

A Revision of the Lichen Family
Thelotremataceae in Panama

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ABSTRACT

Hale, Mason E., Jr. A Revision of the Lichen Family Thelotremataceae in Panama. *Smithsonian Contributions to Botany*, number 38, 60 pages, 15 figures, 1978.—The family Thelotremataceae comprises 99 species in Panama, distributed among four genera, *Ocellularia*, *Phaeotrema*, *Thelotrema*, and *Leptotrema*. It is most common in virgin rain forests at mid-elevations. Phytogeographically there are many species in common with the West Indies and South America. The following species are described as new: *Ocellularia barroensis*, *O. bullata*, *O. congesta*, *O. dactylifera*, *O. dactyliza*, *O. decolorata*, *O. dissuta*, *O. esslingeri*, *O. landronii*, *O. minutula*, *O. neei*, *O. protocetrarica*, *O. pseudoschizostoma*, *O. pulverulenta*, *O. referta*, *O. subwrightii*, *O. uniseptata*, *O. viridis*, *Phaeotrema vulcani*, *Thelotrema hiatum*, *T. maximum*, *Leptotrema chiriquiense*, *L. hypoprotocetraricum*, *L. panamense*, and *L. stellatum*. These new combinations are made: *Ocellularia pachystoma* (Nylander) Hale (basionym: *Thelotrema pachystomum* Nylander) and *O. verrucosa* (Fée) Hale (basionym: *Thelotrema verrucosum* Fée).

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Mason E. Hale, Jr.

Introduction

After completing a field program on the Thelotremataceae in Dominica (Hale, 1974a), I had an opportunity to visit Panama on three separate occasions in 1973, 1974, and 1975. There were only four specimens of the family from Panama on file in the herbarium at the Smithsonian Institution, and no species had ever been reported there (Imshaug, 1956). The prospects for finding many specimens, therefore, seemed poor. Notwithstanding, I was able to collect nearly 600 specimens at 11 localities from the province of Chiriquí in the west to Panamá in the east. Two excellent lichen collectors, Dr. Scott Mori (with Dr. A. Gentry) and Michael Nee, added small but valuable collections, some from the remote Darien region near Colombia, and Dr. T. L. Esslinger and Dr. M. Nakanishi, who accompanied me on different trips, added about 50 more specimens. All of these collections taken together represent 99 species among almost 700 numbers, more than twice as many as I had found in Dominica.

It is very difficult and probably foolhardy to undertake a world monograph of the Thelotremataceae along the usual lines, namely, to locate and examine type collections, annotate available herbarium material, and prepare a monograph from this information. One of the more frustrating aspects of lichenology is that herbarium holdings of tropical groups are notoriously poor. While this is true for almost any plant group, it is especially

true for crustose lichens that are rarely collected in abundance by phanerogamic botanists or naturalists, the main source of lichen specimens in the past. Even in the largest European herbaria, in the case of the Thelotremataceae, one finds mostly sheets of type collections from the 19th century and large holdings of *Thelotrema lepadinum* and some *Leptotrema wightii*.

I have in fact examined most of the type collections of the family Thelotremataceae, representing over 400 species. While about 100 of these have proved to be synonyms, I have already described or will soon add nearly 100 new species to the family and feel confident that another 100 will be discovered as time and resources permit further field work in the tropical rain forests. This particular forest biome, so rich in thelotremes, is being rapidly destroyed and many species will probably become extinct before they can even be collected. My approach has been and will continue to be a detailed examination of the thelotreme floras of specific areas where I have been able to conduct adequate field studies but still including data on synonymy at the world level.

As usual, I am indebted to curators of museums and herbaria who sent collections on loan, as indicated by herbarium acronyms cited under "Specimens Examined." I would like to mention in particular Dr. T. Ahti, Dr. Reino Alava, the late Dr. C. E. Bonner, Mr. M. S. Christiansen, Dr. H. Hertel, Mr. Peter James, Mme. Jovet-Ast, Dr. I. M. Lamb, Dr. H. Riedl, and Dr. R. Santesson. I am also especially thankful for transportation support provided by Dr. Robert Dressler, Smithsonian

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Tropical Research Institute, and by Dr. Michael Nee and Dr. Scott Mori, who were associated with the plant exploration program of the Missouri Botanical Garden at Summit Gardens. Dr. Ove Almborn has kindly read and corrected the Latin descriptions of the new species. Financial support was received from the Smithsonian Institution for the field studies.

Morphological Characters

I have already summarized the main morphological features of the family in my study of the Dominican species (Hale, 1974a) and this information will not be repeated here. The Panamanian species have the same broad characters and any unusual or interesting aspects are summarized below in discussions of the various genera. It is obvious, however, that the terminology for apothecial structure is rather confused at present and cannot be considered as final. As I use the term "lepadinoid," for example, it is only intended to describe semiemergent to emergent apothecia with a free, persistent proper exciple. The "actinoid" columella would perhaps better be called "reticulate," as Salisbury has suggested. "Chroodiscoid," derived from the epiphyllous genus *Chroodiscus*, refers to species with an erect or recurved thalline margin, as in *Ocellularia alborosella* (Figure 4c), while "ascidioid" is used to describe strongly emergent apothecia. All of these terms could be dropped in favor of precise descriptions of the apothecial structures involved.

Chemistry

Chemistry is extremely helpful in routine identifications of specimens of the Thelotremataceae. While morphological characters may vary according to ecological or growth conditions, chemical content of each species is remarkably uniform and stable. The Panamanian species have a chemistry very similar to that of the family in Dominica. For example, the four most common acids, psoromic acid, stictic acid, hypoprotocetraric acid, and protocetraric acid, have almost identical frequency in both areas. Virensic acid, known from *Leptotrema spondaicum* (Nylander) Zahlbruckner in Do-

minica, does not occur in Panama, whereas lichexanthone, a component of five species in Panama, did not occur in Dominica. The acids are tabulated below by chemical groups and further notes will be found in the species discussions. All specimens were studied with precoated Merck silica-gel plates utilizing C. Culberson's A and B solutions. Spots were visualized by spraying the plates with 10% sulfuric acid and heating them for 10 minutes at 110°C. When color tests are used, it is best to expose part of the amphithecial medulla for testing. The thallus is often too thin to evoke a clear test.

DEPSIDES.—This group of lichen substances is extremely rare in the family. For example, only one of 400 known species, *Ocellularia americana* Hale, contains gyrophoric acid. Of the species in Panama, *O. olivacea* contains an unidentified acid (or acids) that I presume to be depsidic in nature because of the chromatographic behavior.

DEPSIDONES.—This group is of frequent occurrence in the Thelotremataceae. The commonest acid is psoromic acid, which occurs with or without norpsoromic acid (Keogh, 1976) in the following 23 species, nearly one-fourth of the family represented in Panama: *Ocellularia antillensis*, *O. berkeleyana*, *O. calvescens*, *O. comparabilis*, *O. glaucophaena*, *O. isidiifera*, *O. latilabra*, *O. minutula*, *O. myriotremoides*, *O. pachystoma*, *O. pulverulenta*, *O. riplei*, *O. subcavata*, *O. subwrightii*, *O. terebratula*, and *O. uniseptata*; *Phaeotrema auberianum*; and *Thelotrema clandestinum*, *T. concretum*, *T. conforme*, *T. cryptotrema*, *T. maximum*, and *T. wrightii*.

The next most common acid is stictic acid, often accompanied by constictic acid in 16 species: *Ocellularia bullata*, *O. conglomerata*, *O. dactylifera*, *O. dilatata*, *O. exanthismocarpa*, *O. neei*, *O. pseudoschizostoma*, and *O. sublilacina*; *Thelotrema erumpens*, *T. glaucopallens*, *T. myriocarpum*, *T. stylothecium*, and *T. subpraestans*; and *Leptotrema deceptum*, *L. reclusum*, and *L. trypaneoides*.

Closely following stictic acid, hypoprotocetraric acid, which is the only P- depsidone, is the main component in 15 species (frequently accompanied by 4-O-demethylnotatic acid (Culberson and Hale, 1973), by unidentified spots, or in *Phaeotrema glypticum* by lichexanthone): *Ocellularia actinota*, *O. aurulenta*, *O. congesta*, *O. domingensis*, *O. fecunda*, *O. glaucula*, *O. microporella*, *O. referta*, and *O. rhodostroma*; *Phaeotrema glypticum* and

P. leiostomum; *Thelotrema myrioporoides* and *T. oclusum*; and *Leptotrema chiriquiense* and *L. hypoprotocetraricum*.

Protocetraric acid occurs in the following eight species: *Ocellularia dactyliza*, *O. perforata*, *O. protocetrarica*, and *O. verrucosa*; *Thelotrema auratum*; and *Leptotrema bahianum*, *L. laeviusculum*, and *L. panamense*. Two of these, *Thelotrema auratum* and *Leptotrema panamense*, also contain epihymenial pigments.

Norstictic acid occurs in only one species, *Thelotrema norsticticum*.

Unidentified (and presumed) depsidones were found in *Thelotrema praestans* (the "praestans" unknown) and in *Ocellularia cavata*, *O. crocea*, *O. decolorata*, *O. rhabdospora*, and *O. subemersa* (the "cinchonarum" or "cavata" unknown). Both of these react P+ red.

XANTHONES.—The only xanthone in the Thelotremataceae is lichexanthone, which reacts brilliant orange under longwave ultraviolet radiation. It is a component of the cortex in five species: *Ocellularia glaucula*, *Phaeotrema glypticum*, *Thelotrema myrioporoides*, *Leptotrema metaphoricum*, and *L. microsporum*.

ANTHRAQUINONES AND OTHER PIGMENTS.—Various red or orange anthraquinone pigments, of which only endocrocin has been positively identified, are present in *Ocellularia crocea*, *O. mordenii*, *O. rhodostroma*, and *O. xanthostroma* (all in the medulla) and in *Thelotrema auratum* and *Leptotrema panamense* (epihymenial) and *L. wightii* (medullary). Unidentified yellow medullary or amphithecial pigments, perhaps related to entothecin, are known in *Ocellularia aurulenta*, *O. cavata*, and *O. fecunda*.

UNIDENTIFIED SUBSTANCES.—Three species, *Ocellularia esslingerii*, *O. recondita*, and *O. viridis*, show distinct P-, H₂SO₄+ gray spots, presumably phenolic in nature and probably new substances.

NO SUBSTANCES PRESENT.—Twenty-one species, as listed below, reacted negative in color tests and produced no substances reacting H₂SO₄ positive on the chromatographic plates: *Ocellularia alba*, *O. alborosella*, *O. barroensis*, *O. chionostoma*, *O. concolor*, *O. dissuta*, *O. landronii*, *O. papillata*, and *O. turgidula*; *Phaeotrema meiospermum* and *P. vulcanum*; *Thelotrema adjectum*, *T. conveniens*, *T. hiatum*, *T. lepadinum*, *T. leucomelaenum*, *T. pycnoporellum*, and *T. tenue*; and *Leptotrema lepadodes*, *L. stellatum*, and *L. urceolare*.

The Thelotrema Flora

One of my goals in tropical field work with the Thelotremataceae has been an attempt to estimate how many species one can reasonably expect to collect out of the total lichen flora. In Dominica I made deliberate efforts to recollect certain areas, make random transects, and otherwise satisfy myself that the number of species finally identified (48) came close to representing the total flora. Rough statistical extrapolations showed that there are probably about 55 species of thelotremes on Dominica and that the seven not yet found could be collected on additional excursions, but since time and financial resources are limiting factors, especially in the tropics, one must obviously be satisfied with a less than complete sampling.

I found that similar estimates are not now possible in Panama, a much larger, more diverse, and less thoroughly collected region than Dominica. As in Dominica, new species comprise 30% of the flora, but I found that each new locality in Panama added at least one new species, not to mention new records of species for Panama. In other words, we are still on the slope of a theoretical sigmoid curve of species distribution, but an estimate of 130–140 species in the flora may not be far off.

The question cannot be answered until more forest sites have been investigated, and the problem of accessibility to virgin forests in Panama prevents us from reaching this goal quickly. I made samples at points where roads were being opened up and felled trees could be easily reached, but the minuteness of this sample is all too evident when one realizes that the 12 collecting sites were taken along a nearly continuous range of forest extending about 600 km.

There is little doubt, however, that a general lichen collector, one who tries to collect all lichen families in a limited amount of time, does justice to none of them, especially with crustose groups such as the Thelotremataceae, which can often only be recognized in the field after careful, time-consuming searching with a hand lens. A general collector could probably be expected to collect no more than 10–30% of the total number of species in the Thelotremataceae in Panama, especially if he did not have access to freshly felled trees.

Details on the number of specimens collected and comparisons with Dominica are given below

under discussions of the genera. About 30 collections were sterile and could not be assigned to genus. An additional 20–30 specimens have not been identified to species level yet for various reasons and will be left for future study.

Collecting Sites

My main aim in Panama was to work only in the virgin rain forests, which occur in large unbroken tracts in the low mountains along the Caribbean side of the country. Unfortunately these sites are often remote from the main east-west Panamerican Highway and can only be reached where new roads are being cut across the isthmus, as at Santa Fe, El Valle, Cerro Jefe, etc., and at Volcán Chiriquí. The entire Pacific side was left unexplored; much of it is dry savanna used for cattle ranches, but good rain forest is reported to occur at higher elevations in the Ocu Peninsula. Nor did I enter the roadless Darien region but had access to collections by Mori and Gentry. My first collecting trip was made in 1973 and included Chiriquí, the two road cuts at Cerro Jefe and El Llano-Cartí, and Barro Colorado Island. The second trip in 1974 included the Gamboa area, Colón, Santa Rita Ridge, and El Valle. The third trip with Dr. T. L. Esslinger covered the sites near Alto Piedra above Santa Fe, the road cut to the Río Calevobora, and second visits to Chiriquí and Barro Colorado Island.

The localities are coded as follows in the list of specimens examined.

1. Virgin oak cloud forest at 1900–2200 m elevation, Volcán Chiriquí, along the trail from Cerro Punto to Boquete, Province of Chiriquí. The first trip is indicated as 1, the second as 1a. On the second trip the oak forest was already being logged and I was able to collect more extensively in the canopy.
2. Recently logged rain forest at about 750 m elevation at La Mesa, north of El Valle, Province of Coclé. This was a very rich locality for the family and much forest remains in spite of recent clearing for chicken farms.
3. Mixed mature secondary and primary rain forest at 100–150 m elevation, Barro Colorado Island, Canal Zone (3 represents the first visit, 3a the second). Specimens were collected primarily along several main trails on the southern half of the island. This forest reserve has recovered from disturbances previous to the closing of the area when the canal was built about 80 years ago.
4. Mature secondary rain forest along the Naval Pipeline Road at 150 m, 9 km northwest of Gamboa, Canal Zone. This forest is very similar to that on nearby Barro Colorado

but few canopy species were collected because of the absence of windfalls.

5. Open secondary groves at Summit Gardens, Canal Zone. As expected, this was a poor site for the family.
6. Recently logged primary forest and remnant stands at about 350 m elevation, Santa Rita Ridge, about 6 km from Roosevelt Highway, Province of Colón. Rather extensive forests remain in this interesting area.
7. Secondary rain forest near sea level, a few kilometers northwest of Colón, Province of Colón. This was the poorest site visited for no obvious reasons.
8. Road cut through primary rain forest at about 300 m elevation, 16–20 km along the El Llano-Cartí road, Province of Panamá. This was a magnificent locality with easy access to understory as well as to freshly felled trees.
9. Roadcut through primary rain forest at about 700 m elevation in the vicinity of Cerro Jefe, Province of Panamá. This was also a rich locality, similar to 8 but with fewer felled trees.
10. Disturbed primary forest and pasture at base of mountain west of Alto Piedra at about 850 m elevation, Province of Veraguas. There was no access to felled trees here and thelotremes were poorly represented.
11. New road cut through primary rain forest at about 800 m elevation, 4–8 km from Alto Piedra going toward Río Calevobora, Province of Veraguas. This was an excellent area since several hectares of trees had just been felled.
12. Primary rain forest in the Serranía del Darien region (near the Tacarcuna River) at about 1800 m elevation, Province of Darien. Specimens from this remote locality, reached only by boat and long hikes, were collected by Mori and Gentry.

Specimens collected by Hale, Mori, and Nee are filed in the Smithsonian Institution (US); those by Esslinger are in his private herbarium. Standard herbarium acronyms indicate location of type specimens seen. Many of these types are illustrated in Figures 1 and 2 and others will be found in Hale (1974a).

Full citations for synonyms of species that also occur in Dominica (Hale, 1974a) are not usually repeated here. Statements on distribution of species outside of Dominica and Panama are based on my own determinations of specimens in BM, FH, G, H, L, LD, M, PC, S, UPS, US, and W. Provisional determinations are indicated by "cf." All species descriptions are taken from populations in Panama and deviations from the types are noted under "Remarks." The chemical components, however, represent results of analyzing the types, and any differences with the Panamanian populations are noted under "Remarks." All literature has been examined in the original to ascertain the exact designation of types.

When identifying species in the Thelotremata-

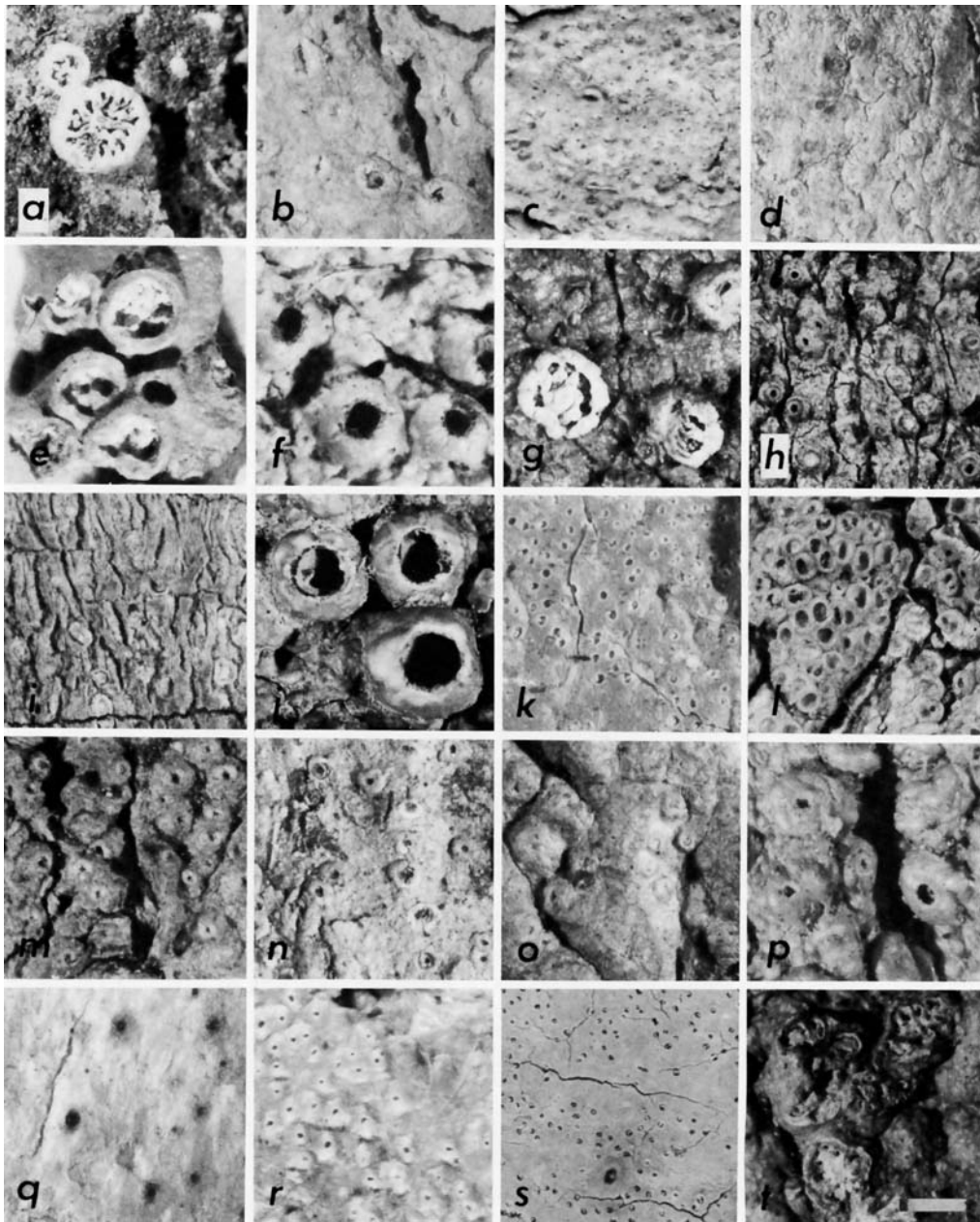


FIGURE 1.—Type specimens of Thelotremataceae (listed alphabetically by species under the original basionym): a, *Thelotrema actinotum* Tuckerman (FH-Tuck); b, *Thelotrema adjectum* Nylander (H-Nyl); c, *Myriotrema album* Fée (G); d, *Thelotrema annulatum* Müller Argoviensis (G); e, *Thelotrema auberianum* Montagne, (H-Nyl); f, *Thelotrema auratum* Tuckerman (FH-Tuck); g, *Stegobolus berkeleyanum* Montagne (BM); h, *Thelotrema calvescens* Fée (G); i, *Thelotrema chionostomum* Nylander (FH-Tuck); j, *Thelotrema citrinodiscum* Redinger (S); k, *Thelotrema clandestinum* Fée (G); l, *Thelotrema concretum* Fée (G); m, *Thelotrema connivens* Nylander (N-Nyl); n, *Ascidium croceum* Krempelhuber (M); o, *Thelotrema cryptotrema* Nylander (H-Nyl); p, *Ascidium domingense* Fée (FH-Tuck); q, *Thelotrema erumpens* Magnusson (UPS); r, *Thelotrema glaucophaenum* Krempelhuber (M); s, *Thelotrema glauculum* Nylander (H-Nyl); t, *Thelotrema glyphicum* Nylander (FH-Tuck). (1 mm scale for all species is given in 1t.)

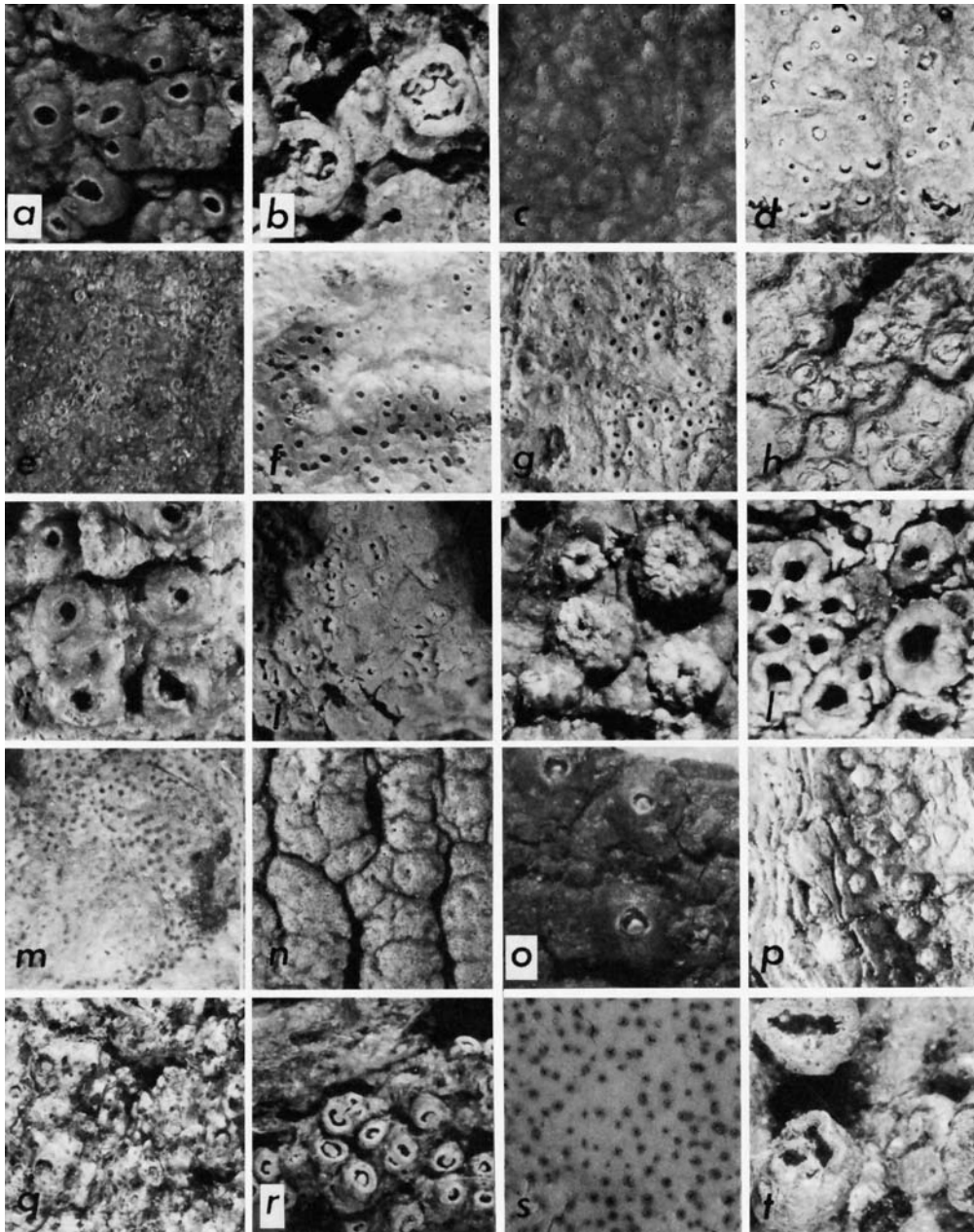


FIGURE 2.—Type specimens of Thelotremataceae (listed alphabetically by species under original basionym): *a*, *Thelotrema intervallatum* Nylander (H-Nyl); *b*, *Thelotrema leucotylum* Nylander (BM); *c*, *Thelotrema microporellum* Nylander (FH-Tuck); *e*, *Thelotrema myriocarpum* Fée (PC); *f*, *Thelotrema myrioporoides* Müller Argoviensis (G); *h*, *Thelotrema oclusum* Nylander (H-Nyl); *i*, *Thelotrema oculatum* Vainio (TUR); *j*, *Thelotrema opacum* Vainio (TUR); *k*, *Thelotrema pachystomum* Nylander (PC); *l*, *Thelotrema porphyrodiscum* Zahlbruckner (W); *m*, *Thelotrema pycnoporellum* Nylander (H-Nyl); *n*, *Thelotrema reclusum* Krempelhuber (H-Nyl); *o*, *Thelotrema reconditum* Stirton (BM); *p*, *Thelotrema secoligella* Müller Argoviensis (G); *q*, *Thelotrema stylothecium* Vainio (FH); *r*, *Ocellularia subemersa* Müller Argoviensis (G); *s*, *Thelotrema trypaneoides* Nylander (FH-Tuck); *t*, *Thelotrema wrightii* Tuckerman (FH-Tuck). (1 mm scale for all species is given in Figure 1t.)

ceae, it is desirable to determine chemical contents with thin-layer chromatography, although thalline color tests are invoked as far as possible in the keys and will suffice up to a certain point.

Ocellularia Meyer

Ocellularia, the most commonly collected genus in the family, includes about 175 species and the 57 species in Panama represent almost 30% of those known. The 400 specimens comprise 60% of the total 700 collected in Panama. This compares with 72% in Dominica, where the perhaps abnormally high frequency of *O. rhodostroma* distorts the percentage somewhat. The 10 commonest species are as follows, compared with the ranking in Dominica (in parentheses): 1 (3), *O. perforata*, 63 collections; 2 (4), *O. papillata*, 45; 3 (2), *O. fecunda*, 24; 4 (not in Dominica), *O. ripleyi*, 17; 5 (not in Dominica), *O. sublilacina*, 16; 6 (12), *O. concolor*, 15; 7 (not in Dominica), *O. glaucophaena*, 15; 8 (5), *O. subcavata*, 12; 9 (not in Dominica), *O. latilabra*, 10; 10 (not in Dominica), *O. microporella*, 10. All of the 10 commonest species in Dominica, excepting *O. nigropuncta*, also occurred in Panama.

Of the 57 species reported here, 21 (37%) are new, either described here or in Hale (1947b), compared with 8 of 22 (36%) in Dominica, virtually identical percentages.

Ocellularia was usually collected at each locality in abundance except for the secondary forest at Summit Gardens. Where sites were visited twice, there was not a high level of duplication, suggesting that while a single visit may turn up a majority of the species, certainly not all will be collected. For example, I collected nearly equal numbers of specimens (about 50) on two separate visits to Barro Colorado Island. On the first I discovered 16 species. On the second trip, seven of these (*O. comparabilis*, *O. glaucophaena*, *O. papillata*, *O. perforata*, *O. recondita*, *O. ripleyi*, and *O. sublilacina*) were rediscovered. These were also the seven commonest species both times; however, a total of nine species (*O. antillensis*, *O. berkeleyana*, *O. calvescens*, *O. concolor*, *O. dilatata*, *O. glaucula*, *O. olivacea*, *O. unispetata*, and *O. verrucosa*) were not recollected on the second visit. Most of these species were represented by a single collection. At the same time 5 of the 12 species collected on the second visit (*O. barroensis*, *O. latilabra*, *O. minutula*, *O. sub-*

wrightii, and *O. xanthostroma*) had not been collected on the first trip.

The richest locality was, in fact, Barro Colorado Island with 21 species, followed by El Valle with 18, Cerro Jefe with 17, El Llano-Cartí road with 16, the Río Calevobora road and Santa Rita both with 15, and Gamboa with 12. Only eight species were collected in the cloud forest at Volcán Chiriquí, where *Thelotrema* and *Leptotrema* predominated. This reinforces my impression that *Ocellularia* is primarily a genus of low to mid elevation rain forest, overshadowed by *Thelotrema* at higher elevations.

