# THE NORTH AND MIDDLE AMERICAN SPECIES OF THE LICHEN GENERA BOMBYLIOSPORA AND LOPADIUM WITH ANTHRAQUINONE PIGMENTS

Thesis for the Degree of M. S. MICHIGAN STATE UNIVERSITY Judith McKillen Burgess 1963





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# ABSTRACT

# THE NORTH AND MIDDLE AMERICAN SPECIES OF THE LICHEN GENERA BOMBYLIOSPORA AND LOPADIUM WITH ANTHRAQUINONE PIGMENTS

by Judith McKillen Burgess

The lichen genus <u>Bombyliospora</u> is composed of two species groups. The North and Middle American members of the group producing anthraquinone pigments were the subject of this study. These species have long been supposed to be closely related to the <u>Lopadia</u> with anthraquinone pigments.

I have found that the genus, as presently constituted, is a natural group. The unifying character of its unique spore is more important than the pigments produced. The spore should be called multilocular rather than multicellular; the locules are formed when the endospore thickens and constricts the sporoplast, as in <u>Caloplaca</u>. The endospore sculpturing may be annular, in which case the original primary locule is divided into several, lentiform secondary locules, or it may be spiroform, in which case the primary locule is not separated into parts, but is only forced to take on a spiralled shape. The fact that similarly variable endospore thickening was found in <u>Caloplaca</u> <u>atroalba</u>, during the course of this study, makes it even more certain that <u>Bombyliospora</u> belongs in the Caloplacaceae. The section Spiroblastia has been erected to include the anthraquinone-producing <u>Bombyliosporae</u>, among which spiroform locules are very common.

Lopadium vulpinum has been transferred to Bombyliospora because

it has the appropriate spore type. The other North and Middle American <u>Lopadia</u> with anthraquinone pigments cannot be transferred, since their spores are of another type.

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by

Judith McKillen Burgess

# A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

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#### INTRODUCTION

The lichen genus <u>Bombyliospora</u> is composed of two species groups which are superficially dissimilar. The group whose North and Middle American species were the subject of this study is traditionally characterized by its yellow or orange apothecia and thallus, and small spores with lenticular cells. <u>Bombyliospora aureola</u>, <u>B. domingensis</u>, and <u>B. flavidula</u> belong to this group. The other group, including the type species, <u>B. pachycarpa</u> Mass., is traditionally recognized by means of its lack of anthraquinone pigments and its large spores with cubical cells.

The genus <u>Lopadium</u> has apparently analogous groups also occurring in the perscribed area, and its species with anthraquinone pigments have often been supposed to be closely related to the <u>Bombyliosporae</u> with anthraquinones or congeneric with them. The <u>Lopadia</u> concerned are <u>L. cfr. dodgei, L. fuscoluteum, L. leucoxanthum</u>, and <u>L. vulpinum</u>.

The purpose of this investigation was to re-evaluate the position of the <u>Bombyliosporae</u> with anthraquinones within the genus, to characterize their unique spore, and to determine their natural relationship with the anthraquinone-producing <u>Lopadia</u>.

I have found that <u>L. vulpinum</u> must be transferred to <u>Bombylio</u>-<u>spora</u>, so to avoid confusion, I will refer to it throughout the paper as <u>Bombyliospora</u> vulpina.

Specimens studied were obtained from these herbaria: University of Michigan (MICH), Missouri Botanical Garden (MO), Michigan State University (MSC), and the Smithsonian Institution (US).

The photographs were taken by Mr. Philip Coleman.

I am grateful for the guidance and encouragement of my advisor, Dr. Henry A. Imshaug, and I wish to thank Dr. Flordeliz R. Uyenco for her fresh collections of <u>Bombyliospora</u> from Florida. Thanks are due to Mr. Dennis Jackson for the camera lucida tracings of fig. 10 and 11 of plate 9.

#### MORPHOLOGY

### Methods.

Freehand sections of the thallus and apothecia of every specimen were made with a razor blade and crushed by gentle pressure on the cover slip. Apothecia of representative specimens of each species were sectioned at 25 µ with a freezing microtome using Wetmore's (1960) method and were permanently mounted in Diaphane (Will Corp., Rochester, New York). Some were stained with 0.1 per cent acid fuchsin in 95 per cent ethanol, and others were mounted unstained in order to demonstrate the natural color of the exciple. Tissues were diagrammed with the aid of a Zeiss drawing apparatus, then stylized diagrams were made with these diagrams for guidance.

Spores were drawn with the aid of a Zeiss drawing apparatus, and were measured, in distilled water. In order to photograph the spores, freehand apothecial sections were mounted unstained in Diaphane and squashed immediately, or were mounted and squashed in Turtox Mounting Medium to which a few crystals of acid fuchsin had been added, or were mounted, unstained, in water. The second medium reacted with the lichen tissues and bubbles were formed after a few days.

Change in spore appearance with addition of 20 per cent aqueous KOH was noted. The location of cytoplasm in spores was verified by mounting in Amann's Medium to which acid fuchsin had been added.

### Thallus

The most conspicuous characteristic of the thallus is its color. Due to the presence of anthraquinones, herbarium specimens are usually orange or gold colored, and K+ rose (K+ means there is a color change with addition of KOH; K- indicates lack of color change). Some are at least partly glaucous, and a few are ochraceous. <u>Bombyliospora aureola</u> has a yellow thallus. <u>Bombyliospora flavidula</u> often has reddiah maculi. Tuckerman must have been referring to these when he wrote (in Nylander, 1863a) "thallo interdum hinc inde intus miniatotincto (erythrinoso)." Acharius (1814), Müller (1887a), Tuckerman (1888), Shirley (1889), Bailey (1891), and Fink (1935) have all pointed out the great variation of thallus color occurring even within one specimen.

Very little fresh material was seen, but without exception it was pale green. The fresh material seen consisted of <u>B</u>. <u>domingensis</u> and <u>B</u>. <u>vulpina</u>, species which have glaucous thalli much less often than does <u>B</u>. <u>flavidula</u>. This material, collected by Uyenco in Florida in February, 1963, had begun to turn yellowish by the end of April, 1963. It was air dried. It is suggested that the change in color is due partly to a slight loss of color by the algae, but mostly to the conversion of the anthraquinone in the thallus from a colorless sugar solution to a colored crystalline state before death of the thallus (see Thomson, 1955).

In some herbarium specimens, birefringent gold or red particles can be seen in the medulla and algal layer.

The thallus is thin (up to 150  $\mu$ ), heteromerous, and has no well defined cortex. The smooth upper surface is composed of indistinct periclinal hyphae. I have seen no rhizinae on the lower surface; in fact, the thallus is sometimes hypophloedal with some hyphae and a

few algal cells among the bark cells.

The thallus may be areolate, in which case the wide, thin, white hypothallus is prominent, or it may be rugose or smooth, becoming areolate. This variation seems to lack significance.

The algal cells are 7-16  $\mu$  in diameter and have lobed chloroplasts. They are thought to be <u>Trebouxia</u>.

Large red-sheathed colonies of <u>Gloeocapsa</u> were seen rather frequently inside the thallus and apothecia of several specimens of <u>B</u>. <u>domingensis</u> and <u>B</u>. <u>flavidula</u>. Apparently it is a common epiphyte which can be accidentally included in the lichen tissue.

<u>Bombyliospora aureola</u> has been described as having a rimose thallus, but the single example I saw was rimose merely because the bark on which it grew was cracked.

Leprose and coralloid varieties of <u>B</u>. <u>domingensis</u> and <u>B</u>. <u>vulpina</u> have been described, but not from this area, and I have not seen any.

### Apothecia

The apothecia always contain an abundance of anthraquinone pigments. Relative colors of the disks and margins are of some help in determining species but are not reliable. A few specimens of <u>B</u>. <u>domin-</u> <u>gensis</u> and <u>B</u>. <u>vulpina</u> have yellow pruina which can be scraped off to reveal dark disks. <u>Bombyliospora aureola</u> disks are heavily yellow pruinose, but disks of <u>B</u>. <u>flavidula</u> are never pruinose. Disks which are not pruinose may appear fuzzy due to the anthrequinone crust on the tips of the paraphyses; this condition should not be confused with pruinosity.

The entire, persistent margin may be yellow, orange, or ochraceous. It is thick, except in <u>B. flavidula</u>, whose mature apothecia

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have thinner margins than those of the other species (plate 2). If the disk is pruinose, the pruina extends onto the inner edge of the margin, which is usually elevated.

There is no significant variation in maximum size of apothecia. Young apothecia are flat and mature ones may remain plane or become slightly (rarely greatly) convex. The outline of mature apothecia is very often extremely gyrose (undulate, flexuous), and columns of sterile tissue the color of the margin rise through the hymenium to appear as raised pads of that color on the disk (plate 1). The apothecia often appear crowled, and many small ones sometimes arise on what seems to be the disk of a larger one. Fee (1324 and 1337) pictured some of the apothecial configurations.

Microscopically, there is a good deal of uniformity in apothecial structure. In general, the exciple is more or less intensely rust colored, although it may be colorless, and a distinct, colorless, narrow subhymenium is usually visible. Malme's collection of <u>B</u>. <u>domingensis</u> in <u>Lichenes Austroamericani</u>, no. <u>41</u> <u>A</u> and <u>B</u> is illustrative; <u>A</u> has a colorless exciple and <u>B</u> an intensely colored one. A stylized diagram of the tissues is presented in plate 5. The terms are used as defined by Imshaug (1957). The apothecial tissues of <u>Lopadium</u> cfr. <u>dodgei</u> and <u>L</u>. <u>leucoxanthum</u> are also of this type, but those of <u>L</u>. <u>fuscoluteum</u> are different (fig. 2).

# Spores: ontogeny

The name <u>Bombyliospora</u> means bulging spore. De Notaris (1849) chose the name, and he used it only in connection with <u>B. pachycarpa</u>. However, the literature and my own observations indicate that the spore wall of this species is smooth, not bulged (see fig. of <u>B. incana</u>,=

<u>B. pachycarpa</u>, in Zahlbruckner, 1905 and 1926). Perhaps the name applies to spores in an intermediate stage of development, where the endospore annuli are just beginning to constrict the sporoplast (plate 10, fig. 4). Körber (1855) and Frank (1886) described the spores of <u>B. pachycarpa</u> as caterpillar-shaped.

<u>Bombyliospora</u> has always been described as having multiseptate spores, in contrast to the muriform spores of <u>Lopadium</u>. These two terms are no longer adequate in view of present knowledge of spore development and morphology. The appearance of mature spores cannot be accurately described without conditeration of how they got that appearance. This is particularly true with muriform spores.

Hue (1912) pointed out that polarilocular and multilocular spores of <u>Licheni blasteniospori</u> Mass. have no true septa and are therefore unicellular: "Les spores des Lichens blasténiosporés sont simples, elles naissent simples et demeurent toujours telles, mais en même temps elles sont polocoelées, c'est-à-dire que, par suite de l'épaississement équatorial de leur tegument, elles présentent aux deux pôles des cavitiés hémisphérique...."

By the same line of reasoning, the spores of <u>Bombyliospora</u> also are unicellular. At first, the spore consists of a single, continuous, cylindrical sporoplast surrounded by a uniformly thin wall of epispore and endospore. Very early in development, the endospore begins to thicken, causing the sporoplast to lose its cylindrical shape and become a tube having protrusions in a characteristic pattern. The protrusions represent locules of the mature spore. I use locule here as Hue used it, to mean a cavity containing a sporoplast within the spore wall, as opposed to cell, which is a unit delimited by a wall laid

down on a middle lamella. The original cylindrical locule of <u>Bombylio</u>-<u>spora</u> will be called the primary locule. In the mature spore it may remain primary, but take on a spiroform shape, or it may be separated by endospore into several lentiform secondary locules. The number of secondary locules depends on the species.

In blasteniosporous lichens, according to Hue, additional concentric layers of wall material are deposited inside the original epispore and endospore, constricting the cylindrical (primary) locule into two polar areas or into several (secondary) docules. The polar areas are usually still connected by a tube at maturity, but sometimes not. Hue based his concept of the concentric layering on betites fentes apparaissant ca et là sur la surface des spores" and considered the idea confirmed when he observed a spore cut transversely. He saw three concentric circles: the outer, of many layers, he interpreted as the outermost spore wall; the middle he called the endospore, which was "de formation plus recente, [and therefore] moins apparentes;" the innermost circle he called the tube. As no species is known to have such a thick epispore, I believe Hue did not see the epispore at all. He probably saw a section showing the tube, a locule above or below it (his endospore), and the endospore. The "petites fentes" were probably folds in the walls of nonturgid spores.

There is no indication of concentric layering of the spore walls in <u>Bombyliospora</u>, but in some way the endospore thickens and constricts the sporoplast, forcing it to assume the shape of the remaining space. The sequence of diagrams in plate8 represents the changes in appearance of one spore type of <u>B. domingensis</u> as it develops; the process is continuous, therefore the diagrams do not represent distinct stages. Photographs of various stages of both spore types of <u>B. domingensis</u>

appear in plate 6, and of <u>B</u>. valpina, in plate 7.

Wall thickenings growing from opposite sides of the spore eventually meet and obliterate the central tube, forming secondary locules. Thus, although the final appearance is of a septate spore, it is no more septate than is a <u>Caloplaca</u> spore; it is unicellular, and multilocular.

Spores of all North and Middle American species of <u>Bombyliospora</u> lack the central tube at maturity. The secondary locules nearly touch each other, and endospore wall material completely fills the very small area between them.

