

Morden-Smithsonian Expedition
to Dominica:
The Lichens (Thelotremataceae)

Mason E. Hale, Jr.



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ABSTRACT

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Morden-Smithsonian Expedition to Dominica: The Lichens (Thelotremataceae)

Mason E. Hale, Jr.

Introduction

The Thelotremataceae comprise a very large family of crustose lichens that has attracted the attention of many lichenologists, beginning with Acharius (Hale, 1972). They have unique crater-like apothecia, but this characteristic feature can usually only be seen under magnification. As a matter of fact, these inconspicuous lichens will often be overlooked in the field unless a hand lens is used. Furthermore, because of the small size of the apothecia, very few species can be recognized at sight. All must be collected and examined later for morphological and chemical characters. Thallus color, however, is rather constant, light greenish or ashy gray. Only a few species have the deep green color of the equally common pyrenocarpous lichens, which, together with the Graphidaceae and Thelotremataceae, account for the majority of crusts that are collected in lowland tropical regions.

This paper is part of an on-going project on a modern treatment of the lichen flora of Dominica. As I mentioned in the first part on the Parmeliaceae (Hale, 1971a), where climate and topography are discussed, Dominica has the greatest remaining areas of virgin or relatively undisturbed forest of all the islands in the Lesser Antilles. Though

easily accessible by car and well-kept trails, these forests have as yet suffered little from human activity. Logging operations in the Dleau Gommier Forest Reserve, for example, have ceased, at least temporarily. Other islands in the Antilles are by contrast much more intensively cultivated and undisturbed forests are confined to higher, often inaccessible mountain slopes.

On my first trip to Dominica in 1969 I was interested primarily in foliose lichens, which proved to be relatively poorly developed. Many of the numerous crusts that I collected more or less randomly and blindly were actually thelotremes. The obvious richness of the family inspired me to undertake a second trip to the island in December 1971, once again under the Morden-Smithsonian Expedition, to concentrate exclusively on this family. A final brief trip for the same purpose was made in May 1972 under National Geographic Society support. Altogether, nearly 550 specimens of thelotremes were collected, making this one of the most intensive collecting programs ever undertaken for a crustose lichen group.

Special thanks are due Mrs. William J. Morden, who supported most of the field work for this project. Assistance is also gratefully acknowledged from the National Geographic Society for a broader study of the evolution of the Thelotremataceae in the Lesser Antilles, which included Dominica. Curators at a number of museums and universities have sent loans of type-specimens, and their help

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and patience are deeply appreciated: Dr. T. Ahti (H), Dr. Reino Alava (TUR), Dr. Ove Almborn (LD), Dr. C. E. Bonner (G), Mr. M. Skytte Christiansen (C), Mr. Peter James (BM), Mme Jovet-Ast (P), Dr. I. M. Lamb (FH), Dr. R. A. Maas Geesteranus (L), Prof. H. Merxmüller (M), Dr. Harald Riedl (W), and Dr. R. Santesson (UPS). I wish also to thank Dr. Chicita Culberson for help in identifying or verifying most of the chemical substances of the various specimens.

Morphological Characters

After curating and labeling each specimen, I studied the various morphological characters that appear to be most important for taxonomic purposes. The descriptions, therefore, are not exhaustive but should be adequate for species identification. Redinger (1936) and Salisbury (1972a, 1972b) have drawn up useful summaries of the essential features of this family and a number of the species which may also be consulted.

THALLUS STRUCTURE

The anatomy of crustose lichens is not as complex as that found in typical foliose lichens. Cortical structure is less distinct, and, lacking a free lower surface, the medullary hyphae usually penetrate the outer layers of bark periderm (or rock substratum). The algal layer (*Trentepohlia*) may also be indistinct. Large colorless crystalline inclusions are commonly found in the medulla, as in *Ocellularia nigropuncta*, new species, and *Thelotrema interpositum*.

Sections examined under a scanning-electron microscope show some of these structures vividly. *Ocellularia olivacea*, *O. perforata*, and *Thelotrema confusum*, new species (Figure 1a,b,c), all with well-developed epiphloeodal thalli, have a cortex consisting of several layers of heavily gelatinized cells appearing almost paraplectenchymatous; the loosely organized medulla penetrates the periderm. The surface is essentially smooth and featureless (Figure 2a-d). In some species the cortex is similar but peculiar aculeate hyphae protrude from the surface in greater or lesser abundance (Figure 3a,b). They appear to be collapsed, perhaps because of vacuum treatment needed for specimen preparation. This aculeate orientation, reported

here for the first time, is characteristic of *Myriotrema* species (*Ocellularia terebratula*, *Thelotrema clandestinum*) as well as a few species with emergent apothecia (*T. depressum*, *T. praestans*). I have observed similar orientation in several species of *Graphis* and *Graphina*. Most thelotremes, however, have an irregularly organized surface, as in *O. mordenii*, new species (Figure 3c,d), and a poorly defined cortex.

Leptotrema wightii has an unusual cortex previously described by many lichenologists. The thallus is very thick (up to 1 mm) and has a grainy surface (Figure 5d). The cortex is arranged in tall columns with algae scattered vertically (Salisbury, 1971) (Figure 1d).

The so-called hypophloeodal species lack the structures described above. The external thallus is reduced to a microscopic layer of hyphae spread thinly over the bark surface (Figure 4), and these hyphae penetrate several layers of periderm with very sparse symbiotic algae apparently located just below the periderm surface. Representatives of this group from Dominica include *Ocellularia concolor*, *O. pyrenuloides*, *Phaeotrema disciforme*, new combination, *Thelotrema leucomelaenum*, and *T. tenue*, new species.

APOTHECIAL CHARACTERS

Several morphologists have studied the internal structure and probable ontogeny of ascocarps in the Thelotremataceae (Redinger, 1936; Johnson and Brown, 1941; Letrouit-Galinou, 1966). The most commonly studied species is *Thelotrema lepadinum*, which has a distinct exciple breaking away free from the apothecial wall. The following Dominican species have more or less similar structure: *Ocellularia conglomerata*, new species, *O. dominicana*, new species, *O. exanthismocarpa* (Figure 5a), *Leptotrema occultum*, *L. subcompunctum*, and *Phaeotrema aggregatum*, new species. I will call this arrangement "lepadinioid" in the descriptions; Salisbury (1972a) uses the term "*Thelotrema lepadinum* group."

What appears to be an extreme stage of this configuration of apothecial wall and exciple is seen in the *Chroodiscus*-type apothecium (here termed "chroodiscoid"). The outer wall or margin is erect and becomes recurved (Salisbury, 1972b), almost as in *Geaster*, and the exciple usually persists as a

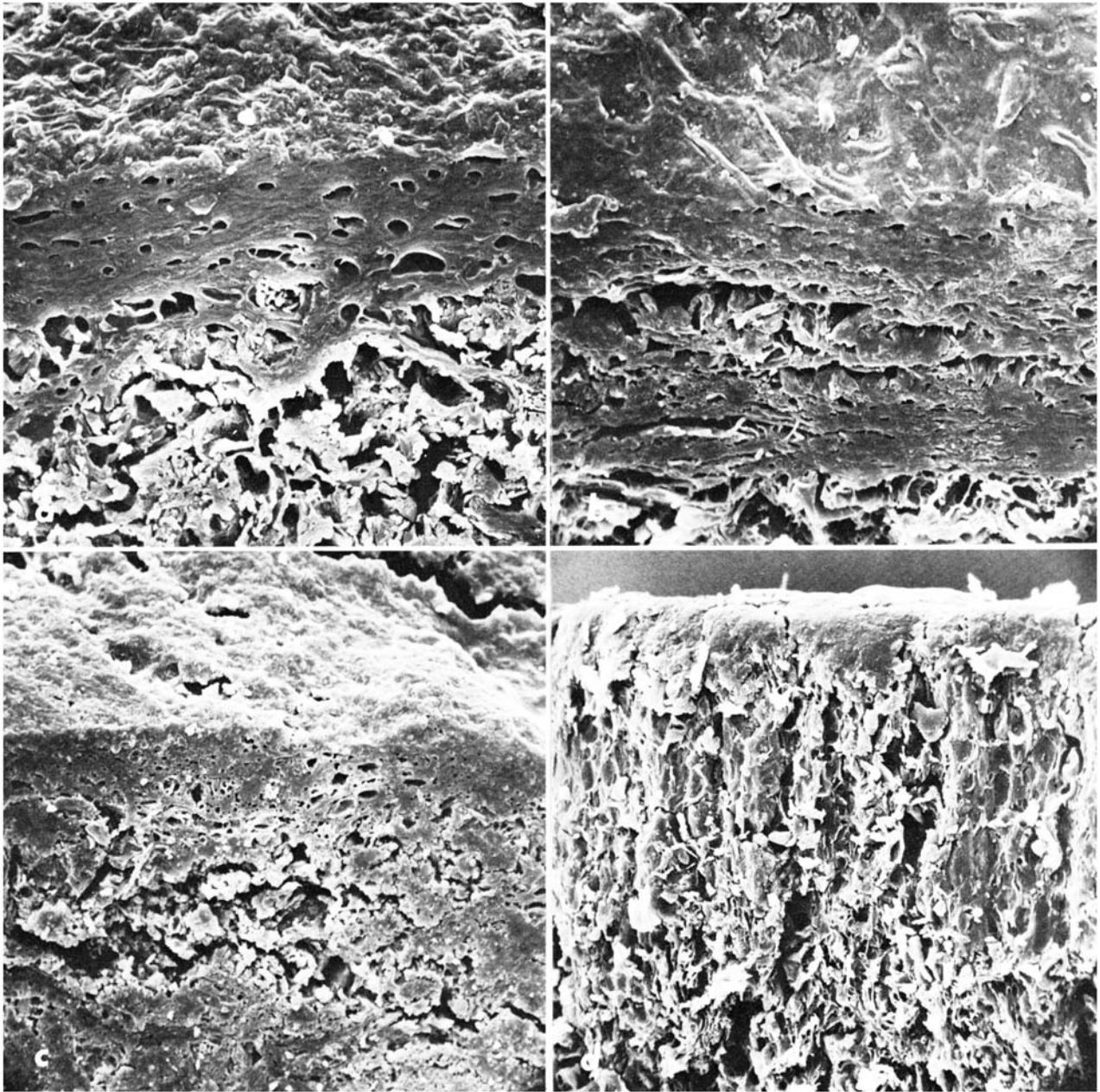


FIGURE 1.—Cross-sections of epiphloeodal lichens viewed with a scanning-electron microscope (a, b, and c, sectioned obliquely; d, vertically): a, *Ocellularia olivacea* (Hale 35226) ($\times 1000$); b, *O. perforata* (Hale 38145) ($\times 1000$); c, *Thelotrema confusum*, new species (Hale 37697) ($\times 500$); d, *Leptotrema wightii* (Hioram 5850 from Cuba) ($\times 500$).

second inner rim. The disc is widely exposed and nothing resembling the discrete pore characteristic of the other thelotremes remains (Figure 5b). This type was first recognized among the foliicolous lichens, but it seems identical to that in the non-

foliicolous species of the Thelotremataceae, including in Dominica *Ocellularia alborosella* and *O. dilatata*. It is called the "*Thelotrema platycarpum* group" by Salisbury (1972b). In the absence of more detailed ontogenetic research,

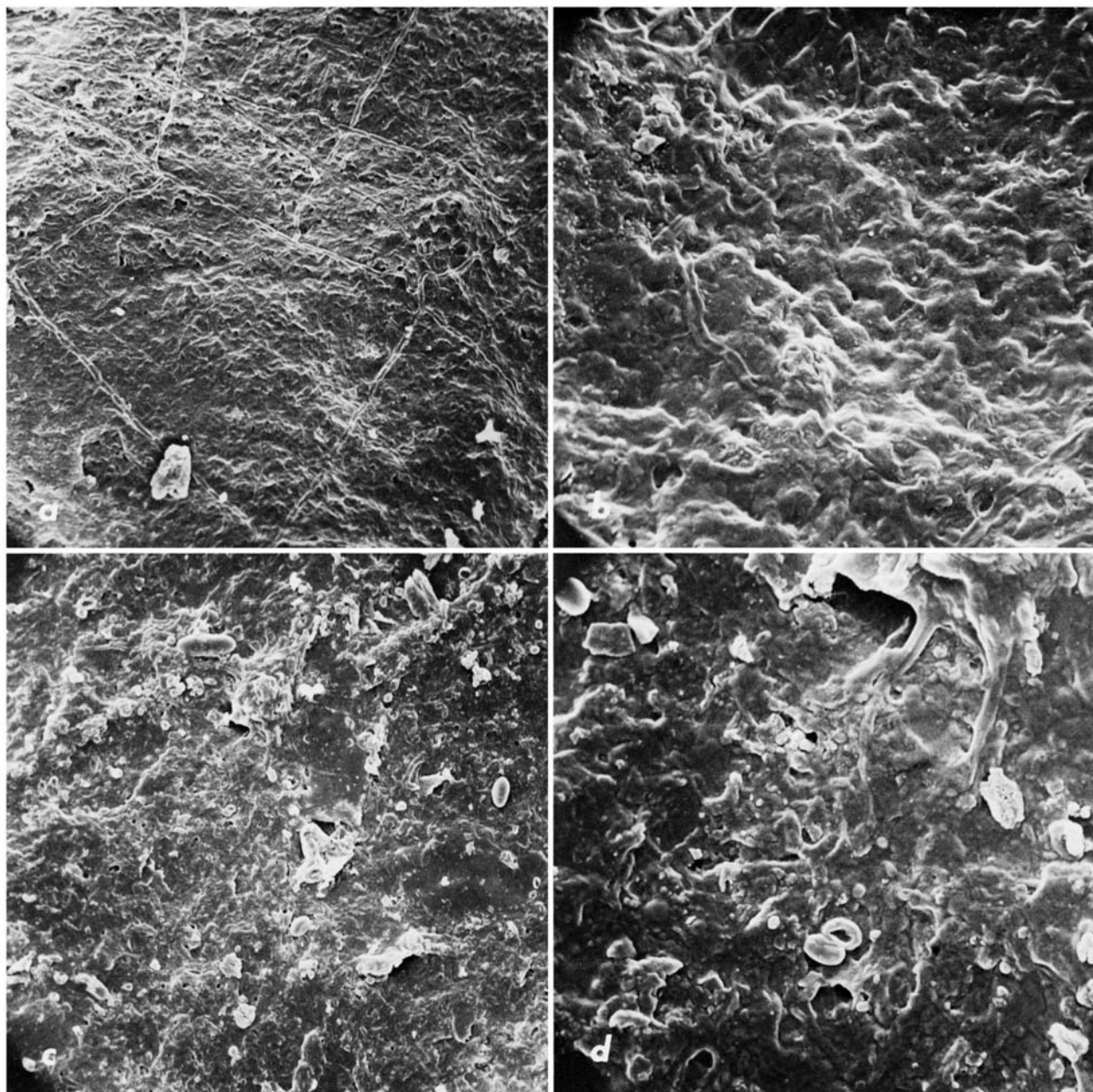


FIGURE 2.—Surfaces of epiphloeodal lichens viewed with a scanning-electron microscope: *a, b*, *Ocellularia nigropuncta*, new species (Hale 35365) ($\times 500$ and $\times 2000$); *c, d*, *O. dominicana*, new species (Hale 37967) ($\times 500$ and $\times 2000$).

however, we cannot yet say that *Chroodiscus* is a good genus, that the *Chroodiscus*-like nonfoliicolous thelotremes should be transferred to *Chroodiscus*, or that *Chroodiscus* should be transferred to *Ocellularia*. Chroodiscoid species, incidentally, are distributed among the four presently recognized

genera, *Ocellularia*, *Leptotrema*, *Phaeotrema*, and *Thelotrema*, on the world level.

The majority of species in the Thelotremataceae are neither lepadinioid or chroodiscoid. The exiple is fused with the receptacle wall and the main rim or margin closes over most of the disc

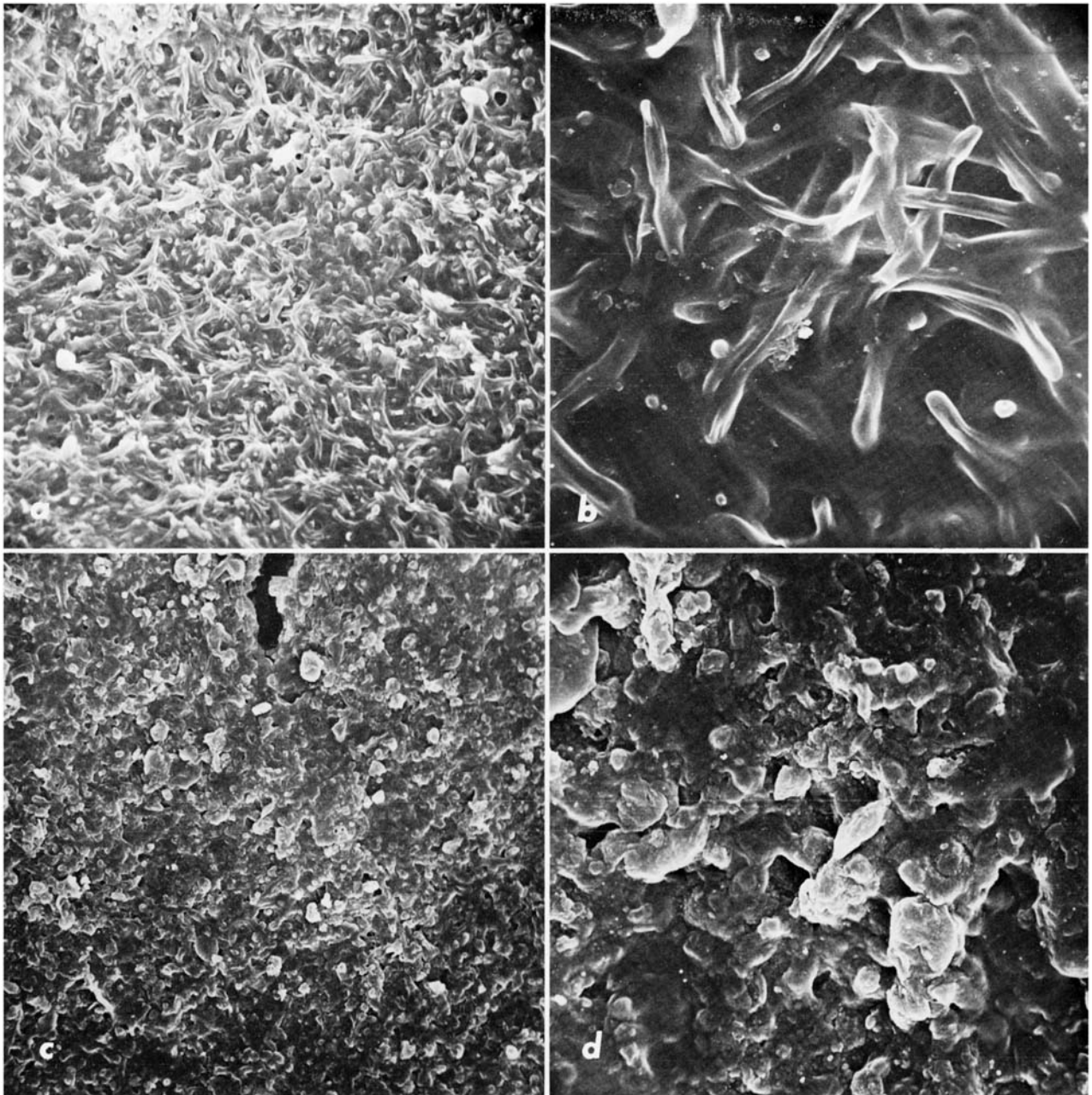


FIGURE 3.—Surfaces of epiphloeodal lichens viewed with a scanning-electron microscope: *a, b*, *Ocellularia olivacea* (Hale 38054) ($\times 500$ and $\times 2000$); *c, d*, *O. mordenii*, new species (Hale 37764) ($\times 500$ and $\times 2000$).

leaving only a small constricted pore. The upper wall is usually carbonized. There are, broadly speaking, three groups that can be recognized for practical purposes on the basis of degree of emergence from the substratum. One, represented by the "Myriotrema" type, has immersed noncarbon-

ized apothecia and a pore flush with the thallus surface (Figure 5*c,d*). The apothecia are always quite small, 0.1–0.3 mm in diameter. Typical examples in Dominica are *Ocellularia olivacea* and *Thelotrema clandestinum*.

A second group, which includes the majority

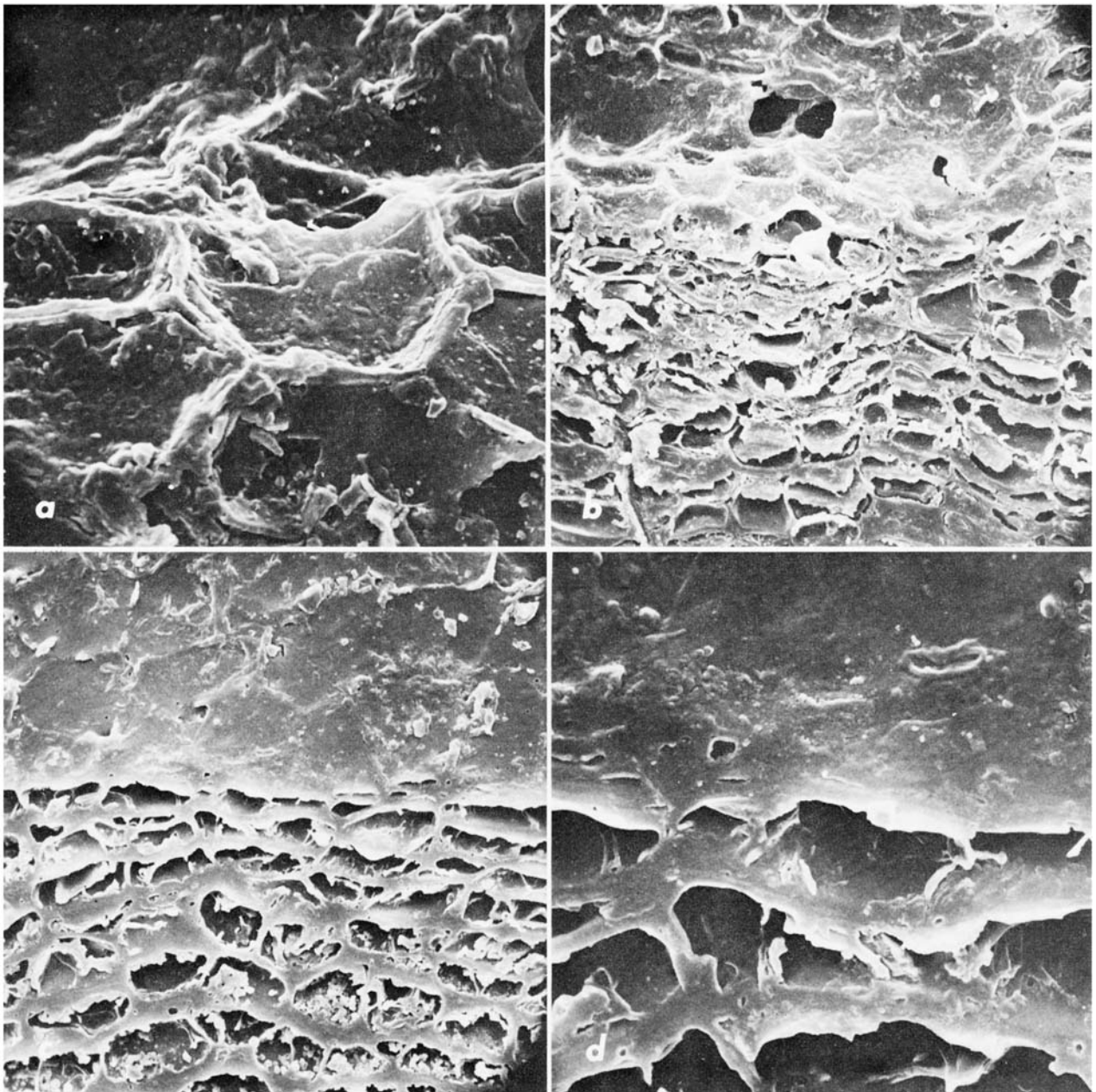


FIGURE 4.—Surface and cross-sections of hypophloeodal lichens viewed with a scanning-electron microscope: a, *Thelotrema leucomelaenum*, surface view (Hale 35491) ($\times 2000$); b, *T. leucomelaenum*, cross-section (Hale 35491) ($\times 500$); c, d, *T. tenue*, new species (Hale 35430) ($\times 500$ and $\times 2000$).

of the species, has emergent apothecia, neither basally constricted or strongly raised (Figure 5e,f). They are usually 0.4–1.0 mm in diameter, although in a few species (for example, *Thelotrema praestans* in Figure 17e) nearly 2 mm in diameter.