The morphology of the genus follows lines similar to those in Dominica. Isidia are clearly developed in *O. dactylifera* and *O. isidiifera* and sorediate structures in *O. pulverulenta*. The thallus is distinct and epiphloeodal in all species except *O. chionostoma*, *O. concolor*, *O. exanthismocarpha*, and *O. neei*, which are hypophloeodal. The species may be grouped according to apothecial structure as discussed in Hale (1947a:2). Chroodiscoid species, those with an open disc, erect to recurved thalline margin, and an often persistent proper exciple (Figures 4c, 5h, 8b), include *O. alborosella*, *O. chionostoma*, *O. conglomerata*, *O. dilatata*, *O. dissuta*, *O. esslingeri*, *O. neei*, *O. pseudoschizostoma*, *O. referta*, and *O. sublilacina*. The lepadinoid type apothecium, where the walls are more incurved to form a more or less distinct pore, through which a free proper exciple is visible, is characteristic of *O. exanthismocarpha* and *O. turgidula*. The myriotremoid species have immersed or flush apothecia: *O. alba*, *O. glaucula*, *O. microporella*, *O. olivacea*, *O. terebratula*, and *O. unispetata*. Here the proper exciple may or may not persist, and there is no carbonized tissue.

Columellate species include *O. antillarum*, *O. cavata*, *O. concolor*, *O. landronii*, *O. papillata*, *O. perforata*, *O. recondita*, *O. ripleyi*, *O. subcavata*, and *O. subemersa*. A weakly developed columella may be present in *O. isidiifera*, *O. minutula*, and *O. mordenii*. The reticulate or actinoid columella (Figure 1a) occurs in *O. actinota*, *O. berkeleyana*, and *O. latilabra* and is imperfectly developed in *O. barroensis*, *O. comparabilis*, *O. protocetrarica*, *O. subwrightii*, and *O. viridis* (Figure 3f).

The species of *Ocellularia* often have strong habitat preferences, as I have found in Dominica, and species in common to these two regions have

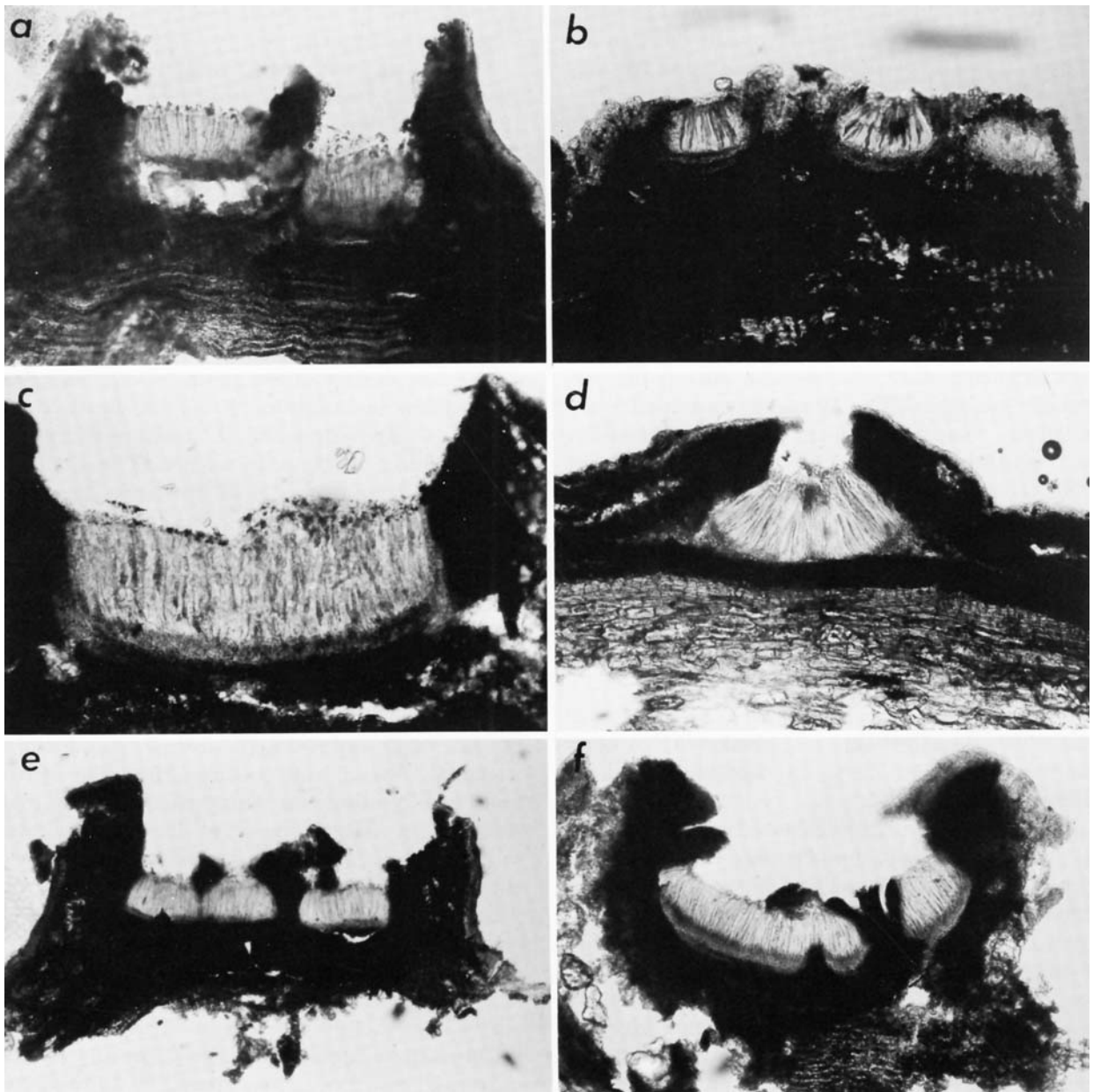


FIGURE 3.—Cross section of apothecia of *Ocellularia* species: a, *O. barroensis* (Hale 46069) ($\times 125$) (hymenium pulled away from hypothecium in left part); b, *O. dactylifera* (Hale 43503) ($\times 125$); c, *O. dactyliza* (Hale 43559) ($\times 125$); d, *O. minutula* (Hale 43341) ($\times 125$); e, *O. prototetrarica* (Hale 44786) ($\times 100$); f, *O. viridis* (Hale 38538) ($\times 125$).

similar behavior. Added to data on habitats of type collections, especially elevation, where this can be determined, it is possible to categorize the more common Panamanian species as follows: restricted to higher elevations (more than 2000 m) are *O. domingensis*, *O. isidiifera*, *O. pachystoma*, and *O.*

rhabdospora; restricted to low elevations (less than 300 m) are *O. glaucophaena*, *O. minutula*, *O. recondita*, *O. ripleyi*, *O. sublilacina*, *O. uniseptata*, and *O. verrucosa*. The remaining species occur in the rain forests at 300 to 1800 m elevation.

Species restricted to the canopy include *O. glau-*

cula, *O. microporella*, *O. mordenii*, *O. olivacea*, *O. subemersa*, *O. subcavata*, *O. terebratula*, and *O. uniseptata*. A few species occur mostly at base level in dense rain forest: *O. dilatata*, *O. concolor*, *O. papillata*, *O. perforata*, and *O. sublilacina*. Much more field work will be needed to categorize the remaining species, although it is obvious that most grow out of normal reach on the mid to upper trunk areas.

Any statements on the phytogeography of *Ocellularia* must be regarded as provisional and subject to modification as more collections of the group are made. One may generalize by saying that

the *Ocellularia* flora shows considerable affinity with those of both the Caribbean and South American area. For example, *O. domingensis*, *O. pachystoma*, *O. recondita*, and *O. verrucosa* were previously known only from South America. *Ocellularia actinota*, *O. fecunda*, *O. glaucula*, *O. landronii*, *O. microporella*, *O. rhodostroma*, *O. subemersa*, and *O. xanthostroma* are all typical Caribbean species. The pantropical element is represented by *O. alba*, *O. berkeleyana*, *O. cavata*, *O. concolor*, *O. crocea*, *O. exanthismocarpa*, *O. glaucophaena*, *O. olivacea*, *O. papillata*, *O. perforata*, *O. subcavata*, and *O. terebratula*.

Key to the Species of *Ocellularia*

1. Spores very large, 100–250 μm long.
 2. Medulla white, unpigmented.
 3. Apothecia emergent; thallus finely verrucose; P+ yellow (psoromic acid)48 *O. ripleyi*
 3. Apothecia strongly emergent to ascidioid; thallus smooth; P– or P+ red.
 4. Distinct central columella present.45. *O. rhabdospora*
 4. Columella lacking.22. *O. domingensis*
 2. Medulla pigmented yellow or red.
 5. Medulla yellow, K– or more intensively yellow.
 6. Apothecia strongly emergent; pore gaping, to 0.4 mm broad.25. *O. fecunda*
 6. Apothecia semi-emergent; pore less than 0.1 mm wide.5. *O. aurulenta*
 5. Medulla red or orange, K+ reddish or purple.
 7. Pigments yellow orange.57. *O. xanthostroma*
 7. Pigments red or deep pink.
 8. Apothecia strongly emergent; pore annulate; medulla deep pink.46. *O. rhodostroma*
 8. Apothecia semiemergent; pore not annulate; medulla blood red.33. *O. mordenii*
1. Spores smaller, less than 100 μm long.
 9. Apothecia chroodiscoid with an erect or recurved thalline margin and often a persistent proper exciple; columella never present (*O. conglomerata*, *O. exanthismocarpa*, and *O. turgidula* have conspicuous lepadinoid apothecia that may appear chroodiscoid; *O. latilabra* has an open disc but it is actinoid-columellate); thalline margin noncarbonized.
 10. Disc very broad, 2–4 mm wide; spores 60–80 μm long.50. *O. sublilacina*
 10. Disc less than 2 mm broad; spores less than 30 μm long.
 11. Apothecia less than 0.3 mm in diameter; disc heavily pruinose.11. *O. chionostoma*
 11. Apothecia 0.5–1.0 mm wide; disc, if pruinose, remaining distinct.
 12. Stictic acid present.
 13. Proper exciple persistent, free.
 14. Apothecia aggregated; disc partially filled with excipular material.15. *O. conglomerata*
 14. Apothecia separate; disc open35. *O. neei*
 13. Proper exciple evanescent.
 15. Thalline rim very coarse, recurved.20. *O. dilatata*
 15. Thalline rim crumbling apically, erect.41. *O. pseudoschizostoma*
 12. Stictic acid lacking.
 16. Thalline margin delicate, recurved.3. *O. alborosella*
 16. Thalline margin coarse, erect.
 17. Thalline margin entire, uniformly thickened.23. *O. esslingeri*
 17. Thalline margin irregular, splitting.21. *O. dissuta*
 9. Apothecia with an incurved thalline margin and more or less closed disc, flush, semi-emergent, or ascidioid with a discrete pore; disc, if open, with an actinoid columella.
 18. Columella present.

Key to the Species of *Ocellularia* (cont'd)

19. Central reticulate columella present; disc relatively open (*O. barroensis* and *O. protocetrarica* have weakly carbonized, mostly superficial actinoid structures; *O. comparabilis* and *O. subemersa* have a main columella with some secondary actinoid formation).
20. Thallus isidiate.28. *O. isidiifera*
20. Thallus lacking isidia.
21. Thallus and disc P-. 1. *O. actinota*
21. Thallus and disc P+ yellow (psoromic acid).
22. Thalline rim irregularly split.30. *O. latilabra*
22. Thalline rim entire.
23. Apothecia 2-5 mm broad.51. *O. subwrightii*
23. Apothecia less than 2 mm broad.7. *O. berkeleyana*
19. Central columella simple (becoming partially actinoid in *O. comparabilis* and *O. subemersa*); disc more or less closed with a distinct pore.
24. Thallus and apothecia P-.
25. Apothecia strongly emergent, urceolate.56. *O. viridis*
25. Apothecia nearly flush to semiemergent.
26. Thallus dull, largely hypophloeodal; pore to 0.4 mm wide, black inside.13. *O. concolor*
26. Thallus distinct, shiny, epiphloeodal; pore 0.1-0.2 mm wide.
27. Apothecia semiemergent to emergent; pore white annulate.43. *O. recondita*
27. Apothecia nearly flush to semiemergent; pore not annulate.
28. Thallus dark greenish; apothecia sunken.29. *O. landronii*
28. Thallus whitish mineral gray; apothecia flush to slightly emergent.38. *O. papillata*
24. Thallus and apothecia P+ orange or yellow.
29. Thallus and apothecia P+ yellow (psoromic acid).
30. Pore annulate; base of columella heavily carbonized, the upper part only partially48. *O. subcavata*
30. Pore not annulate; columella uniformly carbonized.
31. Pore round, 0.1 mm or less in diameter; thallus thin, minutely verrucose. 4. *O. antillensis*
31. Pore larger, irregular, to 0.2 mm wide; thallus rather thick, smooth.12. *O. comparabilis*
29. Thallus and apothecia P+ red (psoromic acid lacking)
32. Apothecia quite emergent, becoming urceolate; spores 4-loculate, 12-15 μm long.49. *O. subemersa*
32. Apothecia barely emergent to strongly emergent; spores 6-18 loculate, more than 20 μm long.
33. Apothecia small, 0.4-0.6 mm broad, flush to semiemergent; protocetraric acid present.39. *O. perforata*
33. Apothecia larger, 0.6-0.9 mm broad, emergent; "cinchonarum" unknown present.10. *O. cavata*
18. Columella lacking (*O. barroensis* and *O. protocetrarica* may have weak actinoid growths on the surface of the disc).
34. Medulla orange throughout16. *O. crocea*
34. Medulla white.
35. Spores 50-70 μm long, 12-28 loculate.
36. Thallus fragile, densely bullate-pustulate 8. *O. bullata*
36. Thallus smooth (coarsely isidiate in *O. dactyliza*).
37. Thallus coarsely isidiate.18. *O. dactyliza*
37. Thallus smooth, nonisidiate.
38. Stictic acid present24. *O. exanthismocarpa*
38. No lichen substances present53. *O. turgidula*
35. Spores 6-30 μm long, 1-9 loculate.
39. Apothecia more or less emergent, large, 0.5-2.0 mm in diameter.
40. Pore relatively wide and open, filled with excipular material.

41. Apothecia aggregated, emergent with a distinct semierect thalline margin.15. *O. conglomerata*
41. Apothecia mostly separate and only weakly emergent; thalline margin not raised.
42. Thallus P+ red19. *O. decolorata*
42. Thallus P-44. *O. referta*
40. Pore discrete, without intruding excipular material.
43. Apothecia becoming strongly emergent with an erect, apically crumbling thalline margin.37. *O. pachystoma*
43. Apothecia emergent, the apex not crumbling.
44. Thallus P-.6. *O. barroensis*
44. Thallus P+ yellow or red.
45. Protocetraric acid present.
46. Pore usually black rimmed; thallus roughened and verrucose.55. *O. verrucosa*
46. Pore not black rimmed; thallus smooth.40. *O. protocetrarica*
45. Psoromic acid present.
47. Thallus becoming coarsely and sparsely sorediate.42. *O. pulverulenta*
47. Thallus smooth, esorediate.
48. Pore about 0.1 mm wide, becoming annulate.9. *O. calvescens*
48. Pore 0.1-0.3 mm wide, not annulate.26. *O. glaucophaena*
39. Apothecia immersed to flush, usually not more than 0.4 mm wide.
49. Thallus P-.
50. No lichen substances present (using TLC).
51. Apothecia about 0.2 mm wide, flush.2. *O. alba*
51. Apothecia 0.2-0.4 mm wide, becoming slightly emergent.38. *O. papillata*
50. Lichen substances present (using TLC).
52. "Olivacea" unknowns present.36. *O. olivacea*
52. Hypoprotocetraric acid present.
53. Apothecia to 0.3 mm wide (or wider in *O. referta*); pore rather open.
54. Apothecia semiemergent, the pore open without intruding excipular material.14. *O. congesta*
54. Apothecia nearly flush with a broad pore area filled with excipular material.44. *O. referta*
53. Apothecia 0.1-0.2 mm wide, flush; pore 0.05-0.1 mm in diameter.
55. Lichexanthone present (UV+ orange); proper exciple often persistent.27. *O. glaucula*
55. Lichexanthone absent; proper exciple evanescent.31. *O. microporella*
49. Thallus P+ orange or yellow.
56. Thallus subsidiate; stictic acid present (a trace of stictic acid may occur with psoromic acid in *O. uniseptata*).17. *O. dactylifera*
56. Thallus smooth, nonisidiate; psoromic acid present.
57. Spores 4-6 μm long, mostly 2 loculate.54. *O. uniseptata*
57. Spores 10-20 μm long, 4-6 loculate.
58. Thallus surface dull, finely scabrid; pore more or less annulate.34. *O. myriotremoides*
58. Thallus shiny, not scabrid; pore not annulate.
59. Apothecia flush to semiemergent at maturity.26. *O. glaucophaena*
59. Apothecia remaining flush.
60. Apothecia sparsely developed; spores more than 20 μm long.32. *O. minutula*
60. Apothecia numerous; spores less than 20 μm long.52. *O. terebratula*

1. *Ocellularia actinota*

FIGURE 4a

Ocellularia actinota (Tuckerman) Müller Argoviensis, 1887b: 397.

Thelotrema actinotum Tuckerman, 1862:411 [type collection: Cuba, Wright 132 (FH, lectotype; isotype in L) (Figure 1a)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, smooth to irregularly warty and cracked, dull greenish mineral gray, 6–8 cm broad; apothecia solitary to clumped in 2–3s, emergent, up to 2 mm in diameter, the thalline margin semierect, the columella reticulate but not strongly carbonized, the exposed surface and apothecial rim whitish ivory, lightly pruinose; spores 8, $6 \times 15 \mu\text{m}$, 3–4 loculate, I+ blue.

CHEMISTRY.—Hypoprotocetraric and 4-O-demethylnotatic acids.

REMARKS.—This is the only reticulate columellate species with hypoprotocetraric acid. Superficially it resembles *O. berkeleyana* (Montagne) Zahlbruckner, which has psoromic acid. Previously known only from Cuba, *O. actinota* was collected by Scott Mori in the remote Darien region of eastern Panama at about 1800 m.

SPECIMEN EXAMINED.—12: Mori 4462.

2. *Ocellularia alba*

FIGURE 4b

Ocellularia alba (Fée) Müller Argoviensis, 1887a:6.

Myriotrema album Fée, 1824:104 [type collection: "America meridionali, ad corticem *Bonplandiae trifoliatae* (Wild.)" G, lectotype; isolectotype in H) (Figure 1c)].

Thelotrema myriotrema Nylander, 1857:107. [Based on *Myriotrema album* Fée].

Thelotrema myrioporum Tuckerman, 1862:412 [type collection: Cuba, Wright 129 (FH-Tuck, lectotype; isolectotypes in BM, G, L, PC, UPS)].

Thelotrema album (Fée) Nylander, 1868:35.

Thelotrema subcrassulum Vainio, 1929:38 [type collection: El Yunque, Puerto Rico, Fink 725 (MICH, lectotype; isolectotypes in F, FH, NY, US)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin, shiny, greenish mineral gray, 3–5 cm broad; apothecia numerous, immersed, dispersed, 0.2–0.4 mm in diameter, noncarbonized, a columella lacking, the pore round, 0.05–0.1 mm in diameter;

spores 8, uniseriate, $5-6 \times 16-18 \mu\text{m}$, 4–5 loculate, I+ blue.

CHEMISTRY.—No substances present.

REMARKS.—The flush, noncarbonized apothecia are similar to those of *O. olivacea* (Fée) Müller Argoviensis and *O. terebratula* (Nylander) Müller Argoviensis, both of which have a thicker thallus and different chemistry. I have identified the species from Brazil, the Philippines, Sarawak, the Solomon Islands, and Australia, occurring from sea level to 1200 m elevation. In Panama I collected it only once, on the base of a large tree at 700 m. Redinger (1936:43) places *Thelotrema viridialbum* Krempelhuber in synonymy under *O. alba*, but I found that Krempelhuber's type in M has muriform spores, coarse, almost isidiate outgrowths, and lichexanthone. He also regarded *O. costaricensis* Müller Argoviensis as a form of *O. alba*, but this species contains psoromic acid, and, as Redinger noted, is columellate.

SPECIMEN EXAMINED.—9: 38433.

3. *Ocellularia alborosella*

FIGURE 4c

Ocellularia alborosella (Nylander) Santesson, 1952:308.

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

Thelotrema platycarpellum Vainio, 1923:138.

Ocellularia platycarpella (Vainio) Zahlbruckner, 1923:598.

[For full citations see Hale (1974a:16).]

DESCRIPTION.—Thallus corticolous, epiphloeodal but very thin, shiny and smooth, whitish gray, 5–8 cm broad; apothecia chroodiscoid, up to 1.5 mm across, round to irregularly shaped, the recurved thalline margin conspicuous, the inner exciple free, entire, the disc flesh colored to white pruinose; spores 8, $5-8 \times 10-20 \mu\text{m}$, 5–6 loculate, I+ weakly blue.

CHEMISTRY.—No substances present.

REMARKS.—Spore size is variable in this widespread species, averaging 10–20 μm long but rarely as short as 6–8 μm or as long as 36 μm . The significance of this degree of variation has yet to be determined. The delicate recurved rim and the rather broad pruinose disc are diagnostic. *Ocellularia chionostomum* (Nylander) Riddle (see page 16) has smaller apothecia and a less conspicuous

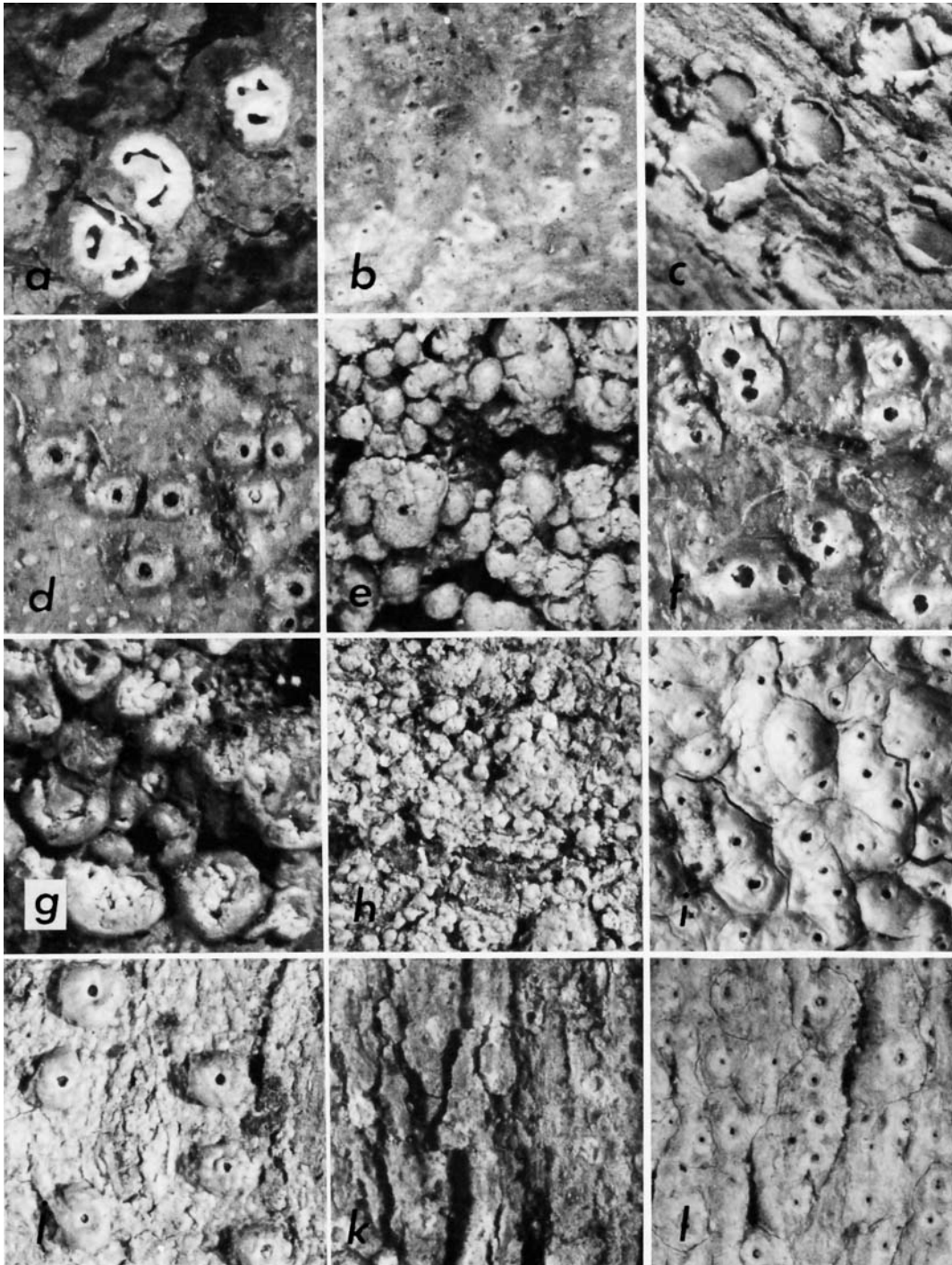


FIGURE 4.—Species of *Ocellularia*: a, *O. actinota* (Mori 4462); b, *O. alba* (Hale 38433); c, *O. alborosella* (Hale 46056); d, *O. antillensis* (Hale 43561); e, *O. aurulenta* (Hale 43567); f, *O. barroensis* (Hale 46069); g, *O. berkeleyana* (Hale 38461); h, *O. bullata* (Hale 34878); i, *O. calvescens* (Hale 38757); j, *O. cavata* (Hale 38466); k, *O. chionostomum* (Hale 43455); l, *O. comparabilis* (Hale 44905) ($\times 10$).

recurved rim. *Ocellularia dilatata* Müller Argovien-
sis is much larger and coarser and contains stictic
acid. The species occurs on lower trunks and sap-
lings in primary and secondary forest at 700–1000
m in Panama. I have also seen specimens from
Louisiana, the West Indies, Venezuela, and Brazil,
where it occurs up to 2500 m.

SPECIMENS EXAMINED.—2: 43494; 10: 46042; 11: 46056.

ILLUSTRATIONS.—Hale, 1974a:18, figs. 5*b*, 9*b*.

4. *Ocellularia antillensis*

FIGURE 4*d*

Ocellularia antillensis Hale, 1974a:17 [type collection: Do-
minica, Hale 35612 (US, holotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal,
minutely verrucose, shiny, grayish white, 3–6 cm
broad; apothecia numerous, separate and regularly
dispersed, 0.3–0.6 mm in diameter, carbonized, the
columella well developed, about 150 μ m in diame-
ter, the pore round, 0.1–0.12 mm in diameter, black
inside; spores 8, 7 \times 12–15 μ m, 5–6 loculate, I+
blue.

CHEMISTRY.—Psoromic and norpsoromic acids.

REMARKS.—The rather open pore and the clearly
visible black top of the columella separate this
species from *O. subcavata* (Nylander) Zahlbruckner,
which has a distinct annulate pore, a partially car-
bonized columella, and a smooth thallus. *Ocellu-
laria antillensis* was collected in Panama on the
upper trunks of palm and evergreen hardwoods at
low to middle elevations.

SPECIMENS EXAMINED.—2: 43561; 3: 38659.

ILLUSTRATIONS.—Hale, 1974a:18, fig. 9*g*.

5. *Ocellularia aurulenta*

FIGURE 4*e*

Ocellularia aurulenta Hale, 1974b:490 [type collection: El
Llano-Cartí Road, Province of Panama, Panama, Hale
38548 (US, holotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal,
thick and irregularly bullate, almost appearing
coarsely isidiate, pale greenish or whitish mineral
gray, up to 15 cm broad; apothecia not common,
occurring inconspicuously among the bullae, semi-
emergent, about 0.5 mm in diameter, carbonized
but without a columella, the pore round, 0.1 mm

in diameter; spores 1–2, 25–35 \times 150–200 μ m, 15–19
loculate, I+ blue.

CHEMISTRY.—Hypoprotocetararic and 4-O-de-
methynotatic acids with unidentified pale yellow
pigments.

REMARKS.—This species has an unusual bullate
thallus that is not fragile but can be easily abraded
to reveal the yellow medulla. It is related to *O.
fecunda* (Vainio) Hale, at least in chemistry. The
distribution area is quite restricted, the low moun-
tains east of the Canal Zone.

SPECIMENS EXAMINED.—6: 43467; 8: 38528, 38536, 38548,
38587. 9: 38441, 38452, 38486, 38495.

ILLUSTRATIONS.—Hale, 1974b:490, fig. 2.

6. *Ocellularia barroensis*, new species

FIGURE 4*f*

DESCRIPTION.—Thallus corticola, epiphloeodes,
nitidus, laevis vel verruculosus, continuus, pallide
cinereo-*viridis*, 6–9 cm latus; apothecia (Figure 3*a*)
numerous, separata vel aggregata, emergentia, 0.6–
0.9 mm diametro, margin thallino suberecto, in-
tegro, decolorato, columella nulla, excipulo proprio
pro parte evoluta sed vulgo evanescenti, disco car-
neo, superficie actinoideo-columellato, albo-prui-
noso; ostiolum apertum, 0.2–0.5 mm diametro;
hymenium ca. 110 μ m altum; sporae 8:nae, 6 \times
17–20 μ m, 5–6 loculatae, I+ caeruleae.

CHEMISTRY.—No substances present.

HOLOTYPE.—Two meters up trunk of tree in
rain forest, Zetek Trail, Barro Colorado Island,
Canal Zone, Panama, elevation 100 m, *M. E. Hale*
46069, 20 February 1975 (US).

REMARKS.—This species is externally similar to
O. glaucophaena, which contains psoromic acid,
but the thalline margin is more erect, thin, and
entire. The apothecia tend to be clumped and at
maturity an actinoid pseudocolumella may develop
on the surface of the disc. It occurred at the base
of a tree at this single locality.

7. *Ocellularia berkeleyana*

FIGURE 4*g*

Ocellularia berkeleyana (Montagne) Zahlbruckner, 1905:118.
Stegobolus berkeleyanus Montagne, 1845:4 [type collection:
Philippines, Berkeley 2185 (BM, lectotype; isolectotype in
G) (Figure 1*g*)].

Thelotrema leucotylium Nylander, 1873:166 [type collection: Andaman Islands, *Kurz* 101 (H, lectotype; isolectotypes in BM, UPS, W, ZT) (Figure 2b)].

Ocellularia leucotylii (Nylander) Müller Argoviensis, 1891b: 51.

Ocellularia radians Müller Argoviensis, 1887b:397 [type collection: Apiahy, Brazil, *Puiggari* 3049 (G, lectotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin and shiny, light greenish mineral gray, 4–8 cm broad; apothecia not common, irregularly dispersed, semiemergent to strongly emergent and basally constricted, 1–2 mm in diameter, the thalline rim entire, distinct, the open flat disc divided by the reticulate columella, becoming white pruinose, the columella carbonized; spores 8, 4–8 × 8–10 μm , 4 loculate, I+ blue.

