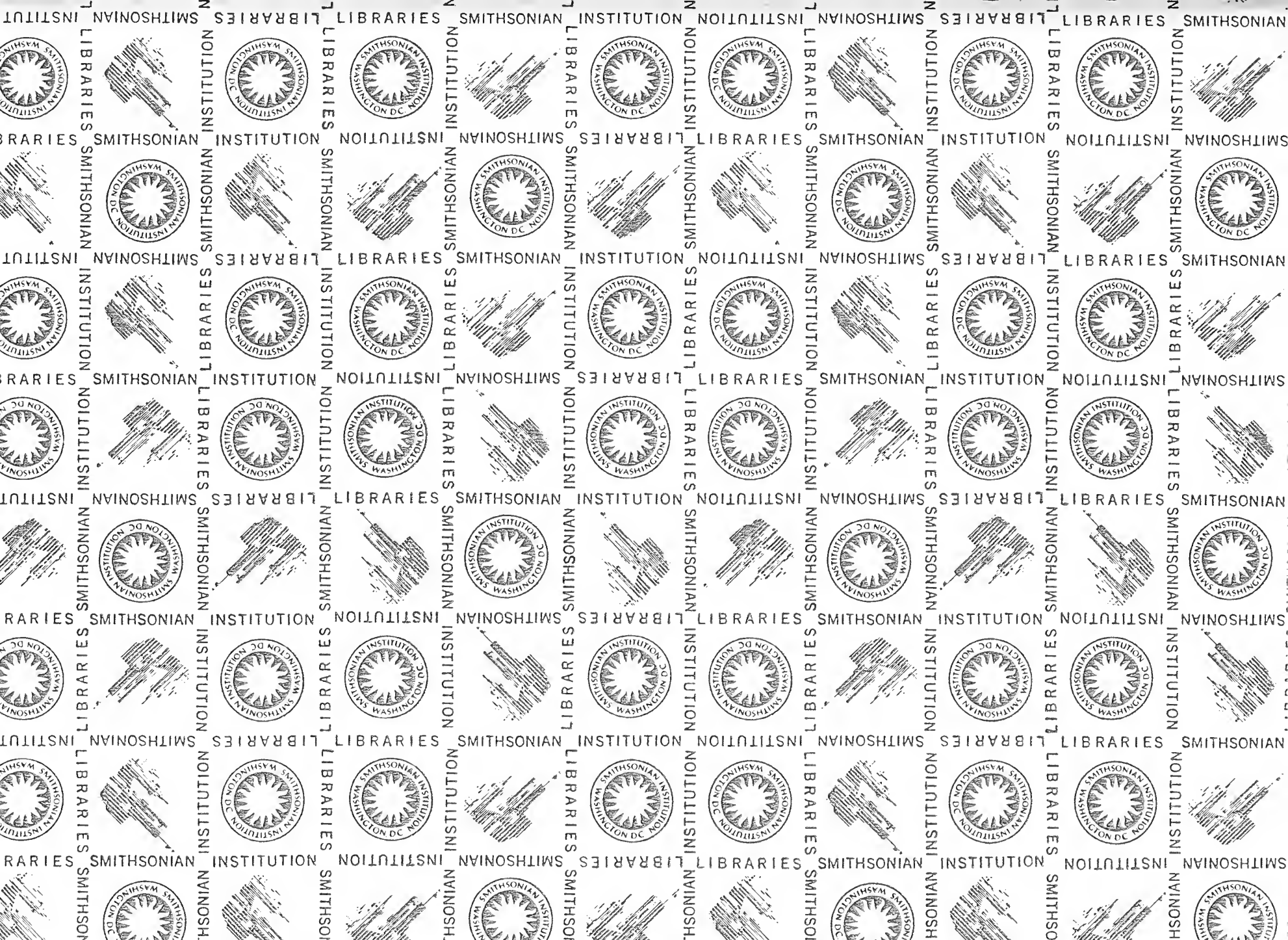
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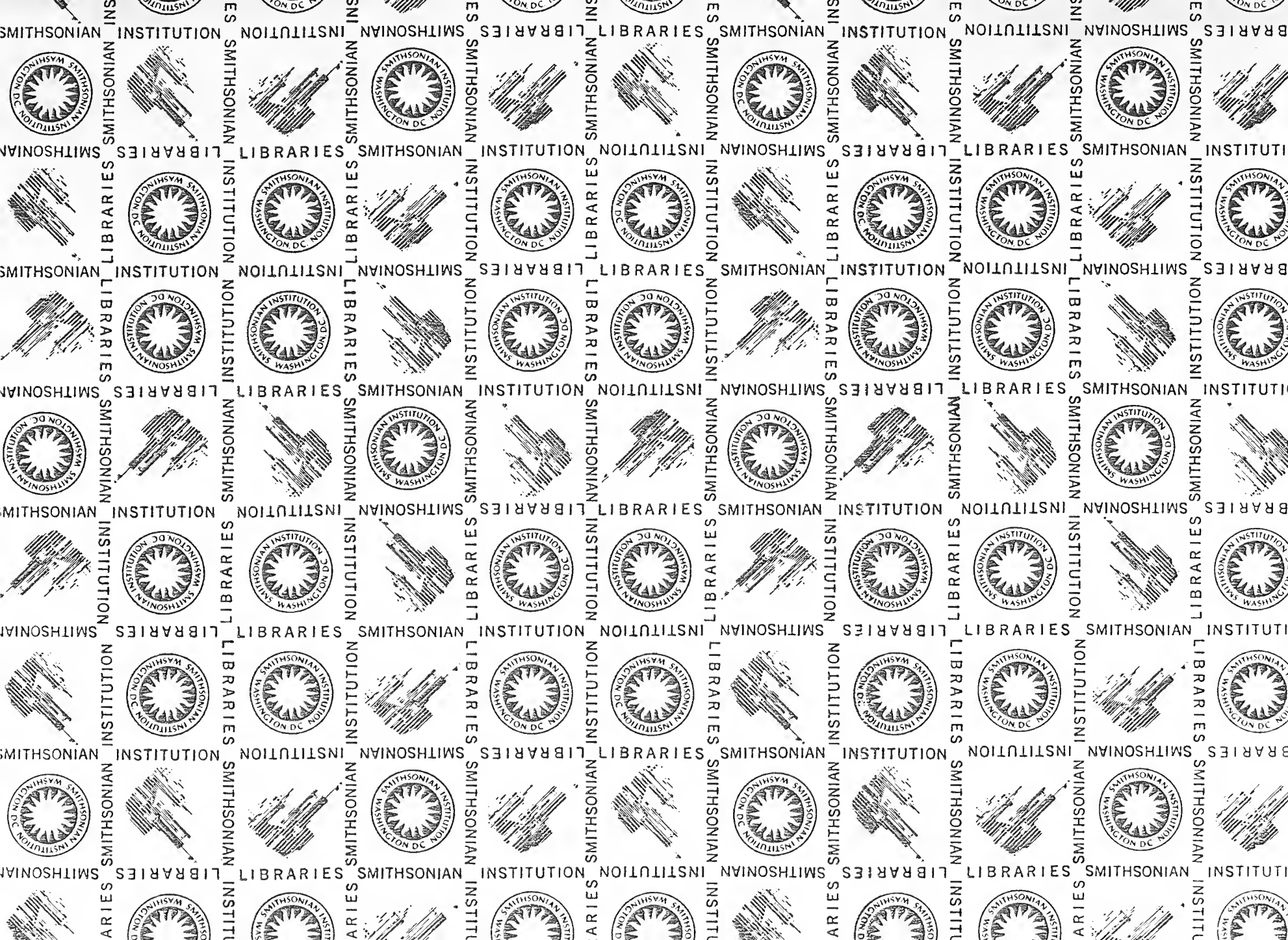
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Morden-Smithsonian Expedition to Dominica: The Lichens (Thelotremataceae)

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

Mason E. Hale, Jr.

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ABSTRACT

Hale, Mason E., Jr. Morden-Smithsonian Expedition to Dominica: The Lichens (Thelotremataceae). *Smithsonian Contributions to Botany,* number 16, 46 pages, 20 figures, 1974.—A revision is made of the lichen family Thelotremataceae in Dominica, based on previously published records by Elliott and on collections by the author. The family comprises 48 species in 4 genera, *Leptotrema, Ocellularia, Phaeotrema,* and *Thelotrema.* The following 15 species are described as new: *Ocellularia antillensis, O. conglomerata, O. dominicana, O. maculata, O. mordenii, O. nigropuncta, O. rimosa, O. sorediata, Phaeotrema aggregatum, P. obscurum, Thelotrema confusum, T. dominicanum, T. papillosum, T. tenue,* and *Leptotrema deceptum.* Three new combinations, *Ocellularia fecunda* (Vainio) Hale, *Phaeotrema disciforme* (Leighton) Hale, and *Leptotrema occultum* (Eschweiler) Hale, are also made. Morphological characters are reviewed and the chemistry of each species is presented in detail. The family is exceptionally well developed in mature rain forest.

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Contents

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 1*a,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 2*a–d*). In some species the cortex is similar but peculiar aculeate hyphae protrude from the surface in greater or lesser abundance (Figure 3*a,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 3*c,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 5*d*). The cortex is arranged in tall columns with algae scattered vertically (Salisbury, 1971) (Figure 1*d*).

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 sparce 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 5*a*), *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

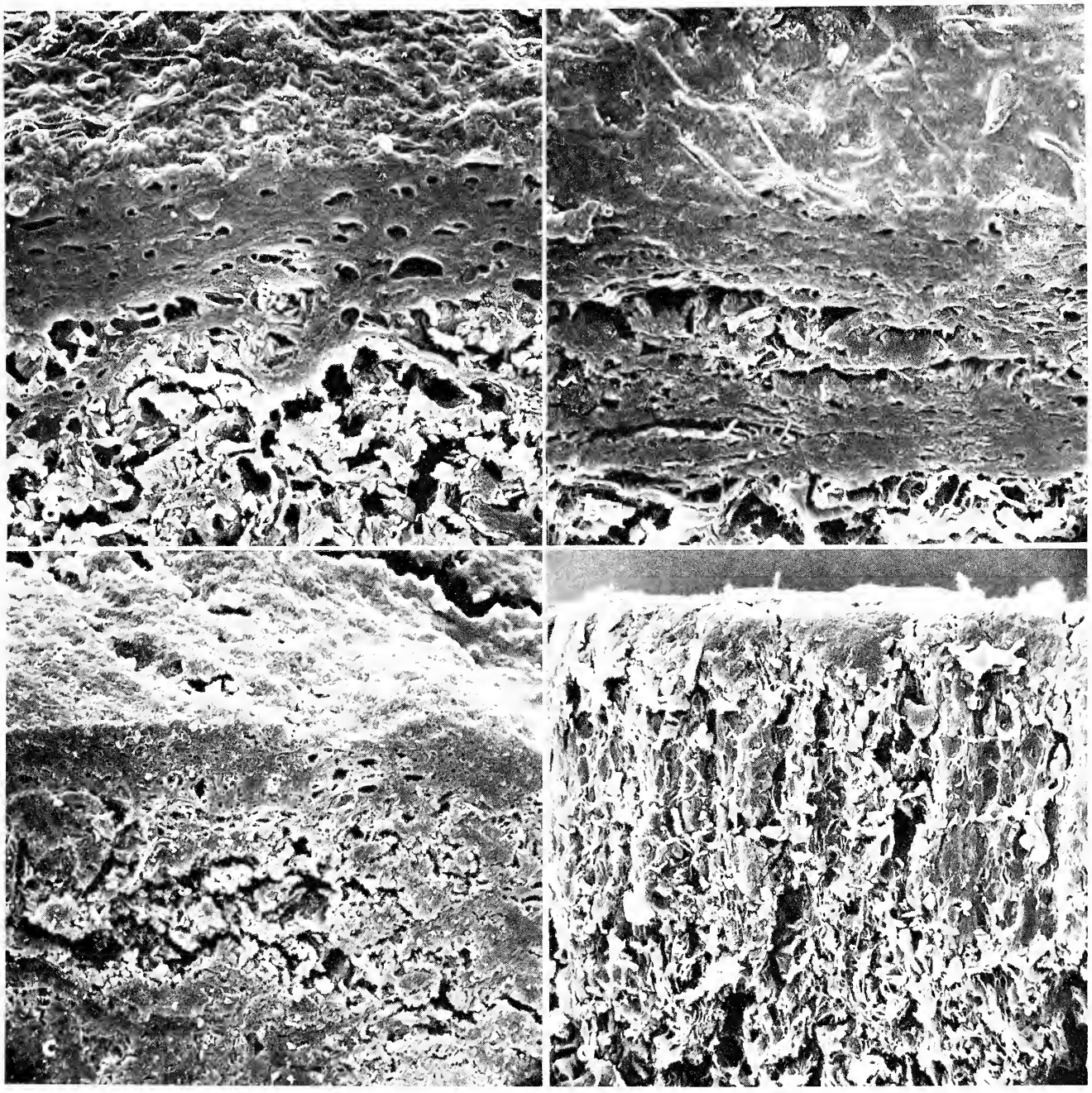

FIGURE 1.—Cross-sections of epiphloeodal lichens viewed with a scanning-electron microscope (*a*, *b*, and *c*, sectioned obliquely; *d*, vertically): *a*, *Ocellularia olivacea* (*Hale* 35226) (× 1000); *b*, *O. perforata* (*Hale* 38145) (× 1000); *c*, *Thelotrema confusum*, new species (*Hale* 37697)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

second inner rim. The disc is widely exposed and nothing resembling the discrete pore characteristic of the other thelotremes remains (Figure 5*b*). 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,

