

A Monograph of the Lichen Genus  
*Bulbothrix* Hale (Parmeliaceae)

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## ABSTRACT

Hale, Mason E., Jr. A Monograph of the Lichen Genus *Bulbothrix* Hale (Parmeliaceae). *Smithsonian Contributions to Botany*, number 32, 29 pages, 7 figures, 1976.—A world-level revision is given for the 29 species of *Bulbothrix*, a generic segregate of *Parmelia* characterized by marginal bulbate cilia and production of atranorin in the upper cortex. The genus is primarily tropical in distribution and best developed in secondary forests. The main center of speciation is Brazil with 14 species, and the genus is also well represented in Africa. The New World species have a high frequency of depsides and orcinol depsidones, whereas the Old World species usually contain  $\beta$ -orcinol depsidones. One new species, *B. klementii* Hale, and one new combination, *B. goebelii* (Zenker) Hale, are proposed.

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# Contents

	<i>Page</i>
Introduction .....	1
Morphology .....	1
Chemistry .....	3
Morph Formation .....	4
Phytogeography .....	5
Classification of <i>Bulbothrix</i> .....	6
Key to the Species .....	7
Taxonomic Treatment .....	9
Literature Cited .....	27
Index .....	29







# A Monograph of the Lichen Genus *Bulbothrix* Hale (Parmeliaceae)

Mason E. Hale, Jr.

## Introduction

This world monograph of the 29 species of *Bulbothrix* is part of my continuing effort to revise the parmelioid genera, utilizing the most up-to-date analytical tools available, in particular the scanning-electron microscope and thin-layer chromatography. Genera already completed include *Hypotrachyna* (Vainio) Hale (Hale, 1975a) (the neotropical species), *Relicina* (Hale and Kurokawa) Hale (Hale, 1975b), and *Pseudoparmelia* Lynge (Hale, 1976). Much of the introductory material in these revisions applies equally well to *Bulbothrix* and will not be repeated here.

I am especially thankful to curators of the various museums and herbaria, as listed by the standard herbarium acronyms under specimens examined, who so generously and promptly lent specimens for study. Special thanks for assistance in carrying out field studies are due Dr. M. López-Figueiras of the Universidad de los Andes, Merida, Venezuela; Dr. P. G. Patwardhan, Maharashtra Association for the Cultivation of Science, Poona, India; and Dr. Flora Uyenco, University of the Philippines, Quezon City. Dr. S. Kurokawa assisted with descriptions and preliminary identifications of many of the species in 1961.

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Smithsonian Expedition to Dominica, National Geographic Society, and the Smithsonian Research Foundation.

## Morphology

THE THALIUS.—Species of *Bulbothrix* have small, adnate to closely adnate thalli. The lobes are sublinear to more rarely subirregular, depending on the width. In these respects *Bulbothrix* is closest to *Relicina* and *Parmelina*. The most characteristic feature, however, is the development of marginal bulbate cilia, which are essentially identical with those of *Relicina* and regularly dispersed around the lobe tips and margins. When rhizines are dichotomously branched, the tips of these bulbae may also be branched.

LOWER SURFACE AND RHIZINES.—The lower surface is black in some of the species, dark or pale brown in others. Rhizines are either simple to sparsely furcate, as in *B. affixa*, *B. chowensis*, *B. decurtata*, *B. fungicola*, *B. hypocraea*, *B. imshaugii* (Figure 1b), *B. isidiza*, *B. meizospora*, *B. pustulata*, *B. sensibilis*, *B. setschwanensis*, *B. subcoronata*, *B. subinflata*, *B. tabacina*, and *B. ventricosa*, or more or less richly dichotomously branched, as in *B. apophysata*, *B. atrichella*, *B. bicornuta*, *B. bulbochaeta*, *B. confoederata*, *B. cornuta*, *B. goebelii*, *B. klementii*, *B. laevigatula* (Figure 1c), *B. schiffneri*, *B. semilunata*, *B. suffixa*, and *B. viridescens*. Branching is a useful and consistent taxonomic character.

There is a close correlation between chemistry and branching pattern of the rhizines. All P+

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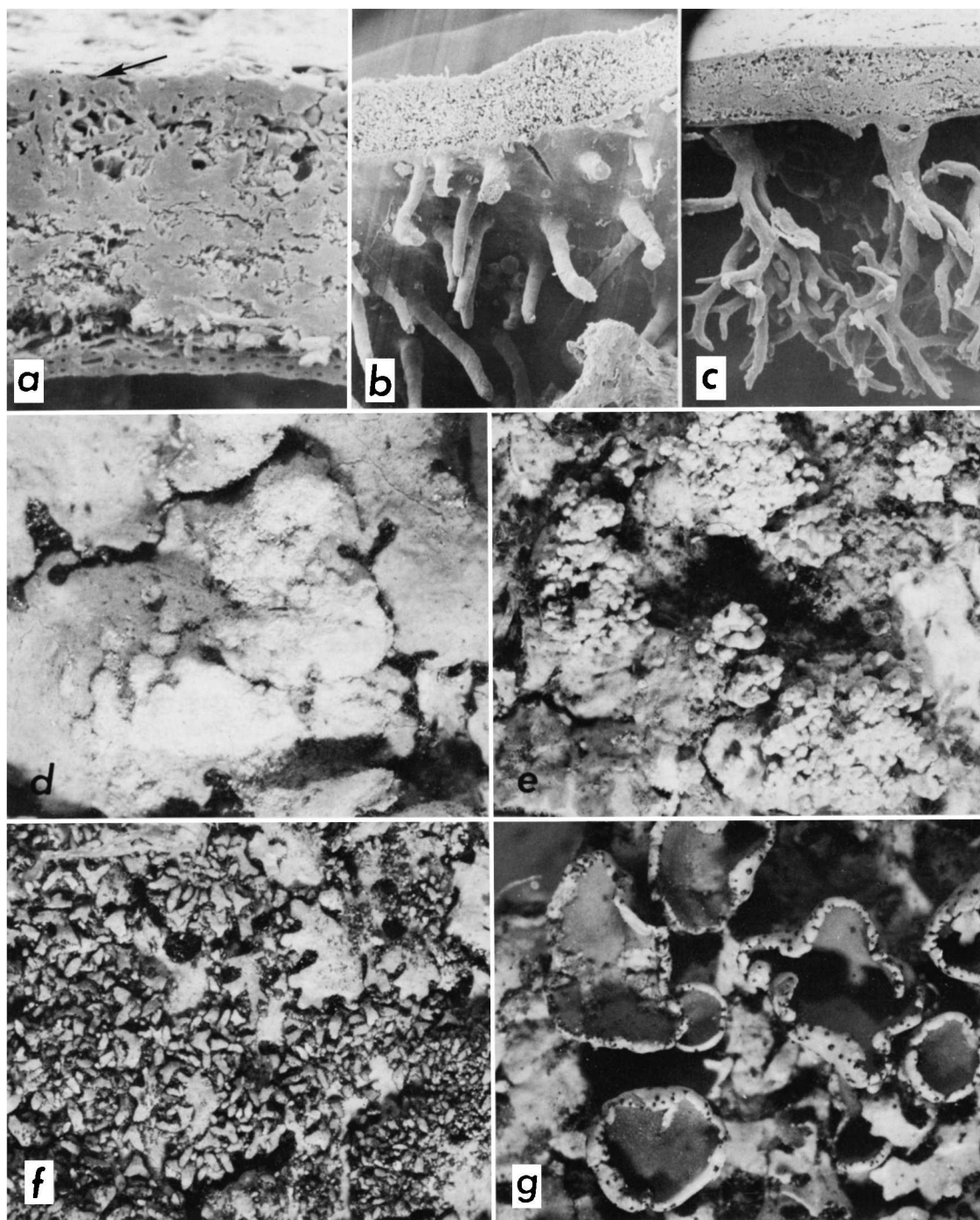


FIGURE 1.—Morphology of *Bulbothrix*: a, cross section of *B. laevigatula* showing epicortex (arrow) (Allard 15992a in US) ( $\times 500$ ); b, simple rhizines of *B. imshaugii* (Mahu 3545 in US) ( $\times 80$ ); c, dichotomously branched rhizines of *B. laevigatula* (Allard 15992a in US) ( $\times 150$ ); d, soralia of *B. imshaugii* (Rundel 7308 in US) ( $\times 10$ ); e, pustules of *B. pustulata* (holotype) ( $\times 10$ ); f, lobules of *B. suffixa* (Hale 42753) ( $\times 10$ ); g, pycnidiate apothecia of *B. viridescens* (Imshaug 42530 in US) ( $\times 10$ ). (Photographs a–c taken with scanning-electron microscope.)



species, that is, those containing norstictic acid, protocetraric acid, or salazinic acid, have simple unbranched rhizines. Most of these are Old World species. On the other hand, the remaining species, all of which are P— and contain gyrophoric acid, lecanoric acid, similar orcinol depsides and depsidones, or only atranorin, have richly branched rhizines and occur predominantly in the New World. The only exceptions are *B. affixa* and *B. fungicola*, which have mostly simple rhizines although they contain gyrophoric acid. As far as I know, no other parmelioid genus shows such a clear-cut correlation between chemistry and morphology except the *Parmelia borrieri* group (Hale, 1965a), which shows a direct correlation between a pale lower surface and the presence of lecanoric acid and a black lower surface with gyrophoric acid.

**VEGETATIVE PROPAGULES.**—Isidia are regularly produced in *B. apophysata*, *B. decurtata*, *B. fungicola*, *B. goebelii*, *B. isidiza*, *B. klementii*, *B. laevigatula*, *B. pigmentacea*, *B. subinflata*, *B. tabacina*, and *B. ventricosa*. They are cylindrical and usually unbranched but become procumbent and nearly dorsiventral in *B. fungicola*. Dense laminal lobules without isidia occur in *B. suffixa* (Figure 1f). These are true lobules since they are corticate and may produce marginal bulbate cilia.

Pustules are found in only one species, *B. pustulata*. These large, inflated structures (Figure 1e) tend to break open apically and seem identical with those described in the genus *Hypotrachyna* (Hale, 1975a:6). They do not form soredia.

Soredia occur only in *B. imshaugii*, a Chilean endemic. The soralia are rather diffuse over the upper surface toward the lobe tips, producing large patches of farinose soredia (Figure 1d).

A rather large percentage of the species in the genus produce no special vegetative propagules other than small adventitious lobules so common in all parmelioid genera. This group includes *B. affixa*, *B. atrichella*, *B. bicornuta*, *B. bulbochaeta*, *B. chowoensis*, *B. confoederata*, *B. coronata*, *B. hypocraea*, *B. meizospora*, *B. subcoronata*, *B. schiffneri*, *B. semilunata*, *B. sensibilis*, *B. setschwanaensis*, and *B. viridescens*. All have abundant apothecia.

**APOTHECIAL CHARACTERS.**—The apothecia of *Bulbothrix* are uniformly small (rarely more than 4 mm in diameter) and sessile or adnate. In a few

species they are almost substipitate because of a constricted base. Pycnidia (coronate apothecia) are always produced around the rim in *B. affixa*, *B. bulbochaeta*, *B. coronata*, *B. fungicola*, *B. schiffneri*, *B. semilunata*, *B. subcoronata*, *B. ventricosa*, and *B. viridescens*. The thalli of these species (and in the case of *B. bulbochaeta*, *B. coronata*, and *B. viridescens* (Figure 1g) the amphithecium) are sometimes heavily pycnidiate with normal immersed pycnidia. These apothecial pycnidia are apparently the same as those I described for *Relicina* (Hale, 1975b:8), the only other parmelioid genus with this trait.

Ecoronate apothecia are characteristic of the remaining 15 fertile species. *Bulbothrix apophysata*, *B. decurtata*, *B. klementii*, and *B. pigmentacea* have never been collected with apothecia.

There is no obvious correlation between chemistry and presence of coronate apothecia, but the geographical correlation is strong. All coronate species, excepting *B. affixa* from Angola and *B. bulbochaeta* from India, are endemic to or more common in the New World. Most species endemic to the Old World are ecoronate.

The spores of *Bulbothrix* are colorless, one-celled, and either ovoid or bicornute. Ovoid spores are rather small, 5–8  $\mu$ m wide and 6–12  $\mu$ m long on the average. Only *B. bulbochaeta*, *B. chowoensis*, *B. confoederata*, and *B. laevigatula* have spores no more than 5–7  $\mu$ m long, the typical range for species of *Relicina* (Hale, 1975b). As a rule, species with salazinic acid, these being largely endemic to the Old World, have the largest spores, 8–20  $\mu$ m long. Bicornute spores are known for three apparently closely related Brazilian species, *B. bicornuta*, *B. schiffneri*, and *B. semilunata*. These spores are quite variable in shape, from nearly ovoid with two short but distinct horns to long, narrow, and semi-lunate. This type of spore has recently been discovered in two species of *Relicina* (Hale, 1975b), but other than these five examples no other species in any parmelioid genera have bicornute spores. We cannot, however, determine the evolutionary significance of unique spores until more is known of their cytology and ontogeny.

### Chemistry

The chemistry of *Bulbothrix* is the least varied



of all the epicorticate parmelioid genera. Only twelve lichen substances, as enumerated below, have been detected. By comparison, the closely related bulbate-ciliate genus *Relicina*, with almost the same number of species, has at least 20 different substances, and of these, only atranorin, gyrophoric acid, norstictic acid, protocetraric acid, and salazinic acid are shared by *Bulbothrix*. For further comparison, the completely unrelated genus *Hypotrachyna* has 39 lichen substances (Hale, 1975a.)

Atranorin: All species in the genus and the main component in *B. bulbochaeta* and *B. viridescens*.

Gyrophoric acid: *B. affixa*, *B. atrichella*, *B. coronata*, *B. fungicola*, *B. goebelii*, *B. schniffneri*, and *B. suffixa*.

Lecanoric acid: *B. bicornuta*, *B. confoederata*, and *B. laevigatula*.

Lobaric acid: *B. apophysata*.

Norlobaridone: *B. decurtata* (as a rare accessory substance with salazinic acid).

Norstictic acid: *B. subcoronata* and *B. ventricosa* (probably accompanied by the unknown substance connorstictic acid).

Protocetraric acid: *B. chowoensis* and *B. subinflata*.

Salazinic acid: *B. decurtata*, *B. hypocraea*, *B. imshaugii*, *B. isidiza*, *B. meizospora*, *B. pustulata*, *B. sensibilis*, *B. setschwanensis*, and *B. tabacina* (rarely accompanied by the unknown substance consalazinic acid, an  $H_2SO_4$  + reddish spot that remains at the point of origin in the usual chromatographic solvents).

Skyrin (rhodophyscin): *B. semilunata*.

Unidentified anthraquinone: *B. pigmentacea*.

On the whole the genus exhibits a relatively low level of evolution in terms of chemistry (Hale, 1966). This is reflected both in the abundance of gyrophoric and salazinic acids, relatively "primitive" substances, and in the lack of biogenetically more "advanced" substances such as alectoronic acid, barbatic acid, divaricatic acid, evernic acid, lichexanthone, perlatolic acid, and stictic acid, as well as the protocetraric acid derivatives fumarprotocetraric acid and succinprotocetraric acid.

On further analysis we can see that the geographical distribution of the acids follows a definite trend. Salazinic acid, for example, predominates in the species endemic to the Old World, and the two species with protocetraric acid (*B. chowoensis* and *B. subinflata*) are also confined there. On the other hand, lecanoric acid, the two orcinol depsidones colensoinic acid and lobaric acid, and norstictic acid are all restricted to species endemic to the New World (North and South

America). The only exception to this generalization is the occurrence of norlobaridone with salazinic acid in the African *B. decurtata*.

Two pantropical species, *B. isidiza* and *B. tabacina*, have salazinic acid and one other, *B. goebelii*, has gyrophoric acid. These differences suggest strongly that the *Bulbothrix* floras of the New and Old Worlds have been separated for a long period of time and deprived of opportunities for gene exchange that might increase chemical diversity. In any event, the New World species have been evolving more rapidly in terms of chemistry than the conservative Old World species.