CHEMISTRY.—Psoromic acid with or without norpsoromic acid.

REMARKS.—This was the first reticulate columellate *Ocellularia* to be described. As Salisbury (1975:59) correctly points out, the genus *Stegobolus* is older than and takes precedence over *Rhabdo-discus* Vainio, if one wished to recognize these species in a separate genus. *Ocellularia berkeleyana* is an extremely variable species and intergrades with several other populations. For example, *O. comparabilis* (Krempelhuber) Müller Argoviensis may develop a rather strongly actinoid disc but would have less emergent apothecia. *Ocellularia latilabra* (Tuckerman) Müller Argoviensis has a more erect to recurved thalline margin and a less carbonized actinoid disc. I have identified the species definitely only from Cuba, Guadeloupe, Java, and South Africa. In Panama it occurs in the mid to upper bole area on larger trees at low to mid elevation.

SPECIMENS EXAMINED.—3: 38693; 9: 38461.

8. *Ocellularia bullata*, new species

FIGURE 4h

DESCRIPTION.—Thallus corticola, epiphloeodes vel evanescens, tenuis, viridi-cinereus, 6 cm latus, isidiato-bullatus, isidiis solidis, integris, usque ad 0.3 mm altis; apothecia rara, emergentia, 0.4–0.5 mm diametro, ecolumellata; ostiolum rotundatum, 0.1 mm diametro; excipulum apice fuligineum; hymenium ca 70 μm altum; sporae 4–8:nae, 10 × 50–65 μm , 7–9 loculatae, I+ caerulescentes.

CHEMISTRY.—Stictic and constictic acids.

HOLOTYPE.—Mature rain forest, Cerro Jefe, Province of Panamá, Panama, elevation 700 m, M. E. Hale 38478, 5 April 1973 (US).

REMARKS.—Externally this species has some resemblance to *O. fragilis* Hale, a Colombian species that has psoromic acid, small spores (12 μm long), and a more fragile thallus. It was collected on the lower trunk of a tree in mature rain forest.

9. *Ocellularia calvescens*

FIGURE 4i

Ocellularia calvescens (Fée) Müller Argoviensis, 1887a:8.

Thelotrema calvescens Fée, 1837:89 [type collection: "America ad cortices *Cinchonarum*" (G, lectotype; isolectotype in H) (Figure 1h)].

Ocellularia sexlocularis Zahlbruckner in Magnusson and Zahlbruckner, 1943:48 [type collection: Haleakala, Hawaii, *Faurie* 678 (UPS, lectotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, smooth or becoming cracked with age, whitish mineral gray, to 10 cm broad; apothecia barely emergent to semiemergent, 0.5–0.8 mm in diameter, carbonized but without a columella, the pore round, about 0.1 mm in diameter, white annulate and vaguely to distinctly raised annulate; spores 8, 6–8 × 15–20 μm , 5–7 loculate, I+ blue.

CHEMISTRY.—Psoromic acid.

REMARKS.—As with most of the Fée types, the original material of *O. calvescens* in G is in very poor condition. It is distinguished by weakly emergent apothecia, a small more or less distinctly annulate pore, and psoromic acid. The spores, as in the Panamanian material, are small. It is a variable species and its limits are still not clearly defined. The specimens collected in Panama, which include some tentatively identified, occurred mostly in the canopy and on lianas from 100 to 2000 m elevation.

SPECIMENS EXAMINED.—1: 38716, 38753, 38757; 3: 38622; 8: 38613; 9: 38506.

10. *Ocellularia cavata*

FIGURE 4j

Ocellularia cavata (Acharius) Müller Argoviensis, 1882:499.

Thelotrema cavatum Acharius, 1812:92 [type collection: Sierra Leone, *Afzelius* (H, lectotype; S, UPS, isolectotypes)].

Thelotrema obturatum Acharius, 1812:92.
Ascidium cinchonarum Fée, 1824:96.
Ocellularia cinchonarum (Fée) Sprengel, 1827:242.
Ocellularia obturata (Acharius) Sprengel, 1927:242.
Ascidium cinchonarum f. *intermedium* Nylander, 1867:319.
Ocellularia lindigiana Müller Argoviensis, 1887a:9.
Ocellularia cinchonarum f. *intermedia* (Nylander) Zahlbruckner, 1923:586.

[For full citations see Hale (1974a:17).]

DESCRIPTION.—Thallus corticolous, epiphloeodal, more or less verruculose, greenish to whitish mineral gray, up to 10 cm broad; apothecia emergent to strongly emergent, 0.7–0.9 mm in diameter, the thalline margin apically carbonized, the exposed medulla either white or pale yellow, a well-developed columella present, about 200 μm in diameter, the pore round, about 0.1 mm in diameter; spores 8, variable, 6–12 \times 24–70 μm , 7–18 loculate, I+ blue.

CHEMISTRY.—The “cinchonarum” unknown, P+ red unknowns, and a faint yellow pigment if pigmented.

REMARKS.—As recently typified (Hale, 1972:188), *O. cavata* has a pale yellowish medulla in the apothecia (which I failed to emphasize) and spores in the range of 30–40 μm long. I have reexamined the type collections of *Ascidium cinchonarum* Fée (PC), *Ocellularia lindigiana* Müller Argoviensis (FH, BM, UPS), and *Thelotrema cavatum* Acharius (S, UPS) and been able to confirm that all have a pale but distinct yellow medullary pigment in the amphithecium. Three specimens from Panama (38444, 38466, and 44921) compare well with the typical population. Two others from Darien (*Mori* 4333 and 4459) have much larger spores (70–80 μm long) and a white amphithecial medulla, although the chemistry is otherwise identical and the apothecia are externally indistinguishable. We obviously need to see more collections before the significance of these differences can be assessed.

SPECIMENS EXAMINED.—1a: 44921; 9: 38444; 12: *Mori* 4333, 4459.

11. *Ocellularia chionostoma*

FIGURE 4k

Ocellularia chionostoma (Nylander) Riddle, 1917:325.
Thelotrema chionostomum Nylander, 1863b:329 [type collection: Cuba, *Wright* 3 (FH, lectotype) (Figure 1i)].

Ocellularia phlyctellacea Müller Argoviensis, 1893b:146 [type collection: Buenos Aires, Costa Rica, *Pittier* 6106 (material in G without collector or number) (G, lectotype)].

DESCRIPTION.—Thallus corticolous, thin and mostly hypophloeodal, whitish gray, 6–10 cm broad; apothecia adnate, chroodiscoid, the thalline and inner exciples short, becoming granular, not recurved, the disc pruinose, 0.2–0.3 mm in diameter; spores 8, 4–6 \times 10–18 μm , 4–5 loculate, I–.

CHEMISTRY.—No substances present.

REMARKS.—The main thallus rim is erect but short, sometimes virtually absent, in contrast, for example, to that of *O. alborosella* (see above). The disc is always white pruinose. It is a lowland species growing near the base of trees in rain forest in Panama.

SPECIMENS EXAMINED.—4: 43455; 8: 38590.

12. *Ocellularia comparabilis*

FIGURE 4l

Ocellularia comparabilis (Krempelhuber) Müller Argoviensis, 1883:318.

Thelotrema comparabile Krempelhuber, 1875:220 [type collection: Rio de Janeiro, Brazil, *Glaziou* 5463 (M, lectotype; isoelectotypes in BM, C, G, M, PC, UPS, W)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth, continuous or cracked with age, whitish mineral gray, 5–12 cm broad; apothecia numerous, emergent, 0.8–1.1 mm in diameter, carbonized with a simple or partially actinoid columella, the pore round and quite open, 0.1–0.2 mm in diameter, the pruinose tip of the columella visible; spores 8, 6–8 \times 15–20 μm , 4–6 loculate, I+ blue.

CHEMISTRY.—Psoromic acid with or without norpsoromic acid.

REMARKS.—*Ocellularia comparabilis* is a variable species, the apothecia varying from nearly immersed to semiemergent and having a distinct thalline margin, open pruinose disc, and imperfect development of an actinoid columella. It intergrades most noticeably with *O. efformata* (Krempelhuber) Müller Argoviensis, which has a jagged, erect thalline margin. It has a broad ecological range in Panama, from near sea level to 2000 m.

SPECIMENS EXAMINED.—1a: 44905, 46025, *Esslinger* 4460; 3: 38684; 3a: 46072, 44846, 44849.

13. *Ocellularia concolor*

FIGURE 5a

Ocellularia concolor Meyen and Flotow, 1843:230 [type collection: Manila, Philippines, *Meyen* (G, lectotype)].

DESCRIPTION.—Thallus corticolous, hypophloeodal, tannish gray and dull, 3–8 cm broad; apothecia numerous, dispersed, emergent, 0.8–1.1 mm in diameter, carbonized with a distinct columella about 160 μm in diameter, the pore round to somewhat irregular, 0.3–0.5 mm broad, the rim blackening and the black tip of the columella easily visible; spores 8, 5–8 \times 13–20 μm , 5–7 loculate, I+ blue.

CHEMISTRY.—No substances present.

REMARKS.—The distinguishing characters are the tannish hypophloeodal thallus and the rather open pore and black disc. As in Dominica, it grows at the base of large trees, on saplings, etc., in low to mid elevation rain forest.

SPECIMENS EXAMINED.—2: 43570, 43579; 3a: 44770; 4, 43431, 43452; 6: 43474, 43478; 8: 38571, 38588; 9: 38460; 11: 44818, 44988, 44995, 46018, 46053, *Esslinger* 4629.

ILLUSTRATIONS.—Hale, 1974a:18, fig. 9j.

14. *Ocellularia congesta*, new species

FIGURE 5b

DESCRIPTION.—Thallus corticola, epiphloeodes, crassus, continuus, cinereo-albus, 6–10 cm latus; apothecia primus immersa, demum congesta et aggregata, semi-emergentia, 0.2–0.4 mm diametro, ecolumellata; ostiolum rotundatum, apertum, 0.1–0.2 mm latum; excipulum distinctum vel evanescent; hymenium 85–95 μm altum; sporae 8:nae, 8 \times 18 μm , 4-loculatae, I+ caerulescentes.

CHEMISTRY.—Hypoprotocetraric and 4-O-demethylnotatic acids.

HOLOTYPE.—Mature secondary rain forest, La Mesa, north of El Valle, Province of Coclé, elevation 750 m, *M. E. Hale* 43470, 13 February 1974 (US).

REMARKS.—This species is very close to *Thelotrema concretum* Fée in external appearance, but *T. concretum*, also a canopy species, contains psoromic acid and has small longitudinally septate spores. *Ocellularia microporella* (Nylander) Zahlbruckner has hypoprotocetraric acid but the apo-

thecia are completely immersed and the spores smaller.

SPECIMEN EXAMINED.—9: 38470 (cf.).

15. *Ocellularia conglomerata*

FIGURE 5c

Ocellularia conglomerata Hale, 1974a:18 [type collection: Dominica, *Hale* 37959 (US, holotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin and shiny, continuous, ashy white, 4–6 cm broad; apothecia not numerous, becoming aggregated in 2s and 3s, 0.5–0.8 mm in diameter, non-carbonized and without a columella, the thalline rim erect, the inner exciple distinct, pulverulent, more or less filling the disc; spores 8, 5 \times 15 μm , 6-loculate, I+ blue.

CHEMISTRY.—Stictic and constictic acids.

REMARKS.—The conspicuous exciples and the aggregated apothecia distinguish this rare species. It is undoubtedly related to *O. exanthismocarpa* (see below) but has much smaller spores and consistently aggregated apothecia with a semierect thalline margin. It occupies the same habitat as the type in Dominica, small branches of understory trees in rain forest at 800 m elevation.

SPECIMEN EXAMINED.—11: 44952.

ILLUSTRATIONS.—Hale, 1974a:18, fig. 9h.

16. *Ocellularia crocea*

FIGURE 5d

Ocellularia crocea (Krempelhuber) C. and D. van Overeem-de Haas, 1922:118.

Ascidium croceum Krempelhuber, 1875:25 [type collection: Sarawak, *Beccari* 31c (M, lectotype) (Figure 1n)].

Phaeotrema croceum (Krempelhuber) Zahlbruckner, 1923:606.

DESCRIPTION.—Thallus corticolous, epiphloeodal, rather thick, shiny, smooth to minutely verruculose, tannish gray, the exposed medulla pale reddish orange, 4–8 cm broad; apothecia numerous, solitary or crowded in 2s and 3s, more or less emergent, 0.4–0.7 mm in diameter, the thalline rim with a dull orange cast, a columella lacking, the inner exciple persisting and more or less filling the pore, the pore 0.1–0.2 mm in diameter; spores 8, 5–8 \times 18–20 μm , 5–7 loculate, I+ blue.

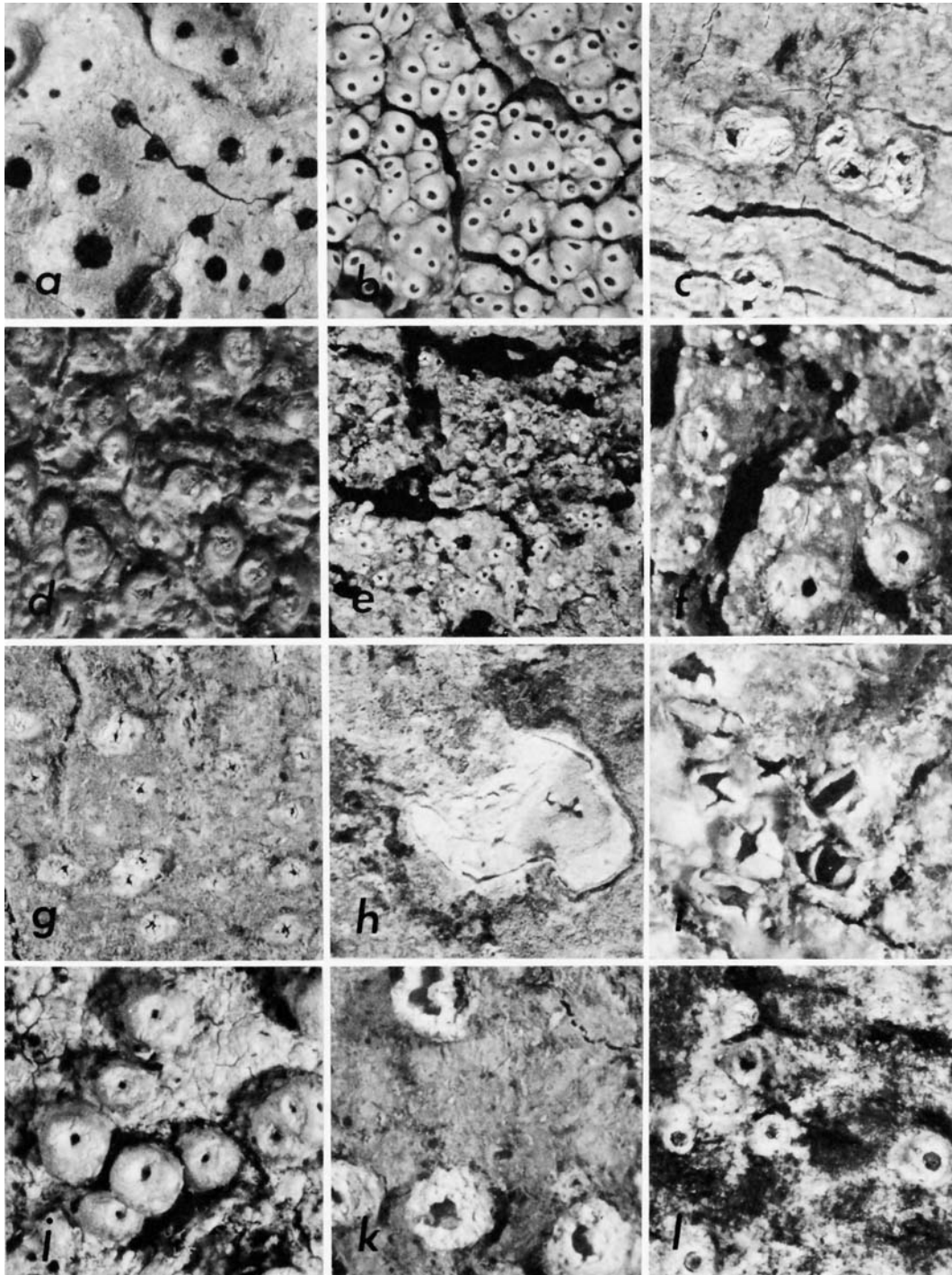


FIGURE 5.—Species of *Ocellularia*: a, *O. concolor* (Hale 46018); b, *O. congesta* (Hale 43470); c, *O. conglomerata* (Hale 44952); d, *O. crocea* (Hale 43091); e, *O. dactylifera* (Hale 43503); f, *O. dactyliza* (Hale 43559); g, *O. decolorata* (Hale 43462); h, *O. dilatata* (Hale 38640); i, *O. dissuta* (Hale 43520); j, *O. domingensis* (Hale 46028); k, *O. esslingeri* (Esslinger 4626); l, *O. exanthismocarpa* (Hale 43542) ($\times 10$).

CHEMISTRY.—“Cinchonarum” unknown and unidentified pigments.

REMARKS.—The material from Panama is identical with the rather fragmentary type from Sarawak. The medulla and apothecial tissues are brilliant orange red and the pore nearly filled with excipular material. It is apparently confined to the upper trunk and canopy.

SPECIMENS EXAMINED.—2: 43583, 43550, 43591.

17. *Ocellularia dactylifera*, new species

FIGURE 5e

DESCRIPTION.—Thallus corticola, epiphloeodes, opacus, minute granulatus, viridi-cinereus, 10–12 cm latus, sparse isidiatus, isidiis cylindricis, usque ad 0.5 mm altis; apothecia (Figure 3b) numerosa, immersa vel leviter emergentia, dispersa vel paulo congregata, eolumellata, 0.1–0.15 mm diametro, margine thallino albo-pruinoso; ostiolum rotundatum, 0.05 mm diametro; excipulum decoloratum, separatum vel pro parte connatum; hymenium 90 μm altum; sporae 8:nae, $5 \times 12 \mu\text{m}$, 5-loculatae, I+ caerulescentes.

CHEMISTRY.—Stictic and constictic acid.

HOLOTYPE.—Rain forest, Santa Rita Ridge, Province of Colón, Panama, elevation 350 m, *M. E. Hale* 43503, 12 February 1974 (US).

REMARKS.—This is one of only several isidiate species in the genus. *Ocellularia bullata* Hale, also from Panama, has peculiar inflated, hollow isidia and stictic acid. From higher elevations we have *O. isidiifera* Hale, which has long, thin isidia and psoromic acid. *Ocellularia dactyliza* Hale (below) has large solid isidia and different chemistry.

18. *Ocellularia dactyliza*, new species

FIGURE 5f

DESCRIPTION.—Thallus corticola, epiphloeodes, nitidus, pallide olivaceo-viridis, 8 cm latus, isidiatus, isidiis crassis, cylindricis vel irregulariter inflatis, facile disrumpentibus; apothecia (Figure 3c) emergentia, 0.7–1.1 mm diametro, eolumellata, amphithecio laevi vel rugoso isidiatoque; ostiolum rotundatum vel irregulare, 0.1–0.3 mm latum, nigro-cinctum; excipulum apice fuligineum; hymenium 120 μm altum, paraphysibus granulato-encrustatis; sporae 6–8:nae, $12 \times 50 \mu\text{m}$, 12–15 loculatae, I+ caerulescentes.

CHEMISTRY.—Protocetraric acid.

HOLOTYPE.—Rain forest, Santa Rita Ridge, Province of Colón, Panama, elevation 350 m, *M. E. Hale* 43559, 12 February 1974 (US).

REMARKS.—This species is characterized by the rather sparse, coarse isidia that break open apically and are easily dislodged, leaving white spots on the thallus. The ostiole is black-rimmed, much as in another protocetraric acid-containing species, *O. verrucosa* (Fée) Hale, which has a roughened but never isidiate thallus and smaller spores (30–42 μm long). It was collected 2 m up the trunk of a medium-sized tree in rain forest.

19. *Ocellularia decolorata*, new species

FIGURE 5g

DESCRIPTION.—Thallus corticola, epiphloeodes, continuus, nitidus, albo-viridis, 6–9 cm latus; apothecia numerosa, irregulariter dispersa, immersa vel vix emergentia, eolumellata, 0.4–0.6 mm diametro, margine thallino erecto, crasso, scabro; ostiolum irregulare, ca 0.1 mm latum; excipulum separatum, laceratum; hymenium 75–85 μm altum; sporae 8:nae, $6 \times 18\text{--}22 \mu\text{m}$, 5–6 loculatae, I+ caerulescentes.

CHEMISTRY.—“Cinchonarum” unknowns.

HOLOTYPE.—Secondary rain forest, La Mesa, north of El Valle, Province of Coclé, Panama, elevation 750 m, *M. E. Hale* 43462, 13 February 1974 (US).

REMARKS.—This species is virtually identical to *Ocellularia crocea* (Krempelhuber) Zahlbruckner, which has the brilliant pigment endocrocin. The disc is largely filled with the apically finely lacerate thallin margin and exciple. The chemistry relates it to the *O. cavata* group. It occurs on the lower trunks of trees in secondary rain forest at low elevation.

20. *Ocellularia dilatata*

FIGURE 5h

Ocellularia dilatata Müller Argovicensis, 1895c:542 [type collection: Rio de Janeiro, Brazil, *Glaziou* 5531 pro parte (G, lectotype; isolecotype in BM)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin, dull, in part evanescent, pale greenish mineral gray, 4–8 cm broad; apothecia not numerous, dis-

persed, chroodiscoid, up to 3.0 mm broad, round to irregularly elongate, the thalline rim thick, erect to recurved, the inner exciple not persisting, the disc flesh colored to heavily white pruinose; spores 8, $5-8 \times 15-25 \mu\text{m}$, 6-9 loculate, I+ blue.

CHEMISTRY.—Stictic and constictic acids.

REMARKS.—The thick, split, recurved thalline margin and irregular shape of the apothecia are typical of the species. The chemical characters are shared by *O. neei* Hale, which has smaller apothecia with a delicate margin and persistent inner exciple, *O. pseudoschizostoma* Hale with a thick, erect thalline margin, and *O. sublilacina* (Ellis and Everhart) Zahlbruckner, a very large species with long spores. Redinger (1936:16) erroneously regarded the species as a *Graphis*. *Ocellularia dilatata* occurs on the lower trunks and on lianas at 100-700 m elevation in Panama.

SPECIMENS EXAMINED.—3: 38640; 9: 38520.

ILLUSTRATIONS.—Hale, 1974a:21, figs. 11a, b.

21. *Ocellularia dissuta*, new species

FIGURE 5i

DESCRIPTION.—Thallus corticola, epiphloeodes, nitidus, continuus, pallide brunneo-olivaceus, 6-10 cm latus; apothecia chroodiscoida, solitaria vel pauce aggregata, 0.6-0.8 mm diametro, margine thallino crasso, irregulariter fisso, non reflexo; ostiolum irregulare, 0.4-0.6 mm latum; excipulum pro parte separatum fissum; disco pallide livido, leviter albo-pruinoso; hymenium 60-70 μm altum; sporae 8-nae, $4-6 \times 10-12 \mu\text{m}$, 3-4 loculae, I-.

CHEMISTRY.—No substances present.

HOLOTYPE.—Rain forest, Santa Rita Ridge, Province of Colón, Panama, elevation 350 m, *M. E. Hale* 43520, 12 February 1974 (US).

REMARKS.—The thalline margin of this species is coarse and split but not recurved, unlike any other species in the genus. It is confined to the lower trunks of small to medium-sized trees in mature rain forests at lower elevations.

SPECIMENS EXAMINED.—6: 43424, 43511, 43512; 8: 38575.

22. *Ocellularia domingensis*

FIGURE 5j

Ocellularia domingensis (Fée in Nylander) Müller Argovien-
sis, 1887b:398.

Ascidium domingense Fée in Nylander, 1857:118 [nomen

nudum; valid publication in Nylander 1863a:455; type collection: Colombia, Lindig 2683 (FH-Tuck, neotype; isoneo-
type in BM, UPS) (Figure 1p)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, rather thick, shiny, verruculose, pale tan, 4-8 cm broad; apothecia fairly numerous, strongly emergent, sometimes subglobose at maturity, about 1 mm in diameter, carbonized but without a columella, pore more or less recessed, about 0.1 mm in diameter, subannulate, the pore area whitish; spores 1-2, $15-45 \times 80-200 \mu\text{m}$, I+ blue.

CHEMISTRY.—Hypoprotocetraric acid.

REMARKS.—*Ocellularia domingensis* was based on an unpublished Fée herbarium name, presumably from Santo Domingo (Dominican Republic?), but no specimen so labeled could be found in Nylander's collections at H or PC or in Fée's at G or PC. The species was validated by Nylander in 1863 in his study of Lindig's Colombian lichens, and I have selected one of these as the neotype of *O. domingensis*. The ascidioid apothecia are large and conspicuous and a columella is lacking; the spores are very large. The only similar species is *O. henatomma* (Acharius) Müller Argovien-
sis from South Africa, which has a distinct columella. The species occurs in cloud forest in Panama and is now known from similar habitats in Guatemala, Venezuela, and Colombia.

SPECIMENS EXAMINED.—1a: 44761, 44892, 44983, 46028.

23. *Ocellularia esslingerii*, new species

FIGURE 5k

DESCRIPTION.—Thallus corticola, epiphloeodes, minute verruculosus, pallide cinereo-viridis, 4 cm latus; apothecia dispersa, chroodiscoida, emergentia, 0.7-1.1 mm diametro, margine thallino crasso, apice pulverulento vel subsorediato, erecto vel pro parte recurvato, excipulo proprio evanescenti, disco leviter albo-pruinoso, carneo; hymenium ca. 90 μm altum; sporae 8-nae, $5-6 \times 18-21 \mu\text{m}$, 5-6 loculae, I+ caeruleae.

CHEMISTRY.—Unidentified P- compound.

HOLOTYPE.—On bark in rain forest at base of ridge west of Escuela de Agrícola, elevation 1000 m, Province of Veraguas, Panama, *T. L. Esslinger* 4626, 24 February 1975 (US).

REMARKS.—No other chroodiscoid species in the genus has quite the same round apothecia with a

thick, more or less entire (as opposed to split and recurved) thalline margin that is subsorediate around the rim. The proper exciple, apparently quite thick, may fuse with the thalline margin or be evanescent. *Ocellularia pseudoschizostoma* Hale, which is superficially similar, has a white, mostly hypophloeodal thallus, stictic acid, and less emergent apothecia.

24. *Ocellularia exanthismocarpa*

FIGURE 5l

Ocellularia exanthismocarpa (Leighton) Zahlbruckner, 1923: 590.

Thelotrema exanthismocarpum Leighton, 1869:169 [type collection: Ceylon, *Thwaites* C. L. 97 (BM, lectotype; isolectotype in H)].

Thelotrema porinoides Montagne and van den Bosch, 1855: 484.

Ocellularia multilocularis Zahlbruckner, 1912:369.

Thelotrema isertii Vainio, 1915: 40.

Thelotrema homothecium Vainio, 1921:190.

Ocellularia homothecia (Vainio) Zahlbruckner, 1923:593.

Ocellularia porinoides (Montagne and van den Bosch) Zahlbruckner, 1923:599.

[For full citations see Hale, 1974a:20.]

DESCRIPTION.—Thallus corticolous, thin and in part hypophloeodal, ashy white, about 3 cm broad; apothecia not numerous, semiemergent, about 0.7 mm in diameter, noncarbonized and without a columella, the thalline rim becoming erect, pulverulent, the inner exciple persistent, free, forming a pore within the main pore, the main pore open, 0.2–0.4 mm in diameter; spores 4–8, $10 \times 40\text{--}50 \mu\text{m}$, about 12 loculate, I+ blue.

CHEMISTRY.—Stictic and constictic acids.

REMARKS.—This very widespread species, so often developed in secondary forests, was collected only once in Panama, in contrast to its abundance in Dominica (Hale, 1974a:20). The pore-within-a-pore configuration of the thalline and inner excipular margins, chemistry, and large spores make identification unmistakable.

SPECIMEN EXAMINED.—2: 43542.

ILLUSTRATIONS.—Hale, 1974a:21, figs. 5a, 11c, g; Salisbury, 1972b:265, fig. 2 (as *Thelotrema porinoides*).

25. *Ocellularia fecunda*

FIGURE 6a

Ocellularia fecunda (Vainio) Hale, 1974a:21.

Thelotrema domingense var. *fecundum* Vainio, 1896:208 [type

collection: St. Vincent, *Elliott* 243 (BM, lectotype; isolectotype in TUR)].

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

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth and shiny, pale greenish gray, 10–20 cm broad; apothecia numerous, solitary and conspicuous, strongly emergent, 1.5–2.0 mm in diameter, heavily carbonized but without a central columella, the exposed medulla light yellowish orange, the pore irregular, 0.4–0.8 mm in diameter; spores 4, $12\text{--}20 \times 80\text{--}150 \mu\text{m}$, 15–30 loculate, I+ blue.

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

REMARKS.—I had found this to be a very common species in Dominica and other islands in the Lesser Antilles with a very wide amplitude in ecological requirements. The large apothecia that abrade easily to reveal a pale yellow-orange medulla make field identification easy. In Panama it was very common in the Cerro Jefe region but surprisingly did not occur west of the Canal Zone in quite similar forests.

SPECIMENS EXAMINED.—8: 38530, 38540, 38542, 38556, 38569, 38584, 38952, 38598, *Mori* 4089; 9: 38430, 38440, 38442, 38448, 38453, 38469, 38472, 38490, 38498, 38503, 38508, 38509, 38513; 12: *Mori* 4268.

ILLUSTRATIONS.—Hale, 1974a:21, fig. 11h, i.

26. *Ocellularia glaucophaena*

FIGURE 6b

Ocellularia glaucophaena (Krempelhuber) Zahlbruckner, 1923: 591.

Thelotrema glaucophaenum Krempelhuber, 1875:19 [type collection: Sarawak, *Beccari* 92 (M, lectotype; isolectotype in G) (Figure 1r)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, often thin, shiny and smooth, continuous or cracked with age, pale greenish mineral gray, 5–15 cm broad; apothecia numerous, separate, nearly immersed to semiemergent, 0.3–1.0 mm in diameter, the thalline rim sometimes semierect and thickening, noncarbonized, a columella lacking, the inner exciple free, sometimes persisting but not conspicuous, the flesh-colored disc visible through the pore, rarely with pseudoactinoid surface markings, the pore 0.1–0.2 mm in diameter; spores 8, $4\text{--}6 \times 10\text{--}24 \mu\text{m}$, 5–6 loculate, I+ blue.