The epispore is thin, and endospore alone is responsible for the formation of secondary locules or distortion of the primary locule into a spiral.

Primary and secondary locules are each surrounded by a membrane. Actually, they seem to be enclosed by a wall as thick as the epispore. There is some reason for thinking this may truly be a wall and not merely a membrane surrounding a plasmolyzed sporoplast; I expect study of the species without anthraquinones to clarify this point.

The spore wall is indented opposite the secondary locules or opposite the spiroform locule, and bulged between, but this is not always apparent. The pattern is so symmetrical that secondary locules look as though they are formed by overlapping circles (plate 6, fig. 3). This is accentuated by KOH.

When the spore wall is ruptured in KOH, locules often may be squeezed out individually (plate 7, fig. 5, and plate 10, fig. 3), each wrapped in its own membrane.

Spore shape, number, and size varies with the species.

# Spore wall sculpture

The manner of thickening of the endospore is striking and most significant. The originally thin endospore has the potential to develop in either of two ways. Annular thickening results in the formation of more or less lens-shaped secondary locules. Thickening in the form of a spiral causes the primary locule to take on a spiralled shape but does not separate it into secondary locules. Both types occur in nearly equal numbers in <u>B. domingensis</u>. The spiroform type is much less common in <u>B. vulpina</u>, while <u>B. flavidula</u> never has the entire endospore spiralled. <u>Bombyliospora aureola</u> never has any portion of the endospore spiralled, but there is indication of that tendency.

It is significant that in at least one species of <u>Caloplaca</u>, too, the andospore may be thickened in either way. I have seen one specimen of <u>Caloplaca atroalba</u> (<u>Wetmore 7432</u>, from South Dakota, MSC), in which some spores have the usual single annular thickening, but many have a spiralled thickening instead. The spores have been described (Fink, 1935) as obscurely one-septate.

Shape and orientation of lentiform locules in <u>Bombyliospora</u> varies between species and the shape also somewhat within species. In <u>B</u>. <u>Aureola</u>, with an ovate spore, \* locule shape depends on location in the spore. All locules are nearly round except the one at the tip of the narrow end of the spore; that one is usually elongated (plate 10, fig. 1). The locules in the smaller half of the spore are smaller than those in the other half.

\*Terms referring to spore shape (except short fusiform) are taken from Chart I: Descriptive Terminology, by the Systematics Assoc., 1962; the terms describe optical sections.

Secondary locules of <u>B</u>. <u>flavidula</u> and <u>B</u>. <u>domingensis</u> are transversely lentiform; that is, each locule looks like a thick, doubleconvex lens whose principal plane is perpendicular to the long axis of the spore. Those of <u>B</u>. <u>domingensis</u> almost always form an acute angle at the edge of the spore, but those of <u>B</u>. <u>flavidula</u> never do (plate 10, fig. 2).

<u>B. vulpine</u> has secondary locules oriented longitudinally; they look like portions of a thick double-convex lens whose principal plane is parallel to the long axis of the spore. Secondary locules of <u>B</u>. <u>vulpine</u> are always subdivided transversely (to the locule) into tertiary locules by extensions of the locule membrane, and are sometimes further divided longitudinally by such extensions. In <u>B. domingensis</u>, one transverse septum rarely divides one or more secondary locules; this condition, when frequent, is the basis for Malme's (1923) South American variety <u>transgressa</u> and Asahina's (1934) variety <u>boninensis</u>, from the Bonin Islands.

Tertiary locules can be easily seen and counted when locules are squeezed out of the spore wall (plate 10, fig. 3). The number is not constant, but in <u>B</u>. <u>domingensis</u> only one ring of tertiary locules forms, while in <u>B</u>. <u>vulpina</u>, two concentric rings are present at maturity.

The spores of <u>Lopadium</u> are superficially similar to those of <u>B. vulpina</u>, but are actually very different. In <u>L. leucoxanthum</u>, material in the ascus shows transverse and longitudinal lines of separation even before a spore wall is laid down. These lines, which become the septations of the spore, are entirely irregular at any age. All walls are uniformly thin; there is no thickening of the endospore and the spore is completely filled with minute cells (plate 7, fig. 7):. In old, necrous spores whose sporoplast has disintegrated, a three dimensional reticulum of irregular septa can be seen throughout the spore.

The spores often break down within asci into oval conidia about  $7 \ge 2/u$ . Apparently healthy spores at all stages of development are often totally brown, and K+ arose. Spores of <u>Bombyliospora</u> never break down into comidia, and although the locules of old spores are rarely brown or red, and K-, the spore wall is never colored.

Spores of <u>L</u>. <u>fuscoluteum</u> and <u>L</u>. cfr. <u>dodgei</u> are similar to each other in that regular transverse septa form before further division proceeds, but at maturity, <u>L</u>. <u>fuscoluteum</u> spores look like those of <u>L</u>. <u>lencoxanthum</u>: as the spore grows in size, the cells become progressively further divided, and the divisions become irregular. The spores are often brown.

In <u>L</u>. cfr. <u>dodgei</u>, all septa originate regular and remain regular, forming right angles (plate 7, fig 6). The mature cells are larger than those of the other two <u>Lopadia</u>, and the spores are never brown, although they are often K+ rose. Further, when pressure is applied to spores of the former two species, they split irregularly through the center, longitudinally, and do not come apart. In <u>L</u>. cfr. <u>dodgei</u>, however, the spores break up in a manner strongly remeniscent of <u>B</u>. <u>vulpina</u>. They sometimes come apart along the seven or nine original transverse septa (the area between is divided into three rows of cells at maturity), or they may be crumbed more completely to yield a flat sheet of locules which remain connected or become separated. In addition, occasionally a wide, colorless, K- ring surrounds the spore; I have not determined the nature of this ring.

The way these spores come apart when crushed implies to me that L. <u>leucoxanthum</u> and <u>L. fuscoluteum</u> spore cells lack a limiting membrane, while <u>L</u>. cfr. <u>dodgei</u>, like <u>Bombyliospora</u>, possesses a limiting membrane around each unit of the spore.

Since Lopadium spore patterns are not due to endospore thickening, the terms primary and secondary locule cannot be applied. No spiralled pattern has been seen in Lopadium.

Spiroform endospore thickening is less common than annular thickening in <u>Bombyliospora</u>, although it is very frequent and easily recognized in <u>B. dominganists</u>. From drawings and notes made by Tuckerman and others on old specimen cards, it is certain that they interpreted spores with spiroform endospores as submuriform. Malme (1923) and Asahina (1934), however, used submuriform to indicate septate secondary locules.

A spiroform locule must be called a primary locule because it is never separated into units by endospore thickening. Spiral thickening of the endospore merely forces the sporoplast to assume a spiral shape. As the single, continuous ridge of endospore develops, it pushes further into the interior of the spore. Until it reaches the midpoint, the sporoplast looks like an auger; it has a cylindrical core with a horizontally flattened ridge running its length spirally. When the endospore reaches and passes the midpoint, the central core is obliterated, leaving only the spiralled part, which is no longer flat but is more or less cylindrical. Invaginations of the locule membrane often form, making the locule transversely septate, but it is still a primary locule. By transverse, I mean the septa are perpendicular to the sides of the locule, no matter what their angle in relation to the spore wall.

The spiroform locule of <u>B</u>. <u>vulpina</u> is always very much septate, often appearing beady. The spiral ridge of endospore is narrower than in <u>B</u>. <u>domingensis</u>, therefore more of the volume of the mature spore is occupied by sporoplast. These facts make the spiroform locule of <u>B</u>. <u>vulpina</u> more difficult to recognize. I have found that slightly oblique

"secondary locules" are a reliable indication of spirals (plate 7, fig. 3). With luck, one can confirm this by squashing the spore to release the locule. Spiroform locules are usually broken at a septum in the process, but retain their form except for unwinding slightly. Lentiform locules are unconnected disks.

Bombyliospore domingensis and <u>B</u>. <u>vulpina</u> both have usually eightlocular spores (sometimes six- or ten-locular), and accordingly, their spiroform locules have eight turns (gyres).

It is not at all unusual to see more than one spiroform ridge of endosporeon one spore wall, especially in <u>B</u>. <u>domingensis</u> (plate 6, fig. 7, 8, 9). In the majority of cases, the two ridges arise on opposite sides of the spore and turn in the same direction: clockwise. I saw one spore with spirals going in opposite directions; the endospore was not thicker at the intersection point. Many spores have one complete ridge the length of the spore plus portions of one or more others. In other words, ridges of spiralled endospore do not always extend from one end of the spore to the other, but may arise and end at any point, joining another ridge if they end in the middleof the spore.

Practically infinite variations and combinations of the two basic spore types--annular and spiroform endospore-- have been seen, most of them in <u>B</u>. <u>domingensis</u>, probably because they are easier to recognize in that species. All of them occur with or without septa dividing the locules. Usually either completely annular or completely spiroform endospore predominates in a given specimen.

Bombyliospora flavidula does not have completely spiroform endospore, but often what would be the two annuli at either end of the spore join to form a short spiral. In <u>B</u>. <u>aureola</u>, the endmost annulus often does not reach the spore midpoint, therefore the

two end locules appear joined (plate 10, fig. 1).

I had thought the number of spiroform locules per ascus might represent the number of nuclei present, but this now seems unlikely; the locale number is a result of the number of ridges of endospore, and that number is inconstant.

The spiroform locule is truly spiralled, not helical. Using Thompson's (1961) definitions, a spiral is "a curve which, starting from a point of origin, continually diminishes in curvature as it recedes from that point; or in other words, whose <u>radius of curvature</u> continually increases." A helix has the same radius of curvature throughout. Since the spore diameter decreases toward an end, the wall thickening must be spiral. Further, the spiroform locule is an equable spiral, or spiral of Archimedes; its shape is that of a coiled cylinder, not a coiled cone.

It should be pointed out that similarly variable wall thickenings are not unknown in plant cells. The secondary wall of tracheary elements of many woody plants is deposited as rings or helices, with the type depending on age of the plant. (Age is not influential in <u>Bombyliospora</u>.) However, Esau (1961) states "...the different types of wall structure intergrade. The annular thickenings may be interconnected here and there; annular and helical...thickenings may be combined in the same cell..." This seems remarkably similar to the situation in <u>Bombyliospora</u>.

Preliminary study of 102 specimens of eight species of <u>Bombylio</u>-<u>Spore</u> which lack anthraquinone pigments has convinced me that their spores are in every way similar to those of the species with anthraquinones. The sporoplast remains cylindrical until the spore is rather large, then three to eleven (rarely more) rings of endospore begin to

pinch the sporoplast into secondary locules. One never gets the impression that they are connected by a central tube, though. As I have attempted to show in plate 10, fig. 4, the reason is purely due to the angles of curvature. Each locule is surrounded by a limiting structure which may become very wide (plate 11, fig. 4), and seems to be a wall rather than a membrane. Secondary locules are longitudinally lentiform. Most investigators have called them cubical, but Zahlbruckner (1905 and 1926) and Fink (1935) called them lenticular.

In a single specimen (<u>Imshaug 15028</u>, from Jamaica, MSC), several spores had completely or partially sporoform endospore, lending strong evidence that the genus is a natural group. Most of the rest of its locudes were distorted like those pictured by Zahlbruckner (1905 and 1926) for <u>B. incana</u>. The spore variations in this specimen are shown in plate 11. Many other specimens have locules distorted like these.

An evolutionary sequence of spore types incorporating some species lacking anthraquinones is presented in plate 12. Not all types of spores known in <u>Bombyliospora</u> are represented because I have not seen them; the types involved are those of <u>B. buelliaceae</u>, <u>B. diplotypa</u>, <u>B. dolichospora</u>, <u>B. expansa</u>, and <u>B. thomensis</u>.

Terms used to describe these spores were chosen so they could be used in other genera also. Thus, one may say of most <u>Caloplacae</u>: primary locule reduced to two polar areas connected by a central tube, i. e., polarilocular; of most <u>Physciae</u>: primary locule mischoblasticmorphic, with or without a median transverse septum, i. e., mischolocular; of some <u>Rinodinae</u>: primary locule reduced to two spheres connected by a narrow tube, with or without a median transverse septum, and if connecting tube is lost, one spherical secondary locule persists in each cell, i. e., pachylocular.

# Pycmidia

The only species seen with pycnidia was <u>B</u>. <u>domingensis</u>, and even then only a very few specimens had pycnidia. The pycnidia are minute, flask shaped, and have carbonaceous walls. The contents are heavily conglutinated, making it very difficult to determine the attachment of the conidia. The conidia are oval,  $7 \times 2/u$ .

Almost none of the literature reports mention pychidia or conidia. For his <u>B</u>. <u>domingensis</u> var. <u>flavocrocea</u>, from Africa, Nylander (1869) describes the pychidia as convex lutescent, with conidia  $5 \times$ 2.5 AL, "adfixa minutissima oblongo-cylindrica" on jointed sterigmata 2.5 AL wide. Zahlbruckner (1905) put <u>Bombyliospora</u> in the Lecideaceae, which he stated are seldom endobasidial, then in 1926, he transferred it to the Caloplacaceae, possibly on account of the conidial attachment. He names only <u>B</u>. <u>domingensis</u> among K+ rose species, and does not describe the pychidia or conidia.

