

MORPHOLOGICAL AND ANATOMICAL
STUDIES IN SOME GENERA
OF THE PANNARIACEAE

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ABSTRACT

MORPHOLOGICAL AND ANATOMICAL STUDIES IN SOME GENERA OF THE PANNARIACEAE

by Carol Mayalata Michael

This study is primarily on the morphology and anatomy of some species of each of the following genera: Coccocarpia, Erioderma, Hydrothyria, Massalongia, Pannaria, Parmeliella, Placynthium and Psoroma. These genera were studied to find some anatomical characters which might be used in the taxonomy of the Pannariaceae. Little anatomical work has been done recently on this family, hence a need was felt for this study. Some species from the West Indies and some from the United States were utilized for this study. There has been no uniformity in the terms used for the different tissues in the thalli and apothecia and it is hoped that the terms used here can be of help as far as uniform terminology is concerned.

First, the anatomical characters of the apothecium and then those of the thallus are used in suggesting any

change in the present circumscription of the Pannariaceae. In addition, phylogenetic advancement in the family is revealed by the increasing complexity of some fungal tissue, e.g., from lower pseudocortex in Hydrothyria venosa to a true lower cortex in Massalongia carnosa. Relationships between the genera are evident. Algal characters can be used to a great advantage along with the fungal characters in identifying the genera and sometimes even the species, but they are of no taxonomic value by themselves.

The apothecial characters are very interesting. Although the apothecia in Pannariaceae were formerly thought to be either lecanorine or lecideine, they appear to me to be lecanorine or mycolecanorine.

Since anatomy and morphology of Placynthium nigrum is quite different from the others, it is suggested that this species be removed from the Pannariaceae and be placed in a family of its own.

It is also suggested to leave Erioderma physioides as a species of Erioderma and not be made the type species of new genus Malmella.

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SOME GENERA OF THE PANNARIACEAE

By

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I

INTRODUCTION

The purpose of this investigation of the family Pannariaceae is 1) to search for new characters that might be used in the taxonomy of the family, 2) to evaluate the advisability of recognizing Placynthiaceae as a family, and 3) to evaluate the advisability of recognizing Malmella as separate genus.

The genera studied were: Coccocarpia, Erioderma, Hydrothyria, Massalongia, Pannaria, Parmeliella, Placynthium and Psoroma. Representatives of available species of these genera were studied both morphologically and anatomically. This paper deals with genus Erioderma in the greatest detail and a key to the species studied is provided; also a key to the genera, based on the species identified, is included. The specimens for this study were obtained from Dr. H. A. Imshaug's collection of West Indian lichens and from the general lichen herbarium at Michigan State University. The type specimen of Erioderma

microcarpa was borrowed from Conservatoire Botanique, Geneva, Switzerland, and the other species of Erioderma seen for this study were obtained from University of Michigan herbarium. Most of the species studied are tropical ones.

The Pannariaceae has been and is in great need of study. Many changes have taken place since this family was established by Tuckerman (1872). New genera have been included and original genera excluded. This has been due to a lack of complete information about any particular genus, and, of course, because of different ideas about morphological and anatomical characters. This study is necessarily of a preliminary nature, but some new characters have been noted which have not been mentioned before and it is hoped that they will be of some help towards more extensive work.

All the original descriptions of the genera, as well as those of species of Erioderma have been obtained and referred to when necessary; a historical survey of the Pannariaceae is also included. The description and the plates of the genera and their species are arranged alphabetically. In the last section detailed drawings

and diagrams are given. Drawings of both thallus and apothecium of each species are included except a few cases where only one or the other is provided.

II

HISTORY OF THE FAMILY PANNARIACEAE

The composite nature of the lichen thallus was not known until 1867 (Schwendener). Prior to this time it was impossible to consider the algal component in the taxonomy of the lichens. When the Pannariaceae was described for the first time by Massalongo (1855), and later by others, only the morphological characters of the thallus and apothecium seemed to be important.

Massalongo (1855) divided lichens into several orders, order No. VII being the Parmeliaceae. He divided the Parmeliaceae into many tribes and one of them was Pannariaceae. The genera he included in this tribe were, Pannaria (this was under Lecidiaceae according to Bory, 1828), Capodium, Massalongia, Polyzosia and Sporoaconia. He put Psoroma in a separate tribe (Psoromae) along with Fulgenia, Gyallolukia, Solenospora, Niospora and Acarospora. Before this Psoroma was often included in the Lecanoraceae. The tribes were mainly separated on the

basis of whether they were foliose or crustose. Sometimes it was hard to separate one growth form from the other, and therefore, foliose species were occasionally put with crustose ones and vice versa.

In the same year (1855), Nylander described Pannariei as a subtribe of Lecanorei and included the following genera: Erioderma, Pannaria, Coccocarpia, Cora and Dichonema.

Koerber, also in 1855, described the Pannariaceae as a subfamily of Lecanoreae including Pannaria and Massalongia. The genus Psoroma was put in the next family, Placodinae.

Mudd (1861) considered the subtribe Pannariaceae in the tribe Lecanoreae and included Pannaria, Massalongia and Amphiloma in it.

Nylander (1861) once again described Pannariei as a subtribe of the tribe Pyxinae and included Heppia and Pannaria.

Reinke (1895) described Pannarieen as a family under the order Cyanophili. Within this category he included Placynthium, Leptoqidium, Polychidium, Heppia, Heterina, Leprocollema, Parmeliella, Stictina, Sticta,

Ricasolia, Pannaria, Lepidocollema, Psoroma, Erioderma, and Hydrothyria. Before this, some species of Erioderma belonged to the Peltigeraceae, some to Stictaceae and some to the genus Lichen. The genus Hydrothyria was put under Collemaceae by Russell (1853).

Zahlbruckner (1907) introduced some better ideas about the classification of lichens and based them on more natural character. He recognized Pannariaceae as a family and included Psoromaria, Psoroma, Lepidocollema, Lepidoleptogium, Pannaria, Hueella, Parmeliella, Placynthium, Erioderma, Coccocarpia and Hydrothyria. He gave the following key for their identification.

A. Thallus with dark green phycobiont.

I. Apothecium biatorine.....Psoromaria

II. Apothecium lecanorine.....Psoroma

B. Thallus with blue-green gonidia.

I. Lower surface of the thallus indistinctly veined; prothallus and rhizoids usually well-developed; spores one-, seldom two-celled, colorless.

a. Upper cortex narrow, indistinct; algal layer almost taking up the entire breadth of the thallus.....Lepidocollema

b. Upper cortex well-developed, distinct.

1. Upper cortex arising from the hyphae which are perpendicular to the surface.

(a) Upper surface of the thallus naked.

(1) Thallus with Nostoc.

[a] Apothecium lecanorine.

[1] Upper cortex paraplectenchymatous, lower cortex lacking.....
.....Lepidoleptogium

[2] Upper and lower cortices well-developed.

a) Spores one-celled
.....Pannaria

b) Spores two-celled
.....Hueella

(2) Thallus with Scytonema.

[a] Apothecium biatorine or lecidienne.

[1] Spores one-celled...
.....Parmeliella

[2] Spores two-celled...
.....Placynthium

(b) Upper surface of the thallus shaggy
.....Erioderma

2. Upper cortex arising from the hyphae which occur horizontally.....Coccocarpia

II. Under surface of the thallus veined; prothallus and rhizoids lacking; spores parallel, 4-celled
.....Hydrothyria

Zahlbruckner (1907) considered the Pannariaceae as closely related to the Heppiaceae and the Stictaceae. The structures of the thallus and the apothecium of members of the Pannariaceae are intermediate between the two families and the Pannariaceae is united to both by the intermediate genera, Lepidocollema of the Heppiaceae and Lobaria of the Stictaceae. This made the correct placement of the Pannariaceae difficult. These three families perhaps represent a monophyletic series, the origin of which Reinke (1895, p. 344) considered as the genus Parmeliella. Reinke (1895) also pointed out the close relationship between the Pannariaceae and the Peltigeraceae, which is clearly indicated by genus Hydrothyria. Zahlbruckner (1907) later suggested that Psoroma should be included in the Pannariaceae in spite of its having dark green algae. Before this Psoroma was placed in the Lecanoraceae as a section of Lecanora.

Hue (1912) reduced the whole family Pannariaceae to one genus, Pannaria. His sections and subsections of the genus corresponded more or less closely to the genera of the other workers.

According to Smith (1921), the Pannariaceae and the Heppiaceae are intermediate between families, with less

developed, gelatinous and homoiomerous thalli and those with advanced and entirely heteromerous thalli. She saw an evolutionary development within the family from genera with blue-green phycobionts (the large majority) to two (Psoroma and Psoromaria) having green phycobionts.

Vainio (1923) included Megalospora, Physcidia and Heterodea in the Pannariaceae. They were shifted to Parmeliaceae by Zahlbruckner in 1926.

Zahlbruckner (1926) included the same genera in the Pannariaceae as he did in 1907; they were Hydrothyria, Lepidocollema, Massalongia, Lepidoleptogium, Placynthium, Parmeliella, Pannaria, Hueela, Psoroma, Psoromaria, Coccocarpia, and Erioderma (listed here according to Zahlbruckner's phylogenetic arrangement of the genera).

Dodge (1933, p. 438) wrote, "In many ways the family (Pannariaceae) seems very homogeneous, so that genus distinctions are often rather arbitrary." He recognized the following seven genera from tropical America: Psoroma, Lepidocollema, Pannaria, Malmella, Parmeliella, Erioderma, and Coccocarpia. He formed the new genus Malmella by combining one species of Erioderma (E. physioides) and one species of Pannaria (P. rubiginosa f. cinerascens) and adding three new species.

Gyelnik (1940) included the following genera in the Pannariaceae: Massalongia, Hueela, Placynthiella, Parmeliella, Pannaria, Molleropsis, and Vestergrenopsis (the last two being gen. nov.). However, he put the genus Psoroma in the Stictaceae. He gave more importance to spore characters in separating the different genera and used thallus characters--heteromerous or homoiomerous. He removed the genus Placynthium from the Pannariaceae and put it in the Lichenaceae. He considered the Pannariaceae as closely related to the Heppiaceae and Lichenaceae.

Räsänen (1943), like Zahlbruckner (1926), placed the Pannariaceae between the Heppiaceae and the Stictaceae. He did not make major differences in the previous circumscription of the family Pannariaceae but included 7 more genera than did Zahlbruckner. The nineteen genera that he included in this family were: Hydrothyria, Coccocarpia (and its two sections Subimbricaria and Umblicularia), Erioderma, Theliodea (which Zahlbruckner considered as a genus of doubtful position), Psoromaria, Psoroma, Hueella, Massalongia, Pannaria, Placynthium, Amphidium (syn. Steinera, which Zahlbruckner had in Lichenaceae), Placynthiopsis, Huillia, Parmeliella, Lepidocollema, Lepidoleptogium, Megalospora, and

Physcidia and Heterodea (the last three genera having been put in the Parmeliaceae by Zahlbruckner).

Dahl (1950) formed the new family Placynthiaceae to include Placynthium, formerly in the Pannariaceae, Porocyphus, formerly in Ephabaceae, Pterygium, formerly in Lichenaceae (Zahlbruckner 1926), and Vestergrenopsis, formerly in Pannariaceae (Gyelnik 1940). When Dahl (1950) was describing Porocyphus from Greenland he was aware that Placynthium and Porocyphus were morphologically and anatomically much alike. He also observed that Placynthium and Pterygium were much too similar to be put in two separate families. According to him the anatomy of the thallus lobes of Vestergrenosis isidiata and those of Placynthium pannariellum are almost alike. He suggested that instead of putting the four closely related genera, Porocyphus, Placynthium, Pterygium, and Vestergrenopsis, in three different families, they should be put together in one separate family which he called Placynthiaceae.

Dahl (1950) presented two major differences between Pannariaceae and Placynthiaceae. He studied the algae in both families by setting them free in a quetsch (crush-mount) preparation. In the Pannariaceae he observed that the algae are true Nostoc (typical rosary-like chains with smooth

globose cells) with no distinct orientation of chains within the thallus. He commented that very often in some species of Pannariaceae scytonemeiform (Scytonema-like) Nostoc occurs. Dahl calls the algae found in Pannaria and other genera of Pannariaceae "nostociform" whereas in Placynthiaceae he calls it "scytonemeiform," because in the latter the algal cells are larger, irregularly globose, and in irregular chains.

The second important difference between the Pannariaceae and the Placynthiaceae that Dahl observed was that in the latter there is a distinct tendency toward forming minute areoles in the thallus; this does not occur in the Pannariaceae.

Dahl further reported that though the external morphology of Coccocarpia in some respects approaches that of the other members of the Pannariaceae, he thought that, according to Bornet's (1909) figures, it has scytonemeiform algae. Dahl does not say clearly whether Coccocarpia should be included in the Placynthiaceae, but if keyed out according to his key it does come under this family rather than under Pannariaceae.

By recognizing Placynthiaceae as a separate family Dahl has made Placynthium the type genus and has included Pterygiopsis, Porocyphus, Pteridium and Vestergrenopsis,

within the family. He also thought that Leptogidium, Lichenodium, Lichenella, Homospella, and perhaps Asirosiphon may belong to this family as well.

Dahl also suggested that Erioderma should be placed in a family of its own, but he did not propose the name. This family, he said, should have a similar relationship to the Placynthiaceae as Peltigeraceae has to Pannariaceae. He came to this conclusion because Erioderma has scytonemiform algae but since the thallus differs considerably from that of members of the Placynthiaceae, he did not recommend including it in that family.

Thus Dahl (1950) put the following genera in the family Pannariaceae; Hydrothyria, Lepidocollema, Lepodoleptogium, Massalongia, Parmeliella, Pannaria, Hueella, Psoroma, Psromaria, and Placynthiella (Gyelnik 1940).

Recently Choisy (1960) recognized Pannariaceae and Placynthiaceae as separate families. His work was mostly concerned with the genera from these families found in a particular region of France.

Hale (1961) included Placynthium in the Pannariaceae. According to him most of the species belonging to the Pannariaceae are crustose or squamulose and very rarely are subfoliose and foliose.

III

MORPHOLOGICAL AND ANATOMICAL CHARACTERS

Methods of Study:

The morphological and anatomical characters of both the thallus and apothecia were studied. Microtome sections were made in the following manner. The specimen was soaked overnight in "Photoflo" (a concentrated liquid wetting agent). The material was mounted on the freezing disk of the microtome in a drop of gum-Arabic. Sections were cut at approximately 15 μ thickness and were picked up with the help of a camel-hair brush, deposited in a watch glass containing water, and selected. The selected sections were stained in acid fucshin (10-15 minutes) and were passed through an alcohol series (from 70 percent to 100 percent) for 10-15 minutes in each of the series. Finally they were put in butyl alcohol for 15-20 minutes and mounted in diaphane. If the material was too small (e.g., Placynthium nigrum) it was embedded in agar and the agar blocks were then mounted on the freezing disk. The sections thus made were studied and drawn by means

of camera-lucida. Both algal and fungal components were noted and compared among the species. The orientation of the hyphae and algal filaments was carefully considered for possible use as a generic or specific character.

Thallus:

The lichen thallus is composed of both fungal hyphae and algal colonies, each with a definite growth form. The thallus characters in the family Pannariaceae have not been uniformly described by lichenologists and different terms have often been used for the same tissue. One of the objectives of this study was to compare the tissues in the various species in the Pannariaceae and describe them by using a uniform terminology.

Morphology of the Thallus:

The thallus in the Pannariaceae varies from foliose to almost crustose. The best example of a foliose thallus is that of Erioderma Wrightii in which the lobes are exceptionally large for the family as a whole; they are 1.0-1.5 cm broad. Other species of Erioderma are also foliose but their lobes are not so large as those of E. Wrightii.

Additional examples in the family having foliose thalli are species of Parmeliella, Pannaria lurida, Massalongia carnosa, and Hydrothyria venosa. These species have thallus lobes 0.6-1.0 cm broad.

Species with thallus lobes smaller than would be found in typical foliose thalli are termed "subfoliose." The lobes of the subfoliose species are 3.0-5.0 mm broad. These species are Pannaria leucosticta, Psoroma hypnorum, and a few others belonging to the genera, Pannaria, Parmeliella and Psoroma.

Species with thallus lobes 1.5-3.0 mm in size are called squamose in this study, examples are: Parmeliella lepidiota, Parmeliella microphylla, and Pannaria pezizoides.

The thallus of Placynthium nigrum is basically crustose, being broken into small areoles. These areoles are 1.0-1.5 mm wide.

Sometimes the defining line between foliose and squamose is very fine and it is often hard to say whether a given thallus is one or the other.

The color of the thallus varies in different genera, even between the species. It can be yellowish-green, brownish, or black.

In foliose species the primary lobes divide dichotomously to form secondary lobes or lobules. Lobes are mostly contiguous, and sometimes imbricate with swollen tips as in Massalongia carnosa or with crenate tips as in Pannaria rubiginosa.

The thallus surface is either tomentose or glabrous. Sometimes the sides of the apothecia have the tomentum though the thallus is without any, as in Hydrothyria venosa and in Massalongia carnosa. Hairs are septate or non-septate, and branched or simple, arranged densely or sparsely and are colorless.

Either isidia or soredia or both may be present. Isidia are mostly marginal and are concolorous with the thallus or are either white or grayish, and globular or cylindrical in shape. In Massalongia carnosa they are concolorous with the thallus and are marginal and corolloid. Isidia were seen in cross-section in Coccocarpia ciliata; they had 1-2 layers of cortical cells and 2-6 algal cells. They do not occur as often as soredia in this family.

Soredia occur on the upper surface, they are farinose and are either marginal or scattered in groups. They are small microscopic bodies consisting of few algal cells

accompanied by few gelatinized hyphae, are non-corticate and often bluish-white. All the genera studied here have sorediate species except Placynthium and Massalongia.

Rhizinae occur on the under side of the lower margins of the thallus. They are usually quite dense and are black, brown, or even pale. Hyphae in the form of cords extend from the lower part of the medulla, pseudocortex or lower cortex, to the substratum and anchor the thallus firmly. They are either on the entire underside, or just on the lower margins, or on the underside exclusive of the margins.

Lichenologists, e.g., Smith (1921) and Hale (1961), have distinguished between a hypothallus and a prothallus, although they both are non-lichenized tissues within the lichenized thallus.

Tulasne (1852) recorded the thallus growth in Verucaria muralis, which is an epilithic crustose species. He observed that the spore on germination produces a delicate branching, septate hypha which produces radiating secondary hyphae on all sides. Zukal (1895) called this beginning of a thallus a prothallus or protothallus. The hyphae of the prothallus adhere to the substratum and form

a kind of plectenchymatous tissue. Algae come in contact with these fungal hyphae and the contact between the two increases their growth and cell division. Zukal (1895) also observed that the hyphae in contact with algae become more and more thin-walled and produce many new branches. Some of these new branches grow upwards and form the cortex and some grow downwards and build up the medulla, but the hyphae at the circumference continue to advance and may start new areas for the algae to come in contact with; these areas he called the prothallus or protothallus.

Smith (1921) said that the prothallus becomes overgrown and obscured by the vigorous increase of the first formed lichenized tissue and can be seen as a white or dark line bordering the thallus. Earlier, Schwendener (1866) stated that the lichens which develop from the spores have a prothallus (protothallus) and those which arise from soredia do not have this first thalline tissue.

Hale (1961) explained that the hypothallus is a thin layer of non-lichenized hyphae which projects beyond the main thallus and appears as a thin black rim, and according to him, its function is unknown. Smith (1921) recognized the hypothallus as formed by an unusual development

of hyphae from the lower medulla or lower cortex. These hyphae become dark-brown and are divided into thick-walled cells. Frequent branching and anastomoses of these hyphae result in a cushion-like structure as in Anzia colpodes and Pannoparmelia anzioides (Fig. 51, Smith, 1921). Fink (1935) said that hypothallus is the first growth of hyphae before any differentiation has taken place, and it often persists as a dark layer below or surrounding a few lichen thalli.

The hypothallus is a special tissue which forms a rather thick, cushion-like structure of thick-walled, branched, and cellular hyphae, as in Pannoparmelia anzioides (Fig. 51, Smith, 1921). A dark line bordering the thallus can be very distinctly seen in Parmeliella plumbea and Parmeliella pannosa. Underneath the thallus, a mat of rhizinae is also formed in these species. This dark line of hyphae bordering the thallus and forming a mat underneath, belong to the prothallus (Dodge, 1933, called this hypothallus). In a cross section of the thallus the mat of rhizoidal tissue is very clearly seen (Plate 19). This tissue is formed of parallel, conglutinate hyphae which do not form a thick cushion-like, arachnoid tissue. Although the tissue appears

Although the tissue appears hypothalline in cross-section, it would seem to be prothalline in origin.

Anatomy of the Thallus:

Wallroth (1825, l. in Smith, 1921) was the first to study and compare different lichen thalli from an anatomical standpoint. He called lichens in which algal cells are distributed uniformly along with the fungal hyphae through the entire thallus "homoiomorous," and those in which they are confined to a distinct zone "heteromorous" Smith (1921, p. 21). The Pannariaceae along with Heppiaceae form a transition between the gelatinous and mostly homoiomorous thallus and the true heteromorous thallus (Smith, 1921, p. 286). In Parmeliella microphylla and Placynthium nigrum (Plates 18 and 21 respectively) the algae occupy the entire thickness of the thallus. In these two cases a cortical layer surrounds the part of the thallus in which the alga and fungus are distributed without any definite layers.

1. The upper cortex in the Pannariaceae is paraplectenchymatous. Lindau (1899) introduced term "plectenchyma," by which he meant any tissue of hyphae. He also introduced

the terms parenchymatous plectenchyma or paraplectenchyma and prosenchymatous plectenchyma or prosoplectenchyma, the former denoting the tissue with more or less isodiametric cells (the more typical "pseudoparenchyma") and the latter denoting that with more elongated cells.

The hyphae in the upper cortex are oriented in different ways. They are parallel to the surface of the thallus in Erioderma physioides (Plate 5), Hydrothyria venosa (Plate 11), Pannaria lurida (Plate 15), and Parmeliella microphylla (Plate 18) and they are almost parallel to the surface of the thallus in Coccocarpia Gayana (Plate 1). The hyphae are vertical to the surface of the thallus in Parmeliella plumbea (Plate 19), Parmeliella pannosa, and Massalongia carnosa (Plate 13). The hyphae of the upper cortex are irregularly arranged or diffuse in Erioderma Wrightii (Plate 9), Erioderma polycarpa and some other species of Coccocarpia.

The upper cortex varies in thickness from one to many cells. In Placynthium nigrum (Plate 21) it is just one cell thick and completely surrounds the areole of the thallus. It is 2-3 cells in Parmeliella microphylla (Plate 18) and the hyphae are thick-walled. The layer is 1-2 cells thick in Massalongia carnosa (Plate 13) and the hyphae here too are rather thick-walled.

In all the species of Erioderma that are studied here, except E. limbatum, the upper cortex is covered with a tomentum. These hairs are cylindrical, either straight or curved. They are mostly unbranched and occasionally septate, and are either dense or sparse. The tomentum is made up of the thickened ends of more or less vertical hyphae.

2. The algal layer comes next to the upper cortex. This layer is usually narrower than the medulla, although in Parmeliella microphylla (Plate 18) and Placynthium nigrum (Plate 21) it is the widest layer. In these species the medullary layer is absent and the whole thickness of the thallus is taken up by the algal layer. In Psoroma pallidum (Plate 24), the algal layer is very narrow and the algal chains are not close together. In some species they are very densely packed, e.g., Parmeliella microphylla (Plate 18). The algae in the genera studied here are Nostoc, Scytonema in the cyanophyta, and Dactylococcus or Coccomyxa in the chlorophyta.

3. Below the algal layer is the medulla. It is usually a thick layer of loosely interwoven thin-walled hyphae, which are generally irregularly arranged. They are periclinal in

Coccocarpia Gayana (Plate 1), parallel to the surface of the thallus in Hydrothyria venosa (Plate 11), almost parallel to the surface in Erioderma physioides (Plate 5) and, parallel, clearly septate and branched in Massalongia carnosa (Plate 13).

In Erioderma physioides (Plate 5) the medullary hyphae are accompanied by special kinds of cells called spheroidal cells by Asahina (1952). He saw them for the first time in Parmelia sublaevigata. Culberson (1961) reported them in Parmelia galbina and called them moniliform cells. These cells are in the form of beaded filaments and take a pink stain with acid fucshin. The significance of these cells in the medulla is not yet clear.

4. All the species of family Pannariaceae that are included in this study except Massalongia carnosa (Plate 14), are without a true lower cortex. The above mentioned species has a true lower cortex since it is exactly like the upper cortex (Degelius, 1954). In some species there is a tissue below the medulla which looks like a cortex but does not resemble the upper cortex. This lower layer is called a pseudocortex by Degelius (1954). There are some doubts and arguments about the presence of a true cortex in different species of the Pannariaceae.

In Hydrothyria venosa (Plate 11), the lower part of the medulla has septate conglutinate hyphae and is best termed a pseudocortex. In some species of Coccocarpia the lower pseudocortex can be seen, Dodge (1933) called this tissue the lower cortex. The lower pseudocortex is an indistinct but easily recognizable layer where it is present.

Placynthium nigrum (Plate 21) has a cortical layer just one cell thick over all the exposed surfaces of the areole of the thallus as the outer most layer surrounding the areole. In Parmeliella microphylla (Plate 18) a lower pseudo cortex is present. The difference between this and the upper cortex is quite clear because the tissue in the lower pseudocortex is loose as compared to the upper cortex.

5. Rhizinae arise from the under surface of the thallus and are either black or brown. They extend from the lower part of the medulla, lower cortex, or the lower pseudocortex. The rhizinae are simple or branched, septate or non-septate, in groups or single; they often anastomose. There is thick prothalline mat formed by the rhizoidal hyphae in Parmeliella plumbea (Plate 19), Parmeliella pannosa and

Coccocarpia pellita. Presence of this tissue is not a diagnostic character for any genus.

Apothecia:

There has been much confusion concerning the usage of the terms for different tissues in the apothecium of the family Pannariaceae. The terms I have used here are those which were adopted by Degelius (1954).