CHEMISTRY.—Psoromic acid.

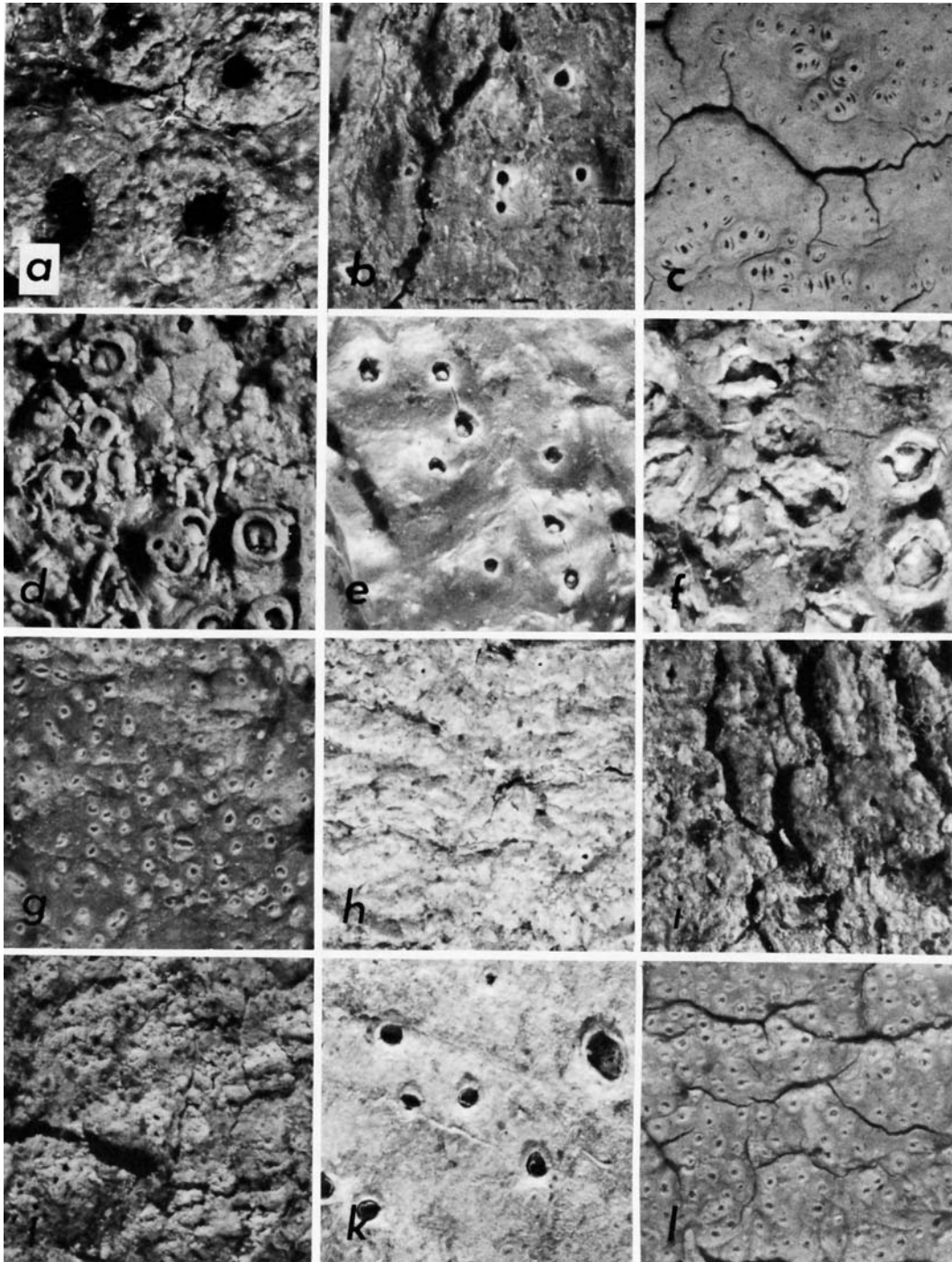


FIGURE 6.—Species of *Ocellularia*: a, *O. fecunda* (Mori 4268); b, *O. glaucophaena* (Hale 43486); c, *O. glaucula* (Hale 43450); d, *O. isidiifera* (Hale 46026); e, *O. landronii* (Landrón 358A); f, *O. latilabra* (Mori 4474); g, *O. microporella* (Hale 44768) h, *O. minutula* (Hale 43504); i, *O. mordenii* (Hale 43446); j, *O. myriotremoides* (Hale 46020); k, *O. neei* (Nee 3710); l, *O. olivacea* (Hale 38434) ($\times 10$).

REMARKS.—While *O. glaucophaena* was first described from Sarawak, it seems to be pantropical with records in US from Florida, Cuba, Java, and the Solomon Islands. There are no strong distinguishing features; the noncarbonized apothecia are usually small but may reach 1.0 mm in Panama. It is a lowland rain forest species occurring on lower trunks. This complex will obviously need more study in the future as more specimens become available.

SPECIMENS EXAMINED.—2: 43576; 3: 38625, 38626, 38647, 38675, 38699; 3a: 44863, 44949, 44998, 46067, *Esslinger* 4347, 4363, 4370; 4: 43437, 43438, 43459, 43486, 43496.

27. *Ocellularia glaucula*

FIGURE 6c

Ocellularia glaucula (Nylander) Zahlbruckner, 1923:591.
Thelotrema glauculum Nylander, 1863b:332 [type collection: Cuba, *Wright* (H, Nylander herbarium 22639, lectotype) (Figure 1s)].
Thelotrema leptoporum Nylander in Leighton, 1869:167 [nomen nudum in Nylander, 1857:118; type collection: Cuba, *Wright* 128 (BM, lectotype; isolectotypes in FH-Tuck, G, L, PC, UPS, US, W)].
Ocellularia leptopora (Nylander) Zahlbruckner, 1923:594.

DESCRIPTION.—Thallus corticolous, epiphloeodal, rather dull, smooth and continuous or cracked, whitish mineral gray, 5–10 cm broad; apothecia numerous, separate, immersed, 0.1–0.2 mm in diameter, noncarbonized and ecolumellate, the inner exciple free, forming a minute pore within the main pore, the main pore round, about 0.1 mm in diameter; spores 8, 5–6 × 10–12 μm , 3–4 loculate, I+ blue.

CHEMISTRY.—Hypoprotocetraric acid and lichenanthone.

REMARKS.—This canopy species is similar to *O. microporella* (Nylander) Zahlbruckner superficially, but the thallus is dull white and the inner exciple distinctly free. I have also seen material from Costa Rica. No. 38491 has larger, more emergent apothecia than normal.

SPECIMENS EXAMINED.—1a: *Esslinger* 4503; 3: 38689; 4: 43450; 8: 38555, 38566; 9: 38491 (cf.).

28. *Ocellularia isidiifera*

FIGURE 6d

Ocellularia isidiifera Hale, 1974b:492 [type collection: Province of Chiriquí, Panama, *Hale* 38709 (US, holotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, rather thick and cracked, whitish to tannish ashy gray, up to 20 cm broad, isidiate, the isidia simple, cylindrical, about 1 mm high, initially erect but becoming decumbent; apothecia rather common, semiemergent, 0.5–1.0 mm in diameter, the thalline rim short but becoming erect, a columella absent or imperfectly developed, the pore round to irregularly elongate, 0.2–0.6 mm in diameter, the exposed disc white pruinose; spores 8, 6–9 × 18–22 μm , 5–6 loculate, I+ blue.

CHEMISTRY.—Psoromic and norpsoromic acids.

REMARKS.—*Ocellularia isidiifera* is amply distinguished by the tall thin isidia. I have collected it in cloud forests at 2500 m elevation in Venezuela as well. The type-locality in Panama was recently logged and the species may become extinct there.

SPECIMENS EXAMINED.—1: 38709, 38742, 38776, 38778, 38896; 1a: 46026, *Esslinger* 4489, 4509.

ILLUSTRATIONS.—Hale, 1974b:492, fig. 7.

29. *Ocellularia landronii*, new species

FIGURE 6e

DESCRIPTION.—Thallus corticola, epiphloeodes, continuous, nitidus, laevis vel minute verruculosus, cinereo-viridis, 6–8 cm latus; apothecia dispersa, immersa vel semi-emergentia, 0.8–1.0 mm diametro, apice fuliginea, columella evoluta, ca 120 μm diametro, apice nigra vel albo-pruinosa; hymenium 80–90 μm altum; sporae 8:nae, 5–6 × 14–19 μm , 5–6 loculatae, I+ caeruleae.

CHEMISTRY.—No substances present.

HOLOTYPE.—On *Dacryodes excelsa*, El Verde, Luquillo Mountains, Humacao District, Puerto Rico, *I. Landrón* 358A (US).

REMARKS.—This species is characterized by the smooth, shiny, dark greenish thallus and the peculiarly sunken apothecia. The distinct, white-tipped columella is typical of an emergent species, but here the apothecia are sunken in the thallus. There are no really comparable species, excepting perhaps *O. groenhartii* Hale, where the apothecia are more clearly semiemergent (Hale, 1975:173). *Ocellularia landronii* grows on the lower bole and base of trees in rain forests in both Puerto Rico and Panama. The species is named in honor of Dr. Ismael Landrón.

SPECIMEN EXAMINED.—6: 43479.

30. *Ocellularia latilabra*

FIGURE 6f

Ocellularia latilabra (Tuckerman) Müller Argoviensis, 1895c: 452.

Thelotrema latilabrum Tuckerman, 1866:269 [type collection: Cuba, Wright 137 (FH-Tuck, lectotype; isolectotypes in BM, G, L, PC, UPS, W)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, continuous or cracked with age, pale greenish gray, 6–10 cm broad; apothecia numerous, separate, semiemergent, 1–2 mm in diameter, the thalline rim erect, firm, splitting with age and in part recurved, the disc densely actinoid-columellate, carbonized, the surface white pruinose, the pore open, irregular, 1–1.5 mm in diameter; spores 8, 6×12 – $24 \mu\text{m}$, 5–6 loculate, I+ blue.

CHEMISTRY.—Psoromic acid.

REMARKS.—This actinoid species differs from *O. berkeleyana* (Montagne) Zahlbruckner in having a tall, erect to recurved thalline margin. It is also related to poorly known *O. schizostoma* (Tuckerman) Müller Argoviensis, described from Cuba, which has a similar irregularly erect, split thalline margin and an open disc. The disc, however, is not distinctly actinoid columellate; it lacks carbonization and is reticulately fissured. These three species are closely related and intergrade broadly. Only study of additional collections will decide the issue. The specimens from Panama occurred at lower to mid trunk in low to mid elevation rain forest. Specimens 44851, 44853, and 44860, all from the area north of Alto Piedra, have a distinct H_2SO_4 + yellow spot above psoromic acid on the TLC plates.

SPECIMENS EXAMINED.—3a: 44832, Esslinger 4350, 4377; 6: 43475; 8: 38568; 11: 44838, 44851, 44853, 44860; 12: Mori 4474.

31. *Ocellularia microporella*

FIGURE 6g

Ocellularia microporella (Nylander) Zahlbruckner, 1923:595. *Thelotrema microporellum* Nylander, 1863b:327 [type collection: Cuba, Wright 126 (FH-Tuck, lectotype; isolectotypes in BM, G, L, PC) (Figure 2c)].

Thelotrema plurifarium Nylander, 1867:315 [type collection: Cuba, Wright (H, Nylander herbarium 22631, lectotype)].

Thelotrema subterebratum Nylander, 1886:174 [type collection: S. Thomé, Möller 51 (H, Nylander herbarium 22772, lectotype; isolectotype in W)].

Ocellularia plurifaria (Nylander) Müller Argoviensis, 1891b: 75.

Ocellularia subterebrata (Nylander) Zahlbruckner, 1923:601.

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, continuous and smooth, pale greenish mineral gray, 5–15 cm broad; apothecia numerous, immersed, 0.1–0.2 mm in diameter, noncarbonized and without a columella, the inner exciple usually evanescent but rarely well developed and filling the pore, the pore round, open, about 0.1 mm in diameter, the pale tan disc visible; spores 8, 5 – 8×12 – $24 \mu\text{m}$, 4–6 loculate, I+ blue.

CHEMISTRY.—Hypoprotocetraric acid.

REMARKS.—This species is obviously related to *O. glaucula* (see above), which contains lichexanthone in addition to hypoprotocetraric acid and has a persistent inner exciple. Both are canopy species, but *O. microporella* generally occurs at higher elevations (380–800 m) than *O. glaucula*. I have identified it from Jamaica also.

SPECIMENS EXAMINED.—2: 43573, 43590; 8: 38611; 9: Mori 4211; 11: 44768, 44807, 44811, 44827, 44984, 46032.

32. *Ocellularia minutula*, new species

FIGURE 6h

DESCRIPTION.—Thallus corticola, epiphloeodes, tenuis, continuous, pallide cinereo-viridis, 6–8 cm latus; apothecia (Figure 3d) solitaria, sparsa, immersa vel semi-emergentia, 0.2–0.3 mm diametro, eolumellata vel rudimentaliter columellata; excipulum non separatum, decoloratum; ostiolum discretum, rotundatum, 0.05 mm diametro, albo-cinctum; hymenium 120–130 μm altum; sporae 8:nae, 7 – 10×22 – $24 \mu\text{m}$, 6–8 loculatae, I+ caerulescentes.

CHEMISTRY.—Psoromic and norpsoromic acids.

HOLOTYPE.—Secondary rain forest, 9 km NW Gamboa along Naval Pipeline Road, Canal Zone, Panama, elevation 150 m, M. E. Hale 43341, 11 February 1974 (US).

REMARKS.—This inconspicuous species has much smaller apothecia than any other psoromic acid-containing species with semiemergent fruiting bodies (nonmyriotremoid). The small but distinct pore, when strongly white annulate, resembles that of *O. umbilicata* Müller Argoviensis, a Costa Rican species with a thicker, warty thallus and larger apothecia. The poorly known *O. albula* (Nylander) Zahlbruckner from Brazil has a white pruinose thallus

and smaller spores. *Ocellularia minutula* occurs on saplings and lower trunks of trees in low to mid elevation rain forest.

SPECIMENS EXAMINED.—3a: 44885; 4: 43504; 7: 43603; 11: 44789, 44801, 44897, 44941.

33. *Ocellularia mordenii*

FIGURE 6i

Ocellularia mordenii Hale, 1974:22 [type collection: Dominica, Hale 37764 (US)].

DESCRIPTION.—Thallus corticolous, epiphloedal, continuous to cracked with age, rather warty and easily abraded, revealing the red medulla, greenish to tannish gray, about 8 cm broad; apothecia dispersed and inconspicuous, immersed to semiemergent in thallus warts, the surface very warty and easily abraded to reveal the red medulla, carbonized, eolumellate or with a weakly developed columella, the pore round, about 0.1 mm in diameter; spores 1–2, 15–20 × 70–150 μm, 24–30 loculate, I+ blue.

CHEMISTRY.—Unidentified anthraquinone pigments.

REMARKS.—This brilliantly pigmented species grows typically in the canopy in virgin rain forest. It is differentiated from *O. xanthostroma* by color of the medulla (red rather than yellow orange) and the somewhat less emergent apothecia.

SPECIMENS EXAMINED.—4: 43446, 43471; 6: 43501.

34. *Ocellularia myriotremoides*

FIGURE 6j

Ocellularia myriotremoides (Nylander) Zahlbruckner, 1923: 596.

Thelotrema myriotremoides Nylander, 1859:221 [type collection: Weddell, Bolivia (PC, lectotype) (Figure 2g)].

Thelotrema opacum Vainio, 1890:85 [type collection: Sitio, Minas Gerais, Brazil, Vainio 808 (TUR, lectotype; isolecotypes in BM, FH, UPS) (Figure 2j)].

Ocellularia opaca (Vainio) Zahlbruckner, 1923:597.

Ocellularia albula (Nylander) Zahlbruckner f. *opaca* (Vainio) Redinger, 1936:46.

DESCRIPTION.—Thallus corticolous, epiphloedal, continuous, dull, the surface becoming minutely scabrid, whitish mineral gray, 4–8 cm broad; apothecia numerous, separate to mostly irregularly aggregated, immersed to barely emergent, 0.3–0.4 mm

in diameter, noncarbonized and without a columella, the pore round, surrounded by a broad white area, slightly raised and white pruinose, 0.1 mm in diameter; spores 8, 3–5 × 12 μm, 4–5 loculate, I+ blue.

CHEMISTRY.—Psoromic acid.

REMARKS.—This species has a characteristic finely scabrid surface. The pore area is rather conspicuously annulate. Redinger (1936:46) reduced it to a forma of *O. albula*, but the type of *O. albula*, a very poor fragment, has semiemergent apothecia with a small pore as well as a pruinose rather than scabrid thallus surface. More closely related is *O. terebratula* (Nylander) Müller Argoviensis, which has a smooth shiny thallus and at the fine structure level aculeate surface hyphae (Hale, 1974:5). The second collection by Weddell that Nylander identified as "*Thelotrema myriotremoides*" is in fact *O. terebratula*, but I have selected the scabrid specimen as the lectotype since he describes the species as "thallo albiore magis opaco subfarinoso." The surface of *Thelotrema terebratulum*, described in 1867 from Colombia, is given as "laevigatus." *Ocellularia myriotremoides* occurs at the mid trunk level in rain forest.

SPECIMENS EXAMINED.—9: 38461; 11: 44788, 46020, Esslinger 4651.

35. *Ocellularia neei*, new species

FIGURE 6k

DESCRIPTION.—Thallus corticola, pro majore parte hypophloeodes, albo-cinereus, 5–7 cm latus; apothecia chroodiscoida, 0.4–0.7 mm diametro, margine thallino sat crasso, erecto vel pauce reflexo; ostium latum, rotundatum, usque as 0.5 mm latum; excipulum separatum, distinctum, disco obscure ferrugineo vel albo-pruinoso, hymenium 60–70 μm altum; spora 8:nae, 5 × 10–14 μm, 4 loculatae, I–.

CHEMISTRY.—Stictic and constictic acids.

HOLOTYPE.—On *Cochlospermum vitifolium* in a thicket, Summit Gardens, Canal Zone, Panama, elevation about 30 m, *M. Nee* and *S. Mori* 3710, 18 March 1971 (US).

REMARKS.—*Ocellularia neei* differs from other chroodiscoid species such as *O. sublilacina* (Everhart and Ellis) Zahlbruckner and *O. dilatata* Müller Argoviensis in being hypophloeodal and in having smaller spores. It is unusual in that it grows on

planted shrubs in an open, heavily used botanical garden near sea level, a lichenologically unpromising area. The species is named for Mr. Michael Nee, an observant lichen collector during his field studies in tropical America.

36. *Ocellularia olivacea*

FIGURE 6*l*

Ocellularia olivacea (Fée) Müller Argoviensis, 1887a:7.
Myriotrema olivaceum Fée, 1824:103 [type collection: South America (G. lectotype)].
Ocellularia olivacea (Fée) C. and D. Van Overeem-De Haas, 1922:118.

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth and continuous or becoming cracked, up to 0.5 mm thick, pale greenish or whitish ashy, 10–30 cm broad; apothecia very numerous, immersed, 0.15–0.3 mm in diameter, noncarbonized and lacking a columella, the inner exciple evanescent, the pore round, flush, about 0.1 mm in diameter; spores 8, uniseriate, 4–6 × 6–12 μm , 4 loculate, I+ blue.

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

REMARKS.—Although this species is common in Dominica, in other islands of the Lesser Antilles, and in Cuba, I found it to be rather rare in Panama. It must be distinguished carefully with spore sections from *Thelotrema clandestinum* Fée and with chemical tests from *O. terebratula* (Nylander) Müller Argoviensis and *O. uniseptata* Hale (both psoromic acid present). They occupy the same habitat, mid bole to canopy of trees up to 750 m elevation in rain forest.

SPECIMENS EXAMINED.—2: 43540; 3: 38641; 9: 38434.

ILLUSTRATIONS.—Hale, 1974a:23, fig. 12c; Redinger, 1936:48, fig. 24.

37. *Ocellularia pachystoma*, new combination

FIGURE 7*a*

Thelotrema pachystomum Nylander, 1863b:325 [type collection: Province Carabaya, Peru, *Weddell* (PC, lectotype) (Figure 2*k*)].
Phaeotrema pachystomum (Nylander) Zahlbruckner, 1923:609.

DESCRIPTION.—Thallus corticolous, epiphloeodal, continuous, shiny, light greenish mineral gray, about 8 cm broad; apothecia common, strongly emergent, separate to clumped in 2s and 3s, 0.7–1.4 mm in diameter, the exciple carbonized, columella lacking, the thalline rim becoming erect, the pore

round, the surrounding area broadly pulverulent or white pruinose, 0.1–0.2 mm in diameter, the pale disc surface visible; spores 8, 4 × 12 μm , 4-loculate, I+ blue.

CHEMISTRY.—Psoromic acid.

REMARKS.—The large emergent apothecia with a conspicuous, erect pulverulent thalline margin characterize this rare species. The type has colorless, not brown, spores. I have collected it in Venezuela at 2000 m elevation and it occurred in the Darien region at about 1800 m.

SPECIMEN EXAMINED.—12: *Mori* 4439.

38. *Ocellularia papillata*

FIGURE 7*b*

Ocellularia papillata (Leighton) Zahlbruckner, 1923:597.
Thelotrema papillatum Leighton, 1869:169 [type collection: Ceylon, *Thwaites* C. L. 129 (BM, lectotype; isolectotypes in G, H, P, S, UPS, W)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth and continuous, shiny, whitish to greenish gray, 3–12 cm broad; apothecia numerous, immersed to slightly emergent, carbonized, a columella usually present, 50–100 μm in diameter, the pore round, 0.1–0.2 mm in diameter; spores 8, 6–10 × 20–32 μm , 6–8 loculate, I+ blue.

CHEMISTRY.—No substances present.

REMARKS.—This was one of the commonest base level species in Panama as it was in Dominica (Hale, 1974a:24). It grows on prop roots, buttresses, lianas, and lower boles of trees in rain forest at low to mid elevation. All specimens had a columella. A chemical test should be used to separate it from *O. perforata* (see below).

SPECIMENS EXAMINED.—3: 38627, 38631, 38657, 38679, 38701; 3a: 44769, 44791, 44797, 44858, 44867, 44868, 44875, 44888, 44889, 44896, 44934, 44937, 44975, 46071, 46075, 46084, *Esslinger* 4398; 4: 3436, 43481, 43499, 43500, 43502, 43587; 6: 43340, 43429, 43463, 43505, 43529, 43531, 43558; 7: 43604, 43605, 43606; 8: 38583; 10: *Esslinger* 4630; 11: 44906, 44968, 45809, 46043, 46054.

ILLUSTRATION.—Hale, 1974a:23, figs. 12*d*, *e*.

39. *Ocellularia perforata*

FIGURE 7*c*

Ocellularia perforata (Leighton) Müller Argoviensis, 1892:284.
Thelotrema perforatum Leighton, 1866:447 [type collection: Casiquiari, Brazil, *Spruce* 254 (BM, lectotype)].

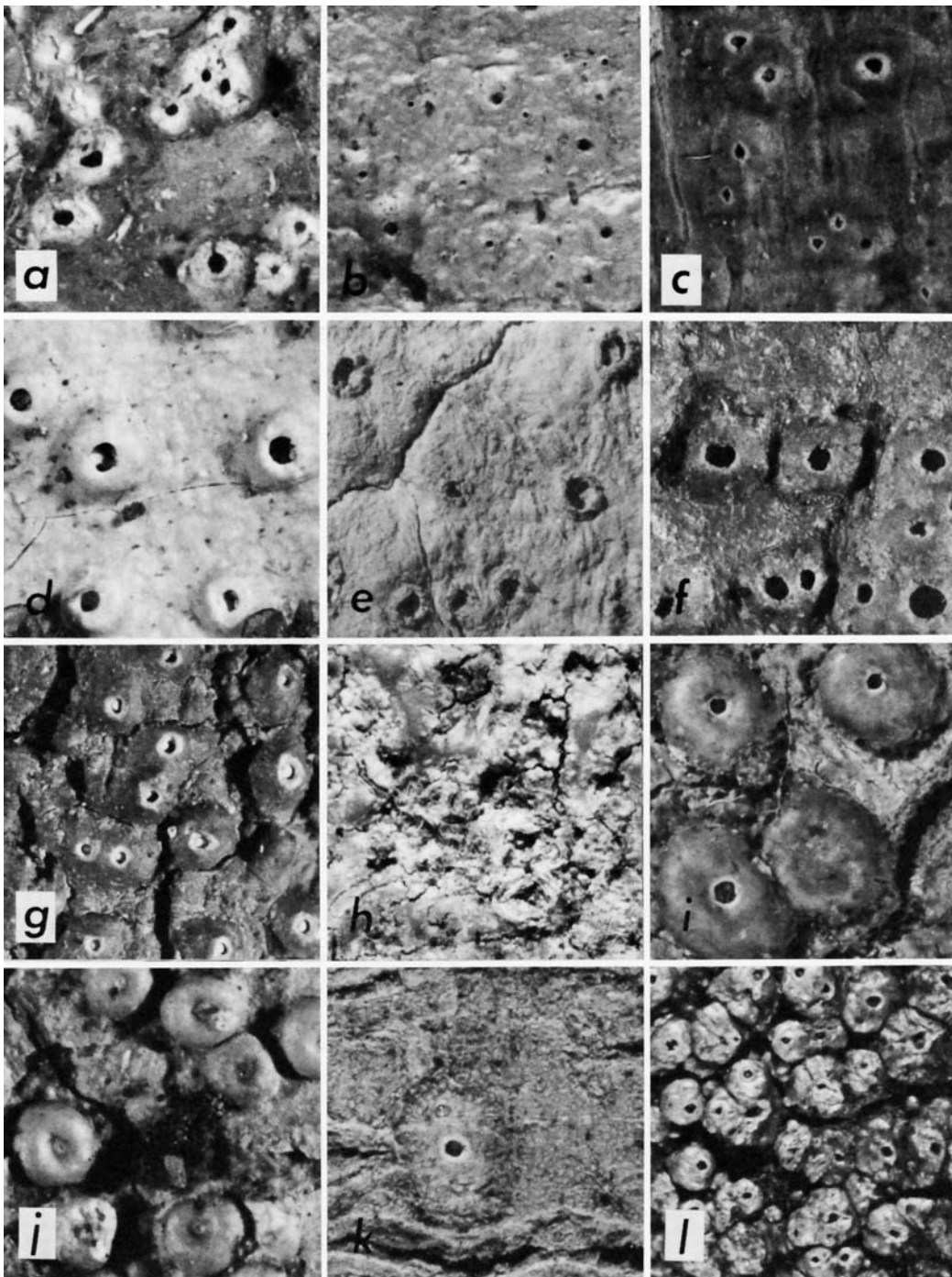


FIGURE 7.—Species of *Ocellularia*: a, *O. pachystoma* (Mori 4439); b, *O. papillata* (Hale 43463); c, *O. perforata* (Hale 46024); d, *O. protocetrarica* (Hale 44786); e, *O. pseudoschizostoma* (Hale 38559); f, *O. pulverulenta* (Hale 46073); g, *O. recondita* (Mori 4293); h, *O. referta* (Hale 43566); i, *O. rhabdospora* (Mori 4448); j, *O. rhodostroma* (Hale 44948); k, *O. ripleyi* (Hale 44836); l, *O. subcavata* (Hale 38516) ($\times 10$).

Thelotrema cavatum var. *planius* Nylander, 1867:316 [type collection: Colombia, Lindig 64 (BM, lectotype; isolectotypes in FH-Tuck, PC)].

Thelotrema terebratum var. *abbreviatulum* Vainio, 1890:83.

Ocellularia rufocincta Müller Argoviensis, 1893b:146.

Thelotrema excavatum Vainio, 1896:208.

Thelotrema excavatum var. *impressulum* Vainio, 1896:208.

Ocellularia cavata var. *planior* (Nylander) Zahlbruckner, 1923:585.

Ocellularia excavata (Vainio) Zahlbruckner, 1923:590.

Ocellularia terebrata var. *abbreviatula* (Vainio) Zahlbruckner, 1923:602. [For full citations see Hale (1974a:25)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, smooth or becoming verrucose with age, whitish or greenish gray, 3–10 cm broad; apothecia numerous, immersed to somewhat emergent, 0.4–0.6 mm in diameter, carbonized, a columella usually developed but variable, 25–160 μm in diameter, or rarely lacking, the pore round, 0.07–0.15 mm in diameter; spores 8, 6–10 \times 20–36 μm , 6–8 loculate, I+ blue.

CHEMISTRY.—Protocetraric acid with or without the “amplior” unknown.

REMARKS.—This is the commonest species of *Ocellularia* and of the family in Panama, occurring on tree bases, buttresses, saplings, lianas, etc., from sea level to 2200 m in rain forest. About 10% of the specimens lacked a columella, much as in Dominica (Hale, 1974a:24). Where it occurs with externally similar *O. papillata*—and the only major locality where they did not was the cloud forests of Volcán Chiriquí—*O. perforata* can be distinguished by the P+ red test. I have identified this pantropical species from Cuba, the Lesser Antilles, Guatemala, Costa Rica, Brazil, and the Solomon Islands.

SPECIMENS EXAMINED.—1: 38711, 38725, 38737, 38744, 38764, 38781; 1a: 44812, 44825, 44826, 44903, 44913, 44923, 44954, 45842, 45877, *Esslinger* 4502; 2: 3535, 43577; 3: 38616, 38623, 38633, 38643, 38665, 38672, 38719; 3a: 44759, 44782, 44817, 44829, 44843, 44872, 44893, 44908, 44953, 44971, 44989, 46076, 46080, *Esslinger* 4339; 6: 43482, 43509, 43523, 43563; 8: 38609; 9: 38437, 38485, 38488, 38496, 38507; 10: 46044, 46063; 11: 44799, 44848, 44854, 44899, 44915, 44931, 44969, 44970, 44997, 46022, 46024.

ILLUSTRATIONS.—Hale, 1974a:23, fig. 12f.