#### CHEMISTRY

# Methods

A 20 per cent aqueous solution of KOH was applied to the upper surface and exposed medulla of the thallus by means of drawn capillary tubes, and the color change was noted. This KOH solution was also added to apothecial sections in distilled water on slides and the color change of each tissue noted. Specific color reactions may be helpful in identifying the anthraquinone, according to Asahina (1954), but were not here.

In an attempt to identify the anthraquinone(s), extractions were made in hot acetone in small test tubes, then a few drops of 0.5 per cent methyl alcoholic magnesium acetate (MgAc) were added. For each specimen, one extraction was made from a few pieces of thallus and another from a few apothecia. According to Asahina, colors gotten in this way may be diagnostic. I found that too much depended on concentration of the substance, and the colors of several standards (species named by Asahina as sources from which a specific anthraquinone has been purified) seemed identical.

I then tried paper chromatography of acetone extracts, using standard techniques. The method of Shibata, Takiko and Tanaka (1950), using petroleum ether saturated with 97 per cent methyl alcohol as solvent and 0.5 per cent methyl alcoholic MgAc to bring out the color of the spots, was not effective. The substances did not dissolve well and there was much streaking.

Three solvents mentioned by Hale (1961) were tried, ascending in tubes, also with little success. They were n-butanol saturated with ammonia, n-butanol-acetone-water, and n-butanol-adcohol-water; for ratios and phases, see Hale, 1961.

The best solvent tried was ethyl acetate-pyridine-water (2:1:1). It dissolved the substances completely and left distinct spots with little streaking. It was tried with ascending technique, in tubes, and descending, on sheets in a tank. The two methods gave comparable results, so I used the descending, since in that way I could run more samples at a time with the equipment available.

Whatman No. 1 chromatography paper was used, and the solvent was allowed to run about 14 inches. One set of specimens was run 19 inches in the hope of separating a double spot, but without success. After drying, the sheets were examined with long wave (3660 A) UV light and the position and color of fluorescent spots were marked. Some sheets were then sprayed with methyl alcoholic MgAc, dryed at 90°C, checked for color reaction, and re-examined for color of fluorescence. Because the colors could not be differentiated, other chromatograms were not sprayed. Drawn capillary tubes containing 20 per cent aqueous KOH, 100 per cent ethyl alcoholic phenylenediamine (PD), or MgAc were used to test each spot. The standards for each anthraquinone named by Asahina were treated in the same way.

In an effort to determine the similarity of anthraquinones in <u>Bombyliospora</u>, <u>Lopadium</u>, and other Caloplacaceae, the pigments of several species not otherwise studied were chromatogrammed. Results are compiled in table 1.

Because the epithecia and margins are not the same color, and sometimes turn slightly different colors in KOH, epithecia and margins

# Chart 1. Anthraquinones

(1) Includes these species:

Bombyliospora domingensis

- B. flavidula
- B. aureola
- B. vulpina
- Lopadium fuscoluteum
- L. leucoxanthum
- L. leucoxanthoides
- L. cfr. dodgei
- Caloplaca ulmorum
- C. stillicicdiorum
- C. feracissima
- C. flavovirescens
- C. aurantiaca
- C. carphinea
- C. pyracea
- C. cerina
- C. elegans
- C. lobulata

(2) Includes these species:

Caloplaca cinnamomea C. tetraspora C. arizonica Elastenia leucoraea Chart 1. Anthraquinones

standard	substance	RP
Xanthoria parietina	parietin	•98
Getraria endocrocea	endocrocin	•70
Solorina crocea	solorinic acid	•98
Xanthoria fallax	fallacin	•97
Teloschistes flavicans	teloschistin	•97
Parmelia formosana	lichenanthone	.80
	unknown I	•95
	unknown II	•95
	unknown III	•95
	unknown IV	•76
	unknown V	•90
	unknown VI	.60

color before treatment	color after MgAc	<u>color after KOH</u>	species
<b>yellow</b> uv-orange	pink u <b>v-</b> pink <b>-ora</b> nge	pink	
bright yellow- orange uv-deep orange	rose uv-deep rose	deep violet	
yellow uv-orange	pink u <b>v-pin</b> k-orange	pink	
yellow uv-erange	pink uv-pink-orange	pink	
yellow uv-orange	pink u <b>v-</b> pink <b>-ora</b> nge	pink	
none uv-	blue uv-	yellow uv-white	
bright yellow uv-bright yellow-orange	pale orange-pink uv-pale pink	pink uv-pink	Protoblastenia rupestrio
yellow uv-orange	pale rose uv <b>-r</b> ose	pale violet u <b>v-v</b> iolet	(1)
<b>yellow-orange</b> u <b>v-yellow-orang</b> e	deep magenta uv-deep rose	deep violet uv-deep purple	(2)
yellow-orange uv-pale`orange	pale rose uv-rose	pale violet uv-violet	(2)
pale yellow uv-pale orange	pale rose uv-rose	pale <b>v</b> iolet u <b>v-viole</b> t	6. cinnamomea
pale yellow uv-pale orange	pale rose uv-pale rose		

were chromatogrammed separately for one specimen of each species of <u>Bombyliospora</u> and <u>Lopadium</u> studied. Apothecia were dissected under magnification to insure that only the appropriate tissue was taken, then the pieces were placed directly on the chromatogram sheet and acetone was applied. Good spots were obtained, showing that enough material was present, but there was no difference in spots from margin and epithecium.

All specimens were inspected macroscopically under UV for fluorescence of thallus surface, medulla, and apothecia.

# Results

When KOH is applied to the thallus surface, orange, gold, or tan thalli turn some shade of red, indicating presence of anthraquinone. The thallus of <u>B</u>. <u>aureola</u> turns purplish. Glaucous and fresh (green) thalli are K-. The medulla of <u>B</u>. <u>vulpina</u> is K+ yellow.

In examining thalli with endothallic <u>Gloeocapsa</u> microscopically, one must take care not to confuse the color of the algal sheath with K reactions. The red sheath does not change color in KOH.

When KOH is applied to apothecial sections, the epithecium turns rose or magenta, or sometimes pale violet. The cortex of the amphithecium turns intensely rose, and immeasurably small purple particles diffuse out. After standing a few minutes, these particles group in small aggregates, but never form large crystals or gain any definite shape, even after standing for several days. Rudolph (1955) has stated that parietin particles form large crystals after standing one half hour, so perhaps the <u>Bombyliospore</u> anthraquinone is not parietin.

The rust colored exciple is K- except in <u>B</u>. <u>aureola</u>, where it is not actually rust colored, but more nearly the color of the amphithecial cortex. This exciple becomes slightly reddish in KOH. In

addition, the thallus of this species is more purple than the margin in KOH.

The pyridine chromatograms eliminated endocrocin as a possible name for the <u>Bombyliospora</u> and <u>Lopadium</u> anthraquinone. Still, parietin, fallacin, and teloschistin could not be differentiated, and the <u>Bombyliospora</u> and <u>Lopadium</u> spots have the same  $R_c$  and colors with every reagent as these three. However, it is not necessary to know the name of the substance; it is enough to know that all K+ rose <u>Bombyliosporae</u> and <u>Lopadia</u> produce the same pigment, and that the same pigment is the most common one among the Caloplacaceae.

It is interesting that <u>Protoblastenia</u> may be separated from <u>Blastenia</u> by its anthraquinone in addition to spore type.

Rudolph (1955) stated that parietin is the only anthraquinone in the Caloplacaceae, but he relied on literature reports which were rather old, published before the days of chromatography. I have found six anthraquionoes among Caloplacaceae with orange or cinnamon apothecia. The cinnamon group is most interesting, having at least two (sometimes four) unique pigments. It seems likely that further study of these will prove them to be a taxon worthy of autonomy.

Spots at R<sub>e</sub>.95 often appear to be double because of the presence of atranorine at the same R<sub>e</sub>; only one anthraquinone is there. Atranorine was proven to be present in the following species by recrystallizing it in G.A.oT. (formula in Asahina, 1954): <u>Bombyliospora</u> <u>domingensis</u>, <u>B. vulpina</u>, <u>Lopadium</u> cfr. <u>dodgei</u>, <u>L. fuscoluteum</u>, <u>Telo-</u> <u>schistes flavicans</u>, <u>Xanthoria parietina</u>, and <u>X. fallax</u>.

The medulla of <u>B</u>. <u>vulpina</u> contains a substance, not an anthraquinone, that is diagnostic for the species. The medulla fluoresces white, and the substance forms a flocculent white precipitate with

MgAc in a test tube. Its R<sub>r</sub> in pyridine in .95. Before treatment, the spot is pale yellow; it is more yellow with MgAc, and fluoresces yellow-white. KOH does not change the color in ordinary light, but changes the fluorescence to purple. PD has no effect. The substance does not crystallize in G.E. or G.A.oT. (both formulas in Asahina, 1954).

Apothecia of L. <u>fuscoluteum</u> yield a gray, non-fluorescing spot at R<sub>f</sub>.07. It is MgAc-, K-, and PD-.

Apothecia of <u>L</u>. <u>leucoxanthoides</u>, whose tissues are K+ blue, yield a streak beginning about  $R_{f}$ .93. It is gray before MgAc and faintly blue after. It absorbs UV, is PD-, and is made colorless by KOH. It is not known whether this substance is responsible for the blue color.

## TAXONOMY

# Families

Massalongo (1852) described <u>Bombyliospora</u> in the Lecideaceae. Zahlbruckner considered it to belong to that family in 1905, but in 1926 he transferred it to the Caloplacaceae on account of its endobasidial conidia and thick spore walls. All members of the Lecideaceae except <u>Megalospora</u>, according to Zahlbruckner, have exobasidial conidia. In addition, members of the Lecideaceae seldom have spores with thickened walls.

Lopadium has always been placed in the Lecideaceae even though its spore walls are often much thickened. The conidia, according to Zahlbruckner (1905 and 1926), are exobasidial. I have not seen direct descriptions of pycnidia or conidia of the species included in this study, but Santesson (1952) stated that the foliicolous species, at least, have exobasidial conidia. Asahina (1934) evidently suspects that the corticolous species may be endobasidial. he proposes that, if they are, Lopadium and Megalospora should be transferred to the Caloplacaceae. Then, according to him, the three genera would represent one evolutionary series within the family. Spore septation would therefore be given less importance than it is now.

Des Abbayes (1951) stated that the position of <u>Bombyliospora</u> in relation to the Caloplacaceae was uncertain because of its "pluricellulaire" spores.

Santesson (1952) pointed out that <u>Brigantiaea</u> Trevis. (1853, not seen) was used before <u>Lopadium</u> Körber (1855). Trevisan intended

<u>Brigantiaea</u> to include all <u>Lopadia</u> with anthraquinone pigments. <u>Bom-</u> <u>byliospora vulpina</u> was not known until 1863, but Santesson includes it in what he calls the Brigantiaea group. He comments also that <u>B</u>. <u>dom-</u> <u>ingensis</u> is probably a member of the group.

Rudolph (1955) stated that <u>Bombyliospora</u> cannot be included in the Caloplacaceae because of its spore type. I have shown this to be untrue.

In my opinion, <u>Bombyliospora</u> is closely related to <u>Caloplaca</u>, and belongs in the Caloplacaceae, as shown by the spore development and by the anthraquinones produced. I believe <u>Lopadium</u> should be left in the Lecideaceae, since it has exobasidial conidia, and its spores do not have thickened endospores.

# Genera

<u>Bombyliospora</u>. Massalongo (1852) credits De Notaris with first recognition of the genus <u>Bombyliospora</u>, but De Notaris never published its description. De Notaris wrote only that <u>B. pachycarpa</u>, "DNtrs. herb.," differed from <u>Biatora icmadophila</u> in the structure of the apothecia and the size and septation of its spores. Massalongo designated <u>B. pachycarpa</u> the type species, and described <u>B. versicolor</u> at the same time. He thought then that <u>Lecidea</u> (=<u>Bombyliospora</u>) <u>versicolar</u> Fee and <u>Lecidea</u> (=<u>Bombyliospora</u>) <u>tuberculosa</u> Fee were synonymous, but in 1860 he recognized <u>B. tuberculosa</u> Fee as a separate species.

<u>Bombyliospora pachycarpa</u> is pictured by Massalongo as having two spore types in the same apothecium: some large spores, with thin walled cubical locules, and some smaller spores, with thick walled transversely lentiform locules.

Obviously Massalongo was mistaken in picturing both types from
one apothecium. I think the source of the error is discernable. He states that he is not sure his concept of the genus agrees with that of De Notaris, and in the legend for the drawing of <u>B. pachycarpa</u>, he states "Queste figure vennero cavate da un examplare favoritomi dal prof. De-Notaris...." Thus it is probably a composite drawing; he observed one spore type and erroneously thought De Notaris' illustration of the other was from the same species.

Massalongo (1852) claims that the spores of <u>B. versicolor</u> are 91.5-122.0 x 24.4-30.5 ~ and one per ascus, but he pictures them with transversely lentiform locules. Massalongo was the only person ever to report seeing such large spores with that type of locule. He wrote that he took his drawing of B. versicolor from Fee's favorite example of Lecanora versicolor, but Fee (1837) made it clear that his L. versicolor had two-celled spores, and this is now the basionym for Megalospora versicolor. Massalongo thought his <u>B. versicolor</u> was the same as Fee's L. tuberculosa, but Fee drew cubical (not longitudinally lentiform) loculed spores for that species. Zahlbruckner (1931) recognized that Massalongo's B. versicolor was not the same as Fée's Lecidea versicolor and Zahlbruckner therefore lists a Bombyliospora versicolor Mass. in his Catalogus. However, Massalongo actually made a new combination of Fee's basionym, so Massalongo's Bombyliospora is without a name. There is reason to believe, however, that no such lichen exists and that Massalongo's description and illustration are the result of compound errors.