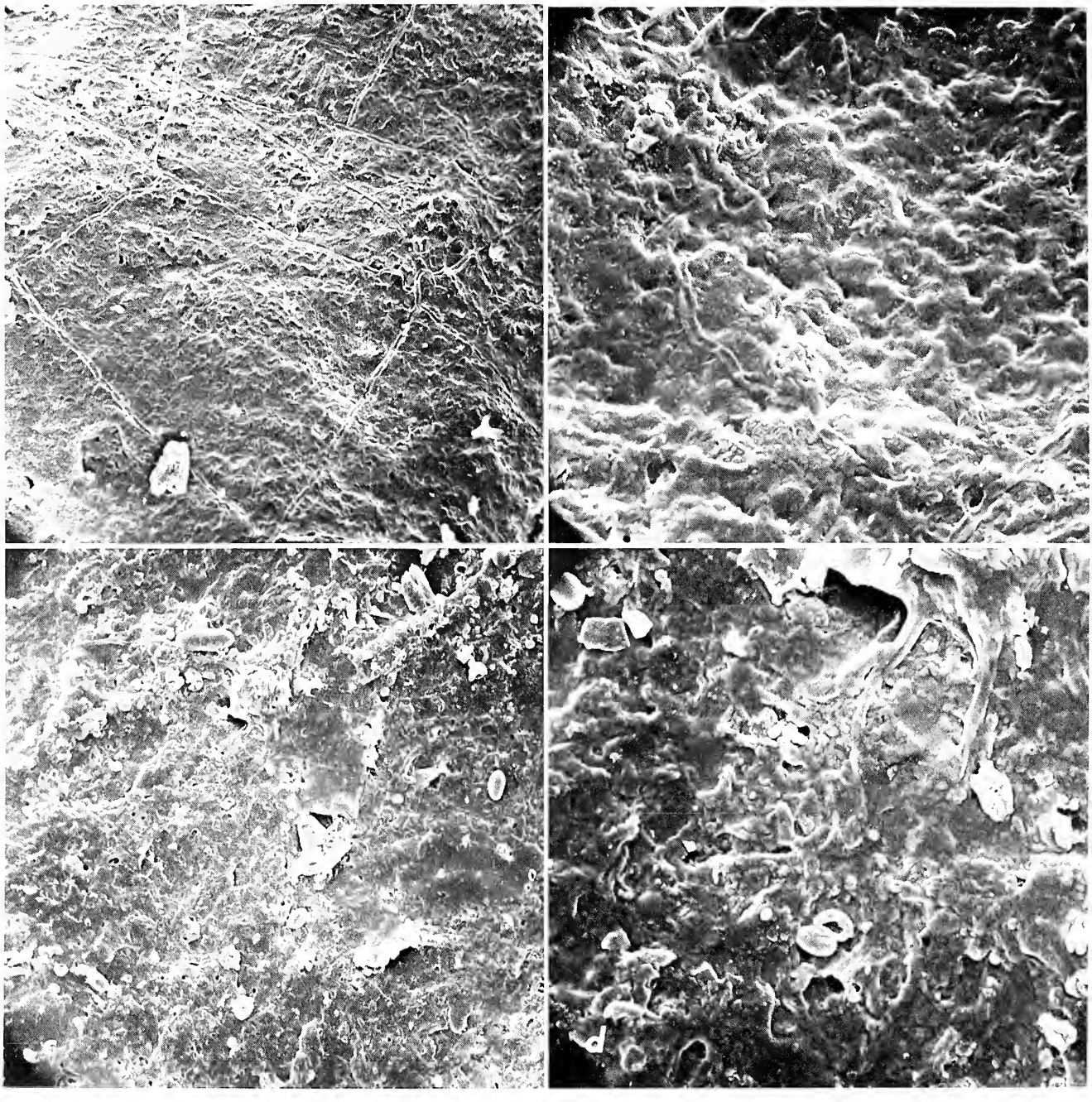

FIGURE 2.—Surfaces of epiphlocodal lichens viewed with a scanning-electron microscope: *a, b, Ocellularia nigropuncta,* new species (*Hale* 35365) (× 500 and × 2000); *c, d, O. dominicana,* new species (*Hale* 37967) (× 500 and × 2000).

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 exciple is fused with the receptacle wall and the main rim or margin closes over most of the disc

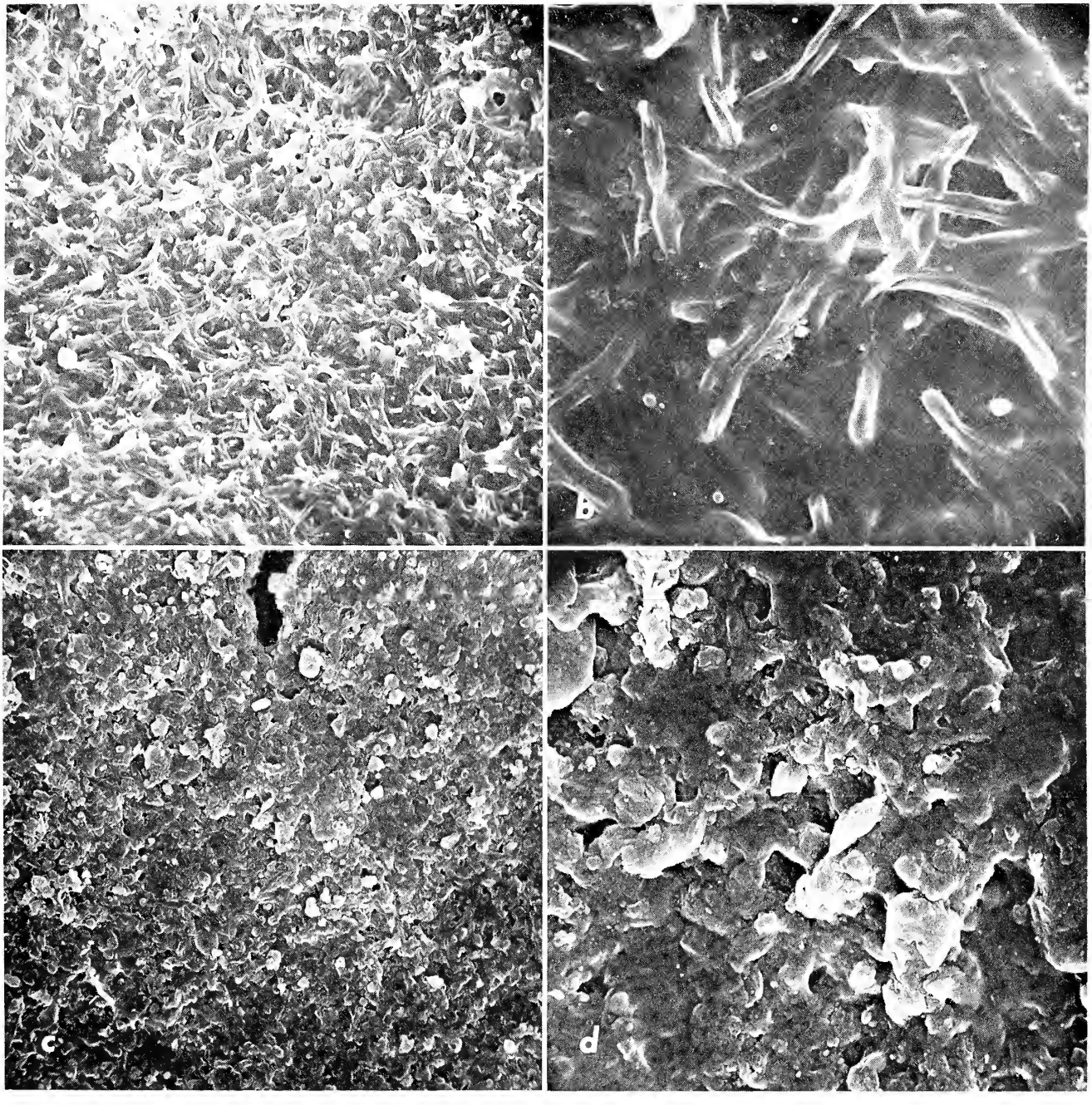

FIGURE 3.—Surfaces of epiphloeodal lichens viewed with a scanning-electron microscope: *a, b, Ocellularia olivacea* (*Hale* 38054) (× 500 and × 2000); *c, d, O. mordenii*, new species (*Hale* 37764) (× 500 and × 2000).

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 noncarbonized 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

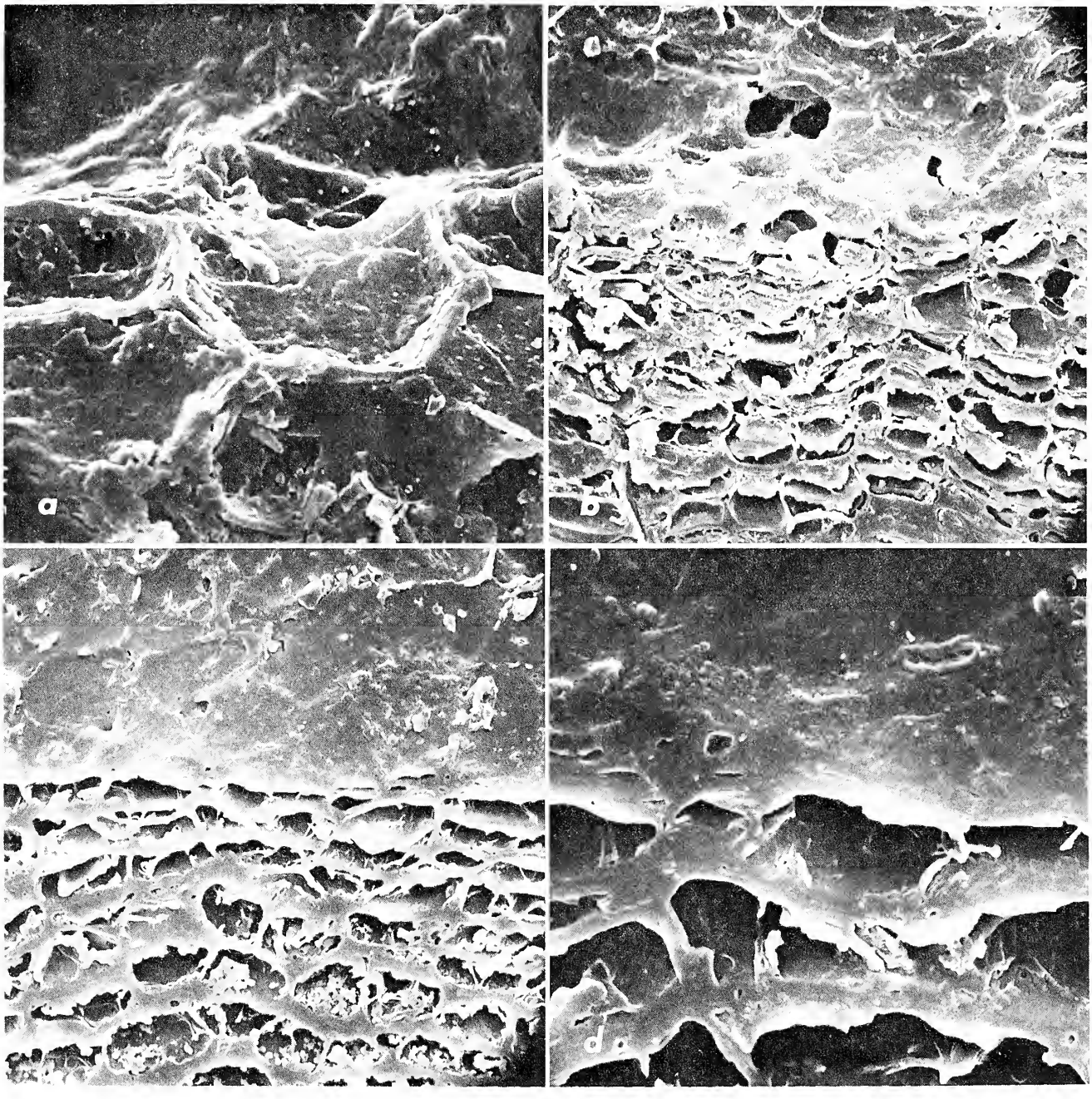

FIGURE 4.—Surface and cross-sections of hypophloeodal lichens viewed with a scanning-electron microscope: *a, Thelotrema leucomelaenum,* surface view (*Hale* 35491) (× 2000); *b, T. leucomelaenum,* cross-section (*Hale* 35491) (× 500); *c, d, T. tenue,* new species (*Hale* 35430) (× 500 and × 2000).

of the species, has emergent apothecia, neither basally constricted or strongly raised (Figure 5*e,f*). They are usually 0.4–1.0 mm in diameter, although in a few species (for example, *Thelotrema praestans* in Figure 17*e*) 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 5*g*). The pore is small and sometimes annulate or open at maturity, as in *O. fecunda* (Figure 11*h,i*).