### Morph Formation

As I explained in studies of *Hypotrachyna* (Hale, 1975a), *Pseudoparmelia* (Hale, 1976), and *Relicina* (Hale, 1975b), speciation in the parmelioid genera may be attributed in large degree to the formation of isidiate and/or sorediate morphs from fertile sexual parents. In comparison with other genera, however, *Bulbothrix*, with relatively fewer species, has not undergone extensive morph formation, and this mechanism has contributed relatively little to speciation in the genus.

There are, for example, an unusually high number of fertile parent species that could give rise to vegetative morphs but have not done so, judging at least from the collections now available. About a third of the species (11) fall into this category: *B. bicornuta*, *B. bulbochaeta*, *B. chowoensis*, *B. coronata*, *B. klementii*, *B. meizospora*, *B. schiffneri*, *B. semilunata*, *B. setschwanensis*, *B. subcoronata*, and *B. viridescens*. The next largest group, five species, *B. apophysata*, *B. decurtata*, *B. pigmentacea*, *B. subinflata*, and *B. ventricosa*, are isidiate species which lack a corresponding nonisidiate parent. The assumption here is that such parents did exist at some stage in the evolutionary history of the genus but have not survived to this time. A similar situation holds for pustulate *B. pustulata*, sorediate *B. imshaugii*, and lobulate *B. suffixa*, none of which appears to have an extant parent.

Finally, four species pairs represent nonisidiate parent-isidiate morph series: *B. affixa* - *B. fungicola*, *B. atrichella* - *B. goebelii*, *B. hypocraea* - *B. isidiza*, and *B. sensibilis* - *B. tabacina*. Except for lobe width differences, *B. confoederata* and *B. laevigatula* also form a plausible parent-isidiate



morph pair. As I remarked in my monograph on *Hypotrachyna* (Hale, 1975a), matching parent morphs and their presumptive vegetative morphs is often quite subjective since minor morphological differences are bound to have arisen in the course of evolution because of adaptations to changing environments, modifications of the parent morph through genetic recombination, etc.

## Phytogeography

*Bulbothrix* is not a commonly collected genus. Even where it is ideally developed, as in the semi-arid scrub forests of Brazil, no species predominate in the vegetation as does, for example, *Hypotrachyna* in the cloud forests of the Andes (Hale, 1975a) or *Relicina* in the dipterocarp forests of the Philippines (Hale, 1975b). One must search with great care to find any specimens of *Bulbothrix* at all. Another measure of its comparative rarity is the fact that few major herbaria have more than a dozen sheets on file. None of the spe-

cies occurs in Europe, where collecting intensity has been high, and few lichenologists have had the opportunity to collect in the tropical regions where *Bulbothrix* does occur. At the same time, collections by some contemporary lichenologists, especially in Africa where I have not collected, were unavailable for this monograph. Consequently, many of the statements made here on species abundance and distribution will be tempered by the results of other workers in the future.

Generalizing, then, from what cannot be considered wholly adequate collections, we find that *Bulbothrix* resembles *Parmotrema* and *Pseudoparmelia* (Hale 1976) in showing highest development in semi-arid woodlands and secondary forests. It appears that the cerrado vegetation of South America and the upland scrub forests of south-central Africa are ideally suited for *Bulbothrix*. Unlike *Pseudoparmelia*, however, the greatest number of species is known from Brazil (Figure 2), less from South Africa, and only one from Australia. The noteworthy point to be made here

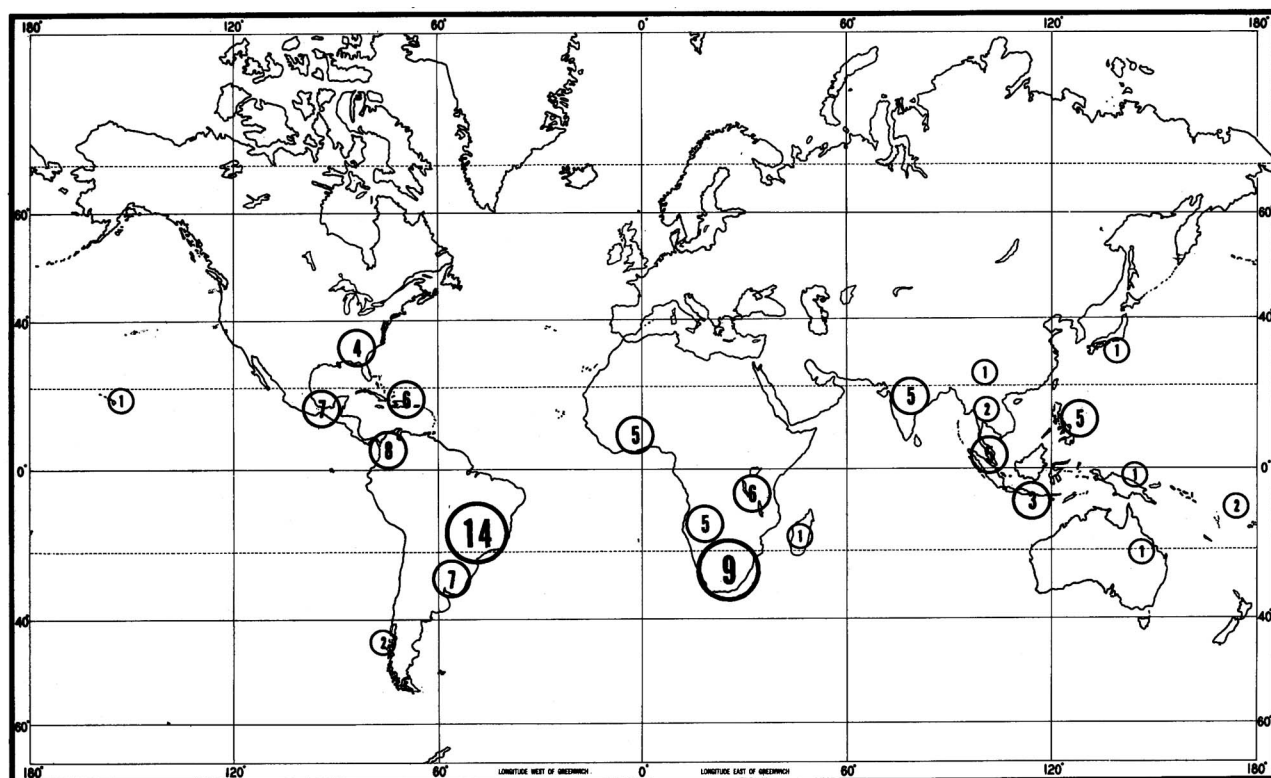


FIGURE 2.—Number of species of *Bulbothrix* in major geopolitical regions (see also list of species in each country in text).



is that the morphologically similar genus *Relicina* has an almost completely separate distribution in the rain forests of Southeast Asia where *Bulbothrix* is rare.

The *Bulbothrix* floras of each geopolitical unit where the genus has been found are as follows.

#### NORTH AND SOUTH AMERICA

- United States: *B. confederata*, *B. coronata*, *B. goebelii*, and *B. laevigatula*.  
 Mexico: *B. coronata*, *B. goebelii*, *B. isidiza*, *B. laevigatula*, *B. tabacina*, and *B. ventricosa*.  
 Guatemala: *B. goebelii*, *B. isidiza*, and *B. suffixa*.  
 Honduras: *B. suffixa*.  
 Costa Rica: *B. ventricosa* and "*Parmelia stenophylla*" (see page 00).  
 Panama: *B. apophysata*, *B. goebelii*, and *B. ventricosa*.  
 Cuba: *B. goebelii*, *B. laevigatula*, *B. suffixa*, and *B. tabacina*.  
 Jamaica: *B. goebelii*, *B. laevigatula*, *B. suffixa*, and *B. tabacina*.  
 Hispaniola: *B. apophysata*, *B. goebelii*, *B. laevigatula*, *B. suffixa*, *B. tabacina*, and *B. ventricosa*.  
 Lesser Antilles and Trinidad: *B. apophysata*, *B. goebelii*, *B. laevigatula*, *B. suffixa*, and *B. tabacina*.  
 Colombia: *B. atrichella*, *B. goebelii*, and *B. laevigatula*.  
 Venezuela: *B. goebelii*, *B. laevigatula*, *B. sensibilis*, *B. suffixa*, *B. tabacina*, and *B. ventricosa*.  
 Peru: *B. atrichella*, *B. coronata*, *B. goebelii*, and *B. laevigatula*.  
 Ecuador: *B. laevigatula*.  
 Guyana: *B. laevigatula*.  
 Brazil: *B. bicornuta*, *B. coronata*, *B. fungicola*, *B. goebelii*, *B. hypocraea*, *B. isidiza*, *B. klementii*, *B. laevigatula*, *B. schiffneri*, *B. semilunata*, *B. subcoronata*, *B. suffixa*, *B. tabacina*, and *B. viridescens*.  
 Uruguay: *B. viridescens*.  
 Paraguay: *B. coronata*, *B. fungicola*, *B. goebelii*, *B. isidiza*, *B. subcoronata*, and *B. suffixa*.  
 Chile: *B. goebelii* and *B. imshaugii*.  
 Argentina: *B. subcoronata*.

#### AFRICA

- Sierra Leone: *B. goebelii*.  
 Ivory Coast: *B. decurtata* and *B. isidiza*.  
 Guinea: *B. sensibilis* and *B. tabacina*.  
 Cameroon: *B. meizospora*.  
 Uganda: *B. decurtata*, *B. hypocraea*, *B. isidiza*, and *B. tabacina*.  
 Urundi: *B. pustulata*.  
 Kenya: *B. isidiza* and *B. sensibilis*.  
 Zaïre: *B. hypocraea*, *B. isidiza*, and *B. sensibilis*.  
 Zambia: *B. chowoensis*, *B. hypocraea*, *B. isidiza*, and *B. sensibilis*.  
 Malawi: *B. isidiza* and *B. sensibilis*.  
 Angola: *B. affixa*, *B. hypocraea*, *B. isidiza*, *B. sensibilis*, and *B. tabacina*.  
 Rhodesia: *B. hypocraea* and *B. isidiza*.

- Tanzania: *B. hypocraea*, *B. isidiza*, and *B. tabacina*.  
 Mozambique: *B. chowoensis*.  
 Union of South Africa: *B. coronata*, *B. decurtata*, *B. goebelii*, *B. isidiza*, *B. suffixa*, *B. tabacina*, and *B. ventricosa*.  
 Madagascar: *B. tabacina*.  
 Mauretius: *B. suffixa*.

#### ASIA

- Pakistan: *B. meizospora*.  
 Nepal: *B. isidiza*, *B. meizospora*, *B. setschwanensis*, and *B. tabacina*.  
 India: *B. bulbothrix*, *B. isidiza*, *B. meizospora*, *B. setschwanensis*, and *B. tabacina*.  
 Thailand: *B. goebelii*.  
 Indochina: *B. isidiza*.  
 Malaysia: *B. goebelii*, *B. isidiza*, *B. pigmentacea*, *B. subinflata*, and *B. tabacina*.  
 Indonesia: *B. goebelii*, *B. isidiza*, and *B. tabacina*.  
 Philippines: *B. goebelii*, *B. isidiza*, *B. pigmentacea*, *B. subinflata*, and *B. tabacina*.  
 New Guinea: *B. goebelii*.  
 Taiwan: *B. goebelii*, *B. isidiza*, and *B. tabacina*.  
 China: *B. setschwanensis*.  
 Japan: *B. isidiza*.  
 Australia: *B. tabacina*.  
 Hawaii: *B. isidiza*.  
 Pacific Area: *B. goebelii* and *B. isidiza*.

The overall breakdown may be summarized as follows: The New World (North and South America) has a total flora of 19 species, 11 of these endemics, 5 also occurring in Africa, and 3 pantropical. Africa has a total of 13 species, 4 of them endemic, 5 also occurring in the New World, 1 shared with Asia, and 3 pantropical. All of Asia has a total flora of 8 species, 4 of them endemic, 1 shared with Africa, and 3 pantropical. The three commonest species are *B. goebelii*, known from 23 countries, *B. isidiza* from 21, and *B. tabacina* from 16. These are the three pantropical species. Eight species are known from only their type localities or, at most, one other collection: *B. affixa*, *B. atrichella*, *B. bicornuta*, *B. bulbochaeta*, *B. chowoensis*, *B. klementii*, *B. pustulata*, *B. schiffneri*, and *B. semilunata*.

#### Classification of *Bulbothrix*

Species now recognized in *Bulbothrix* were previously classified in the collective genus *Parmelia*. The first lichenologist to sense an affinity between some of them was Lynge (1914), who did so, however, on the basis of bicornute spores (as opposed to ovoid) in three species, *B. bicor-*



*nuta*, *B. schiffneri*, and *B. semilunata*. He grouped these three species in section *Bicornuta*, coordinate with section *Amphigymnia*, but overlooked the marginal bulbate cilia characteristic of all three species. He also failed to recognize bulbate cilia in Brazilian specimens of *Parmelia acariospora* (= *B. goebelii*), *P. coronata* (= *B. coronata*), *P. fungicola* (= *B. fungicola*), and *P. viridescens* (= *B. viridescens*), all of which he either identified or described as new. He did make note of coronate apothecia where they occurred.

If we go back to Fée's descriptions (1824 and 1837) of the first two bulbate species to be described, we discover that he correctly described coronate apothecia in *Parmelia coronata* and *P. glandulifera* and possibly marginal bulbate cilia in *P. glandulifera* (= *B. coronata*). Zenker (1827) noticed the richly branched rhizines of *B. goebelii* and their position on the lobe margins. Neither Müller Aargau nor Nylander recognized bulbate cilia in any of the species they described, although Nylander mentioned them for *Parmelia circumnodata* (= *Relicina circumnodata* (Nylander) Hale). Vainio (1890) meticulously described the morphology of *Parmelia coronata* and *P. coronata* var. *isidiosa* Müller Argoviensis (the latter, incidentally, a misidentified *Parmelina*), as well as marginally bulbate *Parmelia abstrusa* (= *Relicina abstrusa* (Vainio) Hale), but failed in all these instances to observe bulbate cilia on the lobe margins.

While Zahlbruckner (1909) did not attempt to group marginally bulbate species, he compared *Parmelia schiffneri* (= *B. schiffneri*) with *Parmelia relicinella* (= *Relicina relicinella* (Nylander) Hale), a marginally bulbate species with usnic acid, *Parmelia coronata* (spores ovoid), and *P. bicornuta* (lobes twice as broad as in *P. schiffneri* and medulla C+ red). In this case, too, Zahl-

bruckner seems to have sensed a close affinity for these species without observing the marginal bulbate cilia. He did not mention these cilia for *Parmelia acariospora* (= *B. goebelii*) either, when describing it as new.

Although Dodge (1959:89) recognized bulbate ("conic") cilia on the lobes of *Parmelia sublaevigatoides* (= *B. tabacina*), he did not see them on other species of *Bulbothrix* that he described.

Hale and Kurokawa (1964) were apparently the first lichenologists to recognize marginally bulbate species as a natural group. I recently separated the usnic acid-containing species as a distinct genus, *Relicina* (Hale and Kurokawa) Hale (Hale, 1975b), leaving the usnic acid-free species as the nucleus of *Bulbothrix* (Hale, 1974).

The chief features of *Bulbothrix* are the marginal bulbate cilia, small, adnate to appressed thallus, adnate imperforate apothecia and frequent occurrence of coronate apothecia, absence of usnic acid in the cortex (and conversely presence of atranorin), variable color of the lower surface (pale brown or black), and simple or branched rhizines. Anatomically the genus is distinguished by a palisade upper cortex overlaid by a pored epicortex (Figure 1a) (Hale, 1973). The unique chemical profile is discussed under "Chemistry" (above).