Morphology of the Apothecia:

When apothecia are present, they are found on the upper surface of the thallus. They are either abundant or rare and can be either marginal or scattered. In most of the species they are sessile, although in all the species of Erioderma they are stipitate. In many species of Coccocarpia they are adnate to the thallus.

The apothecia are usually circular and flattened (disk-shaped). Sometimes they are slightly convex as in Coccocarpia pellita (Plate 3) or slightly concave as in Psoroma hypnorum (Plate 23). The apothecia may become irregular as a result of crowding.

The sizes of the apothecia differ considerably, even in the same species. However the average mature apothecia are 1.0-1.5 mm in diameter in most of the species except Placynthium nigrum where they are 0.3-0.5 mm in diameter.

The development of the apothecia can be either angiocarpic or gymnocarpic. Corner (1929) explained these types, and also the intermediate type, the hemiangiocarpic development. He presented a series of diagrams showing the angiocarpic development of an apothecium in the Discomycetes. Gaumann (1952) labeled the same series of diagrams as those of a hemiangiocarpic apothecium. Whatever the case may be according to the definitions, in the angiocarpic development the hymenium is formed within a mass of interwoven hyphae, called the primary sheath; in the gymnocarpic development the hymenium is superficial from the beginning. The species of Erioderma (E. limbatum, E. physioides, E. polycarpa, and E. microcarpa) have angiocarpic or hemiangiocarpic type of development. Massalongia has hemiangiocarpic type of development of its apothecia (Henssen, 1963), i.e., one in which hyphae do not form a closed sheath.

The margins of the apothecia are usually lighter in color than their disks. The apothecial disk is brown to black in color and is not pruinose generally.

Anatomy of the Apothecia:

Dughi (1952) postulated some new theories about apothecial anatomy. He emphasized that an apothecial cortex is different from a thallus cortex in that the former is produced by the exciple. He divided the different types of apothecia into six categories according to their anatomy.

1. Lecideine apothecia: In which the exciple is uniform and there are no algae in the margins.
2. Superlecideine apothecia: In which the exciple becomes cortical in character.
3. Lecanorine apothecia: In which there are algae in the margins. A cortex and medulla are often developed.
4. Mycolecanorine: In which there are no algae in the margins, but cortex and medulla are developed.
5. Cryptolecanorine apothecia: In which the excipular hyphae come into the thallus for symbiosis-immersed lecanorine.

6. Pseudolecanorine apothecia: In which the exciple is uniform but some algae accidentally occur in the margins.

Apothecia of the Pannariaceae have been called both lecanorine and lecideine. I do not think that any species of this family that I have examined has lecideine apothecia. All the species that I examined have the amphithecium as the outer most margin in the apothecia (though this is questionable in Coccocarpia). The amphithecium has a distinct cortex and medulla and is with or without algae in different genera. Therefore, according to my observations, the apothecia in the Pannariaceae are lecanorine (with algae in the amphithecium), and mycolecanorine (without algae in the amphithecium).

Among the genera I have studied, Pannaria, Massalongia (only M. carnosa studied), and Psoroma have lecanorine apothecia and Erioderma, Parmeliella, Hydrothyra, and Placynthium (only P. nigrum studied), have mycolecanorine apothecia. In the mycolecanorine apothecia the hyphae are not receptive to the establishment of a symbiotic relation with the algae (Imshaug, 1957).

1. Amphithecium is the outer most layer of the apothecia in the genera of the family Pannariaceae that were studied. The amphithecium may be with or without algae, making the apothecia lecanorine or mycolecanorine. The genera having lecanorine apothecia are Massalongia, Pannaria, and Psoroma (Plates 14, 16, and 23). In Massalongia carnosa (Plate 14) and Pannaris lurida (Plate 16) the amphithecium is clearly divided into cortex and medulla. The apothecia in Erioderma (Plates 4, 6, 7, and 8), Hydrothyria venosa (Plate 12), Parmeliella plumbea (Plate 20), and Placynthium nigrum (Plate 21) are mycolecanorine. The hyphal tissue in these species is rather compact on the outside (forming a cortex) and loose towards inside (forming the medulla).

In Hydrothyria venosa (Plate 12) and Massalongia carnosa (Plate 14) a tomentum is seen on the sides of the apothecia, coming from the outer most layer of the amphithecium. These hairs are formed by vertical or horizontal, septate or non-septate, colorless hyphae. The amphithecium is usually paraplectenchymatous and quite often the development of this tissue from the exciple can be seen very well from the orientation of the amphithecial hyphae.

2. The exciple is a very thin, pale tissue between the hymenium and the amphithecium and usually is not prominent. It is usually euthyplactenchymatous and less frequently paraplectenchymatous. Euthyplectenchyma is a hyphal tissue without a "cellular structure." In agreement with Degelius (1954) I consider this tissue to be loose or dense and made up of thin (filiform) or broad hyphae, which are more or less conglomerate. They may be parallel or not and have short or usually more or less long cells. Different kinds of euthyplectenchyma may be distinguished, e.g., a loose euthyplectenchyma of non-parallel hyphae, or dense one of parallel hyphae. The euthyplectenchymatous exciple runs parallel to the surface of the apothecium in the center and is perpendicular to it in the sides. Sometimes it is quite irregular. The limit of the exciple toward the amphithecium is quite sharp, but not so toward the subhymenium above, thus making it difficult to distinguish the subhymenial tissue from the exciple.

There are two other kinds of excipular tissues found in the Collemataceae which are discussed by Degelius (1954): subparaplectenchyma and euparaplectenchyma (Plate 25, redrawn from Degelins, 1954). Most of the species that

are studied here have an exciple of loose or dense euthyplactenchyma and few have of paraplectencyma. Coccocarpia Gayana (Plate 2), Coccocarpia pellita (Plate 3), Erioderma Wrightii (Plate 10), Hydrothyria venosa (Plate 12), Massalongia carnosia (plate 14), Placynthium nigrum and Psoroma hypnorum (Plate 23) have a loose euthyplectenchymatous exciple and the hyphae are parallel or almost parallel. In Pannaria lurida (Plate 16) the exciple is paraplectenchymatous. It is of irregular euthyplectenchymous tissue in Erioderma physioides (Plate 7), Erioderma polycarpa (Plate 8) and Parmeliella plumbea (Plate 20).

The thickness of the exciple varies in different species. In some it is quite wide below the hymenium, and the lateral margins extend right up to the surface of the apothecium as in Placynthium nigrum (Plate 21); in Hydrothyria venosa (Plate 12), the lateral margins of the exciple can not be distinguished from the amphithecium, but below the hymenium it is quite thick and distinct. In Coccocarpia (Plate 2 and 3) it is not easy to separate the exciple from the amphithecium; and, therefore, the labels in the plates for these layers is necessarily approximate and perhaps tentative.

Sometimes the excipular tissue has pigmented hyphae as in Erioderma physioides (Plate 7).

3. The subhymenium is a very thin layer between the hymenium and the exciple but above the hypothecium when the latter is present. In most cases the subhymenium is indistinct from the excipular tissue. It looks somewhat clearer in Erioderma Wrightii (Plate 7) though. Asci and paraphyses develop from this layer.

4. Some authors (Hue, 1906; Fink and Richards, 1915; Vainio, 1921, etc.) have called the central part of the excipular tissue as the hypothecium and its lateral margins as parathecium. But as Degelius (1954) explains, it is a special layer of thick-walled hyphae below the subhymenium and above the exciple. This layer is not seen in any of the species that have been examined.

5. The hymenium (thecium) consists of asci and paraphyses. The thickness of this layer differs in different species, usually varying between 30 and 100 μ . The hymenial layer is colorless, except the tips of the paraphyses and the gelatine which is brown and sometimes even black. This pigmented area forms the epithelial gell or epithecium. The iodine reaction of the hymenium of the species examined is I + blue.

6. The asci are shorter than the paraphyses, but their lengths and widths vary in different species. They are mostly clavate, e.g., Massalongia carnosa (Plate 14), Psoroma hypnorum (Plate 23), Parmeliella plumbea (Plate 20), Pannaria lurida (Plate 16) and Coccocarpia (Plates 2 and 3). The asci are cylindrical in Placynthium nigrum (Plate 21) and Hydrothyria venosa (Plate 12). They are oblong in most species of Erioderma (Plates 7 and 10), and in Erioderma polycarpa (Plate 8) the tips of the asci are pointed.

7. There are eight spores in each ascus arranged in one row (monostichous) or in two rows (distichous). Sometimes both arrangements can be seen in the same apothecium, e.g., Parmeliella plumbea (Plate 20), although one type usually dominates, as is seen in the species of Erioderma (Plates 7 and 10). The spores are usually non-septate. They are 2-celled in Coccocarpia Gayana (Plate 2) and Placynthium nigrum (Plate 22). In Erioderma Wrightii (Plate 7) and Massalongia carnosa (Plate 14), the spores are usually two-celled but three-celled spores can sometimes be seen. For Massalongia the presence of two-celled spores is a generic character. The spores in Coccocarpia Gayana (Plate 2), Erioderma Wrightii (Plate 7) and Parmeliella

plumbea (Plate 20), have a thick epispore, though it is not so thick in the latter two species as in the first one. The spores in all the species are hyaline. The shape of the spores does not vary a great deal in the family. The spores are mostly ellipsoid to oval with rounded or pointed ends. In Massalongia carnosa (Plate 14) and Placynthium nigrum (Plate 21), the spores are elongate elliptical to fusiform with somewhat pointed ends.

8. The paraphyses are numerous and develop from the subhymenium. They are club-shaped to filiform, e.g., Massalongia carnosa (Plate 14) and Psoroma hypnorum (Plate 24) respectively. They are unbranched in all the species studied. They are longer than the asci and almost reach the surface of the hymenium. Sometimes they are septate as in Coccocarpia Gayana (Plate 2). The tips of the paraphyses are thickened and take a dark brown or black pigmentation. The pigmented tips of the paraphyses are responsible for the color of the epithecium (area formed by the tips of the paraphyses). The epithecium can be seen in most apothecia without any difficulty. This region is very thick in Erioderma limbatum and is absent in Placynthium nigrum (Plate 22) and Psoroma hypnorum (Plate 24).

IV

THE PHYCOBIONTS

Most of the genera in the family Pannariaceae have blue-green algae (Nostoc, Scytonema, and maybe Ulothrix). However Psoroma has green algae, (usually called Dactylo-coccus but probably Coccomyxa). In thalli where Nostoc or Scytonema are found, their characteristic forms are not seen many times and correct identification is only possible by making separate cultures of the gonidia.

The cells of Nostoc are usually in the form of short chains (trichomes). The chains which can be from 2 cells to 10 cells long, are arranged irregularly in the thallus and sometimes form lumps or groups. Usually they are vertically arranged but occasional horizontal chains are also seen, as in Hydrothyria venosa (Plate 11). The cells of Nostoc are normally globose, but sometimes become irregular in shape by being compressed together, as in Hydrothyria venosa (Plate 11). Besides Hydrothyria and some species of Erioderma, Pannaria, and Parmeliella have Nostoc. Distinct

chain-sheaths are absent but individual cells are surrounded by a transparent gelatinous covering.

Scytonema, seen in the form of coiled chains, is found in Coccocarpia and in some species of Erioderma, Massalongia and Placynthium. Sometimes the coiled chains can be seen enclosed in thin sheaths as in Massalongia carnosa (Plate 13). Horizontal chains of Scytonema like the chains of Nostoc in Hydrothyria venosa (Plate 11), can be seen in Coccocarpia Gayana (Plate 1).

The cells of Nostoc and Scytonema appear yellowish-green in contrast to those of Dactylococcus (or Coccomyxa) in Psoroma, which are bright green.

The abundance of the algal chains differs in different species. In Parmeliella microphylla (Plate 18) the algal layer occupies the whole of the central part of the thallus so that the medulla is absent. On the other hand the algal layer in Psoroma pallidum is very thin (Plate 24). In all the species of Erioderma examined, the algal cells are not densely packed and the layer is quite thin. Massalongia carnosa (Plate 13) also has a somewhat loose, thin algal layer. Hydrothyria venosa (Plate 11) and Coccocarpia Gayana (Plate 1) have quite a thick algal layer and the algal filaments are closer together.

No work on the culture and identification of the algae was done in this study, therefore all the observations mentioned here are based on previous works. Additional research work on the identification and form details of the algae in Pannariaceae is greatly needed.

LICHEN SUBSTANCES

Not many chemical substances have been reported from the Pannariaceae because not much work has been done on the chemistry of this family. Hesse (1901) reported the presence of hydroxyroccellic acid and pannaric acid from Pannaria languinosa, Yosioka (1941) did not find the above acids but found a new chlorine-containing neutral substance in some species of Pannaria and called it pannarin.

Asahina (1954) reported pannarin from the following species of Pannaria: P. coeruleobadia, P. fulvescens, P. lanuginosa, P. lurida, P. rubiginosa, and P. sublurida. The above species have a PD+ orange-red thalline reaction due to the presence of this chemical.

Asahina (1954) also reported psoromic acid from Psoroma crassum. The thallus of this species gives a PD+ (yellow) color. Runemark (1956) has also reported psoromic acid from Psoroma.

More information on the chemistry of the Pannariaceae is needed before chemical differentiation can be a useful tool in the taxonomy of the family. The only chemical test made in this study was the hymenial iodine reaction. In all species the hymenium was I+ blue.

VI

KEY TO THE GENERA STUDIED

1. Phycobiont Chlorophyta, probably Coccomyxa.
 Thallus subfoliose, greenish in color; lobes corolloid; apothecial disk concave, brown in color, margin concolorous to the thallus; spores one-celled, monostichous or distichous.....Psoroma
1. Phycobiont Cyanophyta.....2
 2. Aquatic. Thallus foliose (but becoming almost fruticose as it grows away from the substrate); filaments of Nostoc occasionally horizontal; apothecia with some tomentum on the sides.....Hydrothyria
 2. Non-aquatic.....3
3. Stipe developed. Thallus foliose, pale green to yellowish-green, upper surface mostly tomentose; algae Scytonema or Nostoc; apothecia mycolecanorine (no algae in the amphithecium...Erioderma

3. Stipe not developed.....4
 4. Apothecia mostly adnate, sessile or constricted below; medulla of periclinical, mostly conglutinate hyphae.
Alage Scytonema.....Coccocarpia
 4. Apothecia not adnate; medulla of loose irregular hyphae or absent.....5
5. Thallus squamulose areolate, areoles granulose; both thallus and apothecia black in color; medulla absent (algal layer occupies the whole thickness of the thallus); apothecia mycolecanorine; spores 1-2 celled; algae
Scytonema.....Placynthium
5. Thallus squamulose to foliose (0.3-1.5 mm wide.....6
 6. Apothecia mycolecanorine; thallus squamulose to foliose, brownish to grayish in color, apothecia black in color, occasionally brown; sometimes prothallus developed and seen as a dark line bordering the thallus; algae Nostoc.....Parmeliella
 6. Apothecia lecanorine.....7

7. Spores mostly 2-celled, rarely 3-celled; thallus foliose, brownish in color; lobes imbricate; isidia corolloid; apothecia brown, quite small as compared to the thallus lobes; algae Scytonema.....Massalongia
7. Spores 1-celled; thallus squamose to foliose, pale green to gray in color; apothecia with cortical tissue clear in the amphithecium; algae Nostoc.....Pannaria

VII

THE GENERA STUDIED

Coccocarpia Pers. in Gaudich.

In Freycinet, Voy. Uranie, Bot. 206, 1826.

Type Species: C. molybdea Pers. apud Gaudich.

Species Studied: C. ciliata, C. cronia, C. Gayana, C. pellita.

Description of the Genus based on the Species Studied:

Thallus: It is squamose to foliose and is quite often isidiate. Color of the thallus is greenish-yellow, olive gray or gray. The upper surface is without any tomentum. The lobes are 1-4 mm wide. Dark or light rhizinae can be seen on the lower surface of the thallus leaving the margins free. They are quite abundant and arise in groups rather than being solitary.

The upper cortex is paraplectenchymatous. The hyphae are loose and are arranged irregularly or are

parallel to the surface of the thallus. The upper cortex is 10-30 μ thick.

The algal layer is 50-70 μ wide and the phycobiont is Scytonema. There are vertical filaments along with occasional horizontal ones. The Scytonema cells have a sheath around them.

In some species the upper part of the medulla has loose hyphae whereas toward the lower part the hyphae are more conglutinate. This lower most layer is called a pseudocortex because it is not like the upper cortex and the hyphae are septate, conglutinate, and form a sort of cortical tissue. Dodge (1933) called it the lower cortex.

From the lower surface of the pseudocortex arise tufts of rhizinae. These are septate and very prominent, and in some species form a dark, thick mat. The tufts are 3-10 μ in width.

Apothecia: The apothecia are scattered on the upper surface of the thallus. They are sessile or adnate, the latter being more frequent. Sometimes they are constricted below. The color of the disk varies from black to brown, or tan. The margins are concolorous with the disk. The diameter of the apothecia is 2-4 mm.

There has been some problem in determining whether the outer most layer is the amphithecium or exciple. That is why it is hard to say with certainty whether the apothecia are lecidiane or mycolecanorine. There are no algae in the outer most layer. Sometimes numerous hair-like appendages arise from the sides of the apothecia. These are cilia or may be considered a dense tomentum. The outermost tissue is paraplectenchymatous. It is quite loose and irregular in some species but in some it is of isodiametric, almost equal sized cells.

The subhymenium is not distinct from the exciple or the amphithecium, whatever the outer most layer should be called.

The hymenium is 80-100 μ thick and has linear, oblong or clavate asci. Each ascus has 8 monostichous or distichous, one or two-celled spores. The paraphyses are also linear or clavate and are septate or non-septate. Sometimes their tips are thickened within forming an epithecium.

Coccocarpia ciliata Wainio

Annal. Acad. Scient. Fennic., Ser. A, 15(6):26.

Material Studied: The material studied was misplaced,
and could not be found to get the collection data.

Detailed Description:

Thallus: The thallus is foliose with lobes about 5 mm broad. The upper surface is grayish. There are numerous whitish isidia scattered on the upper surface. Dark bunches of rhizinae arise from the lower surface of the thallus frequently leaving the margins free.

The upper cortex is of loose paraplectencyma which is parallel to the surface of the thallus. This layer in this species is not very thick (only 2-3 celled or about 10 μ). The upper cortex also continues in the isidium.

The algal layer is formed by very short chains of Scytonema which are not too compact. The layer is 30-40 μ thick and the Scytonema cells are 3-5 μ in diameter. I could not see any horizontal filaments of the phycobiont in this species as I did in C. Gayana and C. pellita var. prolificans.

The medullary tissue is not distinct from the lower most tissue (pseudocortex) which has linear and rectangular hyphae parallel to the surface.

The lowermost hyphae continue downwards vertically, forming strands of rhizinae. The rhizinae are unihyphal, thin-walled, many-celled, and very conspicuous.

Apothecia: The apothecia are scattered over the upper surface. They are black in color (both the disk and the margin). The apothecia are about 4 mm in diameter and they are adnate. The sides of the apothecial disk are tomentose, being covered with long conspicuous free hyphae, hence the name "ciliata." The apothecia are constricted below and at the point of the constriction are joined to the thallus. Sometimes the cilia continue up to the lower surface of the apothecia and almost look like rhizinae. The cilia are long, colorless, generally non-septate, and thin-walled. They are 2.5 μ thick and arise from the outer most layer of tissue.

There is no distinction between the amphithecial and excipular tissue. The margin is paraplectencymatous and extends from below the hymenium downward.

The hymenium is 20 μ wide and has oblong asci and clavate paraphyses. Each ascus has eight, one-celled, minute (about 1 μ in diameter), round, hyaline, and thin-walled spores. They are monostichous or distichous. The paraphyses do not have thick-walled tips hence there is no epithecium.

Coccocarpia cronia (Tuck.) Wainio

C. cronia (Tuck.) Wainio, Annal. Acad. Sc. Fennic., Ser.

A, 6(7):103. 1915.

Syn. Parmelia Cronia Tuck., Proceed. Amer. Acad. Arts &

Sc., 1: 228, 1898; Syn. Lich. New England, 36.

1948.

Material Studied: WEST INDIES. Grenada: Levera Bay,

St. Patrick. Imshaug 16163, 1953 (MSC).

Detailed Description:

Thallus: The thallus is foliose, and the lobes are 2-3 mm wide. The upper surface is grayish-black and the lower surface is black due to presence of a thick mat (prothallus) formed by the rhizinae. Isidia are seen in the center of the thallus and soredia are scattered on the upper surface.

The upper cortex is 10-15 μ wide and is formed of 2-3 layers of paraplectenchyma.

The algal layer is composed of loose coils of Scytonema with cells mostly 10 μ in diameter. The layer is 35-40 μ thick and the phycobiont is more abundant than it is in C. ciliata.

The medullary hyphae are thin-walled, irregular and colorless. The medulla is 20 μ thick and occupies a smaller area than in C. ciliata.

There is cellular tissue below the medulla; this has been called the lower cortex (Dodge, 1933), but since it is not like the upper cortex it is best called a lower pseudocortex. It is formed by thick-walled hyphae and is 10 μ wide. The rhizinae arise from the lower surface of this tissue, forming a tissue which appears to be prothallus.

The rhizinae are long, septate, thick-walled, and form a kind of network. They are branched and arise in groups or are solitary.

Apothecia: They are scattered on the upper surface and are blackish with concolorous margins. The disk is slightly convex and is 1.8-2.0 mm in diameter. The apothecia are

constricted below like C. Gayana. The surface of the apothecium, where not attached to the thallus, is covered with an abundant tomentum.

The outermost layer (with no differentiation between amphithecium and exciple) is composed of irregular and thin-walled paraplectenchyma. This layer extends from below the hymenium to the bottom, and measures 100 μ in thickness.

The hymenium is 90 μ thick and contains oblong asci with eight minute spores in each. The spores are one-celled, hyaline, without a thick episore, and are either monostichous or distichous.

The paraphyses are club-shaped and septate. They are unbranched and without thick-walled apices; hence, there is no epithecium as in C. Gayana (Plate 1).

Coccocarpia Gayana Nyl.

Synop. Lich., 2:41. 1863.

Material Studied: The material studied was misplaced and could not be found to give the collection data.

Detailed Description:

Thallus: The thallus is squamulose, the squamules being 1.2 μ thick. The upper surface is grayish-black and is isidiate. The rhizinae arise from the lower surface of the lower pseudocortex.

The upper cortex is formed of loose, almost parallel paraplectenchyma (Plate 1). The layer is 20-30 μ wide and about 3-4 celled thick.

The algal layer is formed of irregular algal filaments, which were identified by Dodge (1933) as Scytonema. There are coils, short vertical filaments, as well as horizontal filaments (Santesson, 1944) (Plate 1). The algal cells differ quite considerably in size. Their diameters range between 5-10 μ . The algal layer is 70 μ thick, the thickest of all species of Coccocarpia studied here.

It is hard to distinguish between the medulla and the tissue below it, except that there are approximately 2-3 layers of tissue just below the algal layer which have very narrow hyphae grading into a few more layers having broader hyphae. These broad hyphae can be called the pseudocortex. These hyphae are thin-walled, conglutinate, septate, and are parallel to the surface of the thallus.

Rhizinae arise from the lower surface of the pseudocortex and come out in tufts; they are not so conspicuous as in C. cronia.

Apothecia: The apothecia are quite minute (about 0.9 mm in diameter). They are constricted below as in C. cronia. The disk is black and slightly convex.

It is not so difficult here to distinguish between the amphithecium and exciple (Plate 2, diagram) as it is in the preceding species since in the central part of the apothecia one can locate the excipular tissue by the orientation of the hyphae. The outermost layer is formed of thin-walled paraplectenchymatous cells. There are no algal cells seen in the upper parts (above the constriction) of the margins. The exciple is also of loose paraplectenchyma.

The hymenium has clavate asci which are 8-10 μ wide near the centers. There are eight two-celled spores in each ascus. The spores are hyaline with a thick epispore (Plate 2).

The paraphyses are clavate to filiform and are septate but unbranched. There is no differentiated or pigmented epithecium. The hymenium is 80 μ thick.

Coccocarpia pellita (Ach.) Müll. Arg.

Flora 65: 320. 1862.

Parmelia pellita Ach., Lichenog. Univ. 468. 1810. Swartz

Lich. Amer. 7, Pl. 6, 1811.

Material Studied: WEST INDIES. Jamaica, Clarendon, Im-
shaug 13262, 1952 (MSC).

Detailed Description:

Thallus: The thallus is foliose and is greenish-gray in color. The lobes are 3-4 mm wide and are not imbricate. The upper surface is glabrous. The rhizinae are on the lower surface leaving the margins free.

The upper cortex is of loose paraplectenchyma, which is quite irregular and is 20 μ wide.

The algal layer has mostly vertical filaments. The cells are round and are much more uniform in size than those in C. Gayana. The cells are 2-5 μ in diameter and the layer is 65 μ thick.

The medulla is not very distinct from the lower pseudocortex. The latter has thin-walled, parallel conglomerate hyphae. The layer is 60 μ thick and gives rise to rhizinae toward the lower surface.

The rhizinae are mostly seen in groups and are black and 2-4 μ thick.

Apothecia: They are scattered on the upper surface and are adnate. The apothecia are black in color with concolorous disks which are not prominent. They are 1.3-1.6 mm in diameter and are slightly pruinose. The disks are slightly convex.

It seems that in this species one can see the amphithecium and the exciple a little better than in the previous ones but there has been a controversy as to whether the outermost layer is the exciple of amphithecium. Both the "layers" are paraplectencymatous, and the only way one can tell one layer from the other is by the difference in the orientation of the hyphae.

The hymenium is 40 μ wide with club-shaped asci and filiform paraphyses. The eight minute spores in each ascus are round, hyaline, and without an epispore. The spores are monostichous or distichous.

The paraphyses end in thick-walled tips forming a very well developed epithecium.

Erioderma Fée

Essai Cryptog. Ecorc. Officini. 146. 1824.

Type Species: Erioderma polycarpum Fee, Essai Cryptog.

Ecorc. Officini. 146, tab. XXXLV, fig. 2. 1824.

