

A Revision of the Lichen Genus  
*Hypotrachyna* (Parmeliaceae)  
in Tropical America

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## ABSTRACT

Hale, Mason E., Jr. A Revision of the Lichen Genus *Hypotrachyna* (Parmeliaceae) in Tropical America. *Smithsonian Contributions to Botany*, number 25, 73 pages, 20 figures, 1975.—A revision is made for 77 species of *Hypotrachyna* occurring in tropical America. Fifty-eight of these are endemic to the New World. These species are classified loosely in chemical constellations based on the secondary depside-depsidone products. The possible role of hybridization of fertile species and the evolution of vegetative morphs are discussed. Five new species are described: *H. andensis*, *H. lopezii*, *H. partita*, *H. producta*, and *H. protenta*. The remaining 72 species are transferred from the genus *Parmelia* to *Hypotrachyna*.

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# A Revision of the Lichen Genus *Hypotrachyna* (Parmeliaceae) in Tropical America

*Mason E. Hale, Jr.*

## Introduction

I began study of the Parmeliaceae in 1958 with the realization that synonymy and nomenclature of the nearly 600 species in the family could be solved only through a world-level revision. A monograph of the relatively conservative genus *Parmotrema* Massalongo (as *Parmelia* subgenus *Amphigymnia*) was completed in 1964 (Hale, 1965) along with a preliminary study of the other tropical sections of the collective genus *Parmelia* (Hale and Kurokawa, 1964).

Although I had examined all the type specimens and a considerable body of herbarium material, two factors mitigated against a prompt completion of a final monograph for all groups: (1) the inadequacy of chemical techniques available prior to 1965 that were needed to resolve certain chemical groups such as the barbatic and lividic acid groups and even separation of the norstictic acid group; and (2) the lack of sufficient specimens and field experience in tropical America, where many new species were obviously yet to be found.

The development and standardization of thin-layer chromatography has answered the problem of chemical techniques (see C. Culberson, 1972a). We can now routinely achieve resolution heretofore impossible and make accurate identifications of the lichen substances. A number of previously un-

known substances have been isolated and described. The few remaining problems will eventually be solved with high-performance liquid chromatography and mass spectrometry (C. Culberson, 1972b).

The inadequacy of collections will probably never be fully remedied, but we now have access to many more collections than were available in 1965. I have had the opportunity of visiting several tropical areas where I could appreciate more fully the habitats and ecology of the species, data which are only rarely well documented on herbarium labels.

The time has come, therefore, when a "final" summary can be made for the parmelioid genera. This paper summarizes the genus *Hypotrachyna* (Vainio) Hale for tropical America, including the region from the West Indies and Mexico southward to temperate Argentina and Chile. The 19 species known from North America proper are not included, but actually only one (*H. virginica*) is endemic there and the remaining 18 also occur in tropical America.

ACKNOWLEDGMENTS.—I wish to reiterate thanks to the curators—previously acknowledged in Hale (1965) and Hale and Kurokawa (1964)—who so generously loaned and in many cases reloaned valuable specimens. Special thanks are due Dr. S. Kurokawa, whose collaborative help in 1960–1964 speeded up study of hundreds of type specimens. I am extremely grateful to Dr. M. Lopez Figueiras of Universidad de los Andes for the opportunity

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to collect extensively with him in the Venezuelan Andes. Mr. Eric Lewis, Ms. Marianne See, and Dr. Michael Wirth helped at various times with testing of specimens by thin-layer chromatography. The scanning-electron microphotographs were taken by Mr. Walter Brown of the Smithsonian Scanning-Electron Microscope Laboratory.

Field studies in Mexico (1960) were supported by the National Science Foundation, and in Dominica by the Morden-Smithsonian Expedition (Hale, 1971a). The work in the past several years has been supported by grants from the Smithsonian Research Foundation.

### History of *Hypotrachyna* Research

Studies on *Hypotrachyna* (and for all other tropical Parmelias) appeared only as scattered floristic lists prior to 1890. Krempelhuber, Tuckerman, Müller Argau, Nylander, and others received for identification small lots of lichens (usually collected by phanerogamic botanists) and published the results without illustrations, keys, or really useful descriptions. There was little cooperation between workers or sharing of information or specimens.

Vainio (1890) was the first lichenologist to make a truly comprehensive study of tropical lichens. He collected extensively in Rio de Janeiro and Minas Gerais, Brazil, in 1885. The resulting publication, "Étude sur la Classification Naturelle et la Morphologie des Lichens du Brésil," remains a classic and Vainio's well-curated herbarium in Turku and his exsiccate, *Lichenes brasilienses*—distributed, as far as I have been able to determine, to BM, FH, G, K (now at BM), M, P, and UPS—attest his tremendous ability and industry. When identifying specimens, Vainio used Nylander's herbarium and also made a study trip to the Paris museum. This enabled him to present a more definitive study with a low level of synonymy.

Vainio collected 13 species now classified in the genus *Hypotrachyna*: *H. brasiliana* (Nylander) Hale, *H. consimilis* (Vainio) Hale, *H. dactylifera* (Vainio) Hale, *H. flavida* (Zahlbruckner) Hale (as *Parmelia flava* Krempelhuber), *H. gracilescens* (Vainio) Hale, *H. intercalanda* (Vainio) Hale, *H. microblasta* (Vainio) Hale, *H. novella* (Vainio) Hale, *H. pluriformis* (Nylander) Hale, *H. revoluta* (Floerke) Hale, *H. subaffinis* (Zahlbruckner) Hale

(as *Parmelia affinis* Vainio), and *H. velloziae* (Vainio) Hale. Material he identified as *Parmelia gracilis* (Müller Argau) Vainio is misidentified *H. physcioides*. Altogether, Vainio described eight of these species as new. In spite of his efforts, however, only a portion of the *Hypotrachyna* species were collected; the general region of southeastern Brazil is now known to have nearly 40 species.

The next major collecting program also was undertaken by a lichenologist, G. A. A. Malme, under the Regnell expeditions in the 1890s, primarily in Mato Grosso. The magnificently prepared specimens, now preserved in Stockholm, were studied mostly by Malme himself, but *Parmelia* specimens were turned over to B. Lynge, a Norwegian lichenologist who had no previous experience in tropical species, and this at a time when Vainio was the most logical worker and acknowledged authority. Lynge, however, did a creditable job, dealing with 110 species, of which 61 were proposed as new (Lynge, 1914, 1917, 1925). Only 18 of these species are now classified in *Hypotrachyna*. Lynge relied heavily on Vainio's exsiccate preserved at UPS, saw some Nylander types, and visited Zahlbruckner in Vienna. His publications contain much valuable data and some excellent illustrations.

The only other work that could be considered as a flora with keys and descriptions is that by Zahlbruckner (1909), completed just before Lynge's study. It was based on collections made by a non-lichenologist, V. Schiffner, in the São Paulo area. The specimens are preserved at WU and W with duplicates at BM.

More recently, Vareschi (1962) compiled a catalog of Venezuelan *Parmeliae* with many illustrations, but the species identifications have not been checked by a monographer.

My own field experience in tropical America began in Mexico, which has a large *Hypotrachyna* flora. I have also collected intensively in the Lesser Antilles, Trinidad, Guatemala, Panama, and Venezuela. These excursions have given me some idea of the ecological behavior of the genus from sea level to 3700 m, and while the area covered is but a small fraction of the total land mass of tropical America, it seems reasonable to extrapolate from this experience in discussing the habitats where the species might be expected to occur.

## Collections

Any revision is only as good and complete as the specimens available for study. Tropical America is a vast area, some parts of which have been relatively well explored, others are completely unknown and often inaccessible. Even a country as seemingly small as Panama has great tracts of unexplored rain and cloud forest that cannot be reached except by a major expeditionary effort. On the other hand, some areas, while uncollected, would probably have few species of *Hypotrachyna*. Such areas include, in particular, the Amazon Basin, which has a generally low elevation and a hot moist climate, hardly conducive to a rich foliose lichen flora. Deserts or very dry regions as in northern Chile, northern Mexico, and Baja California, and even north-eastern Brazil, also are poor prospects for *Hypotrachyna*.

The major areas of virgin forest in the tropics are, of course, being destroyed—cut over, burned, and colonized—as quickly as they can be reached. Such areas include even the higher elevations where *Hypotrachyna* is so abundant but where the soils are ideal for vegetable farming.

The following list shows the countries where *Hypotrachyna* has been collected, the principal collectors, and the herbaria where their collections are housed:

BAHAMAS: Britton (NY).  
 MEXICO: Arsène (US), Galeotti (P), Hale (US), Wirth (US).  
 WEST INDIES (all islands): Imshaug (MSC).  
 CUBA: Hioram (US), Wright (FH, L, P, UPS, US).  
 JAMAICA: Morton (US), Orcutt (US), Plitt (US).  
 DOMINICAN REPUBLIC: Allard (US).  
 VIRGIN ISLANDS: Raunkiaer and Boergesen (C, TUR).  
 GUADELOUPE: Culberson (DUKE), Duss (TUR), Husnot (H, P).  
 DOMINICA: Elliott (BM, TUR), Hale (US).  
 ST. VINCENT: Elliott (BM, TUR).  
 TRINIDAD: Hale (US).  
 GUATEMALA: Hale (US), Standley (F, US).  
 HONDURAS: Standley (F).  
 COSTA RICA: Culberson (DUKE), Pittier (G, US).  
 PANAMA: Hale (US), Scholander (US).  
 COLOMBIA: Cuatrecasas (US), Killip and Smith (US), Lindig (BM [original], FH, H, M, P), Weir (BM).  
 VENEZUELA: Dennis (BM), Hale (US), Mägdefrau (M), Poelt (M, US), Santesson (S), Vareschi (VEN).  
 FRENCH GUYANA: Leprieur (P).  
 PERU: Bryan (WIS), Gomez (US), Herrera (US), Iltis (WIS).  
 ECUADOR: Jameson (BM), Meyer (W).  
 BOLIVIA: Mandon (H).

CHILE: Gay (P), Imshaug (MSC), Mahu (personal, US), Santesson (S, UPS), Skottsberg (S).

BRAZIL: Damazio (G), Deventer (G), Eiten (US), Glaziou (G, P), Höhnelt (W), Irwin (NY, US), Kurokawa (TNS; specimens not available for study), Malme (S), Puiggari (G), Reitz and Klein (US), Schiffner (W, WU), Spruce (BM, H, NY), Ule (G), Vainio (TUR [original], BM, FH, M, P, UPS), Weddel (P, H), Warming (M).

PARAGUAY: Balansa (G), Malme (S).

URUGUAY: Felippone (W), Herter (H), Hosseus (H), Osorio (MVM).

ARGENTINA: Arechavaleta (G), Balansa (G), Dusén (S), Lamb (CAN), Lorentz and Hieronymus (M).

Noticeable gaps remain in Bolivia, Ecuador, Peru, Venezuela outside the Andes, and areas of Brazil bordering these countries. The unevenness of collecting can also be appreciated by examining lists of species collected in each country (see p. 18).

I have not attempted to evaluate literature reports of species in floristic lists (exclusive of type species) other than to examine the herbarium collections on which these were based and annotate them with revised names as needed. The sheer number of collections involved discourages one from tracing, verifying, and correcting each published name. Because of the extensive synonymy, lack of adequate chemical testing, and the generally low level of accuracy in identification, older published reports are quite untrustworthy.

## Morphological Characters

*Hypotrachyna* is a segregate of the collective genus *Parmelia* characterized by narrow, apically truncate lobes, a black lower surface, and dichotomously branched rhizines (Hale, 1974a). Hale and Kurokawa (1964) had earlier discovered that presence or absence of marginal cilia, type of cilia (normal or bulbate), and branching pattern of rhizines were the most consistent characters that could be used to subdivide the more than 400 species of *Parmelia*. The segregate *Hypotrachyna* is one of the more clear-cut groups in the Parmeliaceae because of the distinctive rhizine branching.