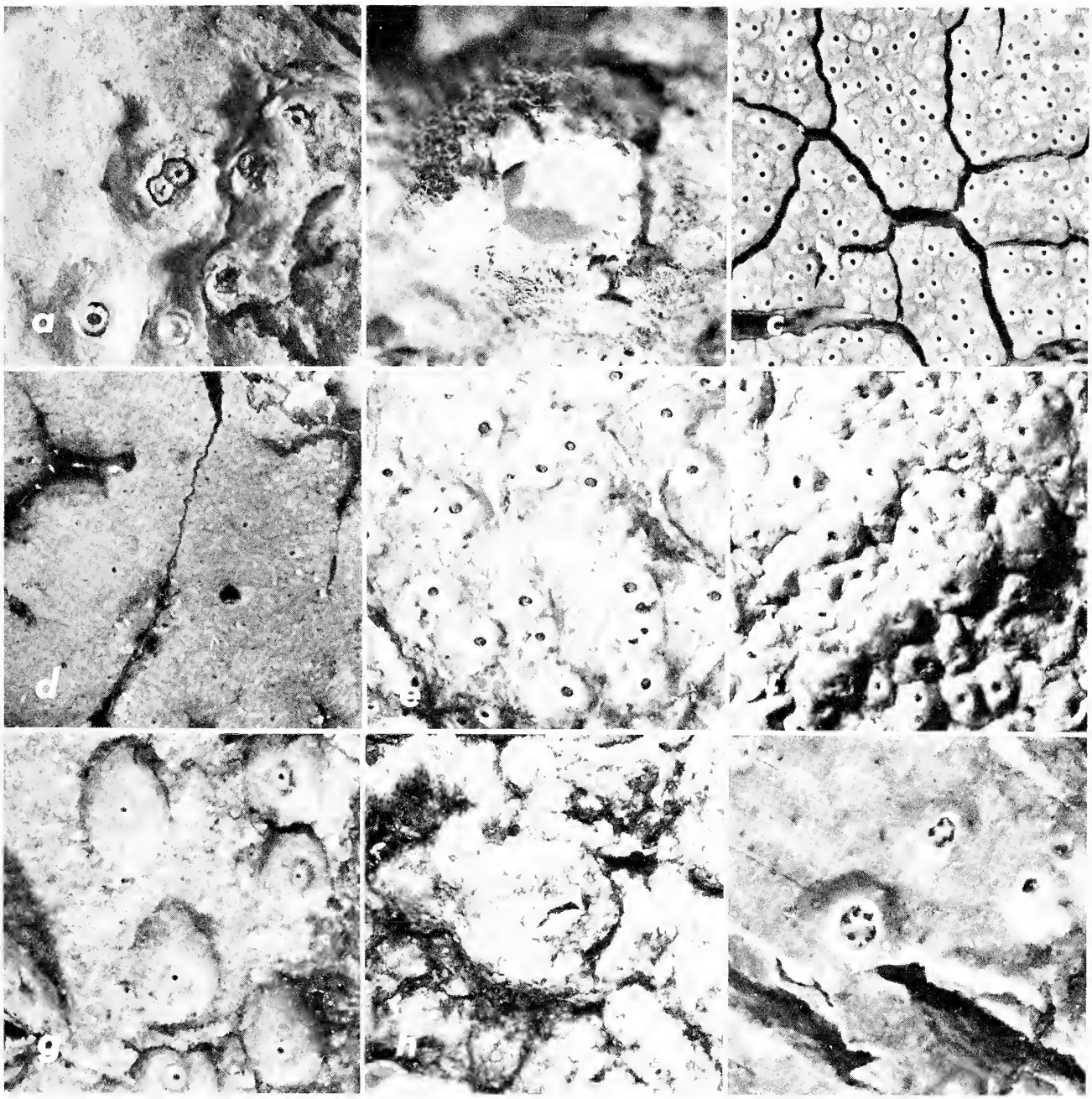

FIGURE 5.—Types of apothecia in the Thelotremataceae (all × 10): *a, Ocellularia exanthismocarpa* (type of *O. multilocularis*); *b, O. alborosella* (*Hale* 35371a); *c, O. olivacea* (*Hale* 35243); *d, Leptotrema wightii,* (type of *L. prevostianum*); *e, O. perforata* (*Hale* 37727); *f, L. bahianum* (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 5*h*). 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 Thelotremataceae.

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 6*f*). 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 ecolumellate 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 5*i*) and *Leptotrema fissum* (Figure 19*a,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 100μ) which may vary between 100μ and 300μ. We can distinguish four very broad categories among the Dominican species: (1) spores less than 20μ long with 4–6 transverse locules, e.g., *Leptotrema wightii, Ocellularia terebratula, Thelotrema clandestinum;* (2) spores 20μ–36μ long with 6–10 transverse locules, e.g., *Ocellularia perforata* (Figure 7*a*), *Thelotrema leucomelaenum;* (3) spores 40μ–90μ long with 12–24 transverse locules, e.g., *Leptotrema deceptum,* new species (Figure 7*d*), *Ocellularia exanthismocarpa;* and (4) spores 80μ–300μ long with numerous locules, e.g., *Ocellularia rhodostroma* (Figure 7*b*), *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 30μ 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 7*d*). In *Phaeotrema disciforme,* new combination, in fact, one often finds a mixture of colorless, mature brown, and shriveled brown spores (Figure 7*c*). Shriveling (Figures 7*c,d*) is characteristic of brown-spored species; I know of no cases where *Thelotrema* or *Ocellularia* spores shrivel.

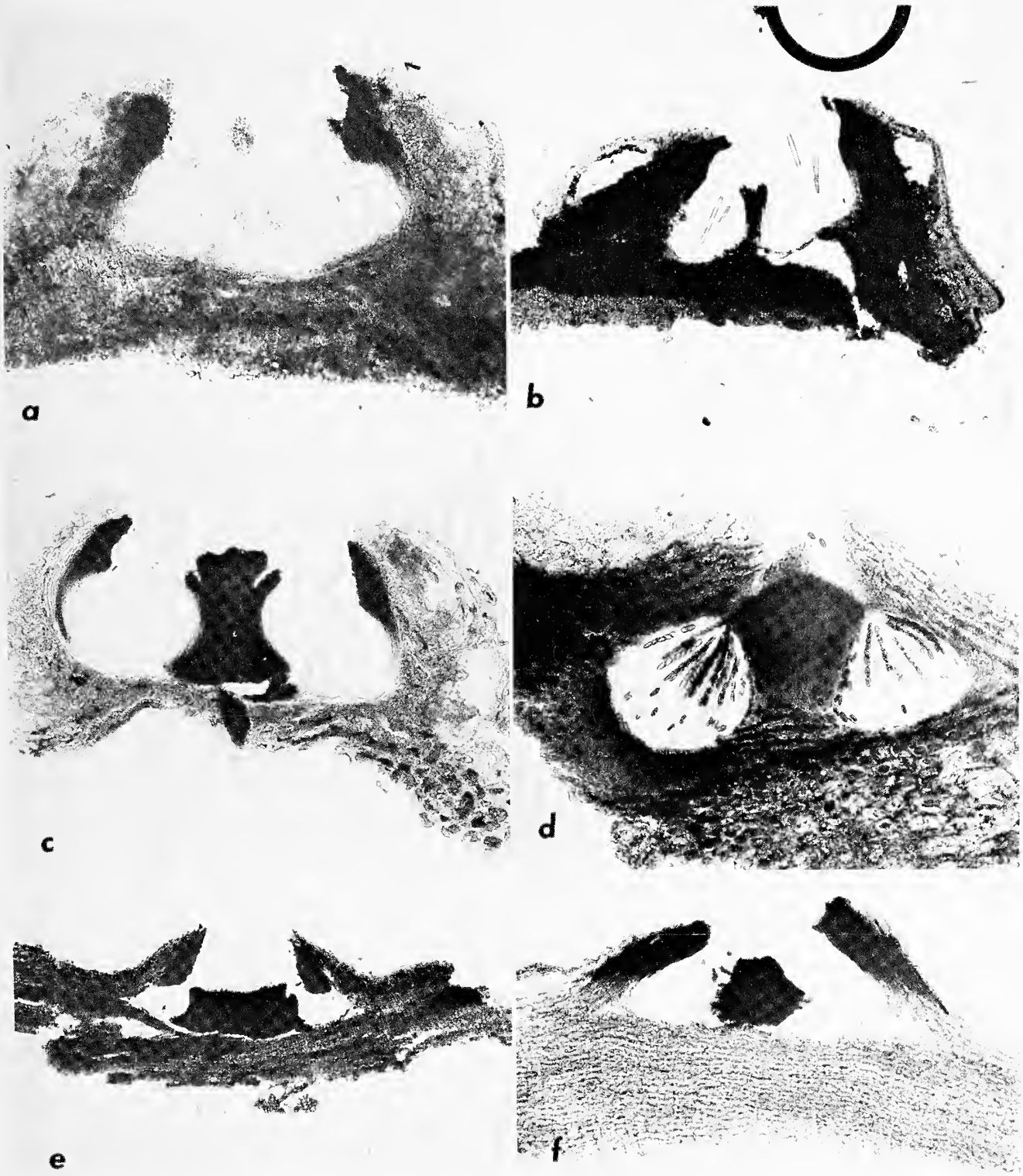

FIGURE 6.—Cross-section of apothecia (all about × 130): *a, Ocellularia nigropuncta,* new species (*Hale* 35365); *b, O. mordenii,* new species (*Hale* 37764); *c, O. cavata* (*Hale* 35134); *d, Phaeotrema leiostomum* (*Hale* 35203); *e, Thelotrema leucomelaenum* (*Hale* 35491); *f, T. tenue,* new species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

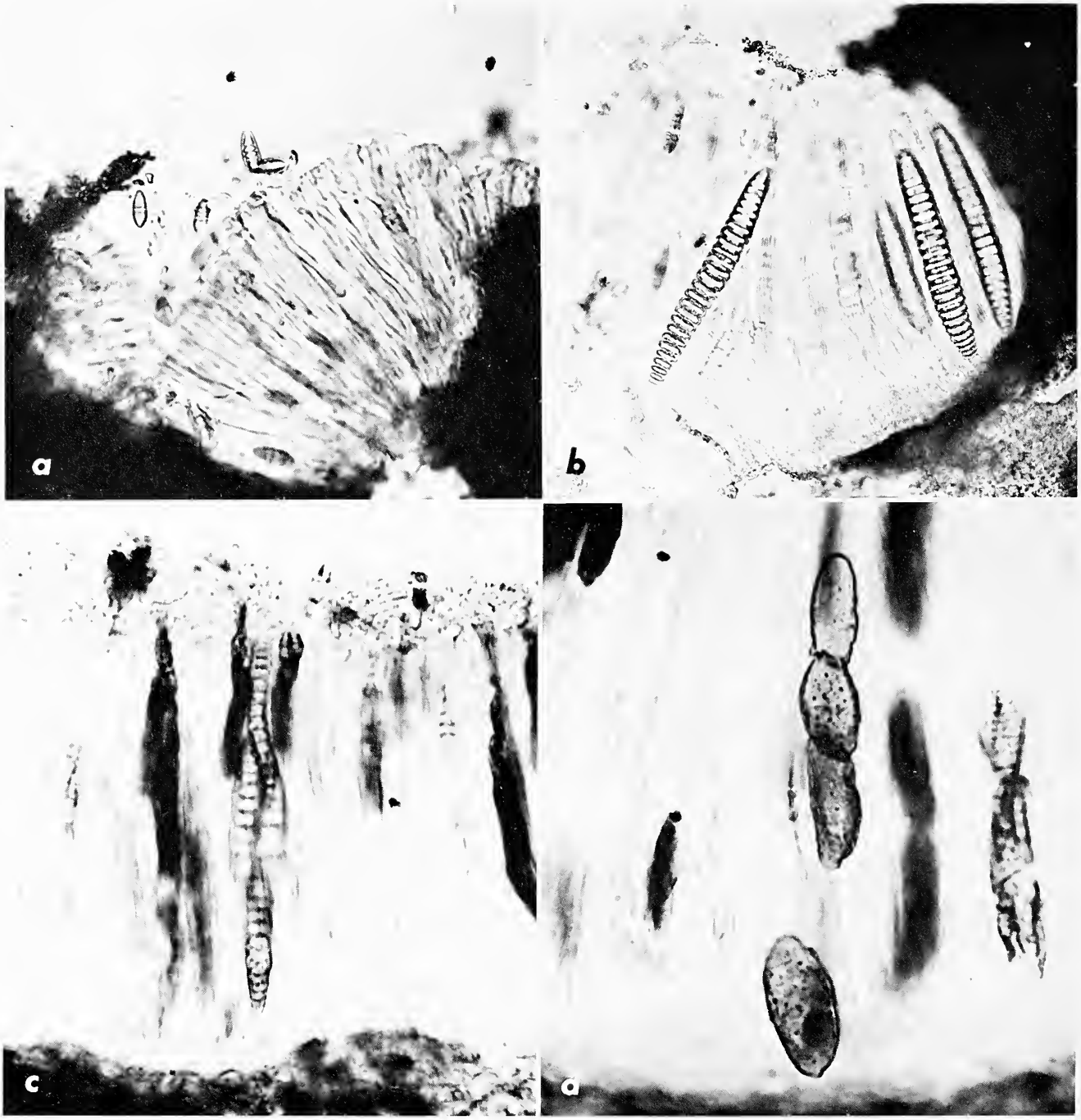

FIGURE 7.—Spores of the Thelotremataceae: *a, Ocellularia perforata* (*Hale* 37784) (× 400); *b, O. rhodostroma* (*Hale* 35440) (× 130); *c, Phaeotrema disciforme,* new combination, with a mixture of colorless spores, brown spores, and shriveled brown spores (*Hale* 37939) (× 400); *d, Leptotrema deceptum,*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