*Bulbothrix* as circumscribed in this monograph is most closely related to *Relicina* in morphology, these being the only two parmelioid genera with bulbate cilia, coronate apothecia, and bicornute spores. However, as I emphasized in my study of *Relicina* (Hale, 1975b), the genera are almost totally different in ecological requirements and in geography. Most species of *Relicina* have evolved in the evergreen rain forests of Southeast Asia. Their chemical profiles are strikingly different, making highly unlikely any significant gene ex-

## Key to the Species

### SPECIES WITHOUT ISIDIA, SOREDIA, OR PUSTULES

1. Apothecia present; spores bicornute.
  2. Medulla C negative ..... *B. semilunata*
  2. Medulla C+ rose or red.
    3. Lecanoric acid present; lobes 1-2 mm wide; apothecial rim ecoronate .... *B. bicornuta*
    3. Gyrophoric acid present; lobes less than 1 mm wide; apothecial rim coronate ..... *B. schiffneri*
1. Apothecia, if present, with ovoid or elliptical spores.
  4. Rhizines richly branched.



5. Medulla C+ rose or red.
  6. Lobes 1 mm wide or less; lecanoric acid present ..... *B. confoederata*
  6. Lobes 1–2 mm wide; gyrophoric acid present.
    7. Apothecia coronate ..... *B. coronata*
    7. Apothecia ecoronate ..... *B. atrichella*
5. Medulla C negative.
  8. Collected in India ..... *B. bulbochaeta*
  8. Collected in tropical America.
    9. Rhizines densely branched; tips of bulbate cilia often branched ..... *B. klementii*
    9. Rhizines simple to sparsely branched; tips of bulbate cilia simple ..... *B. viridescens*
4. Rhizines simple or sparsely furcate.
  10. Apothecia coronate.
    11. Medulla K+ yellow turning red ..... *B. subcoronata*
    11. Medulla K negative.
      12. Lobes 0.5–1 mm wide; collected in Africa ..... *B. affixa*
      12. Lobes 1–2 mm wide; collected in South America ..... *B. viridescens*
  10. Apothecia, if present, ecoronate.
    13. Medulla K negative (protocetraric acid) ..... *B. chowoenensis*
    13. Medulla K+ yellow turning red (salazinic acid).
      14. Lower surface black with at most a narrow marginal brown zone.
        15. Lobes sublinear; spores 7–9  $\mu\text{m}$  long ..... *B. sensibilis*
        15. Lobes broader, subirregular; spores 14–20  $\mu\text{m}$  long ..... *B. meizospora*
      14. Lower surface pale brown.
        16. Lobes more or less sublinear, often crowded, 1–3.5 mm wide; spores 8–14  $\mu\text{m}$  long ..... *B. hypocraea*
        16. Lobes broader, 2–5 mm wide; spores 12–19  $\mu\text{m}$  long ..... *B. setschwanensis*

## SPECIES WITH ISIDIA, SOREDIA, OR PUSTULES

1. Thallus sorediate ..... *B. imshaugii*
1. Thallus not sorediate.
  2. Thallus pustulate ..... *B. pustulata*
  2. Thallus not pustulate.
    3. Thallus isidiate, the isidia becoming procumbent and dorsiventral.
      4. Isidia fine, intermixed with thin, often branched lobulate isidia (Figure 3d) ..... *B. fungicola*
      4. Isidia entirely lobulate (Figure 1f) ..... *B. suffixa*
    3. Thallus isidiate, the isidia erect, cylindrical.
      5. Medulla K+ yellow turning red (salazinic or norstictic acids).
        6. Lower surface brown ..... *B. isidiza*
        6. Lower surface black with at most a narrow brown zone at the margins.
          7. Norstictic acid present ..... *B. ventricosa*
          7. Salazinic acid present.
            8. Thallus usually corticolous; isidia normal ..... *B. tabacina*
            8. Thallus saxicolous; isidia blackening at the tips ..... *B. decurtata*
      5. Medulla K negative.
        9. Medulla C+ rose or red.
          10. Lecanoric acid present ..... *B. laevigatula*
          10. Gyrophoric acid present.
            11. Rhizines richly branched, often pale; isidia uniformly erect and cylindrical ..... *B. goebelii*
            11. Rhizines sparsely branched, black; isidia in part procumbent and dorsiventral ..... *B. fungicola*
        9. Medulla C negative.
          12. Lower surface brown; medulla P+ red (protocetraric acid) ..... *B. subinflata*
          12. Lower surface dark brown to black; medulla P negative.
            13. Lobes appressed, less than 1 mm wide; collected in Southeast Asia ..... *B. pigmentacea*
            13. Lobes adnate, 1–2 mm wide; collected in tropical America ..... *B. apophysata*



change in the past evolution of the two genera. If we look for a parmelioid group with as "primitive" an assemblage of lichen substances as in *Bulbothrix*, it would be *Parmelina* Hale, another genus common in secondary, though more temperate forests, with a comparably small thallus but with normal marginal cilia and simple rhizines. I doubt very much, however, that *Bulbothrix* and *Parmelina* have evolved from a common ancestor or undergone a significant amount of generic hybridization.

### Taxonomic Treatment

#### *Bulbothrix*

*Bulbothrix* Hale, 1974:480.

*Parmelia* section *Bicornuta* Lynge, 1915:17 [type-species: *Parmelia bicornuta* Lynge (= *Bulbothrix bicornuta* (Lynge) Hale)].

*Parmelia* subgenus *Bicornuta* (Lynge) Gyelnik, 1932:219.

*Parmelia* subgenus *Parmelia* section *Imbricaria* subsection *Bicornutae* series *Bicornutae* Hale and Kurokawa, 1964:135.

The 29 presently known species of *Bulbothrix* are listed below in alphabetic order. Chemistry was determined with thin-layer chromatography in two solvent systems, hexane-ether-formic acid and benzene-dioxane-acetic acid. The lichen substances reported are those for the type material, unless otherwise stated. Locations of specimens examined are cited by the standard herbarium acronyms; collections by Hale are all preserved in US and the acronym is not given.

#### *Bulbothrix affixa*

FIGURE 3a

*Bulbothrix affixa* (Hale and Kurokawa) Hale, 1974:428.

*Parmelia affixa* Hale and Kurokawa, 1964:137 [based on *Parmelia coronata* var. *denudata* Vainio].

*Parmelia coronata* Fée var. *denudata* Vainio in Welwitsch, 1901:401 [type collection: Morro de Lopollo, Huila, Angola, Welwitsch 33 (TUR, lectotype; BM, isoelectotype)].

**DESCRIPTION.**—Thallus very closely adnate, corticolous, light mineral gray, 2–3 cm in diameter; lobes sublinear, 0.3–1 mm wide; bulbate cilia dense; upper surface plane, continuous or cracked on older lobes; lower surface black, moderately rhizinate, the rhizines mostly simple, black. Apo-

thecia numerous, adnate, 0.5–1.5 mm in diameter, the exciple coronate, the base retrorsely rhizinate; spores 8, 4–5 × 8–10 μm.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C–, KC+ faint rose, P–, atranorin and gyrophoric acid.

**HABITAT.**—On trees in open areas.

**DISTRIBUTION.**—Angola.

**REMARKS.**—This small species, the only coronate one endemic to Africa, is still known only from Angola. It probably occurs more commonly there and elsewhere in Africa but would be overlooked because of the small size. It may be considered as the presumptive parent morph of *B. fungicola*, a rare New World species. The other nonisidiate species with gyrophoric acid in Africa, *B. coronata*, is significantly larger and has branched rhizines.

**SPECIMENS EXAMINED.**—Angola: Huila, *Degelius* (Degelius herbarium, US).

#### *Bulbothrix apophysata*

FIGURE 3b

*Bulbothrix apophysata* (Hale and Kurokawa) Hale, 1947:480. *Parmelia apophysata* Hale and Kurokawa, 1964:138 [type collection: Piedra Blanca, La Vega, Dominican Republic, Allard 16073 (US, holotype; TNS, isotype)].

**DESCRIPTION.**—Thallus closely adnate, corticolous, light mineral gray, 3–6 cm broad; sublinear-elongate, 0.7–1.5 mm wide; bulbate cilia distinct, numerous; upper surface plane, faintly maculate, irregularly cracked on older lobes, sparsely to moderately isidiate, the isidia simple, less than 0.3 mm high; lower surface variable, usually blackening in the center, dark brown in a broad marginal zone, densely rhizinate, the rhizines pale brown to black, densely branched. Apothecia not seen.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C–, KC+ rose, P–, atranorin and lobaric acid.

**HABITAT.**—On trees in pastures and disturbed areas at 200–1500 m elevation.

**DISTRIBUTION.**—Dominican Republic, Trinidad, and Panama.

**REMARKS.**—This species has so far been collected only in secondary forests. The chemistry is unique in the genus and no nonisidiate morph is extant. Three other isidiate species within the range of *B. apophysata* would be distinguished as follows:



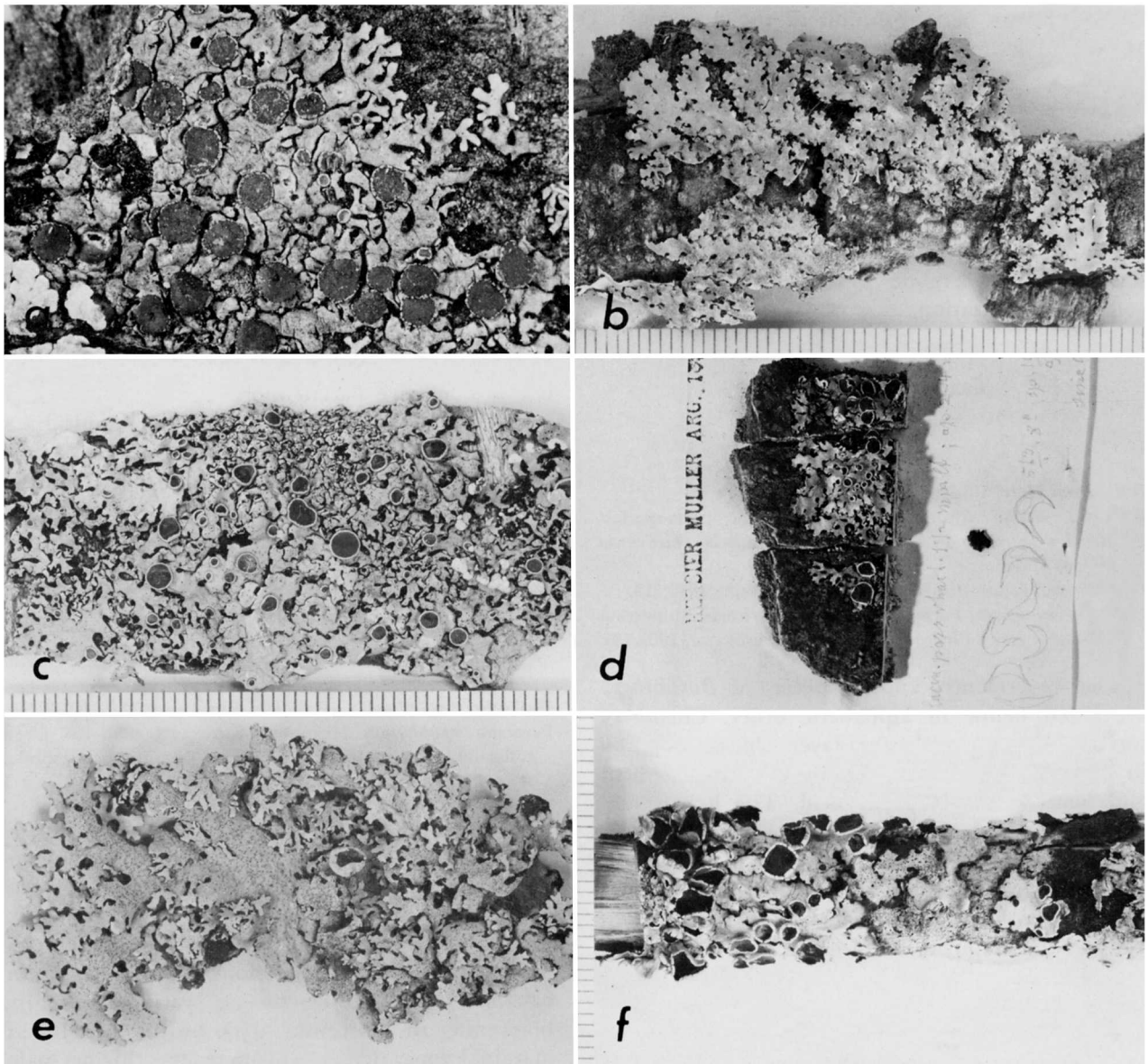


FIGURE 3.—Species of *Bulbothrix*: a, *B. affixa* (lectotype in BM) ( $\times 4$ ); b, *B. apophysata* (Hale 38873); c, *B. atrichella* (Lindig 110 in H); d, *B. bicornuta* (lectotype in G) ( $\times 1$ ); e, *B. bulbochaeta* (holotype in US); f, *B. chowoensis* (isotype in US). (Scale for b, c, e, f in mm.)

*B. laevigatula* is somewhat smaller and more appressed and contains lecanoric acid; *B. goebelii* has a more fragile thallus with a darker, sometimes olivaceous color, and produces gyrophoric acid; and *B. tabacina* has simple black rhizines and contains salazinic acid.

SPECIMENS EXAMINED.—Dominican Republic: La Vega, Allard 18032 (US). Trinidad: Imshaug 32318 (MSC). Panama: Chiriquí, Hale 38873; Veraguas, Hale 45941.

### *Bulbothrix atrichella*

FIGURE 3c

*Bulbothrix atrichella* (Nylander) Hale, 1974:480.

*Parmelia atrichella* Nylander, 1885:614 [type collection: Colombia, Lindig 110 (H, Nylander herbarium 35233, lectotype; FH, BM, M, isolectotypes)].

DESCRIPTION.—Thallus closely adnate on bark, light mineral gray, turning olive-buff in the her-



barium, 3–6 cm in diameter; lobes sublinear-elongate, 0.5–2 mm wide, the margins densely bulbate, sometimes lobulate; upper surface plane, shiny, maculate; lower surface black, densely rhizinate, the rhizines densely branched. Apothecia adnate, 1–2.5 mm in diameter, the disc carob brown, ecoronate; spores 8,  $5 \times 7\text{--}8\text{ }\mu\text{m}$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+ rose, KC+ red, P–, atranorin and gyrophoric acid.

HABITAT.—On trees in open forest at about 2000 m elevation.

DISTRIBUTION.—Colombia and Peru.

REMARKS.—This species is known from only two collections. It is very close to *B. coronata* but lacks coronate apothecia. The upper surface is rather distinctly maculate and the thallus color more olivaceous than in *B. coronata*. *Bulbothrix goebelii* may well be the isidiate morph.

SPECIMENS EXAMINED.—Peru: San Martín, Allard 21472 bis (US).

### *Bulbothrix bicornuta*

FIGURE 3d

*Bulbothrix bicornuta* (Müller Argoviensis) Hale, 1974:480.

*Parmelia bicornuta* Müller Argoviensis, 1891:377 [type collection: Rio de Janeiro, Brazil, Leyland (BM, lectotype; G, isolectotype)].

DESCRIPTION.—Thallus adnate on bark, whitish mineral gray, 4–6 cm in diameter; lobes sublinear-elongate, 0.7–1.5 mm wide; bulbate cilia dense, strongly inflated, becoming apically branched; upper surface plane, shiny, continuous; lower surface black, densely short rhizinate, the rhizines branched. Apothecia adnate, 1–4 mm in diameter, the exciple ecoronate; spores 8, bicornute,  $3\text{--}4 \times 15\text{--}19\text{ }\mu\text{m}$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+, KC+ red, P–, atranorin and lecanoric acid.

HABITAT.—On trees in open forest.

DISTRIBUTION.—Brazil.