INTERNAL STRUCTURE.—Little attention has been paid to differences in internal structure of Parmeliaceae and how they might aid in a more natural classification of the genera. While carefully sectioning the Brazilian collections, Lynge (1914) noted that the species related to *Parmelia microsticta* had a rather thick paraplectenchymatous cortex in con-

trast to a palisade plectenchymatous cortex found in *Hypotrachyna* species. My recent work with the scanning-electron microscope (SEM) showed that all species of *Hypotrachyna* so far examined (Hale, 1972a) have a palisade cortex that is overlain by a thin, pored polysaccharide epicortex (Figure 1a) which cannot be seen with light microscopes. It is the cortex, along with dichotomously branched rhizines, that I use to distinguish *Hypotrachyna*. *Parmelia* sensu stricto has a paraplectenchymatous

cortex without a pored epicortex, as in the type-species of the genus, *P. saxatilis* (L.) Acharius.

The cross sections of *Hypotrachyna* are consequently rather uniform from species to species. The palisade cortical cells form a layer  $12\mu$ – $18\mu$  thick. The *Trebouxia*-containing algal layer is  $12\mu$ – $24\mu$  thick, the medulla  $50\mu$ – $150\mu$  thick, and the paraplectenchymatous lower cortex  $12\mu$ – $18\mu$  thick (Figure 1b). In general, very small species (2–5 cm in diameter) are quite thin (medulla  $50\mu$ – $60\mu$ ),

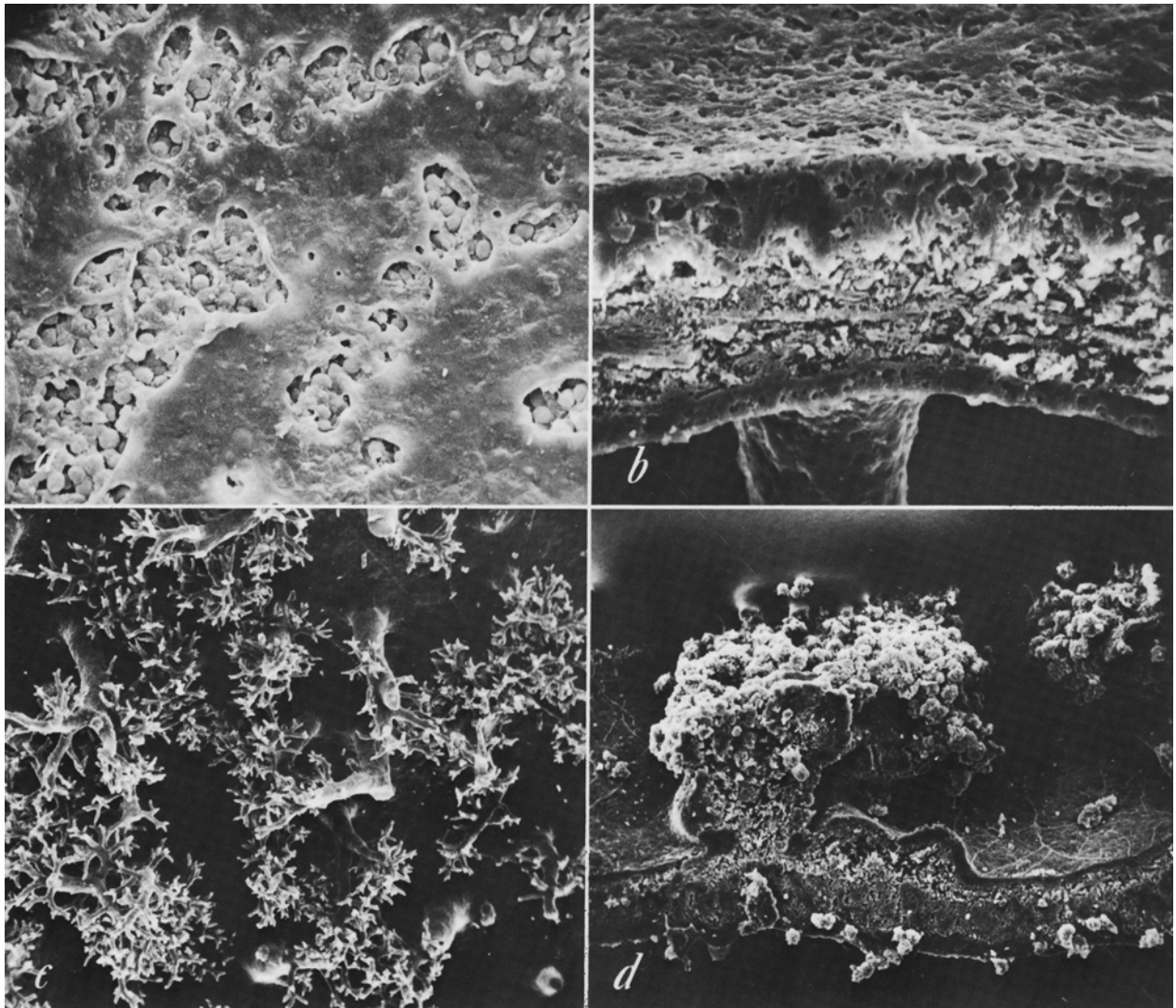


FIGURE 1.—Morphology of *Hypotrachyna*: a, surface of *H. croceopustulata* (Imshaug 22275) ( $\times 500$  with SEM); b, cross section of *H. croceopustulata* (Hale 33269) ( $\times 500$  with SEM); c, rhizines of *H. densirhizinata* (Scholander) ( $\times 100$  with SEM); d, cross section of thallus and a sororium of *H. densirhizinata* (Hale 43194) ( $\times 75$  with SEM).



while larger species (5–25 cm in diameter) have proportionately thicker layers. The rhizines consist of conglutinated strands of prosoplectenchymatous hyphae and are moderately to richly dichotomously branched (Figure 1c).

**LOBE CONFIGURATION.**—*Hypotrachyna* is extremely homogeneous in overall lobe configuration. It is possible, however, to recognize two broad types in tropical America: an extremely elongate, divaricate, and little-branched type as in *H. caraccensis* (Figure

8a) or *H. lopezii* (Figure 13c), and a shorter-lobed, more or less closely branched and imbricate type exemplified by *H. livida* (Figure 13b). There are, of course, numerous intermediates between these two extremes, as in *H. laevigata* (Figure 12f). A third type of configuration is found in the very rare *H. koyaensis*, which has the broader, almost subirregular lobes (Figure 12e) characteristic of many species of *Hypotrachyna* endemic to Asia.

**SOREDIA.**—These vegetative diaspores originate in

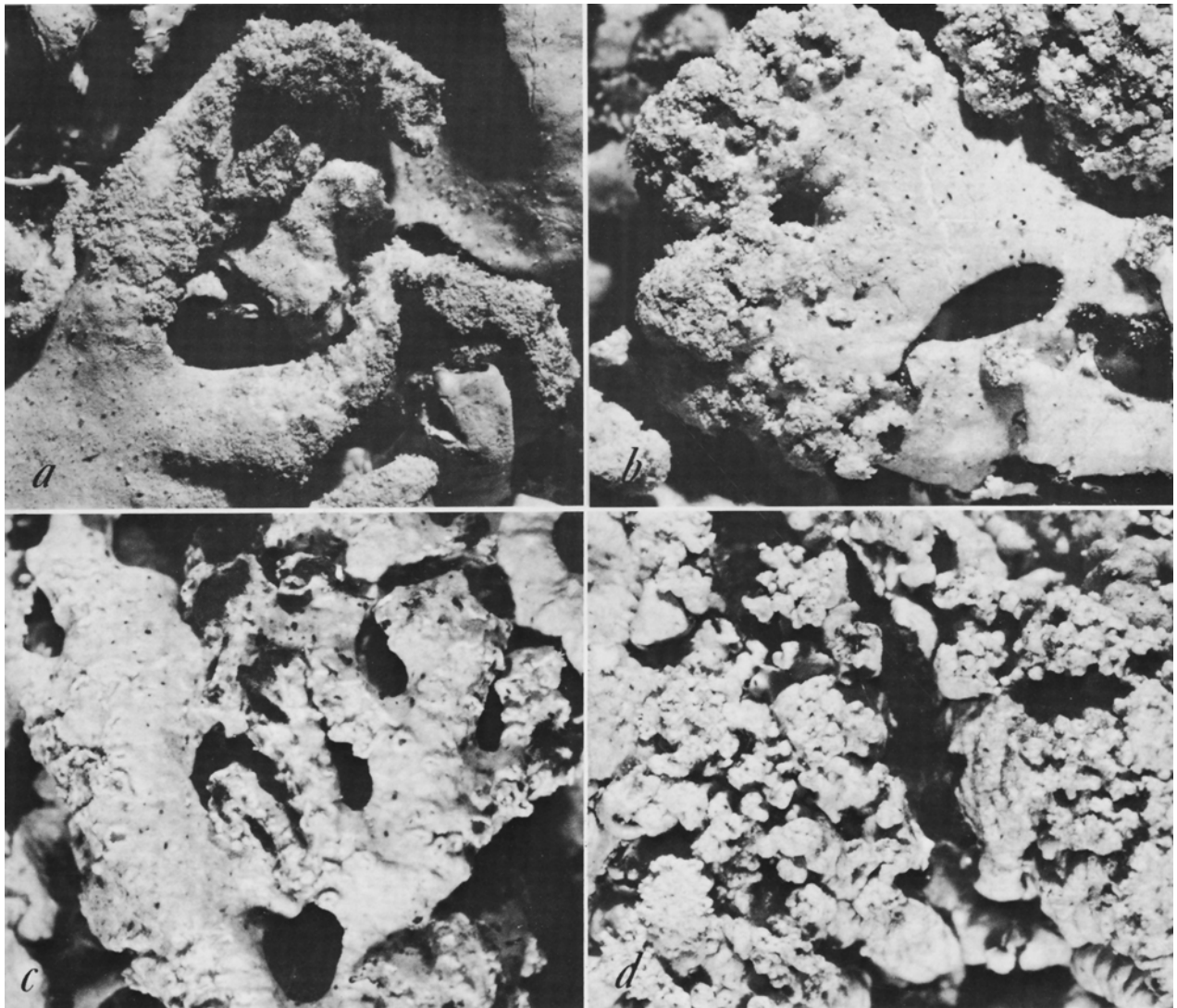


FIGURE 2.—Vegetative structures of *Hypotrachyna* (all  $\times 10$ ): a, diffuse soralia of *H. revoluta* (Hale 43293a); b, orbicular soralia of *H. sinuosa* (Hale 43071a); c, pustulate soralia of *H. croceopustulata* (Hale 33269); d, pustules of *H. dactylifera* (Hale 42075).

soralia (Figure 1d) and erupt as a powder. The shape and location of the soralia on lobes are important taxonomic characters used to recognize species. Soredia occur in 18 of the 77 species of tropical American *Hypotrachyna*: *H. brevirhiza*, *H. croceopustulata*, *H. densirhizinata*, *H. endochlora*, *H. exsplendens*, *H. flavovirens*, *H. gondylophora*, *H. immaculata*, *H. laevigata*, *H. oostingii*, *H. producta*, *H. pseudosinuosa*, *H. revoluta* (Figure 2a), *H. rockii*, *H. sinuosa* (Figure 2b), *H. subaffinis*, *H. thyanota*, and *H. velloziae*. They are

generally subterminal to rarely laminal and produced in orbicular soralia. Soralia rarely become diffuse, as in *H. revoluta*. In a few species pustules are formed initially but later become sorediate, as in *H. croceopustulata* (Figure 2c). Details of abnormal soredial formation will be found in the species discussions.