40. *Ocellularia protocetrarica*, new species

FIGURE 7d

DESCRIPTION.—Thallus corticola, epiphloeodes, nitidus, laevis vel verruculosus, pallide viridi-albus,

5–8 cm latus; apothecia (Figure 3e) numerosa, solitaria vel sparse aggregata, emergentia, 0.9–1.2 mm diametro, apice fuliginea, columella nulla vel rudimentariter actinoides, vix fuliginea, disco albo-pruinoso; ostiolum rotundatum, 0.2–0.5 mm diametro; hymenium ca 120 μm altum; sporae 8:nae, 6–8 \times 20–24 μm , 5–7 loculatae, I+ caeruleae.

CHEMISTRY.—Protocetraric acid.

HOLOTYPE.—Primary rain forest on road to Río Calovebora, 4–8 km from Alto Piedra, Province of Veraguas, Panama, elevation 800 m, *M. E. Hale* 44786, 25 February 1975 (US).

REMARKS.—The disc of the species at maturity has superficial pruinose actinoid divisions or fissures that may be slightly carbonized. The round pore is quite open and concolorous with the thallus. Two other protocetraric acid-containing species may cause confusion. *Ocellularia verrucosa* (see page 33), which also occurs in Panama, has a black rimmed, rather irregular pore and a smooth, entire disc. *Ocellularia nigropuncta* Hale from Dominica has smaller apothecia and a small black-rimmed pore.

SPECIMENS EXAMINED.—11: 46055; 12: *Mori* 4270 (cf.).

41. *Ocellularia pseudoschizostoma*, new species

FIGURE 7e

DESCRIPTION.—Thallus corticola, epiphloeodes vel evanescens, albus, 3–5 cm latus; apothecia dispersa, singularia, chroodiscoidea, 0.5–0.7 mm diametro, margine thallino crasso, erecto, non reflexo, irregulariter fisso; excipulum decoloratum, aetate non separatum; discus lividus, fissus, albo-pruinosis; hymenium 80–90 μm altum, paraphysibus granulato-encrustatis; sporae 8:nae, 12 \times 24 μm , 6–7 loculatae, I+ caerulescentes.

CHEMISTRY.—Stictic and constictic acids.

HOLOTYPE.—Primary rain forest, El Llano-Cartí road at 16–20 km, Province of Panamá, Panama, elevation 300 m, *M. E. Hale* 38559, 6 April 1973 (US).

REMARKS.—Another chroodiscoid species from Panama, *O. neei* Hale, has similar chemistry but differs in having a distinct inner exciple and a dark disc. *Ocellularia subllacina* (Everhart and Ellis) Zahlbruckner has much larger apothecia with a strongly recurved margin. *Ocellularia pseudoschizostoma* grows in the canopy in virgin rain forest.

42. *Ocellularia pulverulenta*, new species

FIGURE 7f

DESCRIPTION.—Thallus corticola, epiphloeodes, verrucosus vel subgranulatus, rimosus, albido-viridis, ca 10 cm latus, pro parte isidiatus, isidiis minutis, sorediatis, soraliis irregularibus, sorediis granulosis; apotheca sparsa, emergentia, amphithecio verrucoso-pustulato, sorediascenti, 0.4–1.0 mm diametro, eolumellata; ostiolum rotundatum, ca 0.1 mm diametro; excipulum decoloratum; hymenium 60–70 μm altum; sporae 8:nae, 6–10 \times 18–24 μm , 6–7 loculatae, I+ caerulescentes.

CHEMISTRY.—Psoromic and norpsoromic acids.

HOLOTYPE.—Secondary rain forest, 9 km NW of Gamboa along Naval Pipeline Road, Canal Zone, Panama, elevation 150 m, *M. E. Hale* 43468, 11 February 1974 (US).

REMARKS.—The small irregular soredial patches and small crumbly masses of isidioid growths are unique in this species. There is, in fact, only one other sorediate species in the genus, *O. sorediata* Hale from Dominica, which has large capitata soralia, immersed apothecia, and no chemical substances. The noncarbonized apothecia, at the same time, are similar to those of *O. glaucophaena* (Krempelhuber) Zahlbruckner, although larger. *Ocellularia pulverulenta* grew at about 1.5 m up on large trees in secondary low elevation rain forest.

SPECIMENS EXAMINED.—3a: 44821, 46073.

43. *Ocellularia recondita*

FIGURE 7g

Ocellularia recondita (Stirton) Zahlbruckner, 1923:600.
Thelotrema reconditum Stirton, 1876:162 [type collection: Amazons, Brazil, *Trail* (BM, lectotype) (Figure 2o)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, minutely rugulose, greenish gray, 6–10 cm broad; apothecia numerous, emergent but not basally constricted, heavily carbonized, 0.6–1.0 mm in diameter, the columella distinct, thick, the pore round, 0.1–0.3 mm in diameter, usually white annulate, the white pruinose tip of the columella clearly visible; spores 8, 7–8 \times 14–20 μm , 5–6 loculate, I+ blue.

CHEMISTRY.—Unknown P– substance. There is

a single strong H_2SO_4 + gray spot near the “olivacea” unknown.

REMARKS.—The emergent apothecia have a distinctive white rim around the pore, but the most important character is the chemistry, a P– unknown. Redinger (1936:37) regarded *O. recondita* as a synonym of *O. cavata* (Acharius) Müller Argoviensis, noting the large apothecia. I do not believe the two species are related at all. Aside from the type, I have seen one specimen from a lowland rain forest in Colombia, the usual habitat in Panama.

SPECIMENS EXAMINED.—3: 38618, 38628, 38687; 3a: 46074, *Esslinger* 4366; 4: 43488; 6: 43517.

44. *Ocellularia referta*, new species

FIGURE 7h

DESCRIPTION.—Thallus corticola, epiphloeodes, nitidus, rimosus, pallide olivaceo-viridis, 5–7 cm latus; apothecia semi-emergentia, subchroodiscoida, solitaria atque 2–3 confluentia, 0.5–0.7 mm diametro, margine thallino crasso, fisso, vix emergenti, non reflexo; ostiolum vix visibile, ca 0.1 mm diametro; excipulum pro parte separatum, fissum, apice fuligineum; hymenium ca 60 μm altum; sporae 8:nae, 8 \times 24 μm , 5–7 loculatae, I+ caerulescentes.

CHEMISTRY.—Hypoprotocetraric and 4-0-demethylnotatic acids.

HOLOTYPE. Secondary rain forest, La Mesa, north of El Valle, Province of Coclé, Panama, elevation 750 m, *M. E. Hale* 43566, 13 February 1974 (US).

REMARKS.—There are no other species with hypoprotocetraric acid similar to this one. *Phaeotrema aggregatum* Hale from Dominica has a similar filled disc but the apothecia are smaller and more aggregated and no lichen substances are produced. This species occurred at mid bole level in the rain forest.

45. *Ocellularia rhabdospora*

FIGURE 7i

Ocellularia rhabdospora (Nylander) Redinger, 1936:17.
Ascidium rhabdosporum Nylander, 1867:320 [type collection: Pie de Cuesta, Colombia, *Lindig* (H. Nylander herbarium 22432, lectotype; isolectotype in BM)].

Phaeotrema rhabdosporum (Nylander) Müller Argoviensis, 1895c:454.

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, verruculose, rimose with age, brownish or greenish gray, 6–10 cm broad; apothecia numerous, separate and dispersed, strongly emergent and ascidioid, up to 2 mm in diameter, heavily carbonized with a distinct central columella, the pore round, 0.2–0.3 in diameter, slightly depressed and narrowly white annulate; spores 1–2, 12×120 –160 μm , 15–20 loculate, I+ blue.

CHEMISTRY.—“Cinchonarum” P+ unknown substances.

REMARKS.—In this Brazilian study Redinger (1936:26) described in detail the specimens on which Krempelhuber based *Ascidium melanostomum* (*Phaeotrema melanostomum* (Krempelhuber) Müller Argoviensis). I propose to typify this species with *Glaziou* 5573 (G). It contains hypoprotocetraric acid (as do the syntypes), even though the basic morphology is very close to that of *O. rhabdospora*, which contains the P+ red “cinchonarium” series. With this hypoprotocetraric acid-containing population excluded and with proper typification of *O. rhabdospora*, we must now refer to the large ascidioid species collected in Panama as *O. rhabdospora*. It is a rare species, occurring only in the type-locality in Colombia and in eastern Darien.

SPECIMENS EXAMINED.—12: *Mori* 4448, 4457, 4460, 4463, 4478, 4492.

46. *Ocellularia rhodostroma*

FIGURE 7j

Ocellularia rhodostroma (Montagne) Zahlbruckner, 1923:600. *Ascidium rhodostromum* Montagne, 1851:75 [type collection: French Guiana, collection 1334 (PC, lectotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth to finely verruculose, continuous, pale greenish tan to gray, the exposed medulla deep pink, 5–10 cm broad; apothecia numerous, ascidioid, 1.0–1.8 mm in diameter, heavily carbonized but without a columella, the thick deep pink medulla easily exposed as the fragile cortex breaks away, the pore round, strongly annulate with a raised ring, 0.05–0.1 mm in diameter; spores 1–2, 20 – 30×100 –140 μm , 20–25 loculate, I+ blue.

CHEMISTRY.—Hypoprotocetraric acid and in

greater concentration 4-O-demethylnotatic acid with unidentified K– pigments.

REMARKS.—This was the commonest species of *Ocellularia* in Dominica (Hale, 1974a:27), but in Panama it was commonly collected only in the mid-elevation rain forests west of the Canal Zone and mostly in the canopy or mid bole area of the trees. Surprisingly I did not collect it at Chiriquí, an area of mossy forest not unlike that in Dominica where it had maximum abundance, and, as expected, it was absent from the low elevation rain forests. The pink medulla and large annulate-pored apothecia are so distinctive that the species can be identified positively in the field.

SPECIMENS EXAMINED.—2: 43454, 43545, 43572, 43578, 43581; 6: 43508, 43533, 43537; 9: 38438, 38443, 38458, 38462; 10: 44990; 11: 44785, 44800, 44841, 44850, 44884, 44929, 44932, 44938, 44948, 44965, 45814, 46050, *Esslinger* 4648.

ILLUSTRATIONS.—Hale, 1974a:26, fig. 13a.

47. *Ocellularia ripleyi*

FIGURE 7k

Ocellularia ripleyi Hale, 1974b:493 [type collection: Canal Zone, Panama, *Hale* 38664 (US, holotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, continuous, uniformly minutely verrucose, dull, whitish gray, 8–14 cm broad; apothecia rather numerous, emergent, 1.0–1.5 mm in diameter, the amphithecium minutely verrucose, carbonized with a distinct columella, the pore round, 0.2 mm in diameter, white annulate; spores 1–2, 12 – 15×80 –200 μm , 8–25 loculate, I+ blue.

CHEMISTRY.—Psoromic acid with or without norpsoromic acid.

REMARKS.—This conspicuous understory species is the dominant *Ocellularia* on Barro Colorado Island. I collected it at only one other site, the adjacent mainland near Gamboa. This high localization suggests that it is a recently revolved population, very successful within a narrow environmental and geographic range, although one record has been made in Cuba. It is externally and chemically similar to *Thelotrema interpositum* Nylander, which does not occur at all in Panama.

SPECIMENS EXAMINED.—3: 38621, 38648, 38650, 38658, 38664, 38688, 38700, *Herre* 14; 3a: 44822, 44828, 44836, 44840, 44856, 44991, 45813, 46081, *Esslinger* 4353A, 4359, 4374, 4406, 4409; 4: 43434.

ILLUSTRATIONS.—Hale, 1974b:493, fig. 8.

48. *Ocellularia subcavata*

FIGURE 71

Ocellularia subcavata (Nylander) Zahlbruckner, 1923:601.
Thelotrema subcavatum Nylander, 1876:561 [type collection: Cuba, Wright 509 (H. Nylander herbarium 22813, lectotype; isoelectotype in FH-Tuck)].
Thelotrema vagum Vainio, 1896:209.
Ocellularia vaga (Vainio) Zahlbruckner, 1923:603.

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, thick, warty and cracked, ashy white, up to 12 cm broad; apothecia very numerous, emergent, 0.6–1.0 mm in diameter, crowded, the walls carbonized but the central columella carbonized only at the base, the apex noncarbonized and white pruinose, the pore round, 0.1–0.2 mm in diameter, white annulate with a raised ring, the center filled with the white pruinose columella tip; spores 8, 4–8 × 8–22 μm , usually uniseriate, 5–6 loculate with narrow locules, I+ blue.

CHEMISTRY.—Psoromic acid with or without norpsoromic acid.

REMARKS.—This species is easily recognized by the numerous, crowded annulate pored apothecia and the basally uncarbonized columella. It was very common in Dominica (Hale, 1974a:28) and has been identified from all the islands in the Lesser Antilles, Jamaica, and Venezuela, generally at mid elevation (300–800 m). I collected it in Panama only west of the Canal Zone, mostly at canopy level.

SPECIMENS EXAMINED.—2: 43469; 8: 38529, 38543, 38551, 38553, 38602, 38603; 9: 38479, 38487, 38500, 38516; 11: 46048.

ILLUSTRATIONS.—Hale, 1974a:26, fig. 13b.

49. *Ocellularia subemersa*

FIGURE 8a

Ocellularia subemersa Müller Argoviensis, 1886:310 [type collection: Gordon Town, Jamaica, Hart 125 (G, lectotype) (Figure 2r)].

DESCRIPTION.—Thallus corticolous or partially muscicolous, epiphloeodal or very thin and in part hypophloeodal, shiny, fragile, tannish, or greenish gray, 5–8 cm broad; apothecia common, solitary or clumped in 2s and 3s, strongly emergent and becoming basally constricted, 0.4–0.7 mm in diameter, the thalline rim carbonized, erect, or becoming

abruptly apically recurved, the entire rim white pruinose, the columella distinct, carbonized, the apex white pruinose, the pore open, irregular, 0.3–0.5 mm in diameter; spores 8, 5–6 × 12–15 μm , 4–6 loculate, I+ blue.

CHEMISTRY.—“Cinchonarum” unknowns.

REMARKS.—This unusual species is characterized by the rather small but distinctly urceolate apothecia with an erect or slightly flared thalline margin surrounding the apically white pruinose columella. It is a canopy species at a 700–800 m elevation in Panama and also occurs in Jamaica, the type-locality, and Trinidad.

SPECIMENS EXAMINED.—2: 43522, 43539, 43552; 9: 38474; 11: 44891, 46060, *Esslinger* 4646, 4647.

50. *Ocellularia sublilacina*

FIGURE 8b

Ocellularia sublilacina (Ellis and Everhart in Smith) Zahlbruckner, 1923:601.

Karstenia sublilacina Ellis and Everhart in Smith, 1896:49 [type collection: Castillo, Nicaragua, *Smith* 49 (BPL, lectotype)].

Thelotrema sublilacinum (Ellis and Everhart in Smith) Vainio, 1923:137.

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, smooth, and continuous, dark olivaceous or greenish mineral gray, up to 15 cm broad; apothecia common, separate, conspicuous, chroodiscoid, 2–5 mm in diameter, the thalline margin usually thick, erect or recurved, the inner exciple well developed, persistent, free, the disc pale tan to flesh colored; spores 2–4, 10–15 × 60–120 μm , 15–20 loculate, I+ blue.

CHEMISTRY.—Stictic and constictic acids with associated unknown substances.

REMARKS.—*Ocellularia sublilacina* is one of the truly remarkable species in the genus. The chroodiscoid apothecia are so large as to appear as disc fungi, leading Ellis and Everhart to describe it as a fungus originally. The thalline rim and inner exciple remain free and form a conspicuous fringe around the disc. It occurs mainly on the lower trunk of trees in dense woods. I have also collected it in Trinidad.

SPECIMENS EXAMINED.—3: 38514, 38597, 38638, 38678; 3a: 44760, 44771, 44794, 44803, 44874, 44901, 46077, *Esslinger* 4352, 4357, 4387; 4: 43343, 43456; 8: 38596; 9: 38468; 11: 44795.

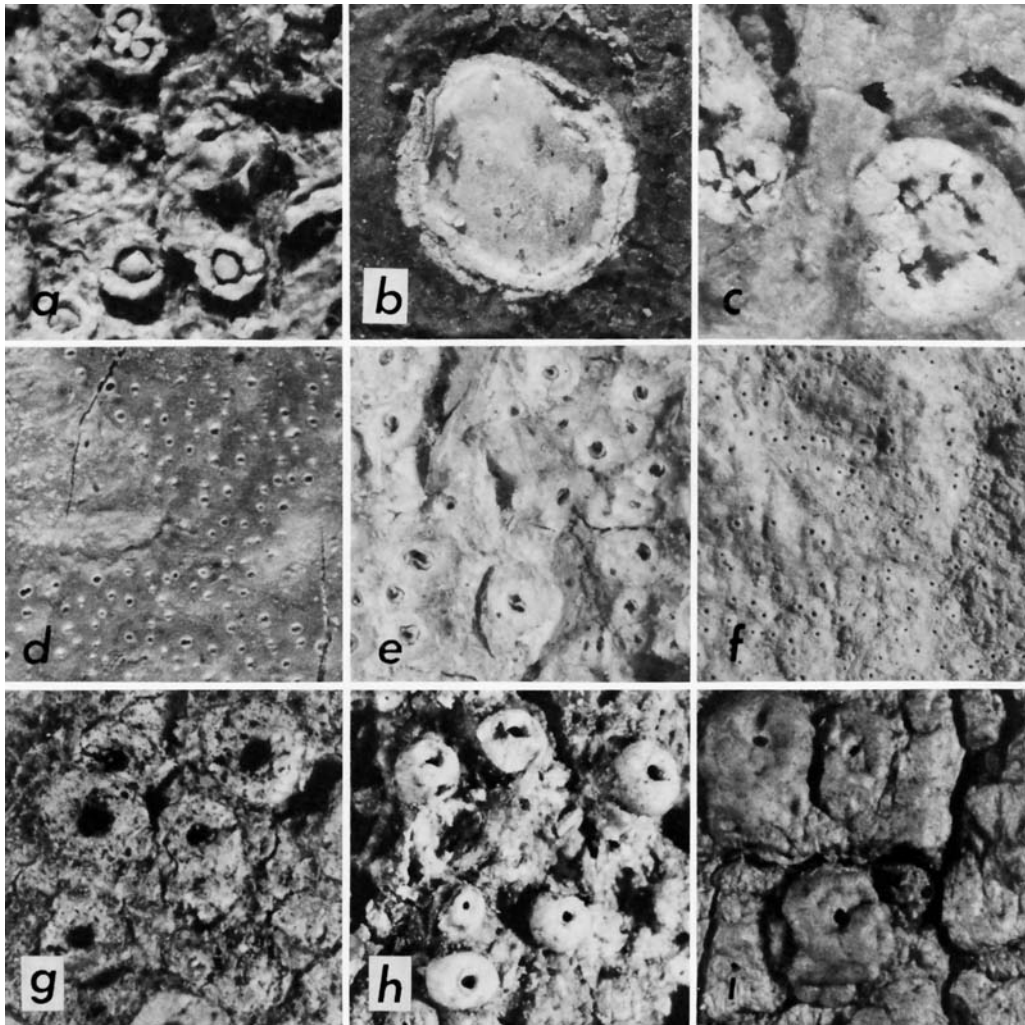


FIGURE 8.—Species of *Ocellularia*: a, *O. subemersa* (Hale 37474); b, *O. sublilacina* (Hale 38597); c, *O. subwrightii* (Mori 4286); d, *O. terebratula* (Hale 44787); e, *O. turgidula* (Hale 45832); f, *O. uniseptata* (Hale 38671); g, *O. verrucosa* (Hale 43433); h, *O. viridis* (Hale 38538); i, *O. xanthostroma* (Hale 44758) ($\times 10$).

51. *Ocellularia subwrightii*, new species

FIGURE 8c

DESCRIPTION.—Thallus corticola, epiphloeodes, sat tenuis et fragilis, laevis vel verruculosus, nitidus, continuus, pallide stramineo-viridis, 5–15 cm latus; apothecia rara, separata, rotundata vel irregulariter expansa, valde emergentia, aetate basi constricta, 2–5 mm lata, margine thallino crasso (usque ad 1 mm lato), scabroso, disco aperto, carneo, actinoide-diviso, columellis subfuliginis, elevatis, pro parte superficialibus, livido-stramineo-pruinosis; hymenium ca. 120 μm altum; sporae 8-nae, 5–7 \times 14–22 μm , 4–5 loculatae, I+ caeruleae.

CHEMISTRY.—Psoromic acid and an unidentified H_2SO_4 + yellow spot near stictic acid in the benzene solvent.

HOLOTYPE.—Cerro Mali, Province of Darien, Panama, elevation 850 m, S. Mori and A. Gentry 4286, 16 January 1975 (US).

REMARKS.—The large apothecia are pale yellowish white and stand out conspicuously from the more greenish thallus. The development of a coarse, partially carbonized, superficial columella is identical with that in *Thelotrema wrightii* (Tuckerman) Zahlbruckner. There are no close relatives in *Ocellularia*; for example, *O. berkeleyana* (see page 14) has smaller, round apothecia with a heavily

carbonized actinoid disc. It occurs rather widely in Panama from 100 m to 1100 m elevation on lower trunk and basal area of large trees.

SPECIMENS EXAMINED.—3a: 44887; 6: 43519; 9: 38473; 11: 46016, 44900 (cf.); 12: *Mori* 4254, 4255, 4279, 4286, 4305.

52. *Ocellularia terebratula*

FIGURE 8d

Ocellularia terebratula (Nylander) Müller Argoviensis, 1887a: 12.

Thelotrema terebratulum Nylander, 1867:315 [type collection: Colombia, *Lindig* 129 (H, Nylander herbarium 22637, lectotype; isoelectotypes in FH, G, M, PC)].

Thelotrema clandestinum f. *remanens* Nylander, 1867:317. *Ocellularia remanens* (Nylander) Müller Argoviensis, 1887a:7. [For full citations see Hale (1974a:28)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, quite thick, shiny, smooth and continuous, pale greenish to whitish ashy, 4–8 cm broad; apothecia very numerous, immersed, 0.2–0.4 mm in diameter, noncarbonized and eolumellate, the inner exciple evanescent or rarely persistent, the pore round, flush, 0.05–0.1 mm in diameter, usually faintly white annulate; spores 8, $5 \times 12 \mu\text{m}$, 3–5 loculate, I+ blue.

CHEMISTRY.—Psoromic and norpsoromic acids.

REMARKS.—This is one of the canopy species of the *Ocellularia alba-Thelotrema clandestinum* type that must be examined carefully for spores and chemistry for positive identification. It is distinguished by the flush apothecia, smooth shiny thallus, and presence of psoromic acid. The fine structure of the cortical surface, semierect aculeate hyphae (Hale, 1974a:2), is distinctive. Closely related *O. myriotremoides* (#34) has a scabrid surface. I have identified specimens from Florida, Costa Rica, the Lesser Antilles, New Caledonia, Java, Sabah, and the Solomon Islands.

SPECIMENS EXAMINED.—2: 43556; 3a: 44787; 6: 43525; 9: 38464, 38476.

ILLUSTRATIONS.—Hale, 1974a:26, fig. 13e.

53. *Ocellularia turgidula*

FIGURE 8e

Ocellularia turgidula Müller Argoviensis, 1893a:94. [type collection: Mont Mou, New Caledonia, *Balansa* (PC, lectotype; isoelectotype in G)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin, shiny, smooth to minutely verruculose, whit-

ish ashy gray, 5 cm broad; apothecia numerous, separate to loosely clustered, semiemergent, 0.5–0.9 mm in diameter, the thalline exciple noncarbonized, somewhat raised, the inner exciple distinct, entire, free; the pore open 0.2–0.3 mm wide; spores 4–8, $10 \times 50\text{--}55 \mu\text{m}$, 10–12 loculate, I+ blue.

CHEMISTRY.—No lichen substances present.

REMARKS.—Externally *O. turgidula* is quite similar to *Thelotrema lepadinum* (Acharius) Acharius but the thallus is more developed and the apothecial pore less open. It seems to occur in more open, secondary habitats. I have another record from Japan: *Hale* 29652, Inohae Valley, Hyuga Province.

SPECIMEN EXAMINED.—11: 45832.

54. *Ocellularia uniseptata*, new species

FIGURE 8f

DESCRIPTION.—Thallus corticola, epiphloeodes, continuous, minute verruculosus, albidus, 6–8 cm latus; apothecia numerosa, regulariter dispersa, immersa, 0.1–0.2 diametro, eolumellata; ostiolum rotundatum, ca 0.07 mm diametro, leviter annulatum, albo-cinctum; excipulum decoloratum; hymenium 45–50 μm altum; sporae 8:nae, 3–4 \times 6 μm , 2–, raro 3-loculatae, I+ caerulescentes.

CHEMISTRY.—Psoromic acid and a trace of stictic acid.

HOLOTYPE.—Secondary rain forest, W. H. Wheeler trail, Barro Colorado Island, Canal Zone, Panama, elevation about 120 m, *M. E. Hale* 38671, 3 April 1973 (US).

REMARKS.—This species seems to be close to *O. terebratula* (see above), a canopy species with a shiny, nongranular thallus and larger spores. *Ocellularia uniseptata* is unusual, however, in having small, mostly uniseptate spores and in occurring lower on the trunks in low elevation rain forest.

SPECIMENS EXAMINED.—3a: 44904, *Esslinger* 4392.

55. *Ocellularia verrucosa*, new combination

FIGURE 8g

Thelotrema verrucosum Fée, 1824:94 [type collection: "America, ad corticem *Cinchonae lancifoliae* (Mutis.)" (G, lectotype; isoelectotype in L)].

Ascidium cinchonarum var. *verrucosum* (Fée) Fée, 1837:91.

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin, minutely verrucose, dull greenish or brown-

ish mineral gray, 5–7 cm broad; apothecia isolated, emergent, about 1.0 mm in diameter, carbonized but without a columella, the pore round, to 0.5 mm in diameter, black rimmed, the lightly pruinose disc visible; spores 8, $8 \times 22\text{--}32 \mu\text{m}$, 6–8 loculate, I+ blue.

CHEMISTRY.—Protocetraric acid.

REMARKS.—The type of this species in G is in poor condition, but the apothecia can be adequately characterized as semiemergent, ecolumellate, and with a black rimmed pore. The granular-verrucose thallus surface was noted by Fée in his original description. Fée himself later reduced it to a variety of *Ascidium cinchonarum* Fée, but that species contains the P+ “cinchonarum” unknowns, not protocetraric acid, and is columellate. Müller (1887a:6) followed Fée’s interpretation, and as far as I can determine no one has investigated the problem since then. The material I collected in Panama matches Fée’s lectotype very closely, as does one other from Colombia, all collected in the canopy or upper bole of trees in lowland rain forest. The closest relative may be *O. lepadinioides* (Leighton) Zahlbruckner, which has larger apothecia and spores.

SPECIMENS EXAMINED.—3: 43492; 4: 43433, 43480; 8: 38544.

56. *Ocellularia viridis*, new species

FIGURE 8h

DESCRIPTION.—Thallus corticola, epiphloeodes, nitidus, continuus, albo-viridis, 4–7 cm latus; apothecia (Figure 3f) numerosa, dispersa, emergentia, aetate basi constricta, globoso-urceolata, 0.6–0.9 mm diametro, ecolumellata vel demum rudimentaliter actinoide-columellata; ostiolum rotundatum, 0.1–0.2 mm diametro, plus minusve depressum, albo-annulatum; excipulum decoloratum vel fuliginascens; hymenium 60–70 μm altum; sporae 8:nae, $4\text{--}6 \times 7\text{--}14 \mu\text{m}$, 4–5 loculatae, I+ caerulescentes.

CHEMISTRY.—An unknown substance.

HOLOTYPE.—Mature rain forest, El Llano-Cartí Road at 16–20 km, Province of Panamá, Panama, elevation 300 m, *M. E. Hale* 38538, 6 April 1973 (US).

REMARKS.—The urn-shaped apothecia are somewhat similar to those of *O. submersa* (see above), a West Indian species with the “cinchonarum” unknown, but the pore is not open. The unknown

substance in *O. viridis* is P– and forms a weak gray spot in the usual solvent systems. The species grows at the mid bole and lower trunk levels in rain forest at low to mid elevation.

SPECIMENS EXAMINED.—6: 43472; 8: 38554, 38601.

57. *Ocellularia xanthostroma*

FIGURE 8i

Ocellularia xanthostroma (Nylander) Zahlbruckner, 1923:603.
Ascidium xanthostromum Nylander, 1891:20 [type collection: Cuba. *Wright* 33 (H, Nylander herbarium 22412, lectotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, verruculose, whitish mineral gray, the medulla bright reddish orange, 5–7 cm broad; apothecia numerous, separate, strongly emergent, 1.1–1.5 mm in diameter, the amphithecium smooth to warty, easily breaking open to reveal the pigmented medulla, the exciple carbonized, a columella lacking, the pore round, 0.1–0.2 mm in diameter, narrowly white annulate, somewhat depressed; spores 2–4, $12 \times 100 \mu\text{m}$, about 18 loculate, I+ blue.

CHEMISTRY.—Endocrocin and a second unidentified pigment.

REMARKS.—The cortical layer on the thallus and apothecia breaks away easily to reveal the brilliant orange-yellow medulla. The chief pigment is endocrocin. It differs from *O. mordenii* (see page 25) in chemistry (different pigments that are red rather than orange) and apparently in having more discrete emergent apothecia, although we must see more collections to comprehend the full range of chemical and morphological variation in this complex. The one specimen from Panama was collected on a liana along an open trail on Barro Colorado Island.

SPECIMEN EXAMINED.—3a: 44755.

Phaeotrema Müller Argoviensis

This genus is recognized by the brown, transversely septate spores. It is the smallest genus in the family, comprising about 50 species worldwide but only 5 in Panama. Of the 28 specimens collected, 21 are *P. auberianum*, which occurred at 7 of the 12 collecting localities. No other species is represented by more than two collections scattered among nine localities, generally at mid elevation.

The genus is rare both at the highest localities in Chiriquí and in the lowland forests.

All of the species except *P. vulcani* have a reticulate columella or a tendency to form one. None are

chroodiscoid or lepadinioid. *Phaeotrema auberianum* and *P. meiospermum* are both pantropical and the remaining species neotropical in distribution.