REMARKS.—The most distinctive feature of this rare species—it is still known only from the type collection—is the bicornute spores. The other two species in the genus with bicornute spores, *B. schiffneri* and *B. semilunata*, have different chemistry and much narrower lobes. It is probably unrelated to lecanoric acid-containing *B. confoe-*

*derata*, a North American endemic which has ovoid spores and narrow lobes (0.5–1.0 mm wide). Müller measured the spores as listed above in the description, but my own examination gave smaller spores, about 8  $\mu\text{m}$  long.

### *Bulbothrix bulbochaeta*

FIGURE 3e

*Bulbothrix bulbochaeta* (Hale) Hale, 1974:480.

*Parmelia bulbochaeta* Hale in Hale and Kurokawa, 1964:138 [type collection: Shembaganur, Madurai District, India, Awasthi 4347 (Awasthi herbarium, holotype; US, isotype)].

DESCRIPTION.—Thallus adnate to loosely adnate, corticolous, coriaceous, mineral gray, 4–8 cm broad; lobes sublinear, crowded, 1.5–2.5 mm wide; bulbate cilia conspicuous, simple or apically branched; upper surface plane, shiny, continuous, usually heavily pycnidiate; lower surface black except for a narrow brown zone along the margins, densely rhizinate, the rhizines dichotomously branched. Apothecia adnate, 2–3 mm in diameter, the exciple coronate; spores 8,  $4 \times 5\text{ }\mu\text{m}$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, KC–, P–, atranorin.

HABITAT.—On trees in secondary forest at 2000 m elevation.

DISTRIBUTION.—India.

REMARKS.—This is the only member of *Bulbothrix* endemic to India. It is characterized by the rather coriaceous thallus and lack of medullary substances. I attempted to recollect the species in 1974 in the Palni Hills of South India, but it is either very rare or has been (or soon will be) destroyed by continued deforestation in the region.

### *Bulbothrix chowoensis*

FIGURE 3f

*Bulbothrix chowoensis* (Hale) Hale, 1974:480.

*Parmelia chowoensis* Hale, 1972:343 [type collection: Nyika Plateau, Zambia, Jellicoe 53 (BM, holotype; US, isotype)].

DESCRIPTION.—Thallus adnate, corticolous, coriaceous, light mineral gray, 4–6 cm broad; lobes subirregular, contiguous or subimbricate, 2–2.5 mm wide; upper surface plane, shiny, emaculate; lower surface brown, moderately rhizinate, the



rhizines brown, simple. Apothecia numerous, adnate to subpedicellate, ecoronate, 2–4 mm in diameter; spores 8,  $3\text{--}4 \times 6\text{--}7 \mu\text{m}$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, P+ red, atranorin and protocetraric acid.

HABITAT.—On branches of trees in open forest.

DISTRIBUTION.—Zambia and Mozambique.

REMARKS.—This species superficially resembles *B. hypocraea* but has smaller spores and different chemistry (*B. hypocraea* is K+ red with salazinic acid). One other species in the genus, isidiate *B. subinflata*, contains protocetraric acid but would not be considered related to *B. chowoensis* because of narrower sublinear lobes and occurrence in the rain forests of Southeast Asia.

SPECIMENS EXAMINED.—Mozambique: *Sandrone* (F, US).

### *Bulbothrix confoederata*

FIGURE 4a

*Bulbothrix confoederata* (Culberson) Hale, 1974:480.

*Parmelia confoederata* Culberson, 1961:169 [type collection: Shallotte, Brunswick County, North Carolina, *Culberson* 9010 (DUKE, holotype; FH, TNS, US, isotypes)].

DESCRIPTION.—Thallus closely adnate on twigs, light mineral gray, 2–5 cm broad; lobes sublinear, 0.5–1 mm wide; bulbate cilia dense, conspicuously inflated, apically branched; upper surface plane, continuous; lower surface black, densely rhizinate, the rhizines dichotomously branched. Apothecia common, 1–3 mm in diameter, the exciple ecoronate; spores 8,  $3\text{--}5 \times 5\text{--}7 \mu\text{m}$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+, KC+ red, P–, atranorin and lecanoric acid.

HABITAT.—On tree branches and small shrubs near sea level in open areas.

DISTRIBUTION.—Southeastern United States.

REMARKS.—This is the only species in the genus endemic to North America. It had been completely overlooked prior to its description in 1961 although sparsely represented in herbaria under such names as "*Parmelia laevigata*." It occurs commonly on small exposed shrubs in a zone back from the shoreline along the Gulf and Atlantic coasts. Because of the similar chemistry, one might be tempted to compare it with *B. bicornuta*, but the spores are ovoid, not bicornute, and the thallus significantly smaller. One might also consider it as the nonisidiate parent morph of leca-

norin acid-containing *B. laevigatula*, a somewhat larger ecoronate species surely not far removed.

SPECIMENS EXAMINED.—United States: Virginia, *Reed* 59656 (Reed herbarium); North Carolina, *Culberson* 5169 (DUKE, US); South Carolina, *Culberson* 10022 (DUKE, US); Georgia, *Skorepa and Folkerts* 2475 (US); Alabama, *Evans* 98 (US), *Hale* 7262, 34193; Florida, *Calkins* 32 (WIS), *Hale* 16710, 17050, 17643, 21661, 21823, 21868, 21868, 21943, *Rapp* (FLAS, US); Texas, *Fisher* 50155 (US). See Moore (1968:219) for additional records from Florida.

### *Bulbothrix coronata*

FIGURE 4b

*Bulbothrix coronata* (Fée) Hale, 1974:480.

*Parmelia coronata* Fée, 1824:123 [type collection: South America (G, lectotype)].

*Parmelia glandulifera* Fée, 1824:123 [type collection: Tropical America, *Humboldt and Bonpland* (G, lectotype)].

*Parmelia appressa* Zenker in Goebel and Kunze, 1827:157 [type collection: Peru (L, lectotype)].

*Parmelia relicina* var. *coronata* (Fée) Müller Argoviensis, 1887b:318.

DESCRIPTION.—Thallus closely adnate on bark, 3–6 cm in diameter; lobes sublinear-elongate, crowded, 0.5–2 mm wide; bulbate cilia distinct; upper surface plane to rugulose, continuous to faintly maculate, cracked on older lobes; lower surface black, moderately rhizinate, the rhizines moderately to densely branched. Apothecia adnate, 1–3 mm in diameter, the exciple coronate; spores 8,  $5 \times 6\text{--}8 \mu\text{m}$ .

CHEMISTRY.—Medulla K–, C+ rose, KC+ red, P–, atranorin and gyrophoric acid.

HABITAT.—On trunks and branches of trees in semi-arid woodlands up to 2300 m elevation.

DISTRIBUTION.—United States, Mexico, Brazil, Paraguay, and South Africa.

REMARKS.—This was the first species described in the genus and the marginal bulbate cilia were recognized by Fée when he used the epithet *glandulifera*. It occurs in the New World with a disjunct locality in South Africa. No vegetative morphs have been discovered. The only confusable species, *B. bicornuta*, *B. schiffneri*, and *B. semilunata*, are all distinguished by bicornute spores.

Müller (1887b:318) was the first lichenologist to synonymize *Parmelia glandulifera* under *P. coronata*. He then reduced them to *P. relicina* var. *coronata*, emphasizing the coronate apothecia



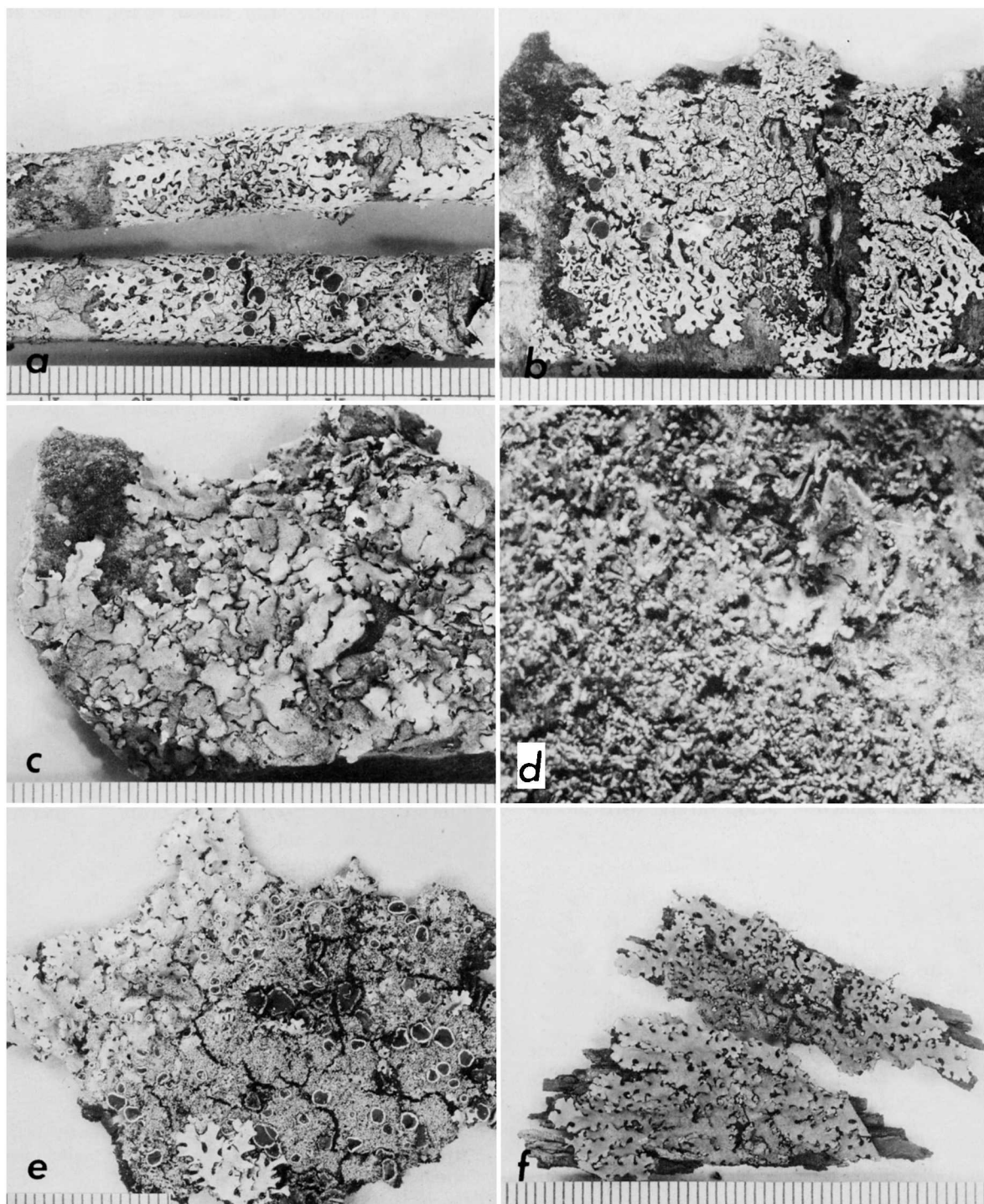


FIGURE 4.—Species of *Bulbothrix*: a, *B. confoederata* (Hale 33845); b, *B. coronata* (Hale 20505); c, *B. decurtata* (isotype in US); d, *B. fungicola* (isolectotype of *Parmelia coronata* f. *isidiosa* in BM) ( $\times 10$ ); e, *B. goebelii* (lectotype of *Parmelia acariospora* in W); f, *B. goebelii* (Ravenel in US). (Scale in mm.)



common to these species but disregarding the yellow color (and different chemistry) of *P. relicina* (= *Relicina relicinula* (Müller Argoviensis) Hale).

**SPECIMENS EXAMINED.**—United States: Texas, *Anderson and Shushan* 18742 (COLO, US), *Wetmore* 18231 (MINN, US). Mexico: Chiapas, *Hale* 20505; Michoacán, *Iltis* 1893 (US, WIS); Oaxaca, *Hale* 20827, *Iltis* 2691 (US). Jamaica: *Imshaug* 14295, 15007 (MSC). Brazil: *Spruce* 158 (BM); Mato Grosso, *Malme* (LD, S, US). For additional records from Brazil see *Hale* (1960:13). Paraguay: *Balsana* 4192 (P). Union of South Africa: Cape Province, *Almborn* 2879 (LD).

### *Bulbothrix decurtata*

FIGURE 4c

*Bulbothrix decurtata* (Kurokawa) Hale, 1974:480.

*Parmelia decurtata* Kurokawa in Hale and Kurokawa, 1964: 139 [type collection: 10 miles southwest of Lydenburg, Transvaal, Union of South Africa, *Almborn* 7388 (LD, holotype; US, isotype)].

**DESCRIPTION.**—Thallus adnate to closely adnate on rock, mineral gray, 3–7 cm broad; lobes subirregular to sublinear, 1–3 mm wide; bulbate cilia sparse to moderate, conspicuously inflated; upper surface plane, continuous or cracked on older lobes, moderately isidiate, the isidia cylindrical to granular, often black-tipped; lower surface dark brown to black in the center, densely rhizinate, the rhizines simple. Apothecia not seen.

**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow turning red, C–, KC–, P+ pale orange, atranorin and salacinic acid, rarely with norlobaridone.

**HABITAT.**—On rocks in semi-arid regions.

**DISTRIBUTION.**—Africa.

**REMARKS.**—*Bulbothrix decurtata* is apparently the only obligately saxicolous species in the genus. The thallus is usually quite adnate and collected with the rock substratum. No parent morph is known. One anomalous specimen from the Ivory Coast (*Santesson* 10485b) contains norlobaridone in addition to salazinic acid but is otherwise indistinguishable from the normal population.

**SPECIMENS EXAMINED.**—Ivory Coast: Man, *Santesson* 10485b (UPS, US). Uganda: Kigezi District, *Swinscow* U 23/73 (BM, US).

### *Bulbothrix fungicola*

FIGURE 4d

*Bulbothrix fungicola* (Lynge) Hale, 1974:480.

*Parmelia fungicola* Lynge, 1914:129 [type collection: Santa Anna da Chapada, Mato Grosso, Brazil, *Malme* 2438B (S, lectotype)].

*Parmelia coronata* f. *isidiosa* Müller Argoviensis, 1888:56 [type collection: Paraguay, *Balsana* 4157 (G, lectotype; BM, M, W, isoelectotypes)].

*Parmelia pseudocoronata* Gyelnik, 1931:289 [based on *P. coronata* f. *isidiosa* Müller Argoviensis].

**DESCRIPTION.**—Thallus closely adnate on bark, olivaceous mineral gray in the herbarium, 2–3 cm broad; lobes sublinear, crowded, 0.5–1.5 mm wide; marginal bulbate cilia dense; upper surface plane, shiny, densely isidiate, the isidia initially erect and cylindrical but soon lobulate and dorsiventral, the procumbent lobules narrow, dichotomously branched; lower surface black, moderately branched, the rhizines simple to sparsely branched. Apothecia adnate, 1–3 mm in diameter, the rim coronate; spores 8, 4–6 × 8–10 µm.

**CHEMISTRY.**—Cortex K+ yellow, medulla C+ rose, KC+ red, P–, atranorin and gyrophoric acid.

**HABITAT.**—On trees in open forest.

**DISTRIBUTION.**—West Indies and South America.

**REMARKS.**—This small, fragile lichen is easily confused with *B. suffixa*, a more widespread species differing in lobule formation without isidia (Figure 1f) and lack of pycnidia on the apothecial rim. Both are rather rare and more collections are needed to decide on their exact relationship. My report of bicornute spores in West Indian material (*Hale*, 1971b:15) is probably incorrect, although I have not checked the specimen cited. The type of *Parmelia fungicola* definitely has ovoid spores; the type of *P. coronata* f. *isidiosa* has apothecia but no spores.