A third group, typified by *Ocellularia rhodostroma* and *O. cavata*, has strongly emergent apothecia with a partially constricted base (Figure 5g). The pore is small and sometimes annulate or open at maturity, as in *O. fecunda* (Figure 11h,i).

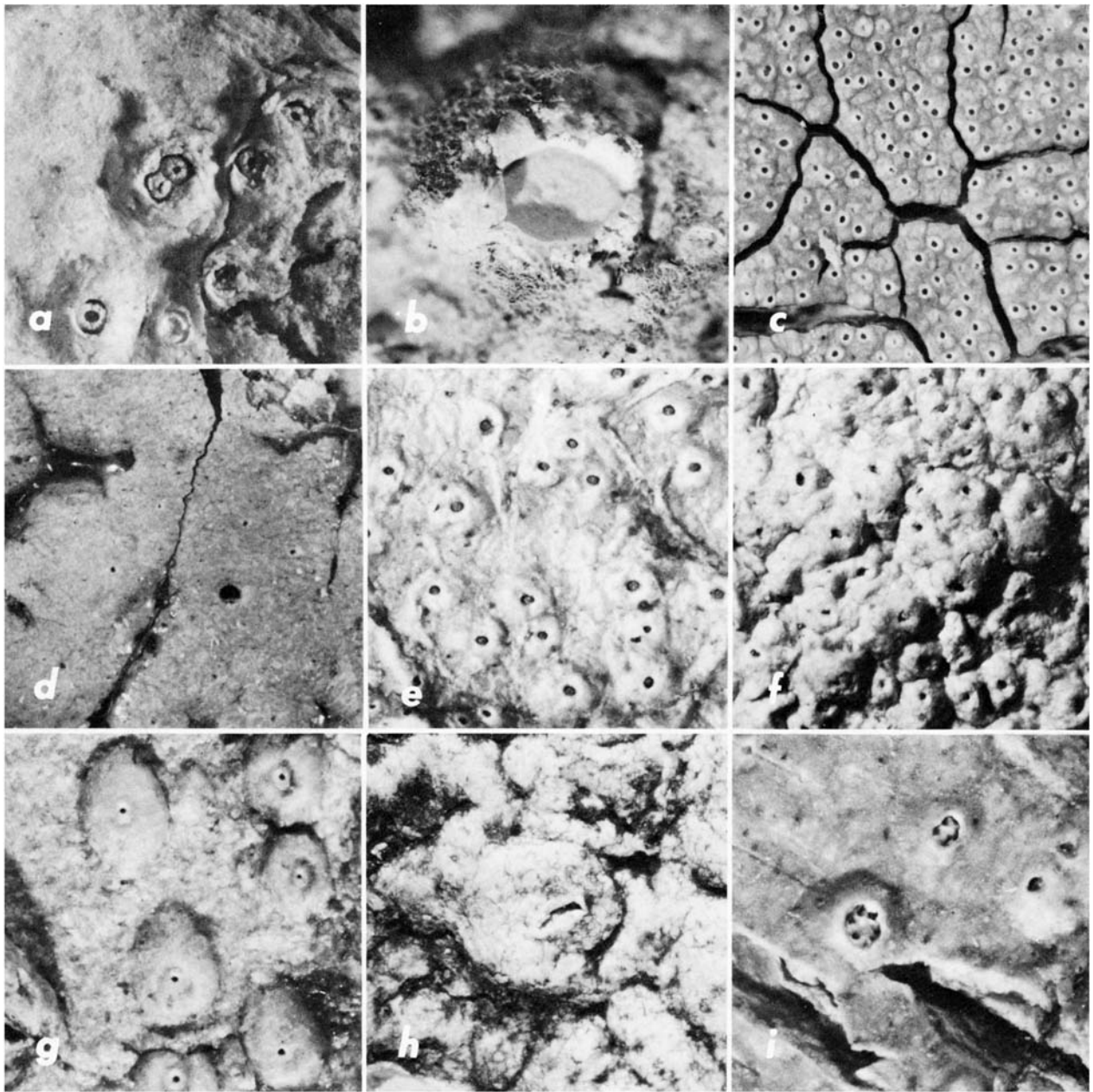


FIGURE 5.—Types of apothecia in the Thelotre mataceae (all $\times 10$): a, *Ocellularia exanthismocarpa* (type of *O. multilocularis*); b, *O. alborosella* (Hale 35371a); c, *O. olivacea* (Hale 35243); d, *Leptotrema wightii*, (type of *L. prevostianum*); e, *O. perforata* (Hale 37727); f, *L. bahianum* (type of *Thelotrema rudius* var. *dominicanum*); g, *O. rhodostroma* (Hale 38122); h, *Phaeotrema leiostomum* (Hale 37956); i, *O. comparabilis* (Hale 37372).

Diameter varies between 0.6 and 2.0 mm. This group was called *Ascidium* by Fée (1824), not so much because of emergence but because of a duplicate membrane in the perithecium (the nature of which is not clear to me) and a marginate pore.

Although Nylander continued to use *Ascidium* for strongly emergent species, no modern lichenologists have employed it. The type of the genus, *A. cinchonarum* Fée, is synonymous with *Ocellularia cavata*. Naturally there are intergradations

between the *Ascidium*-type and the more common emergent type, but I believe the descriptive term "ascidioid" is still useful.

A final group forms a transition to the Graphidaceae. The apothecia become irregularly elongate with a lirelliform dehiscence. In Dominica this includes *Phaeotrema leiostomum*, which can produce both round and elongate apothecia (Figure 5h). Other species from South America have this trait developed much more conspicuously and have been described in the Graphidaceae (as *Phaeographis chionodisca* Redinger (1936:69)). They should probably be transferred to the Thelotrema-taceae.

Redinger (1936) further divides the Thelotremataceae into two groups that differ in position of the ascogonial initial. In one group the initial is located on or just below the periderm surface so that at maturity the apothecial wall develops on and apart from the unbroken periderm (for example, *Ocellularia rhodostroma* and *Phaeotrema disciforme*, new combination). The other group, including most nonchroodiscoid species in Dominica, has ascogonial initials deeply embedded in the periderm. The maturing apothecia must break through this layer to reach the surface. Several layers of periderm cells are thereby included in the apothecial receptacle and can be easily recognized in sections (Figure 6f). This character deserves much more detailed study.

Development of a central cylindrical columella is particularly characteristic of the Thelotremataceae, and for the most part presence or absence of a columella is a good species character (Figure 6). As a rule, columellate species do not have perfect counterparts that lack a columella. Noteworthy exceptions in Dominica are *Ocellularia papillata* and *O. perforata*, each of which has a large population where a columella is clearly developed and a smaller one where it is either absent or very difficult to find. I have not recognized such eolumellate species as new without correlating morphological or chemical characters. Columellate species always have heavily carbonized apothecial walls.

Redinger (1936:6) proposed an interesting hypothesis that the columella plays a role in breaking open the periderm layer in species that develop deeply embedded. As the apothecia mature, the columella pushes up against the upper carbonized

walls and periderm, acting as a kind of ramrod. Not all species with periderm inclusions have a columella, but as Redinger found for the Brazilian species the correlation is high.

The range in development of a columella is very great (Figure 6), from the weak thin columella in *Ocellularia mordenii*, new species, to the multiple actinoid structures of *Ocellularia comparabilis* (Figure 5i) and *Leptotrema fissum* (Figure 19a,c). The most highly developed species is *Ocellularia glaziovii* (Müller-Argau known from South America Vainio (1921:184) recognized these species under a separate genus, *Rhabdodiscus*).

SPORES

Spore size is an important and relatively constant character. The range of spore length, for example, is usually quite small except for very large spores (more than 100 μ) which may vary between 100 μ and 300 μ . We can distinguish four very broad categories among the Dominican species: (1) spores less than 20 μ long with 4–6 transverse locules, e.g., *Leptotrema wightii*, *Ocellularia terebratula*, *Thelotrema clandestinum*; (2) spores 20 μ –36 μ long with 6–10 transverse locules, e.g., *Ocellularia perforata* (Figure 7a), *Thelotrema leucomelaenum*; (3) spores 40 μ –90 μ long with 12–24 transverse locules, e.g., *Leptotrema deceptum*, new species (Figure 7d), *Ocellularia exanthismocarpha*; and (4) spores 80 μ –300 μ long with numerous locules, e.g., *Ocellularia rhodostroma* (Figure 7b), *Thelotrema praestans*, *T. tuberculiferum*.

The number of longitudinal septations in *Leptotrema* and *Thelotrema* varies according to length, from 1 or 2 septae in small spores (up to about 30 μ long) to 4–6 or more in large spores.

Spores are colorless or brown. It is sometimes a problem to determine color in large-spored species of *Leptotrema* and *Thelotrema* where, on the one hand, a *Thelotrema* species might have some senile spores turning brown and on the other a *Leptotrema* will have some colorless spores (Figure 7d). In *Phaeotrema disciforme*, new combination, in fact, one often finds a mixture of colorless, mature brown, and shriveled brown spores (Figure 7c). Shriveling (Figures 7c,d) is characteristic of brown-spored species; I know of no cases where *Thelotrema* or *Ocellularia* spores shrivel.

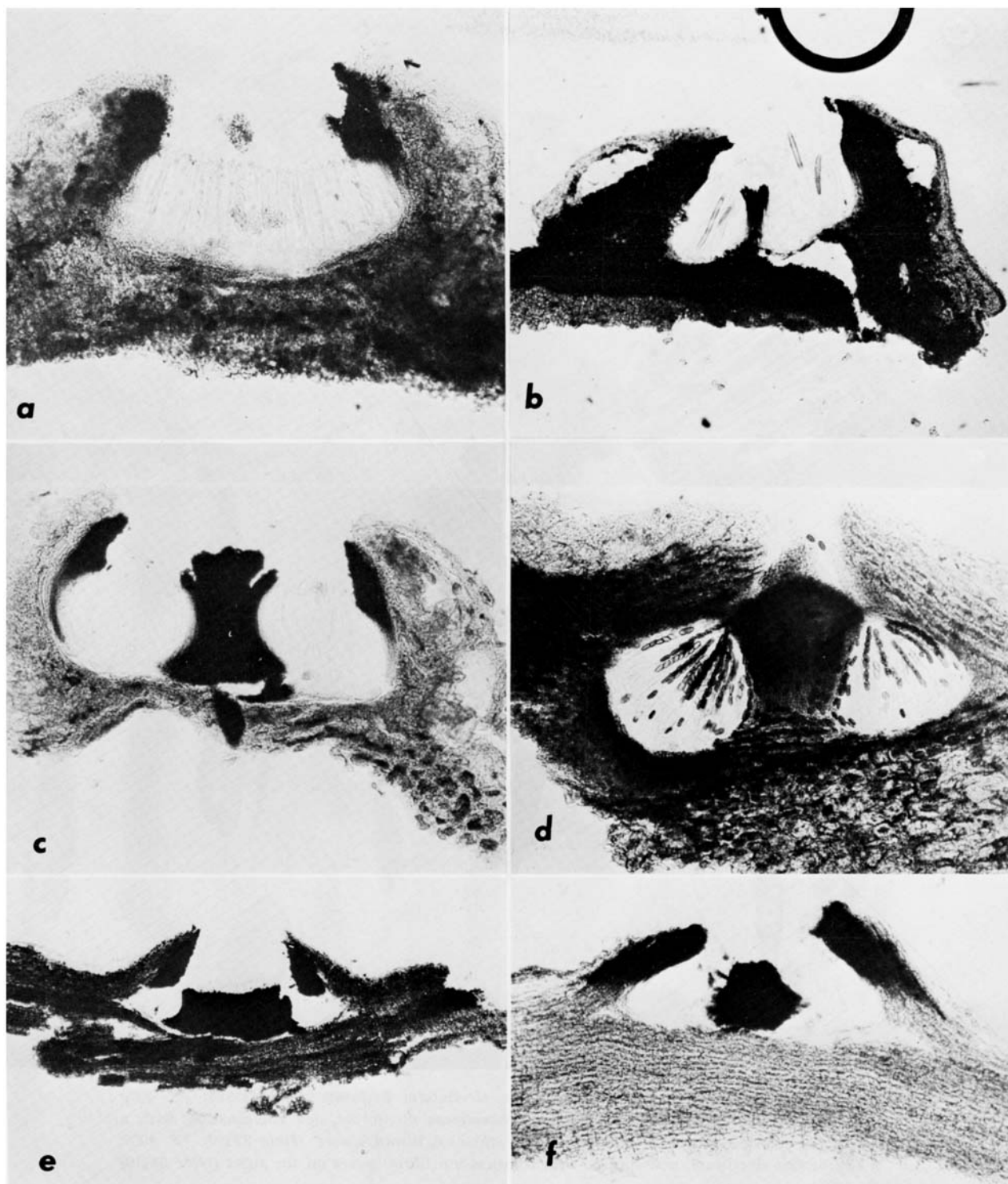


FIGURE 6.—Cross-section of apothecia (all about $\times 130$): a, *Ocellularia nigropuncta*, new species (Hale 35365); b, *O. mordenii*, new species (Hale 37764); c, *O. cavata* (Hale 35134); d, *Phaeotrema leiostomum* (Hale 35203); e, *Thelotrema leucomelaenum* (Hale 35491); f, *T. tenue*, new species (Hale 35430).

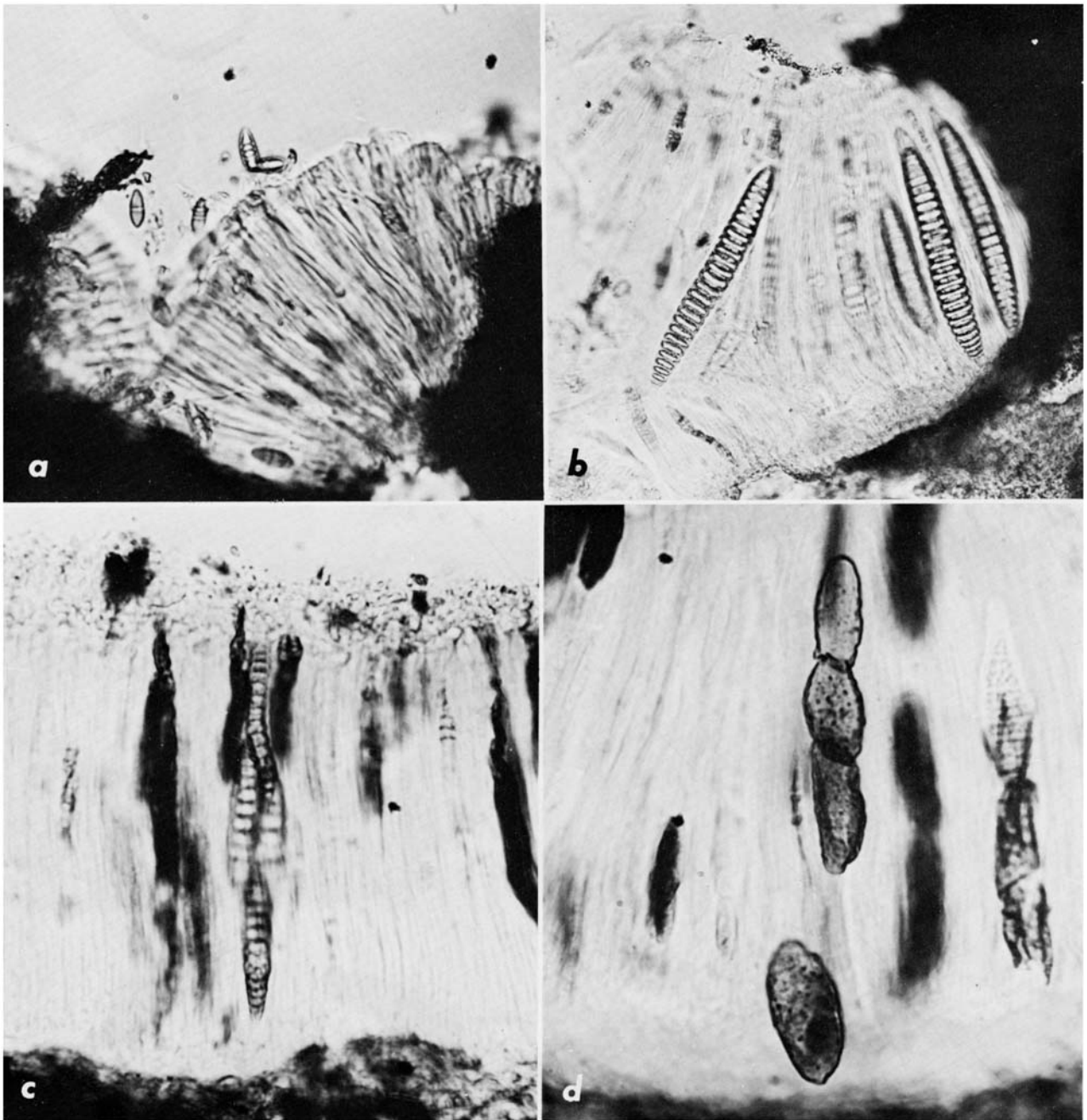


FIGURE 7.—Spores of the Thelotre mataceae: *a*, *Ocellularia perforata* (Hale 37784) ($\times 400$); *b*, *O. rhodostroma* (Hale 35440) ($\times 130$); *c*, *Phaeotrema disciforme*, new combination, with a mixture of colorless spores, brown spores, and shriveled brown spores (Hale 37939) ($\times 400$); *d*, *Leptotrema deceptum*, new species, with colorless muriform spores on the right (Hale 38110) ($\times 400$).

In any event, transitional species should be judged individually, and the presence of a few anomalous brown-spored specimens among many colorless specimens (as in *Ocellularia fecunda*, new combi-

nation, or *O. subcavata* on Dominica) should not be totally unexpected; nor should these isolated cases prejudice the value of spore color as a generic character.

Generic Limits

The generic delimitation of the Thelotremataceae has undergone many changes since the classic work of Acharius. Fée (1824), for example, established two genera, in addition to recognizing *Thelotrema*, based on external features and apothecial characters: *Ascidium* and *Myriotrema*, both presently considered to be synonyms of *Ocellularia*. Müller-Argau (1887a) proposed the most far-reaching changes, using spore septation and coloration to separate four genera (in addition to foliicolous *Chroodiscus*): *Ocellularia* (transversely septate colorless spores), *Phaeotrema* (transversely septate brown spores), *Thelotrema* (muriform colorless spores), and *Leptotrema* (muriform brown spores).

While Vainio, one of the truly creative thinkers in lichen classification, rejected many "spore genera," almost all authors since Müller-Argau have accepted these genera (and, indeed, spore-based genera in other families). Poelt (1973:613) refers to these as "artificial genera," yet almost any character we select is in a sense artificial. I don't believe this term does justice in that it implies spore characters are artificial.

We are, in reality, faced with at least three choices for generic delimitation in the family: (1) one genus (*Thelotrema*) to accommodate all thelotremataceous species; (2) four spore-based genera (*Ocellularia*, *Phaeotrema*, *Thelotrema*, and *Leptotrema*); (3) five or more genera (*Ascidium*, *Chroodiscus*, *Myriotrema*, *Rhabdodiscus*, and *Thelotrema*) based on apothecial emergence and excipular structures. Most lichenologists, as I said, have opted for spore-based genera. While a majority opinion does not necessarily prove the naturalness or validity of such genera, they do represent one possible biological differentiation, broadly correlated with chemical, morphological, and ecological characters (as I will discuss briefly under each genus).

I cannot agree with Salisbury's (1972a) recent rejection of spore-based genera in favor of a single massive genus *Thelotrema* with 400 species subdivided into "groups" according to excipular structure, a character that is difficult to identify. His keys and descriptions show how cumbersome this approach is, for in each instance one must desig-

nate the spore type, e.g., *Thelotrema wightii* with *Leptotrema*-type spores, etc. If one is forced to make this critical distinction every time a species is identified and described, then they should be treated as distinct genera, a more coherent and certainly a more pragmatic, working solution. Spore characters are well proven, even critical, in the taxonomy of nonlichenized fungi. A retrogressive generic concept in lichens will hardly encourage a better understanding of their biology and evolution. My experience in the Thelotremataceae suggests that spore-based genera are reasonably natural, easily manageable units that are probably diverging in terms of habitat requirements and biogenetic characters as reflected in chemical differences.

Chemistry

As in almost every other group of lichens studied, chemistry is an important and fundamental character in understanding the evolution and population biology of the Thelotremataceae. The family has an unexpectedly rich chemistry with a predominance of P+ depsidones and related compounds (Culberson and Culberson, 1968; Culberson and Hale, 1973). I will discuss the possible significance of this chemistry below under the species and hope to explore the broader aspects of biochemical evolution of the family in another paper.

All of the specimens were initially tested with *p*-phenylenediamine and chromatographed on Brinkman thin-layer plates according to the P reaction. I would recommend, however, that lichenologists consider using this reagent as little as possible because of the well-known carcinogenic properties of volatile amines. Identification of the lichen substances can be made just as easily with TLC without recourse to a P test except in doubtful cases.

Standard thin-layer solvent systems (hexane-ether-formic acid, 130:80:20 v/v, and benzene-dioxane-acetic acid, 180:45:5, v/v) were used to identify the chemical content of each specimen.

HYPOPROTOCETRARIC ACID AND 4-0-DEMETHYLNOTATIC ACID.—*Ocellularia fecunda*, new combination, (hypoprotocetraric acid predominating), *O. rhodostroma* (4-0-demethylnotatic acid predominating), and *Phaeotrema leiostomum* (4-0-deme-

thylnotatic acid sometimes lacking). These acids were recently examined in detail by Culberson (Culberson and Hale, 1973), who discusses the biogenesis. *Ocellularia fecunda* and *O. rhodostroma* were not included in that study.

NORSTICTIC ACID.—*Leptotrema occultum*. This is a rare acid in the Thelotremataceae (especially in contrast to the Graphidaceae) and is largely confined to *Leptotrema* on the world level.