Key to the Species of *Phaeotrema*

- 1. A columella lacking5. *P. vulcani*
- 1. A columella present.
 - 2. The disc open, 1–5 mm wide, often elongated, actinoid-columellate.
 - 3. Thallus P+ yellow (psoromic acid).1. *P. auberianum*
 - 3. Thallus P– (hypoprotocetraric acid).2. *P. glyphicum*
 - 2. Disc less than 0.4 mm wide, columella mostly simple.
 - 4. Columella broad, the top clearly visible through the open pore, the pore 0.2–0.4 mm wide4. *P. meiospermum*
 - 4. Columella narrow or weakly developed, the pore 0.1–0.2 mm wide, with a raised annulate rim.3. *P. leiostomum*

1. *Phaeotrema auberianum*

FIGURE 9a, b

Phaeotrema auberianum (Montagne) Müller Argoviensis, 1886:311.

Thelotrema auberianum Montagne in Sagra, 1842:163 [type collection: Cuba, *Auber* (H, Nylander herbarium 22615, lectotype; isolectotype in L) (Figure 1e)].

Thelotrema glyphidellum Stirton, 1876:161 [type collection: Amazons, Brazil, *Trail*, (BM, lectotype)].

Phaeographis chionodisca Redinger, 1935:72 [type collection: Santos, São Paulo, *Malme* 3559 (S, lectotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth to verruculose, shiny, fissured with age, greenish mineral gray, 6–12 cm broad; apothecia common, irregularly dispersed, solitary, emergent

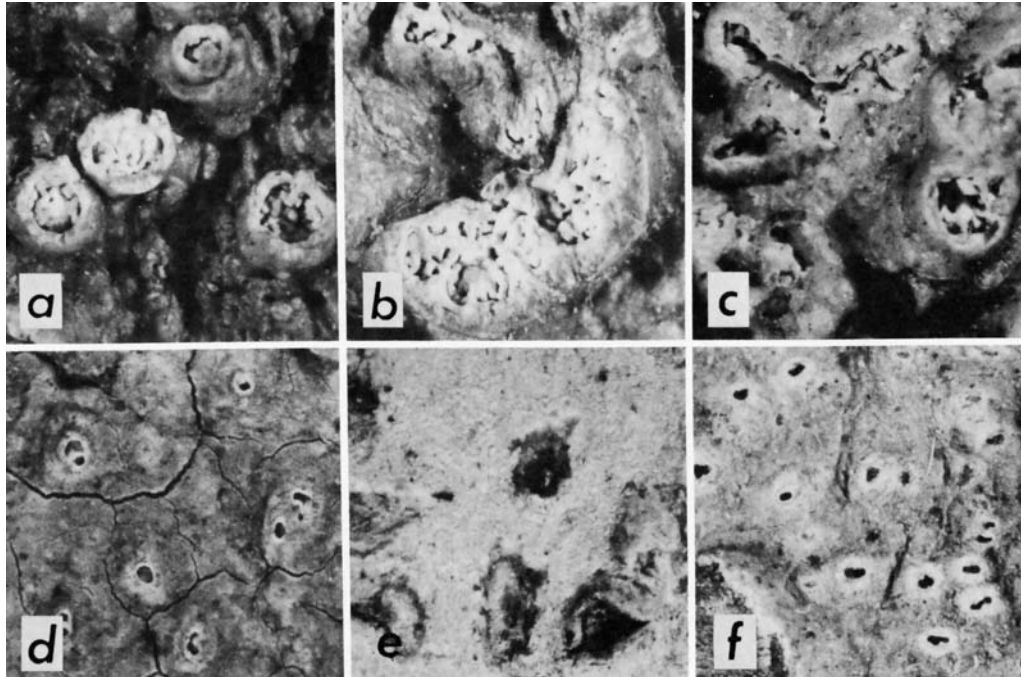


FIGURE 9.—Species of *Phaeotrema*: a, *P. auberianum* (Hale 43487); b, *P. auberianum* with elongate apothecia (Hale 45581); c, *P. glyphicum* (Nakanishi 51); d, *P. leiostomum* (Hale 38600); e, *P. meiospermum* (Hale 46061); f, *P. vulcani* (Hale 43534) (× 10).

to strongly emergent at maturity, 1.0–2.5 mm wide, the thalline margin thick, carbonized, the disc open, conspicuously actinoid-columellate, the columella carbonized; surface of the disc becoming heavy white pruinose; spores 8, 4–8 × 9–14 μm , 4 loculate.

CHEMISTRY.—Psoromic acid.

REMARKS.—This is a conspicuous lichen, easily recognized and widespread in Panama and usually collected on lower trunks of trees in open forest. The actinoid disc is very similar to that of *Ocellularia berkeleyana* (Montagne) Müller Argoviensis. Range in size and shape of the disc is very great, Redinger's type of *Phaeographis chionodisca* and my numbers 38564 and 38581 representing an extreme population with long lirelliform apothecia up to 8 mm long (Figure 9b). It is a pantropical species.

SPECIMENS EXAMINED.—3a: 44793, 44857, 44961; 4: 43487; 6: 43528, 43543, 43544; 8: 38525, 38539, 38573; 38582, 38604; 9: 8475; 11: 44819, 44834, 44880, 44898, 44992, *Esslinger* 4257, 4413.

2. *Phaeotrema glyphicum*

FIGURE 9c

Phaeotrema glyphicum (Nylander) Zahlbruckner, 1923:607.
Thelotrema glyphicum Nylander, 1863a:453 [type collection: Villeta, Colombia, *Lindig* 826 (FH-Tuck, lectotype; isolecotypes in BM, PC, W) (Figure 1t)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thick, smooth to verruculose, white-spotted, ivory to pale tan, 6–10 cm broad; apothecia numerous, more or less clustered, orbicular to lirelliform in outline, immersed to semi-emergent, up to 2 mm broad, the thalline margin becoming white pruinose, forming a low rim, the disc open to somewhat closed, actinoid columellate, the columella carbonized; spores 8, 4–8 × 12–16 μm , 4 loculate.

CHEMISTRY.—Lichexanthone with or without hypoprotocetraric and 4-O-demethylnotatic acids.

REMARKS.—This rare species was previously known only from Brazil (Redinger, 1936:72) and the type collection in Colombia. The large irregularly shaped apothecia have a strongly developed actinoid disc. *Hale* 38465 contains both lichexanthone, the only component in the type collection, and hypoprotocetraric and 4-O-demethylnotatic acids. The normal habitat seems to be the mid and

upper trunk of mature trees in rain forest at higher elevations.

SPECIMENS EXAMINED.—1: *Nakanishi* 51; 1a: 44877; 9: 38465.

3. *Phaeotrema leiostomum*

FIGURE 9d

Phaeotrema leiostomum (Tuckerman) Zahlbruckner, 1923:608.
Thelotrema leiostomum Tuckerman, 1862:407 [type collection: Cuba, *Wright* 149 (FH-Tuck, lectotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, continuous, smooth and shiny, about 5 cm broad; apothecia slightly emergent, 0.3–0.6 mm in diameter, weakly carbonized and with a weakly developed columella, the pore round, 0.1–0.3 mm in diameter, white annulate; spores 8, 8 × 15 μm , 4 loculate.

CHEMISTRY.—Hyproprotocetraric acid.

REMARKS.—The Panamanian material, which lacks 4-O-demethylnotatic acid, is identical to the population in Dominica (*Hale*, 1974a:29) but with less variation in apothecial outline. It also has a similar habitat: mid bole on trees in rain forest at mid elevation.

SPECIMENS EXAMINED.—8: 38600.

ILLUSTRATIONS.—*Hale*, 1974a:30, figs. 14b, c.

4. *Phaeotrema meiospermum*

FIGURE 9e

Phaeotrema meiospermum (Nylander) Müller Argoviensis, 1886:311.

Thelotrema meiospermum Nylander, 1863b:333 [type collection: Cuba, *Wright* 136 (FH-Tuck, lectotype; isolecotypes in BM, G. H. L., PC, UPS)].

Thelotrema phaeospermoides Vainio, 1921:185 [type collection: Prov. Rizal, Philippines, *Ramos and Edaño* 29456 (TUR, lectotype; isolecotypes in BM, FH, US, W)].

Phaeotrema phaeospermoides (Vainio) Zahlbruckner, 1923:609.

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth with a grainy surface, shiny, ivory colored, 6–12 cm broad; apothecia not common, immersed to semiemergent, round to elongate in outline, 0.3–0.5 mm in diameter, the thalline margin carbonized, a columella present, very broad, to 300 μm in diameter, the pore open with the black columella surface clearly visible, round to irregular, 0.2–0.4 mm wide; spores 8, 10 × 16–18 μm , 4 loculate.

CHEMISTRY.—No substances present.

REMARKS.—The apothecia are quite variable in size and may have a single broad columella or a main columella with secondary actinoid growths. I have identified the species from Florida, Cuba, Sri Lanka, Java, and Sarawak. In Panama it occurred on the lower trunk of trees in the rain forest at mid elevation.

SPECIMENS EXAMINED.—11: 46033, 46061.

5. *Phaeotrema vulcani*, new species

FIGURE 9f

DESCRIPTION.—Thallus corticola, epiphloeodes, continuous vel demum rimosus, glauco-viridis, 10 cm latus; apothecia (Figure 10) numerosa, immersa vel semi-emergentia, solitaria vel 2–3 confluentia, 0.5–0.7 mm in diametro, eolumellata; ostiolum rotundatum vel elongatum, 0.2–0.3 mm latum, annulo elevato, albocincto; excipulum decoloratum; hymenium 60–90 μm altum; sporae 8:nae, 4–5 \times 10–12 μm , 2–3 loculatae, I–.

CHEMISTRY.—No substances present.

HOLOTYPE.—Secondary rain forest, La Mesa, north of El Valle, Province of Coclé, Panama, elevation 750 m, M. E. Hale 43534, 13 February 1974 (US).

REMARKS.—The raised, white, round to elongated ostiole is similar to that of *Phaeotrema leiostomum* (Tuckerman) Zahlbruckner but much larger. There are no comparable species in the



FIGURE 10—Section of apothecium of *Phaeotrema vulcani* (Hale 43534) ($\times 125$).

genus. It is confined to canopy branches in the rain forest at mid elevations.

SPECIMENS EXAMINED.—11: 44763.

Thelotrema Acharius

This is the second largest genus in the family, characterized by colorless muriform spores. On the world level there are about 140 species. The 23 species in Panama were collected frequently at all the localities, excepting the Summit Botanical Garden and the pasture above Alto Piedra. About 120 collections were made, 20% of the total for the family compared with 15% in Dominica.

The floristic composition of the genus is quite different from that in Dominica. For example, 7 of the 10 commonest species, *T. erumpens* (4 collections), *T. oclusum* (4), *T. maximum* (12), *T. myrioporoides* (6), *T. stylotheceum* (6), *T. subpraestans* (17), and *T. wrightii* (5) have not yet been collected in Dominica. The three remaining species of the 10 most common, *T. conforme* (8), *T. glaucopallens* (31), and *T. praestans* (3) are among the 10 most common in Dominica. Four of the 23 *Thelotremata* are described as new from Panama, as compared with 4 of 14 in Dominica.

The morphological variation of the apothecia is similar to that in Dominica. One species, *T. hiatum*, is clearly chroodiscoid, while *T. conveniens*, *T. lepadinum*, *T. myriocarpum*, and *T. oclusum* are lepadinoid. *Thelotrema clandestinum*, *T. glaucopallens*, *T. norsticticum*, and *T. pycnoporellum* have flush myriotreroid apothecia. Only *T. leucomelaenum*, *T. praestans*, *T. stylotheceum*, and *T. subpraestans* are strongly columellate, and *T. wrightii* has a weakly actinoid disc.

The lowland species, as represented by the collections made on Barro Colorado Island and nearby Gamboa, include *T. adjectum*, *T. cryptotrema*, *T. glaucopallens*, *T. hiatum*, *T. myrioporoides*, and *T. subpraestans*. The strictly high elevation species include *T. concretum*, *T. conveniens*, *T. erumpens*, *T. lepadinum*, *T. leucomelaenum*, *T. oclusum*, *T. stylotheceum*, and *T. tenue*. *Thelotrema* is best developed at higher elevations, there being a total of eight species among 22 collections made at Chiriquí. Only five species make up the 39 collections made at Barro Colorado Island.

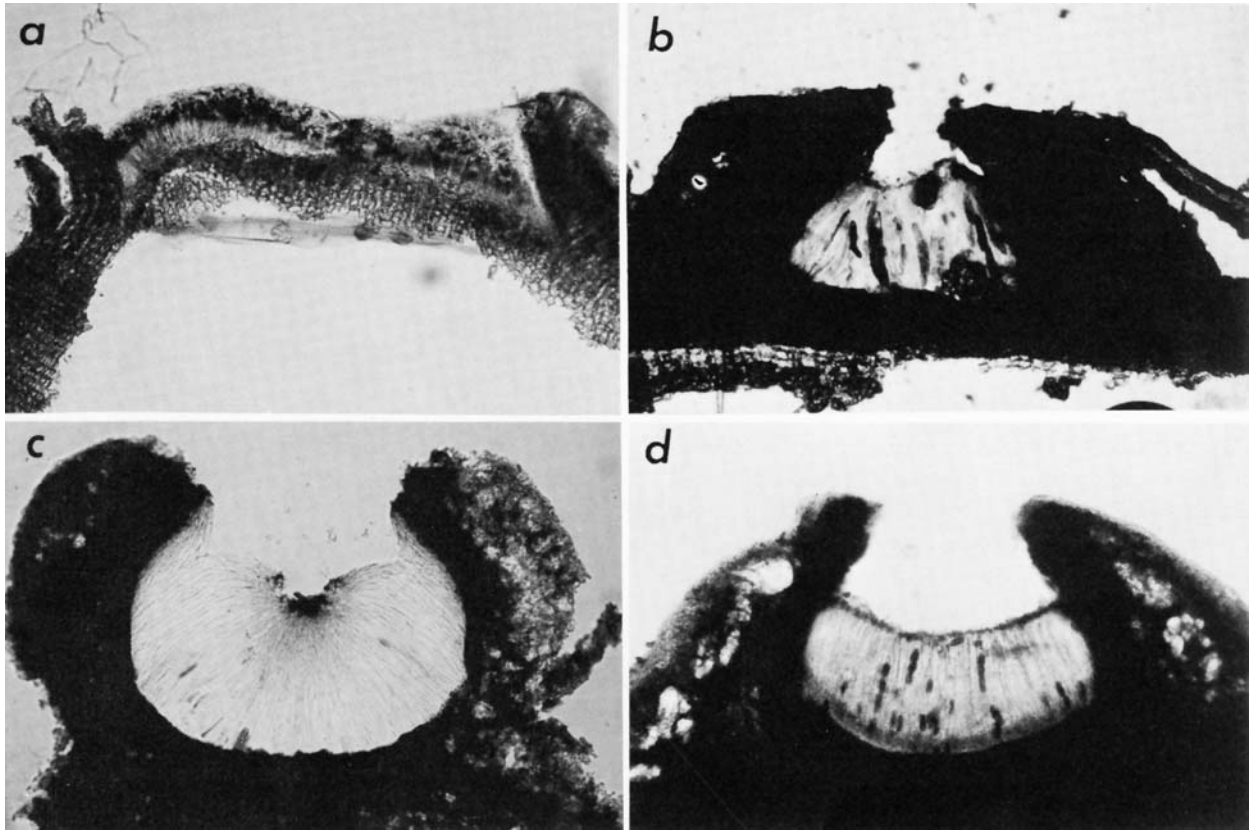


FIGURE 11.—Cross sections of apothecia of *Thelotrema* and *Leptotrema*: a, *T. hiatum* (Hale 43458) ($\times 125$); b, *T. maximum* (Hale 43580) ($\times 100$); c, *L. chiriquiense* (Hale 46035) ($\times 100$); d, *L. panamense* (Hale 43584) ($\times 125$).

The following species are restricted to the canopy: *T. clandestinum*, *T. cryptotrema*, *T. myrioporoides*, *T. praestans*, and *T. subpraestans*. The remaining species grow lower on the trunk but only *T. glaucopallens* is strongly restricted to the base level.

The phytogeography of *Thelotrema* is less well known than for *Ocellularia*, because fewer collections have been made. A rather large group of species were previously known only from South

America, illustrating perhaps the more continental nature of the Panamanian flora as compared with that of Dominica: *T. concretum*, *T. conveniens*, *T. cryptotrema*, *T. oclusum*, and *T. stylothecium*. Caribbean species include *T. adjectum*, *T. myrioporoides*, *T. norsticticum*, *T. pycnoporellum*, *T. tenue*, and *T. wrightii*, most of which were previously known only from Cuba. *Thelotrema auratum*, *T. clandestinum*, *T. erumpens*, *T. glaucopallens*, and *T. lepadinum* form a pantropical element.

Key to the Species of *Thelotrema*

1. Apothecial disc open, the thalline rim erect or recurved.
 2. Apothecia large, 1–3 mm in diameter, the rim coarse.23. *T. wrightii*
 2. Apothecia less than 1 mm wide, the rim thin.10. *T. hiatum*
1. Apothecia with a distinct pore, the thalline rim not erect.
 3. A distinct black central column present (weakly developed in *T. conforme* and *T. tenue*).
 4. Apothecia large and emergent, 2–3 mm in diameter; spores 200–300 μ m long.
 5. Stictic acid present21. *T. subpraestans*
 5. "Praestans" unknown present.18. *T. praestans*

4. Apothecia 1 mm or less in diameter; spores less than 50 μm .
 6. Apothecia to 1 mm in diameter, emergent; psoromic acid present (P+ yellow).5. *T. conforme*
6. Apothecia 0.2–0.8 mm in diameter, nearly flush; stictic acid present (P+ orange) or no substances present.
 7. Stictic acid present.20. *T. stylotheceum*
 7. No lichen substances present.
 8. Pore small, 0.1 mm wide; columella thin and tall; spores less than 20 μm22. *T. tenue*
 8. Pore gaping 0.2–0.4 mm wide; columella thick and broad; spores more than 30 μm12. *T. leucomelaenum*
3. Central columella lacking.
 9. Apothecia large and emergent, 1–4 mm in diameter.
 10. Disc covered with a yellow-orange pruina2. *T. auratum*
 10. Disc unpigmented.
 11. Pore small, about 0.1 mm wide.13. *T. maximum*
 11. Pore open, 0.2–0.4 mm wide, the proper exciple visible.11. *T. lepadinum*
9. Apothecia smaller, 0.2–0.8 mm in diameter, flush to semiemergent.
 12. Spores large and densely muriform, more than 50 μm long.
 13. Thallus P+ yellow (psoromic acid).7. *T. cryptotrema*
 13. Thallus P–.
 14. Spores less than 100 μm long.1. *T. adjectum*
 14. Spores more than 100 μm long.
 15. Pore distinct, the proper exciple forming a small inner pore.6. *T. conveniens*
 15. Pore broader, 0.2–0.4 mm wide, more or less filled with excipular material.17. *T. oclusum*
12. Spores smaller, less than 40 μm long.
 16. Apothecia to 0.5 mm in diameter, slightly emergent and often apically carbonized.
 17. Apothecia with an open pore, to 0.2 mm wide; uncarbonized.4. *T. concretum*
 17. Apothecia with a small pore, less than 0.1 mm wide; apically carbonized.
 18. Stictic acid present.8. *T. erumpens*
 18. No lichen substances present.22. *T. tenue*
16. Apothecia 0.1–0.3 mm in diameter, flush, uncarbonized (slightly carbonized only in *T. pycnoporellum*).
 19. Stictic acid present.
 20. Pore up to 0.1 mm wide, filled with the free proper exciple.14. *T. myriocarpum*
 20. Pore less than 0.1 mm; proper exciple evanescent.9. *T. glaucopallens*
19. Stictic acid lacking.
 21. Thallus P+ yellow or orange.
 22. Psoromic acid present.3. *T. clandestinum*
 22. Norstictic acid present.16. *T. norsticticum*
 21. Thallus P–.
 23. Hypoprotocetraric acid present.15. *T. myrioporoides*
 23. No lichen substances present.19. *T. pycnoporellum*

1. *Thelotrema adjectum*

FIGURE 12a

Thelotrema adjectum Nylander, 1866:290 [type collection: Cuba, Wright ser. 2, 82 (H. Nylander herbarium 22572, lectotype; isolectotype in UPS) (Figure 1b)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, the surface grainy to minutely verruculose, continuous, pale tannish or whitish gray, 6–12 cm broad;

apothecia numerous, solitary, nearly immersed to semiemergent, 0.6–1.0 mm in diameter, the thalline rim coarse, becoming semierect, jagged, the inner exciple well developed, thickened, filling the pore area and forming a double pore, flesh colored, the pore irregular, 0.2–0.3 mm wide; spores 8, 12–15 \times 36–50 μm , 1–2 \times 9–12 loculate, I–.

CHEMISTRY.—No substances present.

REMARKS.—This inconspicuous species is char-

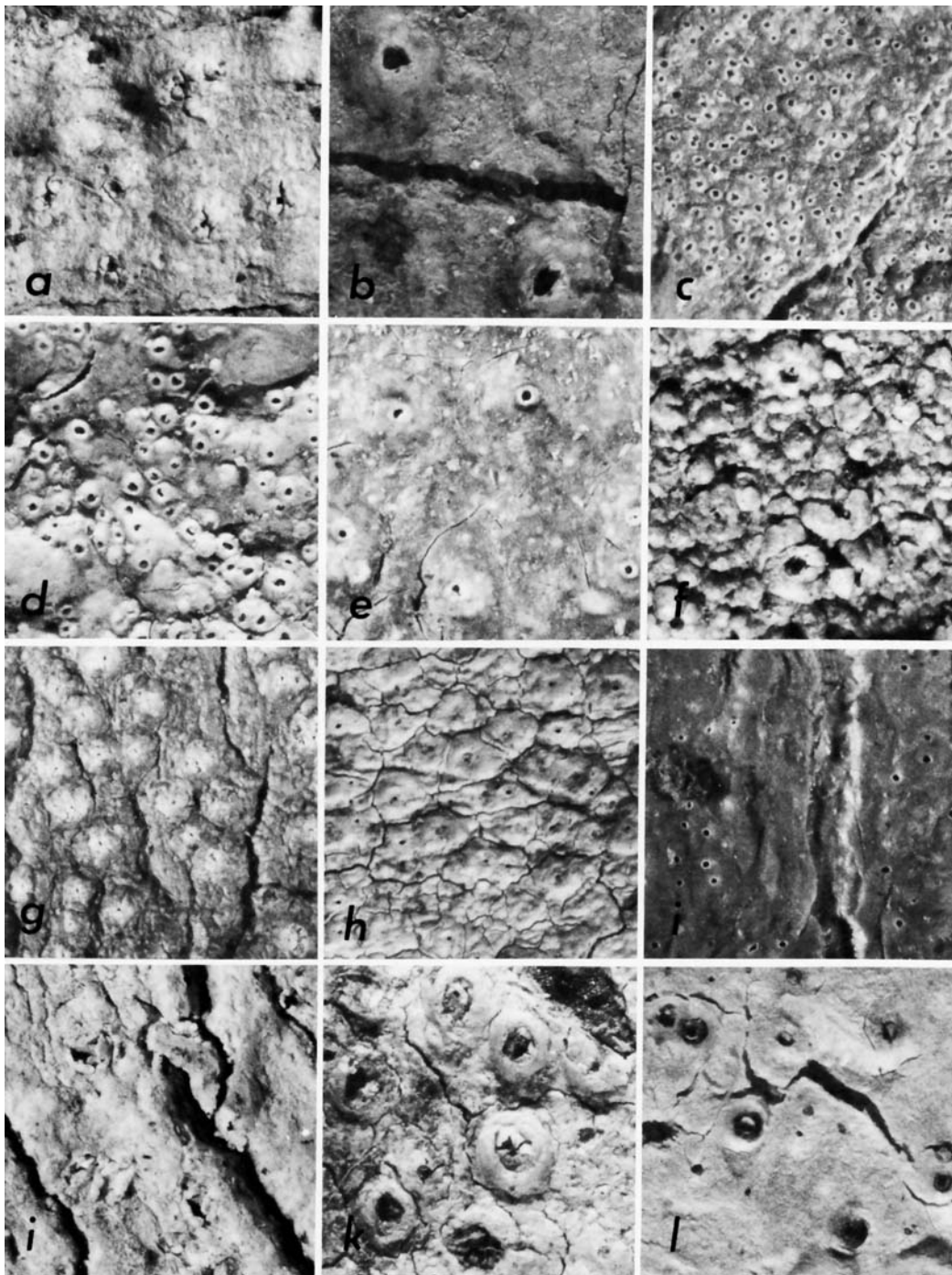


FIGURE 12.—Species of *Thelotrema*: a, *T. adjectum* (Hale 44882); b, *T. auratum* (Hale 43544); c, *T. clandestinum* (Hale 44942); d, *T. concretum* (Hale 43549); e, *T. conforme* (Hale 38463); f, *T. connivens* (Hale 38741); g, *T. cryptotrema* (Hale 43483); h, *T. erumpens* (Hale 38752); i, *T. glaucopallens* (Hale 44873); j, *T. hiatus* (Hale 43458); k, *T. lepadinum* (Hale 44902); l, *T. leucomelaenum* (Hale 38765) ($\times 10$).

acterized by the semiemergent apothecia and the filled disc. The type collection from Cuba has slightly larger spores, 57–78 μm long. In Panama *T. adjectum* occurs at the base of trees in the low elevation rain forest of Barro Colorado Island but at no other sites. It is also known in subtropical United States (Florida and Louisiana).

SPECIMENS EXAMINED.—3a: 44779, 44864, 44882.

2. *Thelotrema auratum*

FIGURE 12b

Thelotrema auratum Tuckerman, 1862:408 [type collection: Cuba, Wright 133 (FH-Tuck, lectotype; isolectotypes in BM, G, L, PC, UPS) (Figure 1f)].

Thelotrema intervallatum Nylander, 1868:36 [type collection: New Caledonia, Marie (H, Nylander herbarium 22458, lectotype; isolectotypes in G, PC) (Figure 2a)].

Thelotrema oculatum Vainio, 1921:179 [type collection: Polillo, Philippines, Robinson 9082 (TUR, Vainio herbarium 26828, lectotype) (Figure 2i)].

Thelotrema porphyrodiscum Zahlbruckner, 1908:245 [type collection: Sawai, Samoa, Reching 2926 (W, lectotype) (Figure 2l)].

Thelotrema citrinodiscum Redinger, 1936:78 [type collection: Corcovado, Rio de Janeiro, Brazil, Malme 88 (S, lectotype) (Figure 1j)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, shiny, continuous, pale brownish mineral gray, 8–11 cm wide; apothecia solitary, dispersed, emergent, 0.9–1.2 mm in diameter, the exciple carbonized, columella lacking, the disc yellow-pruinose, the pore irregular, black rimmed, to 0.5 mm wide; spores 8, $12 \times 24\text{--}26 \mu\text{m}$, $0\text{--}2 \times 6\text{--}7$ loculate, I+ bluish.

CHEMISTRY.—Protocetraric acid and an unidentified epihymenial pigment.

REMARKS.—This species is easily recognized by the large, emergent ascidioid apothecia with a yellowish or orange-red pruinose disc. The chromatograms of *T. auratum* and all the types of the synonyms listed were run together and proved to be identical. Vainio (1921:180) had actually indicated that his *T. oculatum* was very closely related to *T. intervallatum* Nylander. Redinger (1936:80) compares *T. citrinodiscum* with *T. porphyrodiscum* Zahlbruckner, which he differentiates by a deep purplish disc. The disc pigmentation is in fact quite variable but the same pigments seem to be involved. The species is rare in Panama and

occurred on upper trunks of trees in rain forest.

SPECIMENS EXAMINED.—2: 43544, 43574.

3. *Thelotrema clandestinum*

FIGURE 12c

Thelotrema clandestinum Fée, 1837:90 [type collection: "In America ad corticem *Cinchonae lancifoliae* Mutis." (G, lectotype) (Figure 1k)].

Thelotrema subcaesium Nylander, 1869:120.

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

[For full citations see Hale (1974a:32).]

DESCRIPTION.—Thallus corticolous, epiphloeodal, thick and continuous, whitish to pale greenish gray, up to 20 cm broad; apothecia numerous, separate, immersed, 0.15–0.3 mm in diameter, noncarbonized and without a free inner exciple and columella, the pore round, 0.07–0.1 mm in diameter, usually more or less distinctly white annulate; spores 8, $6\text{--}7 \times 14\text{--}22 \mu\text{m}$, $0\text{--}1 \times 4\text{--}5$ loculate, I+ blue.

CHEMISTRY.—Psoromic acid with or without norpsoromic acid.

REMARKS.—This canopy species has a thick continuous thallus similar to that of *Ocellularia terebratula* (Nylander) Müller Argoviensis, and as I had found in Dominica, these species must be carefully separated by examining spores. I have identified *T. clandestinum* from Florida, Guatemala, the Caribbean region, Venezuela, Brazil, South India, the Philippines, and the Solomon Islands.

SPECIMENS EXAMINED.—2: 43597; 1: 44942, 44959.

ILLUSTRATIONS.—Hale, 1974a:32, figs. 14g, i.

4. *Thelotrema concretum*

FIGURE 12d

Thelotrema concretum Fée, 1837:90 [type collection: "In America meridionali ad cortices *Cinchonae lancifoliae* Mutis." (G, lectotype; isolectotype in H-Nyl) (Figure 1l)].

Thelotrema microporoides Nylander, 1863:326 [type collection: Colombia, Lindig 2622 (H, lectotype; isolectotypes in BM, FH, G, PC, S, UPS)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth and continuous, shiny, pale greenish to tannish mineral gray, 10–12 cm broad; apothecia numerous, solitary or becoming clumped, immersed to semiemergent, 0.2–0.4 mm in diameter, noncar-

bonized and lacking a columella, the inner exciple sometimes persistent, the low thalline rim raised and erect at maturity, the pore open, to 0.2 mm wide, the pale flesh-colored disc visible; spores 8, $7 \times 12\text{--}14 \mu\text{m}$, $1 \times 4\text{--}5$ loculate, I+ blue.

CHEMISTRY.—Psoromic acid with or without norpsoromic acid.