**SPECIMENS EXAMINED.**—See *Hale* (1971b:15) for records from Dominica and the Dominican Republic.

### *Bulbothrix goebelii*, new combination

FIGURE 4e,f

*Parmelia goebelii* Zenker in Goebel and Kunze, 1827:134 [type collection: "Auf officinellen Rinden," South America, without collector, (M, lectotype)].

*Parmelia papyrina* Fée, 1837:121 [type collection: tropical America, (G, lectotype)].

*Parmelia subdissecta* Nylander in Nylander and Crombie, 1883:51 [type collection: Tanjong, Malacca, *Maingay* (H, Nylander herbarium 35161, lectotype; BM, isoelectotype)].

*Parmelia granatensis* Nylander, 1885:613 [type collection:



- Socorro, Colombia, *Lindig* (H, Nylander herbarium 35170; BM, PC, islectotypes)].
- Parmelia scortella* Nylander, 1885:615 [type collection: Texas (FH-Tuck, lectotype; H, islectotype)].
- Parmelia addenda* Vainio, 1907:169 [type collection: Lem Dan, Koh Chang, Thailand, *Schmidt* X (C, lectotype; TUR, islectotype)].
- Parmelia acariospora* Zahlbruckner, 1909:169 [type collection: near Barra Mansa, Itapicirica, São Paulo, Brazil *Schiffner* (W, lectotype; US, islectotype)].
- Parmelia marginalis* Lynge, 1914:112 [type collection: Santa Anna de Chapada, Mato Grosso, Brazil, *Malme* 2393\*\*\*\* (S, lectotype)].
- Parmelia njalensis* Dodge, 1959:65 [type collection: Kori, Njala, Sierra Leone, *Deighton* M.5642 (BM, lectotype)].
- Bulbothrix papyrina* (Fée) Hale, 1974:480.
- Bulbothrix scortella* (Nylander) Hale, 1974:481.
- Bulbothrix subdissecta* (Nylander) Hale, 1974:481.

**DESCRIPTION.**—Thallus closely adnate on bark, fragile, whitish mineral gray to olive-buff, 2–8 cm broad; lobes sublinear-elongate, 0.5–1.5 mm wide, the margins often filiform-dissected; bulbate cilia dense, becoming apically branched; upper surface plane, dull to clearly maculate, moderately isidiate, the isidia simple or branched, erect, cylindrical, to 0.7 mm high, sometimes blackening apically; lower surface variable, dark brown to black, moderately to densely rhizinate, the rhizines pale brown, black with pale tips, or black and shiny, moderately to richly branched. Apothecia rare, adnate to sessile, 1–2 mm in diameter, the rim ecoronate (amphithecium rarely pycnidiate); spores 8, 4–6 × 8–10 µm.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C+ rose, KC+ red, P–, atranorin and gyrophoric acid.

**HABITAT.**—On trees and more rarely on rocks in primary or secondary forests at lower elevations.

**DISTRIBUTION.**—Pantropical.

**REMARKS.**—*Bulbothrix goebelii* is a widespread, rather variable species characterized by isidia, branched rhizines, and gyrophoric acid. The New World and African populations tend to be very uniform with a brown to blackening lower surface and richly branched, often pale rhizines, as noted by Zenker in his description. The thallus is usually shiny pale olivaceous mineral gray. While some Asian specimens have these same characteristics, others, as in the types of *Parmelia addenda* and *P. subdissecta* and most specimens collected in the lowland dipterocarp forests of the Philippines, have a somewhat smaller, whitish thallus with a

more consistently black lower surface and coarser, less branched rhizines. The amount of intergradation is so great, however, that I have decided to consider these extremes as part of a larger population. Apothecia are not common in either the New or Old World. Of 80 specimens preserved in US only 9 were fertile. Seven of these were ecoronate and two had immersed pycnidia on the amphithecium rather than strictly on the rim, much as in *B. viridescens*.

**SPECIMENS EXAMINED.**—United States: Tennessee, *Nakanishi* 436 (US); North Carolina, *Culberson* 5051, 5276, 7701, 18016 (DUKE), Ireland 4000 (US); South Carolina, *Culberson* 7801, 10284 (DUKE), *Hale* 7614, 7625, 16518, 16614, *Ravenel* (US); Georgia, *Hale* 21982, *Skorepa* 2924 (US); Florida, *Calkins* (FLAS), *Hale* 21838, *Rapp* (FLAS, US); Alabama, *Hale* 7006, 7197, 33919, 34025, 34102, *Pursell* 3916 (US); Mississippi, *Hale* 7916; Louisiana, *Hale* 34010, *Langlois* (US), *Thieret* 24616d (US), *Tucker* 7247 (US); Texas, *Hale* 5169, 33803, 33885. Mexico: Vera Cruz, *Hale* 19401, 19979, 21230. Guatemala: Baja Vera Paz, *Hale* 38350. Panama: Chiriquí, *Hale* 38874, *Maxon* 5128 (US). Haiti: Ouest, *Wetmore* 2669 (MSC), 2685 (MSC, US). Cuba: Pinar del Río, *Imshaug* 25291 (MSC); Oriente, *Imshaug* 24952 (MSC, US). Jamaica: *Imshaug* 14364 (MSC). Dominican Republic: La Vega, *Allard* 16829, 16830, 16847, 16857, 18032; Puerto Plata, *Wetmore* 3933 (US); Trujillo, *Allard* 17356A, 17357 (US). Puerto Rico: *Fink* 1411 (NY, US), *Britton* 750 (NY), *Heller* 293, 4338 (NY). Martinique: *Imshaug* 30496, 32597 (MSC). Venezuela: *Fendler* (FH); Distrito Federal, *Santesson* 6673 (S, US); Mérida, *Hale* 42752. Peru: San Martín, *Allard* 20701, 22581a (US). Brazil: Goiás, *Weddell* (P); Mato Grosso, *Malme* 2365 (S), 2435C (LD, S), 2509B (S, US), 2522F (S, UPS), 2545 (S); São Paulo, *Robert* (BM), *Schiffner* (W). Paraguay: *Balsan* 4176 (G). Chile: Valparaíso, *Santesson* 2970 (S). Union of South Africa: Cape Province, *Almborn* 1361 (LD), 1381 (LD, US). Thailand: *Schmidt* XXI (TUR, syntype of *Parmelia addenda* Vainio). Malaysia: Sabah, *Hale* 30359, 30365, 30598, 30599, 30600. Indonesia: Java, *Groenhart* 3243 (L, US). Taiwan: *Asahina* (TNS). Philippines: Agusan, *Hale* 24475, 24977, 25438; Basilan, *Hale* 24956; Cagayan, *Hale* 24411; Cavite, *Hale* 26839; Quezon, *Hale* 26915, 26918, 26983; Surigao del Sur, *Hale* 24699; Zamboanga del Sur, *Hale* 24314, 24776, 24824. New Guinea: *Bailey* (BM). New Hebrides: *Wilson* (H).

### *Bulbothrix hypocraea*

FIGURE 5a

- Bulbothrix hypocraea* (Vainio) Hale, 1974:480.
- Parmelia hypocraea* Vainio in Welwitsch, 1901:400 [type collection: Monino River, Huila, Angola, *Welwitsch* 32 pro parte (TUR, lectotype; BM, islectotype)].
- Parmelia continua* Lynge, 1914:109 [type collection: Buriti, Serra de Chapada, Mato Grosso, Brazil, *Malme* (S, lectotype)].



*Parmelia leptascea* Steiner and Zahlbruckner in Zahlbruckner, 1926:514 [type collection: Lake Victoria, Bakoba, Africa, Schröder 319 (W, lectotype)].

*Parmelia proboscidea* var. *saxicola* Cengia Sambo, 1938:380 [type collection: Mahulo, Kipengere, Tanzania, Eusebio 13 bis (FI, lectotype)].

*Bulbothrix continua* (Lyngby) Hale, 1974:480.

**DESCRIPTION.**—Thallus adnate on bark, pale mineral gray, turning deep olive-buff in the herbarium, 3–5 cm in diameter; lobes dichotomously or irregularly branched, sublinear-elongate, often crowded, 1–3.5 mm wide; margins smooth to more or less crenate, with conspicuous, short bulbate cilia; upper surface plane and smooth, shiny, usually distinctly maculate; lower surface pale to dark brown, moderately rhizinate, the rhizines thick, brown, usually darker than the lower surface, simple, about 1 mm long. Apothecia numerous, adnate, 1–5 mm in diameter, margins undulate, the amphithecium ecoronate, smooth; disc burnt umber; spores 8, 5–8 × 8–14  $\mu$ m.

**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow turning red, C–, KC–, P+ orange, atranorin and salazinic acid.

**HABITAT.**—On trees in semi-arid woodlands at mid-elevations.

**DISTRIBUTION.**—Brazil and Africa.

**REMARKS.**—This species is characterized by the rather coriaceous, nonisidiate thallus and the pale brown lower surface with brown rhizines. It may be considered as the parent morph of *B. tabacina*. Although *B. sensibilis* is superficially very similar, it differs in having a black lower surface.

**SPECIMENS EXAMINED.**—Brazil: Mato Grosso, *Malme* (US as a mixture with a specimen distributed as *Parmelia coronata*); Minas Gerais, *Warming* 265 (M); São Paulo, *Eiten* 2976B, 2976C (US), *Puiggari* 1217 (G). Uganda: Toro District, *Swinscow* 2U 5/3 (BM, US). Zaire: *Schmitz* 8069 (US). Angola: Bié, *Degelius* (Degelius herbarium); Huíla, *Degelius* (Degelius herbarium, US). Rhodesia: Höeg (TRH), *Schütte* 37 (LD, US), *Wild* 5806 (LD). Zambia: *Jellicoe* 50a (BM). Union of South Africa: Transvaal, *Wager* 1477 (LD).

### *Bulbothrix imshaugii*

FIGURE 5b

*Bulbothrix imshaugii* (Hale) Hale, 1974:480.

*Parmelia imshaugii* Hale, 1971a:31 [type collection: Montaña Compana, Valparaíso, Chile, *Imshaug* 36670 (MSC, holotype; US, isotype)].

**DESCRIPTION.**—Thallus adnate to loosely adnate

on bark, whitish ashy gray, 4–6 mm broad; lobes subirregular, 3–5 mm wide; upper surface plane to rugulose, shiny, maculate, becoming cracked with age, sorediate, the soralia laminal to sub-apical, diffuse, the soredia farinose (Figure 1d); lower surface black except for a brown zone at the tips, moderately to densely rhizinate, the rhizines black, shiny, simple. Apothecia substipitate, ecoronate, 2–4 mm in diameter; spores 8, 4 × 8  $\mu$ m.

**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow turning red, C–, KC–, P+ orange, atranorin and salazinic acid.

**HABITAT.**—On *Nothofagus* in open areas.

**DISTRIBUTION.**—Chile.

**REMARKS.**—This species has still not been collected outside of Chile. It is unlike any other species in the genus because of the production of laminal soredia.

**SPECIMENS EXAMINED.**—Chile: Curicó, *Mahu* 3545 (US); Valparaíso, *Rundel* 7308 (US).

### *Bulbothrix isidiza*

FIGURE 5c

*Bulbothrix isidiza* (Nylander) Hale, 1974:480.

*Parmelia isidiza* Nylander, 1884:130 [type collection: Serra Chella, Angola, *Newton* (H, lectotype)].

*Parmelia tiliacea* var. *hypoleuca* Müller Argoviensis, 1894:257 [type collection: Usambara, *Holst* 787 pro parte (G, lectotype)].

*Parmelia subglandulifera* Hue, 1899:144 [type collection: Madagascar, *Grandidier* (P, lectotype)].

*Parmelia recurvicens* Harmand, 1928:326 [type collection: Indochina, *Demange* 36 (P, lectotype)].

*Parmelia demangei* Harmand, 1928:327 [type collection: Indochina, *Demange* 37 (P, lectotype)].

*Parmelia subscortea* Asahina, 1957:99 [type collection: Keitau, Taiwan, *Asahina* 3324 (TNS, lectotype)].

*Parmelia gillettii* Dodge, 1959:86 [type collection: Libah Mele Mountain, Somalia, *Gillett* 4699 pro parte (BM, lectotype)].

**DESCRIPTION.**—Thallus adnate on bark or rock, yellowish glaucous to olive bluff, 5–10 cm in diameter; lobes subirregular to sublinear, 1–4 mm wide; bulbate cilia distinctly inflated; upper surface plane, continuous, faintly to distinctly maculate, densely isidiate, the isidia simple or branched; lower surface pale brown or darkening, moderately rhizinate, the rhizines simple, pale brown or darkening. Apothecia adnate, 1–3 mm in diameter, ecoronate; spores 8, 5–8 × 7–14  $\mu$ m.



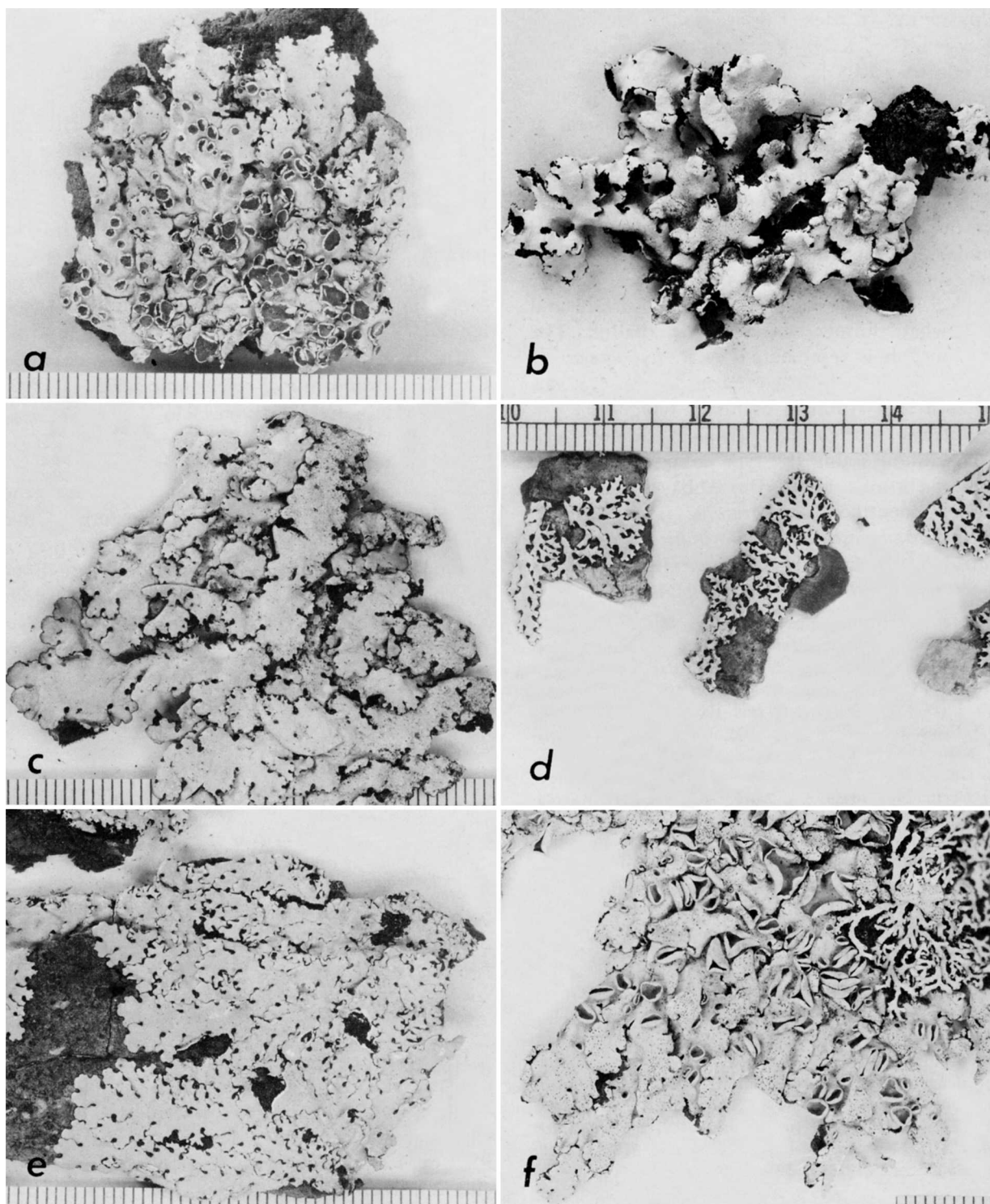


FIGURE 5.—Species of *Bulbothrix*: a, *B. hypocraea* (Degelius in US); b, *B. imshaugii* (isotype in US); c, *B. isidiza* (Hale 31756); d, *B. klementii* (holotype in US); e, *B. laevigatula* (Langlois 53 in US); f, *B. meizospora* (Stainton 4045 in US). (Scale in mm.)