A nomenclatural note concerning <u>B</u>. <u>pachycarpa</u> is in order here. Zahlbruckner (1931) thought <u>B</u>. <u>pachycarpa</u> should be called <u>B</u>. <u>incana</u> because its basionym was <u>Lichen incanus</u> Smith. Actually Smith (in Smith and Sowerby, 1807) stated that his species was based on Lichen

incanus Ach., which is the basionym of <u>Lepraria incana</u>. Therefore incana cannot be used for any <u>Bombyliospora</u>. The correct basionym is <u>Patellaria</u> pachycarpa Del. in Duby (1830).

The only K+ rose taxa now in the genus that were not placed there by Zahlbruckner in his Catalogus (1931) are <u>B. domingensis</u>, which was added as <u>B. gyrosa</u> (Spreng.) Mass., and its variety <u>flavocrocea</u>. which was added as <u>B. flavocrocea</u> (nyl.) Mass., both in 1860. Several other species now in the genus were known before that date, including the K+ rose <u>domingensis</u>, described in 1811, <u>ventosa</u> var. <u>domingensis</u>, 1833, and <u>acervulata</u>, 1829. There is no explanation as to why Massalongo did not include them. His inclusion of <u>B. domingensis</u> (as gyrosa) and its variety <u>flavocrocea</u> was the only indication until Zahlbruckner's monumental work that any K+ rose species belonged to <u>Bombyliospora</u>. I think Massalongo would not have thought them members of this genus except for his confused concept of the locule shape. I see no reason why anyone would have thought the K+ rose and K- species groups related before the spore ontogeny was studied.

Although one might think the difference in pigments produced would indicate that two genera are involved here, I believe the strongly unifying characteristics of spore development and a tendency to spiroform endospore thickening is more important than pigments. Recognition of two subgenera is, however, warranted. I have chosen to call these taxa subgenera rather than sections because the differences between them are too basic to give them only sectional rank.

Lopadium. Until now, <u>B. vulpina</u> was thought to be one of a natural group of K+ rose Lopadia in North and Middle America. I have found that the other members of the group cannot belong to <u>Bombyliospora</u>

since they lack the unique spore type of <u>Bombyliospora</u>. Also, the thallus in <u>Lopedium</u> is thicker and granular or sorediose.

Santesson (1952) stated that <u>Lopadium</u> forms no good taxonomic unit. Three foliicolous genera have already been segregated from it and Santesson saw at least four groups of mainly corticolous species remaining. The type species of <u>Lopadium</u>, <u>L. pezizoideum</u>, is different from all the other species except <u>L. monosporum</u> and probably <u>L. gemellum in having paraphyses with dark, swollen calyptra. Until such time that further study proves that additional genera should be segragated from <u>Lopadium</u>, Santesson proposed <u>Lopadium</u> as a <u>momen conservandum</u> against <u>Brigantiaes</u>. <u>Brigantiaes</u> is the older name, and must be reserved for the K+ rose species. <u>Bombyliospora</u> (1852), however, is older than both, so it it should be decided that the K+ rose <u>Lopadia</u> must be united with the K+ rose <u>Bombyliospora</u>, the latter name will take precedence over <u>Brigantiaes</u>.</u>

In view of the absence of a monographic treatment of the polymorphic "genus" Lopadium, and in the absence of any suitable section name, the species of Lopadium discussed here are merely referred to as the Brigantiaea group.

#### KEY TO SPECIES

This key includes all the North and Middle American species of <u>Bombyliospora</u> and <u>Lopadium</u> with anthraquinone pigments.

- Spores unicellular, multiloculate (may give false impression of being muriform; see text), 12-47 x 6-21/u, two

or more per ascus; thallus glaucous, orange, or ochraceous, smooth.....

- 2. Apothecia stalked, with algae in margin; exciple colorless, with highly refractive white crystals; muscicolous.....L. <u>fuscoluteum</u>
- 2. Apothecia not stalked, no algae in margin; exciple rust colored, without crystals; corticolous....3
- 3. Apothecia up to 0.7 mm across; disks dark ochraceous; margins black; spores (45)59-75 x (18)21-26 n, septa regular at maturity......L. cfr. <u>dodgei</u>
- 3. Apothecia up to 1.6 mm across; disks heavily yellow pruinose or nodular ochraceous; margins orange; spores 54-115(129) x 19-40 /u, wepta irregular at maturity....L. leucoxanthum
- 5. Spores anguste-ovatus, 18-20(24) x 5/u, secondary locules nearly round; disks yellow pruinose......B. <u>aureola</u>
- 5. Spores short fusiform, 12-18 x 6-7 /u, secondary locules transversely lentiform; disks light red to fulvous.....<u>B. flavidula</u>
  - Spores (2-4)6-8: nae, secondary locules trans versely lentiform, rarely septate, spiroform
     locules prevalent; medulla UV-.....<u>B. domingensis</u>
  - Spores 2: nae, secondary locules longitudinal ly lentiform, always much septate; medulla
     UV+ white......
     <u>vulpina</u>

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#### BOMBYLIOSPORA Mass.

Ricerch. Auton. Lich. 114. 1852. <u>Psorothecium</u> sect. Bombyliospora (Mass.) Stizenb. Bericht. Thätigk. St. Gallischen nat. Ges. 160. 1862. <u>Heterothecium</u> sect. Bombyliospora (Mass.) Tuck. Nsy. Lich. 2:55. 1888. <u>Lecidea</u> subgen. Bombyliospora (Mass.) Wainio, Acta Soc. Faun. Fl. Fenn. 7:30. 1890. <u>Patellaria</u> sect. Bombyliospora (Mass.) Mäll. Arg. Bull. Herb. Boissier 2(appendix 1):65. 1894. TYPE SPECIES: <u>B. pachycarpa</u> (Del.) De Not.

Lecania sect. Platylecania Mäll. Arg. Flora 65:327. 1882. TYPE SPECIES: Lecania (=Bombyliospora) amplificans (Nyl.) Mäll. Arg.

Dumoulinia Stein, Schles. Ges. vaterl. Cultur 60:231. 1883. TYPE SPECIES: Dumoulinia (=Bombyliospora) meyeri Stein.

Diagnosis. Thallus crustose, heteromerous, epiphloedal, ecorticate; primary phycobiont trebouxioid. Ascocarp an apothecium of the mycolecanorine type, adnate. Paraphyses simple, nonseptate, not capitate, conglutinated. Spores one to eight per ascus, colorless (locules occasionally red or fuscescent in age), short fusiform, anguste-ovatus, or ellipticus; primary locule cylindrical in earliest stages, becoming scalariform or spiroform; secondary locules 4 to 12 (rarely 14), transversely or longitudinally lentiform, persistently nonseptate or becoming transversely septate, sometimes with a few longitudinal septa; locules occasionally partly lentiform and partly spiroform in the same spore. Conidia endobasidial, according to Zahlbruckner (1905 and 1926).

#### Subgemus SPIROBLASTIA Burgess, subgen. nov.

<u>Diagnosis</u>. Thallus smooth, rugose, or areolate, usually containing an anthraquinone. Hypothallus wide, thin, white. Apothecium up to 1.8 mm across, often in aggregates, often gyrose, with sterile

columns; margins yellow, orange, or ochraceous; epithecia and amphithecial cortices K+ rose or violet, rarely blue. Spores 2 to 8 per ascus.  $12-45 \ge 7-25/a$ .

TYPE SPECIES: <u>B.</u> <u>domingensis</u> (Pers.) Zahlbr.

#### BOMEYLIOSPORA AUREOLA (Nyl.) Zahlbr.

Cat. Lich. Univ. 7:49. 1931. Lecidea aureola Nyl. Ann. Sci. Nat. Bot. IV. 19:353. 1866. <u>Heterothecium aureolum</u> (Nyl.) Tuck. Syn. Lich. 2:159. 1888. <u>Lecanora aureola</u> (Nyl.) Nyl. in Hue, Nouv. Arch. Mus. III. 3:53. 1891. TYPE: collected by Wright, <u>s. n</u>., in Cuba; hb. Tuckerman.

<u>Diagnosis</u>. Thallus yellow, smooth; medulla UV-. Apothecium up to 1.2 mm across, flat, somewhat imbedded in thallus; disk yellow pruinose; margin nearly concolorous with disk, becoming crenulate. Exciple orange-rust colored, K+ orange-red; bark carried up into apothecium. Spores 6+8:nae, anguste-ovatus,  $18-20(24) \ge 5/u$ , with 5-6 nearly round secondary locules, end two locules often joined but not twisted; endospore never spiroform.

<u>Discussion</u>. Stirton (1898) intended this species to be in his genus <u>Miltidea</u> but he failed to make the combination.

This species is rare. It has been reported from Cuba (Tuckerman in Nylander, 1863, and Tuckerman, 1866) and from southern Africa (Stirton, 1898). I doubt that Stirton's material was actually <u>B</u>. <u>aureola</u>; the spores were 5-9 locular. There has been no mention of substrate in the literature.

#### Material seen.

#### WEST INDIES

PUERTO RICO: Albonito, in a wood, <u>Fink 1762</u>, 3 Jan. 1916 (MICH). Mapped in fig. 14.

#### BOMBYLIOSPORA DOMINGENSIS (Pers.) Zahlbr.

in Wawra et Beck, Itin. Princip. Coburg. 2:153. 1888. <u>Patellaria</u> <u>domingensis</u> Pers. Ann. Wetterauisch. Ges. 2:12. 1811. <u>Lecanora</u> <u>domingensis</u> (Pers.) Ach. Syn. Lich. 336. 1814. <u>Parmelia ventosa</u> var. <u>domingensis</u> Eschw. in Martius, Fl. Brasil. 1:189. 1833. <u>Lecidea</u> <u>domingensis</u> (Pers.) Nyl. Acta Soc. Sci. Fenn. 7:462. 1863. <u>Heterothecium sect</u>. Lopadium <u>domingense</u> (Pers.) Tuck. Proc. Am. Acad. 7:229. 1868. <u>Miltidea domingensis</u> Stirt. Trans. Proc. New Zealand Inst. 30: 386. 1898. <u>Placodium domingense</u> (Pers.) Wain. Dansk, Bot. Ark. 4(11): 11. 1926. <u>Lopadium domingense</u> (Pers.) Fink, Lich. Fl. United Stafes 235. 1935. TYPE: collected on trees in Santo Domingo (Hispaniola) by Persoon.

Lecidea gyrosa Spreng. K. Svenska Vet. Akad. Handl. 47. 1820. Parmelia gyrosa (Spreng.) Mont. in Sagra, Hist. l'Ile Cuba, Bot. 212. 1842. <u>Heterothecium gyrosum</u> (Spreng.) Flot. Bot. Zeit. 8:554. <u>Bom-</u> <u>byliospora gyrosa</u> (Spreng.) Mass. Atti I. R. Istit. Veneto III. 5: 262. 1860. TYPE: on bark of <u>Capparis cynosphallophora</u> in Guadalupe; collector not stated.

Lecanora acervulata Raddi, Mem. Soc. Ital. Sci. Modena 20:51, t. 3, f. 2. 1827. Type not stated.

Lecidea domingensis f. glaucotropa Wain. Ann. Acad. Sci. Fenn. A. 6(7):124. 1915. <u>Bombyliospora domingensis</u> var. <u>glaucotropa</u> (Wain.) Wain. Ann. Acad. Sci. Fenn. A. 15(6):103. 1921. TYPE: <u>Duss 473</u>, on bark of <u>Artocarpus incisus</u> in Basse-Terre, Guadalupe.

Bombyliospora domingensis f. transgressa Malme, Ark. Bot. A. 18(12):5. 1923. TYPE: <u>Malme 166</u>, Rio de Janeiro, and <u>Malme 465 B</u> and <u>E</u>, Poirto Alegro.

Bombyliospora domingensis var. inspersa Steiner, Bull. Herb. Bois. II. 7:645. 1907. TYPE: Sanat. sub. no. 995, Cape Province, Africa, Junod, 1900.

<u>Diagnosis</u>. Thallus glaucous, yellow-orange, golden, or rarely ochraceous when dried, smooth, rugose, or areolate; medulla UV-. Apothecium up to 1.8 mm across, flat, slightly convex, or rarely strongly convex; disk dark red to fuscous, rarely sparsely yellow pruinose. Exciple usually rust colored, sometimes colorless, always K-; bark not carried into apothecium; algae sometimes present in stipe. Spores usually 6-8:nae, sometimes 2-4:nae and then larger, 28-45 x 11-14(15-17) /u; endospore thickening annular or spirofrom or a combination of the two, locules nonseptate, or occasionally with a few transverse septa especially in spiroform locules; lentiform locules forming acute angles at edge of spore (rarely not acute).

Discussion. This is the most common of the species studied. It has been reported on <u>Capparis cynophallophora</u> (the type, Sprengel, 1820), <u>Kanthoxylum caribaeum</u> (Fee, 1824), and <u>Artocarpus incisus</u> (Wainio, 1915), and from lable data, on <u>Oxandra</u>, <u>Hyperbena</u>, <u>Liquidambar</u>, <u>Carpinus</u>, <u>Drynetes</u>, <u>Poinciana regia</u>, <u>Acer rubrum</u>, and <u>Citrus</u>.