PUSTULES.—These are coarse, inflated, extremely fragile, isidialike structures (Figures 2d, 3a), but they are related to soralia since they often become sorediate. True pustules are hollow and tend to

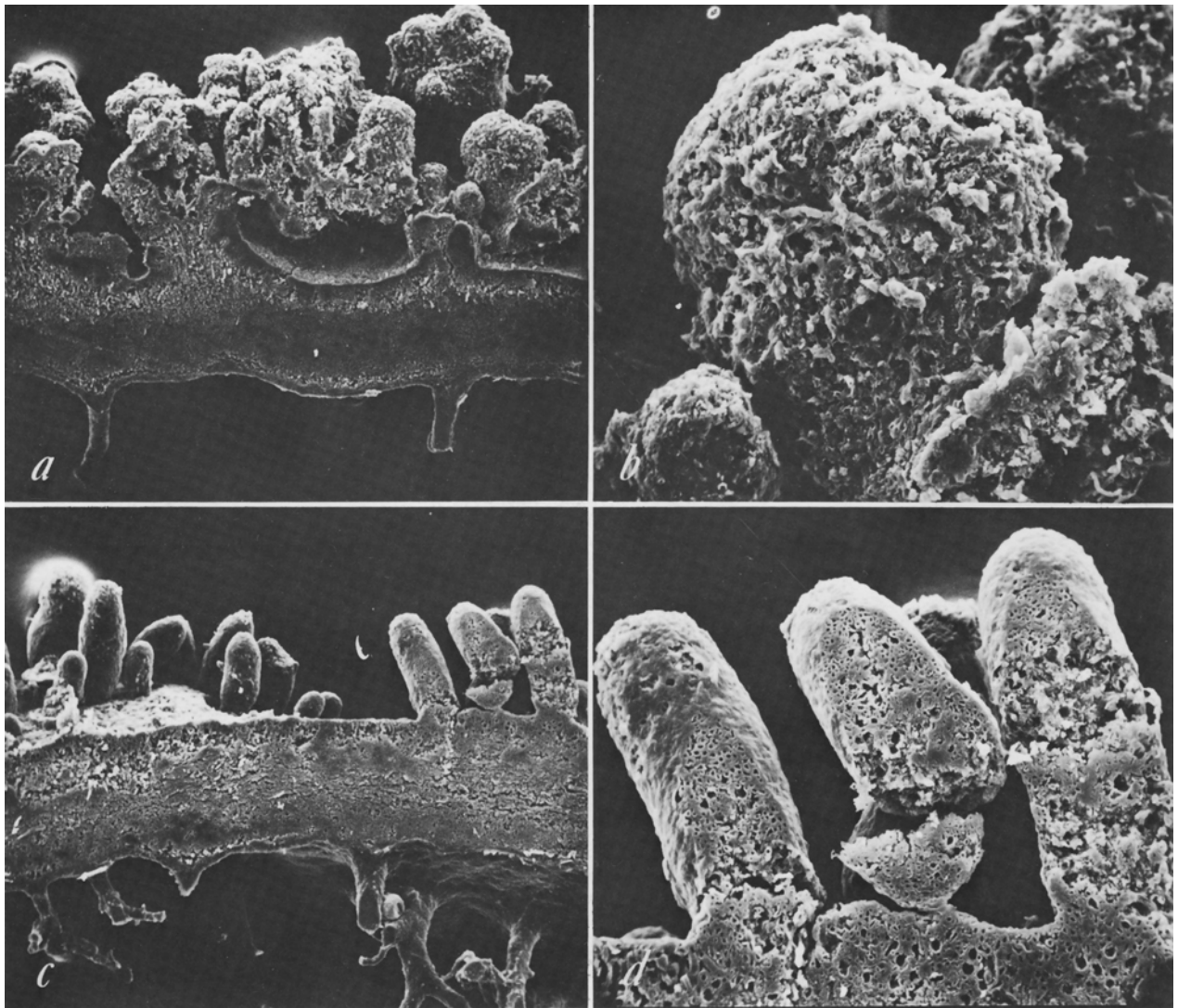


FIGURE 3.—Vegetative structures of *Hypotrachyna*: a, pustules of *H. formosana* (Eiten 7671a) ( $\times 60$  with SEM); b, enlargement of pustule in a ( $\times 300$ ); c, cross section of thallus and isidia of *H. imbricatula* (Quiros 1479) ( $\times 100$  with SEM); d, enlargement of isidia in c ( $\times 300$ ).

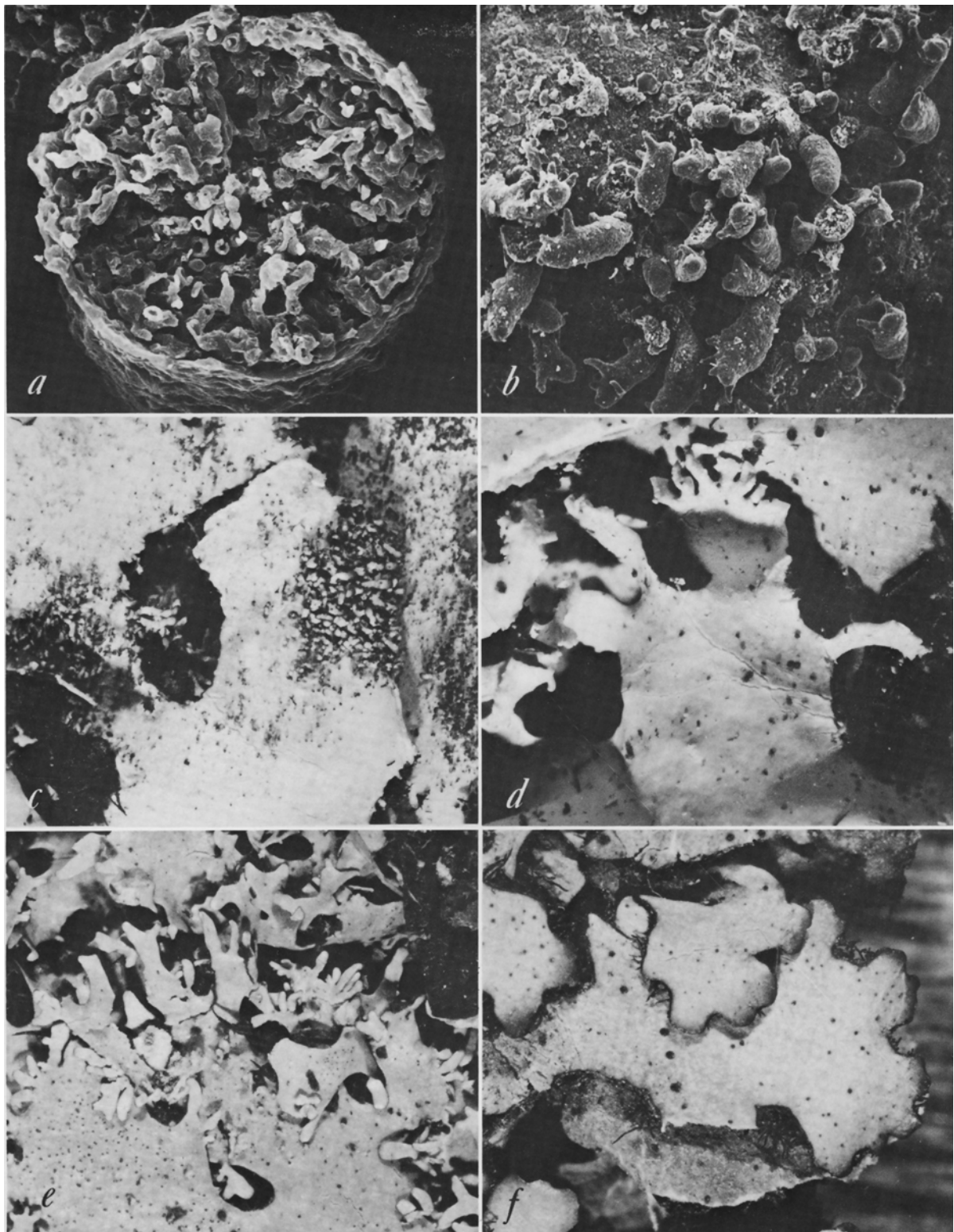


FIGURE 4.—Vegetative structures of *Hypotrachyna*: a, cross section of an isidium of *H. costaricensis* (Hale 42201) ( $\times 1000$  with SEM); b, lobulate isidia of *H. andensis* (Hale 42658a) ( $\times 100$  with SEM); c, lobulate isidia of *H. bogotensis* (Oberwinkler and Poelt 7544) ( $\times 10$ ); d, lobules of *H. rachista* (Hale 43139) ( $\times 10$ ); e, lobules of *H. chlorina* (Hale 43104) ( $\times 10$ ); f, maculae on a lobe of *H. subplumbeata* (Moore and Wood 4944) ( $\times 10$ ).

break open apically without soredial formation. Only three species of *Hypotrachyna* treated here have this type of pustule: *H. dactylifera*, *H. formosana*, and *H. malmei*. Under SEM the surface of pustules is quite rough with loosely aggregated hyphae lacking an outer polysaccharide layer (Figure 3b). More work needs to be done on these structures.

**ISIDIA.**—Fingerlike, cylindrical isidia, densely filled with medullary hyphae and about 0.1 mm in diameter, are well-known lichen structures (Figures 3c, 3d). They occur in 16 species of *Hypotrachyna*: *H. andensis*, *H. bogotensis*, *H. consimilis*, *H. costaricensis*, *H. dentella*, *H. ensifolia*, *H. imbricatula*, *H. isidiocera*, *H. koyaensis*, *H. microblasta*, *H. neodissecta*, *H. osorioi*, *H. partita*, *H. rhabdiformis*, *H. steyermarkii*, and *H. subphysodalica*.

Isidia are often presented in textbooks as containing extensions of thalloid tissues. When viewed with the scanning-electron microscope, however, we see little internal organization (Figure 4a). There is no true cortical structure and no pored epicortex, only a thin, smooth, continuous polysaccharide sheet covering the weakly organized mass of algae and hyphae inside.

While most isidia show little variation except in branching, lobulate isidia sometimes are found to occur in six of the above-named species: *H. andensis*, *H. bogotensis*, *H. ensifolia*, *H. imbricatula*, *H. partita*, and *H. steyermarkii*. In such cases the isidia begin normally but soon become procumbent and even dorsiventral, as in true lobules (Figure 4b,c). Cilia will rarely form (cf. *H. steyermarkii*). When viewed with the SEM, the lobulate isidia appear to have the same level of organization as isidia, lacking, for example, a distinct cortex.

**LOBULES.**—Almost any species of *Hypotrachyna* may develop small adventitious lobes with age. Such lobes can be regarded as regenerative structures with internal structure and a pored epicortex comparable to the main lobes when viewed under the scanning-electron microscope. As defined here, lobules are a consistent species character, abundantly or distinctively produced and not associated with isidia. Four species have them: *H. chlorina* (Figure 4e), *H. prolongata*, *H. rachista* (Figure 4d), and *H. singularis*. I do not mean to imply, however, that these lobules are identical in origin and formation.

**MACULAE.**—These are mottled, light to dark patches in the cortex visible at  $\times 10$  magnification (Figure 4f). They are not detectable as surface features under the scanning-electron microscope but seem to result from darker clumps of algae contrasted with the lighter algae-free hyphal matrix. Although some species of *Hypotrachyna* are always maculate, this is a difficult character to determine in practice and I have avoided using maculae as a primary character.

**APOTHECIAL CHARACTERS.**—Apothecia have been found in 63 species of *Hypotrachyna* but so far are unknown in *H. exsplendens*, *H. gondylophora*, *H. lineariloba*, *H. monilifera*, *H. oostingii*, *H. partita*, *H. physodalica*, *H. producta*, *H. prolongata*, *H. rachista*, *H. steyermarkii*, *H. subphysodalica*, *H. thysanota*, and *H. velloziae*. Apothecia are present, but no spores developed, in *H. croceopustulata*, *H. laevigata*, *H. protoboliviana*, and *H. subplumbeata*.

Apothecia are uniformly small, 1–5 mm in diameter (rarely to 10 mm), adnate (stipitate only in *H. peruviana*), and imperforate. The hymenium is  $40\mu$ – $60\mu$  high. The unicellular spores show a very small range in size, usually  $4\mu$ – $10\mu$  wide and  $8\mu$ – $16\mu$  long. A few species, notably those with yellow pigments (as *H. endochlora*) and *H. pluriformis* have significantly larger spores, up to  $25\mu$  long, but no species of *Hypotrachyna* has spores more than  $30\mu$  long.