**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow-red, C-, KC-, P+ pale orange, atranorin and salazinic acid.

**HABITAT.**—On trees (conifers and hardwoods) in pastures, cerrado woodland, and open areas at 100–2000 m elevation.

**DISTRIBUTION.**—Pantropical.

**REMARKS.**—*Bulbothrix isidiza* is especially common in Africa but also occurs widely in open secondary forests throughout the tropics. The lower surface is uniformly pale brown. Closely related *B. tabacina* has a black lower surface and a somewhat thinner, more fragile thallus. The parent morph is represented by *B. hypocraea*.

Dodge (1959:100) listed *Parmelia tiliacea* var. *hypoleuca* as a synonym of his *P. lythgoeana* (= *Hypotrachyna lythgoeana* (Dodge) Hale), evidently without seeing the type collection since *H. lythgoeana* is nonisidiate. Des Abbayes included a specimen identified as *Parmelia isidiza* in his *Lichenes Madagascarienses Borbonici Selecti Exsiccati* No. 10, but I have determined it to be *Parmelina wallichiana* (Taylor) Hale.

**SPECIMENS EXAMINED.**—Mexico: Chiapas, *Hale* 20170, 20184. Guatemala: Baja Vera Paz, *Hale* 38373. Brazil: Rio de Janeiro, *Ule* 6 (G); São Paulo, *Eiten* 2976C (US). Paraguay: *Balansa* 27 (G), 4176 (PC). Guinea: N'Zérékoré, *Santesson* 10562d (UPS). Ivory Coast: Man, *Santesson* 10616a (UPS). Uganda: East Mengo District, *Lye* L206 (BM, US); West Mengo District, *Swinscow* 2U 1/13 (BM, US). Kenya: Central Prov., *Maas Geesteranus* 4434 (L), 4435 (L, LD, US); Nyanza Prov., *Maas Geesteranus* 10935 (L). Zaire: *Höeg* (TRH). Angola: Bié, *Degelius* (Degelius herbarium, US); Huila, *Degelius* (Degelius herbarium); Moxico, *Degelius* (Degelius herbarium). Malawi: *Jellicoe* 32 (BM, US). Zambia: *Jellicoe* 44 (BM). Tanzania: *Höeg* (TRH). Rhodesia: *Höeg* (LD, TRH, US) *Kofler* (LD). Union of South Africa: Natal, *Almborn* 9642, 9767 (LD, US), *Höeg* (TRH); Transvaal, *Almborn* 6442 (LD), *Höeg* (TRH); Cape Prov., *Höeg* (TRH). Nepal: *Awasthi* 2179 (Awasthi herbarium), *Norkett* 7171 (BM), *Stainton* 3830 (BM). India: West Bengal, *Thomson* 49 (BM), *Togashi* (TNS, US); Maharashtra, *Hale* 43821, 43973; Tamil Nadu, *Hale* 40104, 43757. Malaya: Pahang, *Hale* 30098, 30113, 30209, 30501. Indonesia: Java, *Groenhart* 5678 (L). Philippines: Benguet, *Degelius* (Degelius herbarium, US). Japan: Prov. Bungo, *Kurokawa* 62284 (TNS); Prov. Izu, *Kurokawa* 58628 (TNS, US); Prov. Hyuga, *Hale* 29669, 29670. Tahiti: *Bouffon* (H). Hawaiian Islands: Kauai, *Hale* 31712, 31756; Maui, *Hale* 31247, 31273, 31532.

### *Bulbothrix klementii*, new species

FIGURE 5d

Thallus arcte adnatus, corticola, pallide

stramineo-albidus, 1–2 cm latus, lobis sublineari-bus, dichotome ramosis, separatis, margine conspicue bulbo-ciliatis, bulbis nitidis, orbicularibus, apice furcato-ciliatis, 0.6–1.1 mm latis; superne planus vel aetate transversim rimosus, nitidus, modice isidiatus, isidiis cylindricis, simplicibus; cortex superior 10–12  $\mu$ m crassus, cellulis plus minusve verticalibus, stratum gonidiale 14  $\mu$ m crassum, medulla alba, 80–95  $\mu$ m crassa, cortex inferior paraplectenchymatus, 11–12  $\mu$ m crassus; subtus pallide testaceus, dense rhizinosus, rhizinis pallidis, ca 24  $\mu$ m crassis, dichotome furcatis. Apothecia ignota.

**CHEMISTRY.**—Cortex K+ yellow, medulla K-, C-, P-, atranorin and colensoinic acid.

**HOLOTYPE.**—Cerro Pavón, Rio Atabapo, Venezuela, elevation 110 m, *K. Mägdefrau* 286, 13 February 1958 (M; isotype in US).

**REMARKS.**—This species has narrow lobes and densely branched bulbate cilia that form a mat around the edges of the lobes. The chemistry is unique in the genus: Colensoinic acid, identified by co-chromatography with *Hypotrachyna livida* (Taylor) Hale, is otherwise known only in *Stereocaulon* and *Hypotrachyna*. There are no close relatives in *Bulbothrix*. It is named in honor of Dr. Oscar Klement, who first saw the material at M and correctly placed it in the Parmeliaceae.

### *Bulbothrix laevigatula*

FIGURE 5e

*Bulbothrix laevigatula* (Nylander) Hale, 1974:480.

*Parmelia laevigatula* Nylander, 1885:614 [type collection: French Guiana, *Le Prieur* 504 (H, Nylander herbarium 35653, lectotype; PC, isoelectotype)].

*Parmelia hookeri* Taylor, 1847:169 [type collection: St. Vincent, *Guilding* (FH-Tayl, lectotype; BM, isoelectotype); not *Parmelia hookeri* (Borrer) Sprengel, 1827:282].

**DESCRIPTION.**—Thallus adnate on bark, whitish mineral gray, turning cream-buff in the herbarium, 4–9 cm in diameter; lobes irregularly branched, sublinear-elongate, 0.5–2 mm wide, the margins more or less crenate, with short marginal bulbate cilia less than 0.2 mm long, shiny, often apically branched, strongly inflated at the base; upper surface shiny, emaculate, isidiate, the isidia cylindrical, sometimes branched, less than 0.3 mm high; lower surface black, densely rhizinate, the rhizines



densely and finely branched, forming a woolly mat. Apothecia adnate, 1–5 mm wide, margins crenate and undulate, amphitheciium rugose, ecoronate, isidiate; spores 8, 3–4 × 5–7  $\mu$ m.

**HABITAT.**—On trees (conifers and hardwoods, *Pandanus*, bamboo, coconut) and more rarely on rocks in secondary forests from sea level to 3000 m elevation.

**DISTRIBUTION.**—United States, Mexico, West Indies, and South America.

**REMARKS.**—This isidiate species is one of the most common members of the genus in the West Indies and adjacent United States but it is rare in other parts of tropical America. The thallus is distinctly ashy white in comparison with gyrophoric acid-containing *B. goebelii* which is more greenish or olivaceous whitish gray. It is usually collected sterile, only 7 of 36 specimens in US bearing apothecia. Except for the somewhat broader lobes, *B. laevigatula* might be considered as the isidiate morph of *B. confoederata*, a small lichen endemic to the southeastern United States. The only other species in *Bulbothrix* with lecanoric acid, *B. bicornuta*, has bicornute spores.

**SPECIMENS EXAMINED.**—United States: South Carolina, *Hale* 7624; Georgia, *Hale* 16767, 16769, *Skorepa* 3113 (US); Alabama, *Hale* 33796, 33977, 33980, *McCullough* 1193 (US); Florida, *Hale* 16731, 17742, 17745, 21695, 34117, 34180, *Thomson* 4457 (US, WIS) (for additional records from Florida see Moore, 1968:221); Mississippi, *Langlois* 53 (US). Mexico: Vera Cruz, *Hale* 19833. Cuba: Pinas Del Rio, *Imshaug* 25233 (MSC, US). Jamaica: *Imshaug* 13877 (MSC, US), 14306, 14319, 15791 (MSC), 15952 (MSC, US), 16040, 16250 (MSC). Dominican Republic: *Hassler* (WIS); Cordillera Central, *Imshaug* 23759 (MSC, US); La Vega, *Allard* 15992a, 16548a (US); Santiago, *Imshaug* 23862 (MSC, US), *Wetmore* 3883 (MSC); Trujillo, *Allard* 17356 (US). St. Lucia: *Evans* 71, 83 (FH, US), *Imshaug* 29724, 29991 (MSC). Dominica: *Hale* 35411, 35687. St. Vincent: *Imshaug* 30468, 30729 (MSC). Grenada: *Imshaug* 16234 (MSC). Tobago: *Imshaug* 31388, 31555 (MSC). Trinidad: *Hale* 38206, *Imshaug* 32405, 32431 (MSC). Colombia: Santander, *Killip and Smith* 18075 (US). Venezuela: Mérida, *Hale* 42754. Peru: Churubamba, *Mexia* 8245a (S); San Martín, *Allard* 22256b (US). Ecuador: Galapagos, *Weber* 191 (COLO). Brazil: Rio de Janeiro, *Eiten* 7079 (US), *Schindler* 4577a (US).

### *Bulbothrix meizospora*

FIGURE 5f

*Bulbothrix meizospora* (Nylander) Hale, 1974:480.  
*Parmelia tiliacea* var. *meizospora* Nylander, 1860:383 [type

collection: Nilgherries Mountains, India (H, Nylander herbarium 35107, lectotype)].

*Parmelia meizospora* (Nylander) Nylander, 1869:292.

*Parmelia amplexens* Stirton, 1877-78:201 [type collection: Nilgherries Mountains, India, *Watt* (BM, lectotype; GLAM, isolectotype)].

**DESCRIPTION.**—Thallus adnate on bark, pale glaucous-green, turning olive-buff in the herbarium, 5–8 mm broad; lobes irregularly branched to sublinear-elongate, 1.5–5 mm wide, the margins crenate, with sparse short bulbate cilia; upper surface plane and smooth, more or less shiny, faintly maculate; lower surface black, dark brown and papillate in a broad or narrow zone near the tips, densely to moderately rhizinate, the rhizines brown to black, simple. Apothecia numerous, adnate, 2–8 mm in diameter, ecoronate, amphitheciium more or less wrinkled; disc vandyke-brown; spores 8, 7–11 × 14–21  $\mu$ m.

**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow turning red, C–, KC–, P+ orange, atranorin and salazinic acid.

**HABITAT.**—On trees (rarely on rocks) in open woodlands.

**DISTRIBUTION.**—Africa, Pakistan, Nepal, and India.

**REMARKS.**—This Asian species is rather variable in lobe width and spore size with a close relationship to *B. setschwanensis*, which has a uniformly pale brown lower surface and occurs at higher elevations in the Himalayan region. *Bulbothrix meizospora* has a broader distribution although it too grows at elevations of 2000 m and higher.

**SPECIMENS EXAMINED.**—Cameroon: *Rutherford* 22 (BM). Pakistan: *Iqbal* 828, 835, 844 (US). Nepal: *Banerjee* 1403 (Awasthi herbarium), *Norkett* 5306 (BM, US), 7890, 8231 (BM), *Stainton* 4045 (BM, US). India: Assam, *Blott* (Awasthi herbarium); Sikkim; *Hara* (TNS), *Togashi* (TNS); Uttar Pradesh, *Awasthi* 474, 897, 2683, 3443, 3798 (Awasthi herbarium), *Degelius* AslII (Degelius herbarium, US), *Höeg* 3390, 3403 (Awasthi herbarium), *Stewart* 12298 (NY, US); Tamil Nadu, *Hale* 43877.

### *Bulbothrix pigmentacea*

FIGURE 6a

*Bulbothrix pigmentacea* (Hale) Hale, 1974:480.

*Parmelia pigmentacea* Hale, 1968:325 [type collection: Pagbilao, Sierra Madre, Luzon, Philippines, *Hale* 26895 (US, holotype)].



**DESCRIPTION.**—Thallus closely adnate on bark, thin and fragile, whitish mineral gray, 1–2 cm broad; lobes linear, discrete, 0.5–1.0 mm wide, the margins densely bulbate ciliate, the bulbae apically branched; upper surface plane, shiny, moderately isidiate, the isidia simple, to 0.1 mm high; lower surface black, densely rhizinate, the rhizines dichotomously branched. Apothecia unknown.

**CHEMISTRY.**—Cortex K+ yellow, medulla negative with color reagents, atranorin only present with an unknown red pigment in the rhizines and lower cortex.

**HABITAT.**—On canopy branches of trees in lowland evergreen rain forest from sea level to 300 m elevation.

**DISTRIBUTION.**—Philippines and Malaya.

**REMARKS.**—This is the only species of *Bulbothrix* present in the virgin lowland forests of Southeast Asia. The pigment in the lower cortex and rhizines is exposed when the thallus is cut with a razor blade for cross sections. This unknown pigment and the very narrow lobes would separate it from superficially similar *B. goebelii*. There are no closely related species nor a parent morph.

**SPECIMENS EXAMINED.**—See Hale (1968) for localities in the Philippines and Malaya.

### *Bulbothrix pustulata*

FIGURE 6b

*Bulbothrix pustulata* (Hale) Hale, 1974:480.

*Parmelia pustulata* Hale in Hale and Kurokawa, 1964:140 [type collection: Urundi, Africa, *Deuse* (US, holotype)].

**DESCRIPTION.**—Thallus adnate to loosely adnate on bark, light mineral gray, 6–10 cm broad; lobes more or less subirregular, subrotund, 4–6 mm wide; bulbate cilia moderate, distinctly inflated; upper surface plane to rugose, continuous, moderately isidiate-pustulate (Figure 1e), soredia absent; lower surface black and moderately rhizinate except for a narrow papillate or naked brown zone along the margins, the rhizines simple. Apothecia rudimentary, sessile, to 1.5 mm in diameter; spores not found.

**CHEMISTRY.**—Cortex K + yellow, medulla K + yellow turning red, C–, KC–, P+ pale orange, atranorin and salazinic acid.

**HABITAT.**—On trees in open forest.

**DISTRIBUTION.**—Africa.

**REMARKS.**—This is the only species in *Bulbothrix* with pustules. These are typical pustules, erupting and fragile but without soredial formation. The thallus, although broad lobed, is quite membranous. There is no extant parent or other comparable species in the genus. It is still known only from the type collection.

### *Bulbothrix schiffneri*

FIGURE 6c

*Bulbothrix schiffneri* (Zahlbruckner) Hale, 1974:481.

*Parmelia schiffneri* Zahlbruckner, 1909:167 [type collection: Barra Mansa, Itapepicirica, São Paulo, Brazil, *Schiffner* (W, lectotype)].

**DESCRIPTION.**—Thallus closely adnate on bark and mosses, light mineral gray, 1–2 cm broad; lobes dichotomously branched, sublinear, 0.3–0.5 mm wide, the margins densely bulbate ciliate, the bulbae becoming apically branched; upper surface plane, shiny; lower surface black, densely rhizinate, the rhizines moderately to densely branched. Apothecia numerous, adnate, 1–1.5 mm in diameter, the amphitheciium coronate; spores 8, 5 × 12 µm, bicornute with short upturned tips.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C+ rose, KC+ red, P–, atranorin and gyrophoric acid.