Species Studied: E. limbatum, E. microcarpum, E. physio-
ides, and E. polycarpum, and E. Wrightii.

General Description of the Genus based on the Species
Studied:

Thallus: The thallus is subfoliose to foliose and is greenish-yellow to gray. The lobes vary between 3.0 mm to 1.5 cm. Thick black rhizinae arise from the entire undersurface, the lower margins alone, or the undersurface excluding the margins. All species except E. limbatum have a tomentum on the upper surface of the thallus. The lower surface of the thallus is sometimes veined.

The upper cortex is paraplectenchymatous, with the hyphae either irregular or parallel to the surface of the thallus. The tomentum is formed by vertical hyphae originating from the uppermost layer of the cortex. The hairs are unicellular and colorless. The upper cortex is 3-many celled thick and sometimes appear to have a "cuticle."

Below the upper cortex is the algal layer. The phycobiont is either Nostoc or Scytonema occurring in short chains or filaments. The thickness of algal layer is different in different species.

Below the algal layer is the medulla. This is formed by parallel, almost parallel, or irregular hyphae. These are mostly loose and sometimes are accompanied by special kinds of cells which are moniliform in appearance as in E. physioides. The medulla is exposed as there is no lower cortex. The thickness of the medulla ranges between 30-180 μ within the genus.

Where rhizinae are present, they arise from the lower surface of the medulla. They are black or brown in color and are solitary or in groups. They are non-septate and thin-walled.

Apothecia: The apothecia are conspicuous and are marginal or scattered. Erioderma is the only genus in the Pannariaceae with stipitate apothecia. Usually the apothecial disk is brown in color with a light or dark margin. The sides of apothecia are sometimes covered with light tomentum.

The apothecia are mycolecanorine. [The outermost layer is the amphithecium which is without any phycobiont.]

The amphithecium is paraplectenchymatous. The orientation of the hypahe can be easily followed and it can be established that the amphithecium is developed from the exciple.

The proper margin or the exciple is between the amphithecium and the subhymenium. It is quite a thick layer of tissue in the center but its thickness varies in the lateral arms in different species. The exciple, which is quite distinct from the amphithecium is composed of loose and irregular euthyplectenchyma. Some of the hyphae in some species are even pigmented.

The subhymenium is not distinct in any species except E. Wrightii (Plate 9). In the rest of the species the subhymenium cannot be distinguished from the tissue of the exciple.

The hymenium is between 40-100 μ wide. The asci are oblong, and each contains eight spores which are monostichous or distichous. The spores are usually one-celled, but two-celled spores occur quite often, and rarely even three-celled spores can be found; the spores are ellipsoidal to subspherical, hyaline, and can be with or without an episore. Sometimes they are roughened inside as in E. physioides (Plate 5).

The paraphyses are club-shaped and their tips end in an epithelial cell forming an epithecium. The epithecium appears quite prominent in some species since the thick-walled tip of the paraphyses take a dark stain.

Key to the Species

Studied of Erioderma

1. Upper surface glabrous, Margins sorediate.....limbatum
1. Upper surface tomentose.....2
 2. Rhizinae distributed over the lower surface except at the margins; lobes 1.0-1.5 cm wide.....Wrightii
 2. Rhizinae limited to margins; lobes smaller.....3
3. Lower surface not veined. Spheroidal moniliform cells in the medulla.....physioides
3. Lower surface veined.....4
 4. Veins few, relatively inconspicuous, concolorous with the lower surface of the thallus; apothecia scattered.....microcarpa
 4. Veins yellowish, abundant, prominent; apothecia mostly marginal.....polycarpa

Erioderma limbatum (Nyl) Dodge

E. limbatum, Ann. Missouri Bot. Gard. 20:456, 1933.

E. Wrightii [Tuck.] var. limbatum Nyl. Flora 52:119, 1869.

Material Studied:

U. S. A., Michigan: Chippewa County west of Detour,

Imshaug 3755, 1949 (MSC).

WEST INDIES, Jamaica: Summit of Blue Mt. Peak, Imshaug

13840, 1953 (MSC); East Peak, Imshaug 14820, 1953

(MSC); summit of East Peak, Imshaug 14828, 1953

(MSC); Main Ridge Gap, Imshaug 14750, 1953 (MSC);

summit of St. John's Peak, Imshaug 15164, 1953

(MSC); peak on Main Ridge, Imshaug 15210, 1953

(MSC); slope of High Peak, Imshaug 15227, 1953

(MSC); summit of Sugar Loaf Mt., Imshaug 15449,

1953 (MSC); second ridge below summit of Blue Mt.

Peak, Imshaug 15554, 1953 (MSC) [studied the ma-

terial in detail]; Knife Edge, near Sugar Loaf Mt.,

Imshaug 15498, 1953 (MSC).

Detailed Description:

Thallus: The thallus is subfoliose having lobes 0.3-0.5 cm wide. The lower surface has thick black rhizine except on the margins.

The upper cortex is paraplectenchymatous with a thick "cuticle" on the upper surface, and is 35 μ wide (about 5-celled).

The algal layer has irregular or slightly coiled filaments of Scytonema [?]. The layer is about 40 μ thick and the algal cells are 5-8 μ in diameter.

The medulla in this species is wider than in other species. It is composed of loose, irregular and thin hyphae which become broader towards the lower surface. The layer is about 160 μ thick. The hyphae in the upper part of the medulla are 4-5 μ wide and in the lower part are 6-7 μ . The rhizinae are very abundant covering the entire lower surface except the margin.

Apothecia: The apothecia are stipitate, mostly marginal and are quite large (1.5-2 mm in diameter) as compared to the thallus lobes. The disks are dark gray to black with the margins even darker.

The apothecia are mycolecanorine. The amphithecium is paraplectenchymatous with the hyphae running outward from the internal tissue (the exciple). The hyphal cells are isodiametric.

The exciple is composed of a loose irregular euthyplectenchyma. Some of the hyphae are thick-walled. The exciple is 90 μ wide in the central part and 30 μ in the lateral arms.

The tissue of the stipe is developed below the exciple and inside the amphithecium. It is composed of loose and irregular paraplectenchymatous tissue.

The hymenium is 120 μ wide. The asci are clavate (tapering below), and are 8-10 μ wide and 35-40 μ long. There are eight spores in each ascus, arranged monostichously or distichously with the latter dominating. The spores are mostly one-celled but are occasionally two-celled. They are without an epispore and are hyaline. They are subspherical measuring 2.5 x 2.5 - 3.0 x 2.5 μ . The paraphyses are club-shaped and are 5-10 μ wide near the apex. The tips of paraphyses are thickened inside resulting in an epithecium which is more prominent than in the other species.

Erioderma microcarpa Riddle

Mycologia 4:134. 1912.

The type specimen was collected by C. E. Cummings 189,

Herb. Wellesley College.

Material Studied:

DOMINICAN REPUBLIC. Cordillera Central, (La Vega):

Wetmore 3459, 1958 (MSC); Cordillera Central
(La Vega), summit of Alto de la Bandera, Imshaug
23387, 1958 (MSC); Cordillera Central (La Vega),
Imshaug 23471, 1958 (MSC); Cordillera Central
(La Vega), Imshaug 23363, 1958 (MSC).

HAITI. Massif de la Hotte, Dept. du Sud., Imshaug 23226,
1958 (MSC).

WEST INDIES. Jamaica: Halberstadt, Imshaug 15106, 1958
(MSC).

Detailed Description:

Thallus: The thallus is foliose with the lobes 4-6 mm wide. The upper surface is brownish and the lower surface is whitish or very light. The upper surface is covered with short tomentum. The lower surface is lightly veined. The veins are concolorous with the lower surface. Rhizinae are brown or light in color and they cover the lower surface except the margins.

The upper cortex is paraplectenchymatous. The cells are loosely and irregularly arranged. The layer is 30 μ wide.

The phycobiont is Scytonema, and is in the form of short chains. The layer is 40 μ wide and the algal cells, which are 8-9 x 5 μ , can be seen enclosed in thin sheaths.

The medulla is of loose hyphae, these are elongated and thin-walled, and are almost parallel to the surface of the thallus, making the medulla 60 μ wide. The lower cortex is absent and the rhizinae arise from the lower part of the medulla.

Apothecia: They are scattered on the upper surface. The disk is brown with a lighter colored margin. The apothecia are stipitate and measure 1.0 mm in diameter.

Longitudinal sections of the apothecia show that they are mycolecanorine. The amphithecium is of irregular paraplectenchyma and the orientation of the hyphae is not very clear. The tissue is 20-120 μ wide.

The exciple is quite a wide layer (Plate 4), 30 μ wide laterally and 100 μ wide in the center. It is formed of loose euthyplectenchyma which is vertical to the surface in the sides and parallel to the surface of the apothecium in the center.

The stipe is composed of irregularly arranged paraplectenchyma and is between the exciple above and amphithecium surrounding it.

The hymenium is about 80 μ wide. The asci are oblong and are 40-50 μ long and 5-10 μ wide. Each ascus has eight monostichous or distichous spores. The spores are ovoid in shape and are 8-12 x 5-8 μ in size. They are mostly one-celled or rarely 2 or 3-celled, and are hyaline, and do not have a thick epispore.

The paraphyses have club-shaped and thick-walled tips forming the epithecium. They are 5-8 μ wide near the surface.

Erioderma physioides Wainio

Journ. of Botan. 34:70. 1896.

The type specimen was collected in West Indies, St. Vincent,

Boxwood by W. R. Elliot 150.

Material Studied:

U. S. A., Michigan: Mackinac County, Bois Blamdsland, Imshaug 3261, 1949 (MSC); Imshaug 3725, 1949 (MSC); Chippewa County, Imshaug 3340, 1949 (MSC).

WEST INDIES, Jamaica: Summit of Blue Mt. Peak, St. Thomas, Imshaug 13047, 1952 (MSC); summit of Blue Mt. Peak, St. Thomas, Imshaug 13840, 1952 (MSC); Bellevue to Mt. Rosanna, St. Andrew, Imshaug 14476, 1952 (MSC); summit of Mossmans Peak, St. Thomas, Imshaug 14686, 1953 (MSC); trail of Main Ridge Gap, St. Thomas, Imshaug 14591, 1953 (MSC); ridge between East Pk. and Sugar Loaf Mt., St. Thomas, Imshaug 14890, 1953 (MSC); between High Pk. and Main Ridge Gap, St. Thomas, Imshaug 15209, 1953 (MSC); summit of Sugar Loaf Mt., Imshaug 15259, 1953 (MSC); Knife Edge, near Sugar Loaf Mt., Imshaug 15501, 1953 (MSC).

Detailed Description:

Thallus: The thallus is foliose and the lobes are 2-8 mm wide. The upper surface is pale green and the lower surface is whitish. Soredia can be seen on the margins. Tomentum is seen on the upper surface but some areas are without any. The lobes are divided into lobules and the ultimate size of the lobules is between 2-4 mm. The thallus is attached to the substrate by dense, pennicillate, black rhizinae, which are limited to the margins. Only a few can be seen in the central part of the lower surface.

The upper cortex (Plate 5) is paraplectenchymatous and is 15-25 μ or 2-3 cells wide. The hyphae run parallel to the surface of the thallus. Simple, one-celled, colorless, almost vertical hyphae make up a tomentum which can be seen on the upper surface of this layer.

The algal layer is of short separate chains of Nostoc. The chains are vertical or oblique. The layer is 30 μ wide and the Nostoc cells are mostly 5 x 5 μ . There is no difficulty in identifying the phycobiont in this particular species.

The medulla is formed by loose, nearly parallel hyphae. They are thin-walled, apparently non-septate. Special kinds of cells, called spheroidal cells by Asahina (1952) and moniliiform cells by Culberson (1961), are seen in this layer along with the loose hyphae. The function of these cells is not known. The medullary layer is about 50 μ wide and is exposed to the outside as the rhizinae are mostly marginal and there is no lower cortex. The rhizinae are 5-7 μ thick where they are widest.

Apothecia: They are mostly marginal, peltate, and stipitate. The disk is dark brown to black in color and the margins are lighter. The apothecia are 1-2 mm in diameter.

The upper surface of the apothecia is glabrous but the sides are covered with fine tomentum.

The apothecia (Plates 5 and 7) are mycolecanorine. The outermost layer is the amphithecium and it is paraplectenchymatous. The hyphae run almost parallel to the surface of the apothecium in the center, turning upwards near the top and downward near the bottom of the apothecium. The outer layer of hyphae which form the one or two-celled tomentum are thin-walled, colorless, and 10-12 μ in length. The amphithecium is about 60 μ wide.

The exciple is only a few cells wide in the sides but it is 50-60 μ wide in the center. This is formed of irregular euthyplectenchyma. Some of the hyphae are thick-walled and pigmented.

The tissue below the exciple and within the amphithecium is the stipe. This is formed of loose, irregular, thin-walled, and branched hyphae.

The hymenium is 70 μ wide and has oblong asci. They are 7-10 μ wide and 25-30 μ long. There are eight spores in each ascus and are monostichous or distichous. The spores are ovoid to subspherical in shape and measure 4-5 μ x 5 μ . Generally one-celled spores are found in

this species but occasionally two-celled spores can also be seen (Plate 7). Both kinds are not mixed in the same ascus. The spores are hyaline and minutely roughened within with no thick episore (Plate 7). The paraphyses are filiform, 1.5 - 2 μ wide near the tips, and the tips are thick-walled. The paraphyses form the epithecium.

Erioderma polycarpa Fée

Essai Cryptog. Ecorc. Officin., 146, 1824.

The type specimen was collected in Cuba, Island of Bourbon by Aubert Petite-Thouars in 1824.

Material Studied:

CUBA, Island of Bourbon: Aubert Petite-Thouars in 1824.

Conservatoire Botanique, Geneva, Switzerland

MEXICO. State of Pueblo. Pringle 12344, 1908 (Mich.);

Near Honey Station, Cuyamalaya, Pringle 15578;

1908 (Mich.).

Detailed Description:

Thallus: The thallus is foliose, greenish-yellow above and pale yellow below, with lobes somewhat pleated. The upper surface is tomentose. The lower surface of the thallus is

highly veined. The veins anastomose and are yellowish in color (brighter than the lower surface). The rhizinae are black and abundant and are on the lower surface except the margins.

The upper cortex is 20 - 30 μ thick and is composed of loose paraplectenchymatous tissue which is parallel to the surface of the thallus. There is tomentum on the upper surface as in E. physioides. The hairs are unicellular, straight or curved, colorless, and are 10-20 μ long.

There are filaments of Scytonema in the algal layer. These are short, straight or coiled, composed of 3-6 cells. The filaments are not close together. The layer is 30-40 μ wide and the Scytonema cells are 5-10 μ in diameter; they are almost round.

The medulla is of loose, parallel, thin-walled unbranched hyphae. The layer is exposed to the outside except where there are rhizinae. The medulla is 50-80 μ wide. There is no lower cortex. The rhizinae are abundant and do not occur on the undersides of the margins.

The thallus anatomy is the same as in E. physioides except that here the upper cortex cells are roundish and in E. physioides they are isodiametric, and here (E. polycarpa) the spheroidal cells are absent from the medulla.

Apothecia: There are more apothecia on the margins than on the rest of the upper surface. They are round and small (about 0.5 mm in diameter). The disk is dark brown with black margins. The stipe is much smaller than in the other species. The upper surface of the apothecia is glabrous, but tomentum is present on the sides.

The apothecia are mycolecanorine. The amphithecium is paraplectenchymatous and is highly tomentose on the outside (Plate 8). The orientation of the hyphae follows the growth pattern. The cells are roundish and loosely arranged. This particular layer is reminiscent of the same layer in E. physioides. The amphithecium here is 50 - 80 μ wide. The hairs are 10 - 30 μ long and simple, straight or curved and are colorless.

The exciple is not too distinct in the lateral arms but can be recognized easily in the center where it is 10 - 30 μ wide. It is formed of loose, thin-walled, irregularly arranged euthyplectenchyma.

The subhymenial tissue is not distinguishable from the hymenium above and exciple below.

The hymenium is 30 - 40 μ thick and is composed of ellipsoidal asci and club-shaped paraphyses. The mature

asci are 10 μ wide and 45 μ long. There are eight subsperical, monostichous or distichous spores in each ascus. They are one-celled, hyaline, and without a thick epispore.

The tips of the paraphyses are thick-walled and form the pithecium. The paraphyses are 3-8 μ wide near the tips.

Erioderma Wrightii Tuck.

Amer. Jour. Sc., Ser. 2, 25:423. 1858.

Type collected in Cuba on the tip of Loma del Gato by

C. Wright.

Material Studied:

U. S. A., Michigan: Chippewa County, Imshauq 3341, 3360,
3374, 1949 (MSC); Mackinac County, Imshauq 3294,
1949 (MSC).

HAITI: Massif de la Hotte, Dept. du Sud, Imshauq 23226,
1958 (MSC); Imshauq 23169, 1958 (MSC); Imshauq
23219, 1958 (MSC).

WEST INDIES, Jamaica: Trail of Silver Hill, Plitt, 1932
(Mich.); Spring Trial, Chinchoma, Plitt J-45, 1919
(Mich.); Chestervale, Plitt J-45-13, 1932 (Mich.);
Silver Hill Gap, St. Andrew, Imshauq 14085, 1953 (MSC);

between Clydesdale and St. Helena's Gap, St.

Andrew, Imshaug 15106, 1953 (MSC).

CUBA. Las Villas, Imshaug 24634, 1953 (MSC).

COSTA RICA. Guana-Caste, Dodge and Thomas 6983, 1930

(Mich.).

Detailed Description:

Thallus: The thallus is foliose, pale green in color above and yellowish below (where there are no rhizinae). The lobes are 1.0 - 1.5 cm broad; they are larger than the lobes in the other species studied. There are thick, black rhizinae on the lower surface except on the margins.

The upper cortex is of loose irregularly arranged paraplectenchyma (see Plate 9 for thallus anatomy). Tomentum is developed from the uppermost layer of the hyphae; they are unicellular and colorless. The upper cortex is 25-40 μ thick.

The algal layer is formed of short filaments of Scytonema, irregularly arranged and not so dense as in the other species. The layer is 20-40 μ thick and the Scytonema cells are irregular in shape, ranging between 2 x 3 μ - 5 x 6 μ in size. These are typical scytoneme-form alga as described by Dahl (1950).

The medulla is made up of quite loosely woven, thin-walled, irregularly arranged hyphae. The layer is 50-150 μ wide. The lower margins are arachnoid tomentose, with groups of tomentum covering the lower margins which are otherwise free of rhizinae. Rhizinae arise in groups from the lower surface of the medulla as there is no lower cortex. The rhizinae are 35-50 μ long and 5-7 μ thick.

Apothecia: The apothecia are marginal, peltate and stipitate. The disk is brown or black with lighter margins. The mature apothecia are about 1.5 mm in diameter.

The apothecia are mycolecanorine. The amphithecium is paraplectenchymatous and the hyphae run parallel to the surface in the sides and vertical to the surface below; they are at an angle as they go upward. The development of the hyphae can be very easily traced back to the exciple (Plate 10). Some of the superficial cells are pigmented. The outer surface is tomentose and the tomentum can be seen in groups forming a sort of network. The amphithecium is 20-70 μ in the sides and 100-200 μ below.

The exciple is 20-50 μ thick in the center and only 7-10 μ thick in the sides. It is made up of loose, thin-walled euthyplectenchymatous hyphal tissue, which is somewhat parallel to the surface of the apothecium.

The subhymenium is seen between the hymenium above and the exciple below. The hyphae are thin-walled and loosely arranged. The layer is only about a couple of cells wide.

The hymenium is 100-140 μ thick and has oblong asci with rounded ends. They are 4-5 μ wide and 30-35 μ long with eight spores in each. The spores are mostly monostichous, few are distichous and are ellipsoidal, one or two-celled, and with a thick epispore (Plate 10). They are between 4-5 x 3-4 μ .

Discussion of Species of Erioderma Studied:

Dodge (1933) separated E. physioides and made it the type species for a new genus, Malmella (M. physioides [Vainio] Dodge n. comb). E. physioides should not be removed from its present position as a species of Erioderma. It is evident from the Plates 4-10, the anatomical similarities are so profound within this genus that I cannot

help but disagree with Dodge. The similarities and differences are discussed in detail in Section VIII.

Hydrothyria Russ.

In Proceed. Essex. Instit. 1:188. 1853.

Type Species: H. venosa Russ. Collected in U. S. A.,
Vermont, in a brook on a rocky sterile soil on
slopes of a hill of granite called Bald Mt., near
Dummerston by J. L. Russell and C. C. Frost in
1851.

Species Studied: Hydrothyria venosa, l.c.

Material Studied:

U. S. A., New York: Ulster County, seepage area along
West Neversink Creek, wooded foot of a trail up
Slide Mt., 2410 ft. elev., Smith S. J. and Miller
A. G. 31471 (NYS).

Detailed Description of Hydrothyria Venosa:

Thallus: This is the only aquatic genera in the family.
The thallus is basically foliose, the younger lobes be-
coming almost fruticose as they start growing away from
the substratum. It is gray, becoming blackish sometimes.
Both surfaces are of the same color, but the lower surface

is veined. The veins are a little lighter in color and are very prominent. The lobes are subimbricate and plicate with round margins. They are 6-9 mm. wide. The rhizinae arise from under the surface of the thallus from the veins, mostly in the middle part of the thallus, forming thick tufts.

The upper cortex is paraplectenchymatous, the cells are isodiametric and parallel to the surfaces. The layer is about 5 celled and 20-30 μ thick. There is a thin cuticle on the upper surface.

The algal component is Nostoc (scytonemeiform Nostoc, Dahl, 1950) but the filaments are short, either coiled or straight. Along with many vertical filaments there are occasional horizontal filaments also (as shown in Plate 11). The layer is 60-100 μ thick and the sizes of the algal filaments and cells vary quite a bit. The filaments are 2-many celled long and the cells are anywhere from 5x5 μ - 10x10 μ .

The medulla is of loose, periclinical and thin-walled hyphae, 25-55 μ in thickness.

The lower hyphae in the medulla are septate and are quite distinct from the top portion of the medulla

and can be called pseudocortex (Plate 11). This layer is 10-20 μ thick and is composed of isodiametric, thin-walled and conglutinate hyphae which run parallel to the surface of the thallus. They are quite different from the upper cortex and hence do not form a true lower cortex.

Thick tufts of black rhizinae arise from the central parts of the lower surface of the thallus; they are several mm long and 8-10 μ thick.

Apothecia: The apothecia are marginal, occurring frequently in the notches or sinuses of the thallus. They are sessile, tomentose on the sides and orange to brownish in color. The margins are always darker in color than the disks. The diameter of mature apothecia range between 1.5 and 1.8 μ .

The apothecia are mycolecanorine. The amphithecium is 50 μ thick in the sides and 130 μ in the center and is paraplectenchymatous and tomentose on the sides. The tissue is regular and the hyphae are almost parallel to the surface. The hairs are simple or branched and are straight with pointed tips and 15-25 μ long.

The exciple is not distinct from the amphithecium in the lateral margins but is quite prominent in the center. It is formed by loose and parallel euthyplectenchyma (Plate 11). The layer is 25-35 μ thick.

The subhymenium is not distinguishable from the hymenium above and the exciple below.

The hymenium is 70-90 μ thick and is formed of linear-oblong asci and filiform paraphyses. A mature ascus is 90 μ long and 10 μ wide and has eight elliptical spores. The spores are one-celled, hyaline, and without a thick episporium; they are 9-10 x 5 μ .

The tips of paraphyses are 3-6 μ thick, are thick-walled, and form an epithecium which is about 10 μ thick.

Massalongia Korb.

Syst. Lich. German. 109. 1855.

Type Species: Massalongia carnosa (Dicks.) Korb. l.c.

Lichen carnosus Dicks. Orig. Coll.: Great Britain, Scotland. 1790. p. 21.

Species Studied: Massalongia carnosa.

Material Studied:

U. S. A., Montana: Glacier National Park, over rocks,
Virginia Falls, 5000 ft. elev., Imshaug 6456,
1950 (MSC).

Detailed Description of Massalongia carnosa:

Thallus: The thallus is foliose with imbricate lobes; the lobules are 2-5 mm wide. It is brownish and has globose or cylindrical, marginal isidia. The lower surface is lighter in color and brown rhizinae arise from the middle part leaving the lower margins free.

The upper cortex is almost uniformly 2-celled and 15-20 μ thick (Plate 13). It is covered with a thin cuticle-like layer. The cells are paraplectenchymatous

and pigmented and are vertical to the surface of the thallus.

The phycobiont is Nostoc (Dahl, 1950) and the filaments are distinctly visible enclosed in gelatinous sheaths. The algal layer is 25-30 μ thick and the algal cells are 3-5 μ in diameter.

The medulla is formed by loosely woven, thin-walled, irregular hyphae and 2-3 μ wide hyphae. The layer is 60-70 μ thick.

There is a lower cortex present in this species. It is formed of vertical pigmented, paraplectenchymatous cells. This layer is a little thicker than the upper cortex (25-30 μ) but is mostly one-celled in thickness.

The lowermost hyphae start growing downwards to form the rhizinae. The rhizinae are not very conspicuous as in the other species of the family. They are septate and brown in color.

Apothecia: The apothecia are scattered, peltate, stipitate, and concolorous to the thallus with darker margins. They are about 2 mm in diameter. Tomentum is seen on the sides of the apothecia.

The amphithecium is paraplectenchymatous which is not very regular. Few algal cells are seen in the inner part of the amphithecium making it pseudo-mycolecanorine. The amphithecium is 150 μ thick. The tomentum is very sparse, the hairs are 20-30 μ long and 5 μ thick.

The exciple is of loose, thin-walled, and parallel euthyplectenchyma. It is very narrow in the lateral margins, about 5 μ , but in the center it is about 20 μ thick.

The subhymenial tissue is not distinct from the hymenium above and exciple below.

The hymenium is 30-60 μ thick with clavate to club-shaped asci and club-shaped paraphyses. The asci are 10-12 μ wide and 40-60 μ long. There are eight ellipsoidal two-celled spores (three-celled spores are seen occasionally) in each ascus. They are 11-27 x 3-4.5 μ and are without a thick episporium.

