummings: Decades N. Am. Lich. 267, 267bc (COLO, NY, US), 1897, Cummings, Cummings et al.: Lich. Boreali.-Am. 200, 200bc (COLO, UBC). White Mountains, 1848, Tuckerman (NY), Tuckerman (CANL, NY), 1843-48, 1847, Tuckerman (FH), 1848, Tuckerman, Farlow Herb.: Reliquiae Tuck. 16 (CANL, COLO). *New Jersey*. 1866, Austin (FH). Burlington Co., 1962, Brodo 3558 (CANL, COLO). Cumberland Co., 1982, Buck 8969 (NY), 1982, Brako 4923 (NY), 1982, Harris 16469 (NY). Allenwood, 1907, Plitt 149 (US). Atco, 1882, Green (NY, US). Closter, Austin (CANL, NY), Austin 120, 757 (NY). Newfield, 1880, Ellis (NY). *New York*. 1870, Austin 741 (NY). Essex Co., 1960, Brodo 450 (CANL). Genesee Co., 1946, Muenscher & B. I. B. 525 (NY). Hamilton Co., 1870, Peck (FH), 1986, Harris 19290, 19322, 19324, 19356, 19365 (NY). Suffolk Co., 1960, Brodo 2121 (CANL). St. Lawrence Co., 1981, Harris 13953 (NY), 1983, Harris 16776 (NY). Tompkins Co., 1952, Thomson 4650 (COLO). Ulster Co., 1980, Harris 13229, 13362 (NY). Westchester Co., 1981, Harris 14008 (NY). Alleghany State Park, 1926, Alexander & Herre (US). Belleville, unknown collector (NY), 1868, unknown collector (NY). Buffalo, Wilson (NY). Fort Edward, 1868 (NY). Kirkwille, 1881, Underwood 71 (NY). Manlius, 1887, Cook (US). Shushan, 1906, Dobbin (NY). Penn Yan, 1853, Sartwell (FH). Poughkeepsie, Gerard (NY). *North Carolina*. "Mountains of North Carolina", 1858, Buckley (FH). Avery Co., 1936, Anderson (NY). Camden Co., 1958, Culberson 6950 (US). Forsyth Co., Schweinitz (FH), 1883, Ravenel (FH), 1922, Schallert 5964 (US), 1923, Schallert (WTU), 1932, Schallert (US). Graham Co., 1987, Buck 15342, 15355, 15357 (NY), 1987, Harris 20904, 20915, 20944 (NY). Iredell Co., 1966, Shchepanek 125 (CANL). Macon Co., 1981, Harris 13663 (NY), 1986, Thiers 50220 (SFSU). Macon Co.-Jackson Co., 1981, Gowan 4257 (CANL). Swain Co., 1976, Harris 10927, 11023 (NY), 1987, Harris 20976, 20977, 20978 (NY). Hanes Woods, 1932, Schallert (NY). Hillsboro, Curtis (FH). Tryon, 1927, Evans 416 (UPS), 1928, Evans 406 (UPS). *Ohio*. Lesquereux (FH). Delaware Co., 1894, Bogue 690 (NY). Hocking Co., 1918, Fink 1024 (NY, US), 1968, Wetmore 18071 (MIN), 1968, Brodo 14481 (CANL). Springfield, 1877 (NY). *Oklahoma*. Le Flore Co., 1993, Tønsberg 19290 (BG). *Pennsylvania*. 1852, Michener (FH). Chester Co., Michener (BPI). Delaware Co., 1892, Commons 94 (NY). Pike Co., 1986, Wetmore 55825, 55994 (MIN). Bushkill Falls, 1937 (NY). *South Carolina*. Ravenel (US). Aikens Co. (US). Santee Canal, Ravenel 148 (FH). Society Hill, 1850, Curtis (FH). *Tennessee*. Degelius (MIN). Carter Co., 1976, Buck 1064 (NY), 1976, Harris 10728 (NY). Henderson Co., 1976, Harris 11611 (NY). Monroe Co., 1992, Tønsberg 18034 (BG). Sevier Co., 1935, Sharp 63 (NY). Wilson Co., 1967, Harris 1302 (MIN). Great Smokey Mountain Nat. Park, 1939, Degelius (US), 1986, Thiers 50107 (SFSU). *Texas*. Cass Co., 1989, Tucker 3820 (herb. Tucker). Hardin Co., 1975, Tucker 14027 (herb. Tucker). Houston Co., 1967, Wetmore 17668 (MIN). Nacogdoches Co., 1967, Tucker 7135 (herb. Tucker). Houston, 1872, Hall (FH). *Vermont*. Brattleboro, 1851-53, Tuckerman (FH). 1925, Merrill 2352 (MIN). Brandon, 1924, Dutton, Merrill: Lich. exs. 119 (COLO, MIN). Fairhaven, 1910, Kirk 26 (MIN). Goshen, 1927, Dutton 2624 (US). Jamaica, 1937 (NY). Leicester, 1915, Dutton 863 (COLO, US). Willoughby Lake, 1880, Farlow (FH). *Virginia*. Bedford Co.,1978, Brodo 22812 (CANL). Caroline Co., 1963, Reed 63412 (NY). Charlotte Co., 1955, Culberson 6735 (CANL, COLO, US). Chesterfield Co., 1941, Luttrell 1868 (US). Frederick Co., 1966, Brodo 940, 976 (CANL). Giles Co., 1941, Luttrell 2700 (US), 1978, Harris 12885 (NY). Grayson Co., 1941, Luttrell 2637 (US). Greensville Co., 1941, Luttrell & Allman 1608 (US). Highland Co., 1976, Harris 10670 (NY). King & Queen Co., 1963, Reed 60741 (NY). Madison Co., 1966, Brodo 9526 (CANL, UBC), 1966, Wetmore 15391 (COLO, MIN). Nottoway Co., 1963, Reed 63078 (NY). Page Co., 1981, Guccion 126 (NY). *West Virginia*. Mercer Co., 1963, Brodo A-4615, B-4555 & Brodo (CANL), 1963, Brodo B-4558 & Brodo (CANL, MIN). Pendleton Co., 1976, Harris 10636 (NY). Cass, 1923, Gray (FH, US). Greenbank, 1929, Gray (NY, US), 1930, Gray (US). *Wisconsin*. Ashland Co., 1987, Wetmore 60236, 60245, 60828, 60863 (MIN). Bayfield Co., 1965, Wetmore 13378 (COLO, MIN, US), 1987, Wetmore 61006, 61183 (MIN). Douglas Co., 1946, Thomson, Thomson: Lich. wisconsinenses 36 (CANL, COLO, MIN, US).

25. Bacidia subincompta (Nyl.) Arnold, nom. cons. prop.

Flora, Jena 53: 472 (1870). - *Lecidea subincompta* Nyl., Flora, Jena 48: 147 (1865). – Type: Austria, "An Stämmchen von *Sorbus chamaemespilus* unterhalb der serloswände ober der Waldrast. 5400'. Matrei in Tirol", 1872, Arnold, Arnold: Lich. exs. 505 (H-NYL, typ. cons. prop.; LD, isotype).

Lecidea separabilis Nyl., Flora, Jena 48: 147 (1865). - *Bacidia separabilis* (Nyl.) Arnold, Flora, Jena 53: 472 (1870). – Type: Finland, Tavastia australis, "Hollola", 1863, Norrlin (H-NYL 17424, lectotype selected here).

Lecidea hegetschweileri Hepp, Hepp: Systematische Sammlungen 212 (1852), nom. nudum. - *Biatora atrosanguinea* var. *hegetschweileri* Hepp, Hepp: Flechten Europas no. 23 (1853). - *Bacidia hegetschweileri* (Hepp) Vain., Acta Soc. Fauna Flora fenn. 53 (1): 215 (1922), non auct. – Type: Hepp: Flechten Europas no. 23 (BM, lectotype selected here).

Nomenclature. *Lecidea subincompta* Nyl. was originally made as a nomen novum for *Biatora atrosanguinea* (Schaer.) Hepp (Nylander 1865), since a combination based on the latter name was blocked by the already existing *Lecidea atrosanguinea* (Hoffm.) Nyl. Unfortunately, Nylander based his interpretation of *Biatora atrosanguinea* (Schaer.) Hepp (the basionym of which is *Lecidea anomala* var. *atrosanguinea* Schaer.) on the specimens of Hepp's Flechten Europas 286 in H-NYL, which comprises a mixture of *Bacidia subincompta* in the present sense and *B. circumspecta*. *Lecidea anomala* var. *atrosanguinea* Schaer. was originally based on Schaerer's Lichenes Helvetici exs. 212, which contains nice specimens of *Bacidia incompta* (Borrer ex Hook.) Anzi (syntypes in G and LD studied). Unless conserved, the much used name *Bacidia subincompta* will disappear into synonymy with *Bacidia incompta*. The name *Bacidia subincompta* would then be replaced by *Bacidia separabilis* (Nyl.) Arnold, a name which has hardly ever been used. Ironically, the basionym of this name, *Lecidea separabilis* Nyl., was described on the same page in the same work as *Lecidea subincompta* Nyl.! Magnusson (1936) was the first to list *B. separabilis* (Nyl.) Arnold as a synonym of *B. subincompta* (Nyl.) Arnold. Arnold's Lich. exs. 505 in H-NYL is here suggested as the conserved type of *Bacidia subincompta*, because Nylander himself annotated this specimen "*Lecidea subincompta*", it is a well-developed and typical specimen, and there are isotypes in several other herbaria.

Regarding the nomenclature of the name *Bacidia hegetschweileri*, see *B. vermifera*.

Illustrations. Figs 32 (map), 42F.

Characterization. Thallus granular or ± rimose. Apothecia purple-brown to black. Proper exciple at least laterally with a mixture of greenish and brownish hues. Hypothecium brown, always distinctly darker than the proper exciple below, K+ purplish. Upper part of hymenium ± green. Paraphyses 1.2-2.4 μm wide in mid-hymenium. Spores fusiform, bacilliform, clavate, or acicular, 19-64 × 1.9-6.2 μm, with 3-13 septa.

Thallus indeterminate, rather thin to thick, either discontinuous, of discrete granules or low convex areoles, or continuous, without cracks or ± rimose, wrinkled, warted, tuberculate, or distinctly granular. Granules ± globose or flattened to subsquamulose, (24-)51-74-106(-145) μm (s= 25, N= 11, n= 5), light grey to grey to yellowish grey to green-grey to grey-green to brown-green to brown. Prothallus lacking or present between discrete areoles/granules, thin, endosubstratal, white.

Apothecia (0.3-)0.4-0.6-1.0(-1.2) mm diam. (s= 0.2, N= 18, n= 5), ± plane when young, later becoming convex, epruinose. Disc purple-brown to brown-black to blue-black to pure black, rarely pink-brown or ± grey-brown (± pigment deficient). Margin concolorous with, or paler or darker than disc, grey-brown to dark brown to blue-black to pure black, rarely pink-brown or orange-brown, distinct, level with or raised above disc in young apothecia, later level with the disc, and finally excluded in old and convex apothecia.

Proper exciple laterally (40-)56(-74) μm wide (s= 10, N= 18, n= 1), without crystals. Rim colourless to pale yellow, or orange-brown to red-brown to black-brown, often with a green or blue-green tinge at least in upper part (giving rise to different hues of brown-green or green-brown), along the edge with a single cell layer of of enlarged cells with lumina that are up to 8 × 5 μm. Lateral interior concolorous with or darker than rim (never entirely colourless). Medullary part always paler than hypothecium and lateral interior, colourless to pale yellow to pale brown to pale red-brown. Hypothecium pale to dark (often reddish) brown, sometimes with a green-brown tinge in upper part. Hymenium (45-)54-82-104(-112) μm thick (s= 17, N= 17, n= 5), lower part colourless except for occasional vertical streaks of green to blue-green pig-

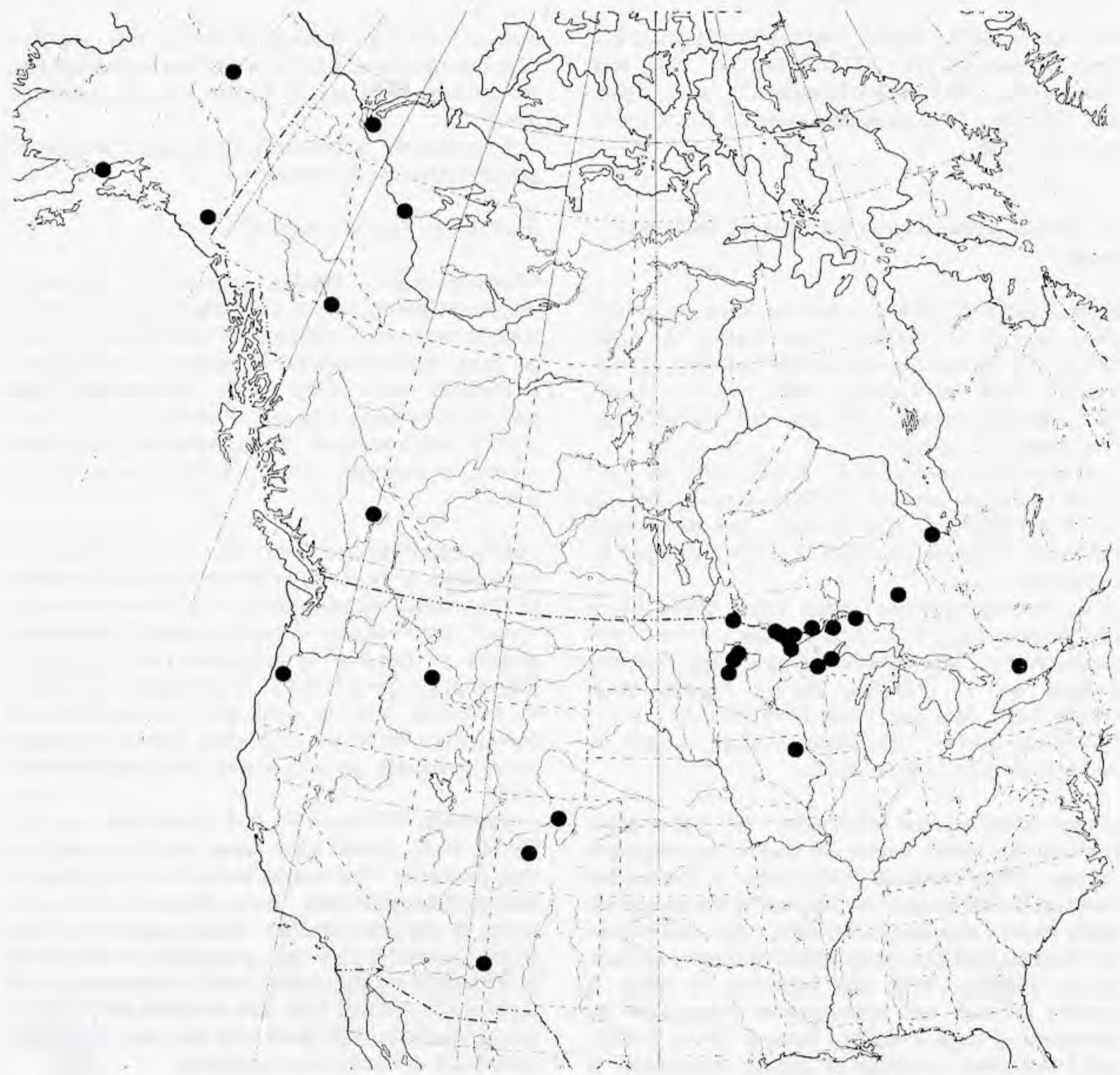


Fig. 32. Known North American distribution of *Bacidia subincompta*.

ment, upper part dirty green to blue-green, indistinctly or distinctly delimited. Paraphyses 1.2-2.4 µm wide in mid-hymenium; apices ± clavate or not at all swollen, sometimes ± moniliform, (1.6-)2.2-3.6-5.6(-6.5) µm wide (s= 1.2, N= 19, n= 5), without internal pigment or with brownish grey internal pigmentation forming a very diffuse cap. Spores fusiform, bacilliform, clavate, or acicular, straight to curved to sigmoid, (19-)23-37-50(-64) µm long (s= 9, N= 17, n= 10), (1.9-)2.1-3.3-5.1(-6.2) µm wide (s= 1.0, N= 17, n= 10), (3.2-)4.6-12.1-19.2(-22.7) times as long as wide (s= 4.5, N= 17, n= 10), with (3-)3.0-5.8-9.7(-13) septa (s= 2.3, N= 17, n= 10).

Pycnidia ± immersed in thallus, uppermost part of wall concolorous with apothecia, c. 50 µm diam. Conidia filiform, curved, non-septate, 10-20 × c. 0.8 µm.

Chemistry: No lichen substances detected.

Pigments: Upper part of hymenium K-, N+ purple (with or without a precipitate of blue crystals). Apices of paraphyses when with brownish pigment K+ purplish, N+ orange-red. Hypothecium and proper exciple K+ purplish, N+ orange-red. – Bacidia Green in hymenium, uppermost part of exciple, and sometimes also upper part of hypothecium. Laurocerasi Brown in hypothecium, proper exciple, pycnidial wall, and apices of the paraphyses.

Ecology. Mainly on rough bark of tree-trunks, preferably in shady and humid forests, but sometimes also in more or less open places like thin forests, forest edges, and solitary trees. *Fraxinus* spp., *Populus* spp, and *Thuja occidentalis* are the most common phorophytes, but it has also been collected on *Abies* sp., *Acer saccharum*, *Alnus* sp., *Quercus garryana*, *Salix* sp., *Ulmus americana*, and lignum of *Pinus* sp.

Distribution. In the Great Lakes region, in the montane or arctic areas from southern Arizona to Alaska, and one outlier in the Willamette Valley of Oregon. – Europe.

Discussion. *Bacidia subincompta* is superficially very similar to *B. schweinitzii*. However, in *B. schweinitzii*, the hypothecium and at least a large part of the proper exciple is continuously and evenly darkly pigmented, whereas in *B. subincompta*, the hypothecium is ± brown in a distinct zone and much paler below.

Bacidia subincompta is a well-defined species, although with an amazing amount of variation in spore shape and thallus appearance. The variation in thallus appearance is similar to that exhibited by the close relative *B. schweinitzii*. The variation in spore shape, however, is unsurpassed by any other species of *Bacidia* that I know of. Within *B. subincompta*, 4-celled and fusiform as well as multicelled and acicular spores can be found. The variation in spore shape is always moderate within the same apothecium, but in some specimens, bacilliform spores are found in young apothecia, whereas acicular spores are found in old apothecia. Consequently, it seems likely that at least part of the variation is due to the age of the apothecium in which the spores are produced. The remainder of the variation must be due to either genetical variation, or environmental influence. Since specimens with very different spore types can be found in similar habitats, and since specimens with the same spore type can be found in very different habitats, it seems probable that a large portion of the variation is actually genetically based.

Partially pigment deficient specimens with pink-brown apothecia have been collected a few times in North America. Entirely pigment deficient specimens with pale pink apothecia have so far only been observed in Europe.

Collections examined. CANADA. *British Columbia*. Wells Gray Provincial Park, 1989, Ekman L794 (LD). *Northwest Territories*. Mackenzie District, Little Gull River, 1966, Scotter 8274c (H). C. 5 mi SE of Norman Wells, 1978, Bird & Thomson (WIS). *Ontario*. Algoma District, Nagagamis Prov. Park, 1968, Brodo 13462 (CANL). Cochrane District, Moose Factory, 1969, Brodo 14682, 14717c (CANL). Lennox & Addington Co., 1972, Wong 855c, Shchepanek & Ley (CANL). Thunder Bay District, 16 km SW of Suomi, 1972, Garton 15327, 15337 (CANL). Slate Islands, 1977, Wetmore 28593 (MIN), 1977, Wetmore 28596 (CANL, MIN). *Yukon*. Tom Creek Tower Area, 1981, Rosie 711 (CANL). – U. S. A. *Alaska*. C. 300 km NNW of Fairbanks,1989, Thor 9081 (S). Chisik Island, 1987, Talbot 87014-2a (WIS). Wrangel-St. Elias Nat. Preserve, c. 390 km E of Anchorage, 1989, Thor 8791 (S). *Arizona*. Apache Co., 1975, Nash 11739 (COLO). *Colorado*. Boulder Co., 1961, Anderson 1513 (CANL, MIN). Gunnison Co., 1955, Weber (COLO). *Iowa*. Fayette, 1894, Fink (NY). *Michigan*. Gogebic Co., 1989, Ekman L971, L976, L978, L979 (LD), + 1989, Ekman L972 (filed with *B. polychroa*, LD). Keeweenaw Co., 1983, Wetmore 47321, 47929 (MIN). Ontonagon Co., 1989, Ekman L987 (LD). *Minnesota*. Beltrami Co., 1900, Fink 596 (MIN). Clearwater Co., 1972, Wetmore 20343 (MIN). Cook Co., 1986, Wetmore 57107 (MIN, NY). Lake Co., 1989, Ekman L952, L959, L961 (LD). + Lake of the Woods Co., 1901, Fink 400 (filed with *B. suffusa*, MIN). Otter Tail Co., 1900, Fink 376 (MIN). Roseau Co., 1901, Fink 234, 323 (MIN). St. Louis Co., 1901, Fink 1468 (MIN), 1986, Wetmore 57637, 57642 (MIN). *Montana*. Ravalli Co., 1980, McCune 10824 (LD). *Oregon*. Benton Co., 1989, Ekman L695 (LD).

26. Bacidia suffusa (Fr.) A. Schneid.

Guide Study Lich. 110 (1898). - *Biatora suffusa* Fr., Syst. Orb. Veget. 285 (1825). – Type: U. S. A., Minnesota, Mahnomen Co., "East of Washington Lake (18 miles NE of Mahnomen). In swamp area with balsam fir, spruce, tamarack", 1976, Wetmore 26404 (US, neotype selected here; CANL, MIN, isotypes).

Lecidea spadicea Ach., Synops. Lich. 34 (1814), nom. rejic. prop. - *Bacidia spadicea* (Ach.) Zahlbr., Denkschr. math.-naturw. Kl. Akad. Wiss. Wien 83: 128 (1909). – Type: North America, specimen marked "*Lecid. spadicea* ns.", ex herb. Muhlenberg (PH, lectotype selected here).

Nomenclature. I have been unable to trace any original material of *Bacidia suffusa*. Therefore, a neotype is selected, a well-developed collection kept in three of the major herbaria in North America.

Lecidea spadicea Ach. was, according to the introduction of *Synopsis Methodica Lichenum*, based on material collected by G. H. E. Muhlenberg. There is no original material in H-ACH, BM, or UPS. The only ex-

Fig. 33. Known world distribution of *Bacidia suffusa*.

tant original material appears to be a small specimen in PH marked "*Lecid. spadicea* ns." This specimen, which is typical *B. suffusa*, was probably collected in Pennsylvania, where Muhlenberg was active as a clergyman. *Lecidea spadicea* Ach. antedates *Biatora suffusa* Fr. by 11 years. Unless an exception is given to the rules of priority, the widely and correctly used name *Bacidia suffusa* will be replaced by *Bacidia spadicea* (Ach.) Zahlbr. Apparently, after the original publication, *Bacidia spadicea* has rarely been used, and never in the correct sense. Instead, *B. spadicea* has been used for various temperate, subtropical, and tropical taxa, none of which are conspecific with the type. Thus, to inhibit further confusion, I suggest rejection of the name *Lecidea spadicea* Ach. (Art. 56.1).