PROTOCETRARIC ACID.—*Ocellularia nigropuncta*, new species, *O. perforata*, *Leptotrema bahianum*, and *Thelotrema confusum*. This well-known P+ red acid is easily identified on TLC plates. It is sometimes accompanied by a higher gray spot that I have termed the "amplior" unknown because of its constant occurrence in *Ocellularia amplior* (Nylander) Redinger. Culberson believes it to be protocetraric acid combined with a carboxylic acid, comparable to fumarprotocetraric acid or the recently described succinprotocetraric acid.

PSOROMIC ACID.—*Ocellularia antillensis*, new species, *O. comparabilis*, *O. subcavata*, *O. terebratula*, *Leptotrema fissum*, *Thelotrema carassense*, *T. clandestinum*, *T. conforme*, *T. leucinum*, and *T. interpositum*. This is the commonest P+ acid in the Thelotremataceae. It is almost always accompanied by an unknown compound "conpsoromic acid," appearing as a spot below psoromic acid. It, too, is P+ yellow.

STICTIC AND CONSTICTIC ACIDS.—*Ocellularia conglomerata*, new species, *O. dilatata*, *O. exanthismocarpha*, *O. pyrenuloides*, *Phaeotrema obscurum*, new species, *Thelotrema glaucopallens*, *Leptotrema deceptum*, new species, *L. microglanoides*, and *L. subcompunctum*. This widespread and well-known acid is actually rather rare in the Thelotremataceae except for the genus *Leptotrema*. Constictic acid, appearing as a H₂SO₄+ yellow spot just below salazinic acid, is a constant accessory compound. One or two other gray spots, as yet unidentified, may occur between stictic and constictic acids on TLC plates. Another rarer accessory is the highest H₂SO₄+ orange-red spot in the "quintaria" series (Hale, 1971b), still unidentified but being discovered in a variety of genera.

VIRENSIC ACID.—*Leptotrema spondaicum*. This acid is P+ red. It was previously unknown in the Thelotremataceae, having been first identified in *Alectoria*.

"CINCHONARUM" UNKNOWN.—*Ocellularia cavata*

and *Thelotrema dominicanum*, new species. Several species of *Ocellularia* and this single *Thelotrema* react P+ red, but neither protocetraric acid or fumarprotocetraric acid can be demonstrated with TLC. Instead there are at least two gray spots above both of these acids on the plates (and often a high H₂SO₄ yellow spot). These are apparently derivatives of protocetraric acid.

"PRAESTANS" UNKNOWN.—*Thelotrema praestans*. This unidentified depsidone reacts P+ red orange and forms a very distinct orange to reddish brown spot below psoromic acid in both solvents.

"OLIVACEA" UNKNOWN.—*Ocellularia olivacea*. This P- compound produces a distinct H₂SO₄ gray spot below lecanoric acid in both solvents. It may be a depside. While the lectotype of *Ocellularia olivacea* contains only this one spot, all West Indian collections, otherwise morphologically indistinguishable, contain a lower gray spot in addition. All specimens have thick white acetone residues.

OTHER P- UNKNOWN.—*Ocellularia rimosa*, new species, and *O. soreliata*, new species. The unidentified spots in these species may or may not represent lichen substances. Some species were examined for fatty acids by dipping the plates in water and trying to detect white water-repellant spots as the water evaporated. Some spots resembling fatty acids were seen but microchemical tests with G.E. and G.A.W. were unsuccessful. Another major group of P- compounds is terpenes. All TLC plates showed numerous terpenes, identifiable as purple, blue, or brown spots falling generally above R^F .5 and fading within a few hours. Probably all of these originate from the bark and are not lichen products, as can be proved by co-chromatographing the lichens with lichen-free bark samples from the same specimen.

NO SUBSTANCES PRESENT.—*Ocellularia alborosella*, *O. concolor*, *O. dominicana*, new species, *O. maculata*, new species, *O. mordenii*, new species, *O. papillata*, *Phaeotrema aggregatum*, new species, *P. disciforme*, new combination, *Thelotrema depressum*, *T. leucomelaenum*, *T. papillosum*, new species, *T. tenue*, new species, and *T. tuberculiferum*.

PIGMENTS.—*Ocellularia mordenii*, new species and *Leptotrema wightii* (anthraquinones) and *O. fecunda*, new combination, *O. rhodostroma*, and *Phaeotrema leiostomum* (K- yellow compounds).

The anthraquinones are generally produced in the thallus, while the yellow compounds occur in the medulla of the apothecia and not in the thallus.

Ecology and Habitats

I paid considerable attention to the ecology of the species and habitat requirements in Dominica in the hope that this information would help in understanding the distribution and evolution of the species on the island. Lichenologists have all too often prepared revisions of tropical lichens on the basis of preserved herbarium specimens alone with little if any opportunity to observe the species in the field. Labels on specimens collected by non-professionals rarely give pertinent information on ecology and habitat. For example, tropical rain forests have distinct layering and great vertical variation in microclimate. Elevational differences are also important and once again such data are rarely given in full on herbarium labels.

Base level species in Dominica form a distinctive group. They grow on roots, lianas, buttresses, prop roots, and saplings within 2–3 m of the forest floor. Characteristic species are *Ocellularia concolor*, *O. papillata*, *O. perforata*, *Thelotrema glaucopallens*, *T. tenue*, new species, and *Leptotrema deceptum*, new species. At the opposite extreme we find canopy species that occur high above the forest floor in tree tops, exposed to great changes in insolation and wetting-drying cycles. These include *Ocellularia mordenii*, new species, *O. olivacea*, *O. subcavata*, *O. terebratula*, *Phaeotrema leiostomum*, *Thelotrema clandestinum*, and *T. praestans*. Other species on Dominica have less stringent habitat requirements or have been collected too infrequently to categorize.

On a broader scale altitudinal differences are also pronounced. The rain forest becomes stunted in Dominica above about 800 m and gradually merges into an elfin mossy forest best developed above 1000 m. Thelotremes become scarce in this wind-swept zone where rain falls almost every day. Two species, however, *Thelotrema leucomelaenum* and *T. tuberculiferum*, are restricted to the highest elevations. *Ocellularia rhodostroma* and *Thelotrema tenue*, new species, occur here as well but also at lower elevation.

The vast bulk of thelotreme collections were made between 300 and 800 m on Dominica, the

zone where rain forest is optimally developed, the trees being 30–40 m high (Figures 2 and 3 in Hale, 1971a, illustrate this forest type). It would appear that this lichen family is totally dependent on undisturbed rain forest as a primary habitat and site for speciation. When this forest is destroyed, it seems inevitable that the lichens associated with it will become extinct. In Dominica, I have seen only two species able to invade disturbed or planted forests; namely, *Leptotrema spondaicum* and *Ocellularia exanthismocarpa*. They have a highly successful means of propagation and become established very quickly.

THE THELOTREME FLORA

As I had found with *Parmelia* (Hale, 1971a), almost all previous collections of the Thelotremataceae on Dominica were made by W. R. Elliott in the 1890s. H. A. Imshaug also made about ten collections in 1963 which are preserved at Michigan State University. I have not had access to these. Elliott collected five specimens, identified by Vainio (1896, 1915) as follows:

Thelotrema excavatum Vainio var. *impresulum* Vainio (Morne Anglais, the type-locality, Elliott 160, specimens in BM and TUR). This is synonymous with *Ocellularia perforata*.

Thelotrema leucomelaenum var. *elevatum* Vainio (Morne Anglais, Elliott 1534, specimen in TUR). This is *T. leucomelaenum*.

Thelotrema rhodostromum (Montagne) Vainio (Morne Anglais, Elliott 521, specimens in BM and TUR, and Prince Rupert, Elliott 1305, specimen in TUR). These are *Ocellularia rhodostroma*.

Thelotrema rudius Vainio var. *dominicanum* Vainio (Prince Rupert, Elliott 1303, specimen in TUR). This is the same as *Leptotrema bahianum*.

The thelotreme flora of Dominica now includes 48 positively identifiable species (and three additional species represented by poor material). I collected all of these except for *Leptotrema bahianum*. No one locality, of course, had anywhere near this number of species (see p. 14, "Collecting Localities"). The richest area was one site (16b) in the Dleau Gommier Forest Reserve which was being logged in December 1971; I collected a total of 19 species there over an area of about 3 hectares. An adjacent site had 14 species as did the trail to Morne Anglais. Dleau Gommier locality 15 had

12 different species. A logged rain forest on the Layou Road (12) had 11 species. Five other localities (11, 16c, 18a, 21, and 24a), all between 350 and 750 m, had 9 species each.

The homogeneity of the flora is remarkably high. Locality 16, for example, contains three adjacent collecting sites. Out of a total flora of 21 species there, 8 were found in common at each site. Three occurred at two of the three sites and 10 were collected at only one of the three sites. The greatest variance in homogeneity obviously comes about when we collect at two very different elevations or sites where habitat conditions are significantly different.

It should be evident that we have not yet inventoried the whole thelotreme flora of Dominica. I would estimate that there are at least 55 species (including the three unidentified collections as possible additions). It would require at least one more intensive collecting trip, possibly two, to reach this number.

COLLECTING LOCALITIES

Specimens were collected at 28 separate localities on the island (Figure 8), and multiple visits were made at different times to six of these, giving a total of 35 collecting sites. These are coded as follows for convenience in citing specimens, going from localities at low elevation in the scrub forest to those at highest elevations.

1. Scrub forest, Rodney's Rock, sea level.
2. Scrub forest near Mero, elevation 15 m.
3. Scrub forest on slopes of Barbers Block, elevation 60 m.
4. Scrub forest near Calibishie, elevation 15 m.
5. Palm forest at Rosalie Bay, elevation sea level.
6. Rain forest along trail to Madjini, elevation 30 m.
7. Virgin rain forest logging area, Newfoundland, elevation 250 m.
8. Rain forest above Newfoundland, elevation 300 m.
9. Rain forest logging area, Castle Bruce Road, elevation 300 m.
10. Dleau Gommier rain forest near Emerald Pool, elevation 450 m.
11. Felled rain forest along new road cut about

- 2 km northwest of Pont Cassé, elevation 430 m.
12. Rain forest logging area on Layou Road, elevation 420 m.
13. Mixed secondary forest logging area at Brant-ridge Estate, elevation 500 m.
14. Rain forest logging area just east of Pont Cassé, elevation about 550 m.
15. Virgin rain forest area at Dleau Gommier Forest Reserve, elevation 500 m.
- 16a, 16b, and 16c. Virgin rain forest logging at Dleau Gommier Forest Reserve, elevation 350–370 m.
17. Remnants of rain forest at Felicité, elevation 370 m.
- 18a and 18b. Remnants of rain forest along road to Jean Estate, elevation 600–700 m.
19. Citrus grove at Laudat, elevation 400 m.

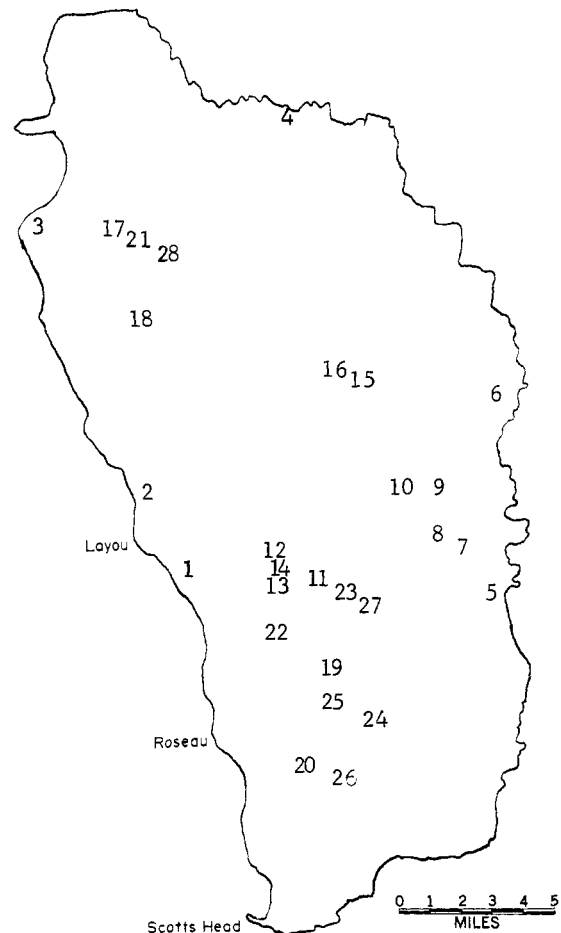


FIGURE 8.—Outline map of Dominica showing localities where specimens of Thelotremataceae were collected.

- 20a and 20b. Remnants of rain forest in pastures above Giraudel, elevation 550–600 m.
21. Virgin rain forest at Syndicate Estate, elevation 650–700 m.
22. Mixed rain forest along trail through Middleham Estate, elevation 650–700 m.
23. Rain forest at the base of Trois Pitons, elevation 650–700 m.
- 24a and 24b. Mixed secondary forest along trail to Boiling Lake, elevation 650–700 m.
- 25a and 25b. Rain forest-mossy forest along trails at Fresh Water Lake, elevation 800–900 m.
- 26a and 26b. Rain forest-mossy forest along trail up Morne Anglais, elevation 800–1000 m.
27. Stunted rain forest-mossy forest on slopes of Trois Pitons, elevation 900–1200 m.
28. Mossy forest area on slopes of Morne Diablotin, elevation 1000–1200 m.

Sixteen localities were visited on the first trip in January 1969 (1, 2, 5, 6, 7, 13, 14, 15, 17, 18b, 19, 20b, 24b, 25b, 26b, and 28). On the second trip seven additional localities were found (3, 11, 12, 16a–c, 22, 23, and 27) and five sites adjacent to localities previously were examined (18a, 20a, 24a, 25a, 26a), all during December 1971. Four new localities were visited in May 1972 (8, 9, 10, 21). All specimens are deposited in US unless otherwise indicated and duplicates will be deposited in the British Museum (BM).

I have provided illustrations of the Dominican species as well as of most type-specimens for comparison. These photographs also serve to show the range of variation in pore size and apothecial emergence. I have found these $\times 10$ photographs to be extremely useful in identification, more so than line drawings of cross-sections. All specimens, including the types listed, were tested with thin-layer chromatography.

Ocellularia

This is the largest genus in the family, comprising about 165 species on the world level or about 40 percent of the total 400 known species. I had almost the same percentage on Dominica (22 of 48 species) but it makes up a disproportionately large percentage of the specimens actually collected, 410 out of 530 (77%). Ecologically the genus is best adapted to mature rain forest and cannot withstand extremes of very dry lowland and wet exposed high elevation. The ten commonest species (with number of specimens collected in parentheses) are: *O. rhodostroma* (93), *O. fecunda*, new combination (64), *O. perforata* (55), *O. papillata* (48), *O. subcavata* (40), *O. exanthismocarpa* (25), *O. nigropuncta*, new species (16), *O. olivacea* (12), *O. mordenii*, new species (10), and *O. terebratula* (10). Rarities, known from single collections each, are *O. antillensis* and *O. cavata*.

Key to the Species of *Ocellularia*

1. Medulla of thallus and/or ascocarps pigmented.
 2. Medulla and ascocarps entirely deep red 12. *O. mordenii*, new species
 2. Medulla of ascocarps yellow or pink but thallus medulla white.
 3. Pigment yellow; pore large, 0.3 mm wide 10. *O. fecunda*, new combination
 3. Pigment deep pink; pore tiny, 0.1 mm wide, annulate. 18. *O. rhodostroma*
1. Medulla of thallus and ascocarps white.
 4. Apothecia lacking a central columella.
 5. Apothecia immersed, 0.2–0.3 mm in diameter.
 6. Thallus P+ yellow 22. *O. terebratula*
 6. Thallus P– 14. *O. olivacea*
 5. Apothecia emergent, 0.6–2.0 mm in diameter.
 7. Disc open with a strongly recurved exciple.
 8. Exciple thick, disc irregularly elongate; stictic acid present 7. *O. dilatata*
 8. Exciple thin and delicate, disc round; stictic acid absent 1. *O. alborosella*
 7. Disc closed, lacking an outer recurved exciple.
 9. Inner lepadinoid exciple strongly developed.
 10. Apothecia aggregated in groups.
 11. Apothecial groups round; stictic acid lacking 8. *O. dominicana*, new species

11. Apothecial groups oblong; stictic acid present 6. *O. conglomerata*, new species
10. Apothecia solitary.
12. Spores large, 55 μ -75 μ 9. *O. exanthismocarpa*
12. Spores small, 15 μ 6. *O. conglomerata*, new species
9. Inner exciple not developed.
13. Thallus P-.
14. Thallus distinctly fissured; pore area black rimmed 19. *O. rimosa*, new species
14. Thallus continuous; pores not black rimmed 15. *O. papillata*
13. Thallus P+ red.
15. Pore area black rimmed 13. *O. nigropuncta*, new species
15. Pore area not black rimmed 16. *O. perforata*
4. Apothecia with a well-developed black central columella.
16. Thallus with large scattered verrucose outgrowths becoming sorediate 20. *O. sorediata*, new species
16. Thallus lacking soredia.
17. Apothecia large, 0.5-1.1 mm in diameter, more or less emergent.
18. Thallus dull tan, hypophloeodal, P- 5. *O. concolor*
18. Thallus distinctly epiphloeodal, P+.
19. Columella becoming actinoid; thallus P+ yellow 4. *O. comparabilis*
19. Columella remaining simple; thallus P+ red 3. *O. cavata*
17. Apothecia smaller, 0.2-0.5 mm in diameter, barely emergent to immersed.
20. Pore annulate; spores small with crowded septae, 5 μ -6 μ \times 9 μ -11 μ 21. *O. subcavata*
20. Pore not annulate; spores generally 20 μ -30 μ long (except smaller in *O. maculata*).
21. Thallus P-.
22. Pore tiny, less than 0.1 mm in diameter; spores 4-loculate 11. *O. maculata*, new species
22. Pore larger, 0.1-0.2 mm wide; spores 6-7-loculate 15. *O. papillata*
21. Thallus P+ red or orange yellow.
23. Thallus very thin to hypophloeodal; P+ orange 17. *O. pyrenuloides*
23. Thallus thick, epiphloeodal.
24. Thallus P+ red; apothecia barely emergent 16. *O. perforata*
24. Thallus P+ yellow; apothecia strongly emergent 2. *O. antillensis*, new species

1. *Ocellularia alborosella*

FIGURES 5b, 9b

Ocellularia alborosella (Nylander) Santesson, 1952:308.

Graphis alborosella Nylander, 1863:372 [type-collection: Colombia, Lindig 2694 (H, lectotype; FH-Tuck, UPS, isotypes); Figure 9b].

Thelotrema platycarpellum Vainio, 1923:138 [type-collection: Arima, Trinidad, Thaxter 57 (TUR, lectotype); Figure 9a].

Ocellularia platycarpella (Vainio) Zahlbruckner, 1923:598.

Thallus whitish gray, thin but continuous, shiny, smooth, forming colonies 5-8 cm broad; apothecia chroodiscoid, up to 1.5 mm across, round to irregular, the marginal flap conspicuous, the disc flesh colored to white pruinose; hymenium about 60 μ

high; spores 8, 5-6 loculate, 4 μ -5 μ \times 8 μ -15 μ , I- or weakly blue (Figure 5b).

CHEMISTRY.—No substances present.

HABITAT.—Tree trunks at mid or higher elevation in rain forest.

This was the first corticolous chroodiscoid species to be described. It is characterized by the small spores and lack of lichen substances. The Dominican collections have a wider disc than the type from Colombia but they fall within a predictable range of variation. It is a rare and easily overlooked species.

SPECIMENS EXAMINED.—8 (38143), 16b (37883), 26b (35371a).

2. *Ocellularia antillensis* Hale, new species

FIGURE 9g

Thallus corticola, albidus, epiphloeodes, planus vel minute verrucosus, nitidus, 3–5 cm latus; apothecia numerosa, emergentia, 0.3–0.5 mm diametro, apice obfusca, columellata, columella 0.15 mm lata; ostiolum 0.1–0.12 mm diametro, intus nigrum; hymenium 70μ – 80μ altum; sporae 8-nae, transversim 7 loculatae, $7\mu \times 20\mu$, I+ coerulescentes (Figure 9g).

CHEMISTRY.—Psoromic and conpsoromic acids.

HOLOTYPE.—Trail to Madjini, low elevation windward rain forest, Dominica, elevation about 30 m, *Hale* 35612, January 1969 (US).

HABITAT.—Upper trunk of stunted rain forest trees (30m).

The whitish minutely verrucose thallus and numerous emergent apothecia with the large contrasting black pore area distinguish this rare species. *Ocellularia comparabilis* var. *microcarpa* Redinger has larger spores ($6\mu \times 30\mu$ – 34μ), sparse apothecia, and a smooth thallus, while *O. terebrata* (Acharius) Müller-Argau has barely emergent apothecia (see Hale, 1972). I later collected this species from Trinidad and Panama, both at low elevation.

SPECIMENS EXAMINED.—3 miles NW of Sangre Grande, Trinidad, *Hale* 37444 (US); Barro Colorado Island, Panama, *Hale* 38659 (US).

3. *Ocellularia cavata*

FIGURES 6c, 9f

Ocellularia cavata (Acharius) Müller-Argau, 1882b:499.

Thelotrema cavatum Acharius, 1812:92 [type-collection: Sierra Leone, *Afzelius* (H, lectotype; S, UPS, isotypes)].—Hale, 1971b, fig. 1a.

Ascidium cinchonarum Fée, 1824:96 [type-collection: On *Cinchona*, South America (G, lectotype; H, L, M, P, isotypes); Figure 9e].

Ocellularia cinchonarum (Fée) Sprengel, 1827:242.

Ascidium cinchonarum f. *intermedium* Nylander, 1867:319 [type-collection: Pie de Cuesta, Colombia, *Lindig* 5 (H, lectotype; BM, G, M, isotypes); Figure 9c].

Ocellularia lindigiana Müller-Argau, 1887a:9 [type-collection: Colombia, *Lindig* 2757 (G, lectotype; BM, FH, UPS, isotypes); Figure 9d].

Ocellularia cinchonarum (Fée) Sprengel f. *intermedia* (Nylander) Zahlbruckner, 1923:586.

Thallus whitish mineral gray, epiphloeodal, continuous, more or less roughened, forming colonies

up to 8 cm across; apothecia ascidioid, 0.7–0.9 mm in diameter, apically carbonized with a large columella (Figure 6c); pore round, 0.07–0.12 mm in diameter, the top of the columella clearly visible; spores 8, 6–8 loculate, 6μ – $8\mu \times 22\mu$ – 28μ , I+ blue. (Figure 9f).

CHEMISTRY.—“Cinchonarum” unknowns A and B and a yellowish pigment.

HABITAT.—Canopy branch in mid-elevation rain forest (about 550 m).

I had previously typified this distinctive but rare Acharian species. It appears to be rare in the Lesser Antilles. The chief diagnostic features are the unusual chemistry, small ascidioid apothecia, and the large columella which protrudes into the pore area.

SPECIMEN EXAMINED.—14 (35134).

4. *Ocellularia comparabilis*

FIGURES 5i, 9i

Ocellularia comparabilis (Krempelhuber) Müller-Argau, 1883:318.