REMARKS.—*Thelotrema concretum* has small, crowded, confluent semiemergent apothecia as so clearly illustrated by Fée (1837, pl. 37). It is part of a complex of similar species with psoromic acid: *T. clandestinum* Fée, which has entirely immersed apothecia, *T. insigne* Zahlbruckner (Redinger, 1936:96), which has long thin isidia, and *T. hartii* Müller Argoviensis, which has sparse, thick isidia. It also resembles the rare *T. halei* Tuckerman, which has a distinct inner exciple and numerous crystal inclusions in the thallus. Redinger (1936:96) also compares it with *T. leucohymenium* Zahlbruckner, a hypoprotocetraric acid-containing species with entirely immersed apothecia, which I place in synonymy under *T. myrioporoides* Müller Argoviensis (see page 45). In addition, while Redinger regards *T. subcaesium* Nylander as a variety of *T. concretum*, I feel it is closer to *T. clandestinum* (see above). Further studies of this species group and other psoromic acid-containing species such as *T. quitoensis* Fée from Ecuador should be made as more specimens become available for study. Incidentally, my spore measurements (taken in part from the lectotype in G) as well as those by Redinger (1936:95) are smaller than Müller's (1887a:11).

Thelotrema concretum is not a commonly collected species but is apparently pantropical. In Panama it occurs at mid elevations on mature trees, generally on the lower trunks. I have seen specimens from the cloud forests of Venezuela (about 2200 m elevation) and from Brazil and Sabah.

SPECIMENS EXAMINED.—1: 38774; 2: 43549.

5. *Thelotrema conforme*

FIGURE 12e

Thelotrema conforme Fée, 1837:89 [type collection: "In America meridionali ad cortices *Cinchonarum*" (G, lectotype)].

Thelotrema consanguineum Müller Argoviensis, 1887b:398 [type collection: Brazil, Puiggari 477 (G, lectotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth and shiny, whitish mineral gray, up to 10 cm broad; apothecia fairly numerous, solitary, emergent, apically carbonized, 0.8–0.1 mm in diameter, the columella distinct to weakly developed, the pore round, 0.1–0.5 mm in diameter, often white annulate; spores 4, $10\text{--}16 \times 24\text{--}50 \mu\text{m}$, $2\text{--}4 \times 7\text{--}10$ loculate, I+ blue.

CHEMISTRY.—Psoromic and norpsoromic acid.

REMARKS.—This is another classic Fée species. It has rather large, more or less emergent apothecia with an annulate pore and intermediate sized spores. As Redinger notes (1936:88), Fée describes the spores as "tetrasporis," apparently referring to a 4-loculate spore. The lectotype material in G, however, examined by Müller (1887a:11) and me, clearly has larger spores and more than four locules. A columella was weakly developed to absent in the specimens from Río Calevobora in Panama, but variability in columella formation is not unusual in *Thelotrema*. The species is usually collected at mid bole or in the canopy and also occurs in Dominica, Trinidad, and Brazil (Redinger, 1936:87).

SPECIMENS EXAMINED.—8: 38537, 38599, 38608; 9: 38463; 11: 44792, 44824, 44830, 46017.

6. *Thelotrema conveniens*

FIGURE 12f

Thelotrema conveniens Nylander, 1873:168 [type collection: Tequendama, Colombia, Lindig in 1863 (H, Nylander herbarium 22496, lectotype) (Figure 1m)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, verrucose to warty, shiny, pale tan, 5–7 cm broad; apothecia not numerous, solitary, emergent at maturity, the thalline margin warty, noncarbonized, 0.6–1.0 mm in diameter, a columella lacking, the inner exciple well developed, entire, leaving a small inner pore, the main pore round, 0.2–0.3 mm in diameter; spores 1, $30 \times 150 \mu\text{m}$, densely muriform, I+ blue.

CHEMISTRY.—No substances present.

REMARKS.—This species was first described in 1873 from the cloud forests near Bogotá and has not, as far as I know, been collected elsewhere. It is distinguished by the small lepadinoid apothecia and the large spores. *Thelotrema rugatulum* Nylander, described at the same time by Nylander

from the Andaman Islands, has smaller apothecia, a less distinct, open pore, and smaller spores (75–85 μm long). It could otherwise be confused with *T. adjectum* Nylander (see above), a lowland species with smaller spores and a filled pore. *Thelotrema conveniens* was collected only at Chiriquí on the mid bole of large oak trees at about 2000 m elevation.

SPECIMENS EXAMINED.—1: 38741; 1a: *Esslinger* 4483.

7. *Thelotrema cryptotrema*

FIGURE 12g

Thelotrema cryptotrema Nylander, 1867:318 [type collection: French Guiana, *Melinou* (H, Nylander herbarium 22490, lectotype; isolectotype in PC) (Figure 1o)].

Thelotrema secoligella Müller Argoviensis, 1895a:31 [type collection: French Guiana, *Leprieur* 722 (G, lectotype) (Figure 2p)].

Thelotrema annulatum Müller Argoviensis, 1895c:453 [type collection: Rio de Janeiro, Brazil, *Glaziou* 5474 (G, lectotype; isolectotype in BM) (Figure 1d)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth, continuous to broadly cracked, whitish mineral gray, 8–12 cm broad; apothecia not common, immersed to semiemergent, 0.4–0.6 mm in diameter, noncarbonized and without a columella, the inner exciple more or less free, apically pruinose, filling much of the pore area, the pore round, 0.05–0.1 mm in diameter; spores 1–4, 15–30 \times 55–80 μm , densely muriform, I–.

CHEMISTRY.—Psoromic acid.

REMARKS.—The pore area is white and more or less closed as in a *Phlyctis*. No other psoromic acid-containing species have this character. The descriptions of Müller's two synonymous species are essentially identical; he compares *T. annulatum* with "*Th. disciforme* Leighton," a quite different species of *Leptotrema* (see p. 53). The species had not previously been reported outside of the type-localities in French Guyana and Brazil. In Panama it occurred in tree tops at lower elevations (100–350 m).

SPECIMENS EXAMINED.—3: 38692; 6: 48483.

8. *Thelotrema erumpens*

FIGURE 12h

Thelotrema erumpens Magnusson, 1955:279 [type collection:

Mauna Kea, Hawaii, *Faurie* 1909 (UPS, lectotype) (Figure 1q)].

Thelotrema leucomelaenum var. *cathomalizans* Nylander, 1863a:452 [type collection: Tequendama, Colombia, *Lindig* (H, Nylander herbarium 22581, lectotype; isolectotypes in BM, FH (as no. 857)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, dull, smooth to verruculose, finely rimose, whitish mineral gray, 8–10 cm broad; apothecia numerous, dispersed to confluent, nearly flush to semiemergent, 0.5–0.7 mm in diameter, the exciple carbonized, columella lacking, the pore round, 0.05–0.1 mm in diameter, becoming blackened; spores 4–8, 12–15 \times 36–50 μm , 1–3 \times 6–8 loculate, I–.

CHEMISTRY.—Stictic acid, constictic acid, and the high "quintaria" unknown.

REMARKS.—The pore of this species is usually heavily carbonized and the surrounding area blackened. Magnusson (1955:279) pointed out its superficial resemblance to *Ocellularia pyrenuloides* Magnusson, which also contains stictic acid and is known from Hawaii and Dominica (Hale 1974a:25). I collected it in Panama on palm trees and evergreen hardwoods at 2200 m elevation in cloud forest.

SPECIMENS EXAMINED.—1: 38752; 1a: 44814, 44955, 45839.

9. *Thelotrema glaucopallens*

FIGURE 12i

Thelotrema glaucopallens Nylander, 1863b:327 [type collection: Cuba, *Wright* 28 (FH-Tuck, lectotype; isolectotypes in L, M, UPS)].

Pyrenula clandestina Acharius, 1814:10.

Thelotrema laevigans Nylander, 1863a:451 [type collection: Bogota, Colombia, *Lindig* 893 (BM, lectotype; isolectotypes in FH, G, PC, W)].

Thelotrema laevigans Nylander var. *avertens* Nylander, 1867:318.

Thelotrema pechueli Müller Argoviensis, 1880:34.

Ocellularia clandestina (Acharius) Müller Argoviensis 1887a:7.

Thelotrema homopastoides Vainio, 1896:207.

Thelotrema butuanum Vainio, 1921:183.

[For full synonymy see Hale (1974a:35).]

DESCRIPTION.—Thallus corticolous, epiphloeodal, very thin and shiny, greenish gray, up to 20 cm broad; apothecia usually numerous, separate, immersed to slightly emergent, 0.2–0.4 mm in diameter, noncarbonized and without a columella, the

inner exciple evanescent, the pore round, 0.05–0.1 mm in diameter; spores 8, 7–10 × 15–25 μm , 1–3 × 6–8 loculate, I–.

CHEMISTRY.—Stictic and constictic acids.

REMARKS.—As I had discovered in Dominica, *T. glaucopallens* is one of the commonest base level species in the rain forests at lower elevations, where it competes with pyrenocarpous lichens. The species was very common in Dominica and I have identified collections from Guatemala, Guyana, Venezuela, Trinidad, Tanzania, Ivory Coast, and the Union of South Africa in addition to localities in the Philippines. It was the most common lichen in the rain forests of Barro Colorado Island in Panama, occurring on prop roots, buttresses, and lower trunks.

SPECIMENS EXAMINED.—3: 38522, 38624, 38646, 38656, 38662, 38667, 38669, 38670, 38680, 38681, 38691; 3a: 44758, 44766, 44774, 44811, 44847, 44873, 44895, 44943, 46079, *Esslinger* 4338, 4340, 4404; 4: 43342, 43447, 43465; 6: 43491, 43527, 43555; 7: 43607; 8: 38606.

10. *Thelotrema hiatum*, new species

FIGURE 12j

DESCRIPTION.—Thallus corticola, epiphloeodes, tenuis, albidus, 8–12 cm latus; apothecia chroodiscoida (Figure 11a), 0.4–0.7 mm diametro, margine thallino crasso, erecto; excipulum interius decoloratum, discretum vel evanescent, disco nigro vel leviter albo-pruinoso; hymenium 180–200 μm altum; sporae 4–8; nae, 6 × 12 μm , longitudine 0–1 loculatae, transversim 2–3 loculatae, I+ caerulescentes.

CHEMISTRY.—No substances present.

HOLOTYPE.—On a felled *Miconia*, along Naval Pipeline Road about 9 km NW of Gamboa, Canal Zone, Panama, elevation 150 m, *M. E. Hale* 43458, 11 February 1974 (US).

REMARKS.—The only apparent relative of this chroodiscoid species is *T. leprocarpum* Tuckerman, known from southern United States, which has large spores (50–80 μm long). The thallus is opaque and crumbly, similar to the whitish bark excrescences characteristic of *Miconia*, a small melanostomaceous tree. It was surprising to find a *Thelotrema* on this weedy roadside tree at low elevation.

11. *Thelotrema lepadinum*

FIGURE 12k

Thelotrema lepadinum (Acharius) Acharius, 1803:132.
Lichen lepadinus Acharius, 1798:30 [type collection: Sweden, Acharius (H-Ach., lectotype; isolectotypes in BM, UPS)].

DESCRIPTION.—Thallus corticolous, epiphloeodal but thin and in part evanescent, pale tannish, 2–5 cm broad; apothecia dispersed, emergent, 0.5–1.0 mm in diameter, noncarbonized, lacking a columella, the proper exciple well developed, free, splitting, the pore open, round, 0.2–0.4 mm in diameter; spores 4–8, 20–26 × 80 μm , with numerous locules, I– or bluish.

CHEMISTRY.—No substances present.

REMARKS.—This pantemperate lichen, by far the most commonly collected member of *Thelotrema*, occurs as a montane species in the tropics, usually in cloud forest. As expected, it was found only at Volcán Chiriquí in Panama.

SPECIMENS EXAMINED.—1: 38777; 1a: 44902, 45968.

12. *Thelotrema leucomelaenum*

FIGURE 12l

Thelotrema leucomelaenum Nylander, 1863b:329 [type collection: Colombia, *Lindig* 2777 (H, Nylander herbarium 22576, lectotype; isolectotypes in BM, FH, G, PC, UPS)].
Thelotrema pauperius Nylander, 1863:329.
Thelotrema leucomelaenum var. *elevatum* Vainio, 1915:137.
[For full citations see Hale (1974a:36).]

DESCRIPTION.—Thallus corticolous, mostly hypophloeodal, whitish, up to 8 cm broad; apothecia immersed to semiemergent, 0.6–0.9 mm in diameter, heavily carbonized with a broad columella about 0.3 mm wide, the pore round, 0.2–0.3 mm in diameter, partially filled by the white-pruinose tip of the columella; spores 8, 12–15 × 24–35 μm , 2–3 × 4–6 loculate, I–.

CHEMISTRY.—No substances present.

REMARKS.—The columella is broad and flat, leaving a narrow ring-shaped hymenial area (Redinger, 1936:92). While this was a rather common species at high elevations in Dominica, it is largely replaced by externally similar but chemically different *T. stylothecium* in Panama (see page 48). I have seen additional material of the species from Jamaica, Colombia, Venezuela, and Brazil.

SPECIMENS EXAMINED.—1: 38765; 1a: 44950.

13. *Thelotrema maximum*, new species

FIGURE 13a

DESCRIPTION.—Thallus corticola, epiphloeodes, crassus, nitidus, continuus, viridi-cinereus, 6–10 cm latus; apothecia (Figure 11b) emergentia, basi non constricta, 1.5–2.0 mm diametro, eolumellata vel rudimentaliter columellata; ostiolum rotundatum, 0.1 mm diametro, plus minusve annulatum, albo-cinctum; excipulum apice fuliginium; hymenium 200–220 μm altum; sporae 1–2:nae, 30–40 \times 100–160 μm , dense murales, I+ caerulescentes.

CHEMISTRY.—Psoromic and norpsoromic acids.

HOLOTYPE.—Top of palm tree in secondary rain forest, La Mesa, north of El Valle, Province of Coclé, Panama, elevation 750 m, *M. E. Hale* 43580, 13 February 1974 (US).

REMARKS.—This is clearly a member of the *T. conforme* Fée complex. It is distinctive in having very large apothecia not at all basally constricted. Of the related species with psoromic acid, *T. conforme* Fée usually has a distinct columella and spores only up to 36 μm long; *T. interpositum* Nylander has comparably large spores (115–160 μm) but the thallus is conspicuously warty; and *T. postpositum* Nylander has smaller (0.6–0.9 mm wide) apothecia with a constricted base (see Hale, 1974a:32). This species was very common at the one site in the Province of Coclé, mostly on canopy branches.

SPECIMENS EXAMINED.—2: 43427, 43495, 43516, 43521, 43541, 43565, 43569, 43575, 43582, 43589, 43595.

14. *Thelotrema myriocarpum*

FIGURE 13b

Thelotrema myriocarpum Fée, 1824:94 [type collection: "In America meridionali ad corticem *Cinchonae rubrae*" (PC, lectotype; isolectotypes in H, L) (Figure 2e)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, dull, smooth to minutely verruculose, becoming rimose, whitish mineral gray, 4–8 cm broad; apothecia numerous, separate, immersed, 0.2 mm in diameter, noncarbonized, the inner exciple entire, free, forming an inner ring, the pore round, 0.05–0.1 mm in diameter; spores 8, 12 \times 24–25 μm , 1–2 \times 5–7 loculate, I– or I+ weakly reddish.

CHEMISTRY.—Stictic and constictic acid.

REMARKS.—*Thelotrema myriocarpum* was described by Fée from South America (probably Venezuela) and has not been reported since. As with most of Fée's types now housed in G, the original material is in poor condition although the PC material is adequate to characterize the species. A single collection from Panama compares well with it; small, more or less immersed apothecia with a persistent inner excipular structure, although the spores in the lectotype are somewhat larger (about 36 μm long). The species is chemically identical with *T. glaucopallens*, which has similar apothecia but no remnants of an inner exciple. They are obviously clearly related but more specimens of the *T. myriocarpum* type must be seen to resolve the problem.

SPECIMEN EXAMINED.—6: 43428.

15. *Thelotrema myrioporoides*

FIGURE 13c

Thelotrema myrioporoides Müller Argoviensis, 1893b:147 [type collection: Boruca, Costa Rica, *Tonduz* in 1893 (G, lectotype) (Figure 2f)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thick and smooth, deeply fissured, whitish to pale greenish mineral gray, 6–10 cm broad; apothecia numerous, immersed, about 0.2 mm in diameter, noncarbonized, the inner exciple free, partially filling the pore, the pore round, white-annulate, 0.1 mm in diameter; spores 8, 6–10 \times 12–14 μm , 0.1 \times 3.5 loculate, I+ blue.

CHEMISTRY.—Hypoprotocetraric acid and 4-O-demethylnotatic acid, with or without lichexanthone.

REMARKS.—First described from Costa Rica, this species inhabits mid elevation rain forests in Panama. Superficially it resembles other canopy species with immersed apothecia such as *Thelotrema clandestinum* Fée and *Ocellularia terebratula* (Nylander) Müller Argoviensis, as noted by Müller (1893:147), who had probably seen the type of *T. subcaesium* Nylander, a synonym of *T. clandestinum*. *Thelotrema subconforme* Nylander, also mentioned by Müller, is an Asian species lacking any lichen substances and having somewhat smaller, more crowded apothecia. One specimen from Panama (45806) is anomalous in producing lichexan-

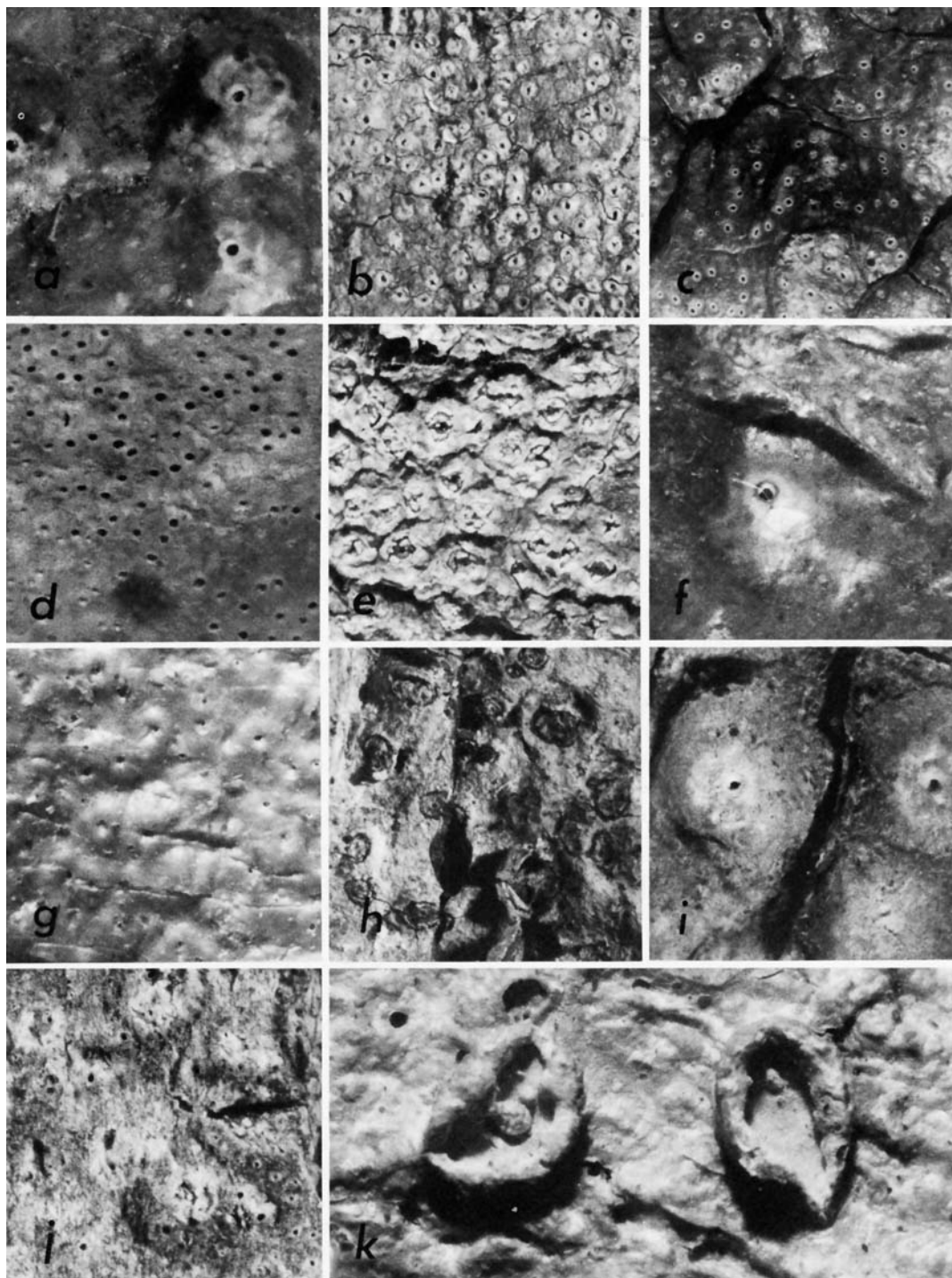


FIGURE 13.—Species of *Thelotrema*: a, *T. maximum* (Hale 43580); b, *T. myriocarpum* (Hale 43428); c, *T. myrioporoides* (Hale 38420); d, *T. norsticticum* (Hale 43592); e, *T. oclusum* (Hale 38736); f, *T. praestans* (Hale 44784); g, *T. pycnoporellum* (Hale 38505); h, *T. stylothecium* (Hale 38724); i, *T. subpraestans* (Hale 44878); j, *T. tenue* (Hale 44810); k, *T. wrightii* (Hale 38449) ($\times 10$).

thone in addition to the normal components, a not unexpected combination.

SPECIMENS EXAMINED.—4: 43435; 7: 43602; 9: 38429, 38494; 11: 45806; *Hunter and Allen* (Province of Panamá).

16. *Thelotrema norsticticum*

FIGURE 13d

Thelotrema norsticticum Hale, 1973:417 [type collection: Trinidad, *Hale* 37369 (US, holotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, about 0.6 mm thick, continuous, whitish mineral gray, about 6 cm broad; apothecia numerous, uniformly dispersed, immersed, 0.1–0.2 mm in diameter, noncarbonized, a columella lacking, the pore round, 0.06 mm in diameter, white annulate; spores 8, 6–8 × 12–14 μ m, 0–1 × 4 loculate, I+ blue.

CHEMISTRY.—Norstictic acid.

REMARKS.—This is the second record for the species. It is differentiated from *T. clandestinum* Fée by having a white annulate pore and different chemistry (*T. clandestinum* has psoromic acid).

SPECIMEN EXAMINED.—2: 43592.

17. *Thelotrema oclusum*

FIGURE 13e

Thelotrema oclusum Nylander, 1867:318 [type collection: Chucuri, Colombia, *Lindig* in 1863 (H, Nylander herbarium 22522, lectotype) (Figure 2h)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin, verruculose, shiny, whitish to ivory colored, 3–8 cm broad; apothecia solitary, dispersed, nearly immersed to semiemergent, 0.6–1.0 mm in diameter, the thalline margin sometimes suberect, the inner exciple well developed, crumbly, filling the pore, columella lacking, the pore round, open, 0.2–0.4 mm in diameter; spores 1, 15–40 × 100–220 μ m, densely muriform, I+ blue.

CHEMISTRY.—Hypoprotocetraric acid and 4-O-demethylnotatic acid.

REMARKS.—This is still another of the Colombian species described by Nylander which occurs in the highlands of Panamá. The disc is filled with the irregular, lacerate inner exciple, as in *Phlyctis*, and the spores are large. No other species in *Thelotrema* with hypoprotocetraric acid have this struc-

ture. It occurs from base to mid bole on large evergreen hardwoods in both Panamá and Venezuela.

SPECIMENS EXAMINED.—1: 38736; 1a: 44993, 45841, 45876.

18. *Thelotrema praestans*

FIGURE 13f

Thelotrema praestans Müller Argoviensis, 1895c:453 [type collection: Rio de Janeiro, Brazil, *Portella* (G, lectotype; isolectotype in BM)].

Thelotrema elliottii Vainio, 1896:207 [type collection: St. Vincent, *Elliott* 246 pro parte (BM, lectotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth and continuous, greenish mineral gray, 6–12 cm broad; apothecia widely dispersed, solitary, becoming strongly emergent, up to 2 mm in diameter, heavily carbonized with a thick columella, the pore round, 0.15–0.3 mm in diameter; spores 1–2, 30–45 × 100–275 μ m, densely muriform, I+ blue.

CHEMISTRY.—“Praestans” unknown.

REMARKS.—*Thelostrema praestans* is a large, easily recognized species. It has large spores, a heavily carbonized exciple and a thick columella, and a tiny depressed pore. As Redinger mentions (1936:91), Müller’s type material has numerous cyphellalike white spots, apparently pycnidia, but I have not seen these in any other specimens. A very closely related species, *T. subpraestans* Hale, which occurs mainly in the lowlands, is even larger and contains stictic acid. *Thelotrema praestans* occurs generally at higher elevations in rain forest and is known from Guatemala, the West Indies, and Brazil.

SPECIMENS EXAMINED.—6: 43524; 11: 44784; 12: *Mori* 4464; Province of Panamá, *Gentry* 4210.

ILLUSTRATIONS.—Hale, 1974a:36, figs. 17e, f, g; Redinger, 1936:90, fig. 54.

19. *Thelotrema pycnoporellum*

FIGURE 13g

Thelotrema pycnoporellum Nylander, 1876:562 ([type collection: Cuba, *Wright* 69 (H, Nylander herbarium 22682, lectotype; isolectotypes in FH, G, UPS) (Figure 2m)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin, shiny, greenish mineral gray, 6–8 cm broad; apothecia numerous, separate, immersed, 0.1–0.5 mm in diameter, the exciple barely carbonized, the

inner exciple evanescent, columella lacking, the pore round, 0.05 mm in diameter, slightly darkened; spores 8, 8–10 × 20–24 μm , 1–2 × 5–6 loculate, I⁺ blue.

CHEMISTRY.—No substances present.

REMARKS.—This species was first described from Cuba and is the only New World *Thelotrema* with immersed apothecia and no lichen substances. It is similar externally to *T. myrioporoides* Müller Argoviensis. Zahlbruckner (1923:628) misspelled the specific epithet as “pyncocarpellum.” In Panama I collected it at the base and on fallen tops of evergreen hardwoods at 700–1000 m elevation.

SPECIMENS EXAMINED.—9: 38505; 11: 46019.

20. *Thelotrema stylothecium*

FIGURE 13h

Thelotrema stylothecium Vainio, 1890:80 [type collection: Carassa, Minas Gerais, Brazil, Vainio 1370 (TUR, lectotype; isolectotypes in BM, FH, UPS) (Figure 2g)].

Thelotrema leucomelaenum var. *stylothecium* (Vainio) Redinger, 1936:92.

DESCRIPTION.—Thallus corticolous, epiphloeodal but in part evanescent or hypophloeodal, whitish mineral gray, 4–8 cm broad; apothecia numerous, solitary, immersed to semiemergent, 0.4–0.7 mm in diameter, the thalline margin coarse, sometimes becoming semierect, carbonized, the columella broad, about 250 μm in diameter with a white-pruinose apex partially filling the pore, the pore round, about 0.3 mm in diameter; spores 8, 10–12 × 20–35 μm , 1–2 × 6–8 loculate, I[–].

CHEMISTRY.—Stictic acid with or without constictic acid.

REMARKS.—In his original description Vainio (1990:81) did not discuss the differences between this species and the very close *T. leucomelaenum*. His Latin diagnoses are almost identical except for spore size, *T. stylothecium* having smaller spores (15–17 μm vs. 28–32 μm long). However, I found that, aside from the basic chemical distinction, the spore sizes overlap to a much greater extent than either Vainio or Redinger (1936:92) showed and I do not believe that this is a valid difference. Both species occur in similar habitats in cloud forests at higher elevations (above about 1500 m). I have identified *T. stylothecium* from

St. Lucia and Guadeloupe in the West Indies—but not from Dominica—and from Venezuela.

SPECIMENS EXAMINED.—1: 38710, 38724, 38767, 38775, 38779; 1a: 45840.

ILLUSTRATION.—Redinger, 1936:93, fig. 56.

21. *Thelotrema subpraestans*

FIGURE 13i

Thelotrema subpraestans Hale, 1974b:497 [type collection: Province of Panamá, Panamá, Hale 38525 (US, holotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, rather thick, rimose with age, pale greenish or whitish gray, 10–20 cm broad; apothecia numerous, solitary, strongly emergent, up to 2.5 mm in diameter, carbonized, a thick central columella present, the pore round, inconspicuous and slightly depressed, 0.1 mm in diameter, white annulate; spores 1, 30–50 × 150–300 μm , densely muriform, I⁺ blue.

CHEMISTRY.—Stictic and constictic acids with or without the high “quintaria” unknown.

REMARKS.—*Thelotrema subpraestans* is the predominant canopy species on Barro Colorado Island and also occurs at higher elevation to the east in the nearby Cerro Jefe region. It appears to represent a recent derivative, perhaps a mutant, of the more widespread *T. praestans* Müller Argoviensis, which contains an unknown P⁺ compound and occurs generally at higher elevations.

SPECIMENS EXAMINED.—3: 38637, 38655, 38660, 38682, 38696; 3a: 44757, 44765, 44809, 44878, Esslinger 4330, 4346, 4381; 8: 38525, 38534, 38549; 9: 38432, 38515.

22. *Thelotrema tenue*

FIGURE 13j

Thelotrema tenue Hale, 1974a:38 [type collection: Dominica, Hale 35439 (US, holotype)].

DESCRIPTION.—Thallus corticolous, hypophloeodal, shiny, whitish gray, 6–8 cm broad; apothecia numerous, immersed to semiemergent, 0.3–0.4 mm in diameter, apically carbonized, the columella weakly developed to absent, the pore round, 0.05–0.1 mm in diameter; spores 8, 10–12 × 20–30 μm , 1–2 × 5–6 loculate, I[–].

CHEMISTRY.—No substances present.

REMARKS.—Previously known only from Dominica, *T. tenue* is represented in Panama by a single collection in the cloud forest at Chiriquí. I have also collected it in Venezuela. The columella is weakly developed to lacking in the Panamanian material.

SPECIMEN EXAMINED.—1a: 44810.

ILLUSTRATIONS.—Hale, 1974a:37, fig. 17k.

23. *Thelotrema wrightii*

FIGURE 13k

Thelotrema wrightii Tuckerman, 1862:409 [type collection: Cuba, Wright 143 (FH-Tuck, lectotype: isolectotypes in BM, G, L, PC, UPS) (Figure 2t)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin and fragile, shiny, smooth to verruculose, pale tannish gray, 10–15 cm broad; apothecia conspicuous, chroodisoid, becoming basally constricted, 1–3 mm in diameter, the thalline margin coarse, erect to slightly recurved, the inner exciple evanescent, the disc white pruinose, becoming superficially actinoid with light carbonization; spores 8, 5–6 × 10–18 μm, 0–1 × 4–5 loculate, I+ blue.