Illustrations. Figs 3C, 33 (map), 42G.

Characterization. Apothecia ± yellow-brown, ± orange-brown or ± purplish to black, sometimes mottled, at least some pruinose. Proper exciple laterally pale yellow to black-brown (along the edge with a 4-6 cell layers thick, distinct zone of enlarged cell lumina), without minute and evenly dispersed crystals (but often with clusters of ± large crystals). Hypothecium ± yellowish, K+ intensifying. Upper part of hymenium pale yellow to black-brown. Spores 38-91 × 2.5-4.3 µm, with 3-17 septa.

Thallus indeterminate, usually ± thick but sometimes thin, continuous, without cracks, ± rimose to areolate or without cracks, smooth to wrinkled to warted to tuberculate, or sometimes subsquamulose, ± yellow-grey to green-grey or pale grey to grey. Prothallus lacking.

Apothecia (0.5-)0.6-1.0-1.2(-1.5) mm diam. (s= 0.2, N= 21, n= 5), ± plane when young, later becoming convex, with thin to thick white pruina on edge and/or disc of at least some young and medium-aged apothecia.

Disc pale yellow-brown, yellow-brown, brown, deep orange-brown, purple-brown, brownish purple, dark purple, brown-black, purple-black, or pure black, sometimes mottled with different colours. Margin concolorous with disc or sometimes slightly darker, ± thin, level with or slightly raised above disc in young apothecia, persistent, excluded only in some old and convex apothecia.

Proper exciple laterally (52-)67(-86) µm wide (s= 12, N= 21, n= 1), usually with radiating clusters of up to 10 µm wide crystals. Rim pale yellow to yellow-brown to orange-brown to dark-brown to black-brown, often darker in upper part than in lower part, along the edge with a 4-6 cell layers thick, distinct zone of cells with enlarged lumina that are up to 12 µm long and up to 6 µm wide. Lateral interior paler than or ± concolorous with rim (rarely darker than rim). Medullary part paler than lateral interior part, almost colourless to pale yellowish. Hypothecium ± yellowish, concolorous with or slightly darker than lateral interior of proper exciple. Hymenium (71-)74-94-115(-127) µm thick (s= 12, N= 21, n= 5), lower part colourless except for occasional vertical streaks with ± orange-brown pigment, upper part pale yellow to pale brown-orange to orange-brown to red-brown to black-brown, pigmentation indistinctly or sometimes distinctly delimited. Paraphyses 1.2-2.0 µm wide in mid-hymenium; apices narrowly clavate or not at all swollen, (1.2-)1.5-1.8-2.0(-2.8) µm wide (s= 0.3, N= 21, n= 5), without internal pigment. Spores acicular, straight, curved, or sigmoid, sometimes coiled in ascus, (38-)48-57-69(-91) µm long (s= 8.0, N= 19, n= 10), (2.5-)2.7-3.2-3.6(-4.3) µm wide (s= 0.4, N= 19, n= 10), (10.3-)14.4-17.9-21.9(-29.5) times as long as wide (s= 3.4, N= 19, n= 10), with (3-)6.3-7.9-12.6(-17) septa (s= 2.5, N= 19, n= 10).

Pycnidia ± immersed in thallus or prothallus, uppermost part of wall concolorous with apothecia, 100-125 µm diam. Conidia filiform, curved, non-septate, 10-27 × c. 0.8 µm.

Chemistry: Atranorin (sometimes only as a trace).

Pigments: Yellow to orange parts of apothecia K+ intensifying, N+ intensifying, ± dark brown parts K+ purplish, N+ orange-red. – Laurocerasi Brown in proper exciple, hymenium, and pycnidial wall. Rubella Orange in proper exciple, hypothecium, hymenium, and pycnidial wall.

Ecology. Mainly on the rough bark of tree trunks in shady and humid forests (often swamp forests). There are a few finds on rock. Many corticolous finds are on *Acer* spp. and *Fraxinus* spp., but it has also been collected on *Carpinus caroliniana*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Populus* sp., *Quercus alba*, *Q. macrocarpa*, *Salix* sp., *Thuja occidentalis*, *Tilia americana*, *Ulmus americana*, and *Zanthoxylum clava-herculis*.

Distribution. In the eastern temperate region, but commonest in the Great Lakes area. In addition, there are two old and probably mislabelled specimens marked "Idaho" and "British Columbia", respectively. – Endemic.

Discussion. The abundance of crystals in the proper exciple, the pigmentation, and the zone of enlarged cells along the edge of the proper exciple indicate that *B. suffusa* is more closely related to the tropical species *B. campalea*, *B. fusconigrescens* (Nyl.) Zahlbr. and *B. millegrana* (Taylor) Zahlbr. than to any of the species occurring within the distribution range of *B. suffusa*. For differences between *B. campalea* and *B. suffusa*, see the former species. *B. millegrana* can be separated from *B. suffusa* by the presence of a narrower, two cell layers thick zone of enlarged lumina along the edge of the proper exciple, and by the absence of crystals and pruina in the apothecia. *B. fusconigrescens* is very similar to *B. suffusa*, also regarding the zone of enlarged cells along the edge of the proper exciple, but is mainly separated by the presence of ± evenly distributed, minute crystals in the proper exciple and by the darker pigmentation (apothecia ± black).

Although perhaps not closely related, *B. suffusa* may be confused also with *B. rosella* (see that species), *B. diffracta*, and *B. polychroa*. The latter two species can be separated by the brown, K+ purple-red hypothecium.

Additional collections examined. CANADA. *British Columbia.* Vancouver Island, 1875, Macoun 2808 (CANL, probably mislabelled). *Ontario.* Renfrew Co., 1983, Brodo 25122, Brodo, Thomson & Thomson (CANL). Algonquin Park, 1900 (CANL). Belleville and Ottawa, 1881, Macoun (US). Belleville, 1882, Macoun 2805 (CANL), 1889, Macoun 3049 (CANL), + 1882, probably collected by Macoun (filed with *B. polychroa*, CANL). Carp, 1907 (CANL). Edmonton, 1893, White 320 (CANL). Navan, 1902 (CANL). Ottawa, 1884, Macoun 2804 (CANL), 1891, Macoun 273-74 (CANL), 1892, Macoun 2807 (CANL), 1896, Macoun (US), 1900, Macoun 221 (CANL, COLO, US), 1902, Macoun 192 (CANL), 1905, Macoun 191 (CANL, US), + 1891, Macoun 102 (filed with *B. polychroa*, US), + 1891, Macoun 275-276 (filed with *B. polychroa*, CANL) + 1901, Macoun 192 (filed with *B. schweinitzii*, CANL). Prescott, Billings (CANL). *Quebec.* Comté Argenteuil, 1984, Brodo 25032 (CANL). Gatineau Co., Brodo 16373 (CANL), 1973, Brodo 19122 & Hawksworth (CANL). Buckinghamn, 1896, Macoun 391 (CANL). – U. S. A. *Arkansas.* Stone Co., 1993, Tønsberg 19258 (BG). *Florida.* + Jacksonville, 1888, Eckfeldt (filed with type specimen of *Lecidea subspadicea* Nyl.= *B. polychroa*, H-NYL). *Idaho*. 1889, Leiberg (US, probably mislabelled). *Illinois*. Calkins 56 (NY). + Calkins 114 (filed with *B. polychroa*, NY). Cook Co., 1897, Calkins (NY). Canton, unknown collector (NY), Wolf (US), + unknown collector (filed with *B. polychroa*, NY), + Wolf 17 (filed with *B. polychroa*, US), + Wolf (filed with *B. polychroa*, US). Deer Park, Calkins 113 (NY). *Iowa*. Bremer Co., 1894, Fink (MIN, NY, US), 1898, Fink (MIN). Fayette Co., 1894, Fink (CANL, MIN, NY, US), 1894, Fink, Cummings: Decades N. Am. Lich. 171 (FH, NY, US), + 1894, Fink (filed with *B. polychroa*, US), + 1894, Fink (filed with *B. schweinitzii*, MIN), 1895, Fink (CANL, NY, US). Henry Co., 1898, Savage (MIN). Iowa City, Shimek (MIN). Fayette, 1894, Fink, Cummings et al.: Lich. Boreali-Am. 102 (COLO), 1894, Fink (MIN, NY). Near Fayette, 1894, Fink (CANL, MIN). *Kansas*. Manhattan, 1893, Waters & Reed 36 (NY). *Louisiana*. Ascension Par., 1981, Tucker 21468, 21473 (herb. Tucker). East Baton Rouge Par., 1980, Tucker 21335 (herb. Tucker). Iberville Par., 1974, Tucker 13317b (herb. Tucker). Sabine Par., 1970, Tucker 8883 (CANL, COLO), + 1970, Tucker 8883 (filed with *B. diffracta*, herb. Tucker). St. Helena Par., 1972, Tucker 10072 (herb. Tucker). West Feliciana Par., 1981, Tucker 21525 (herb. Tucker). + Chenal, 1894, Langlois (filed with *B. schweinitzii*, US). Duchamps, 1894, Langlois 860, s. n. (US). *Maryland*. Montgomery Co., 1902, Maxon 622 (US), 1907, Fink 87 (US). *Massachusetts*. New Bedford, Clarke (FH), Willey (FH, US). *Michigan*. Alger Co., 1987, Wetmore , 58764, 59587 (MIN). Antrim Co., 1965, Swanson (MICH). Delta Co., 1976, Harris 11890 (CANL). Dickinson Co., 1971, Harris 7606 (MIN). Gogebic Co., 1975, Harris 9998a (MIN), 1975, Buck B230 (NY), 1989, Ekman L966, L967, L974, L984 (LD). Ontonagon Co., 1989, Ekman L994, L995 (LD). *Minnesota*. Blue Earth Co., 1899, Fink 29, 37, 130, 138, 141 (MIN), 1899, Gardner 77, 79, 97 (NY). Brown Co., 1899, Fink 274 (MIN). Cass Co., 1976, Wetmore 25951, 25969 (MIN). Clearwater Co., 1963, Hale 22819 (US), 1972, Wetmore 20327, 20354, 20359 (MIN), 1974, Wetmore 22826 (MIN), 1976, Wetmore 25820 (MIN), 1978, Wetmore 36328, 36336 (MIN). Hennepin-Ramsey Co., 1896, Fink 194 (MIN). Hubbard Co., 1957, Anderson (COLO). Itasca Co., 1977, Trana 3130 (MIN). Koochiching Co., 1979, Wetmore 37416 (MIN, NY). Lake of the Woods Co., 1901, Fink 400 (MIN). Olmsted Co., 1975, Wetmore 24163 (MIN), 1977, Trana 2898 (MIN). Otter Tail Co., 1900, Fink 345 (MIN). Pine Co., 1983, Schuster 258 (CANL, MIN). Rice Co., 1975, Wetmore 24224 (MIN). St. Louis Co., 1902, Fink, Hibbard Photo 5443 (MIN), 1973, Wetmore 21696 (MIN), 1978, Wetmore 32669, 32694, 35494, 35502, 35533 (MIN), 1978, Wetmore 31371, 34234, 34255, 34932, 34935 (CANL, MIN), 1979, Wetmore 38899, 40219 (MIN), + 1978, Wetmore 31334 (filed with *B. rubella*, MIN). Winona Co., 1980, Brako 2520 (MIN). Yellow Medicine Co., 1899, Fink 529, 536, 540 (MIN). Cobden, 1878, Earle (NY). Red Lake, 1900, Fink 918, 936, 1015, 1041 (MIN). St. Cloud, 1897, Morgan (US). *Mississippi*. Madison Co., 1971, Tucker 9856 (herb. Tucker). Sharkey Co., 1978, Johnson 7038, 7039, 7044, 7045, 7046, 7066, 7083, 7084, 7089, 7116, 7121 (NY). *New Jersey*. Andover, unknown collector (NY). Closter, 1876, Austin 723 (NY), Austin (NY). Springdale, 1937 (NY). *New York*. Belleville (NY). Buffalo, Wilson (NY, US). East Galway, 1886, 1893, Burt (FH). Fishkill, 1850, Russell (FH). Jamesville, Willey (US). Oneida, Merrill (FH). Shushan, 1907, Fink (NY). *North Carolina*. Swain Co., 1987, Harris 20979, 21000 (NY). *Ohio*. + 1897, Bogue 874, s. n. (filed with *B. polychroa*, NY). Willson 841 (NY). Columbus, 1893, Bogue 215 (NY). + Orwell, 1891, Bogue, Merrill: Lich. exs. 171 (filed with *B. polychroa*, COLO). *Pennsylvania*. Willey (US). *South Carolina*. Curtis (NY). Chester, Green (NY). *Wisconsin*. Ashland Co., 1987, Wetmore 60307, 60902 (MIN), 1965, Denison 862 (CANL). St. Croix Falls, 1897, Baker 138 (NY).

27. Bacidia vermifera (Nyl.) Th. Fr.

Lichenographia Scand. 1: 363 (1874). - *Lecidea vermifera* Nyl., Bot. Notiser 1853: 98 (1853). - Type: Sweden, "Holmiae (Marieberg) ad quercus", Nylander (H-NYL 17507, lectotype selected here).

Bacidia hegetschweileri auct., non (Hepp) Vain.

Nomenclature. The name *Bacidia hegetschweileri* has often been used for this species. This name first appeared as *Lecidea hegetschweileri* Hepp (a nomen nudum) in Hepp's Systematische Sammlungen no. 212 in 1852. In the following year, the name was validly published as *Biatora atrosanguinea* var. *hegetschweileri* in another of Hepp's exsiccates, Flechten Europas no. 23. In the protologue, the collection in Systematische Sammlungen, a collection in herb. Schaerer (Flotow: Lich. exs. no. 91c), and an unspecified number of collections from the vicinity of Zürich in herb. Hepp. are cited. All these specimens are syntypes in addition to Flechten Europas no. 23. The protologue also includes line drawings of spores that are 3-7-septate and straight or only slightly curved.

I have not been able to trace any specimen of Systematische Sammlungen no. 212, nor have I been able to find any schedae. A stray specimen of this "exsiccate" in UPS (no. 126) shows a handwritten label. Clearly, Systematische Sammlungen was not a true exsiccate.

Lynge (1915) saw the series in B, but according to H. Sipman (in litt.) it is no longer present (probably destroyed). All syntypes seen by me (BM, G, LD, M, STR) belong to *Bacidia subincompta*, except one (one of the four in G) which belongs to *B. hegetschweileri* auct., i.e., *B. vermifera*. *Biatora atrosanguinea* var. *hegetschweileri* cannot be typified with a specimen of *B. hegetschweileri* auct., however. The line drawings of spores show that Hepp's intention was to describe the lichen that belongs to *B. subincompta*. A lectotype belonging to *B. hegetschweileri* auct. would thus be in serious conflict with the protologue due to the very different spores (Art. 9.13b).

The use of *Bacidia hegetschweileri* was established by Vainio (1922), who was also the first to combine the name to the species level. *Bacidia vermifera*, on the other hand, was validly published as *Lecidea vermifera* in 1853, and has since been used in a sense consistent with the lectotype selected here. Indeed, the name *Bacidia vermifera* has been in use for this species, parallel to *Bacidia hegetschweileri*, as late as in the 1970s. Consequently, *B. vermifera* is the oldest name at the species level and has never been used in a sense conflicting with its type.

Since the name *Bacidia hegetschweileri* is known by few, and since the name *B. vermifera* has been used for the same taxon also in relatively recent times, I believe the best way to minimize the confusion is to discontinue the use of *Bacidia hegetschweileri* and reduce it into synonymy with *B. subincompta* (see synonymy under this species). Accordingly, the use of *B. vermifera* should be resumed.

Illustrations. Figs 34 (map), 42H.

Characterization. Apothecia (almost) black. Proper exciple laterally red-brown to black-brown (rim darkest). Hypothecium pale. Upper part of hymenium dark red-brown to black-brown; much of the pigment confined to the wall of the parahysis apices. Spores bacilliform to clavate, strongly curved or sigmoid, 14-31 × 2.1-3.1 µm.

Thallus indeterminate, ± thin, either continuous, warted, ± rimose to areolate, or discontinuous, of discrete or contiguous, convex, warted, sometimes subsquamulose, often poorly delimited areoles, white to pale grey to grey to brown-grey. Prothallus lacking or present between discrete areoles, thin, white to pale grey, endosubstratal.

Apothecia (0.2-)0.3-0.3-0.4(-0.5) mm diam. (s= 0.06, N= 8, n= 5), ± plane, remaining so or becoming moderately convex or rarely markedly convex, epruinose. Disc usually pure black, seldom partially or entirely dark purple-brown. Margin concolorous with disc, glossy or matt, distinct, raised above disc in young apothecia, soon level with the disc, persistent or only rarely excluded.

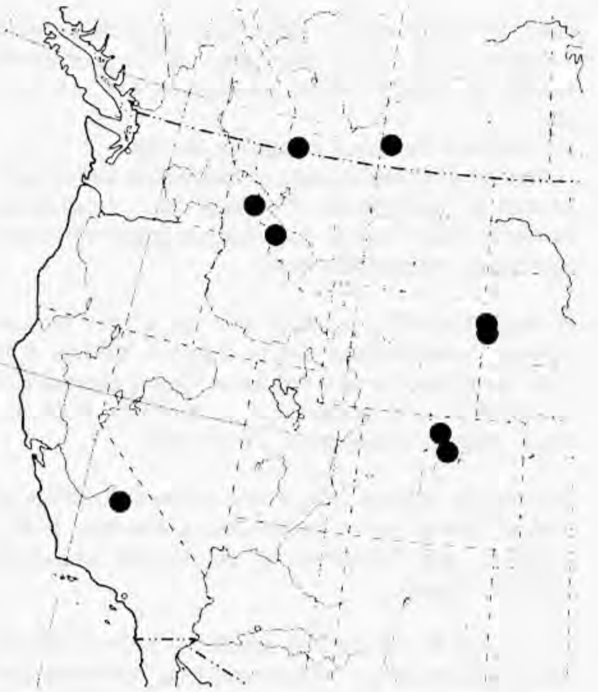


Fig. 34. Known North American distribution of *Bacidia vermifera*.

Proper exciple laterally (26-)35(-45) µm wide (s= 6, N= 8, n= 1), without crystals. Rim black-brown or dark red-brown, downwards sometimes gradually changing to ± red-brown or colourless, along the edge without a layer of enlarged cells. Lateral interior slightly paler than or sometimes concolorous with rim. Medullary part colourless or very pale brownish. Hypothecium colourless or very pale brownish. Hymenium (45-)48-56-64(-68) µm thick (s= 6, N= 8, n= 5), lower part colourless except for occasional vertical streaks with brown pigment, upper part dark red-brown to black-brown, indistinctly delimited. Paraphyses 1.2-2.4 µm wide in mid-hymenium; apices ± clavate (or sometimes a few slightly or not at all swollen), (1.2-)3.1-3.5-4.1(-6.1) µm wide (s= 1.1, N= 8, n= 10), many with brown pigment in the wall. Spores bacilliform to clavate, usually strongly curved or sigmoid but sometimes only slightly curved or almost straight, coiled in ascus, (14-)16-20-27(-31) µm long (s= 4, N= 7, n= 10), (2.1-)2.3-2.6-2.9(-3.1) µm wide (s= 0.3, N= 7, n= 10), (5.2-)6.3-7.8-11.2(-13.5) times as long as wide (s= 2.2, N= 7, n= 10), with (3-)3.0-3.4-4.3(-7) septa (s= 0.9, N= 7, n= 10).

Pycnidia half-immersed in thallus, uppermost part of wall concolorous with apothecia, 40-75 µm diam. Conidia of two types: (1) ellipsoid or short-bacilliform, non-septate, 2.8-3.6 × 1.2-1.6 µm, and (2) bacilliform, straight or slightly curved, non-septate, 6-9 × 0.5-0.8 µm.

Chemistry: No lichen substances detected.

Pigments: All brown parts of apothecium and pycnidial wall K+ purplish and N+ orange-red. – Laurocerasi Brown in proper exciple, hypothecium (small amounts), hymenium, and pycnidial wall.

Ecology. Preferably in shady and humid sites such as canyons, but sometimes also in semiopen habitats. It is often found near streams and lakes. Known phorophytes include *Populus angustifolia*, *P. tremuloides*, *P. trichocarpa*, *Quercus macrocarpa*, and *Salix* sp.

Distribution. Known from a few scattered localities in Alberta, Saskatchewan, South Dakota, Montana, Idaho, Colorado, and California, all at altitudes exceeding 1000 m. – Europe.

Discussion. *B. vermifera* is similar to *B. circumspecta* and *B. igniarii* but can be separated from both these species by the absence of a green pigment (Bacidia Green) in the hymenium and the proper exciple. Furthermore, the spores of *B. circumspecta* are not as strongly curved or sigmoid as in *B. vermifera*.

Collections examined. CANADA. *Alberta*. Waterton Lakes Area, 1964, Jonescu (WIS). *Saskatchewan*. Cypress Hills, 1964, Jonescu (WIS). – U. S. A. *California*. Tulare Co., 1985, Blakeman 360 (MIN). *Colorado*. Boulder Co., 1973, Carmer 757 (CANL, COLO). Larimer Co., 1962, Anderson 2825 (COLO). *Idaho*. Shoshone Co., 1987, McCune 16508 (OSC). *South Dakota*. Lawrence Co., 1960, Anderson (COLO). Pennington Co., 1960, Anderson (COLO, MSC).

Bacidina Vězda, nom. cons. prop.

Folia Geobot. Phytotax. Praha. 25: 431 (1991). – Type: *Bn. phacodes* (holotype).

Lichingoldia D. Hawksw. & Poelt, Pl. Syst. Evol. 154: 203 (1986). – Type: *L. gyalectiformis* D. Hawksw. & Poelt (holotype).

Woessia D. Hawksw. & Poelt, Pl. Syst. Evol. 154: 207 (1986). – Type: *W. fusarioides* D. Hawksw., Poelt & Tscherm.-Woess (holotype).

Woessia and *Lichingoldia*, both described by Hawksworth & Poelt (1986), antedate *Bacidina* by almost five years. Both genera were based on a single collection each in the anamorphic state referred to the type species *W. fusarioides* and *L. gyalectiformis*. Both species were thought to be lichenized "conidial fungi", i.e., fungi not producing ascomata and entirely dependent on conidia for their dispersal. It is clear from the context that the authors did not associate *W. fusarioides* or *L. gyalectiformis* with the *Bacidia phacodes* group.