Pycnidia are often produced by apothecia-bearing species. The microconidia are about  $1\mu$  wide and  $5\mu$ – $7\mu$  long in all species investigated. I have not included them in the descriptions since they seem to have no taxonomic value. Articles by Nylander, Lynge, and Vainio can be consulted for further data on pycnidia and microconidia in various species.

### Chemical Characters

Beginning with Nylander in the 1860s and continuing with Vainio, Zahlbruckner, and Lynge, color tests with KOH and  $\text{Ca}(\text{OCl})_2$  have played an important role in identifying species of *Parmelia*, and information on the tests always has been included in the species descriptions. Only Müller Argau refused to use chemistry, even though it was shown to be a useful aid in identification.

It was Asahina in the few years from 1933–1940 who perfected the microcrystal tests by which

specific lichen substances could be distinguished. This meant, for example, that a KOH+ red species could be shown to contain norstictic acid, salazinic acid, or other component.

The next significant advance in chemical techniques was partition chromatography, first with paper (Wachtmeister, 1952; Mitsuno, 1953) and later on silica gel (thin-layer chromatography or TLC) (Stahl and Schorn, 1961). TLC is now the accepted standard for routine qualitative identification of lichen substances and there is little chance it will be replaced by a more sophisticated technique in the near future. High-performance liquid chromatography (C. Culberson, 1972b) is and will remain far too expensive to be widely available to taxonomists.

My original chemical analyses of *Parmelia* specimens were accomplished with microcrystal tests well before 1965 when TLC was just coming into use. Many of these specimens were returned to herbaria from which they had been borrowed, and it has been necessary in the last few years to borrow them again (especially types) and perform TLC tests. Unfortunately, some which I annotated between 1958 and 1964 were not rechecked. All material examined since 1965 has been studied with TLC.

Culberson's methods have been used exclusively (C. Culberson, 1972a). I have also benefited from being able to consult with Dr. Culberson on numerous occasions on the identification of difficult or unknown acids.

Following is an alphabetical list of all identifiable substances, the species that contain them, and associated substances, that is, those with which they may occur. Unknowns are given at the end. Further details on joint occurrences of substances, accessory substances, etc., are given in discussions of the species.

- Alectoronic acid.—*H. degelii*, *H. densirhizinata*, *H. ensifolia*, *H. exsplendens*, *H. gigas*, *H. lineariloba*, *H. malmei*, and *H. protenta*. Associated substances: atranorin,  $\alpha$ -collatolic acid, gyrophoric acid, lichexanthone, and protocetraric acid. An additional qualitative test for alectoronic acid is bright white to bluish white fluorescence in longwave ultraviolet.
- Anziaic acid.—*H. ducalis*, *H. eitenii*, *H. partita*, *H. producta*, and *H. rachista*. Associated substances: atranorin, lichexanthone, and perlatolic acid. Several unknown spots commonly occur in TLC profiles of anziaic acid.
- Atranorin.—In all species except *H. brasiliiana*, *H. caraccen-*

- sis*, *H. enderythraea*, *H. erythrodes*, *H. flavida*, *H. flavovirens*, *H. formosana*, *H. lopezii*, *H. malmei*, *H. microblasta*, *H. minima*, *H. novella*, *H. osteoleuca*, *H. physodolica*, *H. protoboliviana*, *H. reducens*, *H. silvatica*, *H. subaffinis*, *H. subphysodolica*, and *H. velloziae*. Associated substances: all substances except lichexanthone and usnic acid. Atranorin is the main cortical substance in *Hypotrachyna*; it is absent only when replaced by usnic acid or lichexanthone, although in a few cases it may be present in trace amounts.
- Barbatic acid.—*H. chlorina*, *H. dentella*, *H. endochlora*, *H. imbricatula*, *H. isidiocera*, *H. laevigata*, *H. monilifera*, *H. peruviana*, *H. physcioides*, *H. protoboliviana*, *H. steyermarkii*, and *H. subplumbeata*. Associated substances: Atranorin, 4-O-demethylbarbatic acid, obtusatic and norobtusatic acids (constant accessories except in *H. subplumbeata*), echinocarpic acid, entothecin, usnic acid, and unidentified yellow pigments. A complete discussion of the chemistry of these species is provided by Culberson and Hale (1973). Chromatography of the barbatic group is very difficult; the most promising resolution is obtained with toluene-acetic acid. All specimens usually react C+ orange, a reaction now known to be caused by 4-O-demethylbarbatic acid, not barbatic acid itself.
- Colensoinic acid.—*H. dactylifera*, *H. erythrodes*, *H. formosana*, *H. immaculata*, *H. livida*, *H. novella*, and *H. palmarum*. Associated substances: atranorin, 4-O-demethylphysodic acid, lichexanthone, lividic acid, norcolensoinic acid, physodic acid, rhodophyscin, the "palmarum" unknown, and traces of other unknowns. See the discussion under lividic acid.
- $\alpha$ -Collatolic acid.—*H. degelii*, *H. densirhizinata*, *H. exsplendens*, *H. gigas*, and *H. protenta*. Associated substances: alectoronic acid, atranorin, and gyrophoric acid.  $\alpha$ -Collatolic acid is not a constant accessory component with alectoronic acid, as one may see by comparing the lists of species.
- Constictic acid.—*H. andensis*, *H. lopezii*, and *H. sinuosa*. Associated substances: norstictic acid, salazinic acid, stictic acid, and usnic acid. Constictic acid invariably occurs with stictic acid in *Hypotrachyna*. Its structure is very close to stictic acid.
- 4-O-Demethylbarbatic acid.—See barbatic acid.
- 4-O-Demethylphysodic acid.—See lividic acid.
- Echinocarpic acid.—*H. dentella*, *H. subaffinis*, and *H. thysanota*. Associated substances: atranorin, barbatic acid complex, gyrophoric acid, lichexanthone, and microphyllinic acid. The structure of this P+ orange-red acid is as yet undetermined. It forms a low discrete H<sub>2</sub>SO<sub>4</sub>+ orange spot in hexane-ether and a low, dull gray streak in benzenedioxane solvent systems.
- Entothecin.—*H. chlorina*, *H. endochlora*, *H. isidiocera*, and *H. peruviana*. Associated substances: atranorin, barbatic acid complex, obtusatic acid complex, and unidentified yellow pigments.
- Evernic acid.—*H. bogotensis*, *H. chicitae*, *H. pulvinata*, and *H. rockii*. Associated substances: atranorin, lecanoric acid, norobtusatic acid, obtusatic acid, and rhodophyscin. Lecanoric acid is a constant accessory. Culberson and Hale (1973) discuss this group more fully in relation to the species con-

- taining barbatic acid. They hypothesize that obtusatic acid could be the product of hybridization between evernic acid and barbatic acid.
- Fumarprotocetraric acid.**—*H. gondylophora*. Associated substances: atranorin, rhodophycin, and succinprotocetraric acid. Fumarprotocetraric acid would seem to be an extremely rare substance in *Hypotrachyna*.
- Galbinic acid.**—*H. caraccensis*, *H. enderythraea*, and *H. microblasta*. Associated substances: norstictic acid, salazinic acid, and usnic acid. Galbinic acid was first described from *Parmelina galbina* (Acharius) Hale where it is a primary constituent. It has also been reported in *Usnea*. In *Hypotrachyna* it always occurs with norstictic and salazinic acids. The molecular structure has recently been determined by Dr. Myles Keogh as an acetate of salazinic acid.
- Gyrophoric acid.**—*H. gigas*, *H. neodissecta*, *H. oostingii*, *H. osorioi*, *H. pluriformis*, *H. revoluta*, and *H. thysanota*. Associated substances: alectoronic acid, atranorin, echinocarpic acid, microphyllinic acid, and unknowns. Gyrophoric acid is an accessory substance only in *H. gigas*.
- Lecanoric acid.**—*H. bogotensis*, *H. chicitae*, *H. pulvinata*, and *H. rockii*. Associated substances: atranorin, evernic acid, norobtusatic acid, obtusatic acid, and rhodophycin. Although common as a primary constituent (along with atranorin) in most parmelioid genera, lecanoric acid always occurs in *Hypotrachyna* with and in lesser concentration than evernic acid (C. Culberson, 1972b). The color test with calcium hypochlorite is therefore weak or indistinct.
- Lichexanthone.**—*H. brasiliiana*, *H. eitenii*, *H. erythrodes*, *H. formosana*, *H. malmei*, *H. minima*, *H. novella*, *H. osteoleuca*, *H. silvatica*, and *H. subaffinis*. Associated substances: alectoronic acid, anziaic acid, atranorin, colensoinic acid, 4-O-demethylphysodic acid, echinocarpic acid, lividic acid, norcolensoinic acid, olivetoric acid, physodic acid, protocetraric acid, rhodophycin, and unknown pigments. Lichexanthone is a cortical substance which fluoresces brilliant yellow-orange under longwave ultraviolet. It completely replaces atranorin and usnic acid in the cortex, although traces of atranorin may accompany it in a few species. It is noteworthy that no *Hypotrachyna* species endemic to the Old World produces lichexanthone.
- Lividic acid.**—*H. dactylifera*, *H. erythrodes*, *H. formosana*, *H. immaculata*, *H. livida*, and *H. novella*. Associated substances: atranorin, colensoinic acid, 4-O-demethylphysodic acid, lichexanthone, norcolensoinic acid, physodic acid, rhodophycin, and unknowns. C. Culberson (1966) isolated lividic acid from *H. livida* but its molecular structure (apparently close to physodic acid) is still unknown. It can be identified with TLC, preferably using the hexane and toluene solvent systems. All of the associated substances fall out in this sequence from highest to lowest  $R_F$  in hexane: atranorin or lichexanthone, colensoinic acid, norcolensoinic acid, 4-O-demethylphysodic acid, physodic acid, and lividic acid (see C. Culberson, 1966). Various unknowns may appear below and above lividic acid. In toluene the resolution is not as good and only four or five distinct spots may appear in this sequence: atranorin or lichexanthone, colensoinic acid, 4-O-demethylphysodic acid, norcolensoinic acid, and lividic acid. Perfect resolution of spots is only rarely achieved with these solvent systems, and we must await more satisfactory separation that will come from high-performance liquid chromatography.
- Microphyllinic acid.**—*H. thysanota*. Associated substances: atranorin, echinocarpic acid, and gyrophoric acid. The identity of microphyllinic acid was established by Mr. Jon Dey while comparing the type of *Parmelia nakanishii* with his *P. oostingii*. It is the first reported occurrence outside of *Cetraria*, although C. Culberson postulated its existence in *Hypotrachyna* (Culberson and Hale, 1973).
- Norcolensoinic acid.**—See discussion under lividic acid.
- Norobtusatic acid.**—All species containing obtusatic acid (see lists under barbatic acid). Associated substances: see discussions under barbatic acid and evernic acid.
- Norstictic acid.**—*H. andensis*, *H. brevirhiza*, *H. caraccensis*, *H. enderythraea*, *H. flavovirens*, *H. lopezii*, *H. microblasta*, *H. reducens*, *H. rhabdiformis*, *H. sinuosa*, and *H. sublaevigata*. Associated substances: atranorin, constictic acid, galbinic acid, protocetraric acid, salazinic acid, stictic acid, and usnic acid. One of the first positive results of TLC was the resolution of norstictic acid and its closely related associated substances. Norstictic acid occurs in trace amounts with salazinic acid and in substantial amounts with stictic acid. The accessory substance connorstictic acid has been reported in *Parmotrema* (W. Culberson, 1973). Connorstictic acid is very close to salazinic acid and may occur in *Hypotrachyna* although I have not been able to identify it positively.
- Obtusatic acid.**—All species containing barbatic acid, *H. chicitae*. Associated substances: see discussions under barbatic acid.
- Olivetoric acid.**—*H. intercalanda* and *H. osteoleuca*. Associated substances: atranorin, lichexanthone, rhodophycin, and unknowns. This C+ red acid can be easily identified by means of TLC.
- Perlatolic acid.**—*H. partita*. Associated substances: anziaic acid and atranorin. Perlatolic acid, rare for *Hypotrachyna*, was identified in only one specimen of *H. partita* along with closely related anziaic acid. Its co-occurrence with anziaic acid would not be unexpected.
- Physodalic acid.**—*H. physodalic* and *H. subphysodalic*. Associated substances: protocetraric acid and usnic acid. This acid is biogenetically closely related to protocetraric acid and often occurs with it in *Hypogymnia*. However, only one of the 14 species of *Hypotrachyna* having protocetraric acid contains physodalic acid.
- Physodic acid.**—See discussions under lividic acid.
- Protocetraric acid.**—*H. bahiana*, *H. brasiliiana*, *H. consimilis*, *H. contradicta*, *H. croceopustulata*, *H. flavida*, *H. flavovirens*, *H. koyaensis*, *H. malmei*, *H. minima*, *H. obscurella*, *H. physodalic*, *H. pseudosinuosa*, *H. silvatica*, and *H. velloziae*. Associated substances: alectoronic acid, atranorin, lichexanthone, norstictic acid, physodalic acid, rhodophycin, salazinic acid, and usnic acid. This is the commonest medullary substance in *Hypotrachyna*, although none of the species containing it are especially widespread. The best separation (especially from fumarprotocetraric) is achieved in the hexane solvent system using 10–20 ml more ether than recommended by C. Culberson (1972a).