The paraphyses are about 10 μ thick near the tips and are pigmented in this area forming the epithecium.

Pannaria Del. in Bory

Dictionn. Class. Hist. Nat. 13:20. 1828.

Type Species: Pannaria rubiginosa (Thunberg in Ach.)

Del. in Bory.

Species Studied: P. leucosticta, P. lurida, P. pezizoides,
P. rubiginosa.

Detailed Description of the Genus Based on the Species

Studied:

Thallus: The thallus is squamose, subfoliose or foliose and is olive-green to gray on the upper surface and has a lighter lower surface. The rhizinae are abundant and well developed sometimes forming a black cushion-like structure.

The upper cortex is paraplectenchymatous, 4-5 celled thick with irregular or vertical cells.

The phycobiont is true nostociform Nostoc and the algal layer as such is quite prominent. There are short chains or coils or Nostoc and the algal cells are mostly spherical.

The medulla is composed of loose, irregular, thin-walled, narrow hyphae sometimes forming a loose network (arachnoid). The hyphae in the lower part of the medulla are more densely woven than in the upper.

The lower cortex is absent and the rhizinae arise from the lower surface of the medulla. They are brown, black, or even pale, and are very dense and prominent.

Apothecia: The apothecia are usually abundant, scattered, sessile but constricted below, peltate, orange-brown to dark brown with thalloid margins.

The apothecia are lecanorine with differentiation of a cortex and a medulla (the algae are toward the center of the amphithecium). The amphithecium is paraplectenchymatous and sometimes has a tomentum developing from the outermost hyphae. The amphithecium completely encloses the disk on the sides. There are vertical or parallel filaments of Nostoc which are not so dense as in the thallus.

The exciple is paraplectenchymatous or enthyplectenchymatous. It is colorless, narrow in the sides and wide in the center and quite distinct.

There is no hypothecium and the subhymenium is not distinct from the hymenium above and exciple below.

The hymenium is composed of mostly clavate asci and filiform or club-shaped paraphyses. The surface of the hymenium is flat with the amphithecium coming little above the thecium on the sides. The asci are 10-11 μ wide and 55-75 μ long with eight spores in each of them. The spores are elongate to ellipsoidal or subspherical, hyaline, one-celled and without an epispore, they can be monostichous or distichous. The tips of the paraphyses sometimes form and sometimes do not form an epithecium. Even when the epithecium is developed it is not as conspicuous as in some of the other genera.

Pannaria leucosticta Tuck. in Nyl.

Annal. Scienc. Nat., Bot., Ser. IV, 12:294. 1859.

Material Studied:

U. S. A., North Carolina: Durham County; in Duke Forest near Durham. On Quercus rubra. Culberson 4806, 1958 (MSC).

Detailed Description:

Thallus: The thallus is subfoliose, subimbricate, olive-green and marginally sorediate. The lobules are 0.5-1.0 mm wide. There are black rhizinae on the entire lower surface, forming a network which looks like a hypothallus.

The upper cortex is paraplectenchymatous and is about 32 μ thick. The cells are almost vertical to the surface.

The algal layer is composed of definite coils of Nostoc and is about 65 μ thick.

The medullary hyphae are arachnoid and the layer is 80 μ thick. The hyphae are thin-walled, colorless, and are loosely arranged.

The rhizinae arise from the lower surface of the medulla and form a conspicuous network.

Apothecia: The apothecia are scattered, orange-brown with light colored (concolorous to the thallus) pruinose margin. They are peltate, and constricted below and are 0.3-0.9 mm in diameter.

The amphithecium is 160 μ thick and is paraplectenchymatous and has the algae dispersed almost in the

entire thickness of the amphithecium. It exceeds the surface of the hymenium and is seen like a rim on the sides. There are dense coils of the phycobiont as in the thallus.

The exciple is composed of conglutinate, parallel euthyplectenchyma and is about $32\ \mu$ thick in the sides as well as in the center; it is light brown.

The hymenium is about $95\ \mu$ thick and is almost flat surfaced. There are clavate asci with eight ellipsoidal, hyaline, thin-walled, one-celled spores in each ascus. The spores are mostly monostichous but distichous spores can be seen too. They are $13.8 \times 9.0\ \mu$ in size. The paraphyses are filiform with thickened tips forming an epithecium.

Pannaria lurida (Mont.) Nyl.

Memoir. Soc. Sc. Nat. Cherbourg 5:109. 1857.

Collema luridum Mont. Ann. Sc. Nat. Bot. II, 18:266. 1842.

Material Studied:

U. S. A., North Carolina: Craven County; near Havlock, about 15 ft. up the trunk of a large Quercus falcata felled in the woods during hurricane, Culber-son 10373, 1960 (MSC).

Detailed Description:

Thallus: The thallus is foliose, gray and pruinose with no soredia or isidia. The lower surface is whitish. The lobes are imbricate and the lobules are 2-4 mm wide. The rhizinae are pale to brown and do not develop on the lower margins. They are about 1 mm long and do not form a network.

The upper cortex is paraplectenchymatous, 4-5 celled or about 23 μ thick. The cells are uniform and parallel to the surface of the thallus (Plate 15).

The algal layer is 65 μ thick and is composed of mostly vertical filaments of the phycobiont (Nostoc), the cells of which are 3-7 x 3-6 μ . The filaments are not so dense as in P. leucosticta.

The medullary hyphae are thin-walled, colorless, loose and form a network. The layer is 90 μ thick and the hyphae are 1.5-2.5 μ wide.

The rhizinae are abundant and pale or brown arising in tufts. They do not form a network or cushion-like structure as they do in P. leucosticta.

Apothecia: The apothecia are scattered, orange-brown, pel-tate and constricted below. The margins are pruinose and concolorous with the thallus. Many apothecia become irregular in shape through crowding.

The amphithecium is paraplectenchymatous and is differentiated into a cortical tissue and an inner layer with the algae, the latter come almost in the cortical tissue near the upper tip of the amphithecium. The cells are regular and uniform in size and shape and the whole layer is about 80 μ thick (Plate 16).

The exciple is paraplectenchymatous and is uniform in thickness on the sides and in the center, it is 20 μ thick. The subhymenial layer is not distinguishable.

The hymenium is 120 μ thick and has clavate asci which are about 55 μ long and 10 μ wide. There are eight ellipsoidal, one-celled, thin-walled, hyalline, monostichous spores in each ascus; they are 8-10 x 3-5 μ in size. The paraphyses are filiform and have slightly thickened tips forming a very poorly developed epithecium about 10 μ thick.

Pannaria pezizoides (Wever) Trevis.

Lichenotheca Veneta, 98. 1869.

Lichen pezizoides Weberi, Spic. Fl. Goet. 200. 1778.

Material Studied:

CANADA, British Columbia: Yoho National Park, Twin Falls,
on a mossy soil bank at west of trail is spruce-
fir forest, Lamb 6266, 1951 (MSC).

Detailed Description:

Thallus: The thallus is squamose, The squamules are minute
(0.1-0.2 mm wide), densely imbricate and brown with a smooth
surface.

The upper cortex is paraplectenchymatous and is 20 μ
(3-4 celled) thick and is light brown.

The algal layer, almost 65 μ thick, is composed of
dense coils of Nostoc, which are made up of almost spherical
cells 2.0 x 2.0 μ in size.

The medulla is composed of thin-walled, irregular,
loose hyphae, and the whole layer is about 35 μ thick. The
lower cortex is absent.

The rhizinae are black and shiny and form a narrow
network appearing like a hypothallus, but not as well de-
veloped as in Anzia or Pannoparmelia.

Apothecia: The apothecia, scattered on the upper surface, are usually numerous and brown with the margin concolorous with the thallus. They are peltate and sometimes become irregular in shape through crowding, but a normal spherical apothecium is about 1.2-1.5 μ in diameter.

The amphithecium is paraplectenchymatous and has the algae in the central area where the amphithecium is differentiated into a cortical and medullary tissue (as in P. lurida). The amphithecial cells are regular and uniform in size and the layer is about 105 μ thick.

The exciple is paraplectenchymatous, 10 μ thick in the sides, 70 μ thick in the center, and it is light brown.

The hymenium is composed of clavate asci which are about 75.0x3.0 μ in size, with eight one-celled, ellipsoid (15-25 x 8-13 μ) hyaline spores which are monostichous or distichous and without a thick epispore.

The paraphyses are club-shaped with pigmented and thick-walled tips forming a very well-developed epithecium 20 μ thick. It is best developed of all the species of Pannaria studied here.

Pannaria rubiginosa (Thunb.) Del.

In Bory Dictionn. Class. Hist. Nat. 13:20. 1828.

Lichen rubiginosus Thunb. in Ach., Lich. Suec. Prod. 99,
1798.

Material Studied:

U. S. A., North Carolina: Near Havlock, Graven County,
Culberson 10735, 1960 (MSC).

Detailed Description:

Thallus: The thallus is foliose, olive green and minutely granulose in certain areas. The lobes are imbricate, waved and have crenate margins, they are 0.8 - 1.5 mm wide. The lower surface is light or dark and is covered with pale or black rhizinae on the entire lower surface. The rhizinae are 0.1 - 0.2 mm long and do not form a network or cushion-like structure.

The upper cortex is paraplectenchymatous, 13-25 μ (4-5 celled) thick and the cells are vertical to the surface of the thallus.

The algal layer is about 103.5 μ thick and is composed of dense coils of Nostoc cells which are 4.8 x 3.2 μ in size.

The medulla is composed of loose, thin-walled almost parallel hyphae which make the layer about $70\ \mu$ thick. The rhizinae arise from the lower surface of the medulla, the lower cortex being absent. The rhizinae are about $5\ \mu$ thick and are either pale or brown.

Apothecia: The apothecia are orange-brown to reddish brown, $0.6 - 1.5\ \mu$ in diameter and are scattered. The margins of the apothecia are concolorous with the thallus and are somewhat crenate.

The amphithecium is paraplectenchymatous and is differentiated into a cortical layer and a medulla, the algal filaments and coils are in the inner area (medulla). The outside of the amphithecium is tomentose, the latter being colorless and dense.

The exciple is of irregular paraplectenchyma and is about $13\ \mu$ thick in the sides and $62\ \mu$ thick in the center. It is brownish and quite distinct.

The hymenium is about $131\ \mu$ thick and is composed of clavate asci which are $62\ \mu$ long and $13.8\ \mu$ thick (in the center). There are eight one-celled spores in each ascus, they are ellipsoidal, $14-26 \times 6-11\ \mu$, hyaline, and are arranged in one or two rows.

The paraphyses are filiform and their tips form a brownish epithecium which is 20.5 μ thick but is not so conspicuous as in P. pezizoides.

Parmeliella Müll. Arg.

Memoir Soc. Phys. Hist. Nat. Geneve 36:376. 1862.

Type Species: Parmeliella triptophylla (Ach.) Müll. Arg.

[P. corallinoides (Hoffm.) Zahlbruckner].

Species Studied: P. lepidiota, P. microphylla, P. pannosa,

P. plumbea.

Detailed Description of the Genus based on the Species

Studied:

Thallus: The thallus is squamose to foliose, the tips becoming almost foliose even if the lobes are subfoliose or squamose. The squamules or lobes are quite minute and are brownish-gray. There are abundant black hyphae on the undersurface of the thallus forming a thick mat and extending beyond the thallus as a black margin. This probably is a prothallus; Dodge (1933) called it a hypothallus.

The upper cortex is paraplectenchymatous and is 2-many celled or 10-60 μ thick. The hyphae are vertical or almost vertical to the surface of the thallus.

The phycobiont is Nostoc and the thickness of the algal layer differs considerably in the different species. The Nostoc filaments are densely or sparsely arranged and are mostly vertical to the surface of the thallus. Sometimes there are regular coils of Nostoc filaments as in P. plumbea (Plate 19).

The medullary hyphae are thin-walled, loosely arranged, and irregular or parallel to the surface of the thallus. There are conglomerate, thin- or thick-walled hyphae below the medulla in some species. This tissue is called the "prothallus," (also see pp. 18-21). The prothallus is 5-30 μ thick in different species.

The rhizinae arise from the lower hyphae of the prothallus and are seen on the entire lower surface of the thallus. They are black, thick-walled and very conspicuous.

Apothecia: The apothecia are scattered, peltate, sessile or constricted below, light to dark brown in color with margins concolorous with the thallus. They are quite abundant and conspicuous, their diameter ranging between 0.5-1.2 mm.

The apothecia are mycolecanorine and the amphithecium is para or prosoplectenchymatous. The sizes of the

hyphae and the thickness of the layer differs in different species.

The exciple is distinct and varies in thickness in different species. In P. pannosa the hyphae below the exciple are deeply staining suggesting the presence of hypothecium. The excipular tissue is loose euthyplectenchyma becoming parallel in the lateral margins.

The subhymenium is not distinct from the hymenium above and the exciple below.

The hymenium has linear to oblong asci and paraphyses with club-shaped tips. There are eight ovoid to elliptical, one-celled, mono- or distichous spores in each ascus. The spores are hyaline and are with or without a thick episore.

The tips of the paraphyses may or may not be thick-walled and pigmented, hence the epithecium is developed or undeveloped.

Parmeliella lepidiota Wainio

Termeszetr. Fuzetek, 22:308. 1888.

Material Studied:

CANADA, Alberta: On ridge opposite Angel Glacier on Mt.

Edith Cavell, Jasper National Park, 6500 ft. elev.,

Imshaug 6954, 1950 (MSC).

Detailed Description:

Thallus: The thallus is squamose, the squamules being 0.2-0.3 mm wide and black. The external morphology of the thallus is very reminiscent of Placynthium nigrum. There are black rhizinae on the entire lower surface of the squamules.

The upper cortex is paraplectenchymatous and is 60 μ thick. The hyphal tissue is almost parallel to the surface of the thallus.

The algal layer is 90 μ thick and is composed of regular ensheathed coiled filaments of Nostoc.

The medulla is formed of thin-walled, irregular hyphae, the layer being 160 μ thick. The hyphae are 3-5 μ thick.

There is no prothallus in this species and the rhizinae arise from the lower hyphae of the medulla. The rhizinae are black and about 5 μ thick.

Apothecia: The apothecia are scattered on the upper surface. They are dark brown or black with the same colored margin

and are sessile and the disk is convex. The diameter of the apothecia varies between 0.5-0.7 mm.

The anatomical studies show that the apothecia are mycolecanorine, with a very well-developed epithecium (more than in any other species studied here).

The amphithecium is prosoplectenchymatous and is about 85 μ thick. The exciple is of loose, irregular euthyplectenchyma and is 58 μ thick.

The hymenium is 60 μ thick and is formed by clavate asci and filiform paraphyses. There are eight one-celled, thick-walled, hyaline spores arranged monostichously or distichously in each ascus. The asci are 60-80 μ long and 10-15 μ wide. The spores are 8-10 x 5-8 μ and ovoid.

The tips of the paraphyses are thick-walled and pigmented as to form a very well-developed epithecium which is about 10 μ thick.

Parmeliella microphylla (Sw.) Müll. Arg.

Flora 72:507. 1889.

Lichen microphyllus Sw. Vetensk. Akad. Handl. 301. 1791.

Material Studied:

U. S. A., Michigan: Keweenaw County: Isle Royal National Park, along southwest shore of West Caribou Island, Wetmore 4416, 1959 (MSC).

Detailed Description:

Thallus: The thallus is squamose, the squamules 0.1-0.2 mm wide, sorediate, and gray. There are black rhizinae on the lower surface. The thallus morphology, like P. lepidiota, reminds one of Placynthium nigrum.

The upper cortex is paraplectenchymatous and 3-4 celled or 10 μ thick. The cells are pigmented and parallel to the surface of the thallus. This layer in P. microphylla (Plate 18) is narrowest of all the species of Parmeliella studied here.

The algal layer is 80 μ thick and is composed of vertical filaments of Nostoc, which are very compactly arranged in almost the whole thickness of the thallus, thus reducing the size of the medulla to nil. This is similar in Placynthium nigrum (Plate 21), and different from other species of Parmeliella studied here. The Nostoc cells are 5-6 x 3-4 μ .

There is a paraplectenchymatous hyphal tissue below the algal layer which I suggest should be called the pseudocortex. It is 2-3 celled or 8-9 μ thick.

The rhizinae are very inconspicuous and arise from the lower hyphae of the pseudocortex mostly from the lower margins of the squamules.

Apothecia: The apothecia are scattered, black with margins concolorous with the thallus and are sessile. The disk is 1.0-1.5 mm in diameter and is peltate.

The amphithecium is prosoplectenchymatous with the outer cells pigmented. The layer is about 70 μ thick.

The exciple is formed of irregular euthyplectenchyma. The tissue is very prominent in the central area but is not so much developed in the lateral margins; it is 60 μ thick.

The subhymenial tissue is not distinguishable from the hymenium above and exciple below.

The hymenium is 80 μ thick including the epithecium. There are linear to oblong asci which are 35-45 μ long and 5 μ wide. There are eight one-celled ovoid monostichous or distichous spores in each ascus. They are hyaline and without a thick episore (unlike P. lepidiota) and are 5-6 x 4 μ .

The paraphyses are unbranched and linear with club-shaped tips. The tips of the paraphyses are pigmented and thick-walled forming an 8 μ thick epithecium.

Parmeliella pannosa (Sw.) Müll. Arg.

Flora 64:86. 1881.

Lichen pannosus Sw., Nov. Gen. Sp. Pl. Prodr. 146. 1788.

Material Studied:

U. S. A., Hawaii: island of Oahu in Nūūanu, on Han tree,

Heller A. A. 2107, 1895 (MSC).

Detailed Description:

Thallus: The thallus is subfoliose, the lobes being 0.5-1.0 mm wide, and imbricate. It is brownish and the dark prothallus extends about 1-1.5 mm beyond the thallus forming a black margin. There are black, conspicuous, well developed rhizinae on the entire lower surface of the thallus.

The upper cortex is paraplectenchymatous. The cortical cells are not uniform in size and are vertical to the surface of the thallus. The cortex is several-celled and 32-35 μ thick.

The algal layer is very thin as compared to the algal layer in other species of Parmeliella studied here, being only 12 μ thick and containing short filaments of Nostoc mostly seen as coils which are not densely packed. The algal cells are 5x3-4 μ in size.

There are thin-walled, loose, almost parallel hyphae in the medulla making it about 20 μ thick. There are more conglutinate, parallel and black hyphae below the medulla which form the prothallus. It is 15 μ thick below the medulla.

The rhizinae arise from the lower part of the prothallus. They arise in groups on the entire lower surface of the thallus and are black and quite conspicuous. The rhizinae are 3-5 μ thick.

Apothecia: The apothecia are scattered on the upper surface. They are mostly brown or infrequently black with margins which are concolorous with the thallus. The apothecia are sessile, peltate, and 0.5-1.0 mm in diameter.

The amphithecium is of irregular paraplectenchyma. It is 70 μ thick and the orientation of the hyphae clearly shows its development from the exciple.

The exciple is 15 μ thick and is composed of euthyplactenchyma. It cannot be distinguished very well from the amphithecium in the lateral margins.

There is a layer about 18 μ thick of pigmented, thick-walled cells above the exciple and below the hymenium which probably is the hypothecium. This tissue is absent in all the other species of the family Pannariaceae that are studied here.

The hymenium is 45 μ thick and has clavate asci which are about 55 μ long and 10 μ wide. There are eight oblong, 12-15 x 4-5 μ spores in each ascus. They are thin-walled, one-celled, and hyaline.

The paraphyses have club-shaped tips, 2.5-3.0 μ wide which form the 3 μ thick epithecium. The paraphyses reach the surface of the apothecium, and even extend a little above it.

Parmeliella plumbea (Lightf.) Mull. Arg.

Bullet. Herbar Boissier. 2 (appendix I): 44. 1894.

Lichen plumbeus Lightf., Flora Scotica 2: 826. 1777.

Material Studied:

SCOTLAND, Argyll: shores of Lake Leven near Glen Coe,

Weber W. A. and Grundwell A. C. S. 14300, 1958 (MSC).

Detailed Description:

Thallus: The thallus is foliose, grayish, and has scattered cylindrical isidia and orangish soredia. The thallus lobes are imbricate, 2-4 mm wide and pruinose. The prothallus extends about 1 mm beyond the thallus lobes as a black margin, sometimes appearing like a cushion of hyphae. The rhizinae are abundant, black, and 2.5 mm long. Sometimes they are not seen under the slightly involute margins of the lobules.

The uppercortex is paraplectenchymatous (Plate 20), 20 μ thick and the cells are almost vertical to the surface of the thallus.

The algal layer is 50 μ thick containing Nostoc filaments which are either coiled, vertical, or horizontal. The Nostoc cells are 4-5 x 6-8 μ .

The medulla is 80 μ thick and is composed of thin-walled, almost parallel hyphae.

There are conglutinate and black hyphae below the medulla which form the prothallus which is 20 μ thick and form a mat of hyphae which appears almost cushion-like in the marginal areas at the tips of some lobes.

The rhizinae arise from the lower part of the prothallus and are black and cover the entire lower surface except some marginal tips.

Apothecia: The apothecia are scattered on the upper surface. They are dark brown with the same colored margins and are 0.8-1.0 mm in diameter. The disks are peltate and glabrous and are constricted below.

The apothecia are mycolecanorine, the amphithecium being prosoplectenchymatous and about 60 μ thick.

The exciple is 20 μ thick in the lateral margins and is 80 μ thick in the center. It is composed of euthyplectenchyma and is colorless.

The subhymenium is not distinct from the exciple below and the hymenium above.

The hymenium is 70-100 μ thick and has oblong asci which are 35 μ long and 8 μ wide. There are eight ovoid, one-celled, 4-5 x 4 μ , hyaline, each with a thick epispore. They are monostichous or distichous, often within the same apothecium (Plate 19).

The paraphyses are either fusiform or with club-shaped tips. Their tips are not pigmented or thick-walled in most cases, hence an epithecium is not differentiated.

Placynthium Gray

A Natural Arrangement of British Plants, 1:395. 1821.

Type Species: Placynthium nigrum Gray, l.c.

Species Studied: Placynthium nigrum.

Material Studied:

U. S. A., Michigan: Leelanau County: along the shores of
Lake Michigan at Lighthouse Point, Imshaug 1948,
1958 (MSC).

Detailed Description of Placynthium nigrum:

Thallus: The thallus is crustose but broken into angular areoles. Each areole is composed of several granules. The granules are 0.5-1.0 mm in diameter. The thallus is dark olive-brown, appearing black. It is attached to the substrate by conspicuous rhizinae which are black.

The thallus anatomy is discussed in Section III in detail but some of the important things are repeated here. A thallus section shows that the granules are rather intermediate between being homoiomerous or heteromerous. There is a one-celled paraplectenchymatous cortical layer seen

as the outermost layer of the granule (Plate 21). The thickness of the granule is occupied by the phycobiont and fungal hyphae. The medulla is not seen as a definite layer, since the filaments of Nostoc are dispersed irregularly in the entire central region. The Nostoc filaments are 2-6 cells long and are sometimes in coils. The algal cells are 2-3 x 3.5 - 4 μ . The filaments are mostly vertical.

The rhizinae arise from the lower surface of the areole and are black and conspicuous.

Apothecia: Apothecia are scattered on the upper surface. They are concolorous with the thallus, 0.2-0.3 mm in diameter and with prominent black margins.

The apothecia are mycolecanorine, constricted below and with straight surface. The amphithecium is paraplectenchymatous, and the orientation of the hyphae clearly shows that the amphithecium has developed from the exciple (Plate 22). The tissue of amphithecium is about 15 μ thick laterally and about 90 μ toward the base.

The exciple is composed of thin-walled, loose and almost parallel euthyplectenchyma. It is a very thick

tissue (about 100 μ) in the center of the apothecium and very narrow (20-40 μ) in the lateral margins. Among the species of the Pannariaceae that have been studied here, this species seem to have a unique exciple.

The hymenium is composed of linear asci, pointed at both ends, and filiform paraphyses. The mature asci are 32-35 μ long and 4-5 μ wide. There are eight spores in each ascus. The spores are one-celled or two-celled with both kinds equally common in the same apothecium. They are elliptical, monostichous (arranged side to side slanting in one direction), thin-walled, and hyaline. They are 5-7 x 3-4 ^{μ} ₄ in size.

The paraphyses are without thickened tips hence an epithecium is not differentiated. The tips of the paraphyses are 2-5 μ wide.

Psoroma Nyl.

Mem. Soc. Sci. Nat. Cherb. 3:175. 1855.

Type Species: Psoroma Hyphorum (Vahl). S. F. Gray

Species Studied: Psoroma hyphorum, and Psoroma pallidum.

Detailed Description of the Genus Based on the Species Studied:

Thallus: The thallus is squamose, with minute, glabrous, grayish squamules, having scattered white soredia. The rhizinae are pale and absent from the lower margins, they are few and inconspicuous.

The upper cortex is paraplectenchymatous which is usually several cells thick and the cells are somewhat irregularly placed.

The algal layer is usually narrower than the upper cortex and the medulla. The algal filaments are not so densely packed as in the other genera of the family. The alga is Doctylococcus or more probably Coccomyxa (a green alga).

The medulla is the widest layer and is composed of thin-walled loose hyphae which form a network or are irregular.

The lower part of the medulla is composed of hyphae which form a kind of tissue which is different from the medullary tissue and is not like upper cortex either. This, then, is the pseudocortex.

The rhizinae arise from the pseudocortex and as numerous tufts. They are thin-walled and usually non-septate.

Apothecia: The apothecia are scattered on the upper surface. The disk is concave and the margins are crenate and concolorous with the thallus. They are adnate to sessile.

The apothecia are mycolecanorine, the amphithecium is or is not differentiated into a cortex and a medulla.

The exciple is of loose and parallel euthyphallous tenchyma and colorless.

The asci are linear to oblong and have eight hyaline, thin-walled, monostichous or distichous spores which are usually ellipsoid to almost spherical. The

paraphyses are filiform or with club-shaped ends, they do or do not form an epithecium.

Psoroma hypnorum (Vahl.) Gray.

A Natural Arrangement of British Plants, 1:445. 1821.

Lichen hypnorum Vahl., Icon. Pl. Dan. fasc. 956, 1787.