The type specimen of *Woessia fusarioides* belongs to *Bn. arnoldiana* (according to Sérusiaux 1995 and isotype in priv. herb. of Tschermak-Woess!), whereas the type specimen of *Lichingoldia gyalectiformis* belongs to *Bacidina inundata* (Fr.) Vězda. The describing authors interpreted the type collection of *Lichingoldia gyalectiformis* as a mixture of this species and *Bacidina inundata*. The possibility that these names were conspecific was actually discussed , but it was ruled out due to "the different appearance of the thalli" and since "the conidiomata are not found intermixed with the ascomata". In the type material (isotype in UPS!), I find the apothecia and pycnidia to be mixed on the same thallus, which is not dimorphic. Furthermore, the measurements of conidia provided by the authors refer, according to a slide made by one of the authors and filed with the type, to filaments of an alga overgrown by *Bacidina inundata*! True conidia are, however, present in the same preparation, and they measure 21-36 µm in length (which is normal to *Bn. inundata*), not 70-85 µm as suggested by the authors.

Twenty-five species are presently recognized in *Bacidina* (26 if *Bacidina neglecta* Vězda is considered as distinct from *Bn. chloroticula*), including the species described in or combined into *Bacidina* in this work. Although still a "young" genus, *Bacidina* has gained acceptance also in important reference works (e.g., Farkas & Sipman 1993, Esslinger 1995, Wirth 1995). *Woessia* and *Lichingoldia*, on the other hand, have not received any attention at all, with the recent unfortunate exception of Sérusiaux (1995), who attempted to replace the name *Bacidina* with *Woessia* for exactly the same genus. The reason for doing so was purely nomenclatural, i. e., there were no underlying taxonomical considerations. The present Code strongly discourages this kind of action: "Name changes made for purely nomenclatural reasons... ... are to be avoided" (Greuter et al. 1994: xv). The tools for avoiding an undesirable name change from *Bacidina* to *Woessia* are provided by the Code (Art. 14). I propose that *Bacidina* be conserved against both *Woessia* and *Lichingoldia* (Ekman 1996). Pending the final settlement, I urge that *Bacidina* should be retained.

Lichenized species. Thallus crustose, episubstratal, continuous, without cracks or rimose to areolate to granular, smooth to wrinkled to warted to subsquamulose, sometimes discontinuous, of discrete to contiguous areoles. Prothallus absent. Soredia and isidia absent. Goniocysts common, sometimes covering most of thallus, usually ± pale green. Upper cortex (not present in goniocysts) of one inner layer of anticlinal or irregular hyphae stainable in LCB and an outer epinecral layer (one or the other may be missing), without crystals. Photobiont layer continuous or discontinuous, photobiont chlorococcoid. Medulla and lower cortex absent.

Apothecia ± sessile, biatorine, rarely with an additional, thin thalline margin, when mature 0.1-2.0 mm wide, often weakly pigmented (pale pink or pale yellow to pale orange), sometimes darker (yellow-brown to orange to brown to red-brown to purple-brown to black); pruina absent. Disk plane or slightly concave when young, often soon becoming ± convex. Margin usually slightly raised above disc in young apothecia, later level with the disc, often becoming excluded in old and convex apothecia.

Proper exciple without thick gelatinous layer along rim, without oil droplets, rarely with crystals (c. 1 µm) that are evenly dispersed along the rim of the proper exciple; composed of indistinctly or distinctly radiating, sparingly or abundantly furcate, usually moderately to abundantly anastomosed hyphae. Cell lumina very variable in shape, from narrowly cylindrical to almost globose, 3-15 µm long and 1.5-8 µm wide (lumina near rim of proper exciple excepted), usually 1-8 times as long as wide, but at least partly short and wide (width exceeding 2.5 µm, length less than 4 times the width), widely cylindrical to almost globose or irregular; often distinctly constricted near septa (not in very narrow lumina). Walls ± thin, the distance between two adjacent cell lumina usually less than the width of a lumen. Cell lumina along the rim of the proper exciple rarely ± enlarged in relation to the inner lumina, never forming a distinct zone. Hypothecium usually colourless, sometimes yellowish to brown, without crystals or oil droplets, not chondroid. Hymenium 40-80 µm high, amyloid, usually colourless in lower part and ± pigmented in a diffuse layer in the upper part, rarely with a crystal layer in the upper part, without oil droplets. Paraphyses unbranched or ± branched in upper part, sometimes very sparingly anastomosed; apices not at all swollen to ± clavate, sometimes surrounded by pigment, never containing pigment in the wall, never with thick and gelatinized wall. Asci clavate, surrounded by a thin, amyloid gelatinous sheet; tholus amyloid, with a narrow or wide c-layer, with a high or low, blunt axial body (sometimes penetrating through the entire d-layer), the width of which is more than a third of the entire d-layer; ocular chamber absent or present, low or high, blunt or pointed. Spores eight per ascus, acicular to almost bacilliform, with 0-13 septa, straight, curved, or sigmoid, straight or coiled in ascus (often variable even within the same apothecium), colourless, rather thick-walled, without perispore or ornamentation, 16-60 µm long and 0.9-3.3 µm wide, 9-56 times as long as wide, easily separated from each other at maturity.

Pycnidia ± immersed in thallus, usually concolorous with or paler than apothecia, unilocular. Conidiogenous cells lining the pycnidial cavity, cylindrical, 4-8 × 1.0-1.5 µm, producing conidia apically, lacking distinct conidiophores. Conidia of five different types (one to three types in one species; usually only one type, rarely two types mixed in the same pycnidium): (1) filiform, ± curved, non-septate (rarely 1-septate), 7-30 × 0.5-1.0 µm, (2) bacilliform, 0(-2)-septate, 7-9 × 1.6 µm, (3) filiform, straight or ± curved to slightly sigmoid, distinctly 3-11-septate, 14-57 × 0.6-1.0 µm, (4) filiform, straight or slightly curved to sigmoid, strongly conglutinated, 0-1-septate, 9-14 × 0.6-0.8 µm, and (5) acicular, non-septate, 16-20 × 1.0 µm.

Chemistry: No lichen substances. Negative to K, C, KC, PD, and UV.

Discussion. As with *Bacidia*, the generic description of *Bacidina* presented above is based on my observations on the North American species and must be regarded as provisional.

28. Bacidina aenea S. Ekman, sp. nov.

Type: U. S. A., Florida, Sarasota Co., Myakka River State Park, c. 3 km S of the W end of Upper Myakka lake, seasonally flooded hammock, on *Fraxinus caroliniana*, 1993, Ekman L1207 (LD, holotype).

Thallus per maculas in goniocystas solutus. Apothecia fulva ad cervina ad fusca, pigmentum fulvum (idem quod in *Bacidia arceutina*) continentes. Facile cum *Bacidina crystallifera* confusa, quae stratum crystalliferum in epithecio et in margine excipuli proprii, item cum *Bacidina varia* quae hymenium tenuius, item cum *Bacidina* sp. #1 quae hymenium tenuius; apices paraphysorum latiores, et goniocystas tenuiores habent.

Etymology. *Aeneus*, (here) brazen.

Illustrations. Figs 5E, 36 (map), 43A, 44A.

Characterization. Thallus dissolved into goniocysts in spots. Apothecia brown-yellow to yellow-brown to dark grey-brown. Proper exciple laterally brown-yellow. Hypothecium and upper part of hymenium brown-yellow. Pigment K-. Spores acicular, clavate, or almost bacilliform, 30-43 × 1.9-2.5 µm, with 3-7 septa.

Thallus indeterminate, thin, discontinuous, of discrete or contiguous, convex, sometimes almost granular, dark

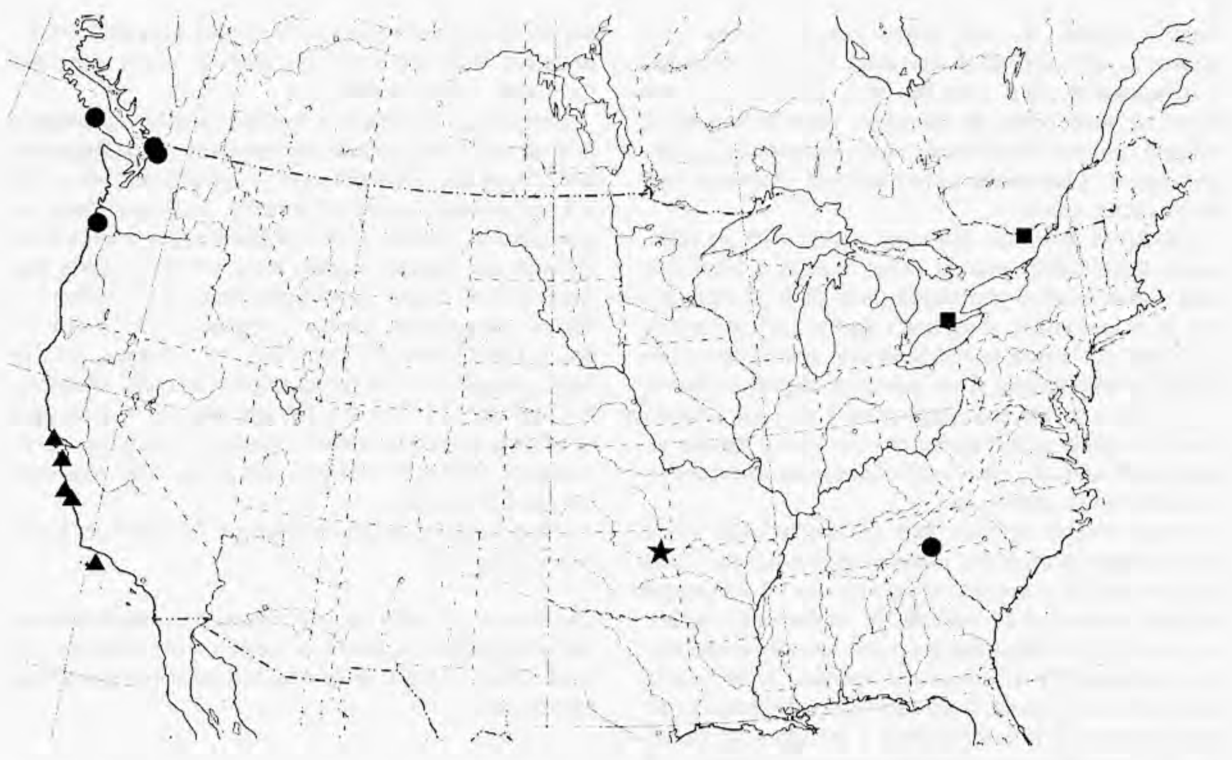


Fig. 35. Known North American distribution of *Bacidina arnoldiana* (dots), *Bn. assulata* (star), and *Bn. chloroticula* (squares). Known world distribution of *Bacidina californica* (triangles).

green to dark grey-green areoles, some of which dissolve into granular goniocysts. Goniocysts pale green, loosely aggregated, (16-)24(-35) µm diam. (s= 6, N= 1, n= 20).

Apothecia (0.3-)0.4(-0.7) mm diam. (s= 0.08, N= 1, n= 20), at first plane, later becoming convex, epruinose. Disk brown-yellow to yellow-brown to dark grey-brown. Margin concolorous with disc, distinct, slightly raised above disc in young apothecia, soon level with the disc, finally excluded.

Proper exciple laterally 43 µm wide (N= 1, n= 1), without crystals. Hyphae with fairly thin walls (2.5-5 µm between adjacent cell lumina), rather distinctly radiating towards edge, with cell lumina of widely differing shapes, gradually expanding towards edge (in lateral interior 1-4 µm wide and up to 15 µm long, 3.5-10 times as long as wide). Rim brown-yellow, downwards gradually changing to colourless. Lateral interior brown-yellow, downwards gradually changing to colourless. Medullary part colourless. Hypothecium pale brown-yellow. Hymenium (71-)73(-76) µm thick (s= 2, N= 1, n= 5), colourless except the uppermost part, which is brown-yellow. Paraphyses rather abundant in relation to the number of asci, 1.2 µm wide in mid-hymenium; apices narrowly clavate or not at all thickened, (1.0-)2.0(-3.2) µm wide (s= 0.5, N= 1, n= 20. Tholus with a narrow c-layer. Ocular chamber lacking or rather wide and blunt; axial body wide and high, conical, blunt or pointed, not penetrating through the entire d-layer. Spores acicular, clavate, or almost bacilliform, straight to curved to sigmoid, (30-)35(-43) µm long (s= 3, N= 1, n= 20), (1.9-)2.2(-2.5) µm wide (s= 0.3, N= 1, n= 20), (13.0-)16.3(-20.0) times as long as wide (s= 2, N= 1, n= 20), with (3-)5.1(-7) septa (s= 1.6, N= 1, n= 20).

Pycnidia not seen.

Pigments: Apothecia K-, N-. – Arceutina Yellow in proper exciple, hypothecium, and hymenium.

Ecology. *Bacidina aenea* was found on the upper side of the leaning branches of a *Fraxinus caroliniana*, at the borderline between a small, open marsh and a seasonally flooded hammock dominated by *Sabal palmetto*, *Quercus virginiana*, and *Fraxinus caroliniana*.

Distribution. Known only from one locality in Sarasota County in southwestern Florida.

Discussion. *Bacidina aenea* can be separated from all other species of *Bacidina* by the presence of fairly large amounts of a brown-yellow pigment in the apothecia

(Arceutina Yellow). Furthermore, *Bn. aenea* is separated from *Bn. crystallifera* by the lack of crystals in the proper exciple and hymenium, and by the wider spores, from *Bn.* sp. #1 by the higher hymenium, narrower paraphysis apices, wider spores, and coarser goniocysts, and from *Bn. varia* by a higher hymenium, and possibly also by slightly larger apothecia and finer goniocysts. The apothecia of *Bn. aenea* are superficially very similar to the apothecia of *Bacidia arceutina* due to the presence of the same pigment.

29. Bacidina arnoldiana (Körb.) V. Wirth & Vězda

Stuttg. Beitr. Naturk. A, 517: 62 (1994) - *Bacidia arnoldiana* Körb., Parerga Lich., fasc. 2: 134 (1860). – Type: Germany, "ad saxa umbrosa calcarea in sylvaticis vallis Rosenthal prope Eichstaedt Bavariae", Arnold, Arnold: Lich. sel. Germ. 131 (L, lectotype selected here).

Woessia fusarioides D. Hawksw., Poelt & Tscherm.-Woess, Pl. Syst. Evol. 154: 207 (1986). – Type: Austria, "Burgenland, Bez. Oberwart, Quercus-Stumpf im Mischwald SW über Bad Tatzmannsdorf, nahe der Strasse nach Oberwart, ± 350 m", 1980, Poelt (herb. Tschermak-Woess, isotype).

Illustrations. Figs 5F, 35 (map), 43B.

Characterization. Thallus entirely dissolving into ± green goniocysts. Apothecia with ± brown disc; margin often paler. Proper exciple colourless or very pale brown. Hypothecium brownish. Upper part of hymenium colourless or pale brown. Brown pigment K+ green-brown. Spores acicular 35-48 × 0.9-1.9 µm, with 0-9 septa. Conidia filiform, curved, 0-1-septate.

Thallus indeterminate, thin, starting as small, convex, discrete or contiguous areoles that very soon dissolve into ± coherent goniocysts that may or may not form coralline or isidia-like structures, grey-green, green-grey, or pale green. Goniocysts (19-)28-32-40(-52) µm diam. (s= 9, N= 4, n= 10).

Apothecia (0.3-)0.4-0.5-0.6(-0.7) mm diam. (s= 0.1, N= 4, n= 10), at first plane, later becoming ± convex, epruinose. Disk grey-brown to brown to dark red-brown. Margin often paler than disc, sometimes concolorous with or darker than disc, distinct, raised above disc in young apothecia, soon level with the disc, usually persistent but sometimes finally excluded.

Proper exciple laterally (36-)57(-77) µm wide (s= 18, N= 5, n= 1), without crystals. Hyphae with rather thin walls (2-5 µm between adjacent cell lumina), rather distinctly radiating towards edge, with cell lumina often of different shapes, usually narrower in upper part than in lower part, in lateral interior 1.5-7 µm wide and up to 13 µm long, 1.5-7.5 times as long as wide. Rim colourless to pale brown. Lateral interior colourless. Medullary part colourless or very pale brown. Hypothecium orange-brown to dark red-brown. Hymenium (42-)43-54-70(-74) µm thick (s= 9, N= 5, n= 5), colourless or pale brown in upper part. Paraphyses usually abundant in relation to the number of asci, 1.0-1.6 µm wide in mid-hymenium; apices ± clavate or only slightly thickened, (1.6-)2.2-2.9-3.4(-4.0) µm wide (s= 0.7, N= 5, n= 10). Tholus with a narrow c-layer. Ocular chamber usually narrow, low, and blunt; axial body wide and high, subcylindrical, blunt, never penetrating through the entire d-layer. Spores acicular, straight to curved to sigmoid, (35-)39-40-42(-48) µm long (s= 3, N= 4, n= 10), (0.9-)1.2-1.3-1.6(-1.9) µm wide (s= 0.2, N= 4, n= 10), (22.3-)28.0-30.6-33.8(-45.7) times as long as wide (s= 5, N= 4, n= 10), with (0-)1.5-3.2-6.4(-9) septa (s= 2.6, N= 4, n= 10), straight or coiled in young asci.

Pycnidia immersed in granular thallus, colourless, 75-125 µm diam. Conidia filiform, curved, 0-1-septate, 21-30 × c. 1.0 µm.

Pigments: Brown parts of apothecia K+ green-brown. – Arnoldiana Brown in proper exciple, hypothecium, and hymenium.

Ecology. Mainly on bark and overgrowing corticolous bryophytes on trunks and branches of trees and shrubs.

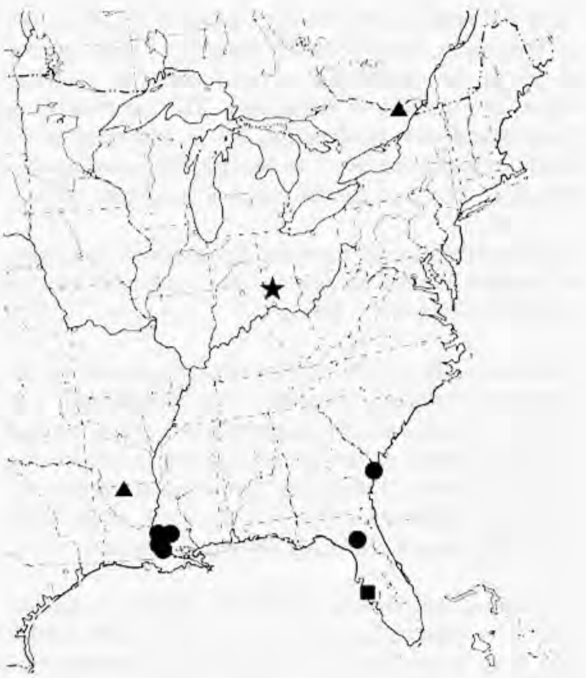


Fig. 36. Known North American distribution of *Bacidina aenea* (square), *Bn. crystallifera* (dots), *Bn. egenula* (triangles), and *Bn. egenuloidea* (star).

Once collected on the wood of a log. It favours shady to semi-open, always humid habitats. Known phorophytes in the western part of the distribution are *Alnus rubra* and *Sambucus callicarpa*. The phorophyte in North Carolina is unidentified, but is, according to the label, a "deciduous tree". In Europe, *Bn. arnoldiana* is frequently found on shaded, more or less basic rocks.

Distribution. Known from the Appalachian mountains of western North Carolina and the coast from Oregon to British Columbia. – Europe.

Discussion. Only likely to be confused with *Bn. egenula*, which also has a distinctly brown hypothecium. Unlike *Bn. arnoldiana*, *Bn. egenula* has a green pigment (Bacidia Green) in the epithecium and a brown, K+ purplish pigment (Laurocerasi Brown) in the proper exciple. *Bn. californica* (q.v.) is the only other North American species producing Arnoldiana Brown.

Collections examined. CANADA. *British Columbia*. Vancouver Island, Ucluelet, 1981, Noble 7299 (UBC). – U. S. A. *North Carolina*. Haywood/Transylvania Co., 1981, Brodo 23794 & Gowan (CANL). *Oregon*. Tillamook Co., 1989, Ekman L713 (LD). *Washington*. Skagit Co., 1989, Ekman L737 (LD). Whatcom Co., 1980, Ryan (WWB).

30. Bacidina assulata (Körb.) S. Ekman, comb. nov.

Bacidia rubella var. *assulata* Körb., Parerga Lich., fasc. 2: 131 (1860). - *Bacidia assulata* (Körb.) Vězda, Lich. sel. exs., fasc. 23, no. 566 (1967). – Type: Poland, Silesia, "Schreibershau", 1835, Flotow (L, lectotype selected here).

Secoliga arceutina f. *intermedia* Hepp ex Stizenb., Nova Acta Acad. Caesar. Leop. Carol. 30 (3): 42 (1863). - *Bacidia intermedia* (Hepp ex Stizenb.) Arnold, Flora, Jena 54: 54 (1871), nom. illeg., non Hampe in A. Massal. 1861. – Type: Not designated; isosyntype in LD studied.

Illustrations. Figs 5G, 35 (map).

Characterization. Thallus dissolving into goniocysts in small spots. Apothecia brown-orange to purple-brown, often mottled. Proper exciple laterally ± orange-brown. Hypothecium colourless or yellowish. Hymenium high, ± orange-brown in upper part. Pigment K+ intensifying. Spores acicular, 36-43 × 1.9-2.5 µm, with 5-9 septa. Conidia filiform, curved, non-septate.

Thallus indeterminate, ± continuous, thin to rather thick, ± warted, in small spots dissolved into loosely aggregated granules (goniocysts). Goniocysts (16-)22(-29) µm diam. (s= 5, N= 1, n= 10).

Apothecia (0.3-)0.4(-0.6) mm diam. (s= 0.09, N= 1, n= 10), plane, epruinose. Disk pink to brown-orange to purple-brown, often mottled with different colours. Margin concolorous with disc, distinct, level with the disc.

Proper exciple laterally 60 µm wide (N= 1, n= 1), without crystals. Hyphae with rather thin walls (2-3 µm between adjacent cell lumina), rather distinctly radiating towards edge, of widely differing shapes (almost globose-ellipsoid-rectangular-elongate), in lateral interior 1.5-6 µm wide and up to 15 µm long, mostly 2-5.5 times as long as wide. Rim ± orange-brown. Lateral interior ± orange-brown. Medullary part colourless. Hypothecium colourless or very pale yellowish. Hymenium (62-)70(-74) µm thick (s= 5, N= 1, n= 5), colourless in lower part, ± diffusely and unevenly orange-brown in upper part. Paraphyses rather abundant in relation to the number of asci, 1.2 µm wide in mid-hymenium; apices ± clavate, (1.6-)2.5(-3.6) µm wide (s= 0.7, N= 1, n= 20), without internal pigment. Tholus with a narrow c-layer. Ocular chamber wide, rather high, blunt; axial body wide and high, conical or subcylindrical, blunt, never penetrating through the entire d-layer, surrounded by a narrow layer that is darker amyloid than the remainder of the d-layer. Spores acicular, straight or curved, (36-)39(-43) µm long (s= 3, N= 1, n= 10), (1.9-)2.3(-2.5) µm wide (s= 0.3, N= 1, n= 10), (14.5-)17.2(-22.7) times as long as wide (s= 3, N= 1, n= 10), with (5-)7(-9) septa (s= 0.9, N= 1, n= 10), straight or coiled in young asci.