In any event, transitional species should be judged individually, and the presence of a few anomolous brown-spored specimens among many colorless specimens (as in *Ocellularia fecunda,* new combination, 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 designate 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. claudestinum, 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. exanthismocarpa, O. pyrenuloides, Phaeotrema obscurum,* new species, *Thelotrema glaucopallens, Leptotrema deceptum,* new species, *L. microglaenoides,* and *L. subconpunctum.* This widespread and well-known acid is actually rather rare in the Thelotremataceae except for the genus *Leptotrema.* Constictic acid, appearing as a H_2SO_4+ 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 H_2SO_4+ 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" Unknowns.—*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 H_2SO_4 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" Unknowns.—*Ocellularia olivacea.* This P− compound produces a distinct H_2SO_4 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− Unknowns.—*Ocellularia rimosa,* new species, and *O. sorediata,* 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 nonprofessionals 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. *impressulum* 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, Rodneys 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 Brantridge 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.

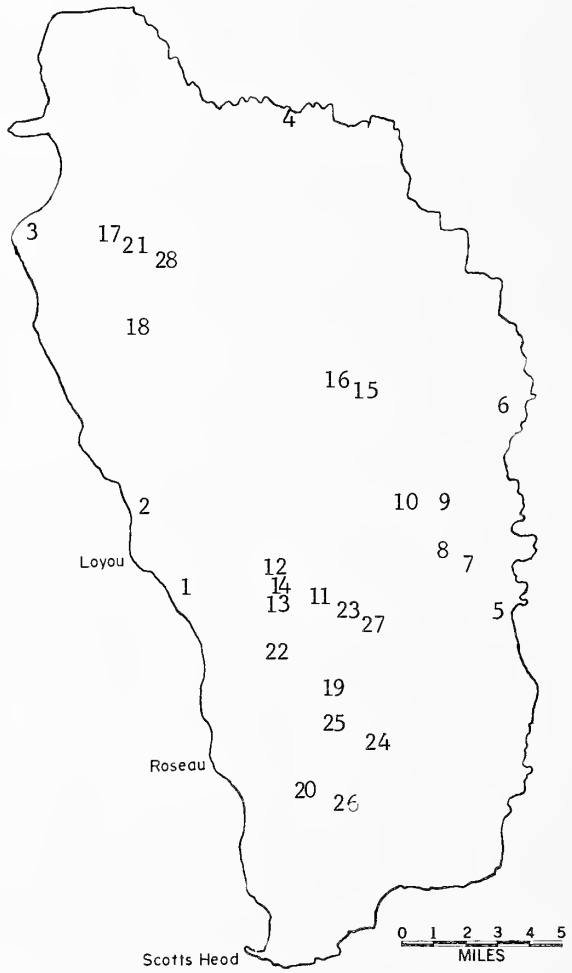

Figure 8.—Outline map of Dominica showing localities where specimens of Thelotremataceae were collected.

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 b.
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 × 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, 55μ–75μ ..... 9. ***O. exanthismocarpa***
12. Spores small, 15μ ..... 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, 5μ–6μ × 9μ–11μ ..... 21. ***O. subcavata***
20. Pore not annulate; spores generally 20μ–30μ 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 5*b*, 9*b*

Ocellularia alborosella (Nylander) Santesson, 1952:308.

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

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

Ocellularia platycarpella (Vaino) 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 60μ high; spores 8, 5–6 loculate, 4μ–5μ × 8μ–15μ, I− or weakly blue (Figure 5*b*).

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 9*g*

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, 7μ × 20μ, I+ coerulescentes (Figure 9*g*).

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 (6μ × 30μ–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 6*c*, 9*f*

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 9*e*].

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 9*c*].

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

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 6*c*); pore round, 0.07–0.12 mm in diameter, the top of the columella clearly visible; spores 8, 6–8 loculate, 6μ–8μ × 22μ–28μ, I+ blue. (Figure 9*f*).

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 5*i*, 9*i*

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 9*i*].

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–6μ × 10μ–14μ, I+ blue. (Figure 5*i*).

CHEMISTRY.—Psoromic 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

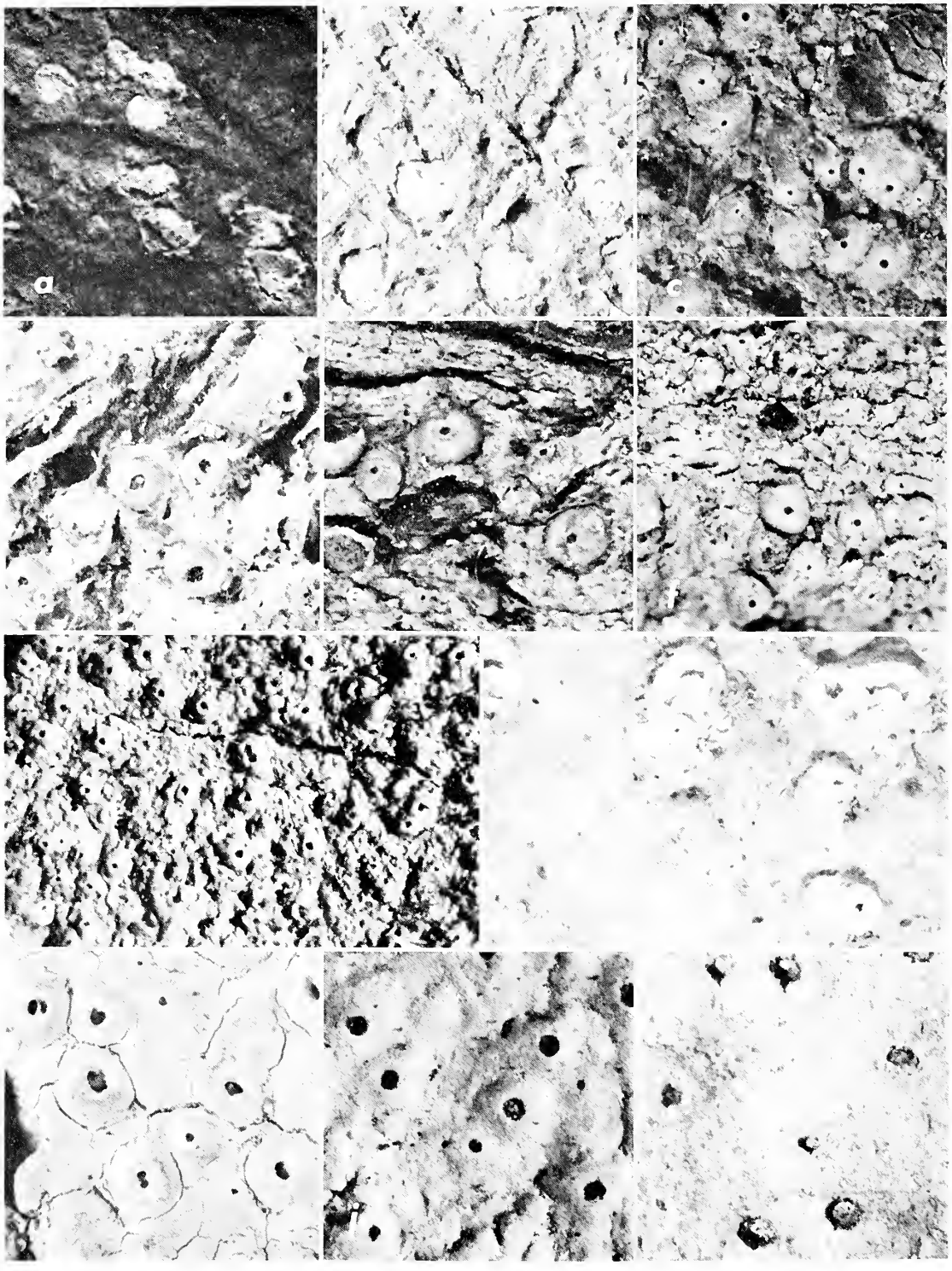

FIGURE 9.—Specimens of Thelotrematacеae (all about × 10): *a, Ocellularia platycarpella* (lectotype in TUR); *b, O. alborosella,* (isotype in FH-Tuck); *c, O. cinchonarum* f. *intermedia* (lectotype in H); *d, O. lindigiana* (lectotype in G); *e, O. cinchonarum* (lectotype in G); *f, O. cavata* (*Hale* 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 9*j,k*

Ocellularia concolor Meyen and Flotow, 1843:230.

Type-Collection.—Manila, Philippines, *Meyen* (G, lectotype) (Figure 9*j*).

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 140μ high; spores 8, 5–7 loculate, 5μ–8μ × 13μ–20μ, I+ blue (Figure 9*k*).

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 9*h*

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 exteriore erecto, excipulo interiore evoluto, pulverulento, disco aperto, carneo; ostiolum irregulare, latum; hymenium 70μ altum; sporae 8:nae, transversim 6–7 loculatae, 5μ–6μ × 15μ–18μ, I+ coerulescentes (Figure 9*h*).

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 11*a,b*

Ocellularia dilatata Müller-Argau, 1895:452.

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

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 60μ high; spores 8, 6–7 loculate, 5μ–6μ × 15μ–17μ, I+ blue (Figure 11*b*).

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 2*c,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 60μ–80μ altum; sporae 8:nae, transversim 6–7 loculatae, 6μ–8μ × 16μ–25μ, I+ coerulescentes (Figure 10).

Chemistry.—No substances present.

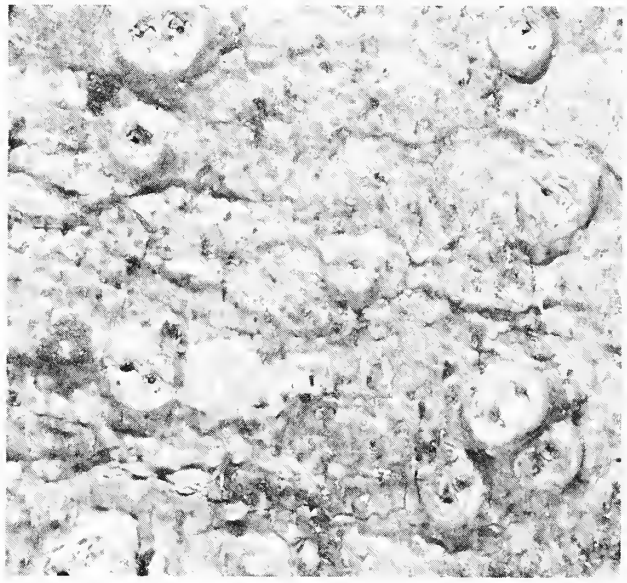

FIGURE 10.—*Ocellularia dominicana*, new species (*Hale* 37841) (about × 10).

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 5*a*, 11*c*,*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 11*c*].

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

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

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

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 11*d*].

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–18μ × 60μ–100μ, I+ deep blue (Figure 11*g*).