Parmelia hypnorum (Vahl.) Ach. Pannaria Hypnorum (Vahl.)

Koerb.

Material Studied:

U. S. A., Colorado: Jackson County: 3 miles north of
Willoe Creek Park, Rabbit Ears Range, Shushan
S-8401, 1956 (MSC).

Detailed Description:

Thallus: The thallus is grayish-green, squamose, the squamules are minute and imbricate with rounded margins and are smooth with occasional globose soredia. The rhizinae are pale and few and are not very conspicuous.

The upper cortex is paraplectenchymatous, 4-5 cells (50 μ) thick with irregular cells.

The algae filaments are quite conspicuous (more than in the thallus of P. pallidum). They are 2-4 cells long and are placed irregularly, the algal cells being 2-4 x 2-5 μ in

size. The algal layer is 40 μ thick (a little less than in P. pallidum).

The medulla is composed of thin-walled, loose arachnoid hyphae, 60 μ thick. There is no pseudocortex below the medulla as in P. pallidum and the rhizinae arise from the lower part of the medulla. The rhizinae are not present on the lower margins and when present are not very conspicuous. However, below the apothecia they are sometimes arachnoid.

Apothecia: The apothecia are reddish brown, 1.5-2 mm in diameter with a concave disk. The margins are crenate and concolorous with the thallus. The margins are involute so as to cover the disk to a great extent.

The apothecia are lecanorine and the amphithecium is not differentiated into a cortex and a medulla. The algae are dispersed through the entire thickness of the amphithecium, which is 225 μ thick. The amphithecium is paraplectenchymatous and short algal chains are found along with the fungal tissue. The hyphae run parallel to the surface of the apothecium. On the sides the amphithecium is tomentose (Plate 24). The tomentum is dense composed of hairs which are short, one-celled, and colorless.

The exciple is euthyplectenchymatous. The tissue is loose and composed of parallel hyphae which are thin-walled and hyalline. It is of equal thickness laterally as well as below the hymenium and is 20 μ thick.

The hymenium is composed of clavate asci. There are eight ellipsoidal one-celled, monostichous or distichous hyalline spores in each ascus. The spores are 15-22 x 7-10 μ in size and are without a thick episore.

The paraphyses are filiform. Their tips are not pigmented or thick-walled, hence an epithecium is not developed here (Plate 24) as it is in P. pallidum.

Psoroma pallidum Nyl.

In Annal. Sc. Nat., Bot., Ser. 4, 12:294. 1859.

Material Studied: Misplaced after making the slides.

Collection data: not available.

Detailed Description:

Thallus: The thallus is squamose, the squamules are 0.1-0.3 mm wide, they are almost corolloid and grayish on the upper surface and pale on the lower. The thallus is glabrous and has occasional scattered, globose, white soredia.

The rhizinae arise from the lower surface leaving the margins free; they are pale and inconspicuous.

The upper cortex is paraplectenchymatous but the cells are irregularly arranged. It is almost 10 cells (about 80 μ) high.

The algal layer is about 35 μ thick and is composed of spheroidal cells of probably Coccomyxa. The algal cells are surrounded by a gelatinous sheath and are usually united in colonies of indefinite extent, which are not very densely packed. The algal cells are 5-10 x 5-8 μ in size.

The medulla is composed of thin-walled, arachnoid hyphae, which are loosely arranged. The layer is 120 μ thick and is the thickest layer in the thallus.

The lower part of the medulla is cellular and 30 μ thick; it appears to be a pseudocortex.

The rhizinae are not very conspicuous, and arise from the pseudocortex.

Apothecia: The apothecia are scattered on the upper surface, and are minute as compared with those of P. hypnorum. The disk is brownish, flat, and the margins are concolorous with the thallus and crenate. The apothecia are adnate.

The amphithecium is differentiated into a cortex and a medulla and the algae are found in the middle areas. The amphithecium is paraplectenchymatous and 160 μ thick. The sides are not tomentose as in P. hypnorum.

The exciple is hyalline and is formed of loose, parallel, thin-walled euthyplactenchyma, 10 μ thick in the sides, and 40 μ thick below the hymenium.

The hymenium is composed of linear asci which are 70-90 x 12-18 μ . They contain eight one-celled, ovoid to spherical, hyalline spores. The spores are mostly monostichous and are without a thick epispore. They are 5-8 μ in diameter.

The paraphyses are linear, unbranched, and non-septate. They have club-shaped tips, forming an epithecium 10 μ thick.

VIII

DISCUSSION

Lichens like any other organism can be classified in many different ways. Ever since these organisms attracted the attention of naturalists, they have been placed in different systems of classification, based on external characters as well as the anatomy of the thallus and apothecium and even the phycobionts. Most of the time the classification was quite artificial (classification based upon characters of convenience without relation to phylogenetic significance or classification based on a single arbitrarily chosen criterion, instead of an evaluation of the totality of characters).

Zahlbruckner (1912) was the first to propose a satisfactory natural classification. Our present knowledge of the lichen ascocarp makes the development of the lichen thallus of secondary taxonomic importance (Santesson, 1954). The micro characters of the fungus in the apothecia, e.g.,

spore septations, nature of the exciple, nature of amphithecial tissue, are very important and must be considered if one has to come to a meaningful phylogenetic grouping of the species. The micro characters of the thallus, e.g., distribution of the algae, presence or absence of a lower cortex, and nature of medullary hyphae, etc., can be of assistance along with the micro-characters of the apothecium. The characters of the phycobionts are more important in identification than in classification. Culberson (1961) in discussing lichen nomenclature proposed, "The algal and fungal components of a lichen shall not be considered discordant elements." Thus, emphasizing the importance of considering both algal and fungal components together, and implying that a lichen thallus is, biologically, something more than just two plants living together. Santesson (1950) emphasized that we have to deal with the lichenized fungi alone and not with the lichen consortium when it comes to taxonomy of lichens. He said that "lichen systematics" based on algal characters is unnatural. My own studies suggest that phylogenetic relationships and development throughout the family Pannariaceae are shown by the development of mycobiont tissue. I have not been able to

see any characters of the phycobiont which can be considered primitive or as as highly advanced.

Naturalness of the family Pannariaceae:

The family Pannariaceae except for the genus Placynthium, seems to be a natural group since phylogenetic relationships can be seen among the genera and a gradual evolution from a less developed to a more developed structure or tissue is quite noticeable. The family probably is of polyphyletic origin and the genera have taken different lines of development. The following characters in the remaining genera show some probable phylogenetic relationships (less highly advanced character given first):

1. The spores range between one to two and three-celled.
2. The exciple is from loose to conglutinate euthyplectenchyma.
3. The amphithecium is prosoplectenchymatous to paraplectenchymatous.
4. The apothecia are lecanorine to mycolecanorine.
5. The thallus is squamose, subfoliose to foliose.
6. The thallus ranges between a less developed heteromerous (Parmeliella microphylla) to a highly

developed heteromerous (Massalongia carnosa) type.

7. The presence of prothallus in some species and its absence in the others.

Placynthium should be removed from the Pannariaceae, because it has many characters (as seen in the type species P. nigrum) which are different from the other genera studied here. They are as follows:

1. The exciple is cup-shaped as compared with a saucer-shaped exciple in the other species.
2. The cortical layers are one-celled thick rather than 2-many celled in the other genera.
3. The medulla is absent, with the whole thickness of the areole being occupied by algal filaments.
4. The thallus is squamose-areolate, rather than squamose, subfoliose, or foliose.

Dahl (1950) also suggested that Placynthium should be removed from the Pannariaceae and be placed in a family of its own--Placynthiaceae. He included other genera in the Placynthiaceae (see p. 10). He separated the two families, Pannariaceae and Placynthiaceae, on the basis of two differences.

Dahl considered the Pannariaceae to have only a nostociform phycobiont and the Placynthiaceae to have only a scytonemeiform phycobiont. He did not consider Psoroma at all which has a green phycobiont. In Coccocarpia the phycobiont is Scytonema (according to Bornet's 1909 figures). Dahl suggested that Coccocarpia be removed from Pannariaceae, though he did not assign it a definite family. If keyed out according to his key it comes under Placynthiaceae. My studies of the anatomy of the apothecium of Coccocarpia show that the apothecial tissues are similar to the other genera, hence Coccocarpia should not be removed from Pannariaceae simply on the basis of its having scytonemeiform alga.

It has not been determined whether the phycobiont of Erioderma is Scytonema or Nostoc or both. Dahl (1950) suggested that Erioderma has scytonemeiform alga but since its morphology and anatomy are different from the members of the Placynthiaceae, it should be put into a family of its own. The characters of the apothecial tissues of Erioderma are closer to the other members of the Pannariaceae and therefore I suggest that Erioderma be left in its present position.

The second criterion that Dahl gave for the separation of Pannariaceae and Placynthiaceae was the orientation of the algal filaments. I found that there are both vertical and horizontal filaments of the phycobiont in the thallus of Placynthium nigrum and other species. The horizontal filaments are quite prominent in Coccocarpia but then they are equally so in Hydrothyria, which was placed in the Pannariaceae.

Choisy (1960) recognized the Placynthiaceae as a separate family with Placynthium as the type genus. Further, he considered the Pannariaceae to contain just one genus, Pannaria, with the other genera formerly included here as sections and subsections of it. I consider the morphological characteristics of these genera support their being kept at the generic level.

Naturalness of the genera:

One of the main characters by which genera of Pannariaceae are identified is the presence of a green or blue-green phycobiont. Only two genera, Psoroma and Psoromaria, possess a green phycobiont, but their mycological characteristics bind them together with the other genera in the Pannariaceae.

The type genus, Pannaria, has the following characters:

1. Thallus squamose to foliose.
2. Thallus almost heteromerous (lower cortex absent).
3. Upper cortex paraplectenchymatous.
4. Phycobiont is blue-green.
5. Medulla of loose, arachnoid hyphae.
6. The outermost layer of the apothecium is the amphithecium.
7. The exciple is distinct.

The characters mentioned above are seen with some variations in the other genera studied here. Some of the distinct differences are mentioned below.

Hydrothyria is an aquatic genus hence one would expect some morphological specializations of the thallus such as, shield-like thallus lobes, prominent veins, thallus becoming frutiose as it grows away from the substrate, etc. However, the anatomy of the apothecium including a paraplectenchymatous amphithecium, a euthyplactenchymatous exciple, etc., follow the same pattern as the other genera in the Pannariaceae.

Dodge (1933) removed Erioderma physioides from the genus Erioderma and made it the type species of a new genus, Malmella, with three new species and another new combination. The way he differentiated between Malmella and Erioderma is that Malmella has less developed tomentum than Erioderma, whereas he has overlooked the fact that E. limbatum which he has included in Erioderma does not have any tomentum at all (although he says it is tomentose). According to him the phycobiont in Malmella is Nostoc and probably Scytonema, though his new combination M. physioides has Nostoc.

The other differences that he gave between Malmella and Erioderma is that the apothecia are scattered in the first, and marginal in the latter. This is not a very distinct difference, because scattered apothecia are seen in E. microcarpa and marginal in E. physioides. Further, he said that amphithecium is absent in Erioderma and present in Malmella. Maybe this is due to differences in terminologies of the tissues of the apothecium, according to the terminologies used here amphithecium is present in all the species of Erioderma that I have examined including E. physioides (Plate 5).

The only difference that is seen between E. physio-
ides and other species is the presence of a special kind
of cells in the medulla of E. physioides. These cells
which have been called moniliform or spheroidal cells,
have not been mentioned by Dodge. Asahina (1952) saw
them in Parmelia sublaevigata and Culberson (1961) noticed
them in Parmelia galbina. The significance of the cells
is still unknown; probably they are of no taxonomic value.

Relationships of the Genera based on the Species Studied:

A phylogenetic arrangement of the genera of the
Pannariaceae was suggested by Reinke (1895), who traced
possible relationships of the genera within the family,
and to other genera and families (see Section II).

Zahlbruckner (1926) also arranged the genera of
the Pannariaceae into a possible phylogenetic order (see
Section II).

This study has revealed some characters which I
considered important in arranging the genera phylogenti-
cally.

If Placynthium is to be included in the Pannaria-
ceae, then it is probably one of the most highly evolved

genera, as shown by its highly developed exciple and what appears to be a retrogressive evolution of the thallus. The latter is indicated by the presence of a cortical layer occupying the whole thickness of the areole. If Placynthium should be removed from the Pannariaceae as suggested by Dahl (1950) and Choisy (1960), and I believe it should, then Massalongia is the most highly evolved genus.

Henssen (1963) treated Massalongia, Koerberia, Vestergreopsis and Placynthium as closely related genera belonging to the family Peltigeraceae. The reasons she gave for including Massalongia and Placynthium in one family were:

1. Both have hemiangiocarpic development of the apothecia, and
2. Their spores are ellipsoid to fusiform and septate.

My studies of Massalongia carnosa and Placynthium nigrum did not show any relationship either between the thalli or the apothecia of these species (see Plates 13, 14, 21, and 22, and the descriptions on pages 81 and 108).

The apothecial anatomy of Massalongia carnosa is quite similar to that of Hydrothyria venosa (Plates 11 and 14 respectively). However, the latter has one-celled spores.

The thallus anatomy of Coccocarpia Gayana (Plate 1) and that of Hydrothyria venosa (Plate 11) show two very strong similarities: the first is the presence of a lower pseudocortex; and the second is the occasional horizontal orientation of algal filaments in the medulla. Coccocarpia Gayana is a more highly evolved species of Coccocarpia, showing the presence of two-celled spores and slightly stipitate apothecia.

The apothecia of Coccocarpia and Erioderma are mycolecanorine (also of Hydrothyria, Massalongia, Parmeliella, and Placynthium) but it is very hard to say whether the outermost margin of the apothecia of Coccocarpia is an amphithegium or exciple. The apothecia of Erioderma have a well-developed stipe which makes them more highly developed than those of Coccocarpia.

The genus Psoroma, though having a bright-green phycobiont as compared to blue-green in other genera, has apothecial characters quite similar to those of Pannaria. Both have lecanorine apothecia but in the amphithegium

of Pannaria lurida (Plate 16) a cortical layer is developed. In Psoroma hypnorum (Plate 23) there is no such differentiation. Two characters which suggest that Psoroma is more highly evolved than Pannaria are larger spores and the presence of a lower pseudocortex (Plate 23).

It seems that Parmeliella is less highly evolved genus than the other genera, because of presence of a prothallus, and prosoplectenchymatous amphithecium. P. microphylla (Plate 18) has a lower pseudocortex, no medulla, and a very thick algal layer, making this species more highly evolved than the others in the genus.

Probably Parmeliella, Coccocarpia, Hydrothyria, and Massalongia follow the same line of evolution, Erioderma being a divergence from somewhere near Coccocarpia. The genus Pannaria falls between Parmeliella and the other more developed genera, and is related to Psoroma.

At this point I would like to make some suggestions for further studies on the Pannariaceae.

1. Extensive research on the chemistry of the family.
2. More work on the isolation and identification of the phycobionts is needed in the Pannariaceae.

3. More intensive works on monographs of some genera.

IX

SUMMARY

This study has been done on morphology and anatomy of some of the species of each of the following genera:

Coccocarpia, Erioderma, Hydrothyria, Massalongia, Pannaria, Placynthium, Parmeliella, and Psoroma, of the family Pannariaceae.

The following conclusions have been drawn after studying the different species.

1. The thallus in Pannariaceae is squamose to foliose, and is heteromerous or between a true homoiomerous and a true heteromerous type. Only Massalongia carnosa has a true lower cortex. Coccocarpia, Hydrothyria, and Psoroma pallidum have a lower pseudocortex and the others do not have a lower cortex at all. In Placynthium nigrum and Parmeliella microphylla, the cortical tissue is present but the algae are not confined to a definite layer.

The hyphal tissue which appears as a dark or pale line beyond the thallus lobes in Parmeliella is a prothallus and not a hypothallus.

2. The apothecia are either lecanorine (algae in the amphithecium), or mycolecanorine (no algae in the amphithecium).
3. The outermost layer in the apothecium is an amphithecium (questionable in Coccocarpia).
4. The genus Placynthium represents many diversities of morphological and anatomical characters from the others, hence should be removed from the Pannariaceae.
5. Erioderma physioides does not present any different characters from the other species of Erioderma, except for the presence of moniliform cells in the thallus, hence should not be made the type species of the new genus Malmella (Dodge, 1933), but should be left as a species of Erioderma.
6. The orientation of the fungal hyphae and algal chains was noted but it is not of any taxonomic value, except that in Coccocarpia Gayana and

Hydrothyria venosa occasional horizontal filaments are seen.

In Section XI are plates of longitudinal and cross-sections of both the thalli and apothecia of Coccocarpia Gayana, Erioderma physioides, Erioderma Wrightii, Hydrothyria venosa, Massalongia carnosae, Pannaria lurida, Parmeliella plumbea, and Placynthium nigrum, cross sections of the thalli of Parmeliella microphylla and Psoroma pallidum, and longitudinal sections of apothecia of Coccocarpia pellita, Pannaria pezizoides, and Psoroma hypnorum. The last plate is of different kinds of tissues that make up the exciple in Collema (redrawn from Degelius, 1954, Fig. 11).

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Plate I

Coccocarpia Gayana. . Cross section of the thallus, illustrated diagrammatically and in detail.

UC = upper cortex

AL = algal layer

M = medulla

PC = pseudocortex

R = Rhizinae

- Note:
1. Upper cortex of irregular paraplectenchyma.
 2. Algal layer with occasional horizontal filaments.
 3. Medulla of parallel hyphae.
 4. Pseudocortex developed.

PLATE I

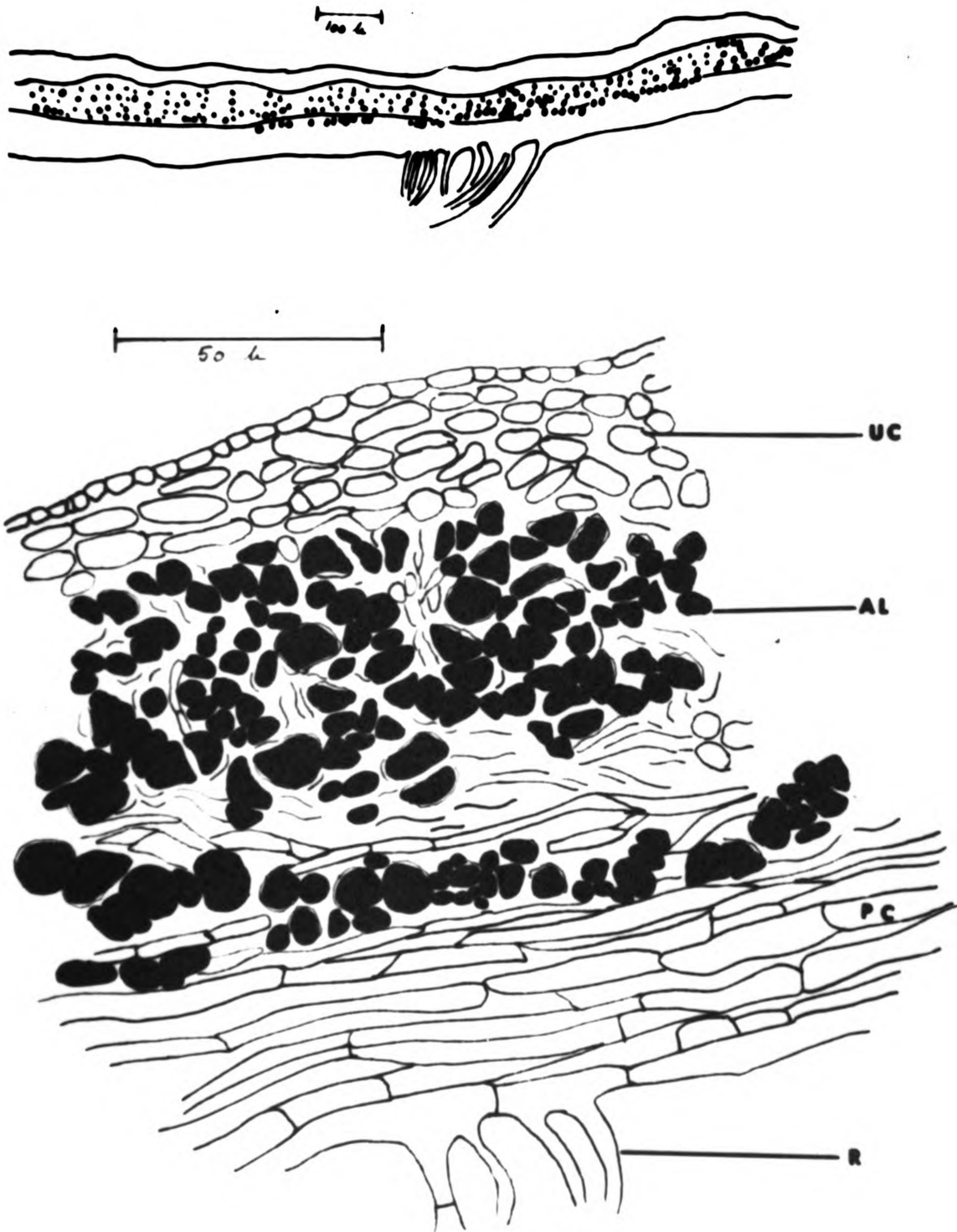


Plate II

Coccocarpia Gayana. Longitudinal section of the apothecium illustrated diagrammatically and in detail.

HYM = hymenium

"EXC"= "exciple"

"AMP"= "amphithecium"

- Note:
1. Mycolecanorine apothecium.
 2. No distinction between "amphithecium" and "exciple."
 3. Septate paraphyses.
 4. Spores two-celled with thick episore.

PLATE II

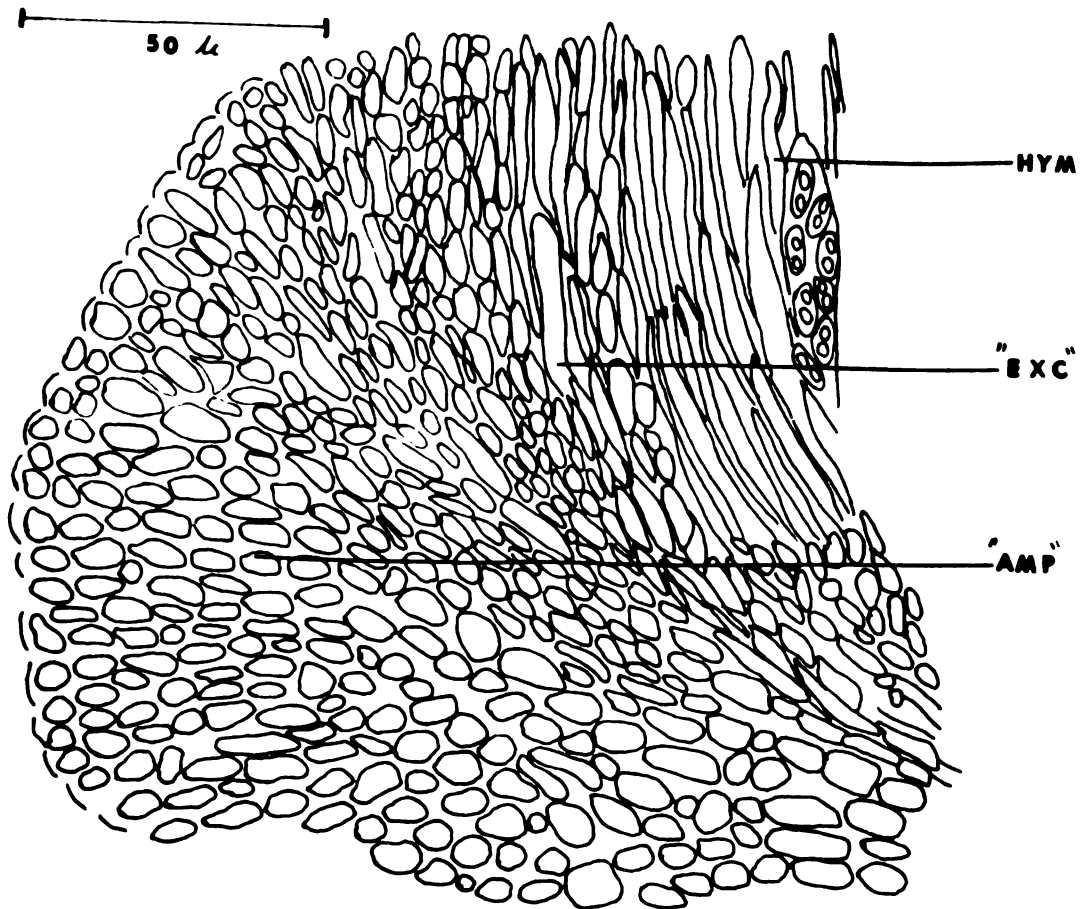
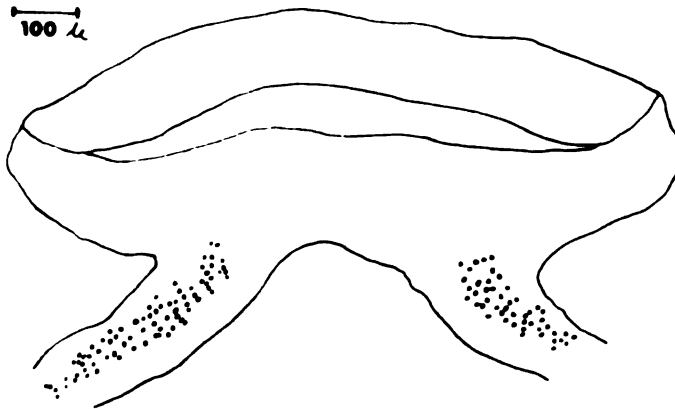


Plate III

Coccocarpia pellita. Longitudinal section of the apothecium illustrated diagrammatically and in detail.

APO = apothecium

THA = thallus

EPI = epithecium

HYM = hymenium

"EXC"= "exciple"

"AMP"= "amphithecium"

- Note:
1. Adnate apothecium.
 2. Well-developed epithecium.
 3. No distinction between amphithecium and exciple.
 4. Spores very minute.