CHEMISTRY.—Psoromic acid.

REMARKS.—This species forms large conspicuous colonies on the lower trunk to mid bole of large trees. The pale flesh-colored apothecia stand out in particular because of the broad chroodisoid disc. The disc becomes irregularly ridged with age, giving the superficial actinoid appearance mentioned by Tuckerman (1862:410). It has been known before only from Cuba. Externally it is extremely close to *Ocellularia subwrightii* Hale (see page 32).

SPECIMENS EXAMINED.—8: 38537, 38589; 9: 38449; 11: 44870, 46052.

Leptotrema Müller Argoviensis

Leptotrema is characterized by brown muriform spores with very close relationships to *Thelotrema*. I recognize approximately 65 species at the world level. In Panama I collected 14 species and 64 specimens, about 9% of the total 700 for the family, comparable to the 7% in Dominica. Four of these are new to science.

The most commonly collected species was *Leptotrema reclusum*, all 13 collections, however, being made at Barro Colorado Island. In the same locality *L. laeviusculum* was collected eight times. While the genus is generally scattered at different localities, most collections were concentrated at just two localities, Chiriquí and Barro Colorado. Three species, *L. chiriquiense*, *L. metaphoricum*, and *L. urceolare*, were confined to the highest elevations in Chiriquí, and *L. laeviusculum*, *L. reclusum*, and *L. wightii* can be considered as typical lowland species.

The apothecial development in *Leptotrema* is varied. *Leptotrema stellatum* is the only strongly chroodisoid species, while *L. hypoprotocetraricum* is generally lepadinoid. *Leptotrema metaphoricum* has an actinoid columella and columellate *L. microsporium* tends toward this condition. Flush myriotremoid apothecia are present in *L. laeviusculum*, *L. trypaneoides*, and *L. wightii*.

As with the other thelotremoid genera, *Leptotrema* has phytogeographical affinities with the Caribbean and South America. *Leptotrema deceptum*, *L. laeviusculum*, and *L. trypaneoides* form a Caribbean group, *L. metaphoricum* and *L. microsporium* are reported here for the first time outside of South America, and *L. reclusum*, *L. urceolare*, and *L. wightii* are pantropical.

Key to the Species of *Leptotrema*

1. Apothecia open and chroodisoid, eolumellate.11. *L. stellatum*
1. Apothecia not chroodisoid; if open an actinoid columella present.
 2. Columella present.
 3. Disc open, large, actinoid, becoming irregularly elongate.7. *L. metaphoricum*
 3. Disc round, not actinoid or open.8. *L. microsporium*
 2. Columella lacking.
 4. Spores large, more than 150 μm long, densely muriform.
 5. Pore 0.1 mm or less in diameter.2. *L. chiriquiense*
 5. Pore open, 0.2–0.3 mm wide, the proper exciple filling the disc partially.4. *L. hypoprotocetraricum*
 4. Spores less than 130 μm long.
 6. Apothecia generally large, emergent, 0.5–1.0 mm in diameter, the pore to 0.5 mm wide.

7. Thallus P+ red (protocetraric acid).
 8. Disc covered with an orange-yellow pruina.9. *L. panamense*
 8. Disc unpigmented.1. *L. bahianum*
 7. Thallus P-.
 9. Spores 80–100 μm large.6. *L. lepadodes*
 9. Spores smaller, 30–30 μm long.13. *L. urceolare*
 6. Apothecia immersed to flush, 0.2–0.5 mm in diameter, the pore 0.05–0.1 mm wide.
 10 Red crystal inclusions in the cortex.14. *L. wightii*
 10. Cortex lacking pigments.
 11. Spores about 100 μm long.10. *L. reclusum*
 11. Spores about 25 μm long.
 12. Cortex shiny, thin; stictic acid present.12. *L. trypaneoides*
 12. Cortex dull, thick and grainy; protocetraric acid present.5. *L. laeviusculum*

1. *Leptotrema bahianum*

FIGURE 14a

Leptotrema bahianum (Acharius) Müller Argoviensis, 1887a:12.

Thelotrema lepadinum var. *bahianum* Acharius, 1803:132.

Thelotrema develatum Nylander, 1863a:454 [type collection: Colombia, Lindig 774 (BM, lectotype; isolecotypes in FH, PC, W)].

Thelotrema rudius Vainio var. *dominicanum* Vainio, 1915:136.

Leptotrema develatum (Nylander) Zahlbruckner, 1923:633.

[For full citations see Hale (1974a:39).]

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin, light tannish or greenish gray, 4–10 cm broad; apothecia numerous, emergent, 0.4–0.8 mm in diameter, noncarbonized and eolumellate, the pore round, about 0.2 mm in diameter; spores 8, 12–14 \times 16–24 μm , 1–3 \times 5–6 loculate.

CHEMISTRY.—Protocetraric acid.

REMARKS.—This is a rather uniform species. It is extremely close to *L. urceolare* (Acharius) Müller Argoviensis, which lacks any lichen substances. *Leptotrema bahianum* is most common in the Caribbean area but also occurs in Venezuela, the Philippines, Sarawak, and other tropical countries. It was collected in Panama over a broad range of elevation (near sea level to 2000 m) on trees in primary and secondary forest.

SPECIMENS EXAMINED.—1: 38726; 3a: 44869, *Esslinger* 4339; 5: 43599; 11: 44845.

ILLUSTRATIONS.—Hale, 1972:193, fig. 2c; 1974a:7, fig. 5f; Redinger, 1936:106, fig. 66.

2. *Leptotrema chiriquiense*, new species

FIGURE 14b

DESCRIPTION.—Thallus corticola, epiphloeodes, nitidus, verrucosus rimosusque, fragilis, stramineo-

albidus, 4–6 cm latus; apothecia (Figure 11c) numerosa, congesta, emergentia vel ascidioida, rotundata vel fere subglobosa, 0.7–1.0 mm diametro, apice fuliginea, columella nulla; ostiolum rotundatum, vix depressum, ca. 0.1 mm diametro; hymenium ca. 300 μm , altum; sporae, 1–2:nae, 35–40 \times 160–190 μm , dense murales, I-.

CHEMISTRY.—Hypoprotocetraric acid and apparently 4-O-demethylnotatic acid.

HOLOTYPE.—Base of exposed tree, remnants of oak forest in pasture at Alto Bepingo, Volcán Chiriquí, Province of Chiriquí, Panama, elevation 2400 m, *M. E. Hale* 46035, 23 February 1975 (US).

REMARKS.—This species is externally somewhat similar to *Ocellularia domingensis* (Nylander) Müller Argoviensis, which also has hypoprotocetraric acid and large spores but with larger, less fragile apothecia. Both species were collected at Chiriquí. This is only the second *Leptotrema* reported to contain hypoprotocetraric acid, the other being *L. hypoprotocetraricum* Hale from the Darien.

SPECIMEN EXAMINED.—1: 38888.

3. *Leptotrema deceptum*

FIGURE 14c

Leptotrema deceptum Hale, 1974a:39 [type collection: Dominica, *Hale* 37860 (US, holotype)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, continuous to cracked with age, smooth and shiny, light tannish gray, 8–10 cm broad; apothecia numerous, immersed to barely emergent, about 0.4 mm in diameter, noncarbonized and eolumellate, the pore minute, about 0.05 mm in diameter, depressed, surrounded by a darkened area; spores 4,

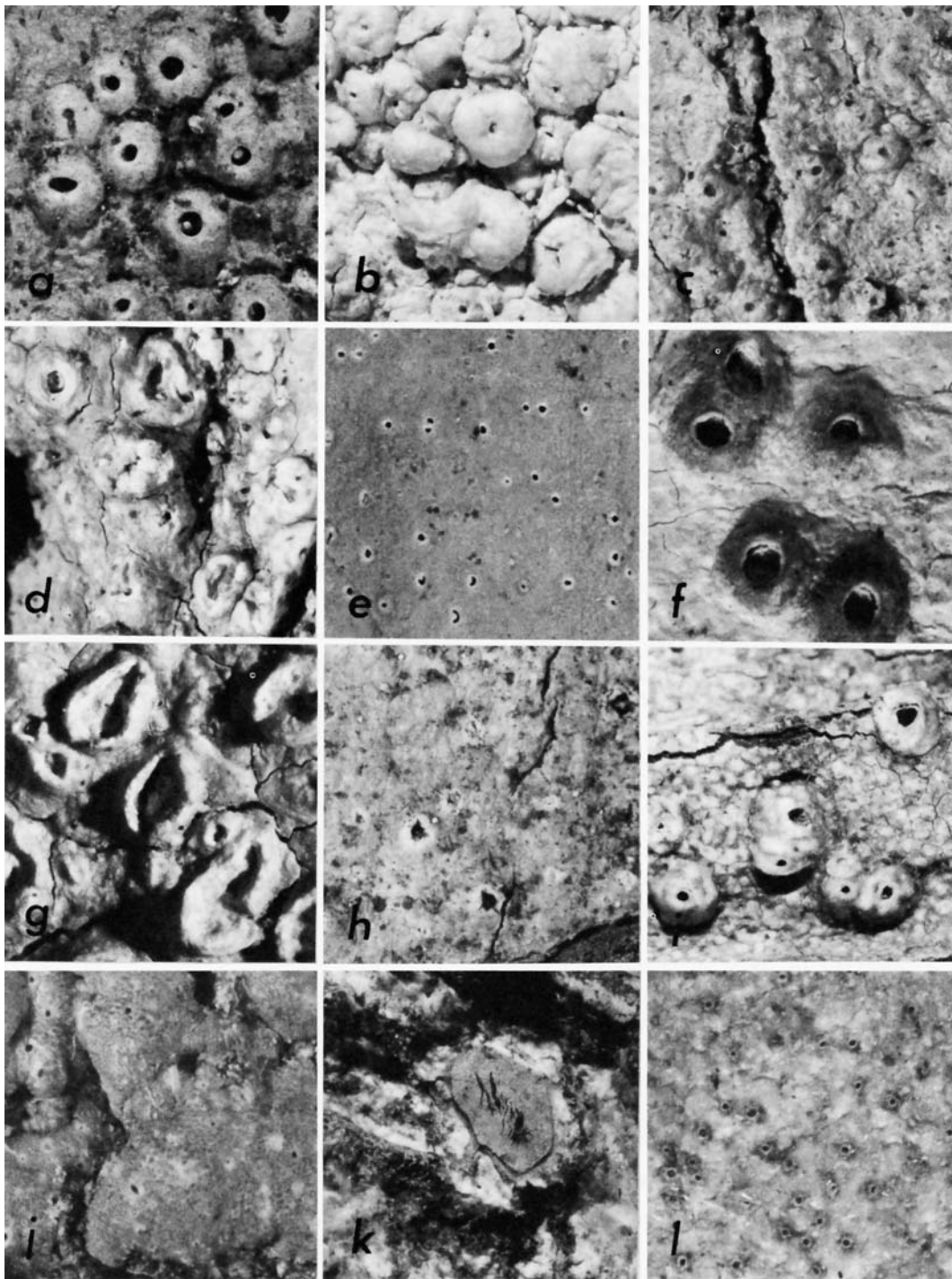


FIGURE 14.—Species of *Leptotrema*: a, *L. bahianum* (Hale 44845); b, *L. chiriquiense* (Hale 46035); c, *L. deceptum* (Hale 43551); d, *L. hypoprotocetraricum* (Mori 4513); e, *L. laeviusculum* (Hale 44973); f, *L. lepadodes* (Hale 46045); g, *L. metaphoricum* (Hale 44911); h, *L. microsporium* (Hale 44936); i, *L. panamense* (Hale 43585); j, *L. reclusum* (Hale 44773); k, *L. stellatum* (Hale 44999); l, *L. trypaneoides* (Hale 46038) ($\times 10$).

25–30 × 60–80 μm, densely muriform, I+ pale blue.

CHEMISTRY.—Stictic and constictic acids.

REMARKS.—This species was previously known only from Dominica and it occurs in Panama in the same type of habitat, base of large trees in rain forest at mid elevations. The pore area is slightly darker and broader than in the typical population. Two other species in Panama have stictic acid: *L. reclusum* (Krempelhuber) Zahlbruckner with larger spores and a grainy appearing cortex and *L. trypaneoides* (Nylander) Riddle with flush apothecia and smaller spores.

SPECIMEN EXAMINED.—6: 43531.

ILLUSTRATIONS.—Hale, 1974a:39, fig. 18.

4. *Leptotrema hypoprotocetraricum*, new species

FIGURE 14d

DESCRIPTION.—Thallus corticola, epiphloeodes, crassus, laevis vel aetate rimosus, pallide cremeo-albidus, 2–4 cm latus; apothecia dispersa, solitaria vel 2–3 aggregata, semi-emergentia, 0.8–1.5 mm diametro, margine thalino crasso, raro semi-erecto, apice pulverulento, albo, excipulo proprio plus minusve distincto, decolorato, separato, columella nulla; hymenium 310–320 μm altum; sporae 1–2: nae, 33–36 × 150–210 μm, dense murales, I–.

CHEMISTRY.—Hypoprotocetraric and 4-O-demethylnotatic acids.

HOLOTYPE.—West ridge of Cerro Tacarcuna massif, Province of Darien, Panama, elevation 1700 m, S. Mori and A. Gentry 4513, 3 February 1975 (US).

REMARKS.—The solitary to clumped apothecia, somewhat reminiscent of those in *Ocellularia conglomerata* Hale, are whitish pulverulent apically and stand out conspicuously from the thallus. No other species of *Leptotrema* have this type of disc, and as pointed out above, only *L. chiriquiense* also contains hypoprotocetraric acid.

5. *Leptotrema laeviusculum*

FIGURE 14e

Leptotrema laeviusculum (Nylander) Zahlbruckner, 1923:635. *Thelotrema laeviusculum* Nylander, 1963b:335 [type collection: Cuba, Wright 155 (FH-Tuck, lectotype; isolectotypes in BM, G, L, PC, UPS)].

DESCRIPTION.—Thallus corticolous, epiphloeodal,

smooth and rather thick with a grainy appearance, sometimes breaking free of the substratum, brittle, pale greenish gray, 6–12 cm broad; apothecia numerous, immersed, separate, 0.2–0.3 mm in diameter, noncarbonized and without a columella, the pore round, 0.8 mm in diameter, white annulate; spores 8, 6–12 × 18–24 μm, 0–1 × 4–5 loculate.

CHEMISTRY.—Protocetraric acid.

REMARKS.—This species is characterized by the dull grainy thallus with crystal inclusions and the small immersed apothecia. Very superficially it might appear to be a member of the *Ocellularia olivacea* group but the habitat is quite different, lianas, exposed roots, and base of trees in low elevation rain forest. I have identified specimens from Cuba, the type-locality, and Trinidad.

SPECIMENS EXAMINED.—3a: 44762, 44764, 44783, 44861, 44865, 44960, 44973, Esslinger 4357.

6. *Leptotrema lepadodes*

FIGURE 14f

- Leptotrema lepadodes* (Tuckerman) Zahlbruckner, 1923:636. *Thelotrema lepadodes* Tuckerman, 1862:405 [type collection: Cuba, Wright (FH-Tuck, lectotype)].
Thelotrema monosporum Nylander f. *album* Nylander, 1861: 46 [type collection: Bonin Islands, Wright (FH-Tuck, lectotype)].
Thelotrema monosporum var. *patulum* Nylander, 1963a:452 [type collection: Cune, Colombia, Lindig in 1860 (H, Nylander herbarium 22715, lectotype)].
Thelotrema disciforme Leighton, 1869:170 [type collection: Central Province, Ceylon, Thwaites (BM, lectotype)].
Leptotrema patulum (Nylander) Müller Argoviensis, 1895b: 315.
Thelotrema aquilinum Vainio, 1915:137 [type collection: St. Croix, Boergesen (TUR, lectotype)].
Leptotrema monosporum f. *album* (Nylander) Zahlbruckner, 1923:638.
Thelotrema rarotongae Räsänen ex Sbarbaro, 1939:101 [type collection: Cook Island, Rarotonga, Parks 2 (H, lectotype)].
Leptotrema pinarocarpum Zahlbruckner in Magnusson and Zahlbruckner, 1944:54 [type collection: Wailuku, Maui, Hawaii, Fairie 679 (UPS, lectotype)].
Phaeotrema disciforme (Leighton) Hale, 1974a:29.

DESCRIPTION.—Thallus corticolous, very thin and mostly hypophloeodal, grayish white, 4–6 cm broad; apothecia common, solitary, emergent, to 1.3 mm in diameter, the thalline margin thick, darker gray and decorticate apically, semierect, carbonized, the inner exciple distinct and persistent, surrounding the open, white pruinose disc that pulls away from

the wall, a columella lacking, the pore gaping, to 0.7 mm in diameter, the disc easily visible; spores 8, 2-4, 15-25 \times 80-100 μ m, densely muriform.

CHEMISTRY.—No substances present.

REMARKS.—The apothecia of this species have an open, gaping pore and a disc that pulls away from the main wall at the periphery. In Panama it occurs in disturbed forest and at canopy level in rain forest. I have seen specimens from the United States, England, West Indies, Hawaii, India, Java, the Philippines, and the Solomon Islands in addition to localities represented by the type collections.

When I first examined the type collection of *Thelotrema disciforme* Leighton, I apparently sectioned the only specimen with transversely septate spores and therefore placed the species in *Phaeotrema*. The remaining material (3 of the 4 pieces in the original collection in BM), however, has muriform spores, as later discovered and annotated by Dr. P. G. Patwardhan. Correctly typified as a species of *Leptotrema*, it is antedated by *L. lepadodes*. I have not yet determined the disposition of the *Phaeotrema* species. In this connection it should be pointed out that the type of *Thelotrema lepadodes* Tuckerman in FH-Tuck definitely has muriform spores, not transversely septate as Salisbury (1972: 272) reports. This is a difficult group that seems to cast doubt on the validity of the spore differences as a generic character. Much more material needs to be examined.

SPECIMENS EXAMINED.—3: 38673; 10: 46045.

7. *Leptotrema metaphoricum*

FIGURE 14g

Leptotrema metaphoricum (Nylander) Zahlbruckner, 1923: 637.

Thelotrema metaphoricum Nylander, 1963a:455 [type collection: Villeta, Colombia, Lindig 2814 (BM, lectotype: isolecotypes in FH-Tuck, G, PC, S, UPS, W)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, rather thick, smooth, fissured with age, pale tannish white, 4-10 cm broad; apothecia common, solitary or in part clumped, semiemergent, chroodiscoid, 0.5-1.5 mm in diameter, round to irregularly elongate in outline, the thalline margin thick, semierect, the inner exciple evanescent, the disc broad, partially actinoid columellate; spores 8, 5-8 \times 10-18 μ m, 0-1 \times 3-4 loculate.

CHEMISTRY.—Lichexanthone.

REMARKS.—The disc is usually large and actinoid columellate with a short thalline margin, much as in *Phaeotrema glyphicum* (Nylander) Zahlbruckner. Older apothecia become irregularly lirelliform. This species was first described from Colombia but has been collected so far in Guatemala and Brazil and in Panama in cloud forest at 2000 m elevation. Only one other comparable species contains lichexanthone, *L. microsporum* Zahlbruckner; it has small round apothecia and a simple columella, but there are obvious and sometimes troublesome intermediates between the two species.

SPECIMENS EXAMINED.—1a: 44911, 44916, 44928.

8. *Leptotrema microsporum*

FIGURE 14h

Leptotrema microsporum Zahlbruckner, 1902:392 [type collection: Rio de Janeiro, Brazil, Höhnelt 148 (W, lectotype) (Figure 2d)].

Thelotrema microsporoides Zahlbruckner, 1923:625 [based on "*Thelotrema microsporum* Zahlbruckner" (not *T. microsporum* Montagne).]

DESCRIPTION.—Thallus corticolous, epiphloeodal, rather thick and smooth to grainy, dull greenish mineral gray, 4-7 cm broad; apothecia mostly solitary, at first immersed but becoming slightly emergent at maturity, to 1 mm in diameter, round in outline, the thalline margin entire, thick, semierect with age, the disc broad, the columella simple to partially actinoid, carbonized, the surface white pruinose, the pore wide, 0.5-1.0 mm wide, white annulate, the tip of the columella often filling the pore; spores 8, 5-8 \times 8-11 μ m, 0-1 \times 2-4 loculate.

CHEMISTRY.—Lichexanthone.

REMARKS.—Typical apothecia, as determined from the type specimen, are flush and 0.5 mm or less in diameter. Some specimens, however, have larger apothecia, which, if strongly emergent, intergrade with those of *L. metaphoricum* (Nylander) Zahlbruckner (see above). These two species may ultimately prove to be part of a large variable population but too few specimens are on hand to make an intelligent judgment. The normal habitat seems to be the lower trunk of trees in open forest. I have identified the species from Mexico, Costa Rica, Cuba, and Colombia.

SPECIMENS EXAMINED.—1: 38735, 38755 (both tentatively identified); 1a: *Esslinger* 4487, 4488; 3a: 44790, 44936; *Marra-ganti*: *Williams* 1103.

9. *Leptotrema panamense*, new species

FIGURE 14i

DESCRIPTION.—Thallus corticola, epiphloeodes, continuous sed demum rimosus, leviter verruculosus, olivaceo-albidus, 6–9 cm latus; apothecia (Figure 11d) numerosa, dispersa, emergentia, 0.7–1.0 mm diametro, basi non valde constricta; ostiolum rotundatum, 0.1–0.2 mm diametro, plus minusve annulato, margin nigro-cinctum vel aurantiaco-cinctum; excipulum apice fuligineum, disco superficie aurantiaco; hymenium 130–140 μm altum; sporae 6–8-nae, 10–12 \times 24–28 μm , longitudine 1-loculatae, transversim 5–6 loculatae, I+ caerulescentes.

CHEMISTRY.—Protocetraric acid and an unidentified pigment.

HOLOTYPE.—Secondary rain forest, La Mesa, north of El Valle, Province of Coclé, Panama, elevation 750 m, *M. E. Hale* 43584, 13 February 1974 (US).

REMARKS.—The rimose thallus and black-rimmed ostiole are similar to those of *O. nigropuncta* Hale and *O. rimoso* Hale, both from Dominica. The reddish orange disc contains a pigment identical to that of *Thelotrema auratum*. It is a canopy species at mid elevations.

SPECIMENS EXAMINED.—2: 43506, 43585; 8: 38567; 11: 46039, 46040, *Esslinger* 4642.

10. *Leptotrema reclusum*

FIGURE 14j

Leptotrema reclusum (Krempelhuber) Zahlbruckner, 1923: 639.

Thelotrema reclusum Krempelhuber in Nylander, 1973:168 [type collection: Andaman Islands, *Kurz* 21 (M, lectotype; isolectotypes in BM, FH-Tuck, H-Nyl, UPS, W, ZT) (Figure 2n)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, well developed and appearing rather thick, broadly warty or bullate, fragile, deeply fissured, the surface shiny but appearing grainy, tannish to greenish mineral gray, 4–8 cm broad; apothecia inconspicuous, immersed to semiemergent, 0.4–0.6 in diameter,

noncarbonized and without a columella, the pore round, 0.05 mm in diameter; spores 1–2, 20–30 \times 70–130 μm , densely muriform.

CHEMISTRY.—Stictic acid, constictic acid, and infrequently the highest “quintaria” unknown.

REMARKS.—*Leptotrema reclusum* is one of a number of species in the genus with stictic acid, a very difficult group that has yet to be well comprehended (see *Hale*, 1974a:40). It is characterized by the large spores, the weakly bullate thallus with a grainy-appearing cortex, and immersed apothecia. The Panamanian material, all collected on Barro Colorado Island at the base of trees, compares very well with the type from the Andaman Islands and specimens from Florida.

SPECIMENS EXAMINED.—3: 38426, 38629, 38644, 38668, 38695; 3a: 44767, 44772, 44773, 44775, 44776, 44780, *Esslinger* 4335, 4354.

11. *Leptotrema stellatum*, new species

FIGURE 14k

DESCRIPTION.—Thallus corticola, epiphloeodes, continuous, nitidus, pallide stramineo-glaucescens, 5 cm latus; apothecia rara, dispersa, chroodisoida, rotundata vel oblonga, usque ad 2 mm lata, margine thallino crasso, stellato-fisso, recurvato, excipulo proprio evanescenti, disco obscuro vel leviter albo-pruinoso; hymenium 220–230 μm altum; sporae 2-nae, 22–26 \times 105–120 μm , dense murales, I–.

CHEMISTRY.—No substances present.

HOLOTYPE.—Top of tree, primary rain forest along road from Alto Piedra to Río Calovebora, Province of Veraguas, Panama, elevation 800 m, *M. E. Hale* 44999, 25 February 1975 (US).

REMARKS.—The chroodisoid disc is lightly pruinose and the thick thalline margin split and recurved as in a *Geaster*. There is some resemblance to *L. mirabilis* Zahlbruckner, which has smaller spores (42–46 μm long) and contains stictic acid.

12. *Leptotrema trypaneoides*

FIGURE 14l

Leptotrema trypaneoides (Nylander) Riddle, 1916:151.

Thelotrema trypaneoides Nylander, 1863b:335 [type collection: Cuba, *Wright* 156 (FH-Tuck, lectotype; isolectotypes in BM, FH, G, L, PC, UPS, US, W) (Figure 2s)].

Thelotrema subterebrans Nylander, 1876:561 [type collection: Cuba, Wright 520 (H, Nylander herbarium 22514, lectotype)].

Leptotrema subterebrans (Nylander) Zahlbruckner, 1923:640.

DESCRIPTION.—Thallus corticolous, epiphloeodal, smooth, shiny and continuous, pale greenish gray, 8–12 cm broad; apothecia numerous, separate, immersed, 0.15–0.2 mm in diameter, sometimes slightly carbonized apically, a columella lacking, the inner exciple evanescent, the pore round, sometimes black rimmed, about 0.1 mm in diameter; spores 8, 10–12 × 24–30 μm, 1–2 × 5–6 loculate.

CHEMISTRY.—Stictic and constictic acids.

REMARKS.—The smooth shiny thallus and the immersed dark-pored apothecia distinguish this species. *Leptotrema phaeosporum* (Nylander) Müller Argoviensis from New Caledonia, a close species, has small apothecia without a distinct bordered pore. It is a rare species in Panama, collected at the base of trees and on saplings in rain forest.

SPECIMENS EXAMINED.—3a: 44815; 11: 44958, 46038.

13. *Leptotrema urceolare*

FIGURE 15a

Leptotrema urceolare (Acharius) Müller Argoviensis, 1887a:12. *Thelotrema urceolare* Acharius, 1812:90 [type collection: "America" on *Cinchona rubra* (H-Ach, lectotype; isolectotypes in C, UPS)].

DESCRIPTION.—Thallus corticolous, epiphloeodal, thin, smooth and continuous, dull, light tannish gray, 6–12 cm broad; apothecia numerous, solitary to irregularly clumped, emergent and sometimes basally constricted to give an urceolate appearance, 0.7–1.1 mm in diameter, carbonized, eolumellate, the whitish pruinose disc usually visible through the pore, the pore wide, round, 0.2–0.5 mm in diameter; spores 8, 10–12 × 20–30 μm, 0–1 × 4–5 loculate.

CHEMISTRY.—No substances present.

REMARKS.—In my study of the Acharian species (Hale, 1972) I expressed reservation on the identity of this species. Since examining more collections, however, I feel that the Panamanian specimens are typical and help establish the characters of *L. urceolare*. The main features are the semiemergent,

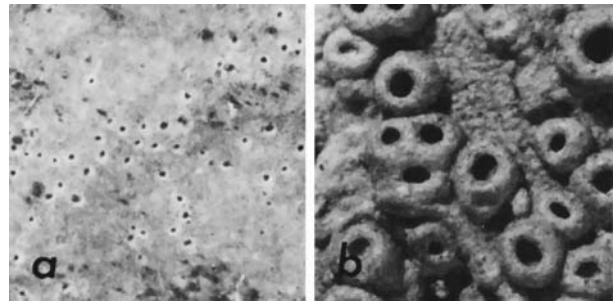


FIGURE 15.—Species of *Leptotrema*: a, *L. urceolare* (Hale 4493); b, *L. wightii* (Hale 38663) (× 10).

often basally constricted apothecia and negative chemistry. I also have specimens from Hawaii and Sarawak. In Panama it occurred on buttresses and bases of large trees, most commonly in the cloud forest at Chiriquí but also near sea level at Barro Colorado.

SPECIMENS EXAMINED.—1: 38712, 38740, 38766; 1a: 44939, 44974, 45815, *Esslinger* 4466, 4500; 3: 38630.

ILLUSTRATIONS.—Hale 1972:195, fig. 3A.

14. *Leptotrema wightii*

FIGURE 15b

Leptotrema wightii (Taylor) Müller Argoviensis, 1882:499. *Endocarpon wightii* Taylor, 1847:155 [type collection: India, Wight (FH-Tayl, lectotype; isolectotypes in BM, G)]. *Thelotrema prevostianum* Montagne, 1849:292. *Leptotrema prevostianum* (Montagne) Montagne, 1956:364. *Thelotrema subconcretum* Leighton, 1869:169. *Thelotrema foraminulosum* Krempelhuber, 1875:20 [type collection: Sarawak, *Beccari* 112 (M, lectotype; isolectotype in G)]. *Phaeotrema subconcretum* (Leighton) Müller Argoviensis, 1887a:10. *Leptotrema flavicans* Müller Argoviensis, 1888:114. *Leptotrema subconcretum* (Leighton) Müller Argoviensis, 1891c:277. *Phaeotrema foraminulosum* (Krempelhuber) Zahlbruckner, 1923:607.

[For full citations see Hale (1974a:43).]

DESCRIPTION.—Thallus corticolous, epiphloeodal, thick, the surface smooth but with a grainy appearance, the cortex columnar, the medulla with conspicuous red crystal masses, greenish mineral gray, up to 10 cm broad; apothecia numerous, separate, immersed, 0.2–0.3 mm in diameter, noncarbonized

and without a columella, the pore round, about 0.1 mm in diameter; spores 8, 9–11 \times 20–28 μm , 0–2 \times 4–6 loculate.

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

REMARKS.—This pantropical species is rare in Panama. As a lichen most commonly collected in dry scrub forests, one would not expect to find it well developed in virgin rain forests.

SPECIMENS EXAMINED.—3: 38663; 3a: 44813.

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