Rhodophyscin.—*H. bahiana*, *H. consimilis*, *H. croceopustulata*, *H. dactylifera*, *H. erythrodes*, *H. gondylophora*, *H. immaculata*, *H. rockii*, and *H. velloziae*. Associated substances: atranorin, colensoinic acid, evernic acid, fumarprotocetraric acid, lecanoric acid, lichexanthone, lividic acid complex, protocetraric acid, succinprotocetraric acid, and usnic acid. This red pigment is assumed to be an anthraquinone first isolated from *Physcia*. It occurs sporadically in the species listed, either in the lower medulla or under soralia.

Salazinic acid.—*H. andensis*, *H. boquetensis*, *H. breviphiza*, *H. caraccensis*, *H. enderythraea*, *H. microblasta*, *H. reducens*, *H. sinuosa*, *H. sublaevigata*, and *H. subsaxatilis*. Associated substances: atranorin, constictic acid, galbinic acid, norstictic acid, stictic acid, and usnic acid. I have not conclusively identified consalazinic acid, an unknown substance that may accompany salazinic acid.

Stictic acid.—*H. andensis*, *H. lopezii*, and *H. sinuosa*. Associated substances: constictic acid, norstictic acid, usnic acid, and two unknowns. This acid is quite rare in *Hypotrachyna* and is accompanied by the same substances that are found in other parmelioid genera.

Succinprotocetraric acid.—*H. gondylophora*. Associated substances: atranorin and fumarprotocetraric acid. This recently described acid (Baker et al., 1973) often accompanies fumarprotocetraric acid in the genus *Xanthoparmelia*.

Usnic acid.—*H. andensis*, *H. caraccensis*, *H. enderythraea*, *H. flavida*, *H. flavovirens*, *H. lopezii*, *H. microblasta*, *H. physodolica*, *H. protoboliviana*, *H. reducens*, *H. sinuosa*, *H. subphysodolica*, and *H. velloziae*. Associated substances: atranorin, barbatic acid complex, constictic acid, galbinic acid, norstictic acid, obtusatic acid complex, physodalic acid, protocetraric acid, rhodophyscin, salacinic acid, and stictic acid. Usnic acid, a common cortical pigment, ordinarily replaces atranorin or lichexanthone, although traces of atranorin may be present in some species. It occurs only with P+  $\beta$ -orcinol depsidones with the sole exception of *H. protoboliviana*, which contains the P- barbatic acid complex.

Fatty acids.—*H. costaricensis*, *H. koyaensis*, and *H. singularis*. Associated substances: atranorin, protocetraric acid. Fatty acids are represented by caperatic and protolichesterinic acids, perhaps others, all difficult to identify with TLC.

"Gracilescens" unknown.—*H. gracilescens*. Associated substance: atranorin.

"Oostingii" unknowns.—*H. oostingii*. Associated substances: atranorin and gyrophoric acid. These unknowns are white fluorescent in longwave ultraviolet but differ from alecatoronic acid.

"Palmarum" unknown.—*H. palmarum*. Associated substances: atranorin and colensoinic acid. This unknown acid forms a distinct spot below colensoinic acid different from any of the other colensoinic-lividic acid complex substances but obviously related to them.

"Prolongata" unknown.—*H. prolongata*. Associated substance: atranorin. This C+ red compound could not be identified with any other lichen substances reacting C+.

"Silvatica" anthraquinones.—*H. silvatica*. Associated substances: atranorin, lichexanthone, and protocetraric acid.

This rusty red pigment occurs throughout the lower medulla.

### Speciation in *Hypotrachyna*

One of the least discussed topics in lichenology is species evolution. As Thomson (1961) points out, we have little of the kinds of cytological or fossil evidence that is so often available in other plant groups. An important clue in lichenology, however, has proven to be chemistry, and, as stated by Culberson and Culberson (1970), comparative phytochemistry is the most useful independent check that exists to evaluate the naturalness of systems based on morphology. This is especially true in lichens, where differentiation of chemical races is a far more obvious and frequent means of evolutionary differentiation than morphology (W. Culberson, 1970).

I will discuss here primarily the origin and direction of speciation in *Hypotrachyna*, although many of the observations and conclusions should apply to other foliose genera. Briefly, I will deal with three aspects: possible hybridization of parent species, formation of vegetative morphs, and habitat selection.

### HYBRIDIZATION

Lichenologists probably would agree that crustose lichens reproduce sexually since most species lack any other obvious means of propagation. On the other hand, it is assumed that foliose and other macrolichens generally reproduce vegetatively by means of diaspores (soredia, isidia, etc.). Little has been said about the reproduction of those foliose lichens which lack vegetative diaspores. If two fertile lichens should hybridize, we would expect gene exchange and possible mutations, processes that could give rise to new variations and species.

Unfortunately, we are not sure how lichens reproduce sexually. There is no way at this time to make experimental crossings and to study cytological details. It is assumed that microconidia (spermatia or pycnidiospores) are capable of migrating to the ascogonial coil, forming a dicaryon with the female element, and existing in a brief one-celled sporophytic stage before meiosis and spore formation take place. Each of the eight ascospores can be germinated and will, at least in theory, reconstitute

a new thallus when a suitable lichenizable alga is entrapped.

Several recent studies have indeed shown that variation in the chemistry of certain populations can best be explained on the assumption of sexual reproduction and hybridization. I can cite my own work in *Cetraria ciliaris* (Hale, 1963) and the Culbersons' recent study of the *Parmelia perforata* group (Culberson and Culberson, 1973). The most convincing evidence for *Hypotrachyna* has been presented by Culberson and Hale (1973) for those species producing evernic acid or barbatic acid. Their data are summarized in Figure 5. Culberson showed that hybridization of plants in the New World with type I Old World chemistry ( $1_M-1$  = evernic acid and  $1-1$  = lecanoric acid) and type II chemistry ( $2_M-2$  = barbatic acid and  $2-2$  = 4-O-demethylbarbatic acid) theoretically could give rise to a new population containing obtusatic acid ( $1_M-2$ ) and norobtusatic acid ( $1-2$ ). Old World populations which had no opportunity to cross with progenitors containing evernic acid also now lack any species with obtusatic acid. On the other hand, these populations free of obtusatic acid are absent in the New World except for rare *H. subplumbeata*, leaving us to conclude that hybridi-

zation produced populations containing obtusatic acid and that such populations had a very significant advantage over those lacking this acid and have displaced them.

Another example of possible hybridization is illustrated by species which previously would have been considered to contain "accessory" substances. One could reasonably postulate, for example, that gyrophoric acid occurring with alectoronic acid in some specimens of *H. gigas* was contributed by a now extinct progenitor which contained gyrophoric acid and which hybridized with the still extant parent containing alectoronic acid. The same reasoning could be applied to *H. physodolica*, which produces protocetraric acid with or without physodalic acid.

A final example concerns the production of cortical substances, principally atranorin, lichexanthone, and usnic acid. While we are totally ignorant of the biogenesis of these substances, one might assume that atranorin is the normal component and that some mutation could block this substance in favor of lichexanthone (see Hale, 1972b, for *H. formosana* versus *H. pustulifera*) or usnic acid. I can cite the following species pairs: *H. livida* (atranorine) and *H. novella* (lichexanthone); *H.*

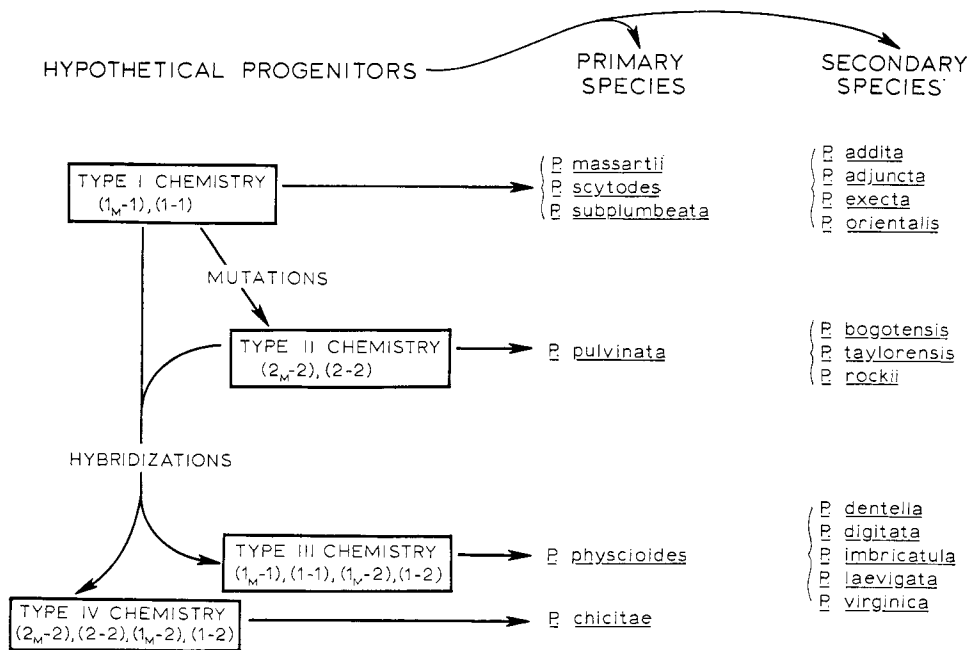


FIGURE 5.—Proposed pathway of chemical and morphological evolution leading to species in the barbatic-evernic-acid complex (from Culberson and Hale, 1973).



*contradicta* (atranorin) and *H. brasiliana* (lichexanthone); and *H. physcioides* (atranorin) and *H. protoboliviana* (usnic acid).

The genus *Hypotrachyna* in tropical America has 36 species that have apothecia and lack the usual vegetative diaspores. These include 26 species endemic to the New World. They represent a gene pool which has produced, and in many cases is still producing, hybridizations and mutations responsible for the creation of new species. As I will show below, many of the extinct sexual morphs in *Hypotrachyna* are survived by their vegetative morphs.

In summary, the evidence now available supports a working hypothesis that sexual reproduction has occurred in *Hypotrachyna* and that it has contributed significantly to the morphological and, especially, chemical diversity of the genus.