Thelotrema comparabile Krempelhuber, 1876:220 [type-collection: Rio de Janeiro, Brazil, *Glaziou* 5463 (M, lectotype; BM, C, G, M, P, UPS, W, isotypes); Figure 9i].

Thallus pale greenish to whitish mineral gray, epiphloeodal, smooth, forming colonies 5–12 cm broad; apothecia emergent, 0.8–1.2 mm in diameter, the walls carbonized, columella simple to actinoid; pore open, 0.2–0.5 mm broad, the white pruinose disc clearly visible; hymenium 50μ – 60μ high; spores 8, 4–5 loculate, 5μ – $6\mu \times 10\mu$ – 14μ , I+ blue. (Figure 5i).

CHEMISTRY.—Psotomic and conpsoromic acids.

HABITAT.—Lower trunks in rain forest (300–700 m).

The columella in this rare species is imperfectly actinoid. To judge from collections made in South America, the range of variation is very great with gradations into related psoromic acid-containing species. For example, *Ocellularia discoidea* (Acharius) Müller-Argau (Hale, 1972) and *O. antillensis*, new species, have a simple columella. *Ocellularia efformata* (Krempelhuber) Müller-Argau has a very similar actinoid columella but the outer margin is semi-erect, leaving an open rather lacerate pore; *O. berkeleyana* (Montagne) Zahlbruckner and *O. glaziovii* Müller-Argau both have highly developed

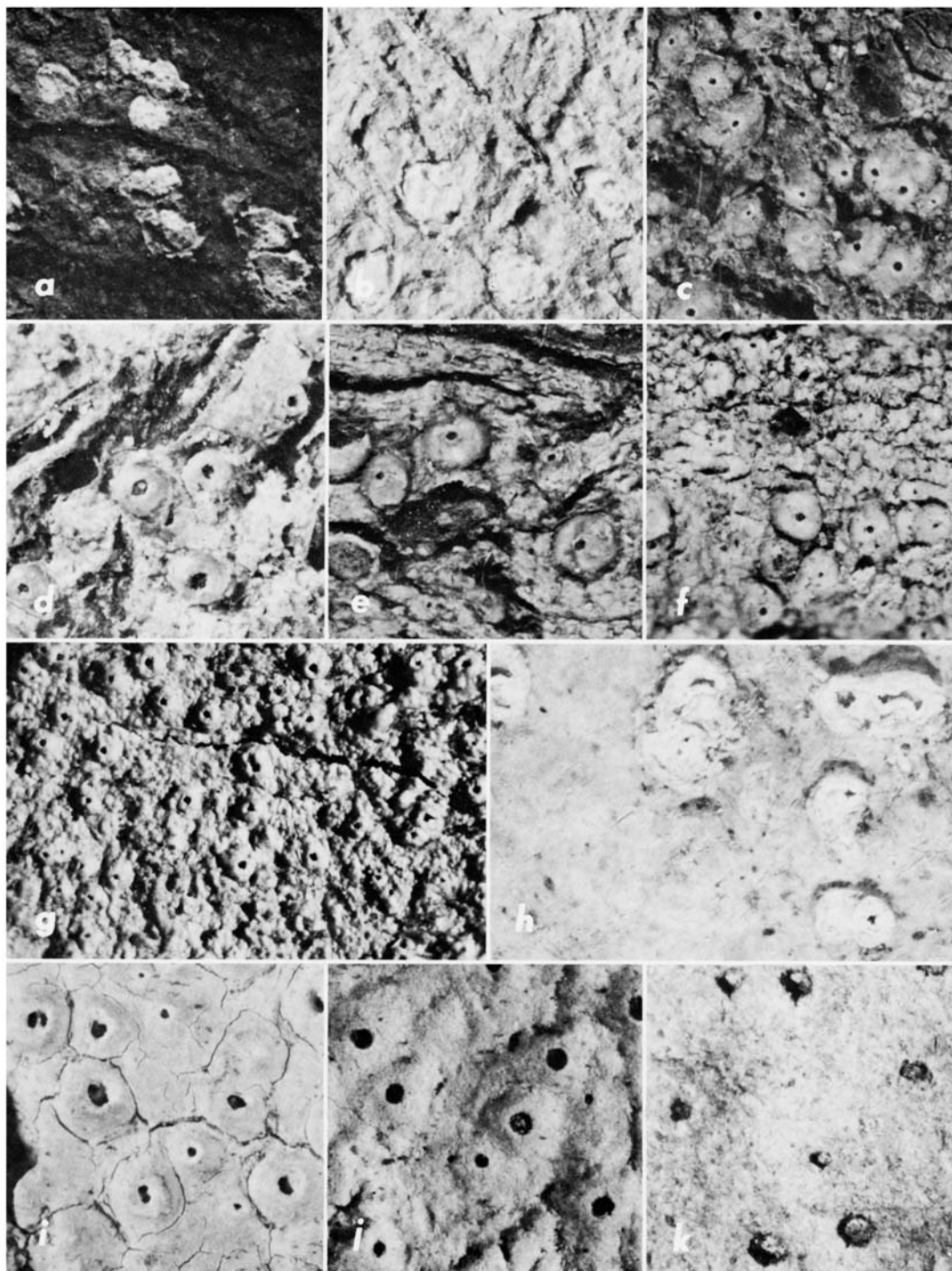


FIGURE 9.—Specimens of Thelotremataceae (all about $\times 10$): *a*, *Ocellularia platycarpella* (lectotype in TUR); *b*, *O. alborosella*, (isotype in FH-Tuck); *c*, *O. cinchonarum* f. *intermedia* (lectotype in H); *d*, *O. lindigiana* (lectotype in G); *e*, *O. cinchonarum* (lectotype in G); *f*, *O. cavata* (Hale 35134); *g*, *O. antillensis*, new species (Hale 35612); *h*, *O. conglomerata*, new species (Hale 37959); *i*, *O. comparabilis* (isotype in BM); *j*, *O. concolor* (lectotype in G); *k*, *O. concolor* (Hale 38167).

actinoid discs; and *O. latilabra* (Tuckerman) Müller-Argau has an actinoid columella and a recurved margin.

SPECIMENS EXAMINED.—9 (38128), 21 (37372, 38144).

5. *Ocellularia concolor*

FIGURE 9j,k

Ocellularia concolor Meyen and Flotow, 1843:230.

TYPE-COLLECTION.—Manila, Philippines, Meyen (G, lectotype) (Figure 9j).

Thallus light grayish tan, dull, mostly hypophloeodal, forming colonies 3–4 cm broad; apothecia numerous, 0.8–1.1 mm in diameter, more or less emergent, apically carbonized, columella present, 0.2–0.3 mm wide; pore open, round to somewhat irregular, 0.3–0.5 mm in diameter, the rim black and the flat black columnar disc easily seen; hymenium 140 μ high; spores 8, 5–7 loculate, 5 μ –8 μ \times 13 μ –20 μ , I+ blue (Figure 9k).

CHEMISTRY.—No substances present.

HABITAT.—Lianas, saplings, base and lower trunk of trees in dense rain forest (300–370 m).

This easily recognizable species was first described from the Philippines and appears to be pantropical. The tannish hypophloeodal thallus and habitat are characteristic. There are no comparable species in this kind of habitat.

SPECIMENS EXAMINED.—8 (38167), 16a (37665), 16b (37801, 37809, 38075).

6. *Ocellularia conglomerata* Hale, new species

FIGURE 9h

Thallus corticola, cinereo-albidus, epiphloeodes, continuus, nitidus, 4–5 cm latus; apothecia primo solitaria, 0.6–0.9 mm diametro, semi-emergentia, mox 2–3:nae conglomerata, margine exteriori erecto, excipulo interiore evoluto, pulverulento, disco aperto, carneo; ostiolum irregulare, latum; hymenium 70 μ altum; sporae 8:nae, transversim 6–7 loculatae, 5 μ –6 μ \times 15 μ –18 μ , I+ coerulescentes (Figure 9h).

CHEMISTRY.—Stictic and constictic acids.

HOLOTYPE.—Trail to Morne Anglais, Dominica, elevation about 900 m, Hale 37959, 13 December 1971 (US).

Chemistry places this species near *O. exanthismocarpa* but the exciple is not so clearly separate from the thick, erect, pulverulent margin, leaving the disc open. The spores are much smaller. Another West Indian stictic acid-containing species, *Ocellularia alboolivacea* (Vainio) Zahlbruckner, has a more typically recurved margin and a thin, entire exciple.

7. *Ocellularia dilatata*

FIGURE 11a,b

Ocellularia dilatata Müller-Argau, 1895:452.

TYPE-COLLECTION.—Rio de Janeiro, Brazil, Glaziou 5531 pro parte (G, lectotype; BM, isotype). (Figure 11a).

Thallus whitish gray, thin, dull, in part hypophloeodal, forming colonies 4–6 cm broad; apothecia chroodiscoid, large, up to 2.5 mm broad, round to elongate, marginal flap rather coarse; disc white pruinose; hymenium about 60 μ high; spores 8, 6–7 loculate, 5 μ –6 μ \times 15 μ –17 μ , I+ blue (Figure 11b).

CHEMISTRY.—Stictic and constictic acids.

HABITAT.—Lower trunk area in higher rain forest zone (850 m).

This rare species is related to *Ocellularia alborosella*, but it has a thicker recurved margin and a different chemistry. I have collected a number of specimens at low elevation in Trinidad, suggesting that the species is more at home on continental land masses.

SPECIMENS EXAMINED.—26a (37695, 37702).

8. *Ocellularia dominicana* Hale, new species

FIGURES 2c,d; 10

Thallus corticola, brunneo- vel viridi-albidus, epiphloeodes, continuus, nitidus, 5–10 cm latus; apothecia semi-emergentia, 0.7–1.1 mm diametro, apice incolores, columella nulla, solitaria vel 2–3 arcte aggregata, habitu similia apothecio singulari, excipulo interiore evoluto, ostiolum complente; ostiolum rotundum, 0.1–0.5 mm diametro; hymenium 60 μ –80 μ altum; sporae 8:nae, transversim 6–7 loculatae, 6 μ –8 μ \times 16 μ –25 μ , I+ coerulescentes (Figure 10).

CHEMISTRY.—No substances present.

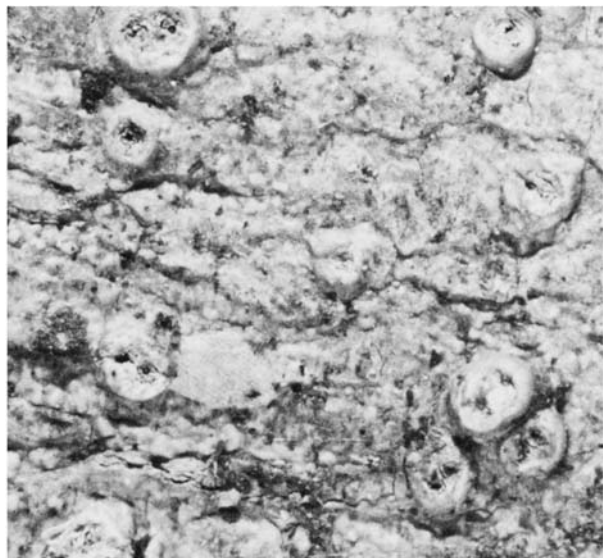


FIGURE 10.—*Ocellularia dominicana*, new species (Hale 37841) (about $\times 10$).

HOLOTYPE.—Submossy forest on upper slopes of Trois Pitons, Dominica, elevation about 1000 m, Hale 37967, 6 December 1971 (US).

HABITAT.—Trunk and lower base of trees in submossy forest (700–1100 m).

The apothecia are so tightly aggregated that I first interpreted the wall between them as a columella. The combined outer margin and exciple are minutely pulverulent and crowded, filling the broad disc but leaving a distinct pore area. The species was rather common at Trois Pitons but not found elsewhere.

SPECIMENS EXAMINED.—23 (38053), 27 (37683, 37688, 37829, 37832, 37841, 38041).

9. *Ocellularia exanthismocarpa*

FIGURES 5a, 11c,g

Ocellularia exanthismocarpa (Leighton) Zahlbruckner, 1923:590.

Thelotrema exanthismocarpum Leighton, 1869:169 [type-collection: Central Province, Ceylon, Thwaites C.L. 97 (BM, lectotype; H, isotype); Figure 11c].

Thelotrema porinoides Montagne and von der Bosch, 1855:484 [type-collection: Java, Junghuhn 151 (L, lectotype; FH, G, P, W, isotypes); Figure 11e].

Ocellularia multilocularis Zahlbruckner, 1912:369 [type-collection: Lanai, Hawaii, Rock 17 (W, holotype); Figure 5a].

Ocellularia isertii Vainio, 1915:40 [type-collection: Guadeloupe, Isert 87 (C, lectotype; TUR, isotype); Figure 11f].

Thelotrema homothecium Vainio, 1921:190 [type-collection: Irosin, Mt. Bulusan, Prov. Sorsogon, Philippines, Elmer 14852 (TUR, lectotype; FH, G, L, S, US, W, isotypes); Figure 11d].

Ocellularia homothecia (Vainio) Zahlbruckner, 1923:593.

Ocellularia porinoides (Montagne and von der Bosch) Zahlbruckner, 1923:599 [not *O. porinoides* (Acharius) Sprengel, 1827:242].

Thallus white to ashy, thin, smooth, in part hypophloeodal, forming colonies 1–4 cm across; apothecia numerous, semi-emergent, the rim becoming erect, noncarbonized and without a columella, the inner exciple distinct, intact, forming an apical pore within the main pore; main pore open, 0.2–0.4 mm in diameter; hymenium 160μ – 180μ high; spores 4–8/ascus, 18–22 loculate, 12μ – $18\mu \times 60\mu$ – 100μ , 1+ deep blue (Figure 11g).

CHEMISTRY.—Stictic and constictic acids and rarely the higher “quintaria” unknown B.

HABITAT.—Trunks, canopy branches, fence posts, and planted trees (300–900 m).

This common pantropical species is unique because of the pore-within-a-pore arrangement. The large spores are also distinctive but it is not unusual to find sterile specimens. It is also one of the few species in the family to invade secondary forests, fence posts, etc., in wet areas up to very high elevation.

SPECIMENS EXAMINED.—8 (38114), 11 (38009), 16b (37982), 17 (35605), 20a (37780, 37781, 37786, 37788, 38019, 38025), 25a (37708, 37709, 37713, 37714, 37715, 37716, 37849, 37996, 38069), 25b (35473, 35516), 26a (37692, 37944), 27 (38042, 38055).

10. *Ocellularia fecunda* (Vainio) Hale, new combination

FIGURE 11h,i

Thelotrema domingense var. *fecundum* Vainio, 1896:208 [type-collection: Richmond Valley, St. Vincent, Elliott 243 (BM, lectotype; TUR, isotype); Figure 11h].

Ocellularia domingensis var. *fecunda* (Vainio) Zahlbruckner, 1923:590.

Thallus light greenish or whitish mineral gray, epiphloeodal, smooth and shiny, forming large colonies up to 30 cm broad; apothecia large, strongly emergent, 1.5–1.8 mm in diameter, the cortex soon breaking away and revealing a light yellowish orange medulla, walls heavily carbonized,

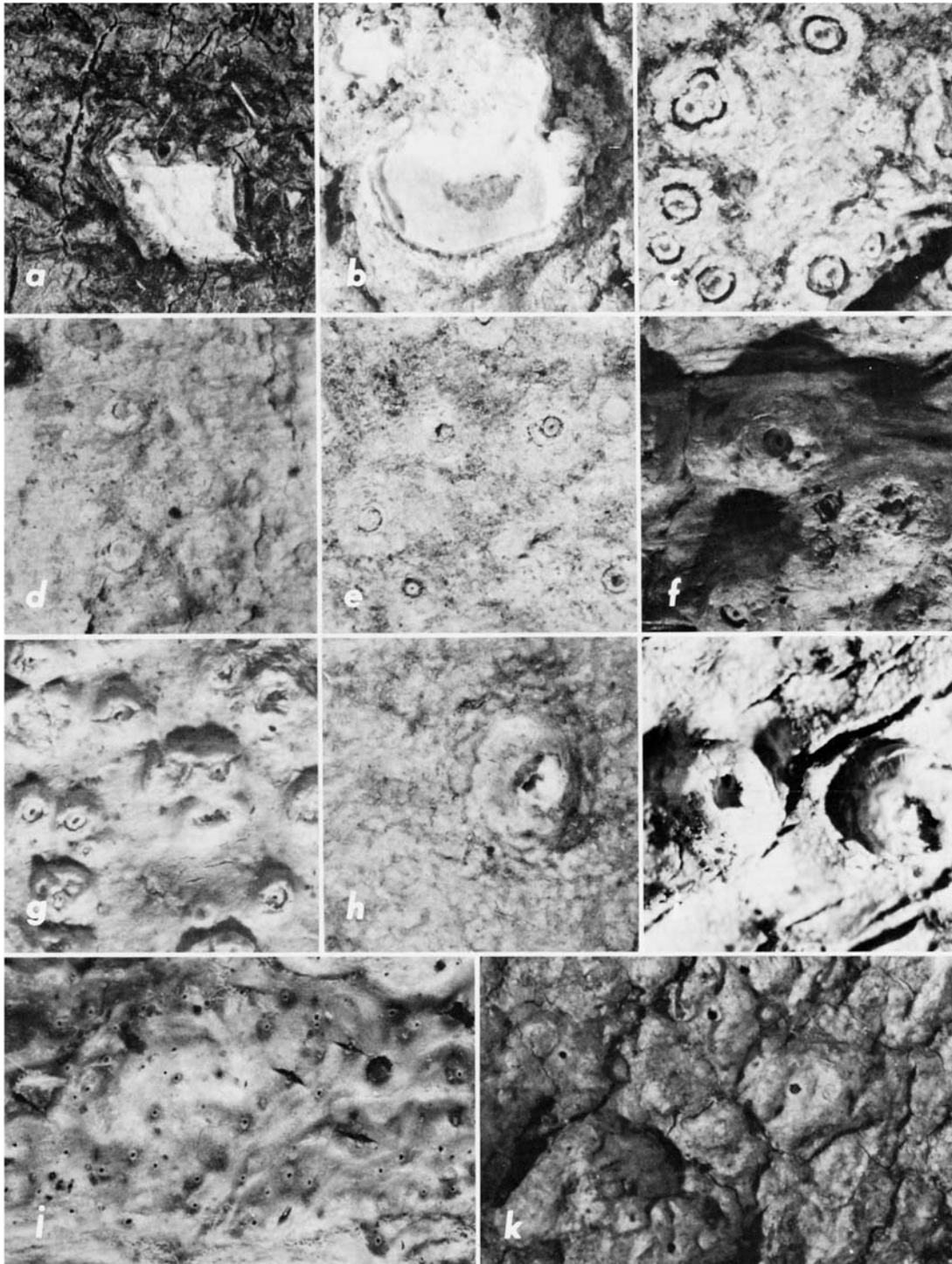


FIGURE 11.—Specimens of Thelotremales (all about $\times 10$): a, *Ocellularia dilatata* (isotype in BM); b, *O. dilatata* (Hale 37702); c, *O. exanthismocarpa* (lectotype in BM); d, *O. homothechia* (isotype in FH); e, *O. porinoides* (lectotype in L); f, *O. isertii* (lectotype in C); g, *O. exanthismocarpa* (Hale 37996); h, *O. fecunda*, new combination (lectotype in BM); i, *O. fecunda*, new combination (Hale 35218); j, *O. maculata*, new species (Hale 38015); k, *O. mordenii*, new species (Hale 37887).

columella absent or weakly and irregularly developed; pore gaping, round to irregular and jagged, 0.4–0.8 mm in diameter, the white pruinose disc clearly visible; hymenium 200μ – 250μ high; spores 1–4/ascus, 30–40 loculate, 12 – $20 \times 80\mu$ – 150μ , rarely turning brown, I+ blue (Figure 11i).

CHEMISTRY.—Hypoprotocetraric acid and in lesser concentration 4–0–demethylnotatic acid along with unidentified pigments.

HABITAT.—Basal area of trees into the upper bole and canopy in the rain forest (300–850 m).

This is one of the few species in the family that can be recognized at sight in the field. The apothecia are very large and the yellow-orange medulla is exposed by rubbing the cortex off. It is the second commonest species in Dominica and forms very extensive colonies. As far as I have determined, the species is restricted to the West Indies and has no close relatives.

SPECIMENS EXAMINED.—8 (38120), 11 (37811, 37816, 37820, 38003, 38046, 38061), 12 (37902, 37906, 37913, 37920, 37921, 37931), 15 (35155, 35167, 35218), 16a (37658, 37942, 37970, 38050), 16b (37796, 37802, 37810, 37874, 37881, 37954), 16c (37765, 37766, 37774, 37943, 37980), 18a (37725, 37957, 37962, 37986, 38039), 21 (38080, 38081, 38089, 38103, 38106, 38107, 38132, 38137), 22 (37639, 37644, 37828, 37838, 37843, 37844, 37844a, 37845, 37856, 37858, 37960, 38026), 23 (37679), 24a (37740, 37743, 37063, 37064), 25a (37711), 26a (38056).

11. *Ocellularia maculata* Hale, new species

FIGURE 11j

Thallus corticola, cinereo-albidus, epiphloeodes, planus, continuus, nitidus, 9 cm latus; apothecia numerosa, minuta, 0.2–0.3 mm diametro, apice obfusca, columellata vel columella parce evoluta; ostiolum rotundum, 0.05–0.1 mm diametro, anguste nigrocinctum, columella protrusa; hymenium 100μ altum; sporae 8:nae, transversim 4 loculatae, 5μ – $7\mu \times 11\mu$ – 13μ , I– (Figure 11j).

CHEMISTRY.—No substances present.

HOLOTYPE.—Remnants of rain forest in pastures above Giraudel, Dominica, elevation 650 m, Hale 38015, 11 December 1971 (US).

Ocellularia maculata might seem at first glance to be *O. papillata* but the apothecia and spores

are much smaller. There are no related species.

SPECIMEN EXAMINED.—18b (35524).

12. *Ocellularia mordenii* Hale, new species

FIGURES 3c,d; 6b; 11k

Thallus corticola, pallide cinereo- vel brunneo-albidus, epiphloeodes, continuus, aetate rimosus, nitidus, usque ad 12 cm latus; medulla omnino sanguinea; apothecia dispersa, vix emergentia, apice obfusca, extus crasse verrucosa, verrucis fragilibus, rumpentibus, columella nulla vel parce evoluta (Figure 6b); ostiolum rotundum, 0.08–0.12 mm diametro; hymenium circa 200μ altum; sporae 1–2:nae, transversim 24–30 loculatae, 15μ – $20\mu \times 70\mu$ – 150μ , I+ coerulescentes (Figure 11k).

CHEMISTRY.—Unidentified anthraquinone pigments only.

HOLOTYPE.—Canopy branches in primary rain forest, Dleau Gommier Forest Reserve, Dominica, elevation about 370 m, Hale 37764, 12 December 1971 (US).

HABITAT.—Canopy branches in rain forest (370–800 m).

The deep red pigment and large warts are distinctive. It is a conspicuous canopy species. A very similar species in Cuba, *O. xanthostroma* (Nylander) Zahlbruckner, differs mainly in containing a K– pale yellow-orange pigment. This lichen is named in honor of Mrs. William J. Morden.