PLATE III

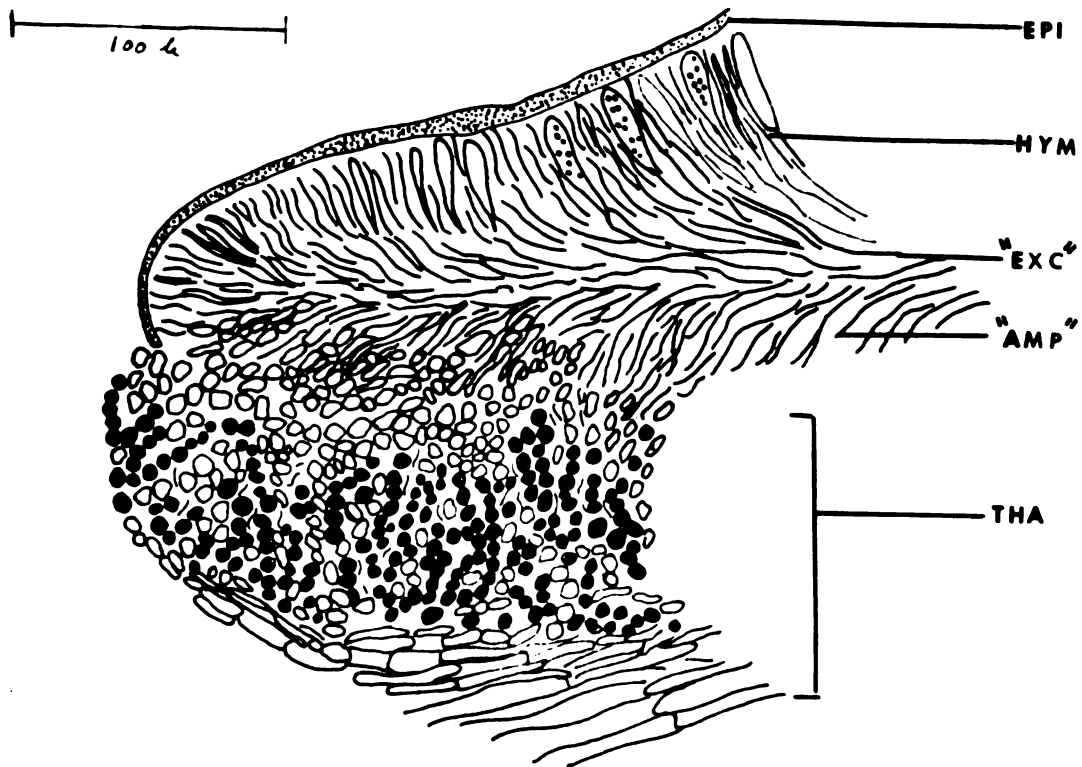
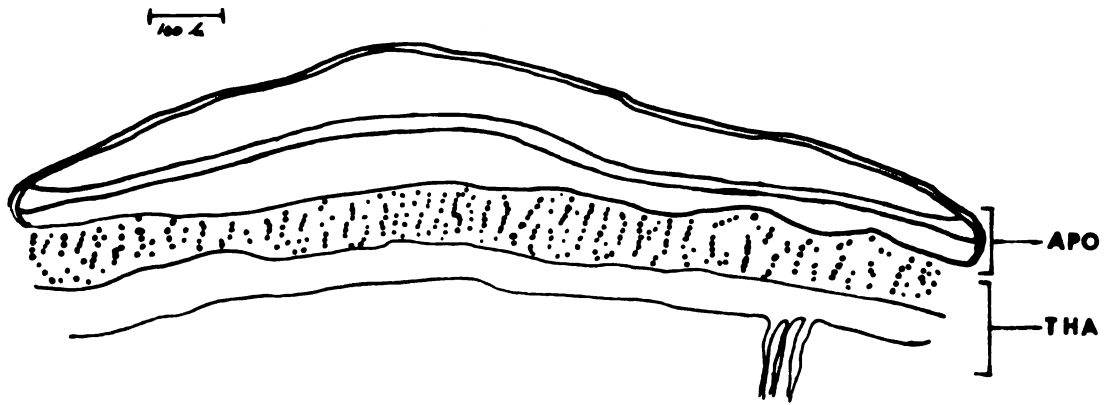


Plate IV

Erioderma microcarpa. Longitudinal section of the apothecium, illustrated diagrammatically.

EPI = epithecium

HYM = hymenium

EXC = exciple

AMP = amphithecium

ST = stipe

- Note:
1. Mycolecanorine apothecium.
 2. Presence of stipe.
 3. Well-developed epithecium.
 4. Exciple almost of uniform thickness.

PLATE IV

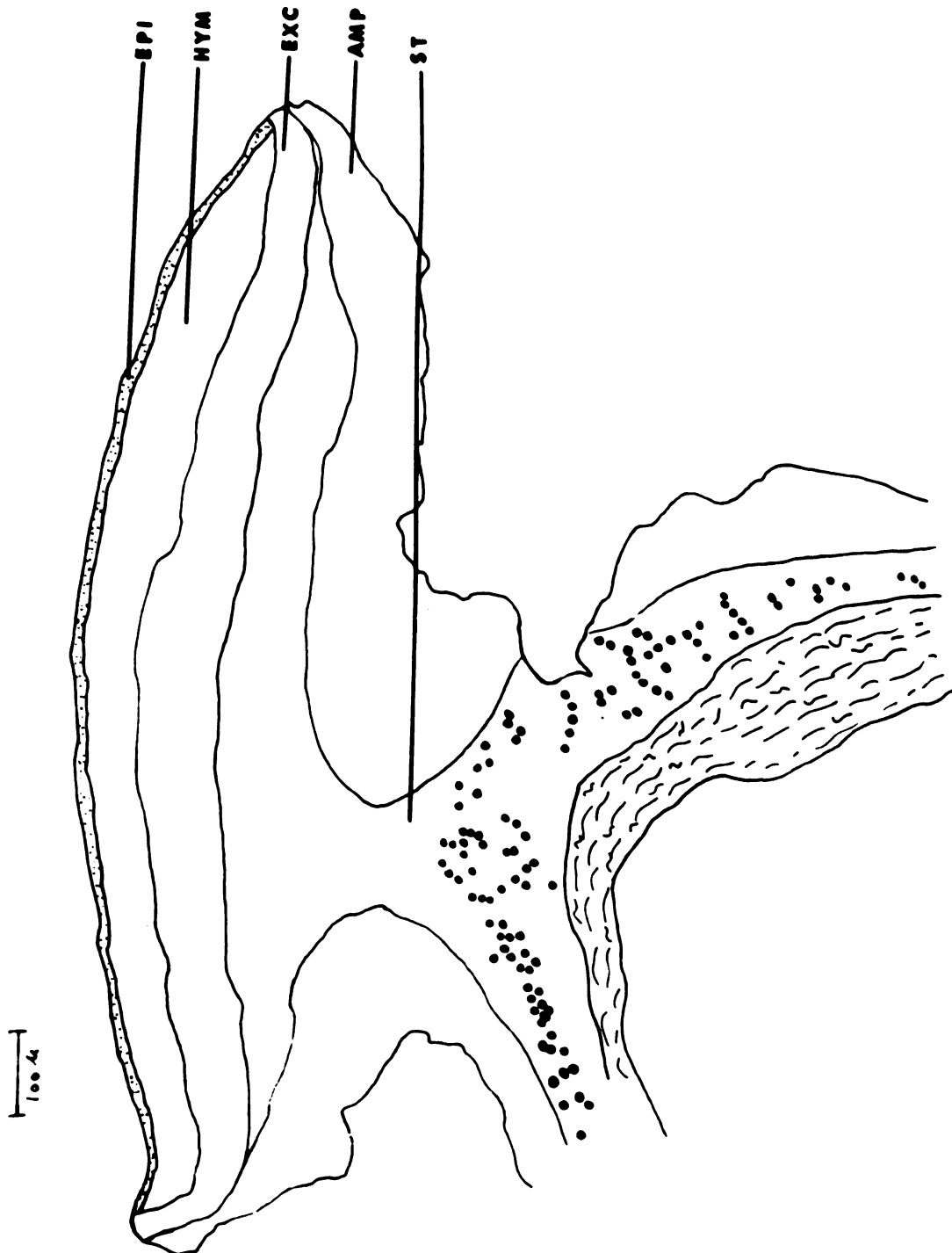


Plate V

Erioderma physioides. Cross section of the thallus illustrated diagrammatically and in detail.

UC = upper cortex

AL = algal layer

M = medulla

SPH.C= spheroidal cells

T = tomentum

- Note:
1. Tomentum developed.
 2. Medullary hyphae almost parallel to the surface of the thallus.
 3. Spheroidal cells in the medulla.

PLATE V

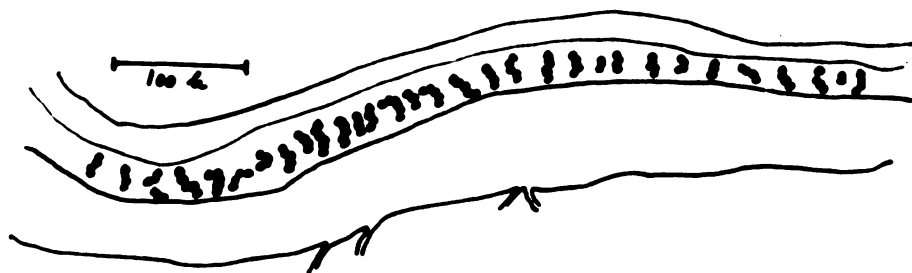


Plate VI

Erioderma physioides. Longitudinal section of the apothecium, illustrated diagrammatically.

EPI = epithecium

HYM = hymenium

EXC = exciple

AMP = amphithecium

ST = stipe

- Note:
1. Mycolecanorine apothecium.
 2. Well-developed epithecium.
 3. Stipe developed.

PLATE VI

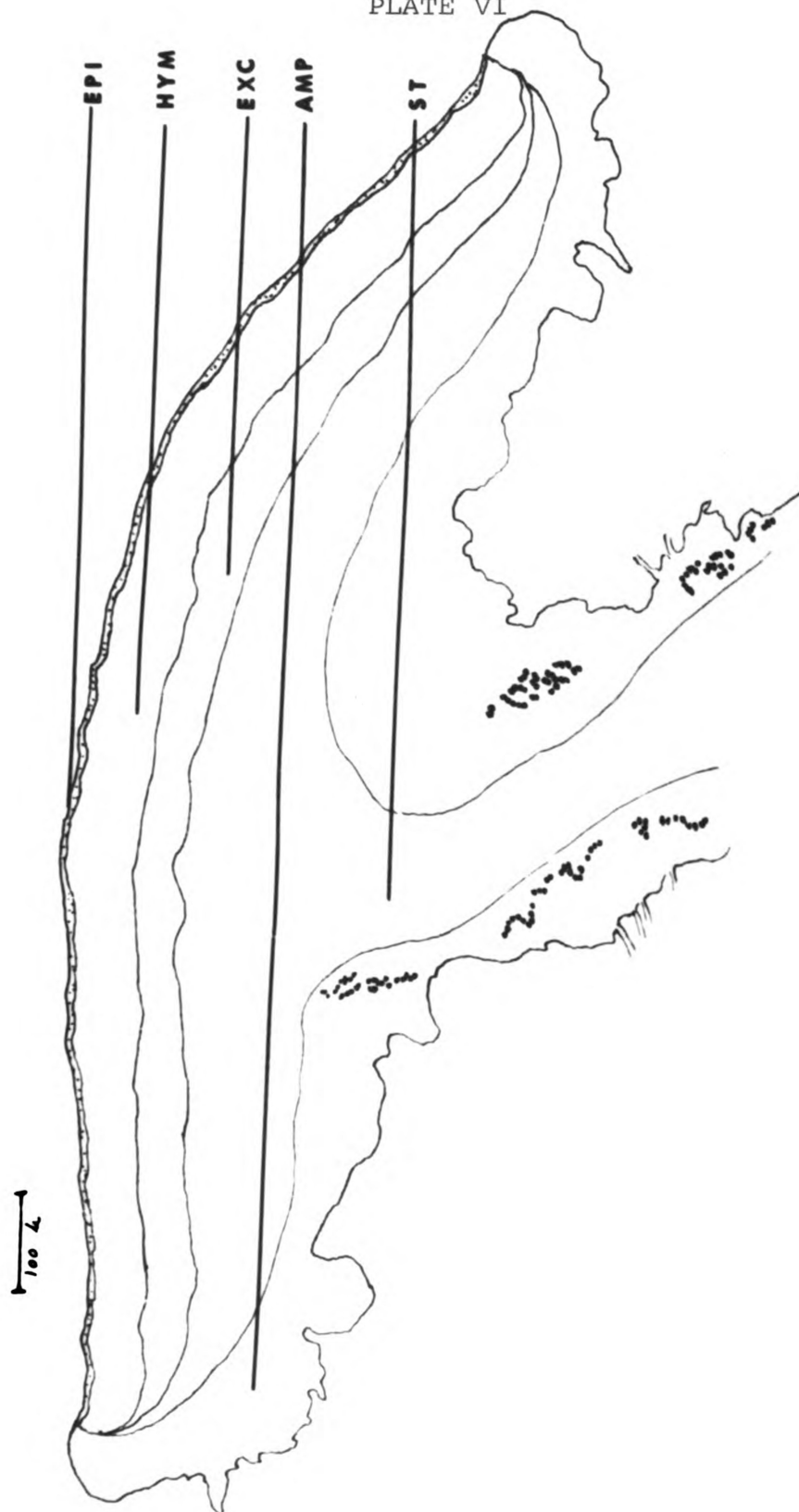


Plate VII

Erioderma physioides. Longitudinal section of the apothecium illustrated in detail.

AMP = amphithecium

EXC = exciple

EPI = epithecium

HYM = hymenium

ST = stipe

SP = spore

- Note:
1. Mycolecanorine apothecium.
 2. Well-developed epithecium.
 3. Exciple narrow at the sides and thicker in the center, of loose, irregular euthyplectenchyma.
 4. Stipe developed.
 5. Diagram of spore (without scale) to show minutely roughened inner wall.

PLATE VII

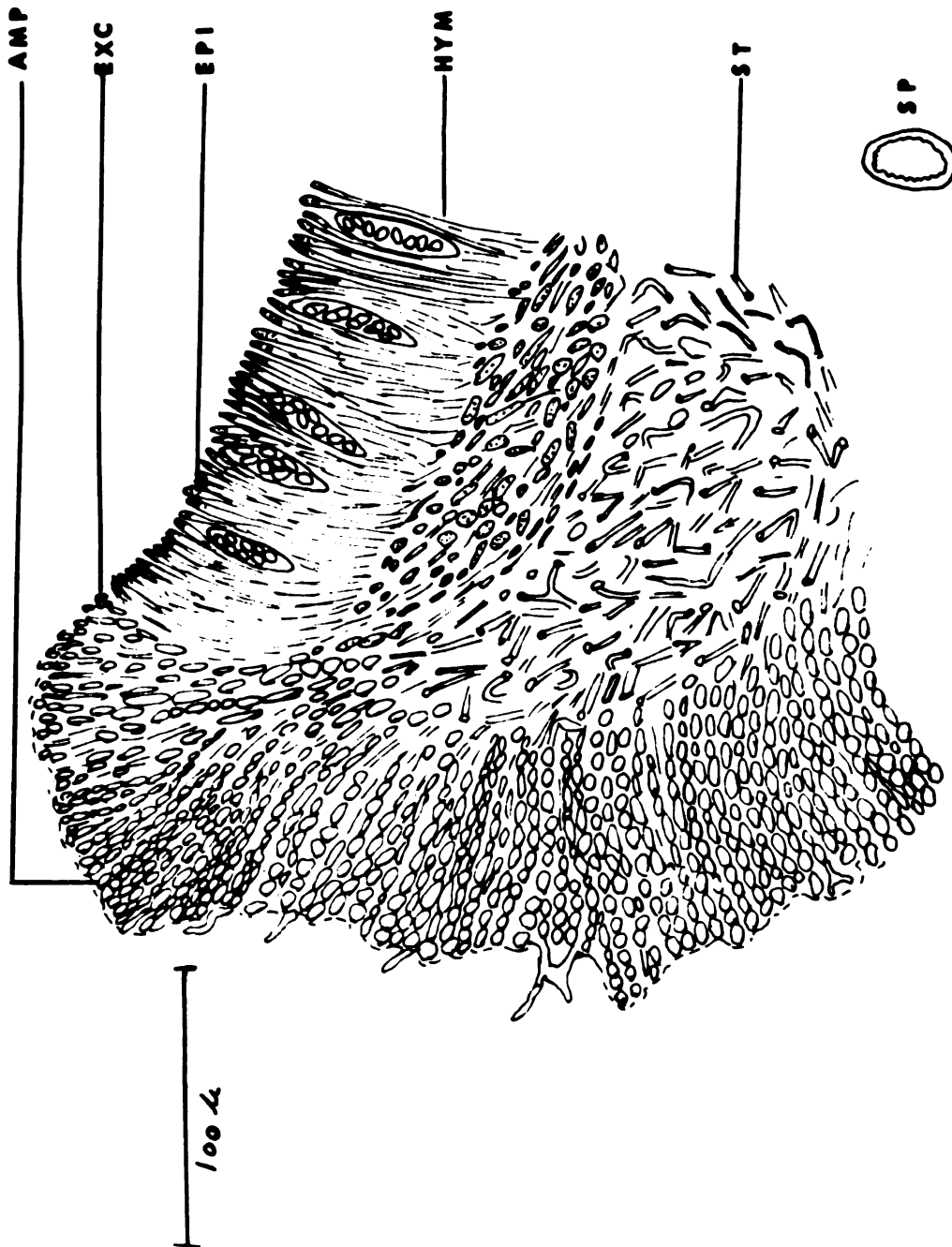


Plate VIII

Erioderma polycarpa. Longitudinal section of the apothecium illustrated in detail.

AMP = amphithecium

EPI = epithecium

HYM = hymenium

EXC = exciple

ST = stipe

T = tomentum

- Note:
1. Exciple of irregular, loose euthyplectencyma.
 2. Stipe developed.
 3. Tomentum well-developed, hairs curved or straight, unicellular, and unbranched.

PLATE VIII

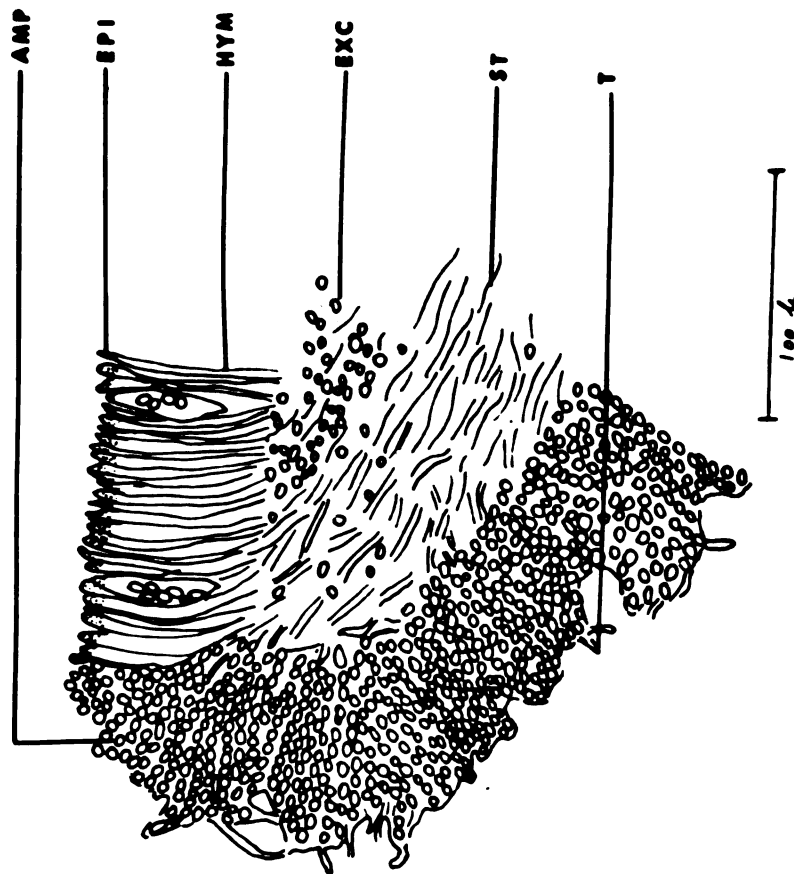


Plate IX

Erioderma Wrightii. Cross section of the thallus illustrated diagrammatically and in detail.

UC = upper cortex

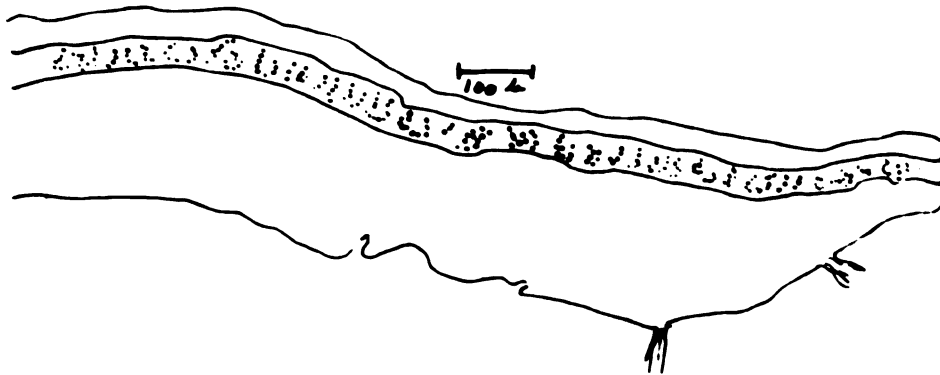
AL = algal layer

M = medulla

R = rhizinae

- Note:
1. Upper cortex of irregular paraplectencyma.
 2. Algal layer of sparse algal filaments.
 3. Medulla of irregular hyphae.

PLATE IX



10 μ

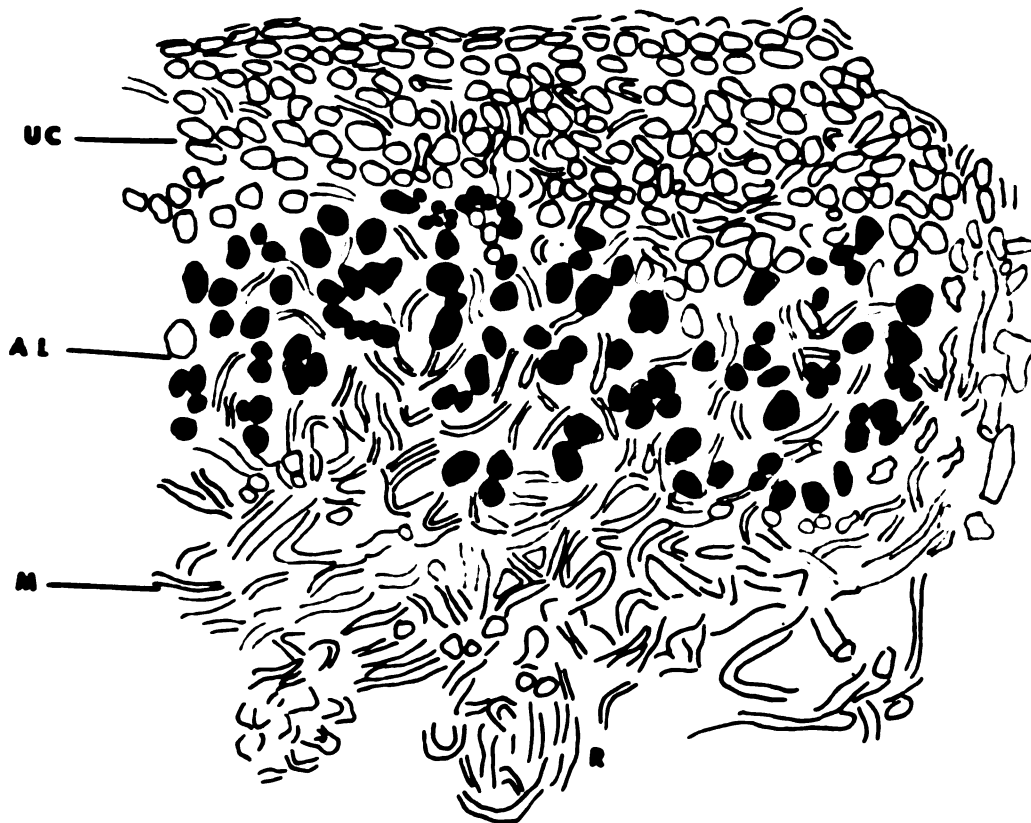


Plate X

Erioderma Wrightii. Longitudinal section of the apothecium illustrated in detail.

EPI = epithecium

HYM = hymenium

EXC = exciple

S.HYM = subhymenium

AMP = amphithecium

T = tomentum

SP = spore

Note: 1. Mycolecanorine apothecium.

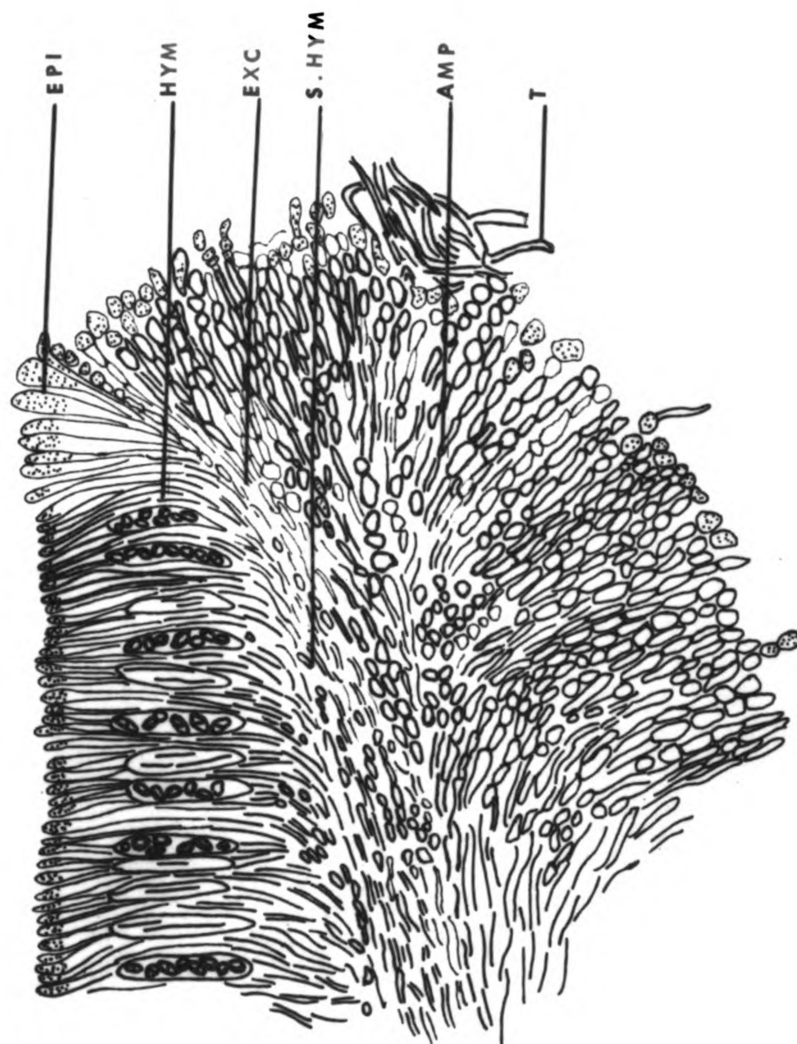
2. Well developed tomentum.