If one were to separate those specimens with mostly spiroform endospore from those with mostly annular endospore, an interesting distribution becomes evident. The former group would be found in large numbers in southeastern United States, but not at all in the West Indies or Middle America. The latter group is found mainly in the West Indies and Middle America, with only a few (5 out of 31) specimens from southeastern United States.

I have examined material from Brazil, Paraguay, Hawaii and the Bonin Islands and find that it is the same as that from North and

Middle America. One specimen (<u>Malme 465 E</u>, from Rio Grande do Sul, Porto Alegro, Brazil, 27 Sept. 1892, in MO), which was listed in Malme's type description of his f. <u>transgressa</u>, looks like normal <u>B</u>. <u>domingensis</u> with locules occasionally septate. The single specimen I have seen from the Bonin Islands (<u>Wright, s. m.</u>, 1853-56, in US) has many spores with spiroform endospores, so perhaps it is not Asahina's (1934) var. <u>boninensis</u>. From the descriptions, I can see no difference between <u>transgressa</u> and <u>boninensis</u> other than locality.

Steiner's var. inspersa is based on the yellow pruinose disk, with a darker color showing when the pruina is scraped off. I have seen this variation and consider it insignificant since it varies greatly within a single specimen.

Wainio's var. <u>glaucotropa</u> is probably not a variety since a single thallus may be partly glaucous and partly orange.

I have seen a specimen (<u>Copeland 848</u>, from the Philippines, April 1904, in US) which was designated and published as f. <u>glauco-</u> <u>tropa</u> by Wainic, but which seems to me to fit the description of <u>B. domingensis</u> var. <u>intermedia</u>. The spores are like those of <u>B</u>. <u>domingensis</u> except for their size--20-30 x 9-13/u, according to Müller (1894). Those of Copeland's specimen were consistently six locular, and the size was 19-21 x 9-12/u. No material like it was seen from the area covered in this study.

No specimens fitting descriptions of other published varieties of this species were seen.

Bombyliospora domingensis has been reported in the literature from Europe (southern France, Zahlbruckner, 1905 and 1926), Africa (northern Africa, Zahlbruckner, 1905 and 1926; Port Natal, Nylander 1896b, Hue, 1891, Stizenberger 1892; Usambara, Mäller 1894; Ivory Coast,

des Abbayes 1955; Bon Spei, Nylander 1859 and 1869b, Hue 1891), southeastern United States (South Carolina and Louisiana, Tuckerman 1872; Florida and Texas, Tuckerman 1888; South Carolina, Louisiana Florida, Texas and Alabama, Fink 1935), Central America (Mexico, Hedrick 1935), West Indies (Guadelupe, Hue 1891; Santa Domingo, Persoon 1811; Cuba, Montagne is Sagra 1842; Bahamas, Riddle 1920), South America (Brazil, Eschweiler in Martius 1833, Müller, 1886, Malme 1923; Argentina, Krempelhuber 1878; Colombia, Nylander 1863b; Argentina and Colombia, Nylander 1869b, Hue 1891; Argentina and Paraguay, Müller 1894), Hawaiian Islands (Oahu, Tuckerman 1868), Asia (Bonin Islands and Taiwan, Asahina 1934), Philippine Islands (Comiran and Samal, Wainio 1921), Australia (Stizenberger 1895; New Caledonia, Nylander 1869b; Queensland, Shirley 1889; Brisbane, Müller 1891; Toowoomba and Queensland, Müller 1882; Queensland , Bmiley 1891), and New Zealand (Hooker 1867, Babington 1855 [pot seen]; north island, Hellbom 1896, Müller 1894).

A nomenclatural note is in order here. Zahlbruckner (1931) was in error in listing Nylander (1869a) as the author of <u>B. leprolyta</u>. He and Hue (1891) called it a subspecies of <u>B. domingensis</u>. Mäller was first to use the name at the specific level, in 1882. Zahlbruckner omitted the homonym <u>Patellaria domingensis</u> var. <u>leprolyta</u> Shirley (1889). The species is mentioned by Bailey (1891) but he misspelled it <u>lepro-</u> <u>lytra</u>, which may account for Zahlbruckner's omission of that reference.

<u>Material seen</u>. Exsiccati. Malme, Lich. Austroam. 41 A & B. UNITED STATES

FLORIDA: county unknown, <u>Calkins 10</u>, 1889 (MSC 119979 and 119984); Mouersit, <u>Calkins 252</u> (MICH); 6 Mile Base, <u>Calkins262</u> (MO); 6 Mile Creek, <u>Calkins 161</u> (US; mixed with <u>B. vulpina</u>); Caloosa River, <u>Austin</u>, 1878 (US ex hb. Willey); southwest Fla., <u>Austin & Smith 40</u>, 1878 (US).

COLUMEIA COUNTY, Lake City, <u>Nash</u> <u>2241</u>, July 11-19, 1895 (MSC, US). DADE COUNTY, Homestead, Owaissa Bauer Hammock, <u>Uyenco</u> <u>102</u>, 9 Feb. 1963 (MSC). HIGHLANDS COUNTY, Highland Hammocks State Park, Sebring, <u>Uyenco</u> <u>79</u>, 11 Feb. 1963 (MSC; mixed with <u>B. vulpina</u> and <u>L. leucoxanthum</u>). POLK COUNTY, Scott Lake near Lakeland, high hammock, <u>McFarlin 40</u>, 4/6/31 (MICH). SEMINOLE COUNTY, Elack Bottom Hammock, 3 mi E of Oveido, <u>Uyenco</u> <u>54</u>, 9 Feb. 1963 (MSC; mixed with <u>B. vulpina</u>). TATLOR COUNTY, Aucilla River on Route 98, <u>Thomson 5228</u>, 4 Sept. 1954 (MSC).

LOUISIANA: parish unknown, <u>Lehnert</u> (MICH); Coteau, <u>Langlois f</u>, 2 Ang. 1892 (US); Duchamps, <u>Langlois c</u>, 17 Sept. 1894 (US); John Durands', <u>Langlois 831</u>, 2 Jan. 1894 (US); Pointe aux Loups, <u>Langlois</u>, 30 Sept. 1895 (US); St. Leo, <u>Langlois</u>, 21 Mar. 1895 (MICH ex hb. Fink 1986). PLAQUEMINES PARISH, Pointe a la Hache, <u>Langlois 304</u>, 20 Nov. 1885 (US). SAINT LANDRY PARISH, Grand Coteau, <u>Langlois b</u>, 6 June 1894 (US), Opelousas, Langlois g, 22 June 1885 (US).

SOUTH CAROLINA: county unknown, <u>Ravenel</u> (MICH ex hb. Fink 15411, mixed with <u>B. vulpina</u>; MO 34146; US; and US ex hb. Willey), Santee Canal, <u>Ravenel</u>, 1849 (MICH, Reliquiae Tuckermanie 104).

TEXAS: county unknown, <u>Hall 6</u>, 1872 (US ex hb. Willey). CENTRAL AMERICA

BRITISH HONDURAS: locality unknown, <u>Mains 3722</u>, 3 July 1936 (MICH); El Cayo District, along Belze River, <u>Mains 3535</u>, 17 June 1936 (MICH); Valenten, <u>Mains 3551</u>, 23 June 1936 (MICH).

MEXICO: locality unknown, Tamasopo, <u>Pringle</u>, 10 June 1890 (MSC 45823); San Luis Potosi, Las Palmas, <u>Pringle 164</u>, 10 June 1890 (US). Yucatan Peminsula, Chichen Itze, in San Yui Cenote, <u>Steere 1701</u>, 29 June 1932 (MICH); Lake Chichancanab, Quintana Roo, <u>Steere 2361</u>, 28-19 July 1932 (MICH); San Miguel, Cozumel Island, Quintana Roo, Steere <u>2657</u>, 6-8 Aug. 1932 (MICH).

#### WEST INDIES

CUBA: Province unknown, <u>Wright</u> (US); <u>Wright II 109</u> (US); <u>Wright</u> 231 (MICH ex hb. Bennett); <u>Wright 231</u>(US). MATANZAS PROVINCE, Camarioca, <u>Britton & Wilson 14021</u>, 7 Feb. 1916 (MO). ORIENTE PROVINCE, Gran Piedra, south slope about halfway up, wooded rocky ravine with small waterfalls, Sierra Maestra, <u>Imshaug 25056</u>, 25057, 25072, 16 Aug. 1959 (MSC).

HAITI: DEPARTMENT DU NORD, hill west of Cap Haitien, <u>Imshaug</u> 22662, 10 July 1958 (MSC).

JAMAICA: HANOVER PARISH, Dolphin Head, 1750 ft, <u>Imshaug 15613</u>, 23 Apr. 1953. ST. ANN PARISH, Albion, 2400 ft, <u>Imshaug 15902</u>, 7 May 1953. ST. CATHERINE PARISH, Montpelier summit, 2300 ft, <u>Imshaug 14296</u>, 28 Jan. 1953; Hollymount, Mt. Diablo, 2754 ft, <u>Imshaug 14208</u>, 28 Jan. 1953, all in MSC.

PUERTO HICO: locality unknown, <u>Earle</u>, summer 1903 (MICH ex hb. Fink 14498). Albonito, in a wood, <u>Fink 1789</u> (MICH ex hb. Fink 8336, mixed with <u>B. flavidula</u>) and <u>Fink 1798</u>, 1/3/1916 (MICH ex hb. Fink 8102); Candelaria, near Bayamon, <u>Britton</u>, <u>Hess & Marble</u> 2883, 11 April 1913 (MICH); near Martin Pena Station, 30 ft, <u>Heller 4337</u>, 19 Jan. 1900 (US, MO); and <u>Heller s. n.</u>, 19 Jan. 1900 (MICH ex hb. Fink 14909); Pela de la Piedra, <u>Drilture & Havre 750</u>, 16 Feb. 1923 (MICH); Rio Piedras, in a wood, <u>Fink 2166</u>, 18 Jan. 1916 (MICH, US).

The localities are mapped in fig. 13.

BOMEYLIOSPORA FLAVIDULA (Tuck.) Zahlbr.

Cat. Lich. Univ. 7:53. 1931. Lecidea flavidula Tuck. in Nyl. Ann. Sci. Nat. Bot. IV. 19:253. 1863. Lecanora domingensis \* flavidula

(Tuck.) Nyl. in Hue, Nouv. Arch. Mus. III. 3:53. 1891. TYPE: collected in Cuba by Wright, s.n.; in hb. Tuckerman.

<u>Diagnosis</u>. Thallus grey-green or glaucous and K-, or occasionally tan and K+ rose, smooth, entire; medulla UV-. Apothecium to up 1.7 mm across, sometimes gyrose, often with sterile columns; disk flat, light red to fulvous, never pruinose; margin rather narrow at maturity; false thalline margin often present, K-. Spores uni- or biseriate, 6-8:nae, short fusiform, 12-18 x 6-8 (rarely 5) u; secondary locules 4-6, transversely lentiform, not forming an acute angle at edge of spore, never septate; end two locules sometimes joined and twisted sprially in 6locular spores.

Discussion. This is a rare species and was previously known only from the original collection. The Puerto Rican specimens were consistently 4-locular except for the one in US, which had a few spores with six locules, the end two joined. The Haitian material was consistently 6-locular except for <u>Wetmore 3194</u>, which had a very few 5- (not six\_) locular spores. Since the other characteristics are identical, I believe that this variation may be interpreted as incipient speciation, but not yet worthy of taxonomic recognition. Populations isolated by water have come to differ by one annular thickening per spore.

I have not seen authentic Colombian material of <u>B</u>. <u>domingensis</u> var. <u>inexplicata</u> (Nyl.) Zahlbr., but the description by Nylander (1863a and 1863b) fits <u>B</u>. <u>flavidula</u>.

#### Material seen.

#### WEST INDIES

HAITI: DEPARTMENT DE L'OUEST, ravine on east slope above road NW of Foret des Pins, <u>Imshaug 22934</u>, 16 July 1958; elfin woodland forest, northof Foret des Pins (Shada Station), near Dominican border,

5800 ft, <u>Wetmore</u> 2912, 2914, 14 July 1958; elfin woodland, ridge above (east of) Foret des Pins, 5800-5900 ft, <u>Wetmore</u> 3181, 3193, 3194, 18 July 1958, all in MSC.

PUERTO RICO: Aibonito, in a wood, <u>Fink 1789</u> (US; MICH ex hb. Fink 8062; and MICH ex hb. Fink 8336, mixed with <u>B. domingensis</u>); Hacienda Pulgillas, Coamo, <u>Chardon 1227</u>, 25 Aug. 1920 (MICH).

The localities are mapped in fig. 14.

BOMEYLIOSPORA VULPINA (Tuck.) Burgess, comb. nov.

Lecidea vulpina Tuck. in Nyl. Ann. Sci. Nat. Bot. IV. 19:354. 1863. Heterothecium sect. Lopadium vulpinum (Tuck.) Tuck. Syn. Lich. 2:57. 1888. <u>Miltidea vulpina</u> (Tuck.) Stirt. Trans. Proc. New Zealand Inst. 30:386. 1898. <u>Sporopodium vulpinum</u> (Tuck.) Wain. Ann. Acad. Sci. Fenn. A. 15(6):88. 1921. TYPE: collected in Cuba by Tuckerman, <u>s. n</u>.; hb. Tuckerman.