SPECIMENS EXAMINED.—12 (37909), 15 (35198), 16a (38051), 16b (37791), 16c (37762, 37886, 37887, 37010), 26a (37863).

13. *Ocellularia nigropuncta* Hale, new species

FIGURES 2a,b; 6a; 12a

Thallus corticola, pallide brunneo- vel viridicinerus, epiphloeodes, continuus vel rarius rimosus, 5–8 cm latus; apothecia numerosa, emergentia, 0.6–0.8 mm diametro, apice obfusca, columella nulla (Figure 6a); ostiolum rotundum, 0.1–0.2 mm diametro, nigrocinctum; hymenium 100μ – 110μ altum; sporae 8:nae, transversim 6–8 loculatae, 6μ – $10\mu \times 20\mu$ – 32μ , I+ coerulescentes (Figure 12a).

CHEMISTRY.—Protocetraric acid.

HOLOTYPE.—Trail to summit of Morne Anglais, Dominica, elevation about 900 m, Hale 35365, January 1969 (US).

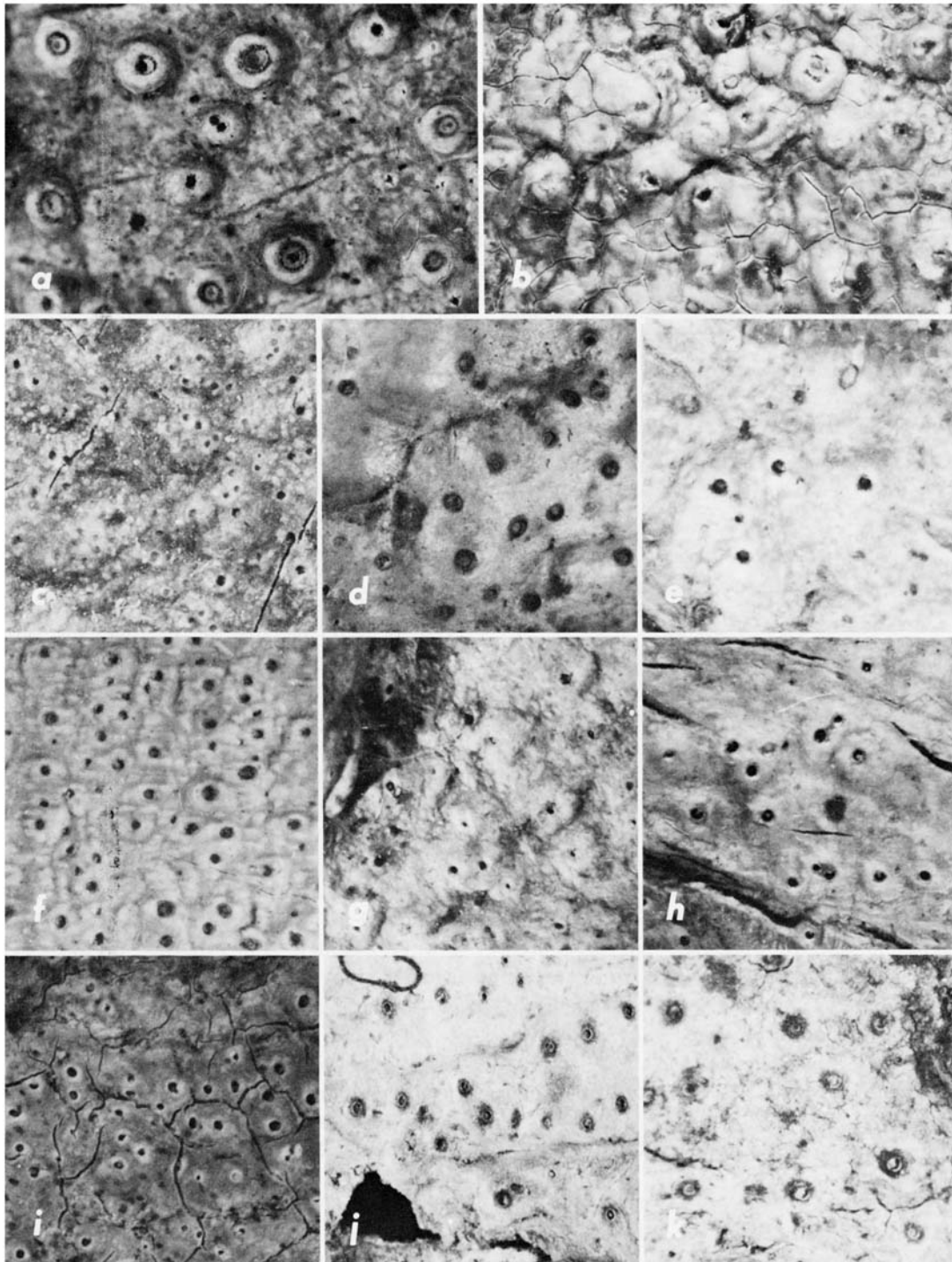


FIGURE 12.—Specimens of Thelotremataceae (all about $\times 10$): a, *Ocellularia nigropuncta*, new species (Hale 35365); b, *O. rimosa*, new species (Hale 38052); c, *O. olivacea* (lectotype in G); d, *O. papillata* (lectotype in BM); e, *O. papillata* (Hale 38098); f, *O. perforata* (lectotype in BM); g, *O. excavata* (lectotype in BM); h, *O. rufocincta* (lectotype in G); i, *O. terebrata* var. *abbreviata* (isotype in FH); j, *O. pyrenuloides* (isotype in W); k, *O. pyrenuloides* (Hale 35524).

HABITAT.—Lianas, lower bole and base, *Symploca* roots, rarely canopy of trees in the rain forest (300–900 m).

The black-rimmed pore area and smooth thallus are diagnostic features. Other ecolmellate protocetraric acid-containing species include *Ocellularia bonplandiae* (Fée) Müller-Argau, which has a grainy surface, and *O. verrucosa* (Fée) Müller-Argau, which has an irregular open pore and larger spores (over 30 μ long). Under the scanning-electron microscope *O. nigropuncta*, new species, has a finely pitted but otherwise smooth surface (Figure 2a,b), whereas *O. verrucosa* appears to have an aculeate orientation and *O. bonplandiae* is verrucose and fissured.

SPECIMENS EXAMINED.—8 (38115, 38158), 10 (38169), 12 (37903), 16a (37660), 16b (37798), 16c (37755, 37770, 37963), 18a (37948), 21 (38092, 38094, 38138), 22 (37852), 24a (37751).

14. *Ocellularia olivacea*

FIGURES 1a; 3a,b; 5c; 12c

Ocellularia olivacea (Fée) Müller-Argau, 1887a:7.

Myriotrema olivacea Fée, 1824:103 [type-collection: On *Bonplandia trifoliata*, South America (G, lectotype); Figure 12c].

Ocellularia olivacea (Fée) C. and D. Van Overeem-De Haas, 1922:118 [superfluous combination].

Thallus light greenish to ashy white, shiny, thick, up to 0.5 mm (Figure 1a), forming extensive colonies up to 50 cm broad, sometimes finely cracked and fissured; apothecia very numerous, immersed, 0.15–0.3 mm in diameter, noncarbonized and without a columella; pore small, flush, about 0.1 mm in diameter; hymenium 65 μ –75 μ high; spores 8, more or less uniseriate, 4 loculate, 4 μ –6 μ \times 8 μ –12 μ , I+ blue (Figure 5c).

CHEMISTRY.—“*Olivacea*” unknown and a second lower spot.

HABITAT.—Canopy branches to mid-bole in rain forest (240–700 m).

This is one of three “*Myriotrema*” species that occur in Dominica, the other two being *O. terebratula* and *Thelotrema clandestinum*, all typically found on canopy branches in dense rain forest. *Ocellularia olivacea* is characterized by the rather small spores and unusual chemistry. The West Indian material all produces a second spot below the “*olivacea*” unknown, probably a related dep-

side. The type-specimen of *O. olivacea* lacks this spot. The surface under the scanning-electron microscope is strongly aculeate (Figure 3a,b).

SPECIMENS EXAMINED.—7 (35226, 35243, 35249), 8 (38164), 9 (38154), 11 (38001), 12 (37965), 15 (35205), 16a (37992, 38054), 18a (37965), 21 (38113).

15. *Ocellularia papillata*

FIGURE 12d,e

Ocellularia papillata (Leighton) Zahlbruckner, 1923:597.

Thelotrema papillatum Leighton, 1869:169 [type-collection: Central Province, Ceylon, Thwaites C.L. 129 (BM, lectotype; H, G, P, S, UPS, W, isotypes); Figure 12d].

Thallus whitish to pale greenish ashy, smooth to more or less warty, shiny, forming colonies 3–12 cm broad; apothecia numerous, 0.6–0.8 mm in diameter, immersed to slightly emergent, the upper walls carbonized, columella present, thin to scarcely developed to absent; pore round, 0.1–0.2 mm in diameter; hymenium 50 μ –70 μ high; spores 8/ascus, 7–9 loculate, 6 μ –10 μ \times 20 μ –36 μ , I+ blue. (Figure 12e).

CHEMISTRY.—No substance present.

HABITAT.—Saplings, prop roots, lianas, and tree bases at mid-elevation in rain forest (300–900 m).

This common species has few outstanding features. The columella is usually present, although often weakly developed and difficult to find. Some specimens, as indicated below, seem to lack it entirely. The apothecia are inconspicuous, almost immersed to slightly emergent, but the pore is always distinct. The thallus is well developed, usually quite whitish, and smooth. There are no close relatives without lichen substances, although *O. perforata*, which has protocetraric acid, is very close in general aspect except perhaps that the apothecia are more often emergent. Both species occupy similar base level habitats in the rain forest and were collected together at 11 of the localities. At eight other localities only one of the species was found.

SPECIMENS EXAMINED (columella present).—8 (38123, 38130, 38165, 38168), 9 (38131), 11 (37825), 16a (37795, 37991), 16b (37662, 37804, 37805, 37808), 18a (37721, 37964); 21 (38084, 38085, 38097, 38098, 38152), 22 (37645, 37837, 37842), 23 (37671, 37681, 37682), 27 (37850, 38072), 28 (35428).

SPECIMENS EXAMINED (columella absent).—7 (35227), 10 (38127, 38150), 16a (37655, 37661), 16b (37792, 38074), 16c (38045) 21 (38086, 38088), 22 (37649, 37834, 37851, 37854, 37855), 23 (37677, 38967), 24a (37746).

16. *Ocellularia perforata*

FIGURES 1b, 5e, 7a, 12f

Ocellularia perforata (Leighton) Müller-Argau, 1892:284.
Thelotrema perforatum Leighton, 1866:447 [type-collection: Casiquiari, Brazil, Spruce 254 (BM, lectotype); Figure 12f].
Thelotrema terebratum var. *abbreviatulum* Vainio, 1890:83 [type-collection: Caraça, Minas Gerais, Brazil, Vainio 1551 (TUR, lectotype; BM, FH, UPS, isotypes); Figure 12i].
Ocellularia rufocincta Müller-Argau, 1893:146 [type-collection: Foret du Rio Général, Tondoiz s.n. (Pittier 6107) (G, lectotype); Figure 12h].
Thelotrema excavatum Vainio, 1896:208 [type-collection: Mt. St. Andrew, St. Vincent, Elliott 153 (TUR, lectotype; BM, FH, isotypes); Figure 12g].
Thelotrema excavatum var. *impressulum* Vainio, 1896:208 [type-collection: Morne Anglais, Dominica, Elliott 169 (BM, lectotype)].
Ocellularia terebrata var. *abbreviata* (Vainio) Zahlbruckner, 1923:602.

Thallus whitish to pale greenish ashy, smooth to more or less warty with age, shiny, forming colonies 3–10 cm broad; apothecia numerous, immersed to moderately emergent, 0.4–0.6 mm in diameter, the upper wall carbonized, columella usually developed, thin 50 μ –70 μ in diameter, but sometimes lacking or difficult to find; pore round, 0.07–0.15 mm in diameter; hymenium 55 μ –70 μ high; spores 8/ascus, 6–8 loculate, 7 μ –10 μ \times 20 μ –34 μ , I+ blue (Figure 5e).

CHEMISTRY.—Protocetraric acid and the “*amplior*” unknown as an accessory substance.

HABITAT.—Buttresses, saplings, and bole to rarely canopy branches in rain forest at mid-elevation (300–850 m).

This is one of the commonest species in Dominica at base level. The smooth whitish thallus (see cross-section in Figure 2b) and the small semi-emergent apothecia resemble *O. papillata*, as discussed above. Some of the specimens as listed below lacked any sign of a columella.

SPECIMENS EXAMINED (columella present).—8 (38149), 11 (37812, 37817, 37997, 38030, 38033), 12 (37899, 38078), 14 (35139), 16a (37651, 37666, 38007, 38032), 16b (37884), 16c (37759, 37761,

37775, 37952), 18a (37727, 37728, 37730, 37732, 37735, 37961, 37969, 37983, 38020), 20a (37784, 37785, 38016, 38017), 21 (38108, 38134, 38145), 22 (37646, 37647, 37830, 35857, 38036), 23 (37675), 24a (37752), 26a (37698, 37701), 27 (37686, 37827).

SPECIMENS EXAMINED (columella absent).—8 (38160, 38163), 16a (38018), 21 (38093, 38140, 38157), 23 (37674), 24a (38066), ?7 (37684, 37847), 26a (37700), 26b (35370).

17. *Ocellularia pyrenuloides*

FIGURE 12j,k

Ocellularia pyrenuloides Zahlbruckner in Magnusson and Zahlbruckner, 1943:46.

TYPE-COLLECTION.—Wailuku, Maui, Hawaii, Faurie 676 (UPS, lectotype; S, W, isotypes) (Figure 12j).

Thallus ashy mineral gray, thin to evanescent, continuous, forming colonies about 5 cm broad; apothecia numerous, nearly immersed to moderately emergent, 0.5–0.7 mm in diameter, walls heavily carbonized, columella present, 130 μ in diameter; pore round, 0.1–0.15 mm wide, pore area surrounded by a blackish ring, in part white pruinose, the pruinose top of columella visible through the pore; hymenium about 60 μ high; spores 8/ascus, 6–7 loculate, 6 μ \times 12 μ –15 μ , I+ blue (Figure 12k).

CHEMISTRY.—Stictic and constictic acids.

HABITAT.—Tree branch in rain forest (650 m).

The darkened pore area is similar to that in *Thelotrema tenue*, new species. There are no related species with stictic acid. It is still surprising to find a Hawaiian species on Dominica, but to me this suggests how poorly the Thelotremataceae have been collected.

SPECIMEN EXAMINED.—18b (35524).

18. *Ocellularia rhodostroma*

FIGURES 5g, 7b, 13a

Ocellularia rhodostroma (Montagne) Zahlbruckner, 1923:600.
Ascidium rhodostromum Montagne, 1851:75 [type-collection: Cayenne, French Guiana, collection 1334 (P, lectotype); Figure 13a].

Thallus light greenish tan to gray, smooth to finely warty, continuous and epiphloeodal, the medulla white or pink, forming colonies 5–10 cm

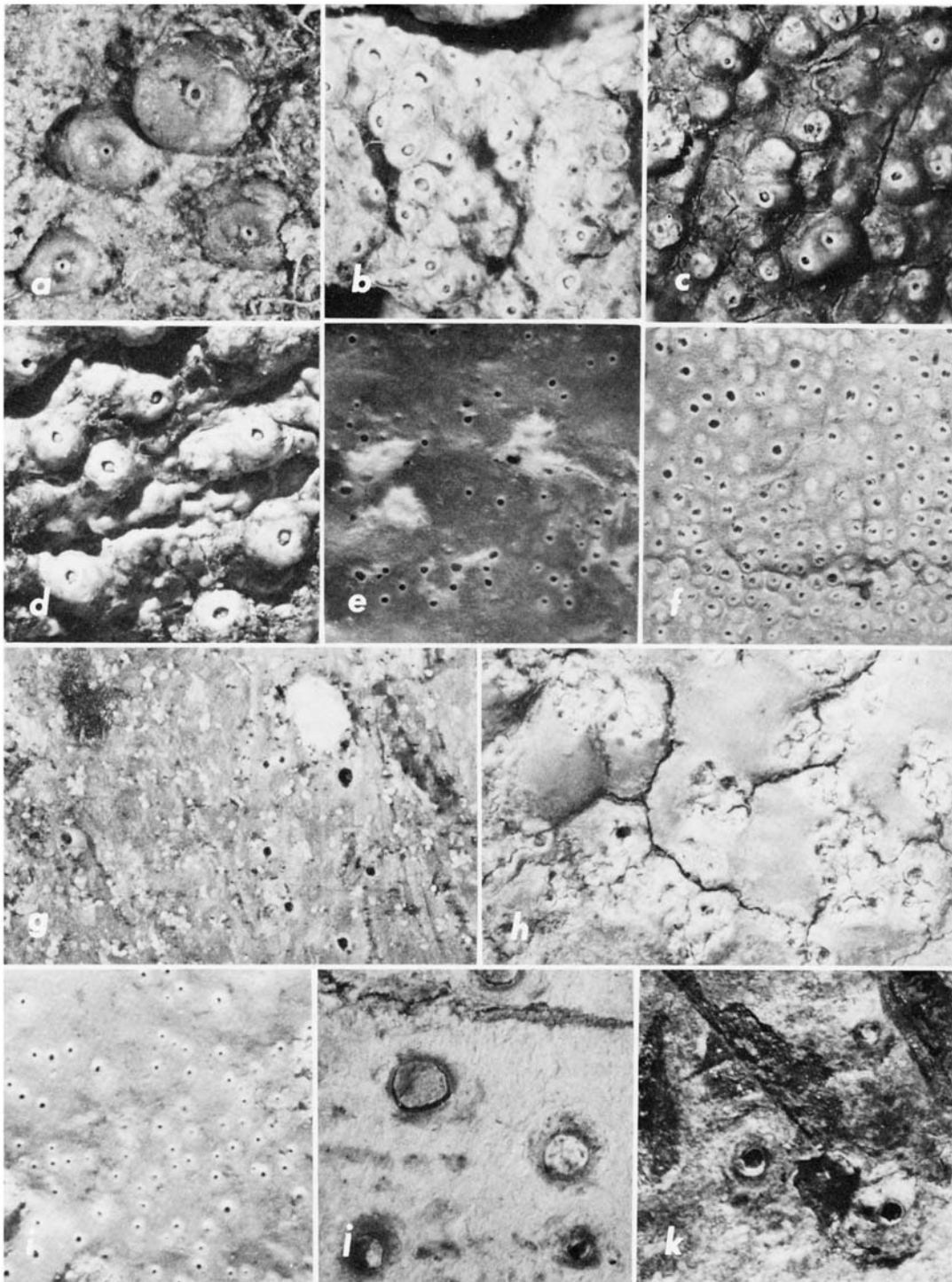


FIGURE 13.—Specimens of Thelotremataceae (all about $\times 10$): *a*, *Ocellularia rhodostroma* (lectotype in P); *b*, *O. subcavata* (lectotype in H); *c*, *O. vaga* (isotype in FH); *d*, *O. subcavata* (*Hale* 37769); *e*, *O. terebratula* (lectotype in H); *f*, *O. remanens* (isotype in G); *g*, *O. sorediata*, new species (*Hale* 37908); *h*, *Phaeotrema aggregatum*, new species (*Hale* 35229); *i*, *O. terebratula* (*Hale* 37793); *j*, *P. disciforme*, new combination (lectotype in BM); *k*, *P. aquilinum* (lectotype in TUR).

broad; apothecia large and easily visible with the naked eye, ascidioid, 1.0–1.8 mm in diameter, the walls heavily carbonized and the medulla deep pink, readily exposed as the fragile cortex breaks away, columella lacking; pore round and small, 0.05–0.1 mm in diameter, surrounded by a raised ring; hymenium 200 μ –275 μ high; spores 1–2/ascus, 25–30 loculate, 25 μ –40 μ \times 100 μ –250 μ , I+ blue (Figures 5g and 7b).

CHEMISTRY.—Hypoprotocetraric acid and in greater concentration 4–0–demethylnotatic acid along with unidentified pigments.

HABITAT.—Canopy branches to lower bole at all elevations on the island.

Ocellularia rhodostroma is the commonest thelotrema on Dominica and the easiest to identify as well. The large ascidioid apothecia have a deep pink medulla exposed when the fragile cortex breaks. The pore is strongly annulate. While occurring at all elevations, it seems best developed at higher elevation into the mossy forest, perhaps because it competes with so few other species there.

SPECIMENS EXAMINED.—7 (35246), 8 (38122, 38146, 38166), 10 (38119), 11 (37815, 37823, 37824, 38004, 38023, 38049), 12 (37894, 37916, 37917, 37927, 37930, 37934), 13 (35279 35448), 14 (35111, 35133), 15 (35160, 35170, 35188, 35314, 16a (37653, 37938), 16b (37800, 37806, 37875, 37994, 37995), 16c (37756, 37870, 37979), 18a (37729, 37731, 37987), 18b (35517, 35522, 35523, 35587), 20a (37777, 38065), 21 (38035, 38147), 22 (37641, 37643, 37650, 37835, 37861), 23 (37672, 38975), 24a (37736, 37742, 37745, 37749, 37754, 38068), 24b (35629), 25a (37705, 37707, 37720, 37840, 37846, 37848, 37862, 37867, 37971, 37975), 25b (35469), 26a (37689, 37690, 37693, 37694, 37699, 37703, 37864, 37866, 37885, 37947 38000, 38014), 26b (35354, 35366, 35371, 35372, 35376), 27 (37831), 28 (35435, 35440).

19. *Ocellularia rimosa* Hale, new species

FIGURE 12b

Thallus corticola, brunneo- vel viridi-cinereus, epiphloeodes, nitidus, continuus sed aetate rimosus, usque ad 15 cm latus; apothecia numerosa, emergentia, 0.7–0.9 mm diametro, apice obfusca, columella nulla; ostiolum rotundum vel irregulare,

0.1–0.2 mm diametro, nigrocinctum; hymenium 110 μ –150 μ altum; sporae 8:nae, transversim 6–8 loculatae, 7 μ –10 μ \times 24 μ –32 μ , I+ coerulescentes (Figure 12b).

CHEMISTRY.—No substances present.

HOLOTYPE.—Base of tree in primary rain forest, Dleau Gommier Forest Reserve, Dominica, elevation 370 m, *Hale* 37978, 1 December 1971 (U.S.).

HABITAT.—Prop roots, tree bases, and lianas in rain forest (370–430 m).

Except for chemistry and slightly larger apothecia, this species is very close to *O. nigropuncta*, new species. Both are base level species, but *O. rimosa* has a more restricted elevational range. The two species were collected together only at Dleau Gommier.

SPECIMENS EXAMINED.—11 (38052), 16a (37654), 16b (37392, 37803), 16c (37758).

20. *Ocellularia sorediata* Hale, new species

FIGURE 13g

Thallus corticola, viridi-albidus, epiphloeodes, continuus, planus, nitidus, usque ad 15 cm latus, sorediatus, soraliis sparsis, verrucosis, circa 1 mm latis; apothecia immersa vel semi-emergentia, 0.4–0.6 mm diametro, apice fuliginea, columellata; ostiolum, rotundum, 0.08–0.11 mm diametro; hymenium 60 μ –70 μ altum; sporae 8:nae, transversim 3–4 loculatae, 6 μ –8 μ \times 12 μ –16 μ , I+ coerulescentes (Figure 13g).