Pycnidia immersed in thallus, colourless, c. 150 µm diam. Conidia filiform, curved, non-septate, c. 10 × 0.5 µm.

Pigments: Yellowish to orange-brown parts of proper exciple, hypothecium, and hymenium K+ intensifying, N-. – Rubella Orange in proper exciple, hypothecium, and hymenium.

Ecology. Collected on the bark of a *Quercus* sp. in a floodplain forest dominated by *Quercus* and *Carya*.

Distribution. Known from a single locality in northeastern Oklahoma. – Central and eastern Europe. Reports from Scandinavia, the British Isles, and the Mediterranean are based on misidentifications.

Discussion. *Bacidina assulata* is an often misused and misunderstood name. It has, above all, been used for specimens of *Bn. phacodes*, *Bn. arnoldiana*, pigment deficient forms of *Bacidia subincompta*, and an undescribed Mediterranean species of *Bacidia* s. str. Apart from the North American specimen, I have seen *Bn. assulata* only from Central and East Europe.

Correctly determined and representative specimens have been distributed by Vězda in *Lichenes selecti exsiccati* no. 566.

Bacidina assulata is closely related and very similar to the type species of *Bacidina*, *Bn. phacodes* (Körb.) Vězda, a species which is known with certainty only from Europe. *Bn. phacodes* differs from *Bn. assulata* in almost completely lacking pigments in the apothecia, and (Swedish and French specimens) in possessing bacilliform to filiform, straight or only slightly curved, 1-5-septate conidia that measure 16-32 × 1.0-1.2 µm. According to Coppins (in Purvis et al. 1992), British specimens of *Bn. phacodes* have conidia up to 60 µm long, 1.5 µm wide, and up to 7-septate. In *Bn. assulata*, on the other hand, the conidia are strongly curved and non-septate. In specimens from Poland (the type specimen) and the Czech Republic, they measure 10-43 × 0.8-1.0 µm (i.e., generally slightly larger than in the American specimen). Furthermore, the thallus of *Bn. phacodes* is never dissolved into goniocysts, whereas in most specimens of *Bn. assulata* small parts of the thallus are dissolved.

Bacidina assulata is also very similar to the North American species *Bn. californica* and *Bn. varia*. Forms of *Bn. californica* with pigmented apothecia can be separated by the brown, K+ green-brown pigment (Arnoldiana Brown). Furthermore, *Bn. californica* differs in the presence of a distinct ocular chamber and a narrow, heavily amyloid zone along the outer edge of the axial body. *Bn. varia* can be distinguished from *Bn. assulata* by the lower hymenium (rarely exceeding 60 µm), the presence of a K+ purplish pigment in the apothecia (Laurocerasi Brown), and the curved to sigmoid, septate conidia.

Collections examined. U. S. A. *Oklahoma*. Cherokee Co., 1988, Harris 21341 (NY).

31. Bacidina californica S. Ekman, sp. nov.

Type: U. S. A., "California. Monterey Co.: on *Umbellularia californica*, floor of canyon at Big Sur", 1966, Weber & Santesson, Weber: Lich. exs. 182 (COLO, holotype; LD, MIN, SFSU, UBC, US, WTU, isotypes). NB! In addition to *Bn. californica*, *Bacidia heterochroa* is present in most type specimens.

Thallus aliquando per maculas in goniocystas solutus, plerumque autem non solutus. Apothecia plerumque pallide rosea ad aurantiaco-brunnea, pigmentum brunneum hydrato kalico viridescens continentia. Pycnidia biformia, conidiis aut filiformibus curvatis non septatis, aut bacilliformibus rectis 0-2-septatis. Facile cum *Bacidina ramea* confusa, cuius apothecia marginem thallinam et pigmentum hydrato kalico intensius coloratum habent.

Etymology. *Californicus*, Californian.

Illustrations. Figs 2C, 5H-I, 35 (map), 43C, 44B.

Characterization. Thallus dissolved into goniocysts or not. Apothecia usually pale pink to orange-brown. Proper exciple usually colourless to pale orange-brown. Hypothecium colourless to pale brown-orange. Upper part of hymenium colourless to ± brownish. Pigment K+ green-brown. Spores acicular, 31-53 × 1.9-3.3 µm, with 0-9 septa. Conidia filiform, curved, non-septate, or bacilliform, straight, 0-2-septate.

Thallus indeterminate, thin to thick, either continuous, wrinkled or warted, ± rimose, or discontinuous, of discrete to contiguous, convex, sometimes almost granular areoles, only seldom dissolved into loosely aggregated granules (goniocysts) in small or large spots; grey, green-grey, grey-green, or yellow-grey, except granular spots, which are pale green. Goniocysts (21-)30(-52) µm diam. (s= 7, N= 1, n= 20).

Apothecia (0.2-)0.4-0.5-0.7(-0.9) mm diam. (s= 0.2, N= 6, n= 10), ± plane when young, later becoming convex, epruinose. Disk pale pink to pale yellow to pale orange to orange-brown, rarely darker (red-brown to purple-brown). Margin concolorous with disc or slightly paler or darker, distinct, level with or slightly raised above disc in young apothecia, later level with the disc, finally excluded.

Proper exciple laterally (29-)48(-69) µm wide (s= 14, N= 5, n= 1), without crystals. Hyphae with rather thin to rather thick walls (1.5-2.5 µm between adjacent cell lumina), rather distinctly radiating towards edge; cell lumina ± homogeneously shaped, in lateral interior 1.5-2 µm wide and up to 12 µm long, 2.5-6.5 times as long as wide. Rim usually colourless to pale orange-brown, sometimes orange-brown to red-brown, then darkest in upper part and downwards gradually changing to colourless. Lateral interior colourless or pale orange-brown. Medullary part colourless. Hypothecium colourless, very pale yellowish, or pale brown-orange. Hymenium (52-)57-64-73(-74) µm thick (s= 8, N= 6, n= 5), in lower part colourless except where vertical streaks of pigment reaches deep down in the hymenium; in upper part colourless, pale yellow-brown, pale orange-brown, rarely orange-brown to red-brown. Paraphyses rather abundant in relation to the number of asci, 1.2-1.6 µm wide in mid-hymenium; apices ± clavate or some not at all or only slightly thickened, (1.6-)2.2-2.5-2.8(-3.7) µm wide (s= 0.6, N= 6, n= 10). Tholus with a narrow c-layer. Ocular chamber wide, low or high, blunt; axial body wide and high, conical, blunt, sometimes penetrating through the entire d-layer. Spores acicular, straight to curved to sigmoid, (31-)35-41-46(-53) µm long (s= 5, N= 6, n= 10), (1.9-)1.9-2.4-2.8(-3.3) µm wide (s= 0.4, N= 6, n= 10), (12.2-)16.7-17.5-19.7(-22.0) times as long as wide (s= 2, N= 6, n= 10), with (0-)3.6-5.7-7.5(-9) septa (s= 2.1, N= 6, n= 10).

Pycnidia ± immersed in thallus, colourless or pale orange to pale brown, of two types: (1) 70-100 in diam; conidia filiform, curved, non-septate, 7-12 × 0.6-0.8 µm, (2) 75-225 µm in diam; conidia bacilliform, straight, non-septate or some 1-2-septate, 7-9 × 1.6 µm.

Pigments: Pigmented parts of apothecia K+ green-brown, N-. – Sometimes Arnoldiana Brown in proper exciple, hypothecium, and hymenium.

Ecology. On tree trunks, mainly on rough bark in shady or open, coastal forests with high air humidity. Known phorophytes include *Aesculus californicus*, *Cupressus macrocarpa*, and *Umbellularia californica*.

Distribution. Known from a few localities in Marin, San Mateo, Monterey, and Santa Barbara Counties in the south and central parts of coastal California. – Endemic?

Discussion. From San Luis Obispo Co., there is a further specimen (Ekman L621, LD), which I have not at the moment included in *Bn. californica*. It differs from other specimens of *B. californica* mainly in having narrower spores (1.2-1.9 µm) and in having different conidia (filiform, straight or slightly curved, non-septate, 27-73 × 0.8-1.0 µm). It was collected on the upper side of a leaning branch of *Quercus agrifolia* in a rather dry coastal oldgrowth. Further collections are needed to establish whether it should be included in *Bn. californica*, or if it represents a distinct species.

Bacidina californica is similar to *Bn. assulata* (see this species) and *Bn. ramea*. The latter species is separated from *Bn. californica* by the K+ intensifying or K+ purplish (not K+ green-brown) pigments in the apothecia and the tendency to produce a thalline margin in the young apothecia. Specimens of *Bn. californica* lacking goniocysts and pigment in the apothecia are very similar to the European *Bn. phacodes*, the type species of the genus. *Bn. phacodes* is then separated mainly by the different conidia (see discussion under *Bn. assulata*) and the thinner hymenium (usually less than 50 µm thick).

Additional collections examined. U. S. A. *California*. Marin Co., 1925, Parks 2883 (COLO), 1989, Ekman L639 (LD), 1989, Ekman L645 (LD). Monterey Co., 1984, Bratt 4271, 4277 (herb. Bratt), 1989, Ekman L632 (LD). San Mateo Co., 1967, Jordan 822 (SFSU). + Santa Barbara Co., 1994, Nimis & Tretiach (filed with *B. insularis*, TSB).

32. Bacidina chloroticula (Nyl.) Vězda & Poelt in Vězda

Folia Geobot. Phytotax. Praha 25: 432 (1991). - *Lecidea chloroticula* Nyl., Flora, Jena 60: 564 (1877). - *Bacidia chloroticula* (Nyl.) A. L. Sm., Monogr. Brit. Lich. 2: 155 (1911). – Type: Ireland, "in rivulo prope Kylemore", 1877, Larbalestier (H-NYL 17648, lectotype selected here).

Lecidea subchlorotica Nyl., Flora, Jena 61: 451 (1878). - *Bacidia subchlorotica* (Nyl.) Flagey, Catal. Lich. Algérie 64 (1896). – Type: France, "Corsica, Ajaccio, super corticem Cupulariae viscosae", 1878, Norrlin (H-NYL 17954, lectotype selected here).

Illustrations. Figs 4A, 5J, 35 (map).

Nomenclature. The lectotypification made by Diederich et al. (1991) is not valid, since the collection chosen (H-NYL 17871) is not original material. It was collected in 1878, the year after the publication of *Lecidea chloroticula* Nyl.

Characterization. Thallus ± dissolving into goniocysts. Apothecia very small, with pale yellow to pale grey disc; margin paler, persistent. Proper exciple, hypothecium, and upper part of hymenium (almost) colourless. Spores acicular, 17-31 × 0.9-1.2 µm, with 0-3 septa. Conidia filiform, curved, 0-1-septate.

Thallus indeterminate, ± thin, continuous, rimose, wrinkled or warted, grey-green or green-grey, not dissolving or partly diffusely dissolving into pale green goniocysts. Goniocysts loosely aggregated, (28-)35(-48) µm diam. (s= 5, N= 1, n= 10).

Apothecia (0.15-)0.19-0.20-0.21(-0.36) mm diam. (s= 0.05, N= 2, n= 10), at first plane, later sometimes becoming moderately convex, epruinose. Disk pale yellow or pale grey. Margin paler than disc, milky white or very pale yellow, distinct, slightly raised above disc in young apothecia, soon level with the disc, persistent.

Proper exciple laterally (24-)29(-33) µm wide (s= 6, N= 2, n= 1), without crystals. Hyphae with very thin walls (0.5-1 µm between adjacent cell lumina), not distinctly radiating towards edge, with cell lumina homogeneously shaped, in lateral interior 2-8 µm wide and up to 15 µm long, 1.5-4 times as long as wide. Rim colourless or very pale brown in uppermost part. Lateral interior colourless. Medullary part colourless. Hypothecium colourless. Hymenium (37-)38-43-48(-51) µm thick (s= 6, N= 2, n= 5), colourless or very pale brown in upper part. Paraphyses few in relation to the number of asci, 1.6-2.0 µm wide in mid-hymenium; apices ± clavate or only slightly thickened, (2.0-)2.4-3.2-4.1(-6.5) µm wide (s= 1.2, N= 2, n= 10). Tholus with a narrow c-layer. Ocular chamber lacking; axial body wide and high, subcylindrical, blunt, never penetrating through the entire d-layer. Spores acicular, straight or slightly curved to sigmoid, (17-)24-26-28(-31) μm long (s= 4, N= 2, n= 10), (0.9-)1.0-1.1-1.2(-1.2) μm wide (s= 0.2, N= 2, n= 10), (16.0-)23.3-23.9-24.5(-30.0) times as long as wide (s= 4, N= 2, n= 10), with (0-)0.6-1.2-1.8(-3) septa (s= 1.1, N= 2, n= 10).

Pycnidia immersed in thallus, colourless, 75-100 μm diam. Conidia filiform, curved, 0-1-septate, 30-43 × 0.8-1.0 μm.

Pigments: All parts of apothecia K-. – Sometimes very small amounts of an unidentified brown pigment in the proper exciple and hymenium.

Ecology. Collected once on the smooth bark of *Fagus grandifolia* and once on rotten wood (probably a log or a stump).

Distribution. Collected twice in southern Ontario. – Europe.

Discussion. Bacidina chloroticula is a rather distinctive species with its pale grey or pale yellow apothecia with persistent margin. It is only likely to be confused with *Bn. egenula* and *Bn. egenuloidea*. The former is separated from *Bn. chloroticula* by the presence of a green pigment (Bacidia Green) in the upper part of the hymenium and by a brown hypothecium. *Bn. egenuloidea* is above all distinguished by the presence of a brown, K+ purplish pigment (Laurocerasi Brown) in the proper exciple, and by the presence of different conidia.

The type of *Bacidia subchlorotica* (Nyl.) Flagey is a typical specimen of *Bacidina chloroticula*.

Collections examined. CANADA. *Ontario*. Norwich, 1978, Wong 2709A, 2712 (CANL). Ottawa, 1897, Macoun 2801 (CANL).

33. Bacidina crystallifera S. Ekman, sp. nov.

Type: U. S. A., Louisiana, "Tunica Hills north of St. Francisville: wooded ravines on Murrill Butler property, on gravel road 1 mi. S of La. route 66; turnoff .25 mi. W of junction of State 66 and U. S. route 61, 30°49'N 91°24'W, West Feliciana Parish, covering vine of muscadine (*Vitis rotundifolia*)", 1981, Tucker 21520 (herb. Shirley Tucker, holotype; LD, isotype)

Thallus nunquam in goniocystas solutus. Apothecia rosea, pigmento destituta vel quasi, strato crystallifero in epithecio et in margine excipuli proprii praedita. Facile cum *Bacidina aenea* confusa, cuius apothecia pigmentum fulvum habent et cum *Bacidina varia*, cuius hymenium tenuius sporaeque breviores et latiores sunt; ambarum apothecia crystallis carent.

Etymology. Crystalliferus, carrying crystals.

Illustrations. Figs 5K-L, 36 (map), 44C.

Characterization. Apothecia ± pink. Proper exciple colourless, at least in the upper part with minute, evenly dispersed crystals along the rim. Hypothecium (almost) colourless. Upper part of hymenium colourless but with a layer of minute crystals between the apices of the paraphyses. Spores acicular, 32-72 × 1.2-1.9 μm, with 3-13 septa.

Thallus indeterminate, thin, either continuous, smooth or warted, slightly rimose or without cracks, or discontinuous, of discrete or contiguous, convex, sometimes almost granular, areoles.

Apothecia (0.2-)0.2-0.3-0.3(-0.5) mm diam. (s= 0.06, N= 5, n= 10), at first plane, later becoming convex, at least when young with thin pruina. Disk pale pink or pale orange-pink. Margin concolorous with disc, distinct, level with or raised above disc in young apothecia, soon level with the disc, finally excluded.

Proper exciple laterally (37-)44(-51) μm wide (s= 5, N= 6, n= 1), without pigment, at least in the upper part with minute and evenly dispersed crystals along the rim (up to 1 μm). Hyphae with rather thin walls (2-3.5 μm between adjacent cell lumina), not distinctly radiating towards edge, with cell lumina that gradually expand towards edge (in lateral interior 1.5-3 μm wide and up to 12 μm long, usually 2-4 times as long as wide). Hypothecium colourless or very pale yellowish. Hymenium (56-)59-66-70(-74) μm thick (s= 5, N= 5, n= 5), colourless, at least partially with minute crystals in the upper part (usually as a distinct, continuous layer). Paraphyses abundant in relation to the number of asci, 1.0-1.4 μm wide in mid-hymenium; apices upwards gradually thickened, (1.6-)2.0-2.1-2.2(-3.2) μm wide (s= 0.4, N= 5, n= 10). Tholus with a rather wide c-layer and a d-layer that is characteristically truncate at the apex. Ocular chamber lacking; axial body very wide and high, conical, pointed with straight or slightly bulging sides, often penetrating through the entire d-layer, the sides of the axial body then collapsing and becoming concave. Spores acicular and straight, curved, or sigmoid, (32-)40-46-52(-72) μm long (s= 7, N= 4, n= 10), (1.2-)1.4-1.6-1.7(-1.9) μm wide (s= 0.3, N= 4, n= 10), (20.0-)26.5-29.9-33.4(-44.6) times as long as wide (s= 5, N= 4, n= 10), with (3-)4.6-5.7-6.7(-13) septa (s= 2.4, N= 4, n= 10).

Pycnidia not seen.

Pigments: All parts of apothecia K-. – Sometimes small amounts of an unidentified pigment (Rubella Orange?) in the hypothecium.

Ecology. On young tree-trunks and vines in shady and humid forests. Known phorophytes include *Fagus grandifolia*, *Liquidambar styraciflua*, *Vitis rotundifolia*, and *Wisteria frutescens*.

Distribution. Known from a few localities in Florida, coastal Georgia, and southern Louisiana. – Endemic?

Discussion. *Bacidina crystallifera* is an easily recognized species due to its crystal layer in the upper part of the hymenium. However, in some apothecia the crystals are rather sparse, and if overlooked, it may be taken for non-goniocystate morphs of *Bn. varia*. Apart from having crystals in the hymenum, *Bn. crystallifera* is separated from *Bn. varia* in having a higher hymenium, and longer and thinner spores. Due to the almost complete lack of pigmentation and the presence of crystals in the apothecia, *Bn. crystallifera* has some resemblance with *Bacidia rosella*. *Bn. crystallifera*, however, has smaller apothecia, narrower spores and lacks an ocular chamber.

Additional collections examined. U. S. A. *Florida*. Alachua Co., 1993, Ekman L1154 (LD). *Georgia*. Chatham Co., 1974, Tucker 12224b (herb. Tucker). *Louisiana*. East Baton Rouge Par., 1982, Tucker 25593 (herb. Tucker), 1993, Ekman L1120 (LD). East Feliciana Par., 1970, Tucker 8478b (herb. Tucker). West Feliciana Par., 1981, Tucker 21520 (herb. Tucker).

34. Bacidina egenula (Nyl.) Vězda

Folia Geobot. Phytotax. Praha 25: 432 (1991). - *Lecidea egenula* Nyl., Flora, Jena 48: 147 (1865). - *Bacidia egenula* (Nyl.) Arnold, Flora, Jena 53: 472 (1870). – Type: France, "Fontainbleau" (H-NYL 17967, lectotype selected here).

Illustrations. Figs 5M, 36 (map), 43D.

Characterization. Thallus entirely dissolved into goniocysts. Apothecia pale brown to black (at least some black). Proper exciple laterally ± brown (K+ purplish), below hypothecium colourless. Hypothecium ± orange-brown. Upper part of hymenium greenish. Spores acicular, 16-31 × 1.2-1.9 µm, with 0-7 septa. Conidia filiform, curved to sigmoid, 0-1-septate, not strongly conglutinated.

Thallus indeterminate, thin to rather thick, entirely dissolved into granules (goniocysts), continuous or of discrete to contiguous granules, grey-green or green-grey. Goniocysts coherent, (24-)45-49-52(-77) µm diam. (s= 12, N= 2, n= 10).

Apothecia (0.2-)0.2-0.3-0.4(-0.5) mm diam. (s= 0.1, N= 2, n= 10), at first plane, later becoming ± convex, epruinose. Disk pale brown to purple-brown to black or occasionally pale pink, often mottled with different hues (at least some apothecia ± black). Margin concolorous or darker than disc, in upper part pale brown-purple to black, in lower part pale pink to pale pink-brown, occasionally entirely pale pink, distinct, slightly raised above disc in young apothecia, soon level with the disc, finally excluded.

Proper exciple laterally (21-)28(-34) µm wide (s= 9, N= 2, n= 1), without crystals. Hyphae with thin walls (1-3 µm between adjacent cell lumina), rather distinctly radiating towards edge, with cell lumina that are narrower in upper part than in lower part, in lateral interior 1-5 µm wide and up to 10 µm long, 3-7 times as long as wide in upper part, 1.2-1.7 times as long as wide in lower part. Rim grey-brown to black-brown in upper part, downwards changing to orange-brown to colourless (entirely colourless in pale pink apothecia). Lateral interior grey-brown to black-brown in upper part, downwards changing to colourless or very pale orange (entirely colourless in pale pink apothecia). Medullary part colourless. Hypothecium ± orange-brown. Hymenium (40-)40-44-47(-50) µm thick (s= 4, N= 2, n= 5), colourless in lower part, upwards usually gradually darkening to pale green, grey-green, or green-brown. Paraphyses rather abundant in relation to the number of asci, 1.6 µm wide in mid-hymenium; apices ± clavate, (2.4-)2.8-3.1-3.4 (-4.9) µm wide (s= 0.7, N= 2, n= 10). Tholus with a narrow c-layer. Ocular chamber rather wide, high, blunt or pointed; axial body wide and high, conical or subcylindrical, blunt, never penetrating through the entire d-layer. Spores acicular, straight or curved, (16-)21-23-25(-31) µm long (s= 5, N= 2, n= 10), (1.2-)1.4-1.5-1.6(-1.9) µm wide (s= 0.2, N= 2, n= 10), (10.0-)15.1-15.3-15.5(-20.0) times as long as wide (s= 3, N= 2, n= 10), with (0-1.1-2.0-2.8(-7) septa (s= 2.0, N= 2, n= 10).

Pycnidia immersed in granular thallus, colourless, 60-75 µm diam. Conidia filiform, curved to sigmoid, 0-1-septate, 9-24 × c. 1.0 µm.

Pigments: Greenish parts of hymenium K-, N+ purple without a precipitate of blue crystals. Dark brown parts of proper exciple and hymenium K+ purplish, N+ orange-red, orange or orange-brown parts of proper exciple and hypothecium K+ intensifying and N-, or K+ slightly green-brown and N-. – Laurocerasi Brown in proper exciple and hymenium. Rubella Orange in proper exciple and hypothecium. Arnoldiana Brown in the hypothecium of some apothecia. Bacidia Green in hymenium.

Ecology. At the locality in Louisiana, it was collected on a hematite rock in a pasture, whereas in Ontario, it was found at the base of an *Ulmus americana*. In Europe, it is usually found on shady, siliceous rocks.