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 11*h*,*i*

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

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,

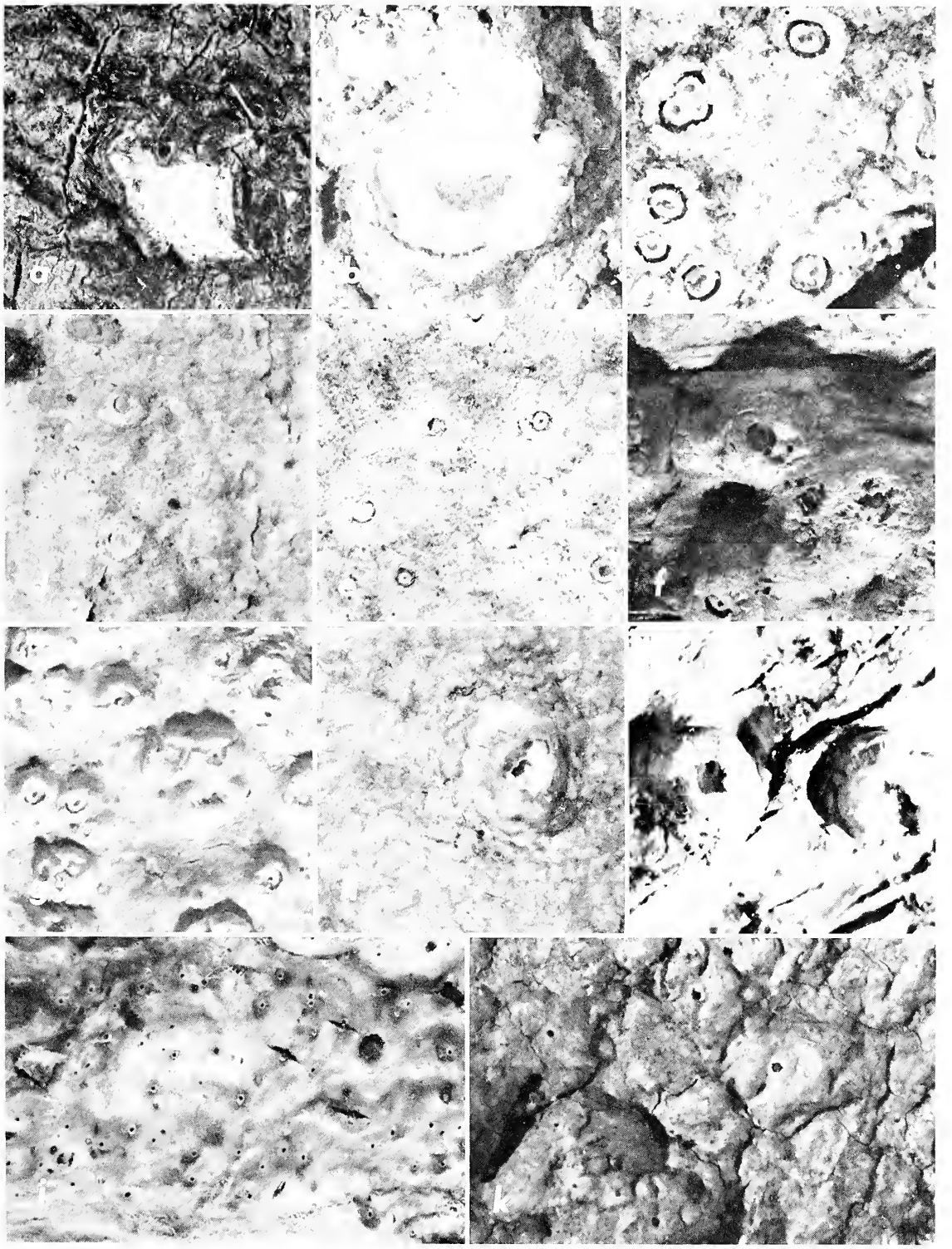

FIGURE 11.—Specimens of Thelotremataceae (all about × 10): *a, Ocellularia dilatata* (isotype in BM); *b, O. dilatata* (*Hale* 37702); *c, O. exanthismocarpa* (lectotype in BM); *d, O. homothecia* (isotype in FH); *e, O. porinoides* (lectotype in L); *f, O. isertii* (lectotype in C); *g, O. exanthismocarpa* (*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 × 80μ–150μ, rarely turning brown, I+ blue (Figure 11*i*).

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 11*j*

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–7μ × 11μ–13μ, I− (Figure 11*j*).

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 3*c,d*; 6*b*; 11*k*

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 6*b*); ostiolum rotundum, 0.08–0.12 mm diametro; hymenium circa 200μ altum; sporae 1–2:nae, transversim 24–30 loculatae, 15μ–20μ × 70μ–150μ, I+ coerulescentes (Figure 11*k*).

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 2*a,b*; 6*a*; 12*a*

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

Chemistry.—Protocetraric acid.

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

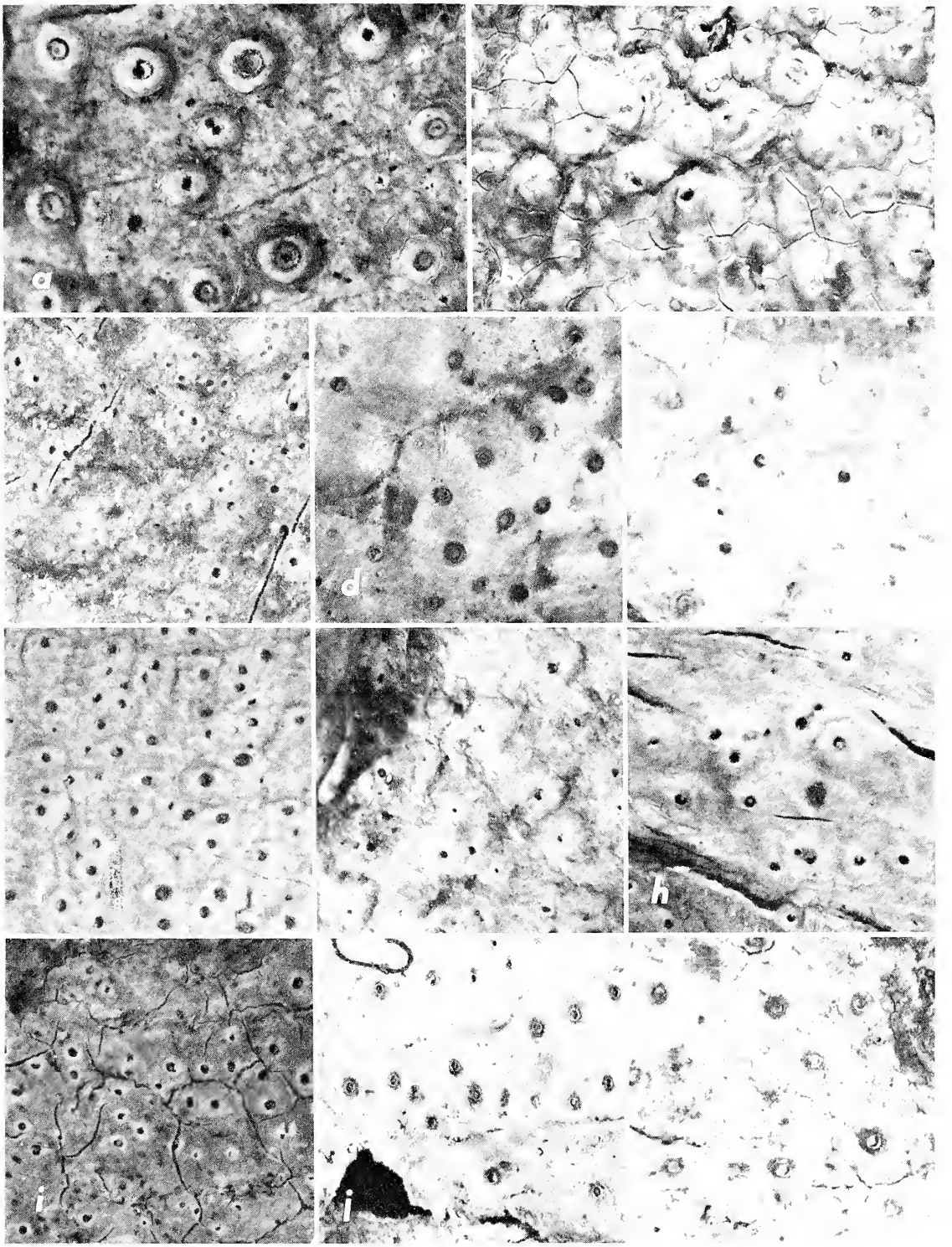

FIGURE 12.—Specimens of Thelotremataceae (all about × 10): *a, Ocellularia nigropuncta,* new species (*Hale* 35365); *b, O. rimosa,* new species (*Hale* 38052); *c, O. olivacea* (lectotype in G); *d, O. papillata* (lectotype in BM); *e, O. papillata* (*Hale* 38098); *f, O. perforata* (lectotype in BM); *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, *Symphonea* roots, rarely canopy of trees in the rain forest (300–900 m).

The black-rimmed pore area and smooth thallus are diagnostic features. Other ecolumellate 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 30μ long). Under the scanning-electron microscope *O. nigropuncta,* new species, has a finely pitted but otherwise smooth surface (Figure 2*a,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 1*a*; 3*a,b*; 5*c*; 12*c*

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

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

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 1*a*), 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 65μ–75μ high; spores 8, more or less uniseriate, 4 loculate, 4μ–6μ × 8μ–12μ, I+ blue (Figure 5*c*).

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 deposide. The type-specimen of *O. olivacea* lacks this spot. The surface under the scanning-electron microscope is strongly aculeate (Figure 3*a,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 12*d,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 12*d*].

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 50μ–70μ high; spores 8/ascus, 7–9 loculate, 6μ–10μ × 20μ–36μ, I+ blue. (Figure 12*e*).

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

Ocellularia perforata (Leighton) Müller-Argau, 1892:284.
Thelotrema perforatum Leighton, 1866:447 [type-collection: Casiquiari, Brazil, *Spruce* 254 (BM, lectotype); Figure 12*f*].
Thelotrema terebratum var. *abbreviatulum* Vainio, 1890:83 [type-collection: Caraça, Minas Gerais, Brazil, *Vainio* 1551 (TUR, lectotype; BM, FH, UPS, isotypes); Figure 12*i*].
Ocellularia rufocincta Müller-Argau, 1893:146 [type-collection: Foret du Rio Général, *Tondoz* s.n. (*Pittier* 6107) (G, lectotype); Figure 12*h*].
Thelotrema excavatum Vainio, 1896:208 [type-collection: Mt. St. Andrew, St. Vincent, *Elliott* 153 (TUR, lectotype; BM, FH, isotypes); Figure 12*g*].
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 50μ–70μ in diameter, but sometimes lacking or difficult to find; pore round, 0.07–0.15 mm in diameter; hymenium 55μ–70μ high; spores 8/ascus, 6–8 loculate, 7μ–10μ × 20μ–34μ, I+ blue (Figure 5*e*).

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 2*b*) 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), 27 (37684, 37847), 26a (37700), 26b (35370).

17. *Ocellularia pyrenuloides*

Figure 12*j*,*k*

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

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

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, 130μ 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 60μ high; spores 8/ascus, 6–7 loculate, 6μ × 12μ–15μ, I+ blue (Figure 12*k*).