#### FORMATION OF VEGETATIVE MORPHS

The primary vegetative diaspores in *Hypotrachyna* are soredia and isidia. These never occur together and seem to represent two separate lines of morphological evolution, as I had previously concluded in *Parmotrema* (Hale, 1965). Most lichenologists of the 19th century treated soredia and isidia as minor characters unworthy of species rank. It was, in fact, not until 1924 that Du Rietz presented a comprehensive discussion of these structures. He not only carefully described their orientation on the thallus but discussed their biological and systematic significance, concluding that sympatric sorediate-nonsorediate, isidiate-nonisidiate populations are best treated as varieties. He felt, however, that allopatric populations should be treated as distinct species.

In the last decade we have gained a new perspective on the significance of soredia and isidia, even if we still do not know why they are produced. When studying *Parmotrema* on a world level, for example, I analyzed a number of "counterpart" species, that is, pairs of sorediate-nonsorediate and isidiate-nonisidiate species which shared otherwise identical morphology and chemistry (Hale, 1965). Fourteen of the 34 sorediate species had fertile nonsorediate counterparts. The sexual morphs were generally endemic to relatively small continental areas while the sorediate counterparts, as a rule, had much wider distributions.

Poelt (1970) expanded these and other examples into a more comprehensive hypothesis of species pairs ("Artenpaare"). Briefly, he postulated that the asexual sorediate and isidiate morphs are derived from sexual morphs and that they behave apomictically without any means of further variation save highly unlikely somatic mutations. These secondary species, to quote Poelt, are blind alleys which have conserved the chemistry of the primary sexual morph. Later, Poelt (1972) expanded this hypothesis to include differentiation of a parent species into two or more chemically different, sexually reproducing species, each of which could produce stable secondary apomictic species. In addition, any or all of the primary species theoretically comprising species pairs may have become extinct.

An upshot of this hypothesis is that morphologically identical but chemically variable sorediate (or isidiate) species, having probably evolved parallel from different parents, would have to be considered polyphyletic. Culberson and Culberson (1973) first suggested this possibility and used it to explain convincingly the origin of speciation in the *Parmotrema perforatum* group. A further consequence is that polyphyletic "chemical species" almost certainly are distinct species.

If the species pair concept is in fact true, it goes far toward explaining the chemical diversity among vegetative morphs. On the other hand, it is supported by no proof other than that offered by comparative biochemistry. As such, it may be an oversimplification that might discourage lichenologists from exploring other evolutionary processes. Some sorediate and isidiate species, for example, do produce pycnidia and microconidia which could act as fertilizing elements of fertile populations. These morphs need not remain simply as "blind alleys." Alternative hypotheses may come to light as we gain a better understanding of soredial and isidial formation, the role of microconidia, and the mechanics and frequency of gene recombination in lichens.

I believe it is profitable, nonetheless, to analyze species pairs in *Hypotrachyna* and see how much they have contributed to the evolution of the genus. The method is very simple: using a list of diaspore-bearing species, a search is made among nondiaspore-bearing fertile species which might be considered perfect morphological and chemical parents.

These parents are defined as strictly as possible with the realization that the sexual morphs may still be evolving and that the pairs may differ because of environmental modifications induced by occupying different habitats.

**SOREDIAE MORPHS.**—There are eighteen sorediate species in *Hypotrachyna* and nine of these can be reasonably paired with presumptive parents (given in alphabetic order of the sorediate species):

<i>H. brevirhiza</i>	–	<i>H. sublaevigata</i>
<i>H. densirhizinata</i>	–	<i>H. gigas</i>
<i>H. exsplendens</i>	–	<i>H. degelii</i>
<i>H. immaculata</i>	–	<i>H. livida</i>
<i>H. laevigata</i>	–	<i>H. physcioides</i>
<i>H. producta</i>	–	<i>H. ducalis</i>
<i>H. revoluta</i>	–	<i>H. pluriformis</i>
<i>H. rockii</i>	–	<i>H. pulvinata</i>
<i>H. sinuosa</i>	–	<i>H. reducens</i>

The remaining nine species cannot be so closely matched. Their origin can be hypothesized in a few cases. *Hypotrachyna flavovirens*, for example, normally contains only protocetraric acid but one specimen contains norstictic acid as well. The norstictic acid probably was contributed by a parent similar to *H. reducens* that crossed with a now extinct progenitor containing protocetraric acid. To cite another example, it is perhaps significant that *H. densirhizinata* is represented by a single chemical population whereas the presumptive parent *H. gigas* has two populations, one with gyrophoric acid in addition to alectoronic acid and one with alectoronic acid only. We are left to conclude that the sorediate morph *H. densirhizinata* evolved before the parent species *H. gigas* acquired gyrophoric acid, probably by crossing with a now extinct progenitor related to *H. thysanota*.

Let us next take a group of very similar species which, for all practical purposes, can be distinguished only by means of chemical tests:

<i>H. endochlora</i>	(barbatic acid and pigments)
<i>H. densirhizinata</i>	(alectoronic acid)
<i>H. gondylophora</i>	(fumarprotocetraric acid)
<i>H. laevigata</i>	(barbatic acid)
<i>H. oostingii</i>	(gyrophoric acid)
<i>H. producta</i>	(anziaic acid)
<i>H. rockii</i>	(evernic and lecanoric acids)
<i>H. thysanota</i>	(gyrophoric, microphyllinic, and echinocarpic acids)

If we accept the species pairs concept to explain this degree of chemical speciation, then we can appreciate how complicated is the evolutionary

pattern involved. Can we assume that these eight species originated from a single sexually reproducing ancestor because of the very similar lobe configuration and mode of forming soredia? Would it follow, then, that the present chemical diversity resulted when the ancestor hybridized with other sexual morphs to give eight chemical populations, each of which produced a vegetative morph? While four of the above species seem to have parents, four (*H. endochlora*, *H. gondylophora*, *H. oostingii* and *H. thysanota*) have no chemically comparable sexual morphs which, we must assume, are either extinct, to be represented now by four chemically stable vegetative morphs, or yet to be discovered in tropical America. If our reasoning is true, then the presumptive parents of the remaining sorediate species in the genus, *H. croceopustulata*, *H. flavovirens*, *H. pseudosinuosa*, *H. subaffinis*, and *H. velloziae*, are probably extinct.

**ISIDIATE MORPHS.**—Although lichenologists are ignorant of the causes of isidial formation, they rarely ever lump isidiate and nonisidiate species in the same taxon. In *Hypotrachyna* we find that seven of the sixteen isidiate species have chemically identical nonisidiate presumptive parents:

<i>H. andensis</i>	–	<i>H. reducens</i>
<i>H. bogotensis</i>	–	<i>H. pulvinata</i>
<i>H. consimilis</i>	–	<i>H. bahiana</i>
<i>H. ensifolia</i>	–	<i>H. gigas</i>
<i>H. imbricatula</i>	–	<i>H. physcioides</i>
<i>H. microblasta</i>	–	<i>H. enderythraea</i>
<i>H. partita</i>	–	<i>H. ducalis</i>

Two of the remaining nine isidiate species, *H. dentella* and *H. isidiocera*, are closely related to the *H. physcioides* group but differ somewhat chemically. *Hypotrachyna neodissecta* may have evolved from *H. pluriformis* but has much smaller spores. All of these vegetative morphs are rather easily distinguished morphologically and no "chemical species" complexes comparable to the *H. laevigata* group discussed above have evolved. We might assume, then, that the progenitors of isidiate morphs have hybridized or mutated to a lesser degree than the parents of sorediate morphs or that the isidiate morphs, once created, have had a lower survival rate.

**PUSTULATE MORPHS.**—Two pustulate species have perfect nonpustulate parents: *H. dactylifera*–*H. livida* and *H. formosana*–*H. novella*. *Hypotrachyna malmei* has no nonpustulate counterpart.

**OTHER MORPHS.**—None of the lobulate species, except perhaps *H. rachista*–*H. ducalis*, has a perfect nonlobulate parent. *Hypotrachyna chlorina* obviously is related to the *H. physcioides* complex because it produces barbatic acid; *H. prolongata* and *H. singularis* stand isolated.

**SERIES OF MORPHS.**—In the following species a progenitor has apparently given rise to more than one kind of morph:

*H. ducalis*–*H. producta* (sorediate)–*H. partita* (isidiate)–*H. rachista* (lobulate)

*H. livida*–*H. immaculata* (sorediate)–*H. dactylifera* (pustulate)

*H. physcioides*–*H. laevigata* (sorediate)–*H. imbricatula* (isidiate)

*H. pulvinata*–*H. rockii* (sorediate)–*H. bogotensis* (isidiate)

*H. reducens*–*H. sinuosa* (sorediate)–*H. andensis* (isidiate)

This seems to imply that most sexual morphs produce either sorediate, isidiate, or pustulate vegetative morphs and only rarely produce two or more different kinds.

In conclusion, we find that *Hypotrachyna* consists of 36 potential sexually reproducing parent or progenitor species. Twelve of these have actually produced 18 morphs, giving a total of 54 species (out of the 77 recognized in this monograph) whose possible evolutionary development can be traced. The remaining 23 asexual species can be assigned to various chemical constellations, but a few simply cannot be explained at this time.

It is my contention that the high rate of development of asexual morphs—involving 66 percent of the sexual morphs—and the coexistence of many of these presumptive progenitors are signs of comparatively recent origin for the genus. In other words, *Hypotrachyna* has been speciating rapidly since the continents drifted apart.

#### HABITAT SELECTION

The concept of habitat selection as first proposed by Culberson and Culberson (1967) helped to explain the microdistribution of chemical populations of *Ramalina siliquosa*. Three species, sympatric over their broad geographic range, segregated at different exposures on rocks into remarkably pure populations, an example of how genetically defined physiological races revealed phenotypically by chemistry (rather than morphology) were associated with distinct habitats.

Given sufficient time and resources, I believe

similar kinds of habitat selection could be demonstrated among *Hypotrachyna* species. For example, species containing barbatic acid, especially *H. physcioides*, seem indiscriminate in selecting habitats, rock, trees, or soil. The tree population seems less robust and has more distinct maculae than the saxicolous population. Two distinct species may eventually evolve because of habitat segregation. Other examples could be cited, as the possible distant relationship between *H. bahiana* (corticolous) and *H. contradicta* (saxicolous) or between *H. degelii* (corticolous) and *H. protenta* (saxicolous).

#### Classification of *Hypotrachyna*

Vainio proposed three sections in his Brazilian study: *Amphigymnia*, *Hypotrachyna*, and *Xanthoparmelia*. *Hypotrachyna* was subdivided into three groups without formal rank: *Irregularis*, *Cyclocheila*, and *Linearis*. It is this last group by which I typified subgenus *Hypotrachyna* (Vainio) Hale and Kurokawa with *Parmelia brasiliiana* Nylander as the lectotype species (Hale and Kurokawa, 1964). I recently elevated this taxon to generic level (Hale, 1974a).

Vainio assigned eleven species to *Hypotrachyna*, and, in fact, only one that he listed, *Parmelia coronata* Fée, does not belong here. Two yellow species, *P. flava* and *P. velloziae*, were placed in section *Xanthoparmelia* but they have dichotomously branched rhizines and belong in *Hypotrachyna*.

While *Hypotrachyna* contains about 110 species, there is no practical internal subdivision into subgenera or sections. The most useful approach is to combine the species into chemical constellations proposed by Culberson and Hale (1973), which are based on the probably biogenetic relationship of the chemicals in *Hypotrachyna* (Figure 6).