Distribution. Known from one station in southern Ontario and one in northernmost Louisiana. Probably much overlooked and possibly with a wide (eastern temperate?) distribution. – Europe.

Discussion. *Bacidina egenula* is very similar to *Bn. egenuloidea*. The latter species differs in lacking Bacidia Green in the hymenium and in having very long and almost straight conidia that are strongly conglutinated. *Bn. egenula* also resembles *Bn. chloroticula* (see this species).

In a European collection of *Bn. egenula* (Oberfranken, Engelhardsberger Brunnen, 1855 Arnold, L), another conidial type has been observed in addition to the one mentioned above and reported by Coppins (in Purvis et al. 1992). It is found mixed in the same pycnidia as the common type. These conidia are straight or curved, evenly thick or slightly thicker towards the proximal end, distinctly 3-7-septate, 32-45 × 1.0-1.6 µm. A very similar type of pycnidium with two conidial stages is found in *B egenuloidea* (see this species).

Collections examined. CANADA. *Ontario*. Ottawa, 1976, Robitaille 149.4 (CANL). – U. S. A. *Louisiana*. Union Par., 1970, Kay (herb. Tucker).

35. Bacidina egenuloidea (Fink) S. Ekman, comb. nov.

Bacidia egenuloidea Fink, Bull. Ohio S. Univ. 25: 346 (1921). – Type: U. S. A., Ohio, Preble Co., "West Alexandria, damp field, granite", 1914, Fink 320 (MU-L608, lectotype selected here).

Illustrations. Figs 5N, 8D, G, 36 (map).

Characterization. Thallus entirely dissolved into goniocysts. Apothecia with pale orange to dark purple-brown disc; margin concolorous or darker. Proper exciple laterally with various brown (K+ purplish) and orange hues (K+ intensifying), below hypothecium colourless. Hypothecium (almost) colourless. Upper part of hymenium pale orange or pale brown. Spores acicular, 20-42 × 0.9-2.1 µm, with 0-5 septa. With three types of conidia, the commonest one filiform, straight or slightly curved to sigmoid, 0-1-septate, strongly conglutinated.

Thallus indeterminate, thin, entirely dissolved into granules (goniocysts) that are ± coherent and form isidia-like or coralline structures, grey-green. Goniocysts (21-)35-46-57(-77) µm diam. (s= 15, N= 1, n= 10).

Apothecia (0.2-)0.3-0.3-0.4(-0.4) mm diam. (s= 0.06, N= 2, n= 10), plane, epruinose. Disk pale orange to brown-orange to dark purple-brown. Margin concolorous or darker than disc, in upper part pale orange to red-brown to purplish black, in lower part pale orange to brown-orange to dark purple-brown, distinct, slightly raised above disc in young apothecia, later level with the disc.

Proper exciple laterally (46-)51(-56) µm wide (s= 7, N= 2, n= 1), without crystals. Hyphae with rather thin walls (1-3 µm between adjacent cell lumina), rather distinctly radiating towards edge, with cell lumina that are narrower in upper part than in lower part, in lateral interior 1-4 µm wide and up to 14 µm long, 4-8 times as long as wide in upper part, 1.5-4 times as long as wide in lower part. Rim orange-brown, grey-brown, or brown in upper part, downwards often gradually changing to colourless. Lateral interior either colourless, or pale orange to pale brown in upper part and downwards changing to colourless. Medullary part colourless. Hypothecium colourless or very pale orange. Hymenium (43-)45-49-54(-56) µm thick (s= 5, N= 2, n= 5), colourless in lower part, diffusely pale orange or pale brown in upper part. Paraphyses rather abundant in relation to the number of asci, 1.6 µm wide in mid-hymenium; apices ± clavate or some not at all or only slightly thickened, (1.6-)3.0-3.1-3.1(-4.9) µm wide (s= 1.0, N= 2, n= 10). Tholus with a wide c-layer. Ocular chamber wide, rather low, pointed; axial body wide and high, conical or subcylindrical, blunt, never penetrating through the entire d-layer. Spores acicular, straight or slightly curved to sigmoid, (20-)25-29-34(-42) µm long (s= 6, N= 2, n= 10), (0.9-)1.1-1.5-1.9(-2.1) µm wide (s= 0.5, N= 2, n= 10), (14.7-)18.3-20.5-22.6(-29.0) times as long as wide (s= 5, N= 2, n= 10), with (0-)0.5-1.5-2.4(-5) septa (s= 1.8, N= 2, n= 10).

Pycnidia immersed in thallus, colourless, 75-200 µm diam. Conidia of three types: (1, the commonest type) filiform, straight or slightly curved to sigmoid, strongly conglutinated, 0-1-septate, 35-49 × 0.8-1.2, µm, (2) filiform, curved, not conglutinated, non-septate, 9-14 × 0.6-0.8 µm, and (3) acicular (thicker at the proximal end), straight or curved, not conglutinated, non-septate, 16-20 × 1.0 µm. Type 1 occur in separate pycnidia, whereas type 2 and 3 occur mixed in the same pycnidia.

Pigments: Brown parts of proper exciple and hymenium K+ purplish, N+ orange-red, pale orange to orange-brown parts of proper exciple, hypothecium, and hymenium K+ intensifying, N-. – Laurocerasi Brown in proper exciple and hymenium. Rubella Orange in proper exciple, hypothecium, and hymenium.

Ecology. At the only known locality, it was collected both on a granite rock and on "old wood" in an "open wood".

Distribution. Known only from the type locality in Ohio. – Endemic?

Fig. 37. Known world distribution of *Bacidina ramea*.

Discussion. *Bacidina egenuloidea* is similar to *Bn. chloroticula* and *Bn. egenula* (see these species).

Additional collections examined. U. S. A. *Ohio*. West Alexandria, 1914, Fink 313 (MICH).

36. Bacidina ramea S. Ekman, sp. nov.

Type: Canada, Vancouver Island, NW of Victoria, Thetis Lake Park, just S of the SE-most part of Thetis Lake, on *Acer macrophyllum*, alt. 80 m, 1989, Ekman L767 (LD, holotype).

Thallus nunquam in goniocystas solutus. Apothecia flava vel pallide rosea ad ferruginea, saepe variegata (pigmentum hydrato kalico intensius coloratum), juniora margine thallina praedita. Pycnidia conidiis filiformibus curvatis non septatis. Facile cum *Bacidina californica* confusa, cuius apothecia margine thallina carent, pigmentumque brunneum hydrato kalico viridescens continent.

Etymology. *Rameus*, belonging to a branch.

Illustrations. Figs 5O, 37 (map), 43E, 44D.

Characterization. Thallus not dissolved into goniocysts. Apothecia with pale yellow to dark red-brown, often mottled disc; proper margin usually paler; margo thallinus present at least in young apothecia, thin, pale greyish. Proper exciple (almost) colourless, except colourless to dark brown rim. Hypothecium (almost) colourless. Upper part of hymenium colourless to red-brown. Spores acicular, 25-57 × 1.2-2.5 μm, with 3-7 septa. Conidia filiform, curved, non-septate.

Thallus indeterminate, thin, usually continuous, wrinkled or warted, ± rimose to areolate, sometimes partly or entirely discontinuous, of discrete or contiguous, convex areoles, pale grey, pale yellow-grey, or pale green-grey, never dissolving into granular goniocysts.

Apothecia (0.3-)0.4-0.5-0.6(-0.7) mm diam. (s= 0.1, N= 9, n= 10), at first plane, later becoming convex, epruinose. Disk pale yellow, pale pink, pale orange, pale to medium brown-orange, pale to medium orange-brown, or pale to dark red-brown, often mottled with different hues. Proper margin usually paler but sometimes concolorous with disc, milky white, pale grey, pale pink, pale yellow, pale brown, seldom orange-brown to dark red-brown, distinct, level with or raised above disc in young apothecia, soon level with the disc, finally excluded, sometimes appearing tomentose due to protruding hyphae. Margo thallinus rather thin, concolorous with the thallus, in at least some of the young apothecia covering 50-100 % of the proper exciple, soon excluded (but easily visible in section even in old apothecia).

Proper exciple laterally (26-)45(-86) μm wide (s= 11, N= 9, n= 1), without crystals. Hyphae with rather thin walls (1.5-4 μm between adjacent cell lumina), not distinctly radiating towards edge, with cell lumina ± of the same shape throughout the entire exciple, in lateral interior 2-3.5 μm wide and up to 9 μm long, 1-3.5 times as long as wide. Rim colourless, pale yellowish, or pale to dark brown. Lateral interior colourless or very pale yellowish. Medullary part colourless or very pale yellowish. Hypothecium colourless or very pale yellowish. Hymenium (55-)57-62-65(-68) μm thick (s= 4, N= 9, n= 5), colourless or diffusely pale yellow to pale brown to red-brown, usually darker in upper part than in lower part. Paraphyses abundant in relation to the number of asci, 1.2-2.0 (occasionally up to 3.2) μm wide in mid-hymenium; apices usually ± clavate sometimes weakly or not at all thickened, (1.6-)2.0-2.8-3.5(-5.3) μm wide (s= 0.7, N= 9, n= 10). Tholus with a narrow c-layer. Ocular chamber lacking; axial body very wide, low, blunt, cushion-like, never penetrating through the entire d-layer. Spores acicular, straight or slightly curved/sigmoid, (25-)31-41-49(-57) μm long (s= 7, N= 9, n= 10), (1.2-)1.6-1.9-2.2(-2.5) μm wide (s= 0.3, N= 9, n= 10), (12.5-)18.5-22.2-28.5(-37.0) times as long as wide (s= 5, N=

9, n= 10), with (3-)3.2-3.9-5.4(-7) septa (s= 1.3, N= 9, n= 10).

Pycnidia immersed in thallus, colourless, c. 100 µm diam. Conidia filiform, curved, non-septate, 9-16 × c. 0.5 µm.

Apothecial and pycnidial pigments: Yellowish parts K+ intensifying, N-. Brownish parts K+ purplish, N+ orange-red. – Sometimes Rubella Orange in proper exciple, hypothecium, and hymenium. Sometimes Laurocerasi Brown in proper exciple and hymenium.

Ecology. Mainly on twigs, branches, and young trunks of shrubs and broad-leaved trees. Occasionally, it has been found on large trunks with coarse bark. It can be found in entirely open habitats, such as coastal sand dunes and shrub-land, as well as in fairly well-lit forests and forest edges (also planted tree-stands). Known phorophytes are *Acer macrophyllum*, *Alnus rubra*, *Casimiroa edulis*, *Eriogonum* sp., *Fraxinus latifolia*, *Heteromeles arbutifolia*, *Oemleria cerasiformis*, *Quercus agrifolia*, *Salix* sp., and *Umbellularia californica*.

Distribution. Along the coast from southern California to southern British Columbia. – Endemic?

Discussion. To my knowledge, *Bn. ramea* is unique within the genus in having a thin, thalline margin on the young apothecia. The thalline margin soon becomes excluded, however, and if overlooked, this species may be confused with *B. californica* (see that species).

Additional collections examined. CANADA. *British Columbia*. Saltspring Island, 1989, Ekman L783 (LD). Vancouver Island, Mount Douglas Park, 1989, Ekman L778, L779 (LD). – U. S. A. *California*. Humboldt Co., 1989, Ekman L658 (LD). Marin Co., 1989, Ekman L643 (LD). Mendocino Co., 1989, Ekman L648 (LD). San Luis Obispo Co., 1981, Tucker 2197 (herb. Bratt). Santa Barbara Co., 1995, Tucker 34302 (herb. Tucker). San Gabriel Range, Sturtevants, 1902, Hasse (NY). Santa Cruz, Anderson (FH). Santa Monica Mountains, 1909, Hasse 2122 (MIN). Santa Monica Range, 1902 Hasse (NY), 1906, Hasse 1789 (FH). Topanga Canyon, 1908, Hasse 2288 (MIN), 1909, Hasse (NY) 1909, Hasse 728 (FH). *Oregon*. Benton Co., 1989, Ekman L685, L687, L688, L690, L691, L692, L701, L704, L705 (LD), + 1972, Pike 3117 (filed with *B. arceutina*, OSC).

37. Bacidina squamellosa S. Ekman, sp. nov.

Type: U. S. A., Florida, Gainesville, just SW of the city, just NW of Lake Kanapaha, on *Cephalanthus occidentalis*, 1993, Ekman L1148 (LD, holotype).

Fig. 38. Known North American distribution of *Bacidina squamellosa* (dots) and *Bn.* sp. #1 (stars).

Thallus squamulis contiguis vel discretis, plerumque ascendentibus, planis, profunde in lobulos 20-30 µm latos, incisis constitutus. Apothecia pallide rosea. Aliquando *Bacidinae variae* similis sed differt apicibus para physorum latioribus, sporis longioribus, cellulorum excipuli proprii luminibus magnis inflatis.

Etymology. *Squamellosus*, minutely scaly.

Illustrations. Figs 5P, 38 (map), 44E.

Characterization. Thallus of prostrate to ascending, small, deeply incised squamules, not dissolved into goniocysts. Apothecia pink. Proper exciple colourless, with large inflated cell lumina in lower part. Hypothecium and hymenium colourless. Spores acicular, 37-60 × 0.9-1.6 µm, with 3-7 septa. Conidia filiform, slightly curved, indistinctly 3-7-septate.

Thallus indeterminate, thin, discontinuous, of discrete or contiguous, prostrate to ascending, small, ± flat, deeply incised squamules, the lobes of which are 20-30 µm wide.

Apothecia (0.2-)0.3-0.4-0.5(-0.7) mm diam. (s= 0.1, N= 3, n= 10), plane, later becoming convex, epruinose. Disk pale pink. Margin concolorous with disc, distinct, somewhat raised above disc in young apothecia, soon level with the disc, finally excluded.

Proper exciple laterally (34-)38(-45) µm wide (s= 6, N= 3, n= 1), without crystals and without internal pigment. Hyphae with rather thin walls (1-3 µm between adjacent cell lumina), distinctly radiating towards edge, with large, inflated lumina in the lower part (3-8 µm wide and up to 24 µm long, mostly 1.5-4.5 times as long as wide) and narrower lumina in the upper part (1-4 µm wide and up to 18 µm long, 2.5-10 times as long as wide). Hypothecium colourless. Hymenium (52-)53-57-62(-62) µm thick (s= 4, N= 3, n= 5), colourless. Paraphyses abundant in relation to the number of asci, 1.2-

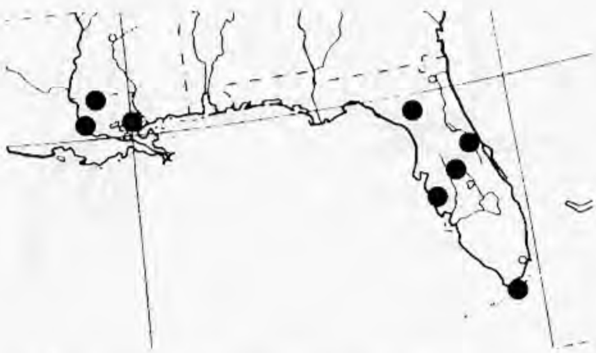


Fig. 39. Known North American distribution of *Bacidina varia.*

1.6 µm wide in mid-hymenium; apices ± clavate, (2.4-)3.1-3.5-4.0(-5.7) µm wide (s= 1.0, N= 3, n= 10). Tholus with an extremely wide c-layer. Ocular chamber lacking; axial body wide and high, conical or semiglobose, blunt or pointed, filling up most of the d-layer but never penetrating at its apex. Spores acicular and straight, curved or sigmoid, (37-)45-46-48(-60) µm long (s= 5, N= 2, n= 10), (0.9-)1.3-1.3-1.4(-1.6) µm wide (s= 0.2, N= 2, n= 10), (26.9-)33.9-36.2-38.5(-55.7) times as long as wide (s= 8, N= 2, n= 10), with (3-)3.2-3.8-4.4(-7) septa (s= 1.4, N= 2, n= 10).

Pycnidia immersed in thallus to sessile, colourless, 75-100 µm diam. Conidia filiform, slightly curved, indistinctly 3-7-septate, 41-58 × 1.0-1.2 µm.

Pigments: All parts of apothecia K-, N-. – Pigments absent.

Ecology. The Gainesville locality is a more or less swampy forest and adjoining, open and grazed areas with a few solitary trees, both dominated by *Planera aquatica*. Here, *Bn. squamellosa* is particularly abundant on trunks of *Planera aquatica* and *Cephalanthus occidentalis* that are subject to periodical flooding. It is not likely that *Bn. squamellosa* can survive a flooding that may last for several years, however. Instead, it is probably a fast colonizer once the water has subsided. The Myakka River locality is similar in being a swamp forest, but here, *Bn. squamellosa* was found on shaded tree trunks of *Fraxinus caroliniana* well above the high-water level.

Distribution. Known from two localities in southern and central Florida. – Endemic?

Discussion. Bacidina squamellosa is an inconspicuous species, but easily identified on account of its finely squamulose thallus. However, the thallus of depauperate morphs may be confused with the coralloid goniocysts of *B. varia*. *B. squamellosa* can then be separated from *B. varia* by the wider paraphysis apices, the longer and narrower spores, and the large, inflated cell lumina in the proper exciple.

Additional collections examined. U. S. A. *Florida*. Alachua Co., 1993, Ekman L1149, L1150, L1151 (LD). Sarasota Co., 1993, Ekman L1206 (LD).

38. Bacidina varia S. Ekman, sp. nov.

Type: U. S. A., Florida, Monroe Co., Lignumvitae Key (N of Lower Matacumbe Key), tropical virgin forest, on *Drypetes diversifolia*, 1993, Ekman L1191 (LD, holotype).

Thallus saepe partim vel totaliter in goniocystas laxe aggregatas solutus. Apothecia pallide rosea ad porphyrea, pigmentum hydrato kalico immutatum vel intensius coloratum, aliquando etiam pigmentum hydrato kalico purpurascens continentes. Pycnidia conidiis filiformibus curvatis ad sigmoideis 0-11-septatis. Facile cum *Bacidina aenea* confusa quae hymenium altius et pigmentum fulvum in apotheciis, item cum *Bacidina* sp. #1 quae goniocystas tenuiores; apices paraphysorum latiores, sporasque angustiores, item cum *Bacidina crystallifera* quae hymenium altius, sporasque longiores et angustiores stratumque crystalliferum in epithecio et in margine excipuli proprii habent.

Etymology. Varius, variable.

Illustrations. Figs 2B, 4B, 5Q, 8C, 39 (map), 44F.

Characterization. Thallus dissolving into goniocysts or not; goniocysts coarse, 17-46 µm diam. Apothecia pink to purple-brown. Proper exciple laterally colourless to pale red-brown, below hypothecium colourless, without large inflated cell lumina in lower part. Hypothecium colourless to pale red-brown. Hymenium colourless to pale brown-orange. Paraphysis apices thin, 1.6-2.7 µm (average of 10). Spores acicular, clavate, or almost bacilliform, 19-50 × 1.2-2.5 µm, with 3-7 septa. Conidia filiform, ± curved or sigmoid, usually indistinctly 3-11-septate.

Thallus indeterminate, thin, usually discontinuous, of discrete or contiguous, convex areoles, sometimes continuous, wrinkled or warted, usually ± rimose but sometimes areolate or entirely without cracks, pale grey to grey-green, often (but not always) partly or entirely dissolving into granular goniocysts, then becoming rather thick. Goniocysts pale green to green, loosely aggregated in coralloid structures, (17-)25-28-29(-46) µm diam. (s= 7, N= 4, n= 10).

Apothecia (0.2-)0.2-0.3-0.4(-0.6) mm diam. (s= 0.09, N= 8, n= 10), at first plane, later becoming convex, epruinose. Disk pale pink, pale grey-pink, pale orange, pale grey-brown, or ± brown-orange to purple-brown, sometimes mottled with different hues. Margin concolorous with or slightly paler than disc, distinct, level with or raised above disc in young apothecia, soon level with the disc, finally excluded.

Proper exciple laterally (25-)40(-52) µm wide (s= 11, N= 9, n= 1), without crystals. Hyphae with rather thin to rather thick walls (1-3.5 µm between adjacent cell lumina), not distinctly radiating towards edge, with cell lumina of widely differing shapes, often shorter and wider in upper part than in lower part, gradually expanding towards edge (in lateral interior 1-3.5 µm wide and up to 15 µm long, 1-11 times as long as wide). Rim colourless, pale yellowish, or pale orange-brown. Lateral interior colourless, pale yellowish, pale brown-orange, or pale red-brown. Medullary part colourless. Hypothecium colourless, pale yellowish, pale brown-orange, or pale red-brown. Hymenium (40-)42-52-61(-62) µm thick (s= 7, N= 9, n= 5), colourless, pale yellowish, or pale brown-orange. Paraphyses usually rather few in relation to the number of asci, 0.8-1.6 µm wide in mid-hymenium; apices ± clavate or not at all thickened, (0.8 -)1.6-2.0-2.7(-4.4) µm wide (s= 0.6, N= 9, n= 10). Tholus with a narrow c-layer. Ocular chamber lacking or wide and blunt, sometimes surrounded by a narrow zone that is more heavily amyloid than the remainder of the d-layer; axial body wide and high, conical, blunt, never penetrating through the entire d-layer. Spores acicular to clavate or sometimes almost bacilliform, straight to curved to sigmoid, (19-)23-29-41(-50) µm long (s= 7, N= 8, n= 10), (1.2-)1.7-2.0-2.4(-2.5) µm wide (s= 0.3, N= 8, n= 10), (8.5-)10.0-14.8-23.5(-33.0) times as long as wide (s= 6, N= 8, n= 10), with (3-)3.0-4.4-6.6(-7) septa (s= 1.7, N= 8, n= 10).

Pycnidia immersed in thallus that is not dissolved into goniocysts, uppermost part of wall concolorous with apothecia, 75-175 µm diam. Conidia filiform, ± curved or sigmoid, indistinctly 3-11-septate or sometimes non-septate, 14-55 × c. 0.6-1.0 µm.

Pigments: All parts of apothecia K- to + intensifying, N-, except pale red-brown parts of proper exciple, hypothecium, and hymenium, which react K+ purplish, N+ orange. – Sometimes small amounts of Rubella Orange, sometimes also Laurocerasi Brown, in proper exciple, hypothecium and hymenium.

Ecology. Usually on trunks or branches of trees and shrubs in shady and humid as well as open and rather dry forests. Sometimes also in more or less open stands of shrubs in man-made habitats. Known phorophytes include *Cephalanthus occidentalis*, *Drypetes diversifolia*, *Fraxinus caroliniana*, *Ilex* sp., *Lagerstroemia indica*, *Magnolia grandiflora*, *Sabal palmetto*, *Sambucus canadensis*, and *Vitis rotundifolia*. One find was made on a polypore on the trunk of a still living *Quercus virginiana*.

Distribution. Known from southern Louisiana and most parts of Florida. – Endemic?