CHEMISTRY.—No substances present.

HOLOTYPE.—Logging area about 3 km northwest of Pont Cassé on the Layout Road, Dominica, elevation 420 m, *Hale* 37908, 10 December 1971 (US).

HABITAT.—Mid-bole of tree in rain forest.

This is, as far as I know, the only sorediate species in the family. Large corticate tubercules are produced first, and some of these become coarsely sorediate. Although these peculiar structures seem to originate from the main thallus, there is still the possibility that they have an extraneous origin.

SPECIMEN EXAMINED.—16b (38029).

21. *Ocellularia subcavata*

FIGURE 13b,d

Ocellularia subcavata (Nylander) Zahlbruckner, 1923:601.

Thelotrema subcavatum Nylander, 1876:561 [type-collection: Cuba, Wright 509 (H, lectotype; FH-Tuck, isotype); Figure 13b].

Thelotrema vagum Vainio, 1896:209 [type-collection: Richmond Peak, St. Vincent, Elliott 260 (BM, lectotype, FH, isotype); Figure 13c].

Ocellularia vaga (Vainio) Zahlbruckner, 1923:603.

Thallus ashy whitish to greenish gray, shiny, more or less warty and cracked, forming colonies up to 12 cm broad; apothecia very numerous, emergent to ascidioid, 0.7–1.0 mm in diameter, crowded, walls carbonized, columella present, basally carbonized but usually colorless in the upper half; pore round, small, 0.1–0.2 mm in diameter, surrounded by a whitish, more or less raised ring, the center filled with the often protruding pruinose columella; hymenium about 100 μ high; spores 8/ascus, usually uniseriate, 5–6 loculate with narrow locules, 4 μ –7 μ \times 8 μ –20 μ , very rarely turning brown with age, I+ blue (Figure 13d).

CHEMISTRY.—Psoromic and consporomic acids.

HABITAT.—Canopy branches and upper bole in rain forest (240–800 m).

This is one of the commonest thelotremes in the canopy and can be recognized in the field with a hand lens because of the numerous crowded apothecia with a white annulate pore and protruding columella. The columella is well developed in cross-section but unique in being more or less noncarbonized in the upper half.

SPECIMENS EXAMINED.—7 (35248, 35252), 9 (38161), 10 (38129), 12 (37893, 37896, 37898, 37900, 37905, 37912, 37924, 37925, 37926, 37928, 37929, 37933), 13 (35294), 15 (35158, 35209), 16a (37652, 37795, 38012), 16b (37662, 37794, 37865), 16c (37767, 37769, 37772, 37773, 37924, 37941, 37972), 18a (37724, 37889, 37949, 38038), 23 (37680), 24a (37737, 37744, 37750), 26a (37691, 37704).

22. *Ocellularia terebratula*

FIGURE 13e,i

Ocellularia terebratula (Nylander) Müller-Argau, 1887:12.

Thelotrema terebratulum Nylander, 1867:315 [type-collection: Rio Negro, Colombia, Lindig 129 (H, lectotype; FH, G, M, P, isotypes); Figure 13e].

Thelotrema clandestinum f. *remanens* Nylander, 1867:317 [type-collection: Monte del Morro, Colombia, Lindig 90 (H, lectotype; BM, G, P, isotypes); Figure 13f].

Ocellularia remanens (Nylander) Müller-Argau, 1887:7.

Thallus light greenish to ashy white, thick and continuous, smooth, shiny, often forming extensive colonies up to 15 cm broad; apothecia numerous, 0.2–0.4 mm in diameter, immersed, noncarbonized and without a columella; pore flush, 0.05–0.1 mm in diameter, usually surrounded by a faint whitish ring; hymenium about 65 μ high; spores 8/ascus, 3–5 loculate, 5 μ –9 μ \times 15 μ –20 μ , I+ blue (Figure 13i).

CHEMISTRY.—Psoromic and consporomic acids.

HABITAT.—Canopy branches and upper bole in rain forest (300–400 m).

Ocellularia terebratula, previously known only from Colombia, is a typical canopy level species. It is very similar to *Thelotrema clandestinum*, as explained below, except for spore characters.

SPECIMENS EXAMINED.—8 (38125), 10 (38126), 12 (37904, 37918), 16a (37668, 37878, 37937, 38011, 38040), 16b (37793).

Phaeotrema

This genus is very similar to *Ocellularia* in spore septation but the spores are brown and sometimes shriveled at maturity, especially in large-spored species. The iodine reaction often seems to be negative, while almost all species of *Ocellularia* are strongly I+ blue. On the world level, *Phaeo-*

Key to the Species of *Phaeotrema*

- | | |
|---|--|
| 1. Apothecia aggregated | 23. <i>P. aggregatum</i> , new species |
| 1. Apothecia solitary. | |
| 2. Apothecia large, about 0.6 mm in diameter, strongly emergent; columella lacking | 24. <i>P. disciforme</i> , new combination |
| 2. Apothecia smaller, less than 0.5 mm in diameter, immersed; columella more or less developed. | |
| 3. Pore 0.1–0.2 mm in diameter, sometimes elongate, with a white annulus | 25. <i>P. leiostomum</i> |
| 3. Pore 0.5–0.1 mm in diameter, round, annulus lacking | 26. <i>P. obscurum</i> , new species |

trema is represented by about 40 species, a rather small group, moreover because few of the species are well represented by herbarium material. In Dominica only six collections (four species) were found, these all occurring below 350 m elevation.

23. *Phaeotrema aggregatum* Hale, new species

FIGURE 13h

Thallus corticola, pallide viridi-cinereus, epiphloeodes, planus, aetate rimosus, 8 cm latus; apothecia irregulariter aggregata, 0.4–0.6 mm diametro, immersa, intus incolores, columella nulla, excipulo interiore bene evoluto; ostiolum 0.1–0.2 mm latum, in centro excipulo interiore congesto, albido-pruinoso; hymenium 110 μ –120 μ altum; sporae 8:nae, transversim 4–5 loculatae, 8 μ \times 16 μ (Figure 13h).

CHEMISTRY.—No substances present.

HOLOTYPE.—Logging area at Newfoundland, Dominica, elevation 250 m, *Hale* 35229, January 1969 (US).

HABITAT.—Upper branches of tree in rain forest.

This unusual species has densely aggregated, immersed apothecia. The pore is usually distinct but may be obscured by the pulverulent exciple and margin, giving the appearance of a *Phlyctis*.

24. *Phaeotrema disciforme* (Leighton) Hale, new combination

FIGURES 7c, 13j, 14a

Thelotrema disciforme Leighton, 1869:170 [type-collection: Central Province, Ceylon, *Thwaites* (BM, lectotype; H, isotype); Figure 13j].

Thelotrema exalbidum Stirton, 1881:184 [type-collection: Assam, *Watt* s.n. (BM, lectotype)].

Thelotrema aquilinum Vainio, 1915:137 [type-collection: St. Croix, *Boergesen* s.n. (TUR, lectotype; C, isotype)].

Leptotrema exalbidum (Stirton) Zahlbruckner, 1923:634.

Thelotrema galactinum Vainio, 1926:24 [type-collection: Maloapan, Mexico, *Liebmann* 7712 (C, lectotype); Figure 13k].

Phaeotrema galactinum (Vainio) Zahlbruckner, 1932:245.

Thallus whitish, dull, very thin and evanescent to hypophloeodal, forming colonies 2–4 cm broad; apothecia large, emergent, 0.7–1.1 mm in diameter, upper walls becoming suberect, carbonized, columella lacking, the inner exciple weakly developed and pulling away from the main margin, the

white-pruinose disc clearly visible; pore open, round, 0.2–0.5 mm in diameter, the rim usually darkened; hymenium 120 μ –140 μ high; spores apparently 4/ascus, 20–24 loculate, 7 μ –12 μ \times 40 μ –55 μ , colorless when immature but mostly turning brown and shriveled at maturity, I— (Figure 14a).

CHEMISTRY.—No substances present.

HABITAT.—Lower trunk area (sea level to 370 m).

A thorough examination of the lectotype showed that the spores are transversely septate without any longitudinal septae. Old shriveled spores, however, give the false impression of being muriform. It is a widespread pantropical species characterized by the large emergent apothecia without periderm inclusions, wide pore, pruinose rim and disc, and lack of a columella.

SPECIMENS EXAMINED.—4 (*Wirth* s.n.), 16b (37939).

25. *Phaeotrema leiostomum*

FIGURES 5h, 6d, 14b,c

Phaeotrema leiostomum (Tuckerman) Zahlbruckner, 1923: 608.

Thelotrema leiostomum Tuckerman, 1862:407 [type-collection: Cuba, *Wright* 149 (FH, lectotype); Figure 14b].

Thallus ashy to pale greenish white, epiphloeodal, continuous, smooth and shiny, forming colonies 2–5 cm broad; apothecia immersed to slightly emergent, 0.3–0.6 mm in diameter, weakly carbonized, columella absent to well developed, noncarbonized (Figure 6d); pore round to irregularly elongate, surrounded by a raised ring, 0.1–0.3 mm long; hymenium 130 μ –150 μ high; spores 8/ascus, brown, 4 loculate, 8 μ –10 μ \times 16 μ –18 μ , I— (Figures 5h, 14c).

CHEMISTRY.—Hypoprotocetraric acid with or without 4–0–demethylnotatic acid along with pale unidentified pigments.

HABITAT.—Canopy and mid-bole branches in rain forest (350–500 m).

A raised annulate pore is characteristic of this species. Elongation of the apothecia was best developed in collection 37956. The extreme form can be seen in *Phaeotrema lirelliforme* (Tuckerman) Zahlbruckner, which lacks any lichen substances. When apothecia are lacking, the thallus of *Phaeotrema leiostomum* alone would not permit identification.

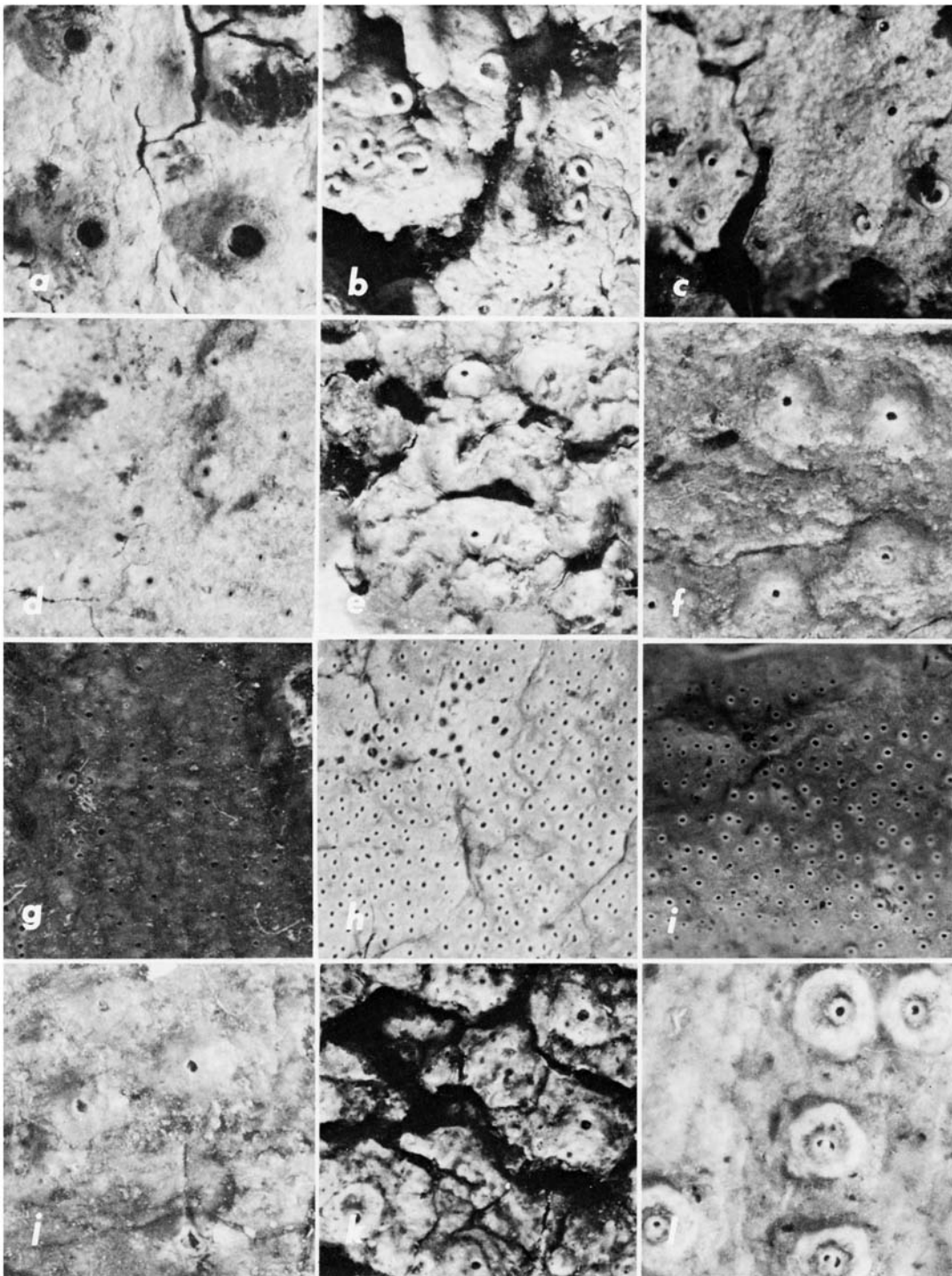


FIGURE 14.—Specimens of Thelotremaaceae (all about $\times 10$): a, *Phaeotrema disciforme*, new combination (Hale 37929); b, *P. leiostomum* (lectotype in FH); c, *P. leiostomum* (Hale 35203); d, *P. obscurum*, new species (Hale 38091); e, *Thelotrema carassense* (isotype in FH); f, *T. carassense* (Hale 37873); g, *T. clandestinum* (lectotype in G); h, *T. subcaesium* (lectotype in H); i, *T. clandestinum* (Hale 35136); j, *T. conforme* (lectotype in G); k, *T. consanguineum* (lectotype in G); l, *T. conforme* (Hale 38062).

SPECIMENS EXAMINED.—15 (35203), 16a (37956), 16b (37993).

26. *Phaeotrema obscurum* Hale, new species

FIGURE 14d

Thallus corticola, pallide brunneo-albidus, tenuis vel hypophloeodes, 5 cm latus; apothecia modice emergentia, 0.3–0.5 mm diametro, apice fuliginea, columellata; ostiolum rotundum, 0.1 mm diametro, intus albido-pruinose; hymenium circa 120µ altum; sporae 8-nae, transversim 5–6 loculatae, 10µ–14µ × 24µ–28µ (Figure 14d).

CHEMISTRY.—Stictic and constictic acids.

HOLOTYPE.—Forty centimeters up trunk of a small tree, Rosalie Road above Newfoundland, elevation 300 m, Hale 38091, 10 December 1972 (US).

HABITAT.—Tree in rain forest.

This tiny species could easily be overlooked. It is unusual to find a well-developed columella in apothecia this small. There are no other species

in the genus with similar morphology. *Phaeotrema albidulum* (Nylander) Müller-Argau also has stictic and constictic acids, but the apothecia are immersed and clustered and the spores larger (40µ).

Thelotrema

Thelotrema is a common genus in Dominica, represented by 14 species among 80 collections. On the world level there are about 130 species. Variation in spore size is as great as in *Ocellularia* but longitudinal septae are always clearly developed (except in *T. clandestinum*). The six commonest species were *T. praestans* (21 collections), *T. glaucopallens* (16), *T. clandestinum* (10), *T. interpositum* (7), *T. leucomelaenum* (7), and *T. depressum* (4).

As I noted for *Ocellularia*, *Thelotrema* avoids the dry lowlands but is widespread in the rain forest. *Thelotrema papillosum* and *T. tuberculiferum* are restricted to the mossy forest.

Key to the Species of *Thelotrema*

- 1. Central columella present.
 - 2. Thallus thin, hypophloeodal; apothecia not emergent, small, less than 0.6 mm in diameter.
 - 3. Columella narrow; spores less than 20µ long 39. *T. tenue*, new species
 - 3. Columella very broad; spores more than 30µ long 36. *T. leucomelaenum*
 - 2. Thallus distinct, epiphloeodal; apothecia emergent, 0.5–1.5 mm in diameter.
 - 4. Spores 20µ–40µ long, 4–8/ascus.
 - 5. Spores about 20µ long; pore not annulate but becoming black rimmed 35. *T. leucinum*
 - 5. Spores about 40µ long; pore becoming annulate 29. *T. conforme*
 - 4. Spores more than 100µ long, 1/ascus.
 - 6. Thallus warty-granular, P+ yellow 34. *T. interpositum*
 - 6. Thallus smooth, P– or P+ orange.
 - 7. Thallus P– 31. *T. depressum*
 - 7. Thallus P+ orange 38. *T. praestans*
- 1. Central columella lacking.
 - 8. Apothecia immersed, the pore flush with thallus surface.
 - 9. Thallus greenish, thin, and shiny 33. *T. glaucopallens*
 - 9. Thallus whitish, thick, dull 28. *T. clandestinum*
 - 8. Apothecia emergent, pores not flush with thallus surface.
 - 10. Spores less than 20µ 30. *T. confusum*, new species
 - 10. Spores more than 70µ long.
 - 11. Thallus P–; collected in mossy forest zone.
 - 12. Apothecia 1 mm tall, eroding around a large area of the pore 40. *T. tuberculiferum*
 - 12. Apothecia barely emergent, pore area not eroding 37. *T. papillosum*, new species
 - 11. Thallus P+ orange or yellow; collected in rain forest zone.
 - 13. P+ yellow; apothecia up to 1.0 mm in diameter 27. *T. carassense*
 - 13. P+ red; apothecia about 0.5 mm in diameter 32. *T. dominicanum*, new species

27. *Thelotrema carassense*

FIGURE 14e,f

Thelotrema carassense Vainio, 1890:79.

TYPE-COLLECTION.—Carassa, Brazil, *Vainio* 1523 (TUR, lectotype; BM, FH, isotypes). (Figure 14e).

Thallus greenish ashy mineral gray, epiphloeodal, continuous and shiny, forming colonies up to 15 cm broad; apothecia semi-emergent, 0.8–1.0 mm in diameter, upper wall weakly carbonized, columella lacking; pore about 0.1 mm in diameter, with a weak raised ring; hymenium 110 μ –130 μ ; spores 8/ascus, muriform, 1–2 \times 8–10 loculate, 12 μ –15 μ \times 30 μ –40 μ , I+ blue (Figure 14f).

CHEMISTRY.—Psoromic and conpsoromic acids.

HABITAT.—Mid and lower bole of trees in rain forest (370–800 m).

The Dominican material is not a perfect fit for the South American type, but it agrees in essential features, lack of columella, intermediate spores, and presence of psoromic acid. The apothecia are larger and spores smaller than in Vainio's specimen (about 70 μ long). The taxonomy of the ecolumellate psoromic acid-containing *Thelotremata* is unfortunately still incomplete. *Thelotrema postpositum* Nylander has large spores (more than 100 μ), but all other species, excluding *T. carassense*, have small spores (less than 20 μ long).

SPECIMENS EXAMINED.—16b (37859), 24b (37738), 26b (37873).

28. *Thelotrema clandestinum*

FIGURE 14g,i

Thelotrema clandestinum Fée, 1837:90.

Thelotrema subcaesium Nylander, 1869:120 [type-collection: Brazil, *Glaziou* 2193 (H, lectotype; BM, C, FH-Tuck, UPS, US, W, isotypes); Figure 14h].

Thelotrema concretum Fée var. *subcaesium* (Nylander) Redinger, 1936:96.

TYPE-COLLECTION.—On *Cinchona lancifolia* in America, without collector (G, lectotype). (Figure 14g).

Thallus whitish to greenish ashy gray, shiny, thick, and continuous, forming colonies up to 20 cm broad; apothecia numerous, immersed, 0.15–0.3 mm in diameter, noncarbonized and without a columella; pore flush, round, 0.07–0.1 mm in diameter, usually with a whitish rim; hymenium

65 μ –75 μ high; spores 8/ascus, uniseriate, 4–5 loculate, muriform with 1–2 longitudinal septae in at least one of the locules, 6 μ –10 μ \times 15 μ –20 μ , I+ blue (Figure 14i).

CHEMISTRY.—Psoromic and conpsoromic acids.

HABITAT.—Canopy branches in rain forest (500–670 m).

Thelotrema clandestinum has small spores with few longitudinal septations. It would, in fact, be classified as an *Ocellularia* unless the spores are carefully examined. Chemically similar *O. terebratula* has only transverse septae. Both species have a thick, continuous thallus and occupy the same kind of habitat. They were collected at a total of ten localities but never together in the same one.

SPECIMENS EXAMINED.—13 (35298, 35393), 14 (35103, 35105, 35136), 15 (35207), 16c (37768, 37872, 37981), 24b (35624a).

29. *Thelotrema conforme*

FIGURE 14j,l

Thelotrema conforme Fée, 1837:89.

Thelotrema consanguineum Müller-Argau, 1887b:398 [type-collection: Apiahy, Brazil, *Puiggari* 477 (G, lectotype); Figure 14k].

TYPE-COLLECTION.—On *Cinchona*, America meridionalis, without collector (G, lectotype) (Figure 14j).

Thallus whitish mineral gray, smooth and shiny, epiphloeodal, forming colonies up to 10 cm broad; apothecia emergent, 0.8–1.0 mm in diameter, apically carbonized, distinct columella present; pore round, 0.1–0.15 mm in diameter, surrounded by a whitish, sometimes raised ring; hymenium 170 μ –200 μ high; spores 4/ascus, muriform, 8–10 loculate transversely, 2–4 loculate longitudinally, 18 μ –20 μ \times 35 μ –50 μ , I+ blue (Figure 14l).

CHEMISTRY.—Psoromic and conpsoromic acids.

HABITAT.—Lower bole and trunk in open rain forest (670 m).

The Dominican material is a satisfactory match for Fée's type-specimen, which has slightly smaller apothecia and a less consistently developed annulate pore. The spores are definitely in the intermediate size range in contrast to related *T. leucinum* which has small spores.

SPECIMENS EXAMINED.—24a (37739, 38062).

30. *Thelotrema confusum* Hale, new species

FIGURES 1c, 15

Thallus corticola, cinereo- vel viridi-albidus, epiphloeodes, planus, continuus vel rimosus, nitidus, 4–8 cm latus; apothecia numerosa, emergentia, 0.8–1.0 mm diametro, apice obfusca, columella nulla; ostiolum rotundum, 0.15–0.2 mm diametro, margine nigrocinctum; hymenium 120 μ –130 μ altum; sporae 4:nae, murales, transversim 6–7 loculatae, longitudinaliter 0–2 loculatae, 6 μ –10 μ \times 12 μ –26 μ , I+ coerulescentes (Figure 15).

CHEMISTRY.—Protocetraric acid.

HOLOTYPE.—Trail to Boiling Lake, elevation 650 m, Hale 37747, 9 December 1971 (US).

HABITAT.—Canopy branches or lower bole in open areas (650–800 m).