3. Subhymenium seen.

4. Spores 2-celled.

5. Diagram without scale of a 2-celled spore.

PLATE X



50 μ

S P

Plate XI

Hydrothyria venosa. Cross section of the thallus illustrated diagrammatically and in detail.

UC = upper cortex

AL = algal layer

M = medulla

R = rhizinae

PC = pseudocortex

- Note:
1. Upper cortex of paraplectenchymatous hyphae, which are running parallel to the surface of the thallus.
 2. Algal filaments horizontal and vertical both.
 3. Medullary hyphae parallel to the surface of the thallus.
 4. Pseudocortex developed.

PLATE XI

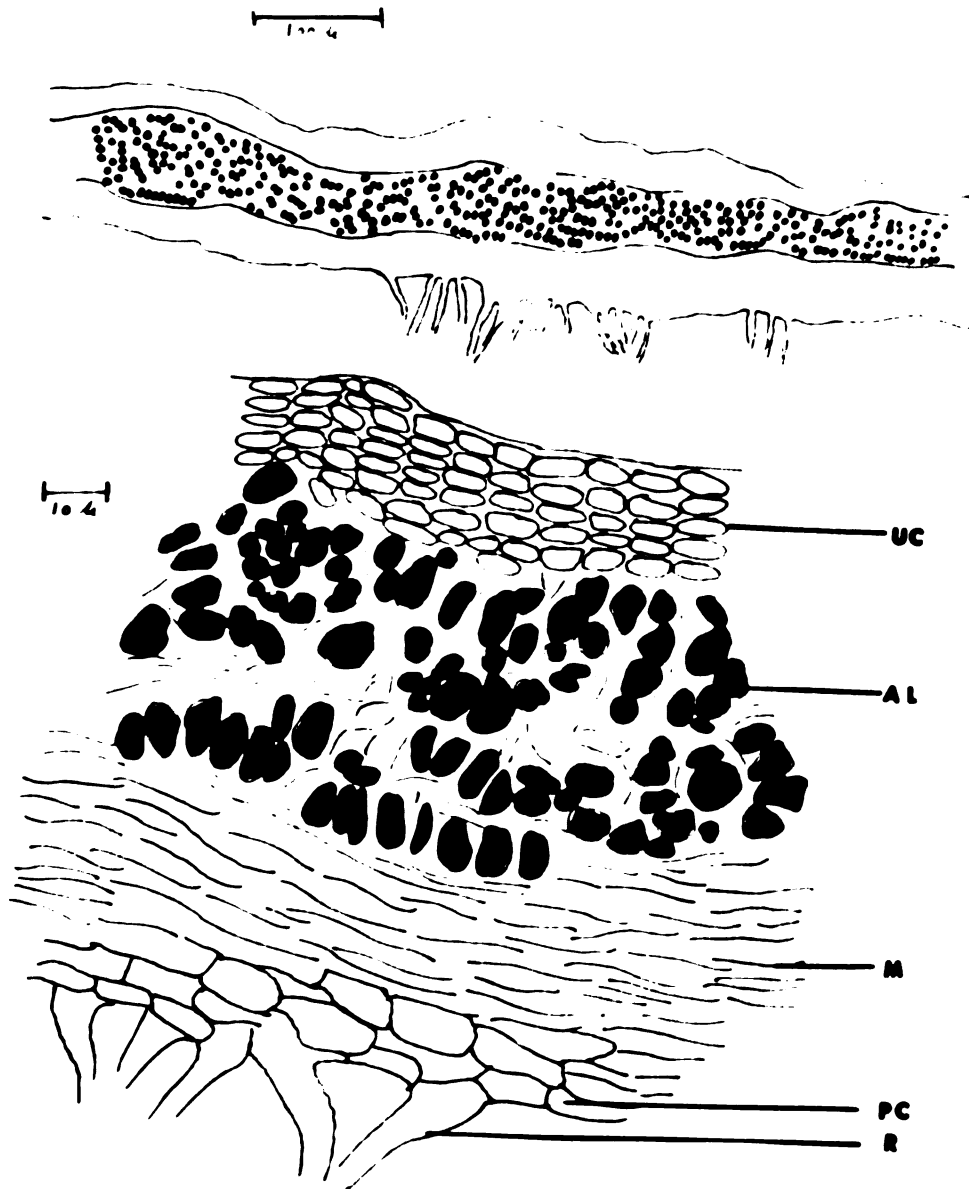


Plate XII

Hydrothyria venosa. Longitudinal section of apothecium
illustrated diagrammatically and in detail.

HYM = hymenium

EXC = exciple

AMP = amphithecium

T = tomentum

- Note:
1. Apothecium mycolecanorine.
 2. The exciple hardly one-celled in the sides,
euthyplectenchymatous.
 3. Amphithecium paraplectenchymatous.
 4. Tomentum well-developed on the sides.

PLATE XII

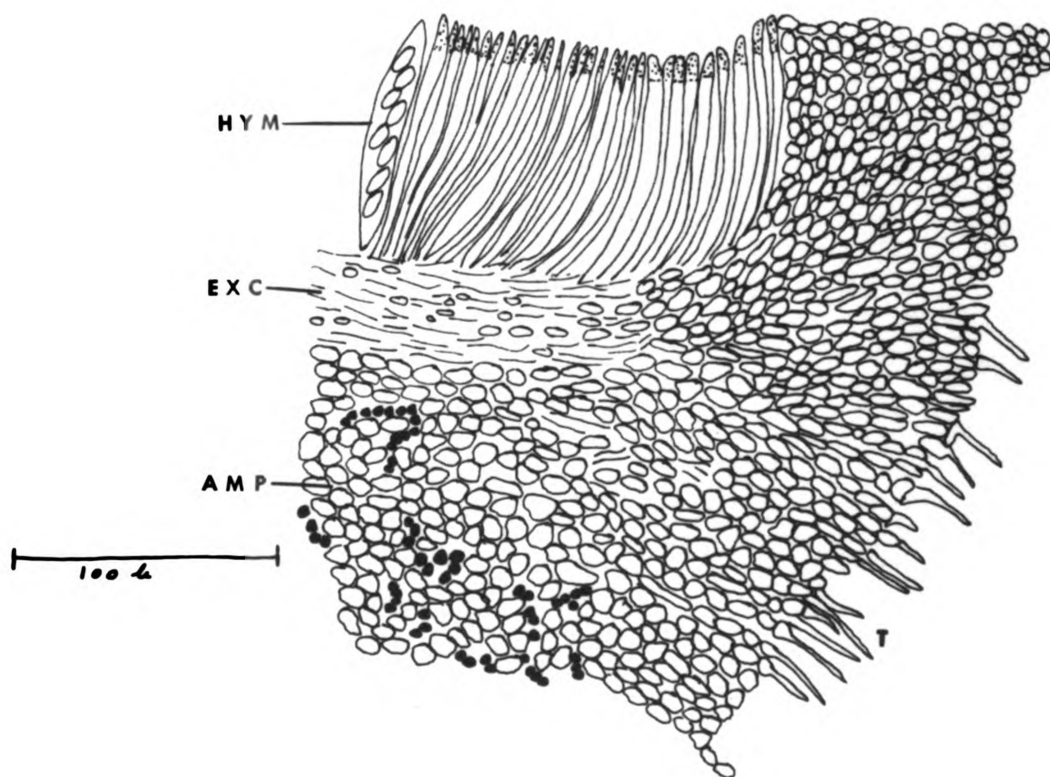
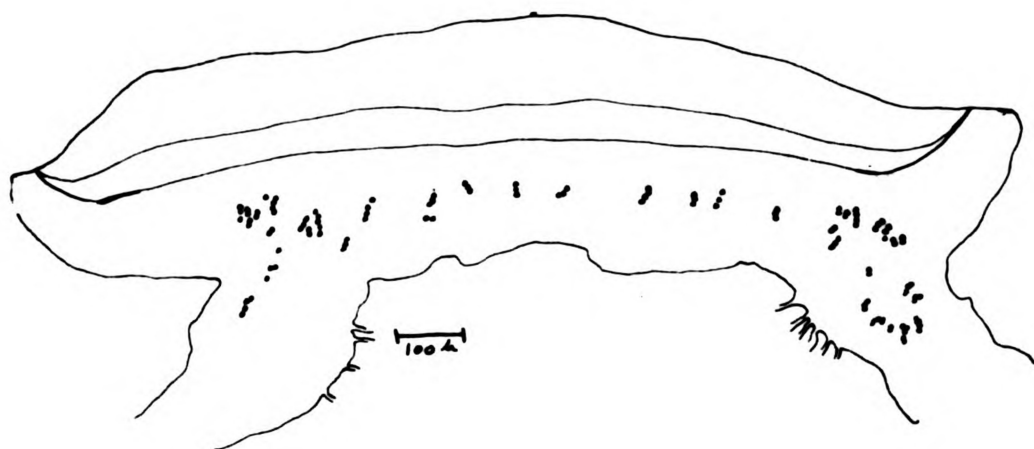


Plate XIII

Massalongia carnosia. Cross section of thallus illustrated diagrammatically and in detail.

UC = upper cortex

AL = algal layer

M = medulla

LC = lower cortex

Note: 1. Lower cortex present, and is exactly like the upper cortex.

2. Medullary hyphae septate and running irregularly.

PLATE XIII

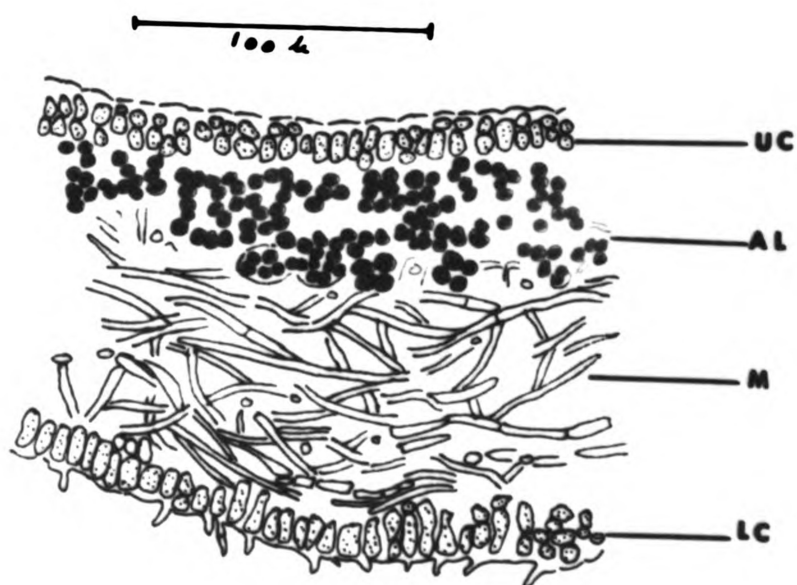
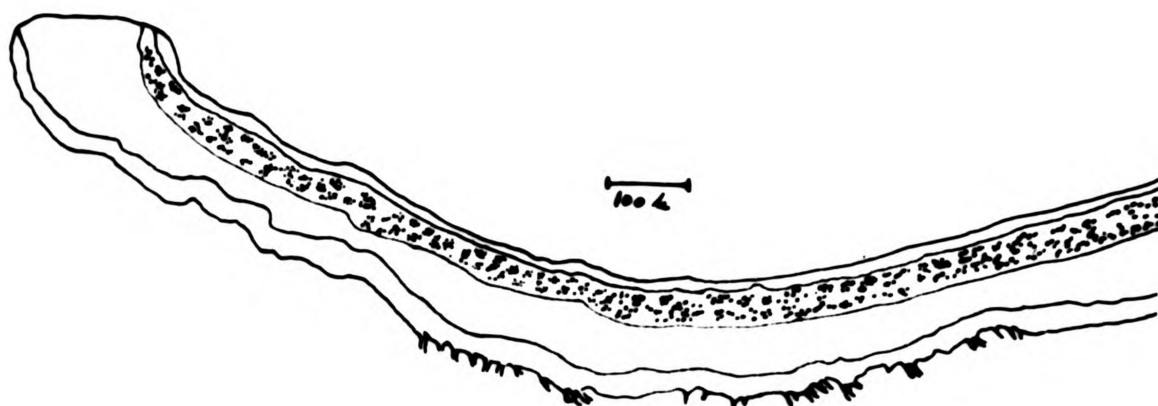


Plate XIV

Massalongia carnosa. Longitudinal section of the apothecium illustrated in detail.

EPI = epithecium

HYM = hymenium

EXC = exciple

AMP = amphithecium

T = tomentum

- Note:
1. Apothecium mycolecanorine.
 2. Exciple narrow.
 3. Amphithecium paraplectenchymatous.
 4. Spores two-celled, rarely three-celled.

Plate XV

Pannaria lurida. Cross section of thallus illustrated
diagrammatically and in detail.

UC = upper cortex

AL = algal layer

M = medulla

R = rhizinae

Note: 1. No lower cortex.

2. Upper cortex paraplectenchymatous hyphae which
are parallel to the surface.

3. Medulla of irregular hyphae.

PLATE XV

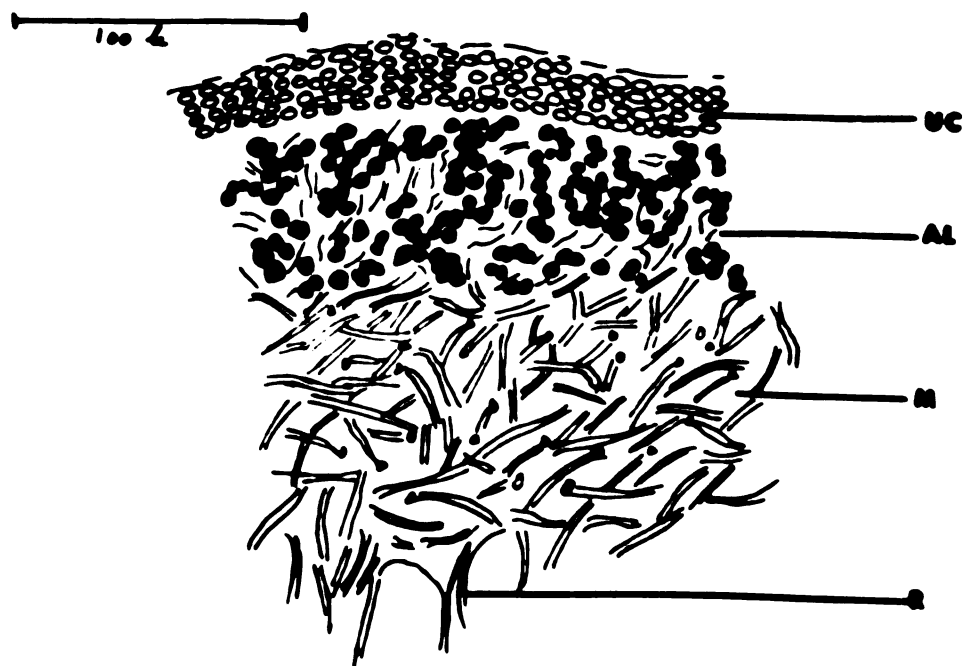
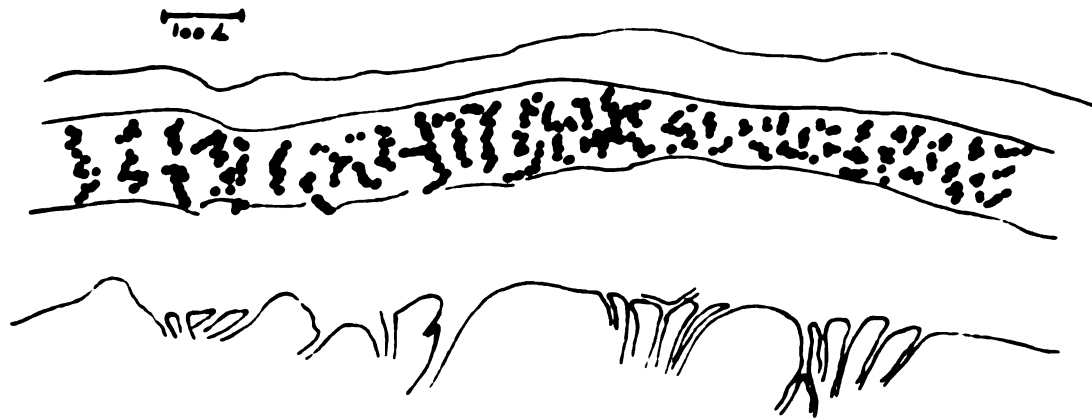


Plate XVI

Pannaria lurida. Longitudinal section of apothecium illustrated in detail.

AMP = amphithecium

EPI = epithecium

HUM = hymenium

EXC = exciple

- Note:
1. Apothecium lecanorine.
 2. A cortical tissue differentiated in the amphithecium.
 3. Exciple paraplectenchymatous.

PLATE XVI

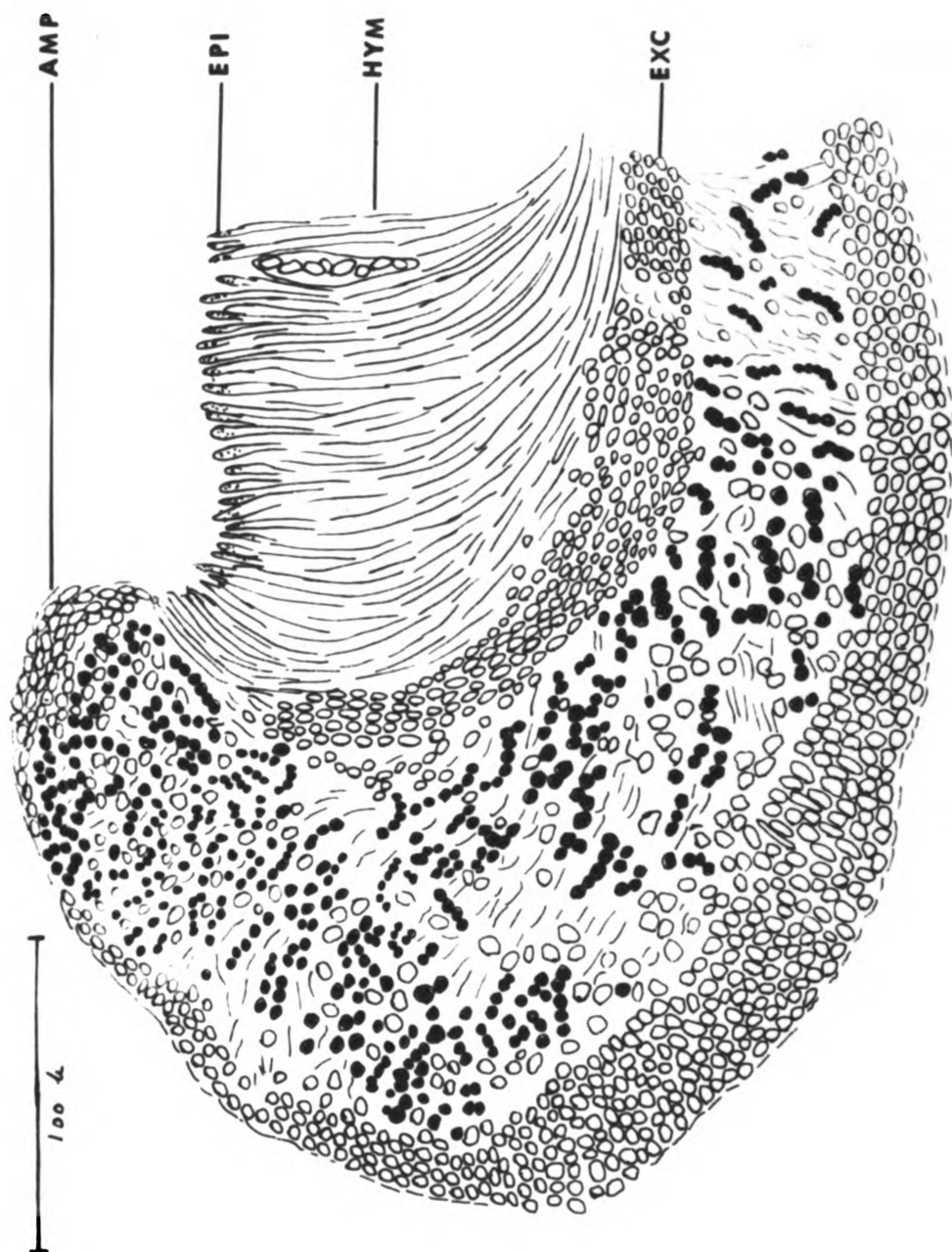


Plate XVII

Pannaria pezezoides. Longitudinal section of apothecium
illustrated diagrammatically.

EPI = epithecium

HYM = hymenium

EXC = exciple

AMP = amphithecium

- Note:
1. Apothecium lecanorine.
 2. Apothecium sessile.
 3. Exciple wide in the center and almost indistinct
in the sides.

PLATE XVII

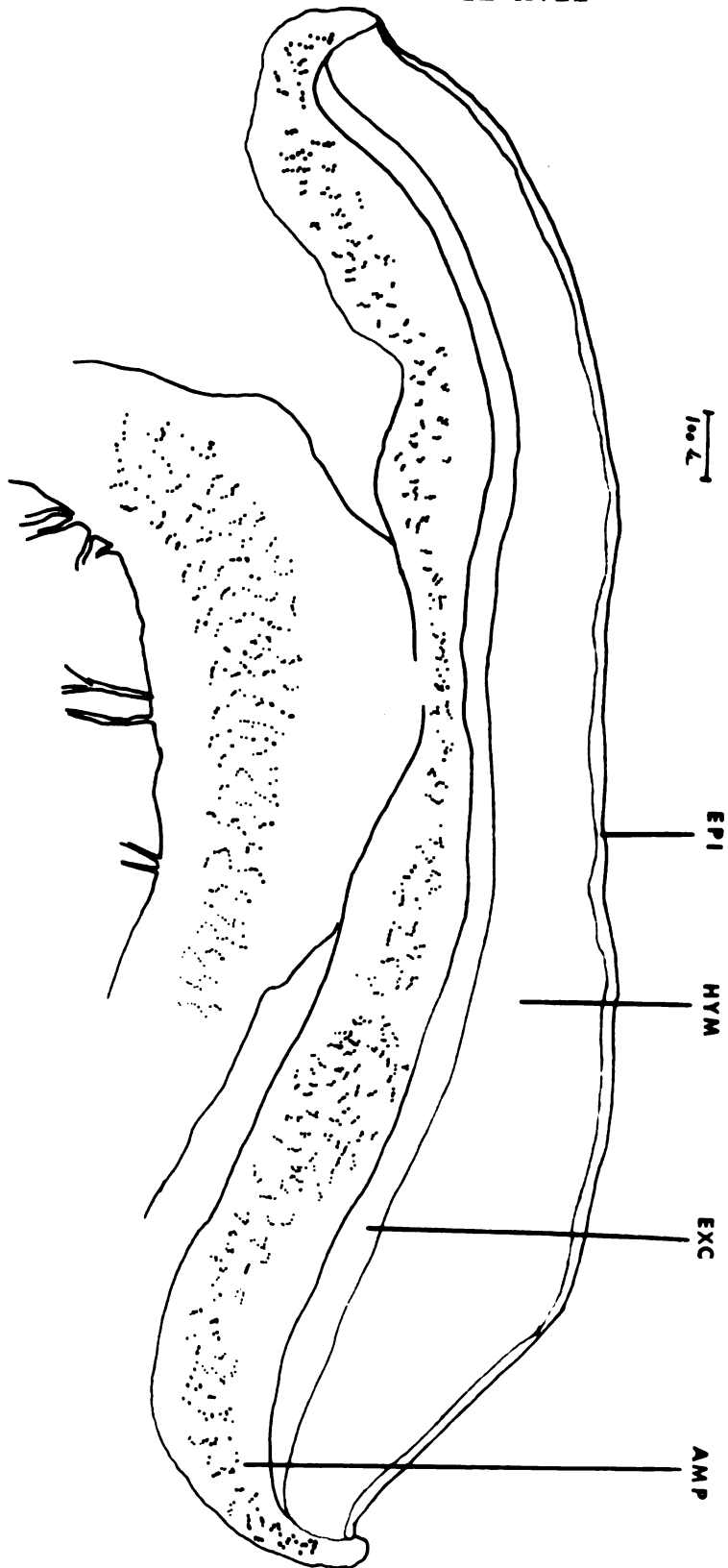


Plate XVIII

Parmeliella microphylla. Cross section of thallus illustrated diagrammatically and in detail.

UC = upper cortex

AL = algal layer

M = medulla

PC = pseudocortex

- Note:
1. Lower cortex absent.
 2. Algal layer very wide, wider than the species, filaments vertical.
 3. Medulla not distinct.
 4. Pseudocortex developed.