**HABITAT.**—On trees in cerrado vegetation.

**DISTRIBUTION.**—Brazil.

**REMARKS.**—This very small lichen is quite similar to *B. semilunata* and is separated from it essentially by the presence of gyrophoric acid. It is still known only from the type collection.

### *Bulbothrix semilunata*

FIGURE 6d

*Bulbothrix semilunata* (Lynge) Hale, 1974:479.

*Parmelia semilunata* Lynge, 1914:23 [type collection: Buriti, Serra da Chapada, Mato Grosso, Brazil, *Malme* (S, lectotype)].

**DESCRIPTION.**—Thallus closely appressed on bark, whitish mineral gray, 1.0–1.5 cm broad; lobes sublinear, 0.2–0.3 mm wide, the marginal bulbate cilia with a branched, ciliate tip; upper surface plane, smooth; lower surface black, moderately



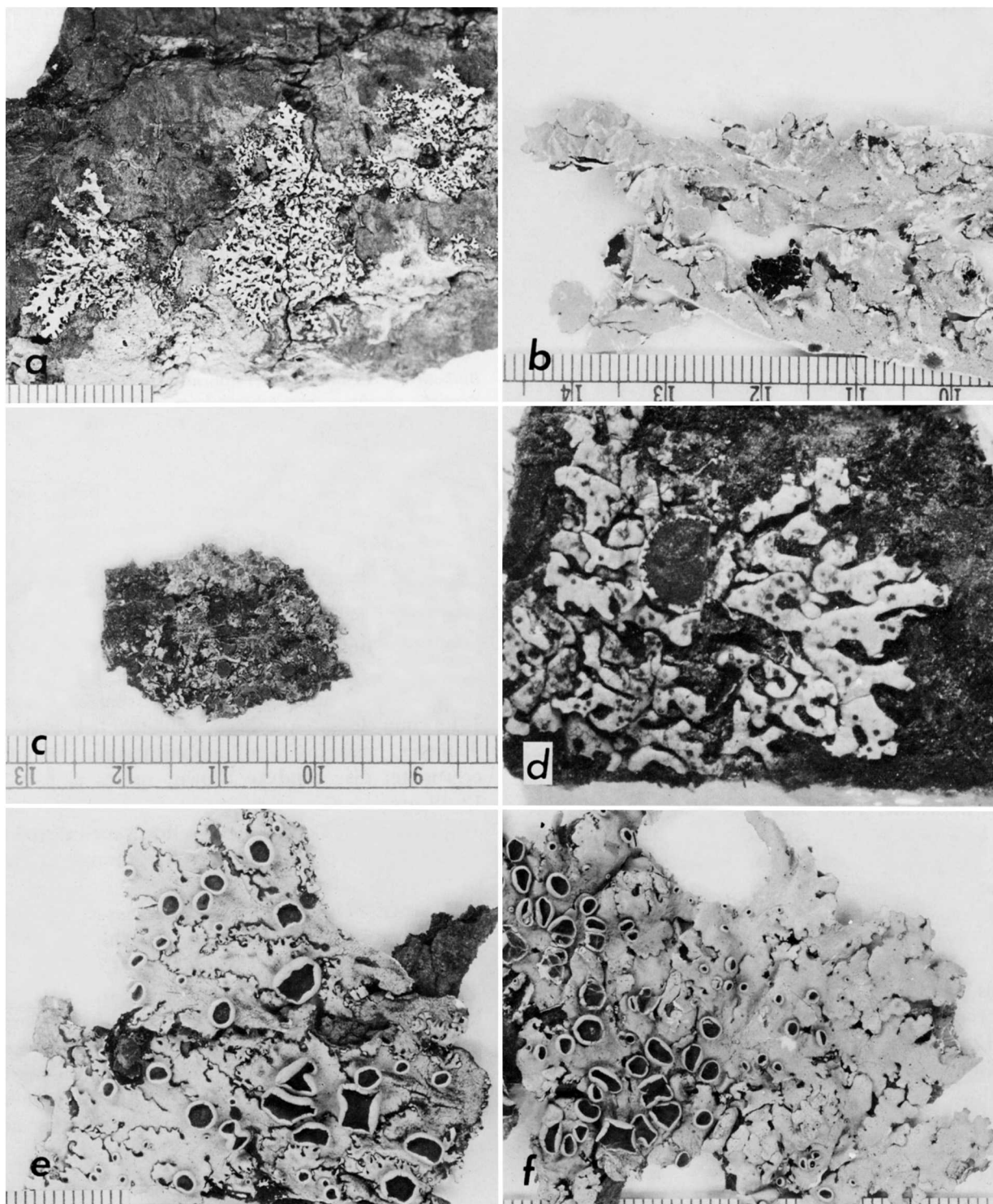


FIGURE 6.—Species of *Bulbothrix*: a, *B. pigmentacea* (holotype in US); b, *B. pustulata* (holotype in US); c, *B. schiffneri* (lectotype in W); d, *B. semilunata* (Malme in US) ( $\times 10$ ); e, *B. sensibilis* (des Abbayes in US); f, *B. setschwanensis* (Awasthi 3316 in US). (Scale in mm.)



rhizinate, the rhizines branched. Apothecia numerous, adnate, about 1 mm in diameter; spores 8, semi-lunate or cornute,  $2-3 \times 9-12 \mu\text{m}$ .

CHEMISTRY.—Cortex and medulla negative with color tests, only skyrin present.

HABITAT.—On trees in cerrado vegetation.

DISTRIBUTION.—Brazil.

REMARKS.—This species is extremely close to *B. schiffneri* in thallus size and lobation. It would be differentiated by the C negative reaction in the medulla and the narrower, more semi-lunate spore outline. Neither species has been collected outside its type-locality.

SPECIMENS EXAMINED.—Brazil: Mato Grosso, *Malme* (US) (discovered as a mixture in a specimen distributed as "*Parmelia coronata*" and probably part of the type collection).

### *Bulbothrix sensibilis*

FIGURE 6e

*Bulbothrix sensibilis* (Steiner and Zahlbruckner) Hale, 1974: 481.

*Parmelia sensibilis* Steiner and Zahlbruckner in Zahlbruckner, 1926:522 [type collection: Bura, British East Africa, *Schröder* 285 (W, lectotype)].

DESCRIPTION.—Thallus adnate on bark, pale olive-buff to pale olive-gray, turning deep olive-buff in the herbarium, rather coriaceous, 4–10 cm in diameter; lobes irregularly branched, more or less imbricate, 1.5–5 mm wide, the margins more or less crenate; bulbae rather sparse, shiny, simple; upper surface more or less shiny, very faintly to moderately maculate, irregularly rugose and cracked on older lobes; lower surface black, densely rhizinate, the rhizines black, simple. Apothecia adnate, 2–6 mm in diameter, the margins more or less undulate, the amphithecium ecoronate, rugose; disc warm-sepia; spores 8,  $5-12 \times 7-18 \mu\text{m}$ .

CHEMISTRY.—Cortex K+ yellow, medulla K+ yellow turning red, C–, P+ orange, atranorin and salazinic acid.

HABITAT.—On trees in open woodlands at 500–2000 m elevation.

DISTRIBUTION.—Venezuela and Africa.

REMARKS.—*Bulbothrix sensibilis* resembles *B. hypocraea* closely in overall appearance but has a distinctly black lower surface. Both have a South

America–Africa distribution pattern, *B. sensibilis* being the much rarer of the two species. It is or would fall very close to the parent morph of *B. tabacina*.

SPECIMENS EXAMINED.—Venezuela: Táchira, *Hale* 45727. Guinea: *des Abbayes* (US). Zaire: *Höeg* (TRH). Malawi: *Brass* 17788 (US). Zambia: *Jellicoe* 52 (BM). Angola: *Benguela*, *Degelius* (*Degelius* herbarium); Bié, *Degelius* (*Degelius* herbarium, US).

### *Bulbothrix setschwanensis*

FIGURE 6f

*Bulbothrix setschwanensis* (Zahlbruckner) Hale, 1974:481.

*Parmelia setschwanensis* Zahlbruckner, 1930:184 [type collection: Otang, Kwapi, Setchwan, China, *Handel-Mazzetti* 2739 (WU, lectotype)].

DESCRIPTION.—Thallus adnate on bark, light mineral gray but turning dark olive-buff in the herbarium, 5–10 cm in diameter; lobes irregularly branched, sublinear-elongate, 2–5 mm wide, the margins crenate with sparse short black bulbate cilia; upper surface plane and smooth, more or less shiny, not maculate, irregularly wrinkled on older lobes; lower surface pale brown, densely rhizinate, the rhizines pale brown, coarse, simple, 1–1.5 mm long. Apothecia adnate, 1–4 mm in diameter, margins and amphithecium smooth, ecoronate; disc vandyke brown; spores 8,  $6-9 \times 12-19 \mu\text{m}$ .

CHEMISTRY.—Cortex K+ yellow, medulla K+ yellow turning red, C–, KC–, P+ orange, atranorin and salazinic acid.

HABITAT.—On trunks and branches of trees in open forests at 2000 m elevation or higher.

DISTRIBUTION.—India, Nepal, and China.

REMARKS.—This species is endemic to the Himalayan region and adjacent China. It has a large coriaceous thallus, very similar to that of *B. meizospora* (see above), which has a blackening lower surface. These two species may indeed prove to be synonymous when careful field studies are conducted.

SPECIMENS EXAMINED.—India: Uttar Pradesh, *Awasthi* 3316 (*Awasthi* herbarium, US); West Bengal, *Togashi* (TNS). Nepal: *Awasthi* 2216 (*Awasthi* herbarium). China: Szechuan, *Handel-Mazzetti* 2017 (W, syntype of *Parmelia setschwanensis* Zahlbruckner).



*Bulbothrix subcoronata*

FIGURE 7a

*Bulbothrix subcoronata* (Müller Argoviensis) Hale, 1974:481.  
*Parmelia subcoronata* Müller Argoviensis, 1887a:135 [type collection: South America (G, lectotype)].

**DESCRIPTION.**—Thallus closely adnate on bark, buff mineral gray but turning pale to deep olive-buff in the herbarium, 3–5 cm in diameter; lobes irregularly branched, sublinear-elongate, 1–3 mm wide, the margins more or less crenate, with moderate short bulbate cilia; upper surface plane and smooth, shiny, slightly to moderately maculate; lower surface brown, moderately rhizinate, the rhizines brown to dark brown, simple. Apothecia adnate, 1–4 mm in diameter, the margins undulate, the amphitheciium coronate; disc verona-brown; spores 8, 5–6 × 7–11 µm.

**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow turning red, C–, KC–, P+ orange, atranorin and norstictic acid.

**HABITAT.**—On trunks and branches of trees in open woodland at lower elevations.

**DISTRIBUTION.**—South America.

**REMARKS.**—This is a rare South American species, occurring apparently in cerrado forests. It is easily recognized by the presence of norstictic acid. Without a chemical test it might be mistaken for *B. hypocraea*, an ecoronate species with salazinic acid. Müller reported smaller spores (to 5 µm long) in the original description, but all the specimens I examined had larger spores as indicated.

**SPECIMENS EXAMINED.**—Brazil: Goiás, Irwin 31977 (NY, US); Mato Grosso, Malme 2271Ba (as a mixture with *Parmelia silvatica*) (S), 2511Ba (S); Rio de Janeiro, Glaziou 1825 (UPS). Paraguay: Handel (G), Kuntze 42 (NY), Kuntze (G), Balansa 4210 (C). Argentina: Misiones, Montes 10060 (MVM, US).

*Bulbothrix subinflata*

FIGURE 7b

*Bulbothrix subinflata* (Hale) Hale, 1974:481.  
*Parmelia subinflata* Hale, 1965b:201 [type collection: 50 miles south of Fabrica, Negros Occidentalis, Philippines, Hale 26641 (US, holotype; TNS, UPS, isotypes)].

**DESCRIPTION.**—Thallus closely adnate on bark, mineral gray, 4–7 cm broad, lobes short, sublinear, 1–2 mm wide, marginally bulbate, the bulbae not

strongly inflated; upper surface shiny, emaculate or faintly maculate, becoming rugose with age, moderately isidiate, the isidia simple to sparsely branched, cylindrical, 0.1–0.2 mm high; lower surface pale brown, moderately rhizinate, the rhizines brown or darkening, simple. Apothecia rare, adnate, to 1 mm in diameter, ecoronate; mature spores not seen.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C–, KC+ rose or KC–, P+ red, atranorin and protocetraric acid.

**HABITAT.**—On branches of evergreen hardwoods in mid-elevation rain forest at 300–1800 m elevation.

**DISTRIBUTION.**—Philippines and Malaysia.

**REMARKS.**—*Bulbothrix subinflata* is the only species outside of *B. pigmentacea* which has evolved in the rain forests of Southeast Asia. It occurs at higher elevations than *B. pigmentacea*, for the most part in cloud forest. The marginal bulbae are not strongly inflated, as with *B. chowoensis*, a broader lobed African species which also contains protocetraric acid.

**SPECIMENS EXAMINED.**—See Hale (1965:201) for localities in the Philippines and Malaysia.

*Bulbothrix suffixa*

FIGURE 7c,d

*Bulbothrix suffixa* (Stirton) Hale, 1974:481.  
*Parmelia suffixa* Stirton, 1877-78:299 [type collection: Knysna, Union of South Africa, Knobel (BM, lectotype; GLAM, isolectotype)].

**DESCRIPTION.**—Thallus closely adnate on bark, fragile, whitish mineral gray, 2–6 cm broad; lobes dichotomously branched, sublinear, 0.5–1.5 mm wide, the margins more or less crenate; bulbate cilia dense, the bulbils shiny, inflated, often apically branched; upper surface plane and smooth, shiny, becoming densely lobulate, the lobules dorsiventral, oblong to spatuliform, marginally bulbate-ciliate (Figure 1f); lower surface black moderately rhizinate, the rhizines black, shiny, dichotomously branched. Apothecia adnate, the amphitheciium becoming lobulate, the rim crenate, coronate; spores 8, 3–5 × 6–12 µm.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C+ rose, KC+ red, P–, atranorin and gyrophoric acid (or if C– no substances present in medulla).



**HABITAT.**—On trees in open areas along trails and roads at up to 2400 m elevation.

**DISTRIBUTION.**—Tropical America and South Africa.

**REMARKS.**—*Bulbothrix suffixa* is characterized by the production of dorsiventral lobules with dense marginal bulbate cilia (Figure 1f). There are no isidia. It has the same chemistry as *B. fungicola*, which is predominantly isidiate and isidiate-lobulate (Figure 3d). As with other small species of *Bulbothrix*, it is not well represented in herbaria and may be subject to revision by future workers. Some specimens are C negative and lack gyrophoric acid but are morphologically identical with the C+ population. I am recognizing these for the present as an acid-free phase.

**SPECIMENS EXAMINED** (gyrophoric acid).—Guatemala: Baja Vera Paz, *Hale* 38376. Honduras: Comayagua, *Standley and Chacón* 5830 (US). Cuba: *Wright* 75 (UPS, US); Pinar del Rio, *Imshaug* 23354 (MSC). Dominican Republic: Santiago, *Imshaug* 23854, *Wetmore* 3881 (MSC). Jamaica: *Imshaug* 15111 (MSC). St. Lucia: *Imshaug* 29820 (MSC). Dominica: *Imshaug* 32758, 32760, 32762 (MSC). Venezuela: Mérida, *Hale* 42257a, 42565d. Union of South Africa: Cape Province, *Almborn* 3444, 3971 (LD), 3961 (LD, US). Mauritius: *Vaughan* 6 (BM).

**SPECIMENS EXAMINED** (lacking gyrophoric acid).—Dominica: *Imshaug* 33330 (MSC). Trinidad: *Imshaug* 32078, 32088 (MSC). Venezuela: Mérida, *Hale* 42753.