The black-rimmed pore and fissured thallus resemble *Ocellularia nigropuncta*, but the spores are clearly muriform. This presents an interesting example of close morphological and chemical convergence with spore septation being the crucial diagnostic character. There are no related species in *Thelotrema*.

SPECIMENS EXAMINED.—16b (37807), 26a (37697).



FIGURE 15.—*Thelotrema confusum*, new species (Hale 37747) ($\times 10$).

31. *Thelotrema depressum*

FIGURE 16b,c

Thelotrema depressum Montagne, 1851:73.

TYPE-COLLECTION.—Cayenne, French Guiana,

Leprieur 701 (BM, lectotype; H, isotype) (Figure 16b).

Thallus and apothecia as in *Thelotrema praestans* (see below); spores 1–2/ascus, muriform with numerous transverse and longitudinal locules, 35 μ –50 μ \times 150 μ –300 μ , I+ blue (Figure 16c).

CHEMISTRY.—No substances present.

HABITAT.—Canopy branches of trees in the rain forest (300–500 m).

The type-material of *Thelotrema depressum* is very fragmentary but color and chromatographic tests established that no P+ compounds were present. The four specimens from Dominica are identical. They may represent only a chemical population of *T. praestans*, which is morphologically identical, as far as we can judge from available specimens, but contains a strong P+ orange-red unknown substance. *Thelotrema praestans* is more common (20 collections) and has a broader altitudinal range (250–800 m).

SPECIMENS EXAMINED.—8 (38141), 12 (37901, 37922), 15 (35150).

32. *Thelotrema dominicanum* Hale, new species

FIGURE 16a

Thallus corticola, pallide brunneo-albidus, epiphloeodes, continuus, nitidus, 4–6 cm latus; apothecia numerosa, emergentia, 0.3–0.4 mm diametro, apice obfusca, columella nulla vel parce evoluta; ostiolum rotundum, 0.05 mm diametro; hymenium 140 μ –160 μ altum; sporae 2–4:nae, murales, transversim 24–30 loculatae, longitudinaliter 2–3 loculatae, 15 μ –20 μ \times 80 μ –90 μ , I+ coerulescentes (Figure 16a).

CHEMISTRY.—“*Cinchonarum*” P+ unknown substances.

HOLOTYPE.—Tree along trail to Morne Anglais, Dominica, elevation about 800 m, Hale 35355, January 1969 (US).

HABITAT.—Tree bole in higher elevation rain forest.

The most unusual feature of this rare lichen is the presence of the “*cinchonarum*” unknown, previously thought to be restricted to the genus *Ocellularia*. Without a chemical test one might identify it with *T. carassense*, which has larger apothecia and a wider pore. Otherwise there are no comparable species in the New World.

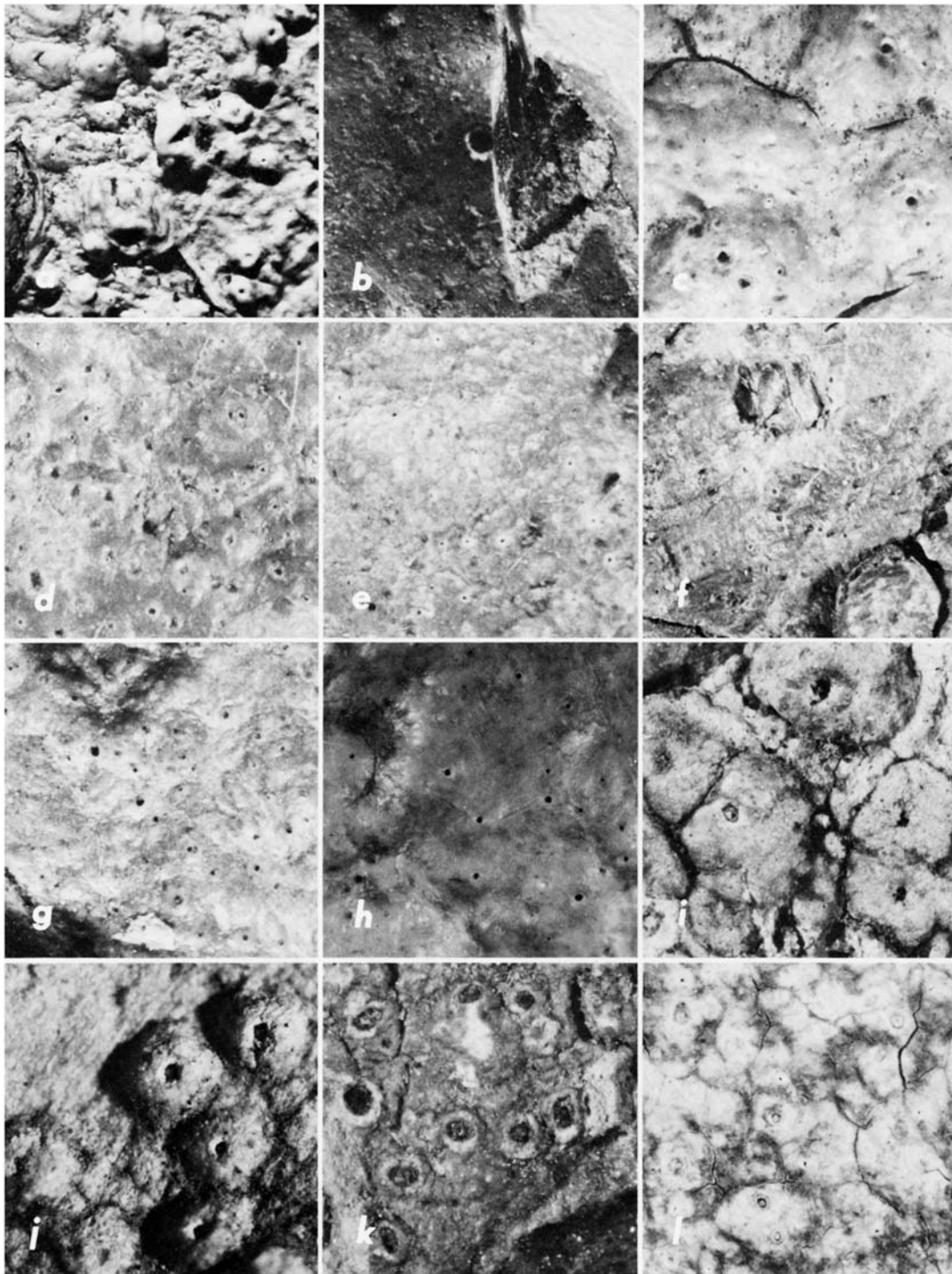


FIGURE 16.—Specimens of Thelotremataceae (all about $\times 10$): *a*, *Thelotrema dominicanum*, new species (Hale 35355); *b*, *T. depressum* (isotype in H); *c*, *T. depressum* (Hale 38141); *d*, *T. glaucopallens* (lectotype in FH-Tuck); *e*, *T. pechueli* (lectotype in G); *f*, *T. butuanum* (lectotype in W); *g*, *T. homopastoides* (lectotype in TUR); *h*, *T. glaucopallens* (Hale 35147); *i*, *T. interpositum* (isotype in L); *j*, *T. interpositum* (Hale 35388); *k*, *T. leucinum* (lectotype in G); *l*, *T. leucinum* (Hale 38100).

33. *Thelotrema glaucopallens*

FIGURE 16d,h

Thelotrema glaucopallens Nylander, 1863:327.*Pyrenula clandestina* Acharius, 1814:10 [type-collection: on *Cinchona flava*, South America (H, lectotype; S, isotype)].*Thelotrema laevigans* Nylander var. *avertens* Nylander, 1867:318 [type-collection: Tequendama, Colombia, Lindig 893 (H, lectotype; BM, FH-Tuck, G, P, W, isotypes)].*Thelotrema pechueli* Müller-Argau, 1880:34 [type-collection: Quillu River, Angola, *Pechuel-Loesche* s.n. (G, lectotype); Figure 16e].*Ocellularia clandestina* (Acharius) Müller-Argau, 1877a:7.*Thelotrema homopastoides* Vainio, 1896:207 [type-collection: Richmond Valley, St. Vincent, Elliott 327 (TUR, lectotype; BM, isotype); Figure 16g].*Thelotrema butuanum* Vainio, 1921:183 [type-collection: Luzon, Philippines, Fenix, BS-28347 (W, lectotype); Figure 16f].

TYPE-COLLECTION.—Cuba, Wright (FH-Tuck, lectotype, as 28; L, UPS, isotypes) (Figure 16d).

Thallus light greenish gray, very thin and shiny, breaking away in thin sheets, forming extensive colonies up to 15 cm broad; apothecia numerous to rather rare, immersed to slightly emergent, 0.2–0.4 mm in diameter, uncarbonized or slightly carbonized apically, without a columella; pore flush to barely raised, round, rarely angular, 0.05–0.12 mm in diameter; hymenium 60 μ –80 μ high; spores 8/ascus, muriform, 6–8 loculate transversely, 2–3 loculate longitudinally, 7 μ –10 μ \times 15 μ –24 μ , I– (Figure 16h).

CHEMISTRY.—Stictic and constictic acids.

HABITAT.—Buttresses, base of large trees, exposed roots, lianas, rarely upper bole and canopy in the rain forest (450–800 m).

The thallus of this pantropical species is unique. It is extremely thin and shiny and tends to break away in thin waxy sheets when bruised or cut. The color is a pyrenocarplike dark yellowish green. Apothecia are usually quite numerous with flush pores having considerable variation in development of a rim, from no distinct annulus to an obviously raised area. Some anomalous specimens may even have semi-emergent apothecia, but the small I– spores and the presence of stictic acid will positively identify them.

SPECIMENS EXAMINED.—10 (38082), 11 (37999, 38008, 38047), 15 (35147), 16a (37670, 37876, 38043, 38044), 20a (37783), 21 (38083, 38095, 38155, 38156), 23 (37678), 26b (35367), 27 (37891), 28 (35431).

34. *Thelotrema interpositum*

FIGURE 16i,j

Thelotrema interpositum (Nylander) Müller-Argau, 1881:526. *Ascidium interpositum* Nylander, 1863:336 [type-collection: Cuba, Wright 28 (H, lectotype; BM, FH, L, M, P, UPS, isotypes); Figure 16i].Thallus light brownish ashy gray, epiphloeodal, smooth to minutely warty, forming colonies 5–8 cm broad; apothecia strongly emergent, 0.8–1.1 mm in diameter, walls heavily carbonized, columella present; pore round, 0.15–0.2 mm in diameter, opening into a tubelike area leading to the pruinose top of the columella; hymenium 200 μ high; spores 2/ascus, muriform with numerous transverse and longitudinal locules, 28 μ –40 μ \times 85 μ –125 μ , I+ blue (Figure 16j).

CHEMISTRY.—Psoromic acid.

HABITAT.—Canopy branches and upper bole area (sea level to 670 m).

The coarsely verrucose thallus and large emergent apothecia with large spores distinguish this species. Two other columnellate psoromic acid-containing species, *T. conforme* and *T. leucinum*, have a smooth thallus and much smaller spores.

SPECIMENS EXAMINED.—5 (35388), 7 (35231), 15 (35148, 35174), 16a (37656, 37657), 16c (37760), 22 (37853, 37976).

35. *Thelotrema leucinum*

FIGURE 16k,l

Thelotrema leucinum Müller-Argau, 1887a:10.TYPE-COLLECTION.—On *Cinchona*, South America (G, lectotype) (Figure 16k).Thallus light ashy gray, epiphloeodal, continuous to cracked with age, shiny, forming a colony about 10 cm wide; apothecia numerous, nearly immersed to semi-emergent, 0.4–0.6 mm in diameter, upper wall carbonized, columella present, 0.2 mm wide; pore round, 0.05–0.12 mm in diameter; hymenium 110 μ –120 μ high; spores 8/ascus, muriform with 4 locules transversely, 2 locules longitudinally, 7 μ –11 μ \times 12 μ –18 μ , I+ blue (Figure 16l).

CHEMISTRY.—Psoromic and conpsoromic acids.

HABITAT.—Canopy branches in rain forest (300 m).

The type of *T. leucinum*, one of Fée's *Cinchona*

bark specimens, is in very poor condition and it is unfortunate that Müller selected it. Identification with the Dominica material is at best provisional, depending largely on the wide columella, small spores, and presence of psoromic acid. A better understanding of the species will come when more specimens are available.

SPECIMEN EXAMINED.—9 (38100).

36. *Thelotrema leucomelaenum*

FIGURES 4a,b; 6e; 17a,d

Thelotrema leucomelaenum Nylander, 1863:329.

Thelotrema pauperius Nylander, 1867:318 [type-collection: Rio Negro, Colombia, Lindig (H, lectotype; BM, M, isotypes); Figure 17b].

Thelotrema leucomelaenum var. *elevatum* Vainio, 1915:137 [type-collection: Morne Anglais, Dominica, Elliott 1534 (TUR, lectotype); Figure 17c].

TYPE-COLLECTION.—Fusagasuga, Colombia, Lindig 2777 (H, lectotype; BM, FH, G, M, P, UPS, isotypes) (Figure 17a).

Thallus white, thin and in part hypophloeodal (Figure 4a,b), forming colonies up to 8 cm broad; apothecia immersed to semi-emergent, 0.6–0.9 mm in diameter, apically carbonized with a broad columella 0.2–0.3 mm wide; pore round to subirregular, 0.2–0.3 mm across, opening to the pruinose columella top (Figure 6e); hymenium 130 μ high; spores 8/ascus, muriform, 4–6 loculate transversely, 2–3 loculate longitudinally, 12 μ –15 μ \times 30 μ –36 μ , I– (Figure 17d).

CHEMISTRY.—No substances present.

HABITAT.—Smaller branches of trees in mossy forest (800–900 m).

A pantropical species, *T. leucomelaenum* has been correctly identified by most lichenologists. The apothecia, while at most semi-emergent, stand out because of the black pore rim. The broad columella occupies most of the interior of the apothecia.

SPECIMENS EXAMINED.—25a (37706, 37710, 37717, 37718, 37871), 25b (35491), 26a (38076).

37. *Thelotrema papillosum* Hale, new species

FIGURE 17j

Thallus corticola, cinereo-viridis, epiphloeodes, minute papillosus, nitidus, 6 cm latus; apothecia vix emergentia, 0.7–0.9 mm diametro, intus in-

colores, columella nulla; ostiolum rotundum vel irregulariter laceratum, 0.1–0.3 mm diametro; hymenium circa 200 μ altum; sporae 1–2:nae, murales, loculis numerosis, 36 μ –40 μ \times 140 μ –150 μ , I– (Figure 17j).

CHEMISTRY.—No substances present.

HOLOTYPE.—Rain forest above Newfoundland, Dominica, elevation about 300 m, Hale 38124, 7 May 1972 (US).

HABITAT.—Canopy branch in rain forest.

This species would be easy to miss in the field. The small greenish warty thallus is not like any *Thelotrema*. The large noncarbonized apothecia are not numerous and seem lost among the thallus irregularities. The closest relative in terms of apothecial structure is *Thelotrema tuberculiferum*, which has large spores but strongly emergent eroding apothecia.

38. *Thelotrema praestans*

FIGURE 17e,g

Thelotrema praestans Müller-Argau, 1895:453.

Thelotrema elliotii Vainio, 1896:207 [type-collection: Richmond Valley, St. Vincent, Elliott 246 pro parte (BM, lectotype); Figure 17f].

TYPE-COLLECTION.—Rio de Janeiro, Brazil, Portella s.n. (G, lectotype; BM isotype) (Figure 17e).

Thallus light greenish to whitish gray, smooth and continuous, epiphloeodal, forming colonies 5–10 cm broad; apothecia semi-emergent to strongly emergent, up to 2 mm in diameter, heavily carbonized with a thick columella; pore 0.15–0.3 mm in diameter, opening through a deep tube into the ascocarp; hymenium about 200 μ high; spores 1–2/ascus, muriform with many transverse and longitudinal locules, 30 μ –45 μ \times 100 μ –275 μ , I+ blue (Figure 17g).

CHEMISTRY.—“*Praestans*” unknown.

HABITAT.—Canopy branches, less commonly bole, liana, or base in rain forest (250–800 m).

This conspicuous thelotreme is related to *T. depressum* but differs in producing a P+ orange-red unknown substance just below psoromic acid in both hexane and benzene solvents. The apothecia are large and heavily carbonized. The fine structure of the cortex is aculeate, as in *T. depressum*.

SPECIMENS EXAMINED.—7 (35237, 35244, 35254, 35273), 8 (38087, 38121, 38159), 9 (38135), 11

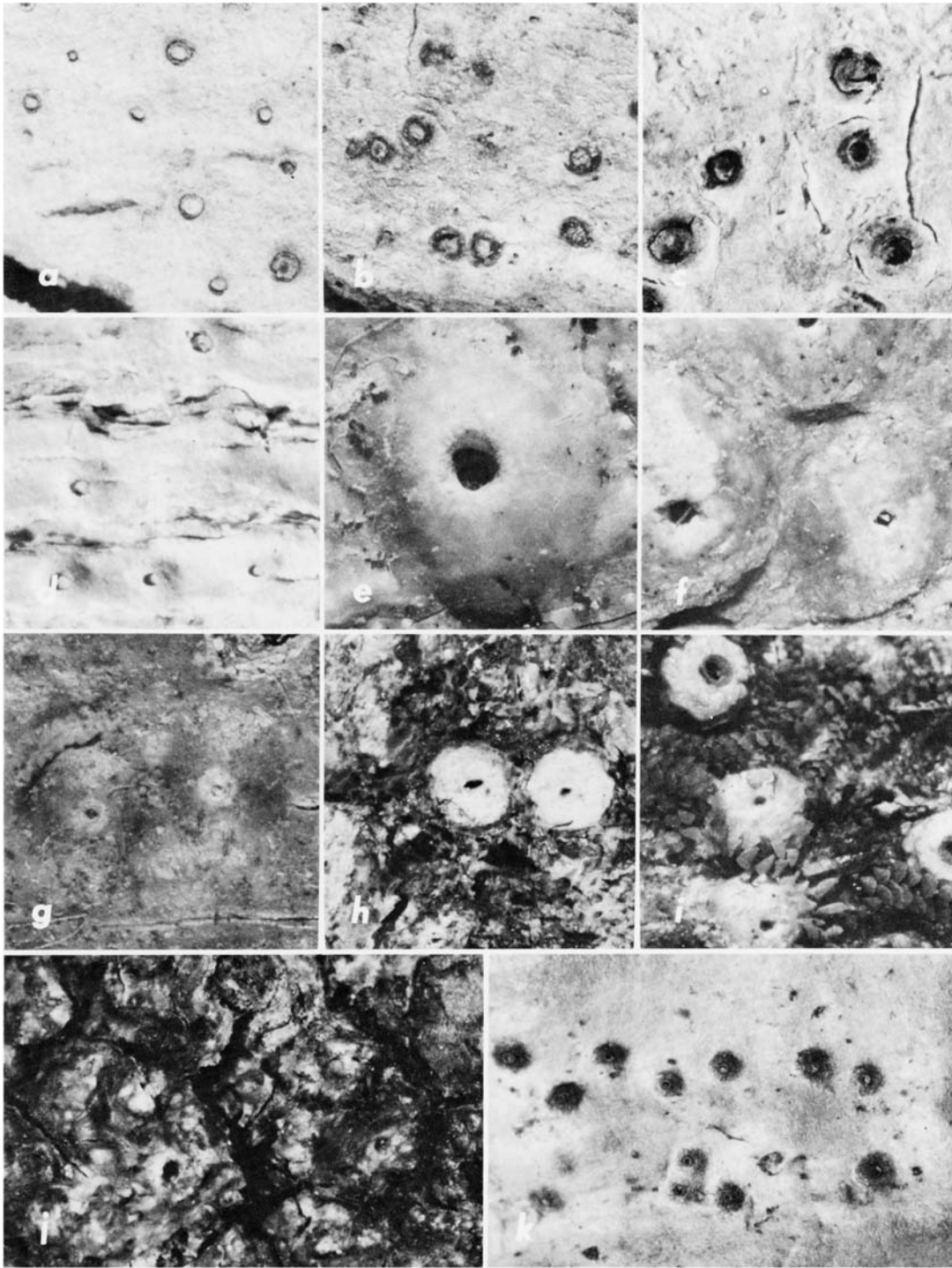


FIGURE 17.—Specimens of Thelotremaaceae (all about $\times 10$): a, *Thelotrema leucomelaenum* (lectotype in H); b, *T. pauperius* (lectotype in H); c, *T. leucomelaenum* var. *elevatum* (lectotype in TUR); d, *T. leucomelaenum* (Hale 35491); e, *T. praestans* (lectotype in G); f, *T. elliotii* (lectotype in BM); g, *T. praestans* (Hale 35273); h, *T. tuberculiferum* (lectotype in TUR); i, *T. tuberculiferum* (Hale 37719); j, *T. papillosum*, new species (Hale 38124); k, *T. tenue*, new species (Hale 35430).

(37821, 37998, 38002, 38048), 12 (37907, 37911), 15 (35171), 18a (37734, 37968), 18b (35521), 20a (37776), 26a (38070).

39. *Thelotrema tenue* Hale, new species

FIGURES 4c,d; 6f; 17k

Thallus corticola, cinereo-albus, hypophloeodes (Figure 4c,d), nitidus, 7 cm latus; apothecia numerosa, immersa vel parce emergentia, 0.3–0.4 mm diametro, apice obfusca, columellata (Figure 6f); ostiolum rotundum, 0.05–0.1 mm diametro; hymenium 90 μ –100 μ altum; sporae 8:nae, murales, transversim 4–5 loculatae, longitudinaliter 1–2 loculatae, 6 μ –7 μ \times 17 μ –19 μ , I– (Figure 17k).

CHEMISTRY.—No substances present.

HOLOTYPE.—Mossy forest zone on trail to Morne Diablotin, Dominica, elevation about 1100 m, Hale 35430, January 1969 (US).

HABITAT.—Lower trunk in rain forest to mossy forest.

Superficially this species resembles *Ocellularia pyrenuloides* in having small blackish apothecia and a thin columella. *Thelotrema leucomelaenum*, another hypophloeodal mossy forest species, has larger spores and a very broad columella. Other than these there are no related species.

40. *Thelotrema tuberculiferum*

FIGURE 17h,i

Thelotrema tuberculiferum Vainio, 1915:136.

TYPE-COLLECTION.—Savane-aux-Ananas, Guadeloupe, Duss 1497 (TUR, lectotype) (Figure 17h).

Thallus ashy whitish, thin and in part evanescent, scattered, forming colonies 4–8 cm broad; apothecia strongly ascidioid, about 1.0 mm in diameter and 1.0 mm high, noncarbonized and lacking a columella, cortex eroding away toward the apex leaving a pulverulent area; pore round, 0.1–0.2 mm in diameter, surrounded by a gray, sometimes raised ring and the broader pulverulent area; hymenium 140 μ –160 μ high; spores 1–2/ascus, muriform with numerous transverse and longitudinal locules, 30 μ –50 μ \times 60 μ –120 μ , I+ pale blue (Figure 17i).

CHEMISTRY.—No substances present.

HABITAT.—Exposed moss-covered branches in mossy forest (800–900 m).

This *Thelotrema* might be mistaken at first for a *Pertusaria*. It was first described from Guadeloupe and is probably endemic to the Lesser Antilles, occurring at high elevations in the upper limit of the mossy forest.