PLATE XVIII

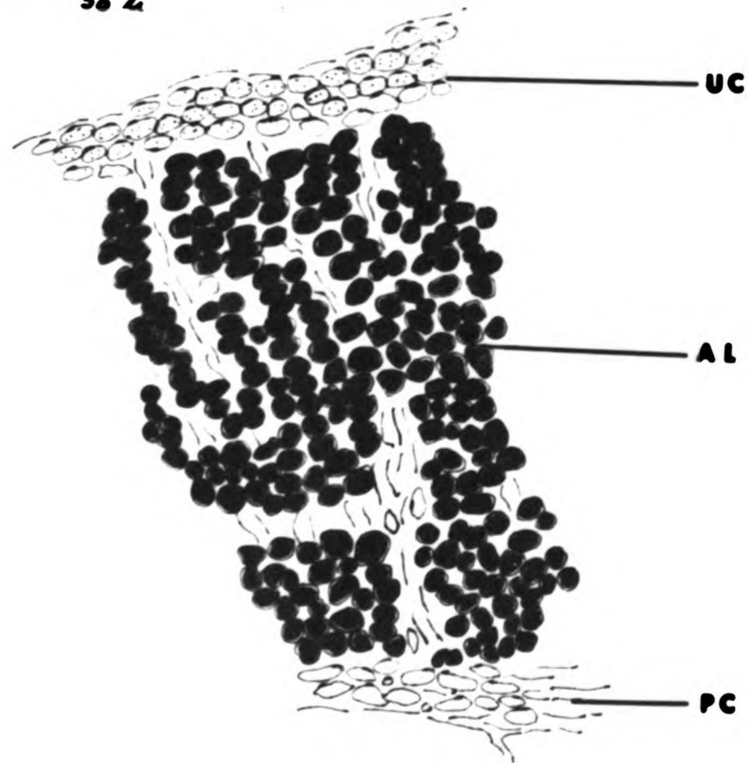
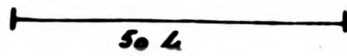


PLATE XIX

Parmeliella plumbea. Cross section of the thallus illustrated diagrammatically and in detail.

UC = upper cortex

AL = algal layer

M = medulla

PT = prothallus

- Note:
1. Upper cortex paraplectenchymatous, hyphae almost vertical to the surface of the thallus.
 2. Medulla of parallel hyphae.
 3. Mat of hyphae forming the prothallus.

PLATE XIX

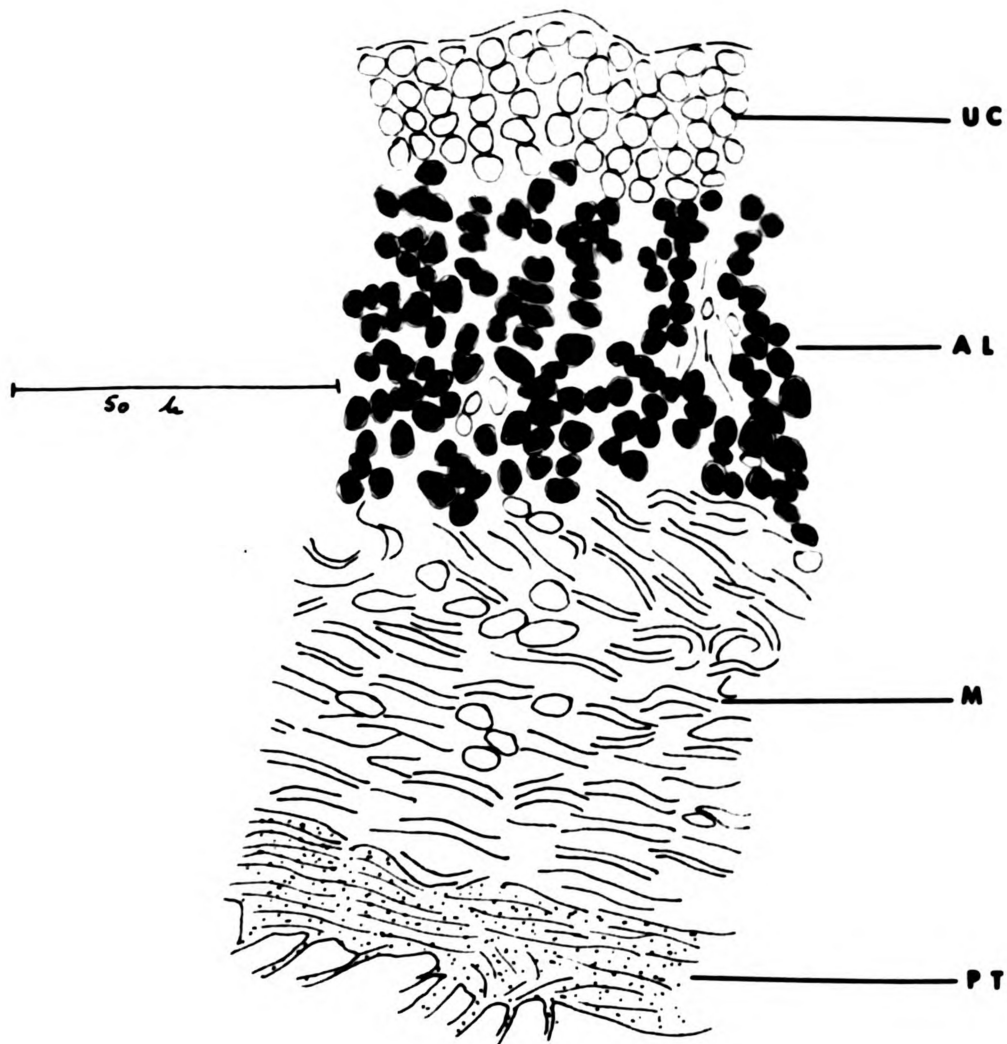
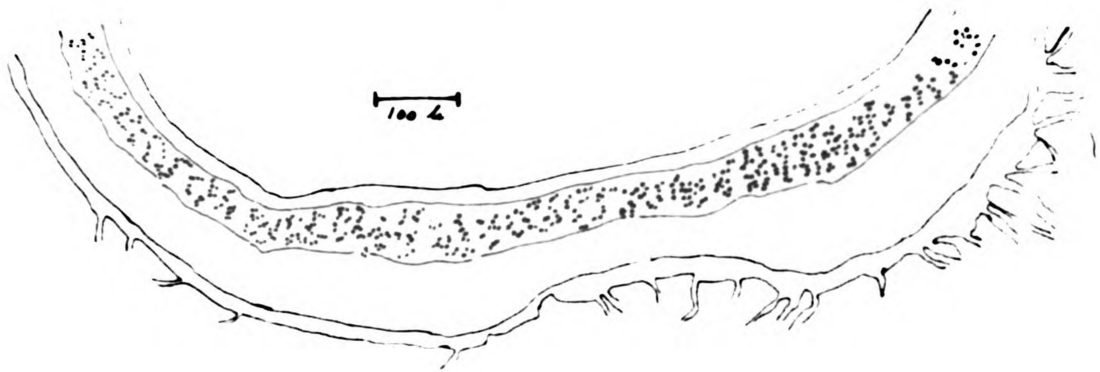


Plate XX

Parmeliella plumbea. Longitudinal section of apothecium
illustrated in detail.

HYM = hymenium

EXC = exciple

AMP = amphithecium

- Note:
1. No epithecium.
 2. Mycolecanorine apothecium.
 3. Spore monostichous and distichous, with thick
epispore.
 4. Amphithecium prosoplectenchymatous.

PLATE XX

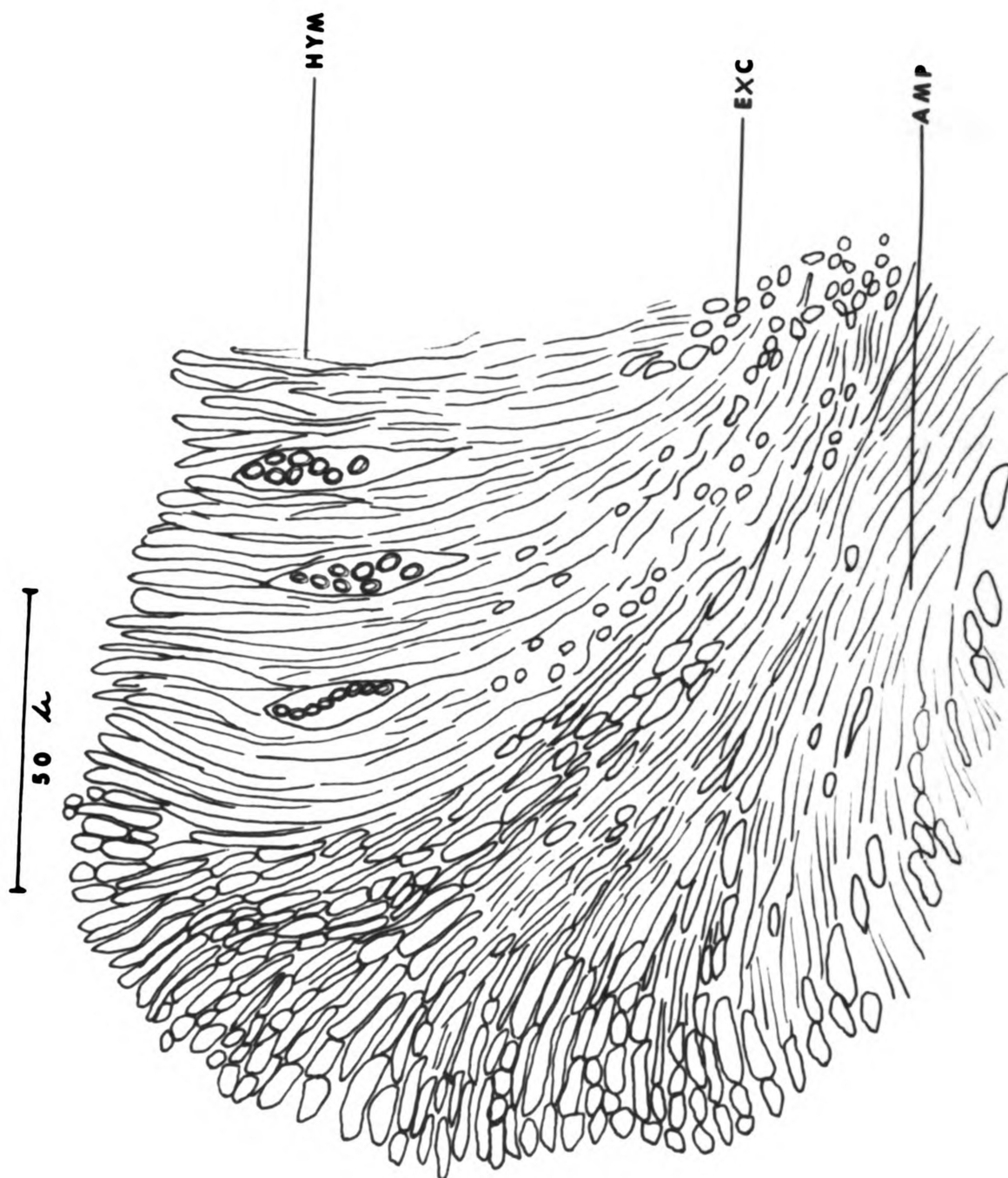


Plate XXI

Placynthium nigrum. Cross section of an areole of the
thallus illustrated in detail.

F = fungal tissue

A = algal filaments

- Note:
1. The cortical layer is one-celled.
 2. Algal filaments are vertical as well as irregular.
 3. Medulla absent.

PLATE XXI

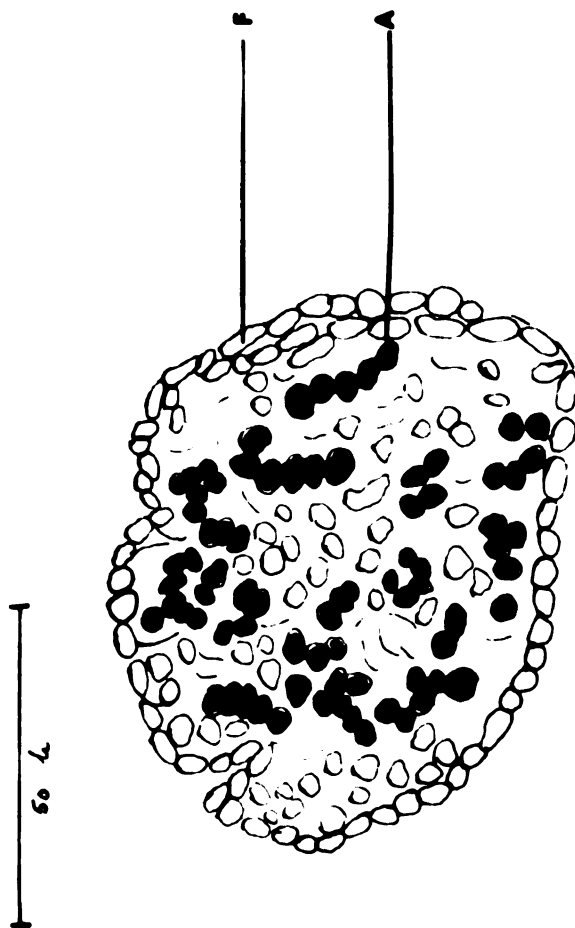


Plate XXII

Placynthium nigrum. Longitudinal section of the apothecium illustrated diagrammatically.

HYM = hymenium

EXC = exciple

AMP = amphithecium

A = areole

- Note:
1. Epithecium absent.
 2. Exciple very wide in the center.
 3. Spores two-celled without thick episore.

PLATE XXII

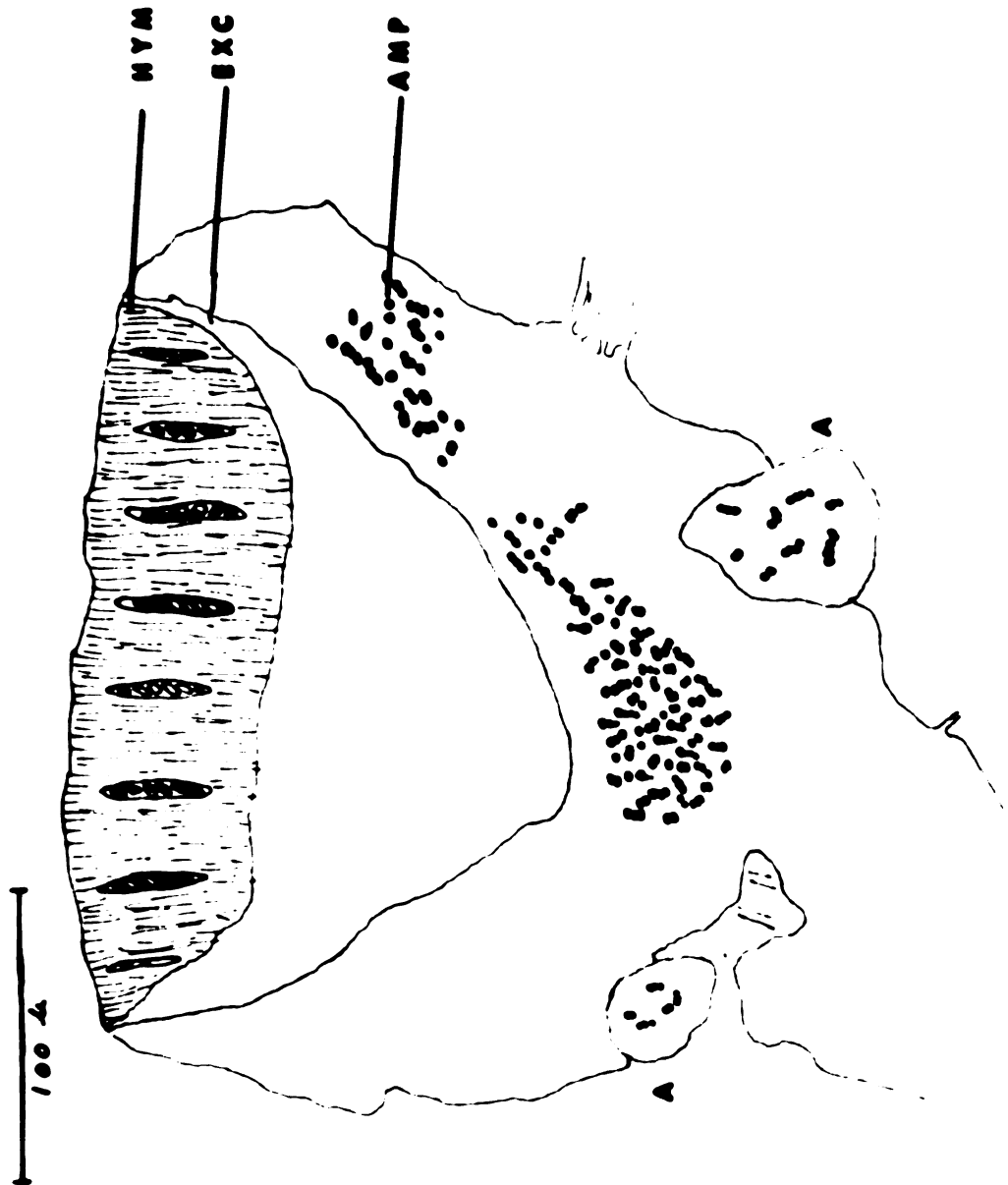


Plate XXIII

Psoroma hypnorum. Longitudinal section of the apothecium
illustrated in detail.

AMP = amphithecium

EXC = exciple

HYM = hymenium

- Note:
1. Apothecium lecanorine.
 2. The tips of the amphithecium curved inwards,
disk concave.
 3. Epithecium absent.
 4. Exciple of parallel and loose euthyplectenchy-
matous tissue.

PLATE XXIII

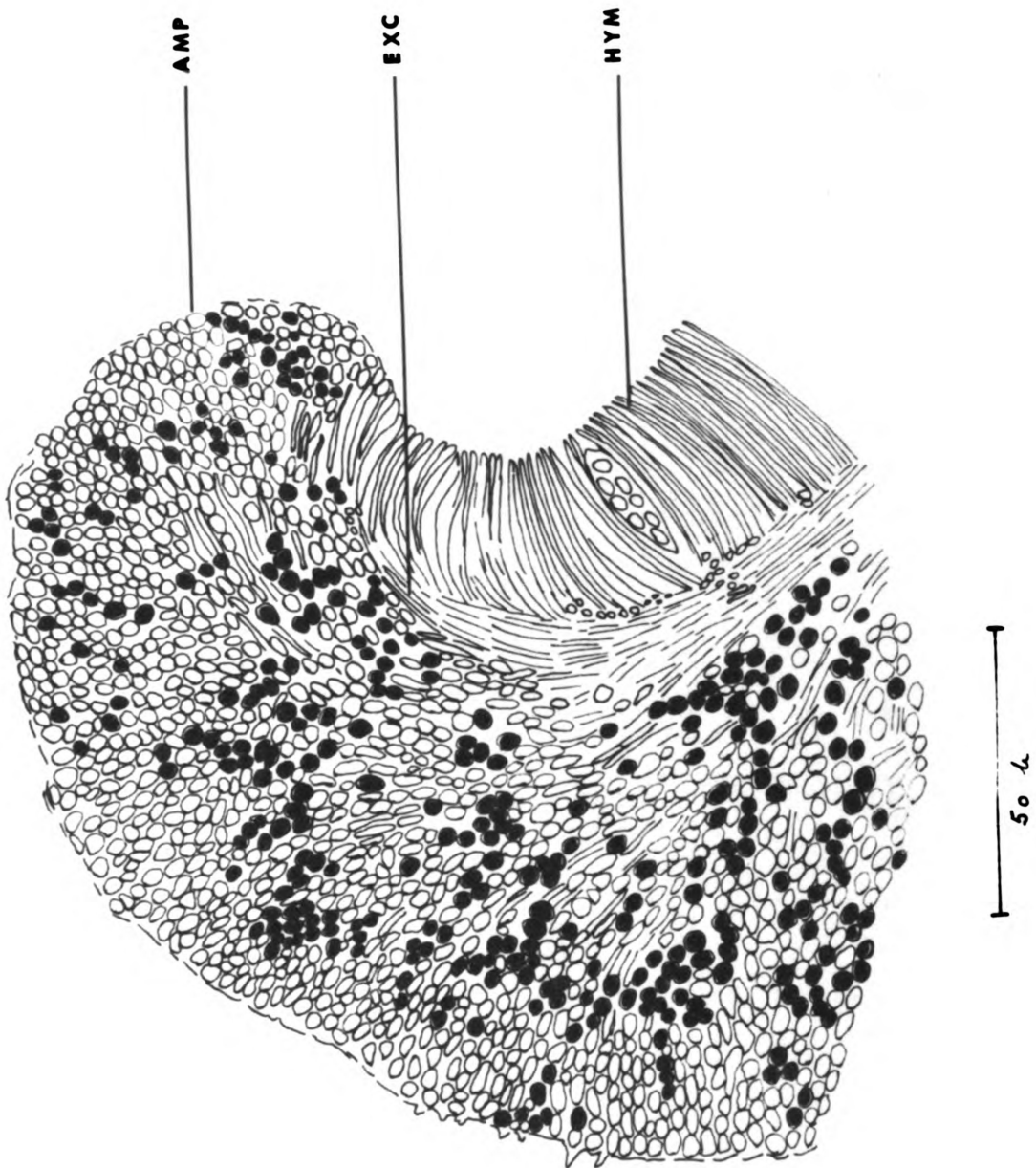


Plate XXIV

Psoroma pallidum. Cross section of the thallus illustrated diagrammatically and in detail.

UC = upper cortex

AL = algal layer

M = medulla

PC = pseudocortex

R = rhizinae

- Note:
1. Upper cortex of irregular paraplectenchyma.
 2. Algal layer narrow.
 3. Medulla of arachnoid hyphae.
 4. Lower pseudocortex developed.

PLATE XXIV

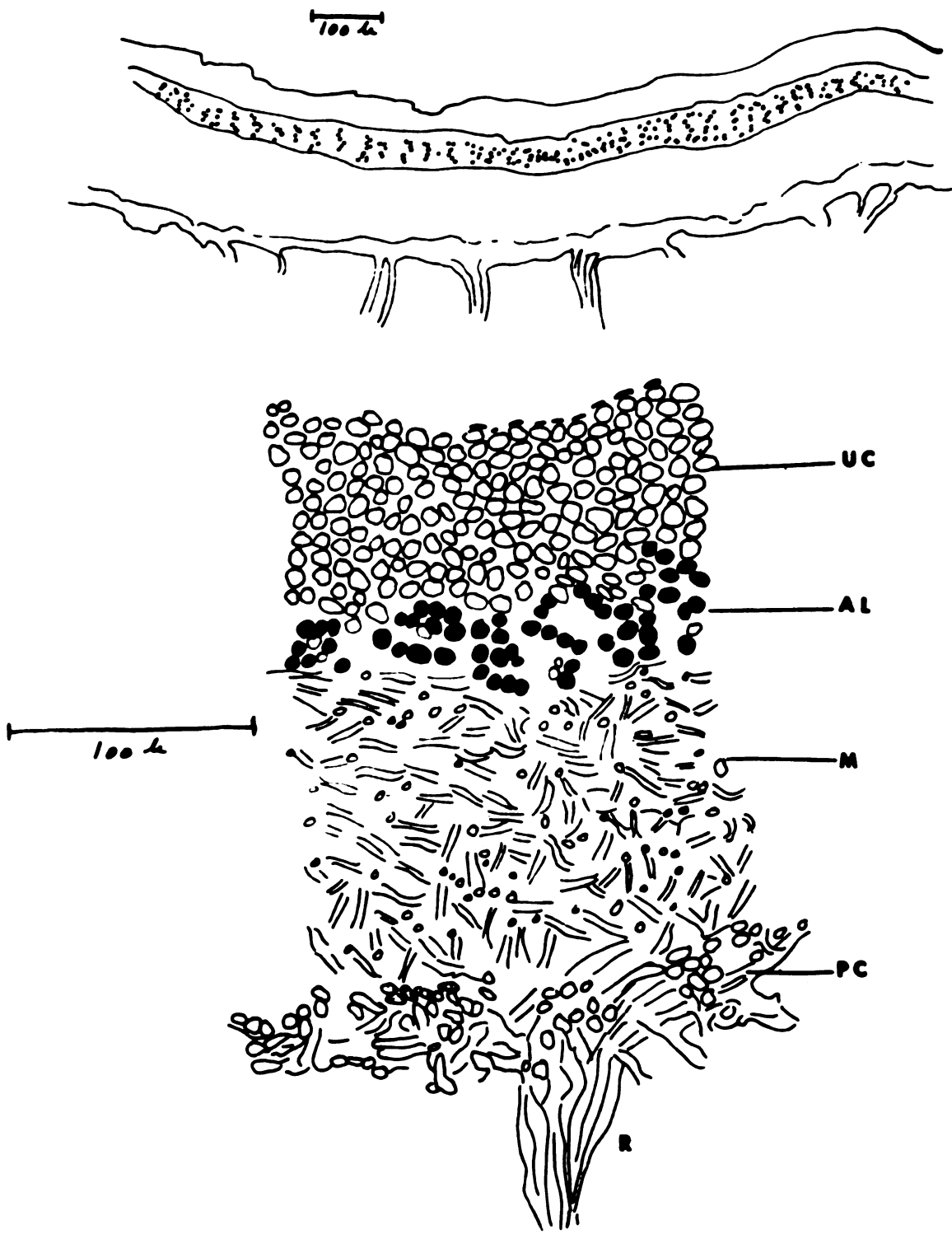
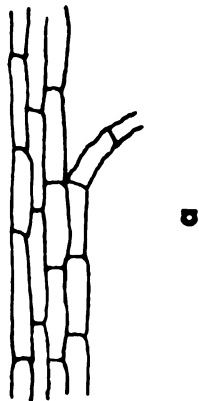
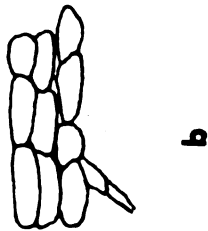
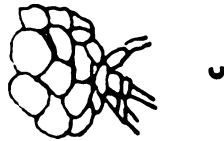


Plate XXV

Collema. Types of excipular tissue (redrawn from Degelius,
1954. Fig. 11, p. 83).

- a. Euthyplectenchymatous.
- b. Subparaplectenchymatous.
- c. Euparaplectenchymatous.

PLATE XXV



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