Lopadium vulpinum var. personatum (Tuck.) Malme, Ark. Bot. A. 29(6):25. 1937. TYPE: <u>Malme 2441</u>, at the edge of a woods, Santa Anna da Chapada, Matto Grosso, Brazil, 28 Feb. 1894.

Locidea subvulpina Nyl. Bull. Soc. Linn. Normandie II. 2:89. 1868. Lopadium vulpinum var. subvulpinum (Nyl.) Zahlbr. Cat. Lich. Univ. 4:317. 1927. TYPE: collected by Tuckerman, <u>s. n</u>.

Diagnosis. Thallus golden, occasionally glaucous; smooth, rugose, or areolate; medulla UV+ white. Apothecium flat to slightly convex; disk fulvous, occasionally sparsely yellow pruinose. Spores 2:nae (rarely 1 or 4:nae), uniseriate, ellipticus, (24-27)28-40(42-47) x (9)12-19(21) u; spiroform or secondary locules much septate transversely, sometimes longitudinally septate; secondary locules longitudinally lentiform. Discussion. This is the second most frequently collected species, but is found far less often than is <u>B</u>. <u>domingensis</u>. Although the type locality is Cuba, Imshaug did not find it in extensive collecting there. It has been reported in the literature from Florida (Tuckerman 1888), the West Indies (Cuba, Tuckerman in Nylander 1863b, Tuckerman 1888, Mäller 1881a, Hue 1891, Lynge 1939; Hispaniola, Wainio 1915), Central America (Mexico, Davis 1936), Asia (Ceylon and East Indies, Mäller 1881a), Africa (Mauritius and Guyana, Tuckerman in Nylander 1863a; Ivory Coast, des Abbayes 1955), and Australia (Shirley 1889, Stirton 1898; New Caledonia, Nylander 1868 and 1869; New Caledonia and Noumea, Mäller 1893a; Brisbane and Queensland, Mäller 1891).

The only substrates identified on the lables were <u>Magnolia</u>, <u>Car</u>-<u>pinus</u>, <u>Citrus</u>, <u>Quercus</u> <u>virginiana</u>, and palm.

The only specimen which had some spores singly in asci was <u>Uyenco</u> <u>51</u>; only the specimen <u>Nash</u>, Fla., had some spores 4:nae.

Müller (1881a) stated that <u>Heterothecium Hampeanum Mass.</u>, <u>H</u>. <u>miniatum Hampe and H. fuscenscens Hampe are synonyms of B. vulpina</u>. These are all <u>nomina nuda</u> not mentioned by Zahlbruckner (1931).

Malme (1937) mistakenly thought a K+ violet blue reaction of the epithecium and amphithecium was normal for <u>B</u>. <u>vulpina</u>, and on that basis he described var. <u>personatum</u> for K+ rose specimens. Tuckerman did not mention the K reaction in the original description, but I have seen Malme's exsiccatum Lichenes Austroamericani no. 195 (MSC) which he called <u>vulpina</u>, and the K reaction of this specimen is distinctly different from that of the isotype. Therefore, Malme's var. <u>personatum</u> is identical to var. vulpina and must be discarded.

Specimens with a K+ violet blue epithecium and amphithecium represent Lecidea subvulpina Nyl., designated as "epithecium et conceptaculum hydrate kalico coerulee tinguntur" by Nylander (1868).

There is some question, however, as to whether or not the name <u>subvulpina</u> was validly published. Nylander's (1868) wording, "Disjuncta scilicet <u>Lecidea subvulpina Nyl.</u>, quae disnoscitur tanquam varietas [of <u>vulpina</u>]" leaves one wondering if he meant to call it a species or a variety. This would fall under Article 4 of the Rules (1956); the name was not validly published since the author failed to recognize the taxon at any certain level. This taxon is for the present treated as a synonym of <u>B. vulpina</u> since the significance of the color reaction is not fully understood. It seems to be analogous to the situation with <u>Lopadium leucoxanthum</u> (K+ rose) and L. leucoxanthoides (K+ blue).

Many authors have commented on the similarity between <u>B</u>. <u>domingen-</u> <u>sis</u> and <u>B</u>. <u>vulpina</u> and their varieties in the past (Tuckerman, 1866, 1868, 1872, 1888; Tuckerman in Nylander, 1863b; Nylander, 1869a; Müller, 1882 and 1891; Shirley, 1889; Stirton, 1898; Malme, 1923; Asahina, 1934; Santesson, 1952), but if they were made members of the same genus, it was <u>B</u>. <u>domingensis</u> that was transferred, because of its "submuriform" spores. It is interesting that the two species have similar forms and varieties reported in the literature, namely glaucescent, ochraceous, and coralloid. None of these were described from North or Middle American material but I have seen both glaucescent and ochraceous forms.

#### Material seen.

#### UNITED STATES

FLORIDA: county unknown, <u>Austin & Smith</u>, Mar. 1878 (US ex hb. Smith); Caloosa River, <u>Austin</u>, 1878 (US ex hb. Willey); <u>Calkins 8</u>, 1889 (MSC); <u>Calkins 8</u>, no date (MSC); <u>Calkins 10</u>, 1889 (MSC); 6 Mile Creek, <u>Calkins 161</u> (US, mixed with <u>B. domingensis</u>). ALACHUA COUNTY, Gainsville, <u>Ravenel</u>, 1877 (US ex hb. Willey). COLUMERA COUNTY, Lake City, <u>Nash 2241</u>, July 11-19, 1895 (MO, US). HIGHLANDS COUNTY, Highland

Hammocks State Park, Sebring, <u>Uyenco 80</u>, 11 Feb. 1963 (MSC); Lime berry trail, Highland Hammocks State Park, Sebring, <u>Uyenco 87</u>, 11 Feb. 1963 (MSC); Wm. Lieder Trail, Highland Hammocks State Park, Sebring, <u>Uyenco 79</u>, 11 Feb. 1963 (MSC, mixed with <u>B. domingensis</u>); LAKE COUNTY, Eustis, <u>Nash 1957</u>, May 28-June 15, 1895 (MO, US). POLK COUNTY, Peace Creek, <u>Smith</u>, Mar. 1880 (US ex hb. Smith). SEMINOLE COUNTY, Black Bottom Hammock, 3 mi E of Oveido, <u>Uyenco 51</u> and <u>54</u>, 9 Feb. 1963 (MSC, <u>54</u> mixed with <u>B. domingensis</u>); Oviedo, <u>Mead</u> (MO ex hb. Moore).

SOUTH CAROLINA: county unknown, <u>Ravenel</u>, on trees (MICH ex hb. Fink 15411).

#### CENTRAL AMERICA

BRITISH HONDURAS: El Cayo District, Cohune Ridge, <u>Mains</u> <u>3784</u>, 10 July 1936 (MICH).

MEXICO: Yucatan peninsula, in forest, Champoton, Campeche, <u>Steere 1826</u>, 7-15 July 1932 (MICH); Yocatan peninsula, San Miguel, Cozumel Island, Quintana Roo, in forest, <u>Steere 1797</u>, 6-8 Aug. 1932 (MICH).

WEST INDIES

CUBA: locality unknown, <u>Wright</u> (US ex hb. Willey ex Miss Wilson; no spores seen by me); <u>Wright II 110a</u> (US); <u>Wright 233</u> (US, ISOTYPE).

Localities are mapped in fig. 14.

<u>Notes on other possible Spiroblastiae</u>. In my study of the literature, I found numerous references to certain species of <u>Bombyliospora</u> and <u>Lopadium</u> commenting on their similarity to one or more of the species just diagnosed. Because they have not been found in North or Middle America, they were not included in this study, and no material was seen. However, since spores with spiral patterns have been mentioned in the literature only in connection with the species below, I feel this discussion is pertinent.

#### LOPADIUM HIFERUM (Nyl.) Zahlbr.

Cat. Lich. Univ. 4:300. 1927. <u>Lecidea bifera</u> Nyl. Ann. Sci. Nat. Bot. IV. 15:47. 1861. <u>Heterothecium biferum</u> (Nyl.) Müll. Arg. Flora 64: 104. 1881. TYPE: collected by Pancher in Mauritius and Guyana.

Ledidea leucoxantha var. <u>bispora</u> Nyl. Mem. Soc. Sci. Nat. Cherbourg 5:123. 1856. (nomen nudum)

<u>Discussion</u>. Nylander's original desceiption (1861) stated that the spores are "transversim pluries divisis vel fere murali-loculosis ..." and two per ascus. He later (1863a) described them as "quasi intus oblique vel spiraliter murali-divisis (seriebus circiter 10)" in comparing the species to <u>B</u>. <u>vulpina</u>. In 1868, he wrote "Sporis binis intus spiraliter (nonnihil oblique) murali divisis mox distinguenda species." His description of the thallus varies from "Similis externe [<u>lopadium</u>] <u>leucoxanthae</u>" (1861) to cinerascent (1863a) to "glancescens tenuis vel glauco-virescens vel macula glauco-flavida indicatur" (1868). The epithecium is K+ purpurascens. The species was originally described from Mauritius and Guyana, as was <u>B</u>. <u>vulpina</u>, and was later reported from New Caledonia and Lifu (Nylander, 1868), Brisbane (Mäller, 1891), and Noumea (Mäller, 1893a). Stirton (1898)stated that <u>L</u>. <u>Miferum</u> and <u>L</u>. <u>parabolum</u> probably belong to the group (muriform-spored <u>Miltidea</u>) of which <u>B</u>. <u>vulpina</u> is the type.

LOPADIUM HIFERUM var. PLURIFERUM (Nyl.) Zahlbr. Cat. Lich. Univ. 4:300. 1927. <u>Lecidea bifera var. plurifera</u> Nyl. Bull. Soc. Linn. Normandie II. 2:89. 1868. TYPE: collected by Nylander in New Caledonia and Lifu.

<u>Discussion</u>. This lichen was described by Nylander (1868) as a variety which has spores 2-6 per ascus, and epithecium K+ "fuscescente (obscuriorem sumente colorem, raro purpurascente)."

#### LOPADIUM PARABOLUM (Nyl.) Zahlbr.

Cat. Lich. Univ. 4:309. 1927. Lecidea parabola Nyl. Bull. Soc, Linn. Normandie II. 2:90. 1868. <u>Heterothecium parabolum</u> (Nyl.) Mäll. Arg. Rev. Mycol. 9:80. 1887. TYPE: collected by Nylander in New Caledonia and Lifu.

<u>Discussion</u>. This species was described as similar to <u>L</u>. <u>biferum</u> but with thallus dilute glauco-flavid, spores "vulgo 8 spiraliter contimuis, parum divisis,"  $30-34 \times 13-15 \times 10^{-15} \times 10^{$ 

LOPADIUM PARABOLUM var. SUBVULPINUM (Mäll. Arg.) Zahlbr. Cat. Lich. Univ. 4:309. 1927. <u>Heterothecium parabolum var. subvul-</u> <u>pinum Mäll. Arg. Flora 70:338. 1887. Lecidea parabola var. subvul-</u> <u>pina (Mäll. Arg.) Shirley, Proc. Roy. Soc. Queensland 6:184. 1889.</u> TYPE: collected by Sayer at Trinity Bay, Australia.

<u>Discussion</u>. The thallus of this variety is "aurantiaco flavus ut in <u>H</u>. <u>vulpino</u> Tuck." (Mäller, 1887a). but the spores are like those of normal <u>L</u>. <u>parabolum</u> or <u>L</u>. <u>biferum</u> except "intus simplicius spiraliter divisae." Shirley's (1889) <u>L</u>. <u>parabola</u> had a golden yellow thallus but he commented on the color variability with single specimens. Mäller (1887a) stated that thallus color is "in tota serie specierum affinium, <u>H</u>. <u>leucoxanthi</u>, <u>H</u>. <u>biferi</u>, <u>H</u>. <u>paraboli</u> et <u>H</u>. <u>vulpini</u> evidenter inconstans et saepe in eodem specimine e flavescenti plus minusve glaucescens v. albicans."

Zahlbruckner (1927) erroneously listed this as var. <u>subalpinum</u>; actually, Mäller and Shirley called it var. <u>subvulpina</u>.

BOMEYLIOSPORA COCCODES (Bel.) Mass.

Atti I. R. Instit. Veneto III. 5:262. 1860. <u>Parmelia coccodes</u> Bel. Voy. Indes-Orient. 2:125, t. 13, f. 2. 1846. <u>Biatora coccodes</u> (Bél.) Mont. Ann. Sci. Nat. Bot. III. 10:126. 1848. <u>Leciden coccodes</u> (Bél.) Nyl. Bull. Soc. Linn. Normandie II. 1:89. 1868. TYPE: collected by Belanger on Reunion.

Discussion. This species is more difficult to interpret because of the lack of clear descriptions of its spores. The thallus surface is different from that of the species just discussed; according to Bélanger (1846), the surface is "subtartare&, granulato-conglomerat&, albo-pallescente," but the granules become "stalactiformes, et verd&tres dans un & ge plus avancé." He did not describe the spores. Montagne (1848) discussed the species briefly in comparison with three other species, but placed emphasis on the characteristics of the thalli, writing only that the spores of <u>B. coccodes</u> have "4 ā 6 mucléms." The species it was com pared with are one-septate, multilocular, and muriform, respectively.

Nylander (1868) evidently felt <u>B</u>. <u>coccodes</u> might be confused with <u>L</u>. <u>biferum</u> var. <u>pluriferum</u>, since he pointed out that the yellow material in the margin of the latter forms a purple liquid with KOH, while in <u>B</u>. <u>ecocodes</u>, the yellow pigment of the margin is "statim violacee purpurascit."