SPECIMENS EXAMINED.—25a (37719), 26a (37868).

Leptotrema

This genus differs from *Thelotrema* in having brown spores which tend to shrivel at maturity regardless of size and appear to be I–. Eight species occur on Dominica among my 36 collections (in-

Key to the Species of *Leptotrema*

1. Columella present, simple to actinoid 43. *L. fissum*
1. Columella lacking.
 2. Pore wide, 0.5–0.8 mm in diameter, the exposed disc dark brown to black 46. *L. spondaicum*
 2. Apothecia immersed to emergent with pores 0.1–0.2 mm in diameter.
 3. Thallus thick with a columnar cortex; red crystalline inclusions often present 48. *L. wightii*
 3. Thallus thin with a normal cortex lacking pigments.
 4. Apothecia with an inner lepadinoid exciple.
 5. Spores about 20 μ long 45. *L. occultum*
 5. Spores about 45 μ long 47. *L. subcompunctum*
 4. Apothecia lacking a lepadinoid exciple.
 6. Pore distinct, 0.1–0.2 mm in diameter; spores 20 μ –30 μ long 41. *L. bahianum*
 6. Pore very tiny, less than 0.1 mm in diameter; spores large, more than 40 μ long.
 7. Pore depressed in a darker area 42. *L. deceptum*, new species
 7. Pore not depressed, surrounding area the same color as the thallus.
 8. Apothecia immersed with flush pores 47. *L. subcompunctum*
 8. Apothecia more or less emergent 44. *L. microglauoides*

cluding the collection of *L. bahianum* by Elliott). It is rarer than would guess from this number of collections since one species, *L. deceptum*, is represented by 21 specimens. *Leptotrema spondaicum* was found 8 times, *L. wightii* 3 times, and the remainder once each. On the world level the genus has about 50 species.

Leptotrema behaves in a peculiar way on Dominica. It is virtually the only thelotreme (5 of 7 collections) in the dry scrub forest. It then essentially skips the rain forest zone and reappears in the submossy forest. Only 5 collections were made in the broad rain forest zone in contrast to 25 above 900 m.

41. *Leptotrema bahianum*

FIGURE 5f

Leptotrema bahianum (Acharius) Müller-Argau, 1887a:12.
Thelotrema lepadinum var. *bahianum* Acharius, 1803:132
 [type-collection: Bahia, Brazil, without collector (H, lectotype; L, UPS, isotypes)].—Hale, 1972:193, fig. 2c.
Thelotrema rudius Vainio var. *dominicanum* Vainio, 1915: 136 [type-collection: Prince Rupert, Dominica, Elliott 1303 (TUR, lectotype); Figure 5f].

Thallus corticolous, epiphloeodal, light tannish white, about 4 cm broad; apothecia numerous, emergent, 0.4–0.6 mm in diameter, noncarbonized and without a columella; pore round, about 0.1 mm in diameter; hymenium 150 μ high; spores 8/ascus, muriform with 5–6 transverse locules and 2–3 longitudinal locules, 12 μ –14 μ \times 16 μ –24 μ , I– (Figure 5f).

CHEMISTRY.—Protocetraric acid.

HABITAT.—Tree branch in dry scrub forest near sea level.

This well-known Acharian species (Hale, 1972) seems to be very rare on Dominica since it has not been found since Elliott's time. It is generally a lowland species in drier areas of the tropics.

42. *Leptotrema deceptum* Hale, new species

FIGURES 7d, 18

Thallus corticola, brunneo-cinereus, epiphloeodes, planus, nitidus, continuus vel rimosus, usque ad 12 cm latus; apothecia immersa, 0.3–0.4 mm diametro, intus incolores, columella nulla; ostiolum minutum, 0.02–0.05 mm diametro, depressum,

ambitu obfuscans; hymenium 100 μ –120 μ altum; sporae obfuscae, 4:nae, murales, loculis numerosis, 14 μ –28 μ \times 40 μ –70 μ , I– vel I+ pallide coerulescentes (Figure 18).

CHEMISTRY.—Stictic and constictic acids.

HOLOTYPE.—*Sloanea* buttress, disturbed primary forest at Middleham Estate, elevation about 670 m, Hale 37860, December 1971 (US).

HABITAT.—Buttresses and exposed roots, saplings, lianas, lower bole in higher elevation rain forest (about 670 m).

This species belongs to a large group of difficult species characterized by a very tiny pore and presence of stictic and constictic acids, including in Dominica *L. microglanoides* and *L. subcompunctum*. It is separated from related species by the smooth, usually fissured thallus and a distinct darker depressed area surrounding the pore, this area in turn surrounded by a whitish ring. Spent apothecia remain as large, open corticate pits.

At first I had considered this (and similar species) as having closer relationships to the Pyrenulaceae. Mr. Richard Harris, a student of the Pyrenulaceae, gave the following opinion in support of placing *L. deceptum* in the Thelotremataceae:

Most pyrenocarpous lichens have some sort of carbonized "wall" surrounding the hymenium [*L. deceptum* is noncarbonized]. The spores react with IKI; a few pyrenocarps have this reaction also but have entirely different paraphyses. The paraphyses [of *L. deceptum*] are unlike those in the pyreno-

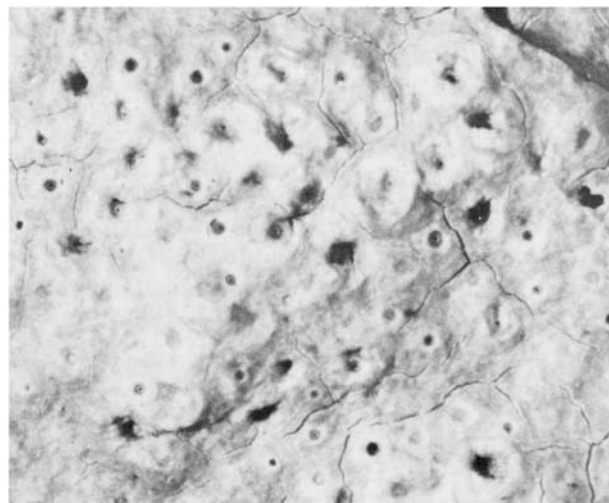


FIGURE 18.—*Leptotrema deceptum*, new species (Hale 37860) ($\times 10$)

carpous lichens in the relative lack of branching and especially in the very thick, coherent gelatinous wall or sheath around them (also found in the Graphidaceae). The asci are also unlike any pyrenocarpous asci. They are closest to *Porina* but lack any "chitinoid" apical ring. *Thelotrema lepadinum* has asci very like those in your specimen. Finally I have never found depsides or depsidones in any pyrenocarpous lichens.

SPECIMENS EXAMINED.—21 (37373, 38104, 38105, 38109, 38110, 38112, 38117, 38133, 38136, 38139, 38142, 38148, 38151, 38153), 22 (37640, 37648, 37836, 37839, 38037), 23 (37673).

43. *Leptotrema fissum*

FIGURE 19a,c

Leptotrema fissum (Nylander) Müller-Argau, 1882a:333.

Thelotrema fissum Nylander, 1859:258 [type-collection: Bourbon, Richard s.n. (H, lectotype; G, P, isotypes); Figure 19a].

Leptotrema integrum Müller-Argau, 1887b:399 [type-collection: Australia, Sayer (G, lectotype; S, isotype); Figure 19b].

Leptotrema fissum (Nylander) Zahlbruckner, 1923:634 [superfluous combination].

Thallus greenish ashy gray, epiphloeodal, smooth, continuous or cracked with age, forming colonies 4–6 cm broad; apothecia semi-emergent, round to irregular, 0.7–1.2 mm wide, with thick erect to coarsely recurved carbonized upper walls, columella variable, barely developed to actinoid, the disc white pruinose; pore initially round but opening at maturity, up to 1 mm broad; hymenium about 100 μ high; spores brown, muriform with 4–6 transverse locules and 0–2 longitudinal locules, 6 μ –7 μ \times 10 μ –13 μ , I– (Figure 19c).

CHEMISTRY.—Psoromic and conpsoromic acids.

HABITAT.—Canopy branches in rain forest (430 m).

The diagnostic features of this pantropical species are the open, often imperfectly actinoid disc, semi-erect lacerated margin, and presence of psoromic acid. It is close in these respects to *Ocellularia comparabilis*.

SPECIMEN EXAMINED.—11 (38031).

44. *Leptotrema microglanoides*

FIGURE 19d,e

Leptotrema microglanoides (Vainio) Zahlbruckner, 1923:637.

Thelotrema microglanoides Vainio, 1896:206 [type-collection: St. Vincent, Elliott 266 (BM, lectotype); Figure 19d].

Thallus light whitish tan, epiphloeodal, continuous and shiny, forming a colony about 6 cm broad; apothecia semi-emergent, 0.8–1.0 mm in diameter, walls not carbonized, columella lacking; pore very tiny, 0.02–0.05 mm in diameter, depressed but with a tiny darker ring at the periphery; hymenium 150 μ –170 μ ; spores brown, 4/ascus, muriform with numerous transverse and longitudinal locules, 18 μ –22 μ \times 36 μ –48 μ , I– (Figure 19e).

CHEMISTRY.—Stictic and constictic acids.

HABITAT.—Branches of tree in rain forest (430 m).

The lectotype of this species is rather fragmentary with very few well-developed apothecia. The thallus is continuous, but with a faint grainy appearance, thin and shiny. The Dominican material is close to the type-specimen, although Vainio reported spores in the range of 120 μ long. I found spores about 50 μ long in the lectotype. The large complex of stictic acid-containing species (e.g. *Leptotrema monosporum* (Nylander) Müller-Argau, *L. phaeosporum* (Nylander) Müller-Argau, and *L. reclusum* (Krempelhuber) Zahlbruckner) is still far from resolved.

SPECIMEN EXAMINED.—11 (37984).

45. *Leptotrema occultum* (Eschweiler) Hale, new combination

FIGURE 19f,g

Thelotrema occultum Eschweiler in Martius, 1833:174 [type-collection: South America (M, lectotype; G, isotype); Figure 19f].

Thallus tannish white, epiphloeodal, continuous, smooth to minutely pitted, forming colonies 3–5 cm broad; apothecia numerous, immersed, 0.2–0.3 mm in diameter, noncarbonized and without columella, inner lepadinoid exciple well developed and pulling away from the wall, lightly pruinose surface of hymenium visible; hymenium 65 μ –70 μ high; spores 4–8/ascus, brown, muriform with 5–7 transverse locules, 2–3 longitudinal locules, 9 μ –10 μ \times 18 μ –21 μ , I– (Figure 19g).

CHEMISTRY.—Norstictic acid.

HABITAT.—Trees in dry scrub forest near sea level.

Leptotrema occultum can be typified with the Martius specimen in Munich and the isotype fragment in Geneva. It is virtually indistinguishable

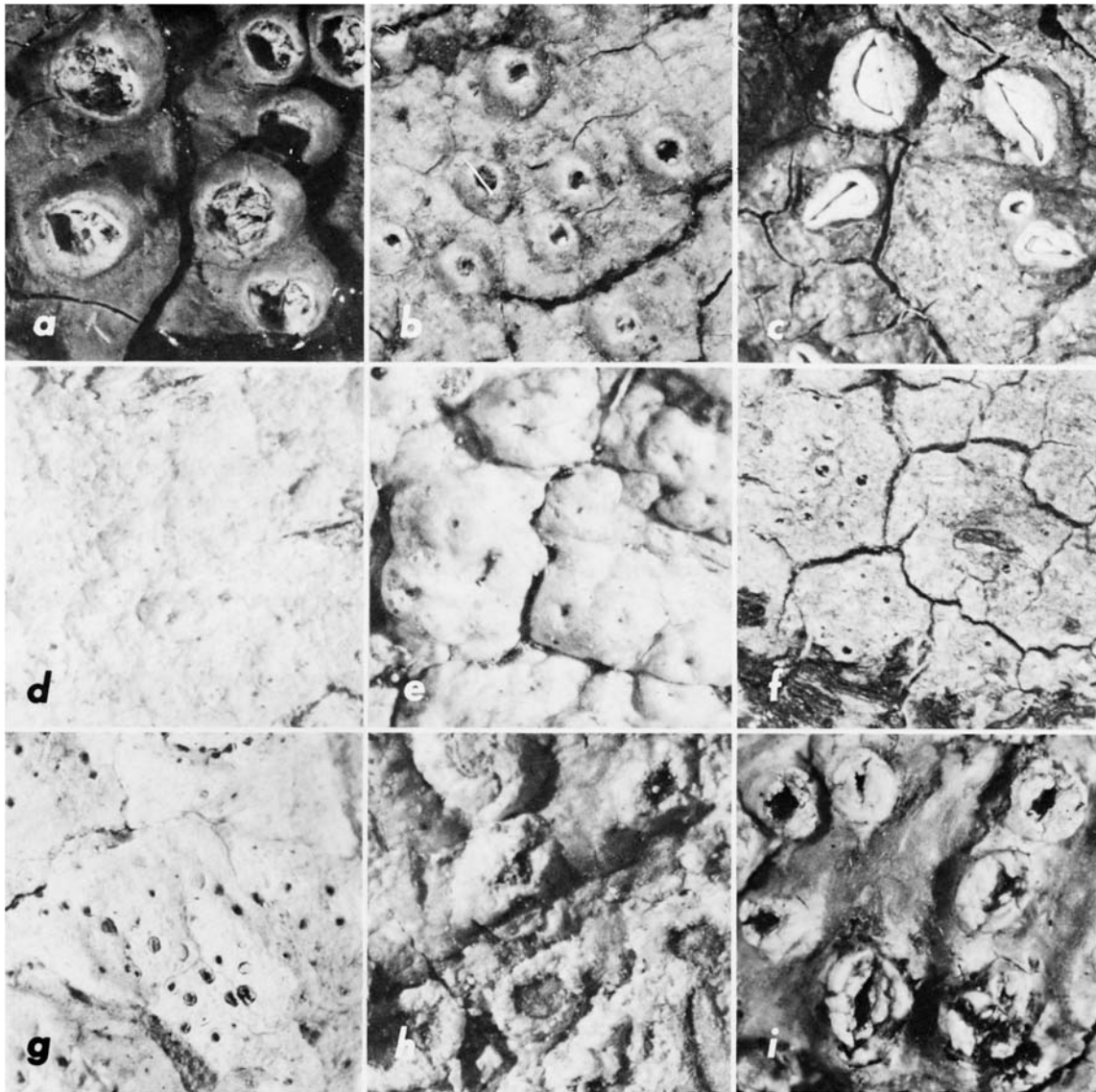


FIGURE 19.—Specimens of Thelotremataceae (all about $\times 10$): a, *Leptotrema fissum* (lectotype in H); b, *L. integrum* (isotype in S); c, *L. fissum* (Hale 38031); d, *L. microglaenoides* (lectotype in BM); e, *L. microglaenoides* (Hale 37984); f, *L. occultum* (isotype in G); g, *L. occultum* (Hale 35718); h, *L. spondaicum* (lectotype in FH-Tuck); i, *L. spondaicum* (Hale 35503).

from pantropical *L. compunctum* (Acharius) Müller-Argau, which contains stictic acid in addition to norstictic acid. I am keeping *L. occultum* separate until study of more material shows whether the chemical and spore variation (spores being generally smaller in norstictic acid-containing specimens) are valid or not. The *L. compunctum* group is very characteristic of dry scrub forest throughout the tropics.

SPECIMEN EXAMINED.—2 (35718).

46. *Leptotrema spondaicum*

FIGURE 19h,i

Leptotrema spondaicum (Nylander) Zahlbruckner, 1923:640.
Thelotrema spondaicum Nylander, 1863:330 [type-collection:
 Cuba, Wright 35 (FH-Tuck, lectotype); Figure 19h].

Thallus ashy white, epiphloeodal to evanescent, waxy, smooth, forming colonies 3–15 cm wide; apothecia numerous, round to irregular, 0.8–1.4

mm across, emergent, walls weakly carbonized, columella lacking; pore initially distinct, about 0.2 mm wide, but soon opening, wide and irregular, to 0.5 mm wide, exposing the dark brown disc, outer rim becoming pulverulent; hymenium 150 μ –170 μ high; spores 1–2/ascus, brown, muriform with numerous transverse and longitudinal locules, 30 μ –40 μ \times 80 μ –130 μ , I– (Figure 19i).

CHEMISTRY.—Virensic acid.

HABITAT.—Trunks of primary and secondary trees in open pastures and citrus groves at higher elevations (600–700 m).

Leptotrema spondaicum stands apart from all other thelotremes in having an open blackish disc surrounded by a thick, often pulverulent margin. One might be tempted to treat it as a species of *Diploschistes*. The chemistry is unique in the family. It is also different ecologically in that the primary habitat seems to be planted trees in disturbed areas.

SPECIMENS EXAMINED.—18b (35590), 19 (38077), 20a (37779, 37789, 37790), 20b (35492, 35503), 26a (37696).

47. *Leptotrema subcompunctum*

FIGURE 20a,b

Leptotrema subcompunctum (Nylander) Zahlbruckner, 1923: 640.

Thelotrema subcompunctum Nylander, 1868:76 [type-collection: Lifu, Loyalty Islands, *Thiebaut* s.n. (H, lectotype; G, P, isotypes); Figure 20a].

Thallus light tannish mineral gray, epiphloeodal, continuous, smooth, dull, forming colonies 4–5 cm broad; apothecia numerous, 0.3–0.4 mm in diameter, immersed to slightly emergent, noncarbonized and without a medulla, the inner lepadinioid exciple clearly developed; pore round, 0.05–0.1 mm in diameter; hymenium 140 μ –160 μ high; spores

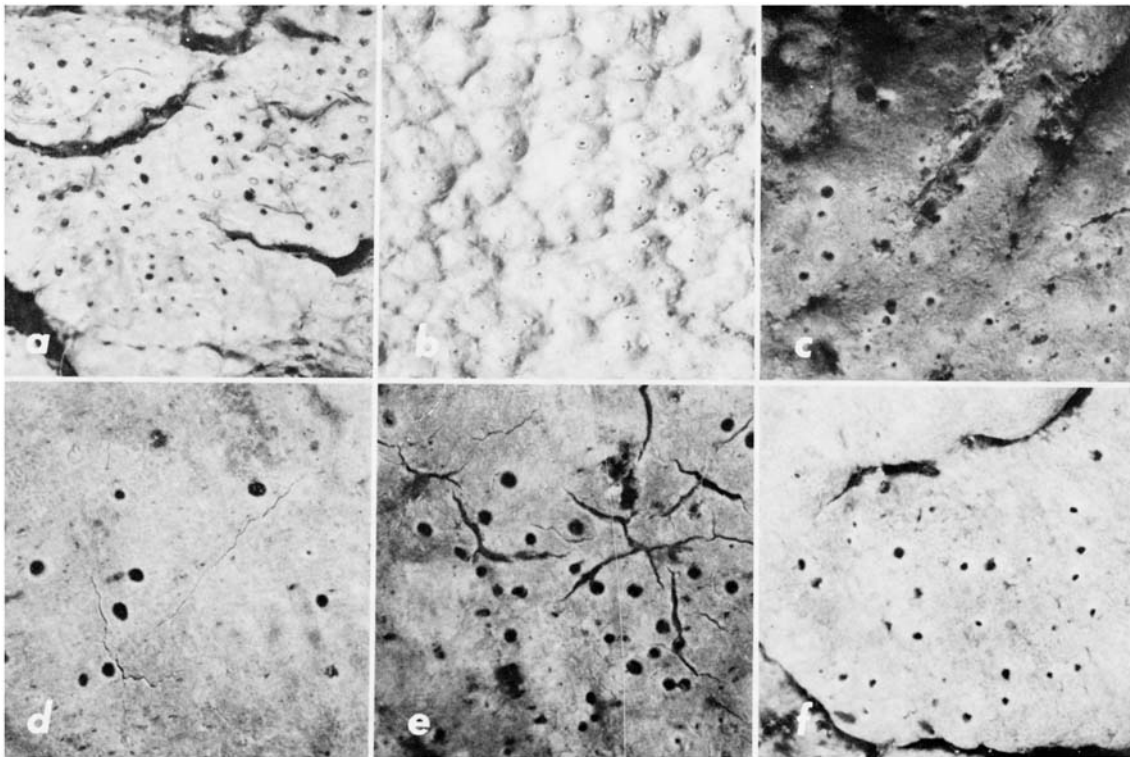


FIGURE 20.—Specimens of Thelotremataceae (all about \times 10): a, *Leptotrema subcompunctum* (isotype in P); b, *L. subcompunctum* (Hale 37888); c, *L. wightii* (lectotype in FH); d, *L. flavicans* (lectotype in G); e, *L. subconcretum* (lectotype in BM); f, *L. wightii* (Hale 35882).

brown, 1–2/ascus, muriform with 8–11 transverse locules and 2–4 longitudinal locules, $10\mu\text{--}13\mu \times 45\mu\text{--}55\mu$, I– (Figure 20b).

CHEMISTRY.—Stictic and constictic acids.

HABITAT.—Tree bole in open rain forest (600 m).

Except for the inner partially free exciple this species would probably be identified as *L. microglaenoides*. The thallus, however, is dull and the ascocarps barely emergent to immersed. This is the only collection that I have seen from the New World.

SPECIMEN EXAMINED.—18a (37888).

48. *Leptotrema wightii*

FIGURES 1d, 20c,f

Leptotrema wightii (Taylor) Müller-Argau, 1882:499.

Endocarpon wightii Taylor, 1847:155 [type-collection: Madras, India, Wight (FH, lectotype; BM, G, isotypes); Figure 20c].

Thelotrema prevostianum Montagne, 1849:292 [type-collection: Antilles, Prévost s.n. (P, lectotype); Figure 5d].

Leptotrema prevostianum (Montagne) Montagne, 1856:364.

Thelotrema subconcretum Leighton, 1869:169 [type-collection: Central Province, Ceylon, Thwaites 89 (BM, lectotype; H, G, P, S, UPS, W, isotypes); Figure 20e].

Phaeotrema subconcretum (Leighton) Müller-Argau, 1887a: 10.

Leptotrema subconcretum (Leighton) Müller-Argau, 1891:277.
Leptotrema flavicans Müller-Argau, 1888:114 [type-collection: Guarapi, Paraguay, Balansa 4170 (G, lectotype; BM, M, W, isotypes); Figure 20d].

Thallus pale greenish mineral gray, thick and epiphloeodal, bulging up and flaking away with age, surface smooth but grainy in appearance, the columnar cortex with or without red crystal masses (Figure 1d), forming colonies up to 10 cm broad; apothecia immersed, 0.2–0.3 mm in diameter, non-carbonized, without a columella; pore round, 0.08–0.11 mm in diameter, flush; hymenium about 100 μ high; spores brown, 8/ascus, muriform with 4–6 transverse locules and 1–2 longitudinal locules, $9\mu\text{--}11\mu \times 20\mu\text{--}28\mu$, I– (Figure 20f).

CHEMISTRY.—No substances present except for the unidentified anthraquinone pigment.

HABITAT.—Tree trunks in dry scrub forest near sea level.

This pantropical species has been discussed in detail by Salisbury (1971). It seems to occur at low elevations in dry scrub forest and extends northward into temperate forests of North America and southward into Argentina.

SPECIMENS EXAMINED.—1 (35582, 35584), 3 (32918).

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