Discussion. Bacidina varia is remarkably variable in thallus structure and apothecium pigmentation. The thallus varies from being not at all dissolved to entirely dissolved into goniocysts. The apothecia are usually pale pink but can sometimes become much darker. Some morphs of *Bn. varia* resembles the European "*Bacidia* "*caligans* (Nyl.) A. L. Sm. (a species of *Bacidina*, but the combination has not yet been made). In the latter species, however, the apothecial margin is generally darker than the disk due to a concentration of Laurocerasi Brown to the uppermost part of the proper exciple. *Bn. varia* is also similar to *B. aenea*, *Bn. crystallifera*, and *Bn.* sp. # 1 (see these species).

Additional collections examined. U. S. A. *Florida.* Alachua Co., 1993, Ekman 1152 (LD). Polk Co., 1993, Ekman L1169, L1170, L1171 (LD). Sarasota Co., 1993, Ekman L1208 (LD). Sanford, 1914, Rapp (FH, US). *Louisiana.* East Baton Rouge Par., 1993, Ekman L1116, L1122, L1123, L1124 (LD), 1983, Tucker 25618 (herb. Tucker), 1992, Tucker 32181 (herb. Tucker). St. Helena Par., 1986, Tucker 27953 (herb. Tucker). St. Tammany Par., 1993, Ekman L1135 (LD); 1993, Tucker 33490 (herb. Tucker).

39. Bacidina sp. # 1

Illustrations. Figs 5R, 38 (map).

Characterization. Thallus partly dissolving into goniocysts; goniocysts fine, 9-21 µm diam. Apothecia ± pink. Proper exciple, hypothecium, and hymenium (almost) colourless. Paraphysis apices wide, 3.2-3.3 µm (average of 10). Conidia filiform, straight or ± curved, indistinctly 5-11-septate

Thallus indeterminate, thin, either discontinuous, of discrete or contiguous, convex areoles, or continuous, wrinkled or warted, without cracks, green to grey-green, partly dissolving into granular goniocysts. Goniocysts loosely aggregated, pale green, (9-)12-14-16(-21) µm diam. (s= 3, N= 2, n= 20).

Apothecia (0.3-)0.3-0.3-0.3(-0.4) mm diam. (s= 0.03, N= 2, n= 10), plane, later becoming convex, epruinose.

Disk pale pink to pink. Margin concolorous disc, distinct, raised above disc in young apothecia, soon level with the disc, finally excluded.

Proper exciple laterally 43 µm wide (N= 1, n= 1), without crystals and without internal pigment. Hyphae with rather thin walls (2.5-4 µm between adjacent cell lumina), ± distinctly radiating towards edge, cell lumina gradually expanding towards edge (in lateral interior 2-5 µm wide and up to 11 µm long, 1.5-3.5 times as long as wide). Hypothecium colourless or very pale yellowish. Hymenium (51-)53(-57) µm thick (s= 2, N= 1, n= 5), colourless. Paraphyses abundant in relation to the number of asci, 1.2-2.0 µm wide in mid-hymenium; apices ± clavate, (1.6-)3.2-3.2-3.3(-5.7) µm wide (s= 1.0, N= 2, n= 10), without pigment. Tholus with a rather wide c-layer. Ocular chamber narrow or wide, ± blunt; axial body very wide and high, conical, blunt, filling up most of the d-layer but never penetrating at its apex. Spores acicular, curved or sigmoid, (30-)37(-43) µm long (s= 4, N= 1, n= 10), (1.2-)1.4(-1.9) µm wide (s= 0.2, N= 1, n= 10), (22.7-)27.9(-33.0) times as long as wide (s= 4, N= 1, n= 10), with (3-)3.4(-5) septa (s= 0.7, N= 1, n= 10).

Pycnidia immersed in thallus that is not dissolved into goniocysts, uppermost part of wall concolorous with apothecia, 50-125 µm diam. Conidia filiform, straight or ± curved, indistinctly 5-11-septate, 41-57 × c. 1.0 µm.

Pigments: All parts of apothecia K-, N-. – Sometimes small amounts of an unidentified yellowish pigment (Rubella Orange?) in the hypothecium.

Ecology. The specimen from Sanford was collected on *Sambucus canadensis*, where it grew together with *Bacidia heterochroa* and *Bacidina varia*. At the locality in Baton Rouge, I observed *Bn.* sp. # 1 growing on old stems of *Vitis rotundifolia* in a dense, shady and rather humid forest, forming rather large sterile patches with few apothecia. Few other lichens were present near *Bn.* sp. # 1.

Distribution. I know of only two sparsely fertile collections, one from Sanford, Florida, and one from Baton Rouge, Louisiana. – Endemic?.

Discussion. I am fairly certain that the taxon I refer to here as *Bn.* sp # 1 is a distinct species, although obviously closely related to *Bn. varia*. The reason for not describing it is that the material presently available is very sparse and includes only a few apothecia. None of these collections is suitable as a holotype. Additional specimens with abundant apothecia are needed before this lichen can be formally described.

Bacidina sp. # 1 is similar to *Bn. aenea*, *Bn. crystallifera*, and, above all, *Bn. varia*. *Bn.* sp # 1 is separated from *Bn. varia* by the finer goniocysts, the wider paraphysis apices, the narrower spores, and the wider cell lumina in the proper exciple, from *B. aenea* by the lower hymenium and the lack of a brown-yellow pigment (Arceutina Yellow) in the apothecia, and from *Bn. crystallifera* by the lower hymenium, wider paraphysis apices, and the lack of crystals in the hymenium and proper exciple.

Collections examined. U. S. A. *Florida.* Sanford, 1914, Rapp (FH). *Louisiana.* East Baton Rouge Par., 1993, Ekman L1121 (LD).

Exsiccates

This is an account of all the exsiccate specimens I have seen containing North American *Bacidia* and *Bacidina*. The exsiccates listed are those that were accepted by Lynge (1915) or Sayre (1969), with the exception of J. Macoun's "Canadian Lichens", which I do not consider to be an exsiccate. Also included here, but not listed by Lynge or Sayre, is Plitt's "Lichenes Exsiccati ex Herbario Dr. H. E. Hasse, relicti". The exsiccate numbers below are followed by the name of the taxon under which it was issued, the herbaria in which I have seen this collection, and finally my determination.

Cummings: Decades of N. Am. Lich.
171. *Biatora suffusa* (FH, NY, US), *Bacidia suffusa*
208. *Biatora rubella* (NY, US), *Bacidia polychroa*
228. *Biatora rubella* (NY, US), *Bacidia polychroa*
247. *Biatora schweinitzii* (NY), *Bacidia schweinitzii*
258. *Biatora rubella* (FH, NY, US), *Bacidia polychroa*
267. *Biatora schweinitzii* (COLO, NY, US), *Bacidia schweinitzii*

Cummings et al.: Lich. Boreali-Am.
102. *Biatora suffusa* (COLO), *Bacidia suffusa*
169. *Biatora schweinitzii* (COLO), *Bacidia schweinitzii*
195. *Biatora rubella* (COLO), *Bacidia polychroa*
200. *Biatora schweinitzii* (COLO, UBC), *Bacidia schweinitzii*

Farlow Herb.: Reliquiae Tuckermanianae
16. *Biatora schweinitzii* (CANL, COLO), *Bacidia schweinitzii*

Merrill: Lich. Exs.
30. *Bacidia rosella* (COLO, MIN, NY, US, WIS), *Bacidia rubella*
119. *Bacidia atrosanguinea* (COLO, MIN), *Bacidia schweinitzii*
171. *Biatora rubella* (COLO, US), *Bacidia polychroa*, in COLO also with an admixture of *B. suffusa*
214. *Biatora schweinitzii* (COLO, FH, US), *Bacidia schweinitzii*

226. *Biatora atrogrisea* (COLO, US), *Bacidia laurocerasi* subsp. *laurocerasi*
260. *Biatora fuscorubella* (COLO), *Bacidia laurocerasi* subsp. *laurocerasi*

Plitt: Lich. Exs. ex Herb. Hasse, relicti
52. *Bacidia endoleuca* (COLO), *Bacidia insularis*

Thomson: Lich. Wisconsinenses Exs.
36. *Bacidia schweinitzii* (CANL, COLO, MIN, US), *Bacidia schweinitzii*

Weber: Lich. Exs. Boulder
182. *Bacidia albescens* (COLO, MIN, SFSU, UBC, US, UW), *Bacidina californica* (holotype and isotypes)+ *Bacidia heterochroa*

Excluded or not examined species

Listed here are species (1) that have previously been referred to *Bacidia* or *Bacidina* but do not belong with certainty to these genera, (2) that belong in *Bacidia* or *Bacidina* but have been erroneously published for North America, or (3) that belong in *Bacidia* or *Bacidina* but are not corticolous or lignicolous in North America. Some species fulfil more than one requirements. I have chosen to restrict the selection of species mainly to those accepted as *Bacidia* by Egan (1987), i.e., listed in boldface by him, but I have added *Bacidia globulosa* (Flörke) Hafellner & V. Wirth, a few species traditionally treated as *Bacidia* but referred to *Mycobilimbia* by Hafellner (1984, 1989), and the long forgotten names *Bacidia pallidula* and *Bacidia niveocincta*. For other North American species that have sometimes been referred to *Bacidia*, see Egan (1987) and Esslinger (1995). Note that the synonymy of "*Bilimbia artyta* (Ach.) Fink" was discussed by Timdal (1991: 122). The species are treated in alphabetical order according to the epithet.

Bacidia accedens sensu R. C. Harris, non (Arnold) Lettau

Bacidia accedens in the sense of Harris (1977) is not synonymous with *Bacidia accedens* (Arnold) Lettau, but constitutes a separate species, which still remains to be described. It appears to be mainly corticolous.

Bacidia akompsa (Tuck.) Fink

Contr. U.S. natn. Herb. 14: 90 (1910). - *Biatora akompsa* Tuck., Synops. N. Am. Lich. 2: 47 (1888). – Type: U. S. A., California, "in *Pini insigni*, Pescadero", 1867, Bolander 33b (FH-TUCK, lectotype selected here).

Bacidia akompsa is a corticolous species of *Lecanactis*.

Herteliana alaskensis (Nyl.) S. Ekman, comb. nova

Lecidea alaskensis Nyl., Bull. Soc. linn. Normandie, sér. 4, 1: 283 (1887). - *Bacidia alaskensis* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 171 (1926). – Type: U. S. A., Alaska, "ad Fret. Behringii", 1880, Bean (H-NYL 17389, lectotype selected here; FH, isotypes).

This species is closely related to *Herteliana taylorii*, but differs in having consistently 3-septate spores that are only 2.5-4 µm wide, and a different secondary chemistry (negative to K, C, and PD; not examined by HPTLC). It is characteristic of seashore rocks from Washington to Alaska (Noble 1982), where it is mainly found on slightly shady surfaces at the upper edge of the *Verrucaria* belt. See also the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level.*

Bacidina apiahica (Müll. Arg.) Vězda

Folia Geobot. Phytotax. Praha 25: 432 (1991). - *Patellaria apiahica* Müll. Arg., Lich. Epiphylli Novi 9 (1890). - *Bacidia apiahica* (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 4: 174 (1926). – Type: Brazil, Puiggari 1025 (G, lectotype selected by Santesson 1952).

This foliicolous species occurs in the southeasternmost United States, where it is sometimes encountered on the leaves of above all *Sabal palmetto* and *S. minor*. Santesson (1952) mentioned that *Bn. apiahica* has sometimes been found growing on twigs. I have never seen any corticolous herbarium material from the United States. Furthermore, my own attempts to find corticolous specimens in the field have been unsuccessful, even in localities where *Bn. apiahica* was abundant on palm-leaves.

Bacidia augustinii (Tuck.) Zahlbr.

Cat. Lich. Univ. 4: 102 (1926). - *Biatora augustinii* Tuck., Synops. N. Am. Lich. 2: 42 (1888). – Type: U. S. A., Florida, "Caloosa River", 1878, Austin (FH-TUCK, lectotype selected here).

Short description of lectotype specimen: Thallus of grey, placoid squamules that are adpressed to a black prothallus consisting of a web of hyphae that are purple-brown in the microscope. Apothecia slightly concave to flat, with orange-brown disc and a thick, red-brown to black margin. Proper exciple orange-brown to red-brown along rim, internally colourless to pale yellow, without crystals or oil droplets, consisting of hyphae with lumina that are ± ellipsoid (3.0-3.5 µm wide), often protruding from the lower part (anchorage hyphae?). Hypothecium pale yellow. Hymenium colourless to pale yellow, c. 50 µm high. Paraphyses sparsely branched in upper part, apical cell sometimes swollen to 3 µm, the wall of which is not thick and gelatinized. Spores filiform, distinctly 1-3-septate, 25-30 × c. 1.2 µm.

The affinities of this corticolous taxon are unclear, but it does not belong in *Bacidia* or *Bacidina*. It should possibly be referred to *Sporacestra*.

Bacidia bagliettoana (A. Massal. & De Not. in A. Massal.) Jatta

Sylloge Lich. Ital. 421 (1900). - *Scoliciosporum bagliettoanum* A. Massal. & de Not. in A. Massal., Memor. Lichenogr. 126 (1853). – Type: Not seen.

This species is a member of *Bacidia* s. str. It grows directly on soil or, more often, on bryophytes overgrowing soil. North American determinations are generally correct.

Bacidia beckhausii Körb.

Parerga Lich., fasc. 2: 134 (1860). – Type: Germany, "Westphalen", Beckhaus (L-910.137 1363, lectotype selected here).

This corticolous species belongs in the *Bacidia beckhausii* group; see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*.

Bacidia brouardii (de Lesd.) Zahlbr.

Cat. Lich. Univ. 10: 359 (1939). - *Bilimbia brouardii* de Lesd., Annls Cryptog. exot. 5: 105 (1932). – Type: Not seen.

I have not been able to trace any original material of this species. It was described from New Mexico, where it was found on siliceous rocks (Bouly de Lesdain 1932). Unfortunately, the diagnosis gives no clue as to the generic affinities.

Bacidia carneoalbida (Müll. Arg) Coppins

Lichenologist 21: 99 (1989). - *Patellaria carneoalbida* Müll. Arg., Flora, Jena 51: 50 (1868). - *Biatora carneoalbida* (Müll. Arg.) Coppins in Coppins, P. James & D. Hawksw., Lichenologist 24: 367 (1992). – Type: Switzerland, Bern, Thun, "Stockhorn", 1867, Fischer (G, lectotype selected by Gilbert et al. 1988 as "holotype"; not seen by me).

Bacidia sphaeroides auct., non (Dicks.) Zahlbr.

This muscicolous and corticolous lichen, often referred to as *Bacidia sphaeroides*, belongs in *Mycobilimbia* (Printzen 1995); see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*.

Ropalospora chlorantha (Tuck.) S. Ekman

Bryologist 96: 586 (1993) - *Biatora chlorantha* Tuck., Proc. Am. Acad. Arts Sci. 1: 252 (1848). - *Bacidia chlorantha* (Tuck.) Fink, Contr. U.S. natn. Herb. 14 (1): 91 (1910). – Type: U. S. A., New Hampshire, "White Mts", 1847, Tuckerman (FH-TUCK, lectotype selected by Ekman 1993)

This corticolous species, which has traditionally been treated as *Bacidia chlorantha*, was transferred to *Ropalospora* by Ekman (1993). Since the publication of that paper, one additional species traditionally treated in *Bacidia* has turned out to belong in *Ropalospora*, namely the Japanese corticolous species *Ropalospora phaeoplaca* (Zahlbr.) S. Ekman comb. nova (*Bacidia phaeoplaca* Zahlbr., Botan. Magaz. Tokyo 41: 333, 1927; type: Japan, "Insula Nippon, Takayu", 1904, Faurie 5882, W, lectotype selected here). It is obviously closely related to *R. chlorantha*, but differs in having the proper exciple inspersed with minute K-soluble crystals and in usually having eight (in some asci up to 12 or 16?) spores per ascus.

Bacidia clementis Hasse

Bryologist 13: 61 (1910). – Type: U. S. A., California, "on *Heteromeles*, San Clemente Island", 1903, Trask (FH, syntype).

This is a younger synonym of *Bactrospora patellarioides* var. *patellarioides*.

Lecania cuprea (A. Massal.) P. Boom & Coppins in P. Boom

Nova Hedwigia 54: 234 (1992). - *Bilimbia cuprea* A. Massal., Lotos 6: 77 (1856). - *Bacidia cuprea* (A. Massal.) Lettau, Hedwigia 52: 132 (1912). - *Lecidea cupreorosella* Nyl ex Stizenb., Nova Acta Acad. Caesar. Leop. Carol. 34 (2): 9 (1867), made as a nomen novum due to the existence of *Lecidea cuprea* Sommerf. - *Biatora cupreorosella* (Nyl. ex Stizenb.) Tuck., Genera Lich. 164 (1872). - *Bacidia cupreorosella* (Nyl. ex Stizenb.) A. Schneid., Guide Study Lich. 109 (1898) – Type: Not seen.

This saxicolous species has traditionally been treated as a species of *Bacidia*, but it belongs in *Lecania*; see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*. I have not checked the determinations of the North American specimens.

Bacidia declinis (Tuck.) Zahlbr.

Cat. Lich. Univ. 4: 109 (1926). - *Lecidea declinis* Tuck., Genera Lich. 182 (1872). – Type: U. S. A., Massachusetts, "NB" (= New Bedford), 1867, Willey (FH-TUCK, lectotype selected here).

This name is a younger synonym of *Catillaria nigroclavata* (Nyl.) Schuler.

Bacidia epixanthoides (Nyl.) Lettau

Hedwigia 52: 133 (1912). - *Lecidea epixanthoides* Nyl., Flora, Jena 48: 5 (1865). - *Biatora epixanthoides* (Nyl.) Diederich, Trav scient. Mus. nat. Hist. nat. Luxemb. 14: 57 (1989). – Type: Not seen.

This mainly corticolous species has for a long time been treated as a *Bacidia*, but belongs in *Mycobilimbia* (Printzen 1995); see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*. I have not checked the determinations of the North American specimens.

Bacidia flavens (Willey in Tuck.) Zahlbr.

Cat. Lich. Univ. 4: 112 (1926). - *Biatora flavens* Willey in Tuck., Synops. N. Am. Lich. 2: 34 (1888). – Type: U. S. A., Massachusetts, "New Bedford", Willey (US, lectotype selected here).

This saxicolous taxon belongs in *Lecania*. I am not sure whether it is just a depauperate form of *Lecania erysibe* (Ach.) Mudd or a separate species.

Fellhanera floridana (Tuck.) S. Ekman, comb. nova

Biatora floridana Tuck., Synops. N. Am. Lich. 2: 39 (1888) - *Bacidia floridana* (Tuck.) Zahlbr. in Engler & Prantl, Natürl. Pflanzenfam. I (1): 135 (1905). – Type: U. S. A., Florida, "Caloosa River", 1878, Austin (FH-TUCK, lectotype selected here).

Bilimbia finkii Vain., Mycologia 21: 35 (1929). - *Bacidia finkii* (Vain.) Zahlbr., Cat. Lich. Univ. 8: 401 (1932). – Type: Puerto Rico, "Rio Piedras", 1915, Fink 534 (TUR-V, lectotype selected here).

Bacidia laeticolor Malme, Ark. Bot. 27A (5): 8 (1935). – Type: Paraguay, "inter Lambaré et Asuncion", 1893, Malme 1647 (LD, paratype).

Fellhanera floridana is transferred here to the genus *Fellhanera* on account of the distinctly paraplectenchymatic proper exciple, tholus structure (dark tubular structure that fades towards the tip of the ascus), abundantly branched paraphyses, and short, 3-septate spores. It is exclusively corticolous and lignicolous, but appears to be closely related to the foliicolous *Fellhanera lisowskii* (Vězda) Vězda (described as *Bacidia lisowskii* by Vězda 1980). *F. floridana* differs slightly from the latter in the pigmentation of the thallus and the apothecia, and in the non-halonate spores.

Short description of the type specimens studied: Thallus thin, ± granular, yellowish. Apothecia up to 0.6 mm wide, orange-brown to red-brown, margin concolorous with disc or slightly paler. Proper exciple of hyphae with almost sphaerical lumina ("paraplectenchymatic"), yellow to orange-brown along rim, pale yellow inside. Hypothecium pale yellow. Hymenium 40-50 µm high, with yellow to orange-brown epithecium (this and rim of proper exc. K+ citrine yellow), pigment when in high concentration appearing crystalline. Paraphyses abundantly branched. Spores 3-septate, slightly constricted at septa, 12-14 · 3-5 µm.

Bacidia globulosa (Flörke) Hafellner & V. Wirth in Wirth

Flecht. Baden-Württemb. 511 (1987). - *Lecidea globulosa* Flörke, Deutsche Lich. 10: 1 (1821). - *Catillaria globulosa* (Flörke) Th. Fr., Lichenogr. scand. 2: 575 (1874). – Type: Not seen.

This lichen has traditionally been called *Catillaria globulosa*, but the name *Bacidia globulosa* has been used in some works in recent time. It does not belong neither in *Bacidia* s. str. nor in *Catillaria* s. str. Printzen (1995: 183) hypothesized a close relationship with *Lecidea albohyalina* (Nyl.) Th. Fr. and *L. meiocarpa* Nyl.

Bacidia granosa (Tuck.) Zahlbr.

Cat. Lich. Univ. 4: 203 (1926). - *Lecidea granosa* Tuck., Proc. Am. Acad. Arts Sci. 5: 420 (1862). – Type: U. S. A., South Carolina, "Santee Canal", Ravenel 191 (FH-TUCK, lectotype selected here).

Bilimbia pammellii Fink in Hedrick, Mycologia 26: 156 (1934). - *Bacidia pammellii* (Fink in Hedrick) Zahlbr., Cat. Lich. Univ. 10: 365 (1939). – Type: U. S. A., Iowa, "The Ledges, Boone Co.", 1903, Fink 1407 (MU-L1397, lectotype selected here; MICH, isotype).

This saxicolous species occurs in eastern North America. It is very similar to some species of *Bacidia*, and it is with some hesitation that I exclude it. It differs from *Bacidia* mainly in having a proper exciple built up of hyphae with cell lumina that are wide relative to the length and lack constrictions at the septa. Thus, the excipular hyphae are very similar to those of *Toninia*, but unlike this genus, they are abundantly furcate, non-anastomosed, and have thicker cell walls. Timdal (1991), however, excluded it from *Toninia* due to the more conglutinated paraphyses and minor differences in the tholus. Its affinities appears to lie with the European *Bacidia coprodes* (Körb.) Lettau, with which it shares a very similar apothecium pigmentation and the excipular structure. *B. granosa* and *B. coprodes* are separated by pycnidial characters. Without pycnidia, however, they are very difficult to tell apart.

Pachyphiale gyalizella (Nyl.) S. Ekman, comb. nova

Lecidea gyalizella Nyl., Sertum Lich. Trop. Labuan et Singapore 38 (1891). - *Bacidia gyalizella* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 114 (1926). – Type: U. S. A., Massachusetts, "New Bedford", Willey (H-NYL 21313, lectotype selected here; FH, UPS, isotypes).