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 5*g*, 7*b*, 13*a*

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

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

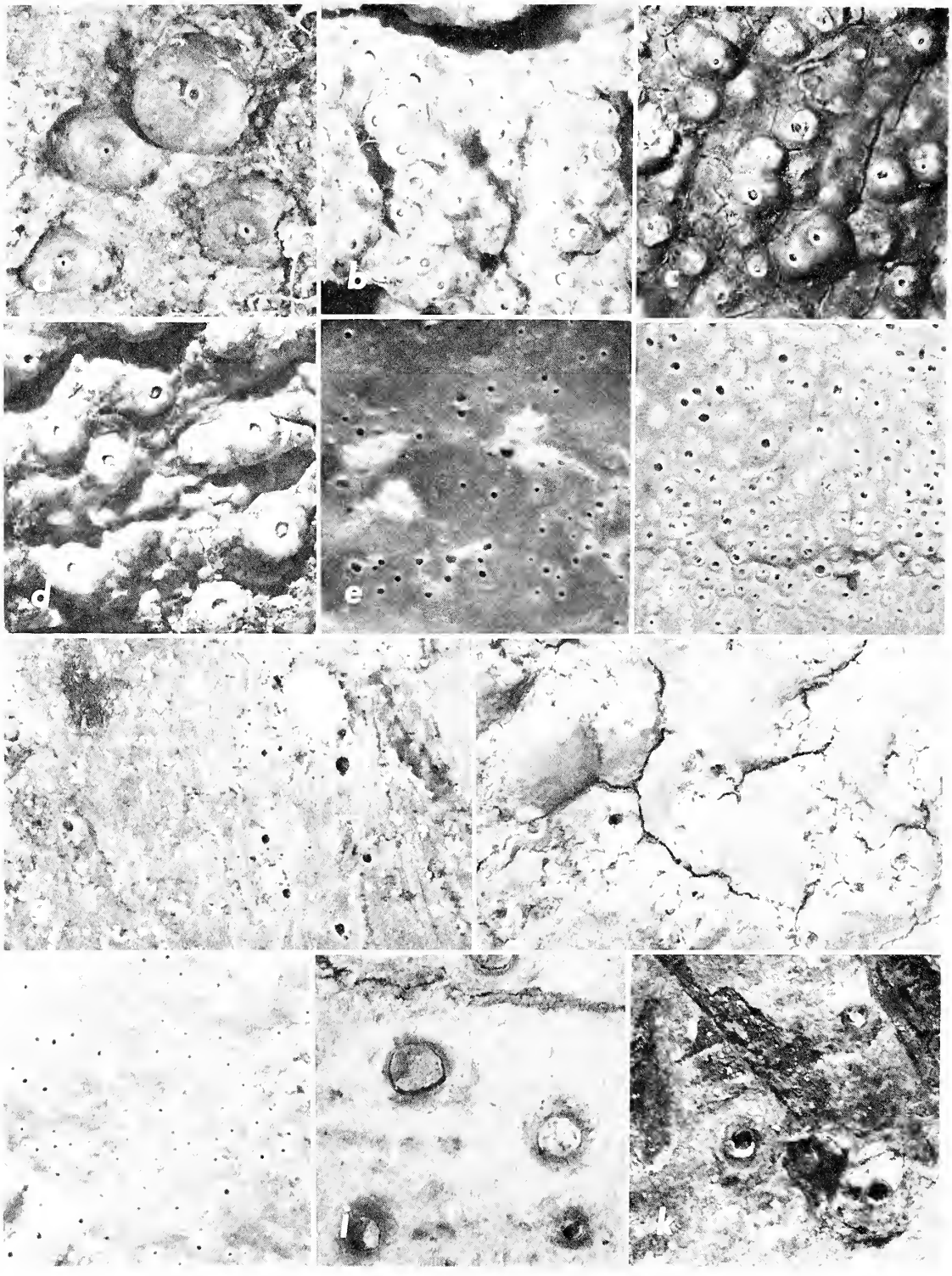

FIGURE 13.—Specimens of Thelotremataceae (all about × 10): *a, Ocellularia rhodostroma* (lectotype in P); *b, O. subcavata* (lectotype in H); *c, O. vaga* (isotype in FH); *d, O. subcavata* (*Hale* 37769); *e, O. terebratula* (lectotype in H); *f, O. remanens* (isotype in G); *g, O. sorediata,* new species (*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 200μ–275μ high; spores 1–2/ascus, 25–30 loculate, 25μ–40μ × 100μ–250μ, I+ blue (Figures 5*g* and 7*b*).

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 thelotreme 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 12*b*

Thallus corticola, brunneo- vel viridi-cinereus, epiphloeodes, nitidus, continuus sed aetate rimosus, usque ad 15 cm latus; apothecia numerosa, emergentia, 0.7–09 mm diametro, apice obfusca, columella nulla; ostiolum rotundum vel irregulare, 0.1–0.2 mm diametro, nigrocinctum; hymenium 110μ–150μ altum; sporae 8:nae, transversim 6–8 loculatae, 7μ–10μ × 24μ–32μ, I+ coerulescentes (Figure 12*b*).

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 13*g*

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 60μ–70μ altum; sporae 8:nae, transversim 3–4 loculatae, 6μ–8μ × 12μ–16μ, I+ coerulescentes (Figure 13*g*).

Chemistry.—No substances present.

Holotype.—Logging area about 3 km northwest of Pont Cassé on the Layou 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 13*b,d*

Ocellularia subcavata (Nylander) Zahlbruckner, 1923:601.

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

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

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 100μ high; spores 8/ascus, usually uniseriate, 5–6 loculate with narrow locules, 4μ–7μ × 8μ–20μ, very rarely turning brown with age, I+ blue (Figure 13*d*).

Chemistry.—Psoromic and conpsoromic 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 13*e,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 13*e*].

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

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 65μ high; spores 8/ascus, 3–5 loculate, 5μ–9μ × 15μ–20μ, I+ blue (Figure 13*i*).

Chemistry.—Psoromic and conpsoromic 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. ***P. aggregatum,*** new species
1. Apothecia solitary.
   2. Apothecia large, about 0.6 mm in diameter, strongly emergent; columella lacking ..... 24. ***P. disciforme,*** 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. ***P. leiostomum***
      3. Pore 0.5–0.1 mm in diameter, round, annulus lacking .... 26. ***P. obscurum,*** new species

trema is represented by about 40 species, a rather small group, moreso 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 13*h*

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 110μ–120μ altum; sporae 8:nae, transversim 4–5 loculatae, 8μ × 16μ (Figure 13*h*).

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 7*c*, 13*j*, 14*a*

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

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 13*k*].

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 120μ–140μ high; spores apparently 4/ascus, 20–24 loculate, 7μ–12μ × 40μ–55μ, colorless when immature but mostly turning brown and shriveled at maturity, I− (Figure 14*a*).

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 5*h*, 6*d*, 14*b*,*c*

Phaeotrema leiostomum (Tuckerman) Zahlbruckner, 1923: 608.

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

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 6*d*); pore round to irregularly elongate, surrounded by a raised ring, 0.1–0.3 mm long; hymenium 130μ–150μ high; spores 8/ascus, brown, 4 loculate, 8μ–10μ × 16μ–18μ, I− (Figures 5*h*, 14*c*).

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.

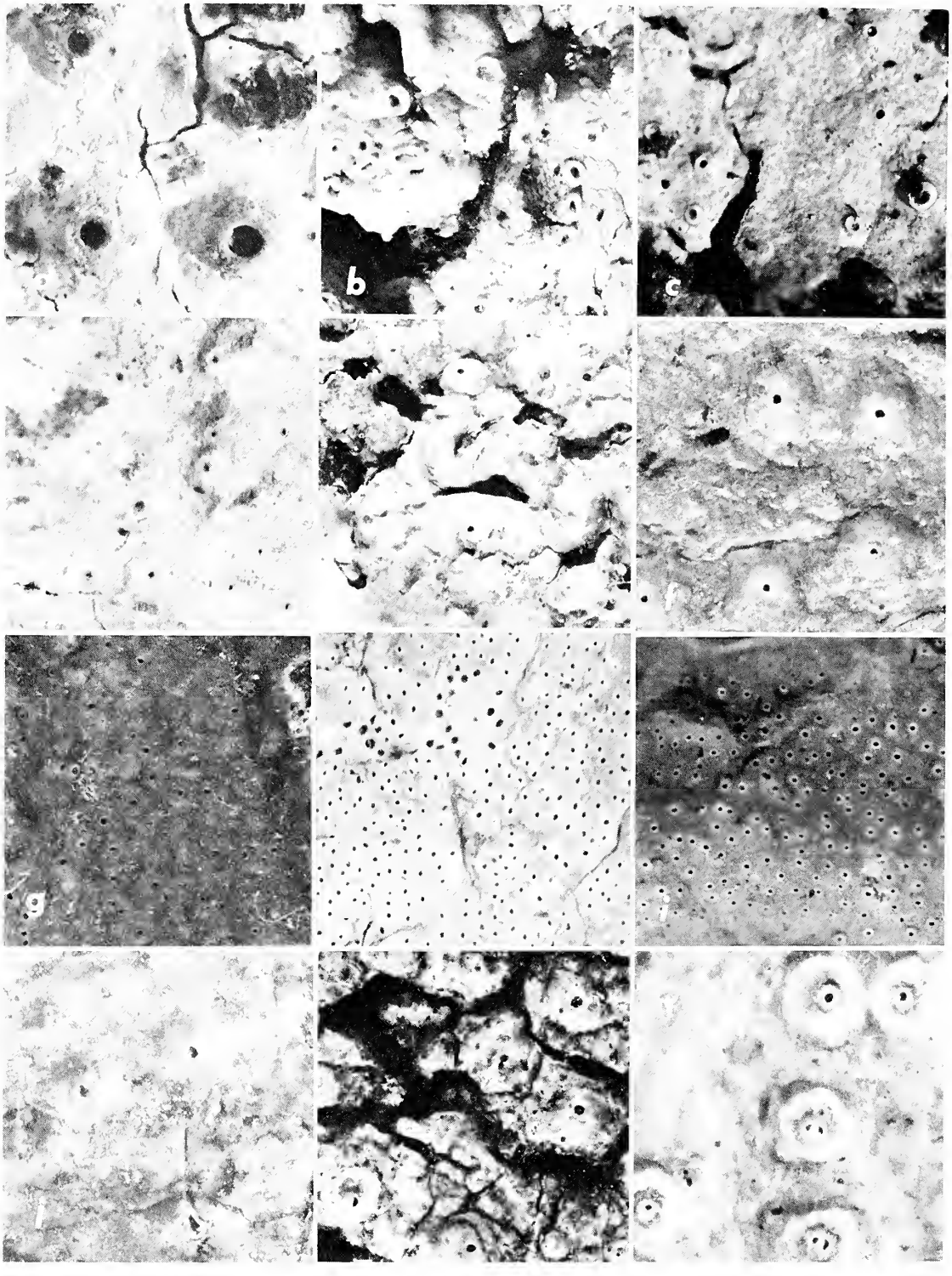

FIGURE 14.—Specimens of Thelotremataceae (all about × 10): *a, Phaeotrema disciforme,* new combination (*Hale* 37929); *b, P. leiostomum* (lectotype in FH); *c, P. leiostomum* (*Hale* 35203); *d, P. obscurum,* new species (*Hale* 38091); *e, Thelotrema carassense* (isotype in FH); *f. T. carassense* (*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 14*d*

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-pruinosum; hymenium circa 120μ altum; sporae 8:nae, transversim 5–6 loculatae, 10μ–14μ × 24μ–28μ (Figure 14*d*).

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 14*e,f*

Thelotrema carassense Vainio, 1890:79.

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

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 110μ–130μ; spores 8/ascus, muriform, 1–2 × 8–10 loculate, 12μ–15μ × 30μ–40μ, I+ blue (Figure 14*f*).

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 70μ long). The taxonomy of the ecolumellate psoromic acid-containing *Thelotremata* is unfortunately still incomplete. *Thelotrema postpositum* Nylander has large spores (more than 100μ), but all other species, excluding *T. carassense,* have small spores (less than 20μ long).

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

28. *Thelotrema clandestinum*

FIGURE 14*g,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 14*h*].

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

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

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

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 14*j,l*

Thelotrema conforme Fée, 1837:89.

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

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

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 170μ–200μ high; spores 4/ascus, muriform, 8–10 loculate transversely, 2–4 loculate longitudinally, 18μ–20μ × 35μ–50μ, I+ blue (Figure 14*l*).

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 1*c*, 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 120μ–130μ altum; sporae 4:nae, murales, transversim 6–7 loculatae, longitudinaliter 0–2 loculatae, 6μ–10μ × 12μ–26μ, 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) (× 10).

31. *Thelotrema depressum*

FIGURE 16*b,c*

Thelotrema depressum Montagne, 1851:73.

TYPE-COLLECTION.—Cayenne, French Guiana, *Leprieur* 701 (BM, lectotype; H, isotype) (Figure 16*b*).

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

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 16*a*

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 140μ–160μ altum; sporae 2–4:nae, murales, transversim 24–30 loculatae, longitudinaliter 2–3 loculatae, 15μ–20μ × 80μ–90μ, I+ coerulescentes (Figure 16*a*).

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.