It is assumed that simple depsides, for example, represent the lowest evolutionary level and mixed depsidones the highest. Accordingly, in my opinion, species in the lividic acid complex (including the boxes for colensoinic acid and 4-O-methylphysodic acid) should and do represent the highest level of evolution in the genus. Without question, the barbatic-evernic acid complex has the highest level of speciation. Another advanced group, with alectoronic acid (*H. gigas*, *H. degelii*, etc.), seems to have evolved in parallel along different lines

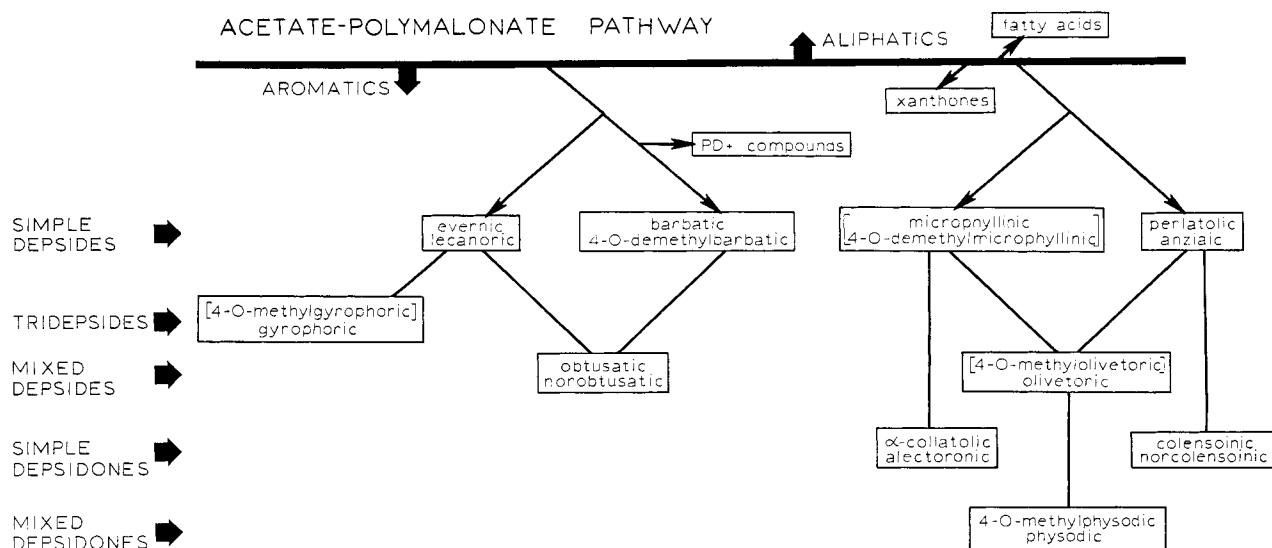


FIGURE 6.—Biogenetic relationships among secondary products in *Hypotrachyna*. Compounds connected by lines have similar chemical structures but are not necessarily derivable from the other.

and has a lower level of speciation. As one might expect, the P+ acid series represented by *H. brasiliana*, *H. enderythraea*, *H. reducens*, *H. sublaevigata*, etc., seems to include more conservative species, some pantropical.

The various species of *Hypotrachyna* are grouped provisionally (below) according to the biogenetic chart (Figure 6) and a consideration of morphological traits. The groups joined by dashes have a generally higher level of internal homogeneity than those separated by commas.

Fatty acids.—*H. costaricensis* and *H. singularis*.

PD+ compounds.—Norstictic acid derivatives: *H. andensis*—*H. reducens*—*H. rhabdiformis*—*H. sinuosa*, *H. boquetensis*—*H. brevirhiza*—*H. sublaevigata*, *H. caraccensis*—*H. enderythraea*—*H. microblasta*, *H. lopezii*, *H. subsaxatilis*. Protocetraric acid derivatives: *H. brasiliana*—*H. bahiana*, *H. consimilis*—*H. contradicta*—*H. croceopustulata*—*H. pseudosinuosa*—*H. silvatica*, *H. flavida*, *H. flavovirens*, *H. gondylophora*, *H. koyaensis*, *H. malmei*—*H. minima*, *H. obscurella*, *H. physodatica*, *H. subaffinis*—*H. velloziae*, *H. subphysodatica*.

Evernic-lecanoric.—*H. bogotensis*—*H. chicitae*—*H. pulvinata*—*H. rockii*.

Gyrophoric: *H. neodissecta*—*H. osorioi*—*H. pluriformis*—*H. revoluta*.

Barbatic: *H. subplumbeata*.

Obtusatic: *H. chlorina*—*H. dentella*—*H. endochlora*—*H. imbricatula*—*H. isidiocera*—*H. laevigata*—*H. monolifera*—*H. peruviana*—*H. physcioides*—*H. steyermarkii*, *H. protoboliviana*.

Microphyllinic: *H. thysanota*.

Alectoronic: *H. degelii*—*H. exsplendens*—*H. protenta*, *H. densirhizinata*—*H. ensifolia*—*H. gigas*—*H. lineariloba*, (?)*H. oostingii*.

Perlatolic-anziaic: *H. ducalis*—*H. partita*—*H. producta*—*H. prolongata*—*H. rachista*, *H. eitenii*.

Olivivetonin: *H. intercalanda*—*H. osteoleuca*.

Colensoinic: *H. dactylifera*—*H. erythrodes*—*H. formosana*—*H. gracilescens*—*H. immaculata*—*H. livida*—*H. novella*—*H. palmarum*.

More detailed discussions of some of these groups will be found in the section on species treatment.

## Habitats and Ecology

*Hypotrachyna* is primarily a genus of higher elevations throughout its range in the tropics. It grows near sea level only at its northern limits in southern United States and southern limits in Chile and Argentina. It is absent or very rare in xerophytic areas and in lowland (0–500 m elevation) rain forest.

The optimal area for *Hypotrachyna* is the zone between 1300 and 2400 m elevation in the major mountain chains of tropical America. The climate here is quite uniform throughout the year and precipitation comes in the form of rain and frequent clouds or mists. There are about 55 species here. Most are corticolous. Where rock outcrops are

abundant, however, a number of obligately saxicolous species may occur: *H. brasiliiana*, *H. contradicta*, *H. erythrodes*, *H. flavida*, *H. obscurella*, *H. osteoleuca*, *H. protenta*, *H. subsaxatilis*, etc. Even some typically corticolous species may grow on rocks: *H. formosana*, *H. imbricatula*, *H. microblasta*, *H. physcioides*, *H. revoluta*, etc.

The area above 2400 m in the American tropics becomes more sparsely forested and intergrades with the true treeless paramo. The *Hypotrachyna* flora here consists of 36 species, including many from the lower zone.

The high paramo has much greater climatic extremes than other zones. The 20 species occurring here (3600–4500 m elevation) include some of the most showy and spectacular ones: *H. caracensis* and *H. gigas*. *Hypotrachyna chicitae*, *H. physodalica*, and *H. subplumbeata* are the only species apparently restricted to high paramo. These paramo lichens grow on rocks, over grass and moss tussocks, and at the base of small shrubs, forming a conspicuous part of the vegetation.

The zone below 1000–1200 m in the tropics is largely true rain forest and, relatively speaking, is poor in terms of number and diversity of foliose species. Only 14 species of *Hypotrachyna* have been recorded below 1000 m. These include those from temperate and subtropical latitudes in the United States and southern South America as well as "weedy" species with broad elevational amplitude such as *H. costaricensis*, *H. formosana*, *H. laevigata*, *H. microblasta*, *H. revoluta*, and *H. rockii*.

### Phytogeographical Relationships

*Hypotrachyna*, primarily a tropical genus, is concentrated in the New World. There are 58

species that occur only in the Americas, while Asia and Africa together have only 32 endemics.

The American tropics, however, differ considerably in floristic composition and degree of endemism. Six major regions can be recognized, as shown in Table 1, where comparisons are made with pantropical elements and Europe and Africa. Europe has only one endemic, *H. taylorensis*, and four other species, *H. endochlora*, *H. laevigata*, *H. revoluta*, and *H. sinuosa*, all pantropical.

Two regions of high endemism stand out: the Andean region (Colombia, Venezuela, Peru, Ecuador, and Bolivia) and the area from Minas Gerais and Mato Grosso in Brazil to adjacent Uruguay. The farther one goes from these centers the lower the degree of endemism and speciation. Actually, the Andes and southeastern Brazil have many species in common and this number surely will be increased as more collecting is done.

Nineteen of the 77 species of *Hypotrachyna* occur outside the New World: *H. bogotensis* and *H. laevigata* are known from Europe; *H. brevihiza*, *H. costaricensis*, *H. endochlora*, *H. formosana*, *H. koyaensis*, *H. microblasta*, *H. pseudosinuosa*, *H. revoluta*, *H. rockii*, and *H. sinuosa* are pantropical or occur on at least one Old World land mass; and the most interesting group, comprising *H. dactylifera*, *H. degelii*, *H. densirhizinata*, *H. exsplendens*, *H. immaculata*, *H. livida*, and *H. subplumbeata*, occurs outside of the New World only in southern Africa, a classic pattern for plants which evolved before the continents drifted apart. In the latter group there is a preponderance of species with the lividic acid complex.

TABLE 1.—Total *Hypotrachyna* flora, number and percentage of endemic species, and number and percentage of species also occurring outside the neotropics, according to the major phytogeographical regions.

Phytogeographical region	Total flora	Endemic species		Extranetrotropical species	
		No.	Percent	No.	Percent
North America .....	19	1	5	6	32
West Indies .....	29	2	7	12	41
Mexico/Central America .....	40	4	10	14	35
Andes .....	46	9	20	11	24
Brazil/Uruguay .....	38	11	29	8	21
Chile/Argentina .....	15	2	13	7	47

### The *Hypotrachyna* Flora

The flora as presented at this time comprises 77 species. The most commonly collected ones (with number of collections examined) are *H. imbricatula* (81+), *H. costaricensis* (65+), *H. bogotensis* (60+), *H. microblasta* (52+), *H. rockii* (50+), *H. physcioides* (35+), *H. laevigata* (35), *H. sinuosa* (33), *H. caraccensis* (32), *H. gigas* (31), *H. pulvinata* (31), *H. densirhizinata* (25), and *H. livida* (25). It is noteworthy that the four commonest species are isidiate.

The rarities in the *Hypotrachyna* flora, found only once or twice, include *H. contradicta*, *H. ducalis*, *H. eitenii*, *H. malmei*, *H. minima*, *H. monilifera*, *H. neodissecta*, *H. prolongata*, *H. protoboliviana*, *H. singularis*, *H. subsaxatilis*, and *H. subplumbeata*.

The number of species in each country or political entity in tropical America varies from highs of 42 species in Venezuela and 37 in Brazil to only one species in Honduras, Puerto Rico, and Trinidad. These differences obviously reflect the intensity of collecting and not necessarily a poor flora. The following listing of the *Hypotrachyna* flora of each country shows how much work remains to be done, and hopefully it will stimulate further collecting efforts:

ARGENTINA: *H. breviphiza*, *H. densirhizinata*, *H. gigas*, *H. intercalanda*, *H. livida*, and *H. pluriformis*.

BOLIVIA: *H. caraccensis*, *H. costaricensis*, *H. densirhizinata*, *H. enderythraea*, *H. gigas*, *H. gondylophora*, *H. physcioides*, *H. pulvinata*, *H. revoluta*, and *H. sinuosa*.

BRAZIL: *H. bahiana*, *H. brasiliana*, *H. caraccensis*, *H. chlorina*, *H. consimilis*, *H. contradicta*, *H. costaricensis*, *H. dactylifera*, *H. degelii*, *H. dentella*, *H. eitenii*, *H. enderythraea*, *H. endochlora*, *H. erythrodes*, *H. flavida*, *H. formosana*, *H. gracilescens*, *H. imbricatula*, *H. immaculata*, *H. intercalanda*, *H. isidiocera*, *H. laevigata*, *H. livida*, *H. malmei*, *H. microblasta*, *H. minima*, *H. novella*, *H. obscurella*, *H. palmarum*, *H. peruviana*, *H. pluriformis*, *H. protenta*, *H. pulvinata*, *H. rockii*, *H. silvatica*, *H. subaffinis*, and *H. velloziae*.

CHILE: *H. bogotensis*, *H. breviphiza*, *H. dactylifera*, *H. densirhizinata*, *H. flavovirens*, *H. formosana*, *H. imbricatula*, *H. laevigata*, *H. oostingii*, *H. pseudosinuosa*, *H. revoluta*, *H. rockii*, *H. sinuosa*, *H. sublaevigata*, and *H. subphysodalica*.