Pachyphiale gyalizella is a very inconspicuous corticolous species, which is closely related to *P. fagicola* (Hepp) Zwackh, the type species of the genus. It differs from the latter in having smaller apothecia (not exceeding 0.25 mm in diam.), 1-3-septate, blunt-ended spores that measure 9-15 × 4-7 µm, narrower paraphyses (c. 1.0 µm), and smaller pycnidia (25-40 µm in diam.) containing ellipsoid conidia measuring 1.5-2.0 × 0.8-1.0 µm. As far as I know, it is known only from the type collection, which was collected on the smooth bark of *Acer rubrum*.

Bacidia herbarum (Stizenb.) Arnold

Flora, Jena 48: 596 (1865). - *Secoliga herbarum* Stizenb., Nova Acta Acad. Caesar. Leop. Carol. 30 (3): 46 (1863). – Type: Not seen.

This species overgrows bryophytes and detritus on the ground, and belongs in *Bacidia* s. str. I have not checked the identity of the North American collections.

Bacidia illudens (Nyl.) Lynge

Meddr Grønland 118 (8): 85 (1937) - *Lecidea illudens* Nyl., Flora, Jena 53: 34 (1870). – Type: Not seen.

Toniniopsis obscura Frey, Ber. schweiz. bot. Ges. 35: 73 (1926). – Type: Switzerland, "Val Cluozza, auf Kalkfelsgesimsen im Pinetum mont. 1850 m. ü. M.", 1923, Frey 442 (BERN, lectotype selected here).

This species overgrows bryophytes in arctic environments. It belongs in *Bacidia* s. str. and has been correctly reported from Northwest Territories, Canada.

Bacidia incompta (Borrer ex Hook.) Anzi

Catal. Lich. Sondr. 70 (1860). - *Lecidea incompta* Borrer ex Hook, Suppl. Engl. Bot. 2, tab. 2699 (1834). – Type: Not seen.

B. incompta is a corticolous species that appears to be exclusively European. Several North American collections have been named *Bacidia incompta*, but none that I have seen is correct. The content of such collections is usually *B. schweinitzii*.

Bacidina inundata (Fr.) Vězda

Folia Geobot. Phytotax Praha 25: 432 (1991). - *Biatora inundata* Fr., K. svenska VetenskAkad. Handl. 1822: 270 (1822). - *Bacidia inundata* (Fr.) Körb., Syst. Lich. Germ. 187 (1855). – Type: Not seen.

This is one of the most frequently used names in *Bacidia* and *Bacidina* in North America. I have studied only a few North American collections named *Bn. inundata*, but it is clear that this name has been used for a mixture of saxicolous species. *Bn. inundata* inhabits shores of lakes and streams, where it is predominantly saxicolous. In Europe, however, it is occasionally found on the lower parts of tree-trunks or on exposed tree-roots etc. in similar habitats.

Bacidia ioessa Herre

Proc. Wash. Acad. Sci. 12: 98 (1910). – Type: Not seen.

I have been unable to trace any original material of this saxicolous species. Judging from the diagnosis, it probably does not belong neither in *Bacidia* nor *Bacidina*.

Bacidia jacobi (Tuck.) Hasse

Contr. U.S. natn. Herb. 17: 51 (1913). - *Biatora jacobi* Tuck., Synops. N. Am. Lich. 2: 48 (1888). – Type: U. S. A., California, "San Diego", 1875, Palmer (FH-TUCK, lectotype selected here).

Short description of the lectotype: Thallus rather thick, pale, wrinkled to warted. Apothecia black, c. 0.5 mm in diam., flat, with margin level with the disc. Proper exciple mostly colourless, but the interior gradually merging into the pigmentation of the hypothecium, with crystals in the rim and as radiating clusters in the interior. Hypothecium brown, K-. Hymenium c. 75 µm high, colourless except for brown spots in the epithecium, which is also inspersed with crystals. Paraphyses unbranched or sparsely branched in upper part, with apical swelling to c. 4 µm, some apical cells with a distinctly delimited, brown (K-) hood. Ascus with a pointed, conical ocular chamber and a rather narrow axial body that reaches all through the d-layer. Spores acicular with both ends pointed, 5-septate, c. 30 × 2.5 µm.

This is a corticolous species, the affinities of which I do not understand. I exclude it from *Bacidia* and *Bacidina* on account of the tholus, the pure brown and K- pigment in the hypothecium, and the spores having both ends pointed.

The isolectotype in US is a different taxon, which belongs in the Arthoniales. This specimen was probably never seen by Tuckerman.

Bacidia kingmanii Hasse

Bryologist 14: 101 (1911), as "*kingmani*". – Type: U. S. A., California, "Mt. Wilson Trail Road, San Gabriel Mts", 1910, Kingman (FH, 3 syntypes).

This is a saxicolous species with unclear affinities. It is excluded from *Bacidia* and *Bacidina* on account of the densely packed and thin-walled excipular hyphae, the richly branched paraphyses, and the tholus, which, although similar to *Bacidia*, lacks a discernable c-layer.

Byssoloma meadii (Tuck.) S. Ekman, comb. nova

Biatora meadii Tuck., Synops. N. Am. Lich. 2: 129 (1888) - *Bacidia meadii* (Tuck.) Zahlbr., Cat. Lich. Univ. 4: 122 (1926). – Type: U. S. A., Florida, Mead (FH-TUCK, lectotype selected here).

This poorly known species is transferred here to *Byssoloma* on account of the tholus (a dark tubular structure that fades towards the tip of the ascus), byssoid proper exciple, short 3-septate spores, and drop-shaped to short-bacilliform conidia. It is very closely related to the much more common and widespread *Byssoloma leucophlebarum* (Nyl.) Vainio. I have been in doubt whether *B. meadii* should be recognized as a distinct species. I have, however, seen both species several times in Florida and Louisiana, where they are often found in the same localities, and it has not been a problem to keep them apart. This has convinced me that they are in fact different species. *Byssoloma meadii* is found in southeastern United States, and appears to be exclusively corticolous, contrary to *B. leucophlebarum*. In localities where *B. meadii* is found on bark, I have searched for it in vain on leaves, even if the foliicolous lichen flora as a whole has been rich. *B. meadii* does not seem to agree with any of the species treated by Kalb & Vězda (1990) and Lücking (1992). The differences between *B. meadii* and *B. leucophlebarum* are summarized in Tab. 18.

Bacidia microcarpa (Th. Fr.) Lettau

Hedwigia 52: 132 (1912). - *Bilimbia obscurata* var. *microcarpa* Th. Fr., Nova Acta R. Soc. Scient. upsal., ser. 3, 3: 283 (1861). – Type: Norway, "Ø. Finmark, Varanger, Mortensnaes", 1857, Th. M. Fries (UPS, syntype).

This is an arctic species overgrowing terricolous bryophytes, and belongs in the *Bacidia sabuletorum* group; see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*. I have not examined the North American specimens. The name *Bacidia microcarpa* has been widely misused for forms of *B. sabuletorum* with predominantly 3-septate spores. The specimen depicted as "*Mycobilimbia obscurata*" by Hafellner (1984: 309, note the warted perispore) is probably such a form. *B. microcarpa* can be distinguished from *B. sabuletorum* on account of the regularly 3-septate spores lacking a perispore, slightly thinner paraphyses (only a few exceeding 2 µm in width), and the dominance of a brown pigment over a green

Tab. 18. A comparison between *Byssoloma leucophlebarum* (Nyl.) Vainio and *B. meadii* (Tuck.) S. Ekman.

	B. leucophlebarum	*B. meadii*
Apothecia	0.3-0.5(-0.6) mm wide, greyish or brownish, rarely yellowish (pigment deficient morphs)	0.2-0.3(-0.5) mm, pale dirty yellow
Proper exciple	Not prominent, outer part byssoid, spreading over the thallus surface, gradually thinner towards edge	Prominent, raised above thallus, moderately byssoid, not spreading over the thallus
Hypothecium	Pale to dark brown, rarely colourless (pigment deficient specimens)	Colourless or pale yellowish
Pycnidia	Common, 100-150 µm wide	Rare, 50-75 µm wide
Ecology	Mostly foliicolous or corticolous, rarely saxicolous	Corticolous, preferring twigs and branches

pigment (the latter patchily distributed) in the epithecium of darkly pigmented apothecia. In *B. sabuletorum*, on the other hand, the spores often possess a warted perispore and more than three septa, the paraphyses often exceed 2 µm in width, and the epithecium of dark apothecia is dominated by a green pigment.

Lecania naegelii (Hepp) Diederich & P. Boom

Bull. Soc. Nat. luxemb. 95: 154 (1994). - *Biatora naegelii* Hepp, Hepp: Flecht. Eur. 19 (1853). - *Bacidia naegelii* (Hepp) Zahlbr., Öst. bot. Z. 59: 439 (1909). – Type: Not seen.

This corticolous species has traditionally been named *Bacidia naegelii*, but belongs in *Lecania*; see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*. North American specimens are generally correctly determined.

Bacidia nivalis Follmann

Philippia 4: 30 (1979). – Type: U. S. A., Washington, "....im Bereich der Sommerschneegrenze am Nordosthang des Mount Baker über dem Austinpass, Whatcom County", 1969, Follmann, Follmann: Lichenes exsiccati selecti a museo historiae naturalis Casselensi editi 262 (LD, isotype).

The pigmentation, the structure of the proper exciple, and the tholus appearance shows that this saxicolous lichen is related to *Porpidia*. Contrary to the claims by its author, it bears no close relationship with *Bacidia trachona*.

Bacidia niveocincta G. Merr. in Zahlbr. & Redinger, nom. nud.

Lich. Rar. exs. 311 (1933). - *Biatora niveocincta* G. Merr., Merrill: Lich. exs. 270 (1913), nom. nud.

Even though this species has been distributed in two exsiccates, its name has not been validated. It may, however, prove to have been validly published under a different name. *Bacidia niveocincta* is a corticolous species of *Fellhanera*, apparently closely related to the foliicolous *F. stanhopeae* (Müll. Arg) Lücking, also known as *Badimia stanhopeae* (Müll. Arg.) Vězda (see Lücking et al. 1994: 400).

The material distributed in the two exsiccates is probably part of the same collection made by Rapp in 1907. *Bacidia niveocincta* was listed by Lamb (1963).

Bacidia pallens (Kullh.) Zahlbr

Cat. Lich. Univ. 4: 134 (1926). - *Bilimbia pallens* Kullh., Not. Sällsk. Fauna Fl. Fenn. Förh. 11: 274 (1871). – Type: Finland, Tavastia australis, "Mustiala, ad corticem tiliae", 1869, Kullhem (H, lectotype selected by Printzen 1995: 203 as "holotype"; UPS, isotype).

The lichen traditionally called *Bacidia pallens*, a corticolous species, is excluded here from *Bacidia* and *Bacidina* on account of the "paraplectenchymatic" proper exciple composed of hyphae with ellipsoid, globose, or irregular cell lumina, the usnic acid containing apothecia, the crystal-inspersed proper exciple and epithecium, and the bacilliform to narrowly elliptical to narrowly drop-shaped conidia. The affinities of *Bacidia pallens* are almost surely with *Cliostomum*.

Bacidia pallidula Zahlbr.

Cat. Lich. Univ. 4: 231 (June 1926), nom. illeg., non (Kremp.) Zahlbr. (Feb. 1926). - *Biatora pallida* Arnold ex Eckfeldt, Bull. Torrey bot. Club 22: 254 (1895). – Type: Canada, Newfoundland, 1894, Waghorn 13 (PH, lectotype selected here).

Zahlbruckner (June 1926) made *Bacidia pallidula* as a nomen novum, since *Bacidia pallida* (Müll. Arg.) Darb. 1912 was blocking the use of a combination based on *Biatora pallida* Arnold ex Eckfeldt Unfortunately, Zahlbruckner forgot that the name *Bacidia pallidula* was already occupied for a quite different species made by himself a few months earlier (Zahlbruckner Feb. 1926). *Bacidia pallidula* Zahlbr. (June 1926) is a younger taxonomic synonym of *Scoliciosporum umbrinum* (Ach.) Arnold.

Bacidina phacodes (Körb.) Vězda

Folia Geobot. Phytotax. Praha 25: 432 (1991). - *Bacidia phacodes* Körb., Parerga Lich., fasc. 2: 130 (1860). – Type: Germany, (1) "München", 1853, Arnold, (2) Eichstädt, 1858, Arnold (L, syntypes).

?*Secoliga arceutina* var *albescens* Stizenb., Nova Acta Acad. Caesar. Leop. Carol. 30 (3): 43 (1863). - *Bacidia albescens* (Stizenb.) Bausch, Verhandl. naturw. Ver. Karlsruhe 4: 106 (1869). – Type: Not seen.

The few North American collections labelled *Bacidia phacodes* or its probable synonym *B. albescens* generally contain other species of *Bacidina*, such as *Bn. californica*, *Bn. varia*, or *Bn.* sp. #1. *Bacidina phacodes* is a corticolous species that does not occur in North America.

Arthrosporum populorum A. Massal.

Memor. Lichenogr. 128 (1853). - *Bacidia populorum* (A. Massal.) Trevis., Trevisan: Lichenotheca Veneta no. 163 (1869). – Type: Not seen.

This corticolous species appears to be rather widespread in boreal North America. For a discussion on its exclusion from *Bacidia*, see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*.

Bacidia ravenelii (Tuck.) Zahlbr.

Cat. Lich. Univ. 4: 138 (1926). - *Biatora ravenelii* Tuck., Synops. N. Am. Lich. 2: 34 (1888). – Type: U. S. A., Florida, "Gainesville", 1877, Ravenel 65 (FH-TUCK, two syntypes).

This is a saxicolous species with unclear affinities. It is distantly related to *Bacidia* and *Bacidina*.

Bacidia rubidofusca (Willey) Zahlbr.

Cat. Lich. Univ. 4: 139 (1926). - *Biatora rubidofusca* Willey, Enum. Lich. New Bedford 23 (1892). – Type: U. S. A., Massachusetts, New Bedford, Willey (US, holotype, not seen by me).

I have not seen any material of this species, but according to Printzen (1995: 215) it probably belongs in *Gyalidea*. It is apparently a terricolous lichen ("on naked earth", Willey 1892).

Ophioparma rubricosa (Müll. Arg.) S. Ekman, comb. nova

Patellaria rubricosa Müll. Arg., Hedwigia 34: 142 (1895). - *Bacidia rubricosa* (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 4: 139 (1926). – Type: U. S. A., Idaho, "Lake Pend d'Oreille", 1880, Eckfeldt 28 (G, holotype)

Bacidia herrei Zahlbr., Annls mycol. 6: 130 (1908). - *Ophioparma herrei* (Zahlbr.) Kalb & Staiger, Biblthca lichenol. 58: 193 (1995). – Type: U. S. A., California, Santa Cruz Mountains, Devil's Cañon, on dead *Adenostoma fasciculatum*, 2300 ft., 1906, Herre 943 (W, holotype, not seen by me; FH, isotype, seen).

Haematomma pacificum Hasse, Bryologist 13: 62 (1910), as "*pacifica*". – Type: U. S. A., California, Santa Cruz Mountains, near Grizzly Peak, on bark of *Pseudotsuga taxifolia*, 2700 ft., 1906, Herre 1033 (F, lectotype selected by Kalb & Staiger 1995: 194, not seen by me).

Haematomma californicum Sigal & D. R. Toren, Bryologist 78: 71 (1975). – Type: U. S. A., California, Lake County, north shore of Lake Pillsbury, at Sunset Campground, 551 m, 1973, Thiers 30899 (SFSU, holotype, not seen by me).

This species was recently treated by Kalb & Staiger (1995) as *Ophioparma herrei*. I agree with their conclusion that this species should be included in *Ophiopar-*

ma. It is similar to the type species of the genus, *O. ventosa* (L.) Norman, and differs mainly in having a thinner thallus with a more or less granular surface and a different ecology. *O. rubricosa* is characteristic of dry, hard lignum and acid bark. It is found from southern California to southern British Columbia (Noble 1982), and in humid areas of the western slopes of the Rocky Mountains.

Bacidia sabuletorum (Schreb.) Lettau

Hedwigia 52: 132 (1912). - *Lichen sabuletorum* Schreb., Spicil. Flor. Lipsiensis 134 (1771). - *Mycobilimbia sabuletorum* (Schreb.) Hafellner, Beih. Nova Hedwigia 79: 310 (1984). – Type: Not seen.

?Bilimbia accedens Arnold, Flora, Jena 45: 391 (1862). - *Bacidia accedens* (Arnold) Lettau, Hedwigia 52: 131 (1912). – Type: Not seen.

Secoliga fuscorubella var. *propinqua* Stizenb., Nova Acta Acad. Caesar. Leop. Carol. 30 (3): 58 (1863). - *Bacidia propinqua* (Stizenb.) Arnold, Flora 49: 531 (1866). – Type: Switzerland, "Zürich, an der Rinde von *Pop. tremula*", Hegetschweiler, Hepp: Flecht. Eur. 519 (LD, syntype).

This muscicolous and corticolous species belongs in the *Bacidia sabuletorum* group; see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*.

I agree with Coppins (in Purvis et al. 1992) that the European *Bacidia accedens* is just an intensely pigmented morph of *B. sabuletorum*. The variation from *B. sabuletorum* to "*B. accedens*" is occasionally seen in a single specimen. I have, however, not seen the types involved, and that is why I have listed *B. accedens* with a query above. The North American *B. accedens* sensu Harris (1977) is a distinct species awaiting formal description.

Bacidia saxicola Looman

Bryologist 65: 297 (1963). – Type: Canada, Saskatchewan, "Lamond C. P., 1700 feet, on granite rock", 1960, Looman 600128 (USAS, holotype).

This saxicolous species is excluded from *Bacidia* and *Bacidina* on account of the very wide and richly branched paraphyses, the occurrence of oil droplets in the hymenium, and a very peculiar tholus. It is almost entirely non-amyloid, but contains a faint, central structure comprised of a small cone just above the spore mass with a long, pointed extension at its apex. I do not understand the affinities of this species, but it is distantly related to *Bacidia* and *Bacidina*.

Bacidia scopulicola (Nyl.) A. L. Sm.

Monogr. Brit. Lich. 2: 156 (1911). - *Lecidea scopulicola* Nyl., Flora, Jena 57: 312 (1874). – Type: Not seen.

This species is a member of *Bacidia* s. str. It is characteristic of marine rocks, where it occurs in the *Verrucaria* zone, preferrably on shady surfaces. In North America, it is found along both the west and the east coast.

Lecania stigmatella (Tuck.) S. Ekman, comb. nova

Biatora stigmatella Tuck., Genera Lich. 167 (1872). - *Bacidia stigmatella* (Tuck.) Zahlbr., Cat. Lich. Univ. 4: 241 (1926). – Type: U. S. A., Louisiana, 1853, Hale (FH-TUCK, lectotype seected here).

This is a corticolous species found in the southeastern United States. It is closely related to *Lecania naegelii*, and their apothecia are almost identically pigmented. *L. stigmatella*, traditionally treated as a *Bacidia*, differs from *L. naegelii* in having narrower spores, filiform, curved, 0-1-septate conidia, and a thallus that often disintegrates into goniocysts. For a discussion on its inclusion in *Lecania*, see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*.

Lecania subfuscula (Nyl) S. Ekman, comb. nova

Lecidea subfuscula Nyl., Flora, Jena 48: 604 (1865). - *Bacidia subfuscula* (Nyl.) Th. Fr., K. svenska VetenskAkad. Förh. 7 (2): 35 (1867). – Type: Iceland, "Reikjavik", 1860, Lindsay (H-NYL 17363, lectotype selected by Printzen 1995: 223 as "holotype").

Biatora siberiensis, Willey in Rothr., Proc. U.S. natn. Mus. 7 (1): 6 (1884). - *Bacidia siberiensis* (Willey in Rothr.) Zahlbr., Cat. Lich. Univ. 4: 146 (1926). – Type: U. S. A., Alaska (as "Siberia"), 1880, Bean (US, lectotype selected here).

This species, long known as *Bacidia subfuscula*, belongs in *Lecania*; see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*. It is usually terricolous or saxicolous, but the type of *Biatora siberiensis* was collected on bone.

Bacidia subgranulosa (Tuck.) Riddle

Mycologia 4: 131 (1912). - *Lecidea microphyllina* var. *subgranulosa* Tuck., Proc. Am. Acad. Arts Sci 6:278 (1864). – Type: Not seen.

A lectotype in FH-TUCK was selected by Lois Brako in 1987, and, according to her label, synonymized with *Psorella pertexta* (Nyl.) Müll. Arg. To my knowledge, the lectotypification has not yet been validly published. It was reported as *Biatora subgranulosa* from a single locality in Georgia by Tuckerman (1888), but I have not examined this specimen. *Lecidea microphyllina* var. *subgranulosa* Tuck. should not be confused with *Lecidea parvifolia* f. *subgranulosa* Tuck., described in the same work. The latter is a synonym of *Phyllopsora canoumbrina* (Vain.) Brako (Brako 1989).

Bacidia tetramera (De Not.) Coppins in Gilbert et al.

Lichenologist 20 237 (1988). - *Bilimbia tetramera* De Not., Giorn. Bot. ital. 2: 191 (1846). – Type: Not seen.

Lecidea sphaeroides var *obscurata* Sommerf., Suppl. Fl. Lapp 165 (1826). - *Mycobilimbia obscurata* (Sommerf.) Rehm, Rabenh. Krypt.-Fl. 2, 1 (3): 328 (1890). - *Bacidia obscurata* (Sommerf.) Zahlbr. in Engler, Nat. Pflanzenfam. 1 (1*): 135 (1905). – Type: Not seen.

Bacidia fusca auct.

This species belongs in *Mycobilimbia* (Printzen 1995). It usually overgrows bryophytes and plant debris on the ground in boreal or arctic areas. I have not examined any North American material.

Bacidia trachona (Ach.) Lettau

Hedwigia 52: 133 (1912). - *Verrucaria trachona* Ach., Meth. Lich., suppl. 16 (1803). – Type: Sweden (H-ACH 823, lectotype selected here).

All North American collections named *Bacidia trachona* are saxicolous. I have studied only a few of them, and they have turned out to belong to *B. granosa*. It seems likely that *Bacidia trachona* should be excluded from *Bacidia* s. str. on account of the pycnidia, which are are large, multi-chambered, and contain narrow, 0.8-1.0 µm wide, conidiogenous cells producing small, ellipsoid conidia with two guttulae. I have not seen any fertile material of this species.

Bacidia verecundula (Th. Fr.) H. Magn.

Förteckn. Skandinaviens växter, 4. Lavar 38 (1936). - *Bilimbia verecundula* Th. Fr., Lich. Scand. 1: 387 (1874). – Type: Norway, " W. Finm.: Alten, Bosekop", 1864, Th. M. Fries (UPS, lectotype selected here).

Bacidia verecundula is a member of the *Bacidia beckhausii* group; see the section *Related genera and species groups* in the chapter *Taxonomic delimitations above species level*. It is similar to *Bacidia hemipolia* (Th. Fr.) Malme but differs in having shorter and wider spores. It is known only from the corticolous type collection from northern Norway. It has been reported from Northwest Territories, Canada, but this record refers to an undescribed member of the *Bacidia sabuletorum* group.