In his (1868) description of <u>L</u>. <u>parabolum</u>, Nylander noted that its spores are almost the same as those of <u>B</u>. <u>coccodes</u>. If one assumed that the specific name was chosen with regard to the spore shape, then incorporated hints from the literature, one would expect the spores to be cocciform and to have a spiroform endospore. This invites curiosity as to the similarity between <u>B. coccodes</u> and <u>L. vulpinum</u> f. <u>corallinum</u> (Müll. Arg.) Zahlbr., which has a yellowish thallus. Tuckerman (1866 and 1838) described the spores of <u>B. vulpina</u> as cocciform to elongateellipsoid. I have seen one specimen from the Philippines (McGregor, 1914, in US), whose spores must be called cocciform except for occasional ones which are alone in the ascus, and then ellipsoid; its yelloworange thallus in smooth rather than coralloid. It seems possible that <u>B. coccodes</u> could have either white and granular, or yellow and smooth thalli; the thallus of <u>L. leucoxanthum</u> has greatly variable surface texture, from my observations, and its color ranges from white to sulfur yellow if one accepts <u>Lecidea bicolor</u> Spreng. as a synonym of <u>L. leucoxanthum</u>.

Trevisan'a 1853 report on <u>B. coccodes</u> in Spighe e Paglie was not available.

Many facts about each of these species and varieties---the spiralled appearance of the spore interior, spore size, K reactions, the sometimes yellowish thallus, and the distribution---indicate that they are probably members of <u>Bombyliospora</u> sect. Spiroblastia.

#### LECIDEA QUADRILOCULARIS Nyl.

Ann. Sci. Nat. Bot. IV. 11:224. 1859. <u>Bombyliospora quadrilocularis</u> (Nyl.) Mass. Atti. I. R. Istit. Veneto III. 5:262. 1860. <u>Lecanora</u> <u>quadrilocularis</u> (Nyl.) Nyl. Ann. Sci. Nat. Bot. IV. 16:378. 1861. <u>Callopisma</u> sect. Tetrophthalmidium <u>tetramerum</u> (Nyl.) Mäll. Arg. Bull. Soc. Bot. Belgique 32:135. 1893. <u>Callopisma quadriloculare</u> Malme,

Ark. Bot. A 20(9):9. 1926. <u>Elastenia quadrilocularis</u> (Ny.) Zahlbr.
Cat. Lich. Univ. 7:48. 1931. <u>Caloplaca quadrilocularis</u> (Nyl.) Eahlbr.
Cat. Lich. Univ. 7:202. 1931. <u>Triophthalmidium</u> sect. Tuckermannia
<u>quadrilocularis</u> (Nyl.) Gyel. Acta Faun. Fl. Univ. II. 1(5-6):8. 1933.
TYPE: collected by Wedd on <u>Cinchona ovata</u> in Tipuani, Bolivia.

<u>Discussion</u>. In my conception of the genus <u>Bombyliospora</u>, this species would belong to it only if the spores develop in the characteristic manner. I have not been able to see any <u>L</u>. <u>quadrilocularis</u>, but the literature information does not exclude it from <u>Bombyliospora</u>, where it was placed by the author of that genus.

Nylander (1859) described the species as having spores "solidae 4-loculares loculis contractis sphaeroideis invidem saepius tubulo junctis." Malme (1926) left out that important word "saepa," writing "4-loculares, loculis tubo contrali conjunctis, intermediis lenticularibus, membrana in apicibus tenui." Hue (1912) stated that Nylander was wrong to call the spores 4-locular; he thought Nylander saw, but didn't understand the significance of, the tube.

The spores are eight per ascus, ellipsoid,  $24-30 \ge 9-11(12)/u$ ; the thallus is ashy and rugose, the apothecial disk fuscous, the margin pale. The original description includes no mention of algae, but Malme (1926), who saw the type, stated that algae are numerous in the medulla of the margin.

Zahlbruckner (1931) took <u>Callopisma tetramerum</u>, from Brazil, to be the same as <u>L</u>. <u>quadrilocularis</u>, although Mäller (1893b) thought it was not. It has spores  $22-25 \times 12-15/u$ , middle locules distinctly larger, thallus white and granular, and there are algae in the apothecial margin.

Thus there is a possibility that <u>Lecidea</u> <u>quadrilocularis</u> Nyl. belongs to <u>Bombyliospora</u>, but I cannot tell at this time.

It should be pointed out that Zahlbruckner (1931) erroneously based all the synonyms except the <u>Bombyliospora</u> and <u>Lecanora</u> <u>quad</u>-<u>rilocularis</u>. Nylander (1861) clearly stated, however, that his <u>Lecanora</u> <u>quadrilocularis</u> was based on his <u>Lecidea</u> <u>quadrilocularis</u>.

#### LOPADIUM Körb.

Syst. Lich. Germaniae 10. 1855. <u>Heterothecium</u> sect. Lopadium (Körb.) Tuck. Syn. Lich. 2:57. 1888. <u>Lecidea</u> subgen. Lopadium (Körb.) Wain. Acta Soc. Faun. Fl. Fenn. 7:25. <u>Diplotomma</u> sect. Lopadium (Körb.) Jatta, Syll. Lich. Ital. 432. 1900. <u>Lecidea</u> subgen. Biatora E. Lopadium (Körb.) Harm. et Claud. Guide Elem. Lich. 71. 1904 (not seen) TYPE SPECIES: <u>L. pezizoideum</u> (Ach.) Körb.

<u>Brigantiaea</u> Trevis. Spighe e Paglie 7. 1853 (not seen). TYPE SPECIES: (selected) <u>Biatora tricolor</u> Mont. (=<u>Lopadium leucoxanthum</u> Spreng. Zahlbr.

Lecidea subgen. Lopadium I. Gymnothecium Wain. Acta Soc. Faun. Fl. Fenn. 7:25. 1890. TYPE SPECIES: Lecidea leucoxantha Spreng.

<u>Diagnosis</u> (adapted from Santesson, 1952). Thallus crustose, heteromerous, epiphloedal, ecorticate, K+ yellow (atranorine); medulla UV-; primary phycobiont trebouxioid. Ascocarp an apothecium of the mycolecanorine type. Spores usually 1:nae, sometimes 2-8:nae, ellipticus, hyaline, fuscescent in age, muriform or submuriform, endospores not thickened. Paraphyses almost simple, or richly branched. Conidia exobasidial, ellipticus to flask shaped or dumbbell shaped; uppermost part of spores or entire spores sometimes breaking into conidia within asci. Cephalodia containing species of Scytonemataceae sometimes present.

#### BRIGANTIAEA GROUP

Diagnosis. Thallus K+ yellow (atranorine), corticolous or muscicolous. Apothecium adnate or stalked, up to 3.5 mm wide, often gyrose and with sterile columns; margin yellow, orange, ochraceous, or black; disk gold, ochraceous, or nearly black; epithecia and amphithecial cortices K+ rose, rarely K+ blue. Spores 1:nae, rarely 2:nae, often fuscescent and K+ rose. Cephalodia not present.

#### LOPADIUM cfr. DODGEI Herre

Bryologist 53:296. 1950. TYPE: collected by <u>Herre s.n.</u>, on <u>Quercus</u> <u>agrifolia</u>, Pacific Grove, Calif.; in Herre hb., isotypes in Dodge hb. and US.

Diagnosis. Thallus ashy, sorediose, corticolous. Apothecium up to 0.7 mm across, adnate; disk ochraceous pruinose, becoming black; margin black. Epithecium and ampithecium K+ rose; exciple rust colored; hymenium with clusters of colorless needles in KOH; paraphyses branched. Spores 1:nae, rarely 2:nae, always hyaline, sometimes K+ rose, (45)59-75 x (18)21-26/u, all septa regular in young and mature spores, making cells nearly round; spores sometimes with wide, colorless halo; spores not breaking into conidia.

<u>Discussion</u>. I am not sure the material I have seen is <u>L</u>. <u>dodgei</u>, but that is the only name available. The type description does not include K reactions or descriptions of apothecial tissues.

The spore of this species is very interesting; its appearance and the way it breaks when crushed is very much like <u>B</u>. <u>vulpina</u>. I cannot justify inclusion of <u>L</u>. cfr. <u>dodgei</u> in <u>Bombyliospora</u>, however, because the locules are not formed by endospore thickening.

Material seen.

MONTANA: Glacier National Park, Snyder Creek, 3400 ft, on cottonwood, <u>Imshaug 7306</u>, 25 July 1950.

WASHINGTON: Mt. Ramier National Park, Nisqually River, 2700 ft, Imshaug 1381, 11 Aug. 1948; both in MSC.

#### LOPADIUM FUSCOLUTEUM (Dicks.) Mudd

Manual Brit. Lich. 190, t. 3, f. 73. 1861. <u>Lichen fuscoluteus</u> Dicks.
Fasc, Flant Crypt. Brit. 2:18, t. 6, f. 2. 1790. <u>Patellaria fuscolutea</u> (Dicks.) Hoffm. Descr. Adumbr. Plant. Lich. 3:10, t. 65, f. 1. 1801 (not seen). <u>Parmelia fuscolutea</u> (Dicks.) Ach. Meth. Lich. 180. 1803.
<u>Lecidea fuscolutea</u> (Dicks.) Ach. K. Svenska Vet. Akad. Handl. 266.
1808 (not seen). <u>Lecidea aurantiaca var. fuscolutea</u> (Dicks.) Schaer.
Lich. Helvet. Spicil. 4-5:179. 1833(not seen). <u>Biatora fuscolutea</u>
(Dicks.) Fries, Summ. Veget. Scandin. 1:112. 1846. <u>Lecanora cerina</u> var. <u>fuscolutea</u> (Dicks.) Linds. Trans. Bot. Soc. Edinb. 7:122. 1863. <u>Het-</u> <u>erothecium fuscoluteum</u>(Dicks.) Tuck. Gen. Lich. 176. 1872. <u>Lecidea</u> *TTT*Bombyliospora <u>fuscolutea</u> (Dicks.) Shirley, Proc. R. Soc. Queensland 6:
175. 1889. <u>Sporepodium fuscoluteum</u> (Dicks.) Wain. Acta Soc. Faun. Fl.

<u>Diagnosis</u>. Thallus smooth, muscicolous. Apothecium stalked, up to 3.5 mm across, thalline margin with algae and with warts containing algae; only this white false thalline margin showing on young apothecia; amphithecium ochraceous. Exciple colorless, full of large white crystals usually visable only in polarized light, crystals sometimes faintly pink, always K-; paraphyses simple. Spores 1:nae, 82-106 x 28-35/u, thin walled, septa regular in young spores, irregular in mature ones; spores often fuscescent and K+ rose, not breaking into conidia.

<u>Discussion</u>. Stirton (1898) meant to include this species in <u>Miltides</u>, but failed to make the combination.

The abundance of algae in the margin makes one wonder what is the true relationship of this species with <u>Caloplaca</u>. The apothecium has a different structure from the other two <u>Lopadia</u> discussed; see fig. 5.

#### Material seen.

#### UNITED STATES

ALASKA: near terminus of Mendenhall glacier, elev. 150 ft, Juneau, <u>Imshaug 28575</u>, 12 July 1963; alpine summit of Mt. Juneau, <u>Imshaug 28764</u>, 15 July 1963, both in MSC.

#### LOPADIUM LEUCOXANTHUM (Spreng.) Zahlbr.

Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Cl. 111(1):398. 1902. <u>Lecidea leucoxantha</u> Spreng. K. Svenska Vet. Akad. Handl. 46. 1820. <u>Patellaria leucoxantha</u> (Spreng.) Spreng. Syst. Veget. 4(1):267. 1827. (not seen). <u>Biatora leucoxantha</u> (Spreng.) Bél. Voyag. Indes-Orient. Crypt. 2:128. 1846. <u>Heterothecium leucoxanthum</u> (Spreng.) Mass. Misc. Lich. 39. 1856 (not seen). <u>Xanthocarpia leucoxantha</u> (Spreng.) C. Mäll. Bot. Zeit. 15:386. 8157. <u>Sporopodium leucoxanthum</u> (Spreng.) Wain. Ann. Acad. Sci. Fenn. A. 15(6):88. 1921. TYPE: on <u>Cinchona oblongifolia</u> Mutis, no locality given except "tropicarum pugillus;" no collecter stated.

Lecidea bicolor Spreng. K. Svenska Vet. Akad. Handl. 48. 1820. Heterothecium bicolor (Spreng.) Flot. Bot. Zeit. 8:554. 1850. TYPE: on rock in Guadalupe; collector not stated.

<u>Parmelia chrysocarpa</u> Meyer in Spreng. Syst. Veg. 4(1):329. 1827 (not seen).

Lecidea <u>olivaceorufa</u> Zenk. in Goebel et Kunze, Pharmazeut. Waarenk. 1:152, t. 17, f. 6. 1829 (not seen).

Lecanora desquamescens Fee, Suppl. Essai Crypt. Ecorc. Offic.

111, t. 42, f. 35. 1837. <u>Heterothecium desquamescens</u> (Fee) Mass. Atti I. R. Istit. Veneto III. 5:262. 1860. TYPE: on <u>Cinchona</u> in Peru; collector not stated.