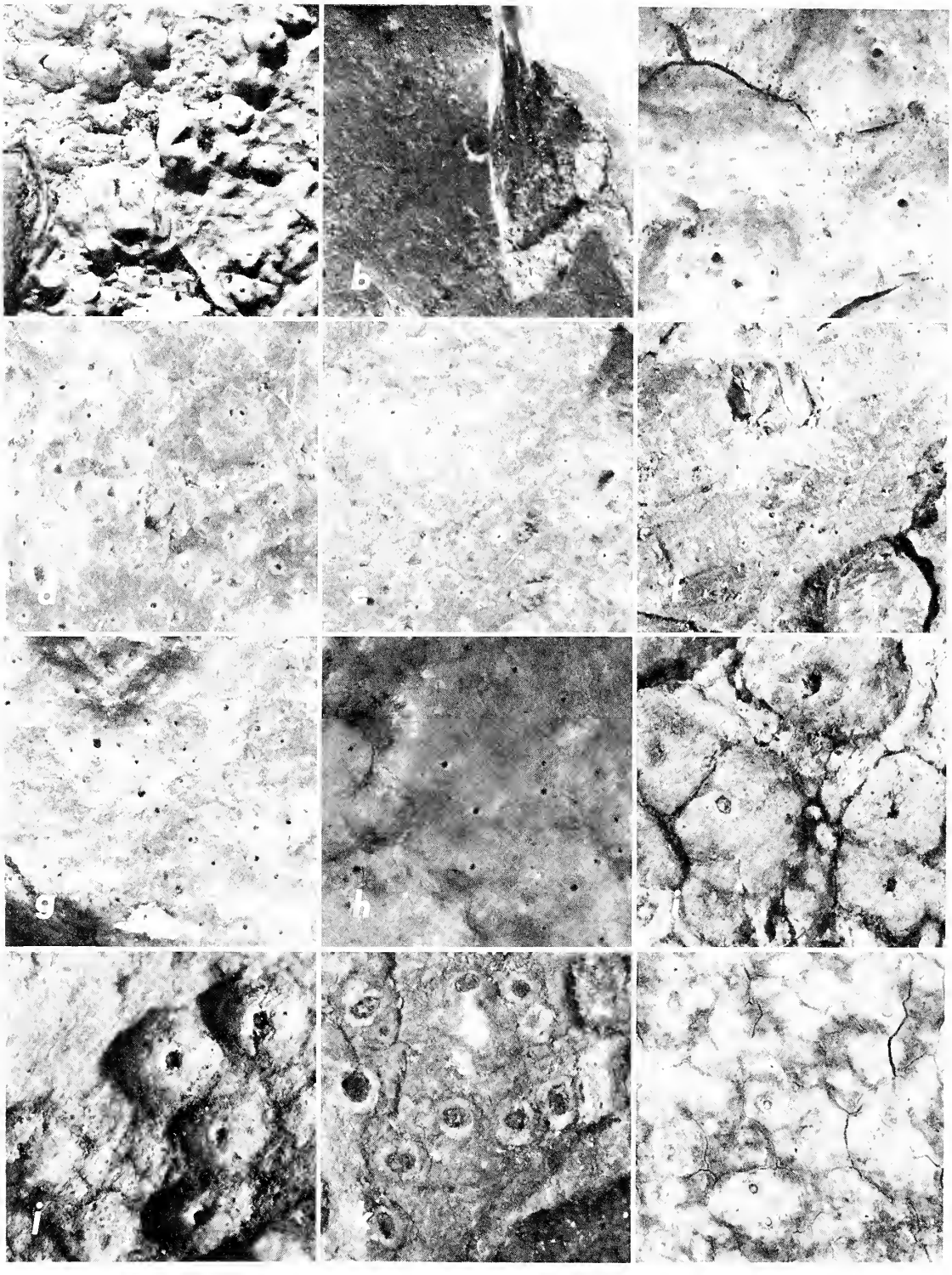

FIGURE 16.—Specimens of Thelotremataceae (all about × 10): *a, Thelotrema dominicanum,* new species (*Hale* 35355); *b, T. depressum* (isotype in H); *c, T. depressum* (*Hale* 38141); *d, T. glaucopallens* (lectotype in FH-Tuck); *e, T. pechueli* (lectotype in G); *f, T. butuanum* (lectotype in W); *g, 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 16*d,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 16*e*].
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 16*g*].
Thelotrema butuanum Vainio, 1921:183 [type-collection: Luzon, Philippines, *Fenix,* BS-28347 (W, lectotype); Figure 16*f*].

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

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 60μ–80μ high; spores 8/ascus, muriform, 6–8 loculate transversely, 2–3 loculate longitudinally, 7μ–10μ × 15μ–24μ, I− (Figure 16*h*).

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 16*i,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 16*i*].

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 200μ high; spores 2/ascus, muriform with numerous transverse and longitudinal locules, 28μ–40μ × 85μ–125μ, I+ blue (Figure 16*j*).

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 16*k,l*

Thelotrema leucinum Müller-Argau, 1887a:10.

TYPE-COLLECTION.—On *Cinchona,* South America (G, lectotype) (Figure 16*k*).

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 110μ–120μ high; spores 8/ascus, muriform with 4 locules transversely, 2 locules longitudinally, 7μ–11μ × 12μ–18μ, I+ blue (Figure 16*l*).

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

Thelotrema leucomelaenum Nylander, 1863:329.

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

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

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

Thallus white, thin and in part hypophloeodal (Figure 4*a,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 6*e*); hymenium 130μ high; spores 8/ascus, muriform, 4–6 loculate transversely, 2–3 loculate longitudinally, 12μ–15μ × 30μ–36μ, I− (Figure 17*d*).

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 17*j*

Thallus corticola, cinereo-viridis, epiphloeodes, minute papillosus, nitidus, 6 cm latus; apothecia vix emergentia, 0.7–0.9 mm diametro, intus incolores, columella nulla; ostiolum rotundum vel irregulariter laceratum, 0.1–0.3 mm diametro; hymenium circa 200μ altum; sporae 1–2:nae, murales, loculis numerosis, 36μ–40μ × 140μ–150μ, I− (Figure 17*j*).

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 17*e,g*

Thelotrema praestans Müller-Argau, 1895:453.

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

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

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 200μ high; spores 1–2/ascus, muriform with many transverse and longitudinal locules, 30μ–45μ × 100μ–275μ, I+ blue (Figure 17*g*).

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

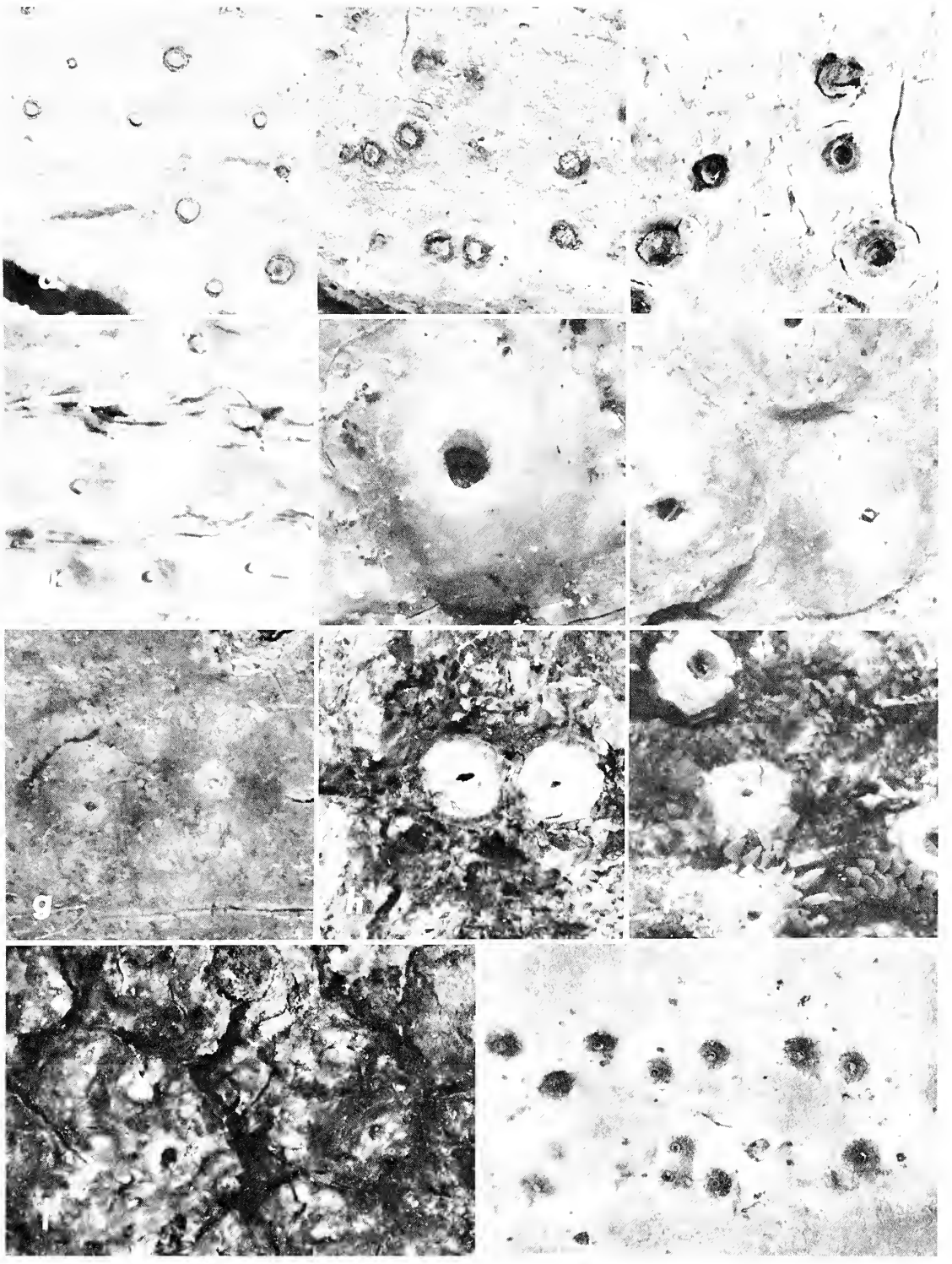

FIGURE 17.—Specimens of Thelotremataceae (all about × 10): *a, Thelotrema leucomelaenum* (lectotype in H); *b, T. pauperius* (lectotype in H); *c, T. leucomelaenum* var. *elevatum* (lectotype in TUR); *d, T. leucomelaenum* (*Hale* 35491); *e, T. praestans* (lectotype in G); *f, T. elliottii* (lectotype 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 4*c,d*; 6*f*; 17*k*

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

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 17*h,i*

Thelotrema tuberculiferum Vainio, 1915:136.

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

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 140μ–160μ high; spores 1–2/ascus, muriform with numerous transverse and longitudinal locules, 30μ–50μ × 60μ–120μ, I+ pale blue (Figure 17*i*).

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 20μ long ..... 45. ***L. occultum***
            5. Spores about 45μ long ..... 47. ***L. subcompunctum***
         4. Apothecia lacking a lepadinoid exciple.
            6. Pore distinct, 0.1–0.2 mm in diameter; spores 20μ–30μ long ..... 41. ***L. bahianum***
            6. Pore very tiny, less than 0.1 mm in diameter; spores large, more than 40μ 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. microglaenoides***

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 5*f*

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. 2*c*.
Thelotrema rudius Vainio var. *dominicanum* Vainio, 1915: 136 [type-collection: Prince Rupert, Dominica, *Elliott* 1303 (TUR, lectotype); Figure 5*f*].

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 150μ high; spores 8/ascus, muriform with 5–6 transverse locules and 2–3 longitudinal locules, 12μ–14μ × 16μ–24μ, I− (Figure 5*f*).

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 7*d*, 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 100μ–120μ altum; sporae obfuscae, 4:nae, murales, loculis numerosis, 14μ–28μ × 40μ–70μ, 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. microglaenoides* 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-

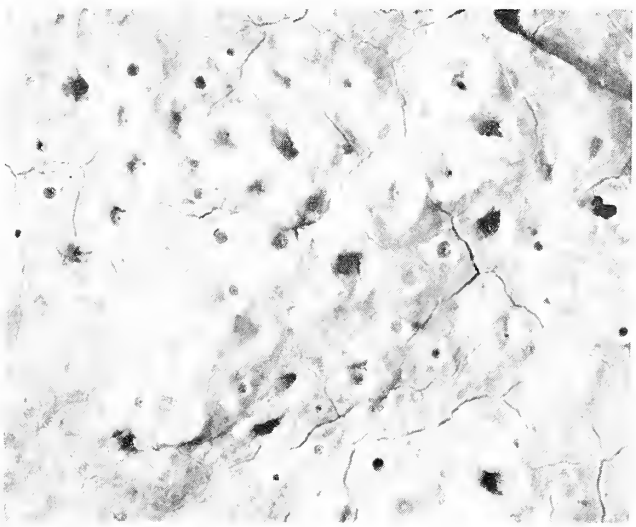

FIGURE 18.—*Leptotrema deceptum,* new species (*Hale* 37860) (× 10)

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 19*a,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 19*a*].
Leptotrema integrum Müller-Argau, 1887b:399 [type-collection: Australia, Sayer (G, lectotype; S, isotype); Figure 19*b*].
Leptotrema fissum (Nylander) Zahlbruckner, 1923:634 [superflous 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 100μ high; spores brown, muriform with 4–6 transverse locules and 0–2 longitudinal locules, 6μ–7μ × 10μ–13μ, I− (Figure 19*c*).

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 microglaenoides*

FIGURE 19*d,e*

Leptotrema microglaenoides (Vainio) Zahlbruckner, 1923:637.
Thelotrema microglaenoides Vainio, 1896:206 [type-collection: St. Vincent, *Elliott* 266 (BM, lectotype); Figure 19*d*].

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 150μ–170μ; spores brown, 4/ascus, muriform with numerous transverse and longitudinal locules, 18μ–22μ × 36μ–48μ, I− (Figure 19*e*).