### *Bulbothrix tabacina*

FIGURE 7e

- Bulbothrix tabacina* (Montagne and Bosch) Hale, 1974:481.  
*Parmelia tabacina* Montagne and Bosch in Montagne, 1856: 327 [type collection: Java, *Junghuhn* (L, lectotype; P, isotype)].  
*Parmelia meizospora* f. *isidiosa* Müller Argoviensis, 1884:620 [nomen nudum].  
*Parmelia ochrovestita* Zahlbruckner, 1928:200 [type collection: Botanical Garden, Bogor, Java, *Overeem* 335 (W, lectotype)].  
*Parmelia meizosporoides* Dodge, 1959:83 [type collection: Imerina, Andrangolaoka, Madagascar, *Hildebrandt* (FH, lectotype)].  
*Parmelia sublaevigatoides* Dodge, 1959:88 [type collection: Mt. Eglon, Uganda (BM, lectotype)].

**DESCRIPTION.**—Thallus adnate to closely adnate on bark, rarely on rock, 4–7 cm in diameter; lobes sublinear to subirregular, 1.5–5 mm wide; bulbate cilia large, conspicuously inflated; upper surface

plane, faintly to moderately maculate, sparsely isidiate, the isidia mostly simple, less than 0.5 mm high; lower surface black, shiny, moderately rhizinate except for a narrow papillate or naked zone along the margins, the rhizines mostly simple. Apothecia adnate, 1.5–4 mm in diameter, the amphithecium ecoronate, isidiate; spores 8, 5–8 × 9–15 µm.

**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow turning red, C–, KC–, P+ orange, atranorin, salacinic acid, and consalazinic acid.

**HABITAT.**—On trees (hardwoods and conifers) or rarely on rocks in open woodland and pastures at sea level to over 2000 m elevation.

**DISTRIBUTION.**—Pantropical.

**REMARKS.**—This isidiate species is one of the most commonly collected members of the genus. The lower cortex is black in contrast to that of *B. isidiza*, which is uniformly pale brown and has a somewhat more robust thallus. It may also be confused with *B. laevigatula*, which has dichotomously branched rhizines, a white cast to the thallus, and lecanoric acid (medulla C+ red). It is the only species of *Bulbothrix* so far discovered in Australia.

Zahlbruckner (1928:174) saw a “type specimen” in M and considered it to be close to *Parmelia cetrata* (= *Parmotrema cetratum* (Acharius) Hale, an amphigymnioid lichen with marginal cilia). Dodge (1959:83) cited *Parmelia meizospora* f. *isidiosa* Müller Argoviensis as a synonym of *Parmelia meizosporoides* Dodge, but Müller's name is a nomen nudum without a description or designated type.

**SPECIMENS EXAMINED.**—Mexico: Vera Cruz, *Hale* 19475; Chiapas, *Hale* 21067 (US), 20122 (S, US). Cuba: Oriente, *Hioram* 5887 (US). Jamaica: *Imshaug* 16014 (MSC). Haiti: Ouest, *Imshaug* 22619 (MSC). Dominican Republic: La Vega, *Allard* 18169, 18172 (US). Tobago: *Imshaug* 31332 (MSC). Venezuela: Distrito Federal, *Ernst* (G); Mérida, *Hale* 42514a; Miranda, *Dennis* 1524A (BM); Táchira, *Hale* 45724. Brazil: São Paulo, *Osorio* 4920 (MVM). Guinea: N'Zérékoré, *Santesson* 10516a (UPS, US), 10507, 10573b, 10594b (UPS). Angola: Cuanza Norte, *Degelius* (Degelius herbarium). Tanzania: *Santesson* 23409, 23422 (UPS). Union of South Africa: Natal, *Höeg* (TRH); Transvaal, *Almborn* 6546 (LD, US). India: Uttar Pradesh, *Mehra* 9 (US). Nepal: *Poelt* 117 (M). Malaya: Pahang, *Hale* 30134; Selangor, *Hale* 31182, 31183, *Maingay* (BM). Philippines: Leyte, *Edano* 16051, 16053 (US); Agusan, *Hale* 25052. Indonesia: Java, *Groenhart* 4356 (L, US), *Neervoert* 926, 1414 (BOR), *Overeem* 676 (BOR), *van Steenis* 5597 (BOR); Sumatra, *Groenhart* 9098 (BOR). Tai-



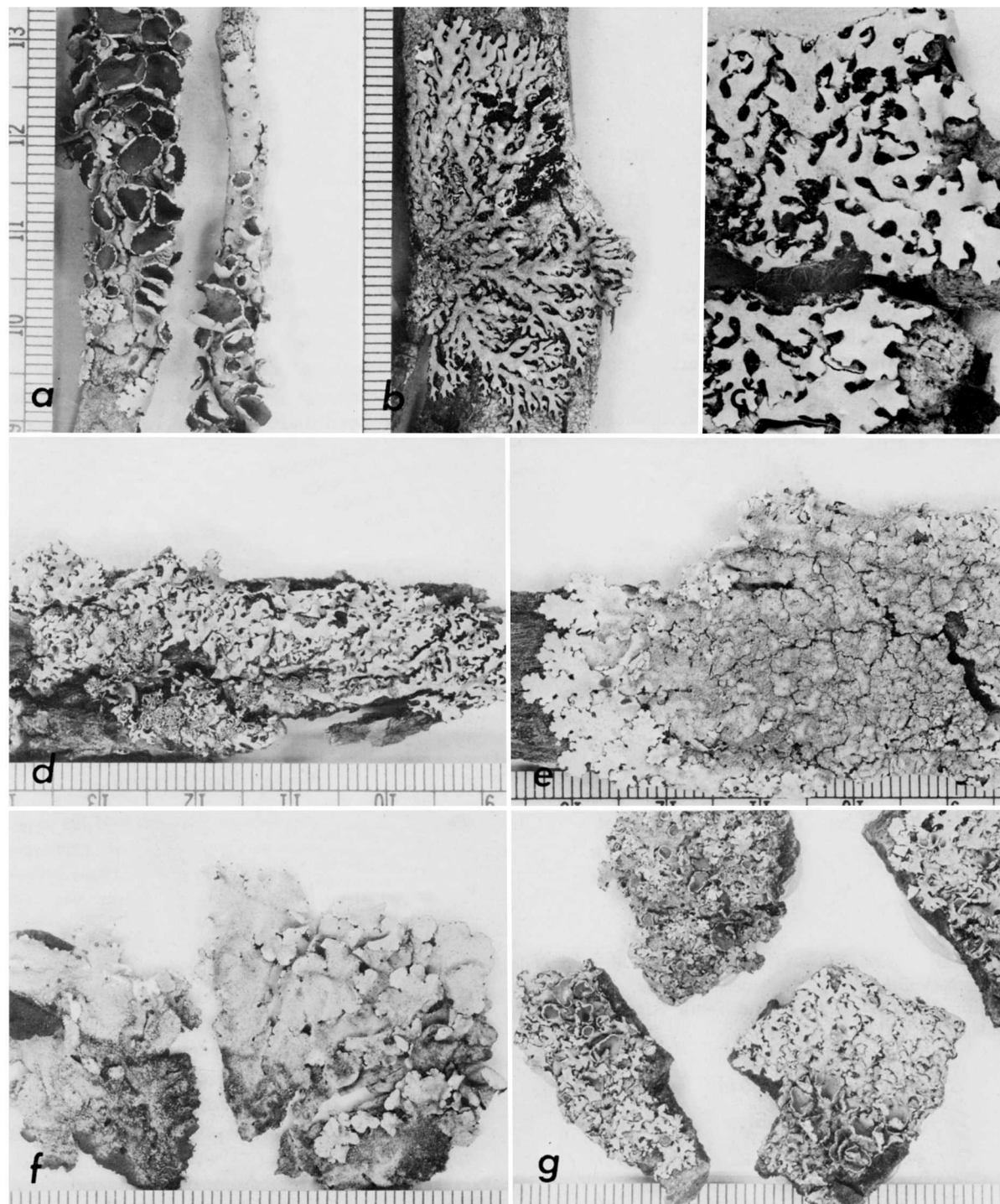


FIGURE 7.—Species of *Bulbothrix*: a, *B. subcoronata* (Montes 10060 pro parte in US); b, *B. subinflata* (Hale 33711); c, *B. suffixa* (lectotype in BM) ( $\times 4$ ); d, *B. suffixa* (Almborn 3961 in US); e, *B. tabacina* (Kurokawa 2730 in US); f, *B. ventricosa* (Hale 43080); g, *B. viridescens* (Imshaug 42530 in US). (Scale in mm.)



wan: Kurokawa 1299, 1363, 2818, 2932 (TNS). Australia: Queensland, Bailey 32 (BM).

### *Bulbothrix ventricosa*

FIGURE 7f

*Bulbothrix ventricosa* (Hale and Kurokawa) Hale, 1974:481.

*Parmelia ventricosa* Hale and Kurokawa, 1964:140 [based on *P. isidiza* var. *domingensis* Vainio].

*Parmelia isidiza* var. *domingensis* Vainio, 1915:17 [type collection: La Cumbra, Dominican Republic, *Raunkiaer* 492 (TUR, lectotype; C, isoelectotype)].

DESCRIPTION.—Thallus adnate on bark, pale glaucous green, 3–5 cm broad; lobes subirregular, 1–5 mm wide, the margins crenate; bulbate cilia distinctly inflated; upper surface plane, shiny, faintly maculate, moderately isidiate, the isidia fine, simple; lower surface black, moderately rhizinate, the rhizines black, mostly simple. Apothecia adnate, 2–3 mm in diameter, the exciple corolate; spores 8, 7–8 × 13–17  $\mu$ m.

CHEMISTRY.—Cortex K+ yellow, medulla K+ yellow turning red, C–, KC–, P+ orange, atranorin and norstictic acid.

HABITAT.—On trunks and branches of trees in open primary cloud forest or secondary forest at 900–2600 m elevation.

DISTRIBUTION.—Mexico, Central America, Venezuela, and Union of South Africa.

REMARKS.—*Bulbothrix ventricosa* occurs chiefly in higher elevation cloud forests in tropical America, although there is a disjunct record from South Africa. While it would appear to be related to *B. subcoronata* because of the presence of norstictic acid, it has much broader lobes and a black lower surface. No parent morph is extant.

SPECIMENS EXAMINED.—Mexico: Chiapas, Hale 20166. Costa Rica: Cartago, Flenniken (US). Panama: Chiriquí, Hale 38763, Nakanishi (US). Venezuela: Mérida, Hale 43080; Táchira, Hale 45727a. Union of South Africa: Transvaal, Almborn 6813 (LD).

### *Bulbothrix viridescens*

FIGURE 7g

*Bulbothrix viridescens* (Lynge) Hale, 1974:481.

*Parmelia viridescens* Lynge, 1914:117 [type collection: Santa Anna da Chapada, Mato Grosso, Brazil, *Malme* 2453 (S, lectotype; W, isoelectotype)].

*Parmelia marginalis* var. *laeviuscula* Räsänen, 1947:45 [type collection: Canelones, Carrasco National Park, Uruguay, *Lamb* 3081 (H, lectotype)].

DESCRIPTION.—Thallus closely adnate, corticolous, pale buff or olivaceous ashy, 3–5 cm broad; lobes sublinear, contiguous to imbricate, 1–2 mm wide, the marginal bulbate cilia distinct, round, becoming apically ciliate; upper surface shiny, plane to distinctly rugulose, becoming heavily pycnidiate; lower surface dark brown or blackening, moderately rhizinate, the rhizines pale brown or darkening, simple or branched. Apothecia numerous, sessile to substipitate, the amphithecium and rim pycnidiate (Figure 1g); spores 8, 4 × 6  $\mu$ m.

CHEMISTRY.—Cortex K+ yellow, medulla negative with color tests, atranorin only present.

REMARKS.—This is one of the few species of *Bulbothrix* lacking any medullary substances. It is a rare lichen with a limited range in Brazil and Uruguay but with more careful collecting should eventually be found in adjacent countries.

SPECIMENS EXAMINED.—Uruguay: Floresta, *Herter* 61467 (S); Montevideo, *Imshaug* 42530 (MSC, US).

### Nomen Inquirendum

*Parmelia stenophylla* Müller Argoviensis 1893:128 [type collection: Boruca, Costa Rica, *Pittier* 5434 (G, lectotype)].

*Parmelia stenophyllizans* Zahlbruckner, 1929:75 [based on *Parmelia stenophylla* Müller Argoviensis, not "*Parmelia stenophylla* (Acharius) Heugel"].

The material in G is fragmentary and sterile but has distinct apically branched bulbate cilia. The thallus lacks isidia, the lobes are 0.17–0.25 mm wide, the medulla reacts C–, KC–, and the lower surface is black with branched rhizines. It is very close to or the same as either *B. schiffneri* or *B. semilunata*, but a positive identification cannot be made without apothecia.



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# Index

(Synonyms in *italics*)

*Bulbothrix affixa*, 9  
*apophysata*, 9  
*atrichella*, 10  
*bicornuta*, 11  
*bulbochaeta*, 11  
*chowoensis*, 11  
*confoederata*, 12  
*continua*, 16  
*coronata*, 12  
*decurtata*, 14  
*fungicola*, 14  
*goebelii*, 14  
*hypocraea*, 15  
*imshaugii*, 16  
*isidiza*, 16  
*klementii*, 18  
*laevigatula*, 18  
*meizospora*, 19  
*papyrina*, 15  
*pigmentacea*, 19  
*pustulata*, 20  
*schiffneri*, 20  
*scortella*, 15  
*semilunata*, 20  
*sensibilis*, 22  
*setschwanensis*, 22  
*subcoronata*, 23  
*subdissecta*, 15  
*subinflata*, 23  
*suffixa*, 23  
*tabacina*, 24  
*ventricosa*, 26

*viridescens*, 26  
*Hypotrachyna livida*, 18  
*lythgoeana*, 18  
*Parmelia acariospora*, 15  
*addenda*, 15  
*affixa*, 9  
*apophysata*, 9  
*appressa*, 12  
*atrichella*, 10  
*bicornuta*, 11  
*bulbochaeta*, 11  
*chowoensis*, 11  
*confoederata*, 12  
*continua*, 15  
*coronata*, 12  
*coronata* var. *denudata*, 9  
*coronata* f. *isidiosa*, 14  
*decurtata*, 14  
*demangei*, 16  
*fungicola*, 14  
*gillettii*, 16  
*glandulifera*, 12  
*goebelii*, 14  
*granatensis*, 14  
*hookeri*, 18  
*hypocraea*, 15  
*imshaugii*, 16  
*isidiza*, 16  
*isidiza* var. *domingensis*, 26  
*laevigatula*, 18  
*leptascea*, 16  
*lythgoeana*, 18  
*marginalis*, 15

*marginalis* var. *laeviuscula*, 26  
*meizospora* f. *isidiosa*, 24  
*meizosporoides*, 24  
*njalensis*, 15  
*ochrovestita*, 24  
*papyrina*, 14  
*pigmentacea*, 19  
*proboscidea* var. *saxicola*, 16  
*pseudocoronata*, 14  
*pustulata*, 20  
*recurviscens*, 16  
*relicina* var. *coronata*, 12  
*schiffneri*, 20  
*scortella*, 15  
*semilunata*, 20  
*sensibilis*, 22  
*setschwanensis*, 22  
*stenophylla*, 26  
*stenophyllizans*, 26  
*subcoronata*, 23  
*subdissecta*, 14  
*subglandulifera*, 16  
*subinflata*, 23  
*sublaevigatoides*, 24  
*subscortea*, 16  
*suffixa*, 23  
*tabacina*, 24  
*tiliacea* var. *hypoleuca*, 16  
*tiliacea* var. *meizospora*, 19  
*ventricosa*, 26  
*viridescens*, 26  
*Parmelina wallichiana*, 18