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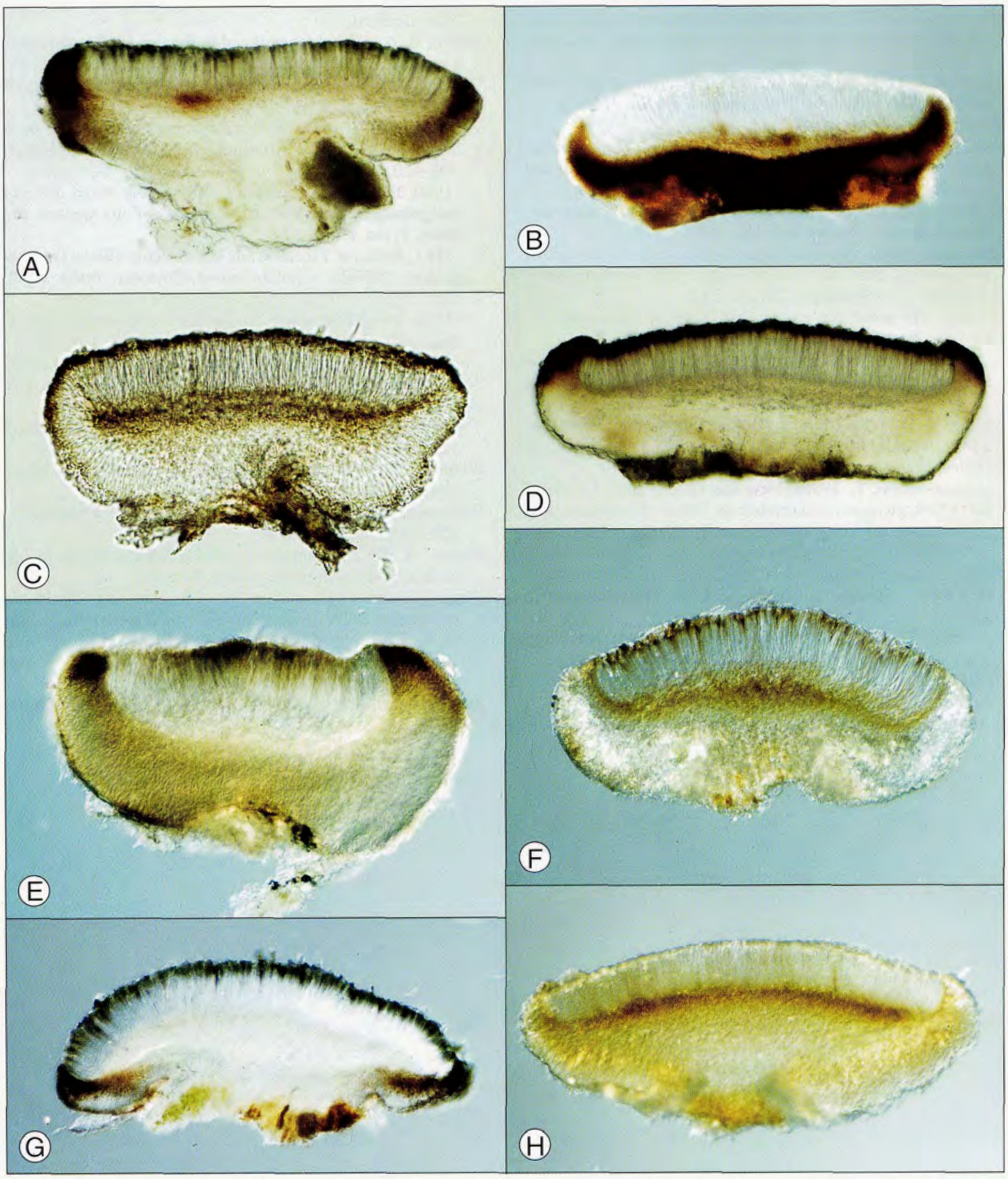

Fig. 40. Apothecial sections of North American species of *Bacidia*. Specimens collected in North America were used. – A. *B. absistens*, ×103 (Ekman L656, LD). – B. *B. aggregatula*, × 85 (Ekman L1188, LD). – C. *B. arceutina*, × 108 (Ekman L696, LD). – D. *B. auerswaldii*, × 78 (Ekman L788, LD). – E. *B. biatorina*, young apothecium, × 115 (Ekman L661, LD). – F. *B. campalea*, crystals brilliant white, × 108 (Ekman L1117, LD). – G. *B. circumspecta*, × 98 (Ekman L634, LD). – H. *B. diffracta*, × 70 (Ekman L1050, LD, holotype).

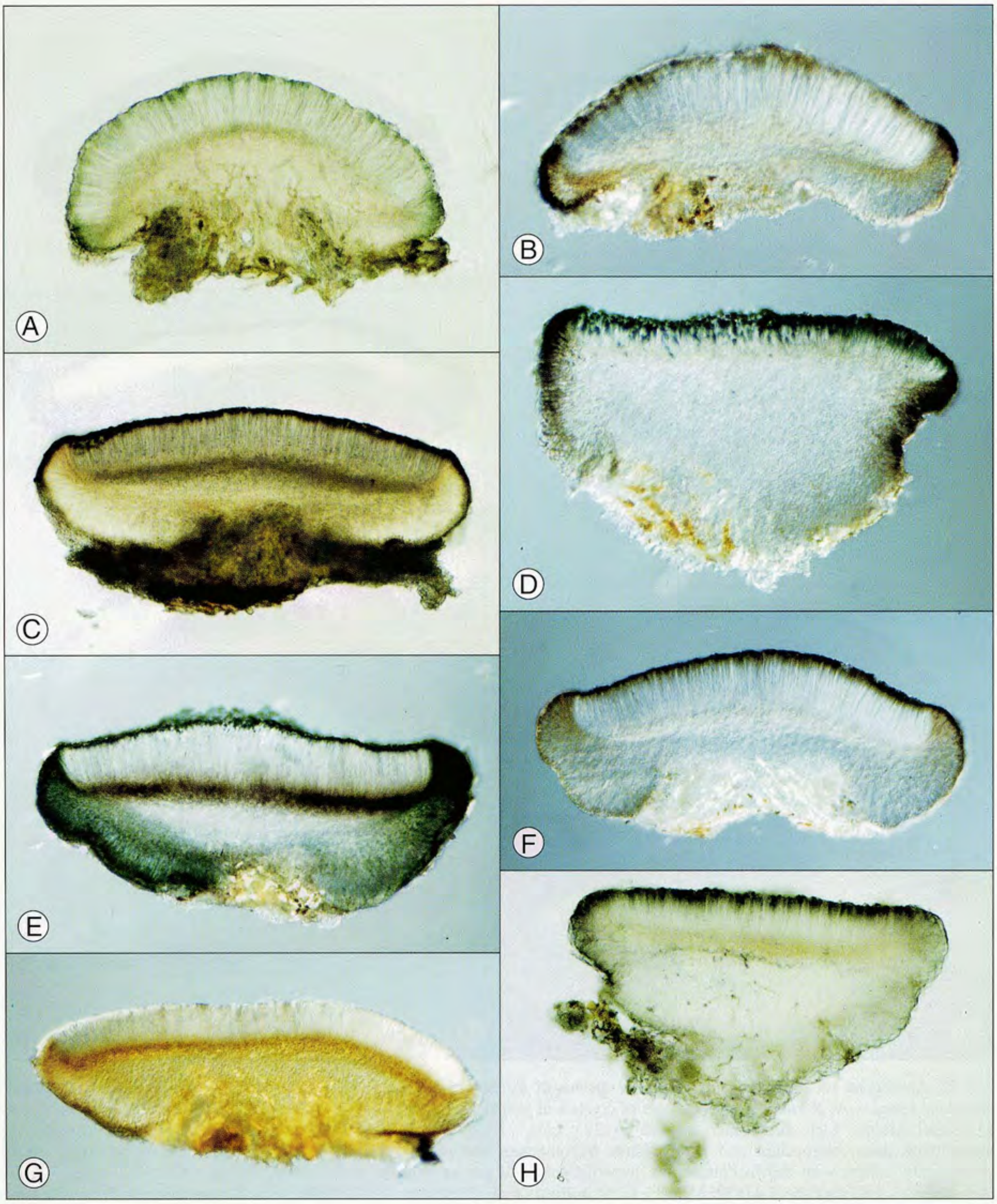

Fig. 41. Apothecial sections of North American species of *Bacidia*. Specimens collected in North America were used, unless otherwise stated. – A. *B. friesiana*, unusually weakly pigmented specimen, but similar to the only North American one, × 140 (Sweden, 16.IIX.1942, Almborn, LD). – B. *B. helicospora*, × 108 (Tucker 11315 & Jones, herb. Tucker). – C. *B. heterochroa*, × 75 (Tucker 24442a, herb. Tucker). – D. *B. igniarii*, × 103 (Sweden, 1866, Blomberg, LD). – E. *B. insularis*, × 85 (1994, Nimis & Tretiach, TSB-18385). – F. *Bacidia laurocersi* subsp. *laurocerasi*, × 78 (Gowan 3188, CANL). – G. *B. polychroa*, × 83 (Wetmore 34668, MIN). – H. *B. reagens*, · 130 (Wetmore 65677, MIN).

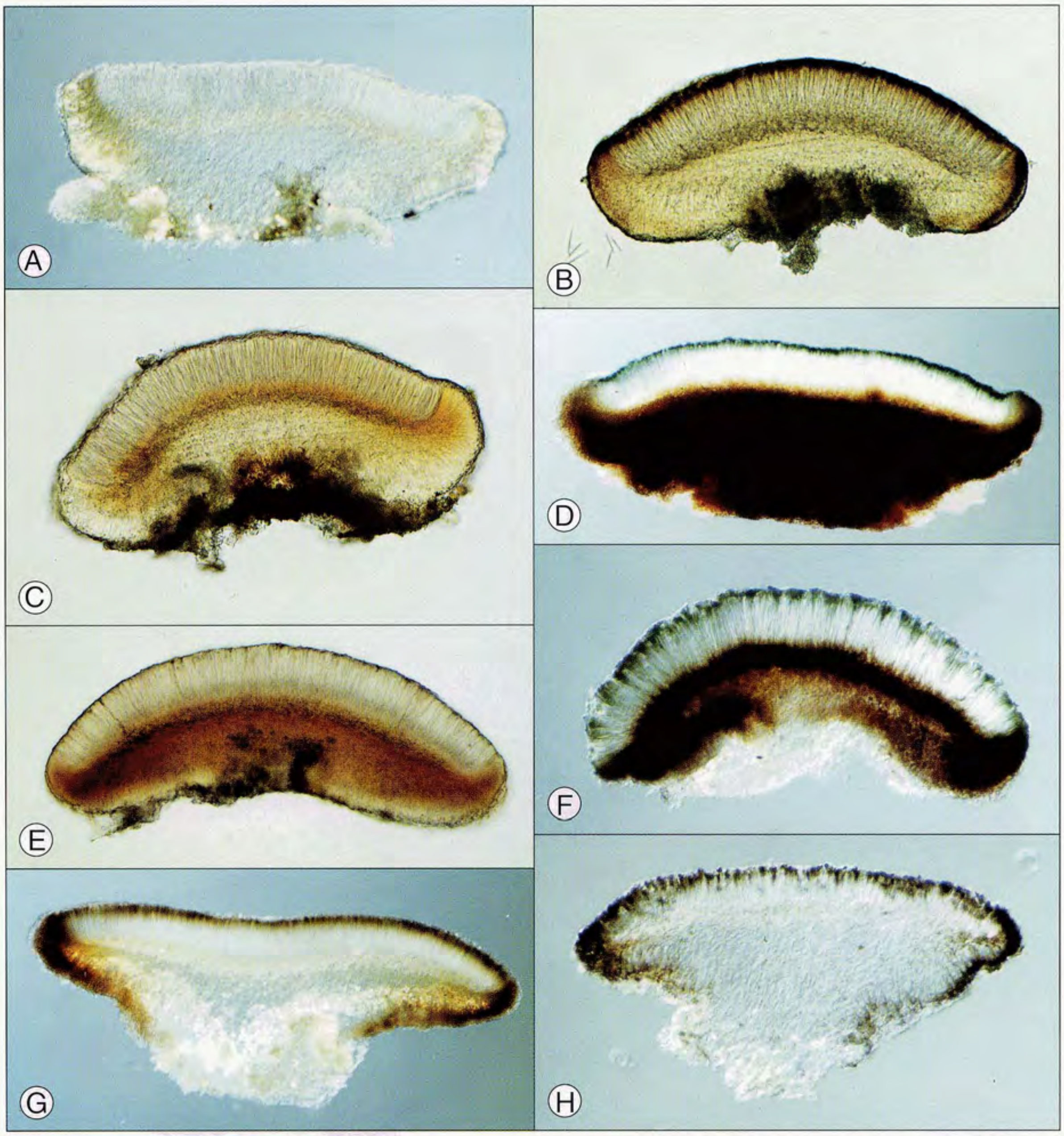

Fig. 42. Apothecial sections of North American species of *Bacidia*. Specimens collected in North America were used, unless otherwise stated. – A. *B. rubella*, note clusters of crystals in proper exciple, × 83 (Shchepanek 203a, CANL). – B. *B. russeola*, × 93 (Brazil, Malme: Lich. austroamer. Regnell no. 243, LD). – C. *B. salmonea*, × 88 (Ekman L710, LD). – D. *B. schweinitzii*, morph with green epithecium and almost black hypothecium and proper exciple, × 60 (Wetmore 35510, MIN). – E. *B. schweinitzii*, morph with brown epithecium, hypothecium, and proper exciple, × 75 (1963, Weber, COLO-L36608). – F. *B. subincompta*, × 88 (Wetmore 47929, MIN). – G. *B. suffusa*, × 60 (Wetmore 31371, MIN). – H. *B. vermifera*, × 103 (Anderson 2825, COLO).

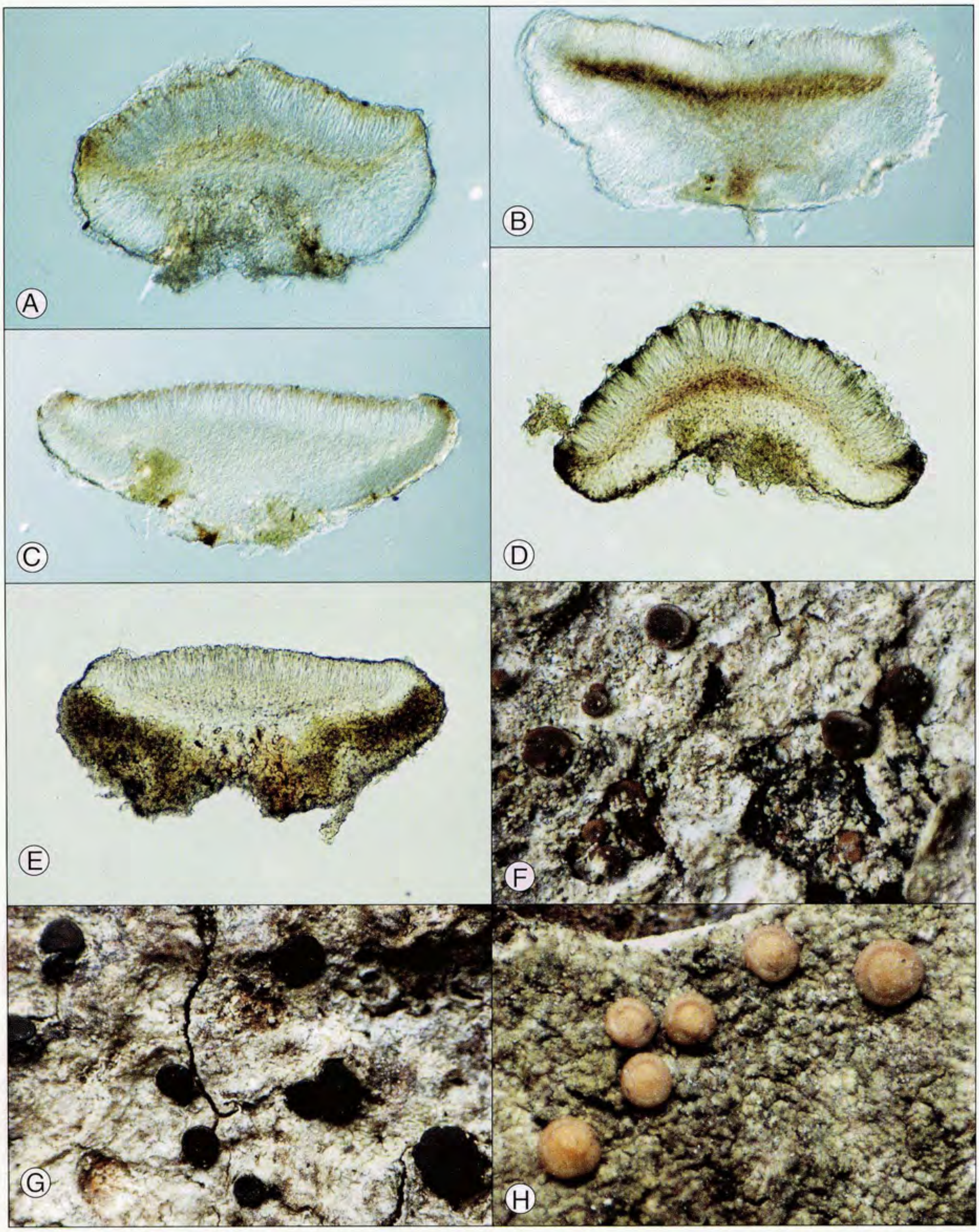

Fig. 43. Apothecial sections (A-E) and habitus (F-H) of North American species of *Bacidia* and *Bacidina*. Specimens collected in North America were used. – A. *Bn. aenea*, × 130 (Ekman L1207, LD, holotype). – B. *Bn. arnoldiana*, × 98 (Brodo 23794, CANL). – C. *Bn. californica*, unusually darkly pigmented specimen (this species is often pigment deficient), × 103 (Bratt 4277, herb. Bratt). – D. *Bn. egenula*, × 150 (Robitaille 149.4, CANL). – E. *Bn. ramea*, young apothecium with well-developed thalline margin, × 123 (Ekman L643, LD). – F. *B. diffracta*, × 12 (Ekman L1050, LD, holotype). – G. *B. helicospora*, × 12 (Tucker 11315 & Jones, herb. Tucker). – H. *B. salmonea*, × 19 (Ekman L753, holotype).

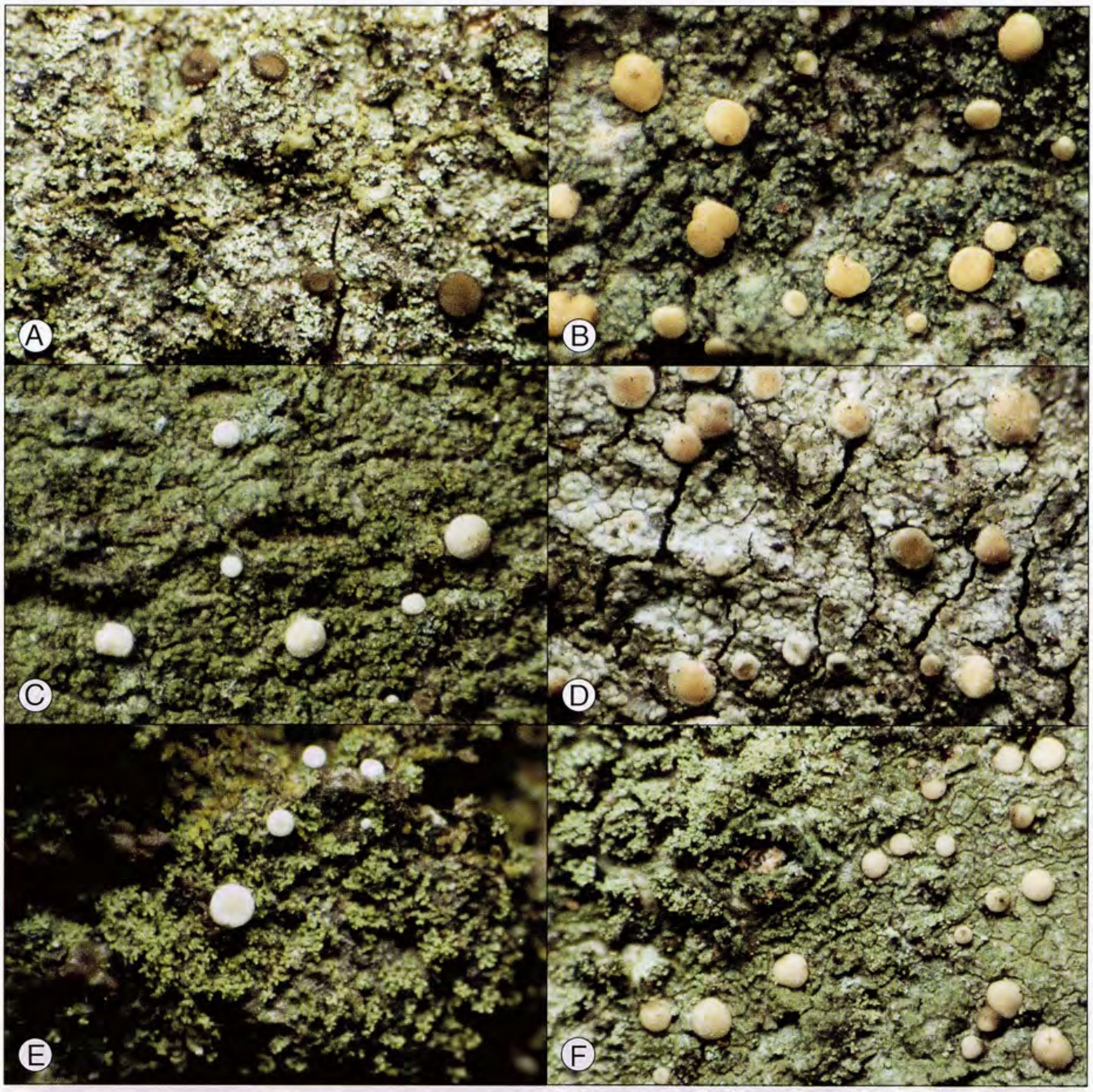

Fig. 44. Habitus of North American species of *Bacidina*. – A. *Bn. aenea*, × 15 (Ekman L1207, holotype). – B. *Bn. californica*, × 16 (Ekman L632, LD). – C. *Bn. crystallifera*, × 20 (Ekman L1120, LD, holotype). – D. *Bn. ramea*, × 14 (Ekman L767, LD, holotype). – E. *Bn. squamellosa*, × 20 (Ekman L1206, LD). – F. *Bn. varia*, × 13 (Ekman L1191, LD, holotype).

Index

Only names of lichens have been included. Unless otherwise stated, epithets of species and taxa of lower rank are treated in *Bacidia* or *Bacidina* (but combinations in other genera may also occur). Names that have been lectotypified, neotypified, or suggested for conservation with a conserved type in this work have been marked with an asterisc. Reference in bold is to taxonomic treatment.