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 120μ long. I found spores about 50μ 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 19*f,g*

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

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 lepadinioid exciple well developed and pulling away from the wall, lightly pruinose surface of hymenium visible; hymenium 65μ–70μ high; spores 4–8/ascus, brown, muriform with 5–7 transverse locules, 2–3 longitudinal locules, 9μ–10μ × 18μ–21μ, I− (Figure 19*g*).

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

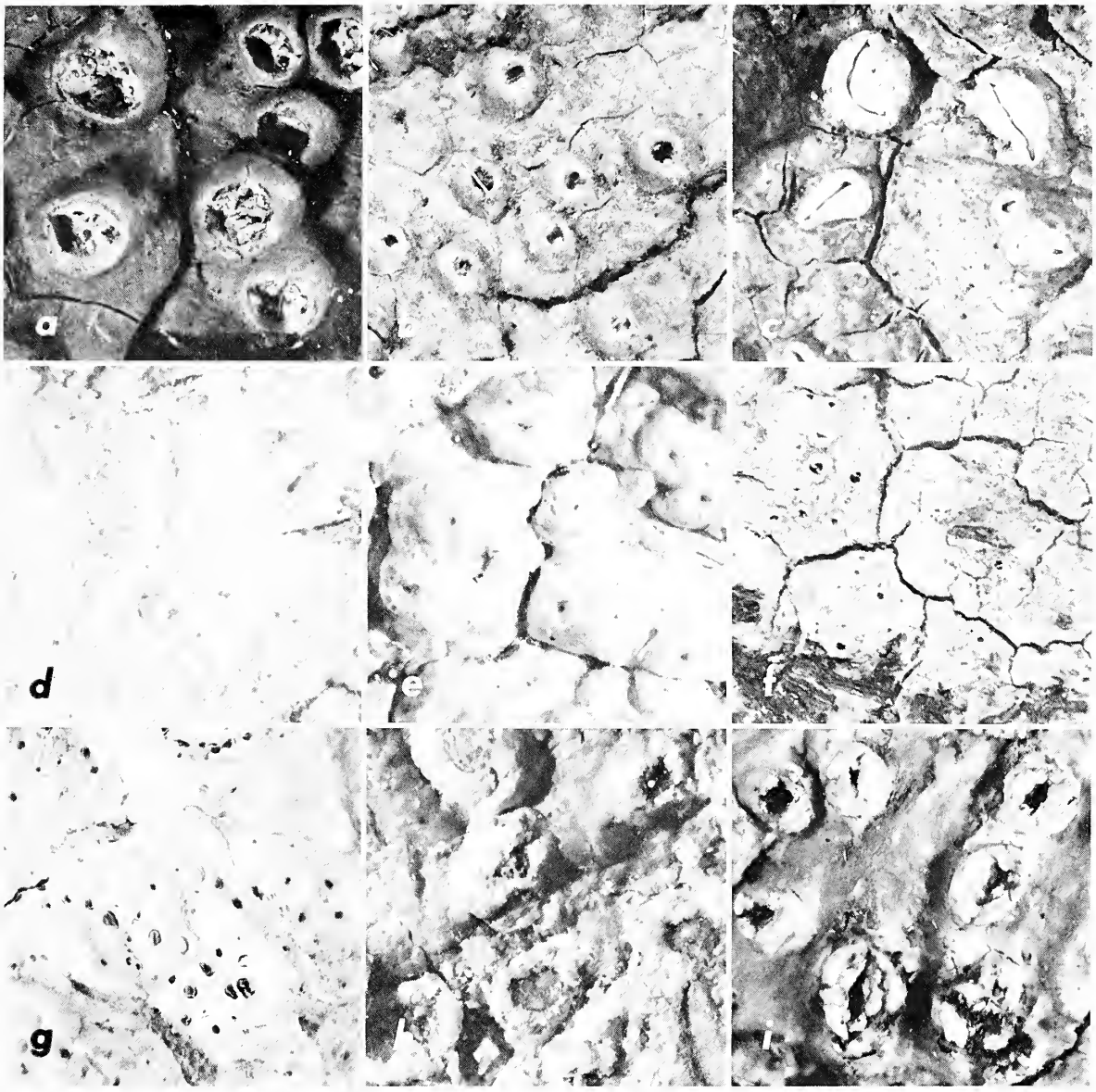

FIGURE 19.—Specimens of Thelotremataceae (all about × 10): *a, Leptotrema fissum* (lectotype in H); *b, L. integrum* (isotype in S); *c, L. fissum* (*Hale* 38031); *d, L. microglaenoides* (lectotype in BM); *e, L. microglaenoides* (*Hale* 37984); *f, L. occultum* (isotype in G); *g, L. occultum* (*Hale*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

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

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 150μ–170μ high; spores 1–2/ascus, brown, muriform with numerous transverse and longitudinal locules, 30μ–40μ × 80μ–130μ, I− (Figure 19*i*).

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 20*a,b*

Leptotrema subcompunctum (Nylander) Zahlbruckner, 1923: 640.

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

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 140μ–160μ high; spores

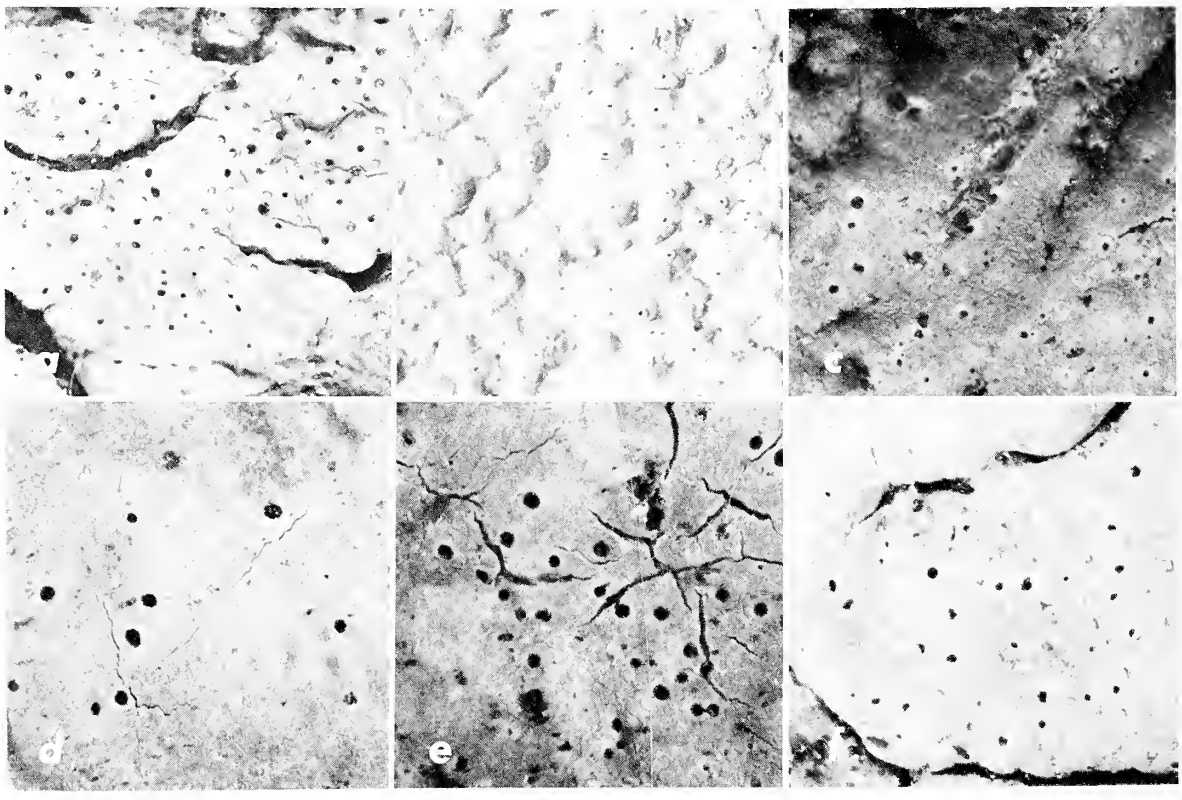

FIGURE 20.—Specimens of Thelotremataceae (all about × 10): *a, Leptotrema subcompunctum* (isotype in P); *b, L. subcompunctum* (*Hale* 37888); *c. L. wightii* (lectotype in FH); *d, L. flavicans* (lectotype in G); *e, L. subconcretum* (lectotype in BM); *f, L. wightii* (*Hale* 35882).

brown, 1–2/ascus, muriform with 8–11 transverse locules and 2–4 longitudinal locules, 10μ–13μ × 45μ–55μ, I− (Figure 20*b*).

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 1*d*, 20*c,f*

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

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

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

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 20*e*].

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 20*d*].

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 1*d*), forming colonies up to 10 cm broad; apothecia immersed, 0.2–0.3 mm in diameter, noncarbonized, without a columella; pore round, 0.08–0.11 mm in diameter, flush; hymenium about 100μ high; spores brown, 8/ascus, muriform with 4–6 transverse locules and 1–2 longitudinal locules, 9μ–11μ × 20μ–28μ, I− (Figure 20*f*).

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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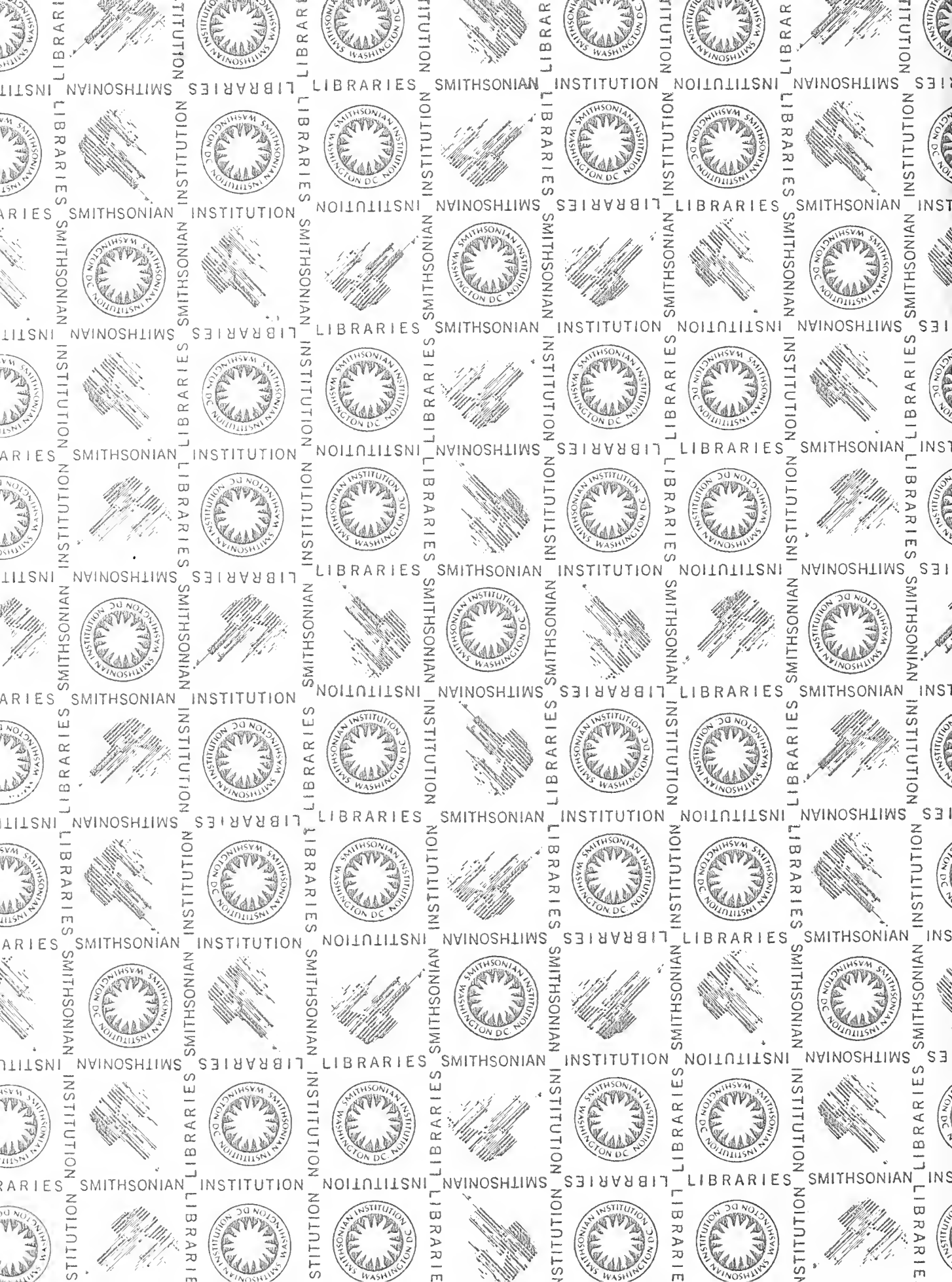
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