<u>Biatora tricolor</u> Mont. Ann. Sci. Nat. Bot. II. 18:266. 1842. <u>Brigantiaea tricolor</u> (Mont.) Trevis. Spighe e Paglie 9. 1853 (not seen) TYPE: collected by Gaudichaud, on bark in the Sandwich Islands.

<u>Megalospora lutea</u> Flot. Linnaea 17:21. 1843. TYPE: no data. <u>Lecanora crocata</u> Fée, Bull. Soc. Bot. France 20:315. 1873.

TYPE: Fee 2204, from Brazil.

Lecidea crocata var. tabacina Fée, Bull. Soc. Bot. France 20: 315. 1873. TYPE: Fée 1913, from Brazil.

Sporopodium leucoxanthoides Wain. Ann. Acad. Sci. Fenn. A. 15(6): 87. 1921. Lopadium leucoxanthoides (Wain.) Zahlbr. Cat. Lich. Univ. 4:305. 1927.

<u>Diagnosis</u>. Thallus granular, often becoming coralloid, corticolous. Apothecium adnate, up to 1.6 mm across; disk yellow pruinose or with ochraceous nodules. Exciple rust colored; ampithecium without algae; paraphyses simple. Spores 1:nae,  $54-115(129) \ge 19-40$  u, thin walled, septa irregular even in young spores, spores often fuscescent and K+ rose, often breaking into conidia.

<u>Discussion</u>. Stirton (1898) meant to include this species in his <u>Miltidea</u> but he failed to make the combination.

I have seen one specimen of <u>L. leucoxanthoides (Heller 2165</u>, Hawaii, in MSC). Wainio described that species as differing from <u>L</u>. <u>leucoxanthum</u> only in the blue color reaction with KOH. The two "species" have the same variation, as noted by Wainio, namely with ochraceous disks or with fuscescent disks ( the latter variety of <u>L. leucoxanthum</u>, var. <u>epiphaeizae</u> Wain., is apparently a nomen nudum), and they have the same distribution. As Wainio pointed out, the situation

seems to be analogous to that with <u>B</u>. <u>vulpina</u> and its variety <u>subvul</u>-<u>pina</u>, but incongruously, Zahlbruckner allowed <u>L</u>. <u>leucoxanthoides</u> to be listed in his Catalogus as an autonomous species. This taxon is for the present treated as a variety of <u>L</u>. <u>leucoxanthum</u> since the significance of the color reaction is not fully understood. It is thought to be a matter of monoquinones vs. diquinones.

<u>Material seen</u>. Exsiccati. Malme, Lich. Austroam. 42 & 393; Merr. II. 101.

#### UNITED STATES

FLORIDA: county unknown, <u>Eckfeldt</u>, 1886 (US); Faulkner's High Hammock, east of Kissinger Springs, <u>McFarlin 103</u>, 14 July 1931 (MICH). ALACHUA COUNTY, San Felasco Hammock, 14 mi NW of Gainsville, <u>Uyenco 38</u>, 6 Feb. 1963 (MSC); scrub oak forest, 8 mi SE of Gainsville, <u>Uyenco 49</u>, 7 Feb. 1963 (MSC). HIGHLANDS COUNTY, Highland Hammocks State Park, Sebring, <u>Uyenco 79</u>, 11 Feb. 1963 (MSC mixed with <u>B. vulpina</u>and <u>B</u>. <u>domingensis</u>). LAKE COUNTY, Eustis, <u>Nash 1957</u>, May 28-June 15, 1895 (MSC).

NEW JERSEY: county unknown, Lehnert 188 (US).

NORTH CAROLINA: DUPLIN COUNTY, 1 mi E. of Beulaville, <u>Culberson</u> <u>10257</u>, June 1960 (MSC).

#### WEST INDIES

CUBA: LA VILLAS PROVINCE, near Topes de Collantes (TB sanatorium), Trinidad Mts., <u>Imshaug 24624</u>, 2 Aug. 1959. ORIENTE PROVINCE, Loma del Gato, Armenia-cultivated area on slope of El Gato (towards sea), Sierra Maestro, <u>Imshaug 24813</u>, 12 Aug. 1959, both in MSC.

HAITI: DEPT. DE L'OUEST, elfin woodland type thicket, ca. 5300 ft, road from Foret des Pins to Savane-Zombie, <u>Wetmore 3002</u> pr. p. DEPT. DU SUD, Massif de la Hotte, near summit of Morne Macaya, 7000 ft, <u>Wetmore 3345</u>, 27 July 1958, both in MSC.

JAMAICA: HANOVER PARISH. Birchs Hill, 1809 ft. Imshaug 15680 and 15698, 24 Apr. 1953. ST. ANDREW PARISH, Bellvue to Mt. Rosanna, 3800 ft, Imshaug 14470, 4 Feb. 1953; Bloxburgh Ridge, 3100 ft, Imshaug 15051, 3 Mar. 1953; west of Coopers Hill, Red Hills, 2500 ft, Imshaug 14133, 27 Jan. 1953; Flora River, 2700 ft, Imshaug 14422, 3 Feb. 1953; Halberstadt House to Bloxburgh Ridge, 2800 ft, Imshaug 15027, 3 Mar. 1953; John Crow Peak, 5750 ft, <u>Imshaug</u> 15356, 27 Mar. 1953; New Haven Gap, 5750 ft, Imshaug 15115, 4 May 1953. ST. ANN PARISH, Green Park to Claremont, 1400 ft, Imshaug 15874, 7 May 1953; Alexandria to Brown's Town, 1800 ft, Imshaug 15941, 7 May 1953. ST. CATHERINE PARISH, Hollymount, Mt. Diablo, 2754 ft, Imshaug 14230, 28 Jan. 1953; Montpelier summit, 2300 ft, Imshaug 14301, 20 Jan. 1953; Mount Diablo, 2600 ft, Imshaug 13776, 18 Dec. 1952. ST. THOMAS PARISH, north slope below Cuna Cuna Gap, 2300-2500 ft, Imshaug 13219; Farm Hill, 4000. ft, Imshaug 14791, 21 Feb. 1953; south slope of Mossmans Peak, 5000 ft, Blue Mts., <u>Imshaug 14657</u>, 19 Feb. 1953, all in MSC.

PUERTO RICO: near Barranquitas, <u>Jelliffe</u>, 22 Feb. 1927 (MICH ex hb. Fink 15649).

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Bombyliospora domingensis, showing rugose thallus, and gyrose apothecia with sterile columns.


Bombyliospora flavidula, showing aggregated apothecia with rather thin margins. The apothecia are more regular in shape than those of other Spiroblastiae.



Bombyliospora vulpina, showing gyrose and aggregated apothecia, smaller than those of other Spiroblastiae, with fuzzy disks.



Lopadium leucoxanthum, showing large apothecia with fuzzy disks; pruina clings to the inner edge of the margins. The thallus is white and granular.



Plate 5. Apothecial Types

epi--epithecium, hym--hymenium, sbh--subhymenium, exc-exciple, alg--algae, med--medulla, cor--cortex, amp-amphithecium, sub--substrate.

- Fig. 1. Represents all K+ rose <u>Bombyliosporae</u> and <u>Lopadia</u> except <u>L. fuscoluteum</u>.
- Fig. 2. Represents L. fuscoluteum.





Plate 6. Spores of Bombyliospora domingensis

- Fig. 1. Young spores in an ascus. The endospore has just begun to thicken; three lines of thickening are visible.
- Fig. 2. Bulges on the inner wall are ridges of endospore.
- Fig. 3. A mature spore with annular endospore thickenings separating eight secondary locules.
- Fig. 4. An oblique view of an immature spore like the one in fig. 5, where the endospore thickenings are approaching each other from the sides of the spore, but have not yet met.
- Fig. 5. An immature spore with eight protrusions connected by a central tube. (The above all in Turtox medium)
- Fig. 6. A mature spore with two annuli, and the rest of the endospore spiroform. The primary locule has become septate. Freshly mounted in Diaphane.
- Fig. 7. A mature spore with a combination of annular and spiroform endospore. A week-old mount in Diaphane.
- Fig. 8. A mature spore with two ridges of spiroform endospore, starting opposite each other. In Diaphane.
- Fig. 9. A mature spore crushed in water; the outer wall has broken, allowing the two spiroform locules to extend like released springs, and curve slightly to the right.

The scale units represent 10 microns.

Plate 6. Spores of Bombyliospora domingensis



Plate 7. Other Spore Types

- Fig. 1-5 are Bombyliospora vulpina
- Fig. 1. Young spore in ascus. All the endospore annuli have met in the center except the top one. In Diaphane.
- Fig. 2. Two young spores in an ascus. The secondary locules have a few transverse septa. (The below were all mounted in water.)
- Fig. 3. Two mature spores in an ascus. Several locules of the lower spore are situated at an angle to the long axis of the spore, indicating that the endospore there is probably spiroform.
- Fig. 4. A mature spore with the falsely-muriform appearance.
- Fig. 5. The outer wall is ruptured, and individual secondary locules are released. Four are in the picture; one is lying nearly flat.
- Fig. 6. <u>Lopadium</u> cfr. <u>dodgei</u>, showing the minute, round, regularlyarranged spore cells, and the wide "hale."
- Fig. 7. <u>Lopadium leucoxanthum</u>, showing the minute, variously-shaped, irregularly-arranged spore cells and the thin wall.
- Fig. 8. A single secondary locule of <u>B. domingensis</u>, lying flat; eight tertiary locules are present, with one circle around a central locule.
- Fig. 9. A single secondary locule of <u>B</u>. <u>vulpina</u>, showing two concentric circles of tertiary locules.

The scale units represent 10 microns.



Plate 8. Spore development in Bombyliospora domingensis

- Fig. 1. Very young spore; the endospore has not begun to thicken.
- Fig. 2-5: the spiroform tendency
- Fig. 2. endospore has just begun to thicken
- Fig. 3. primary locule has the appearance of an auger; the central tube is visible.
- Fig. 4. central tube has been obliterated.
- Fig. 5. primary locule has become septate
- Fig. 6-9: the lentiform tendency
- Fig. 6. primary locule has just become scalariform
- Fig. 7. future secondary locules are becoming lentiform; the central tube is still present
- Fig. 8. central tube has been obliterated; secondary locules are complete
- Fig. 9. secondary locules have a few septa



Plate 9. Spore variation in Bombyliospora domingensis

- Fig. 1. only one annulus is complete
- Fig. 2. half the spore has spiroform endospore, half, annular.
- Fig. 3. both ends have spiroform endospore, the middle, annular.
- Fig. 4. a young spore in KOH; the ends have annular endospore, the middle, spiroform.
- Fig. 5. ends spiroform, middle, annular.
- Fig. 6. upper end with annular endospore, lower with spiroform; one annulus incomplete.
- Fig. 7. most of spore with lentiform secondary locules not forming acute angle at spore edge, and some septate; lower end with spiroform endospore.
- Fig. 8. half the spore has septate lentiform locules forming acute angles at spore edge, half has septate spiroform locule.
- Fig. 9. septate locules not forming acute angles at spore edge, all thickenings annular.
- Fig. 10. sparsely septate primary locules; one complete spiroform locule, part of an additional one.
- Fig. 11. much septate, single spiroform locule; all thickenings spiroform.



## Plate 10

- Fig. 1. Mature spores of <u>Bombyliospora</u> <u>aureola</u>; the end two each have one incomplete annulus.
- Fig. 2. Mature spores of <u>B</u>. <u>flavidula</u>.
- Fig. 3. Septate secondary locules of <u>B. domingensis</u> var. <u>transgressa</u> (<u>Malme 1500 Aa</u>, MO) escaping from ruptured spore wall.
- Fig. 4. Stylized diagram of typical young spore of a member of section Bombyliospora; the endospore annuli are beginning to pinch the primary locule apart, but the spore does not appear to contain a tube.











Plate 11. Spore variation in <u>Bombyliospora</u> sp., Imshaug 15028

- Fig. 1. Spore type found in most specimens, of least frequency in this specimen.
- Fig. 2. Spore type most frequent in this specimen, similar to that pictured by Zahlbruckner in Engler and Prantl 1905 and 1926, for <u>B. incana</u>.
- Fig. 3. One end has spiroform locule, becoming septate; the remaining has annular thickenings. One spore was seen with entirely spiroform thickening.
- Fig. 4. The "membrane" surrounding each locule is greatly enlarged; it is a structure and not a cavity. The lines between are not cell walls, as shown by the fact that they do not extend into the endospore (compare <u>Nephroma helveticum</u> var. <u>helvaticum</u> in Wetmore, 1960).

Plate 12. Lines of evolution in Bombyliospora

- Fig. 1. young spore, represents all species
- Fig. 2. <u>B. domingensis</u>, lentiform type
- Fig. 3. <u>B. vulpina</u>
- Fig. 4. <u>B. flavidula</u>
- Fig. 5. <u>B. aureola</u>
- Fig. 6. <u>B. pachycheila</u>
- Fig. 7. <u>Bombyliospora</u> sp., represents <u>B. porphyrites</u>, <u>B. tuberculosa</u>, <u>B. incana</u>, <u>B. amplificans</u>, and others.



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Plate 13. Distribution Map of Bombyliospora domingensis



Plate 14. Distribution Map of Other Spiroblastiae

solid circles = <u>Bombyliospora</u> <u>vulpina</u> open circles = <u>B. flavidula</u> solid triangle = <u>B. flavidula</u> and <u>B. aureola</u>



Plate 15. Distribution Map of Lopadium leucoxanthum

All maps are Good's Base Map No. 213.



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