COLOMBIA: *H. andensis*, *H. bogotensis*, *H. caraccensis*, *H. costaricensis*, *H. degelii*, *H. densirhizinata*, *H. endochlora*, *H. ensifolia*, *H. flavida*, *H. gigas*, *H. imbricatula*, *H. isidiocera*, *H. laevigata*, *H. microblasta*, *H. osteoleuca*, *H. physcioides*, *H. physodalica*, *H. producta*, *H. protenta*, *H. pulvinata*, *H. rachista*, *H. reducens*, *H. rockii*, and *H. sinuosa*.

COSTA RICA: *H. andensis*, *H. bogotensis*, *H. caraccensis*, *H. chicitae*, *H. costaricensis*, *H. dactylifera*, *H. densirhizinata*, *H. endochlora*, *H. ensifolia*, *H. exsplendens*, *H. gondylophora*, *H. imbricatula*, *H. laevigata*, *H. microblasta*, *H. partita*, *H. physcioides*, *H. protenta*, *H. protoboliviana*, *H. pulvinata*, *H. rockii*, and *H. sinuosa*.

CUBA: *H. costaricensis*, *H. formosana*, *H. imbricatula*, *H. microblasta*, and *H. rockii*.

DOMINICAN REPUBLIC: *H. bogotensis*, *H. consimilis*, *H. costaricensis*, *H. densirhizinata*, *H. endochlora*, *H. ensifolia*, *H. gondylophora*, *H. imbricatula*, *H. isidiocera*, *H. laevigata*, *H. lineariloba*, *H. microblasta*, *H. physcioides*, *H. pseudosinuosa*, *H. rachista*, *H. revoluta*, *H. rockii*, *H. sinuosa*, *H. subaffinis*, and *H. velloziae*.

ECUADOR: *H. bogotensis*, *H. breviphiza*, *H. caraccensis*, *H. densirhizinata*, *H. enderythraea*, *H. gigas*, *H. microblasta*, *H. pulvinata*, and *H. sinuosa*.

GUATEMALA: *H. caraccensis*, *H. costaricensis*, *H. densirhizinata*, *H. exsplendens*, *H. formosana*, *H. imbricatula*, *H. isidiocera*, *H. microblasta*, *H. physcioides*, *H. pulvinata*, *H. rockii*, and *H. subaffinis*.

GUYANA: *H. imbricatula* and *H. laevigata*.

HAITI: *H. bahiana*, *H. bogotensis*, *H. chlorina*, *H. costaricensis*, *H. croceopustulata*, *H. densirhizinata*, *H. ensifolia*, *H. formosana*, *H. imbricatula*, *H. microblasta*, *H. physcioides*, *H. prolongata*, *H. pseudosinuosa*, *H. rockii*, *H. sinuosa*, *H. subaffinis*, and *H. velloziae*.

HONDURAS: *H. imbricatula*.

JAMAICA: *H. bogotensis*, *H. costaricensis*, *H. enderythraea*, *H. ensifolia*, *H. exsplendens*, *H. imbricatula*, *H. isidiocera*, *H. laevigata*, *H. microblasta*, *H. pseudosinuosa*, *H. pulvinata*, and *H. rockii*.

LESSER ANTILLES (Dominica, Grenada, Guadeloupe, Martinique, and St. Vincent): *H. costaricensis*, *H. imbricatula*, *H. laevigata*, *H. microblasta*, *H. pseudosinuosa*, and *H. rockii*.

MEXICO: *H. bogotensis*, *H. consimilis*, *H. costaricensis*, *H. croceopustulata*, *H. dactylifera*, *H. densirhizinata*, *H. dentella*, *H. endochlora*, *H. ensifolia*, *H. exsplendens*, *H. formosana*, *H. gigas*, *H. gondylophora*, *H. imbricatula*, *H. isidiocera*, *H. koyaensis*, *H. laevigata*, *H. microblasta*, *H. physcioides*, *H. pluriformis*, *H. pseudosinuosa*, *H. pulvinata*, *H. rachista*, *H. rockii*, *H. sinuosa*, *H. subaffinis*, *H. sublaevigata*, *H. subplumbeata*, *H. subsaxatilis*, and *H. thysanota*.

PANAMA: *H. boquetensis*, *H. caraccensis*, *H. chlorina*, *H. costaricensis*, *H. dactylifera*, *H. densirhizinata*, *H. endochlora*, *H. ensifolia*, *H. formosana*, *H. gigas*, *H. imbricatula*, *H. isidiocera*, *H. microblasta*, *H. partita*, *H. physcioides*, *H. protenta*, *H. pulvinata*, *H. rachista*, *H. reducens*, *H. rhabdiformis*, *H. rockii*, and *H. sublaevigata*.

PERU: *H. andensis*, *H. bogotensis*, *H. caraccensis*, *H. chicitae*, *H. chlorina*, *H. costaricensis*, *H. degelii*, *H. densirhizinata*, *H. ducalis*, *H. enderythraea*, *H. erythrodes*, *H. flavida*, *H. formosana*, *H. gigas*, *H. imbricatula*, *H. microblasta*, *H. peruviana*, *H. physodalica*, *H. protenta*, *H. pulvinata*, *H. rachista*, *H. reducens*, *H. rhabdiformis*, *H. rockii*, and *H. singularis*.

PUERTO RICO: *H. consimilis*.

TRINIDAD: *H. imbricatula*.

URUGUAY: *H. dactylifera*, *H. endochlora*, *H. livida*, *H. osorioi*, and *H. pluriformis*.

VENEZUELA: *H. andensis*, *H. bogotensis*, *H. brevihiza*, *H. caraccensis*, *H. chicitae*, *H. chlorina*, *H. consimilis*, *H. costaricensis*, *H. dactylifera*, *H. densirhizinata*, *H. dentella*, *H. ducalis*, *H. enderythraea*, *H. endochlora*, *H. ensifolia*, *H. erythrodes*, *H. flavida*, *H. formosana*, *H. gigas*, *H. gondylophora*, *H. imbricatula*, *H. immaculata*, *H. isidiocera*, *H. laevigata*, *H. livida*, *H. lopezii*, *H. microblasta*, *H. monilifera*, *H. neodissecta*, *H. novella*, *H. obscurella*, *H. osteoleuca*, *H. partita*, *H. physcioides*, *H. physodalica*, *H. protenta*, *H. pulvinata*, *H. rachista*, *H. revoluta*, *H. rockii*, *H. sinuosa*, and *H. steyermarkii*.

### Nomenclature

One of the most time-consuming tasks in any monographic effort is unraveling problems in nomenclature and typification. The literature must be searched as completely as possible, the identity and location of type specimens must be determined, and, where needed, lectotypes must be selected. I have decided to use a narrow interpretation of the Code of Botanical Nomenclature in defining types.

A holotype, as I employ the term here, is the specimen actually designated as such by an author. This includes all species described since 1958 when the designation "holotype" became mandatory for a single element on which a new taxon is based. Before 1958 Gyelnik seems to be the only lichenologist who consistently used this term in a correct, modern sense. All other authors either failed to cite a holotype collection or left to later workers the job of deciding which of two or more specimens cited in a species description is the lectotype.

A lectotype, then, in my definition, includes two cases, one in which one of the published syntypes is selected as the lectotype and another where the author listed only one collection in his description but failed to call it a holotype and often did not state clearly where the specimen was housed. In other words, I am often selecting one specimen out of several duplicate collections as the lectotype.

The point of departure here is that I had formerly applied the term "holotype" to a collection which represented the only material cited by an author. Because of the element of selection involved, even as to location of the specimen, I feel the use of the term "lectotype" is justified.

It should be emphasized that selection of lectotypes is not binding on later workers. The Code allows us to lectotypify a species again if better evidence can be produced to support the change. This may happen, for example, when a second worker discovers a specimen in another collection that is in better condition or is more appropriate than the previously designated lectotype. A possibly undesirable amount of nomenclatorial instability may be introduced in these circumstances, but this seems a better course than rigidly following a lectotypification which the earlier worker himself admits may be faulty.

### Keys to the Species

The following keys are divided into three major groups: sorediate, isidiate, and nonsorediate-nonisidiate species. The main division under each group is presence or absence of usnic acid (cortex greenish yellow or whitish to ashy gray). Following this, a combination of pigment and morphological characters is used, but ultimately chemical tests are called for. The standard color tests with KOH, calcium hypochlorite (or other bleach), and p-phenylenediamine suffice to identify a number of species and species groups, but below this level it is highly desirable, if not sometimes mandatory, to identify the substances with microchemical tests, preferably thin-layer chromatography. Further clues as to the species identity can be gained by comparing the specimens with the photographs and by consulting the descriptions and geographical distribution. The geographic ranges of many species will undoubtedly be extended as more collections are made, but geography is still a valuable aid.

### Key to Species with Thallus Sorediate or Sorediate-Pustulate

1. Thallus greenish yellow (usnic acid present).
  2. Lobes very narrow, less than 1 mm wide; medulla K- ..... 77. *H. velloziae*
  2. Lobes 1-3 mm wide; medulla K+ red or K- .
    3. Medulla K+ yellow turning red ..... 69. *H. sinuosa*
    3. Medulla K- (protocetraric acid) ..... 26. *H. flavovirens*

1. Thallus whitish to ashy gray (usnic acid lacking).
4. Medulla uniformly yellow .....21. *H. endochlora*
4. Medulla white.
  5. Soralia distinct, generally terminal or subterminal, soredia powdery.
    6. Medulla K+ red (salazinic acid) .....6. *H. brevibriza*
    6. Medulla K- or slowly dull yellowish.
      7. Medulla C+ rose, red, or orange-red.
        8. Soralia orbicular, distinct .....*H. laevigata* group  
(Barbatic acid: 36. *H. laevigata*; evernic-lecanoric acids: 66. *H. rockii*; gyrophoric acid: 47. *H. oostingii*; anziaic acid: 56. *H. producta*; gyrophoric-echinocarpic acids: 76. *H. thysanota*.)
        8. Soralia more irregular and diffuse (Figure 2a); gyrophoric acid present .....  
.....64. *H. revoluta*
    7. Medulla C- .
      9. Medulla P+ red.
        10. Lobes narrow, 1-2 mm wide; thallus closely adnate .....  
.....60. *H. pseudosinuosa*
        10. Lobes 2-5 mm wide; thallus loosely attached .....29. *H. gondylophora*
      9. Medulla P- .
        11. Thallus adnate; lobes short .....24. *H. exsplendens*
        11. Thallus loosely attached; lobes long-divaricate .....16. *H. densirhizinata*
  5. Soralia laminal toward the center of the thallus.
    12. Soralia with powdery soredia.
      13. Lobes narrow, about 1 mm wide; thallus closely adnate .....71. *H. subaffinis*
      13. Lobes 1-5 mm wide; thallus loosely adnate.
        14. Medulla C+ red (gyrophoric acid) .....64. *H. revoluta*
        14. Medulla C- .
          15. Medulla P+ red .....13. *H. croceopustulata*
          15. Medulla P- .....32. *H. immaculata*
    12. Soralia pustulate with sparse coarse soredia or pustules present.
      16. Lichexanthone present (thallus yellow in UV light).
        17. Lobes narrow, 1-2 mm; confined to Brazil .....40. *H. malmei*
        17. Lobes 1-5 mm wide; pantropical .....27. *H. formosana*
      16. Lichexanthone absent (no fluorescence in UV).
        18. Medulla C+ rose (gyrophoric acid); isidiate pustules solid ....48. *H. osorioi*
        18. Medulla C- .
          19. Pustules becoming sorediate (Figure 2c) .....13. *H. croceopustulata*
          19. Pustules not sorediate (Figure 2d) .....14. *H. dactylifera*

### Key to Species with Thallus Isidiate, Isidiate-Lobulate, or Pustulate

1. Thallus greenish yellow (usnic acid present).
  2. Medulla K- .....73. *H. subphysodalica*
  2. Medulla K+ red.
    3. Isidia distinctly lobulate .....1. *H. andensis*
    3. Isidia remaining cylindrical .....41. *H. microblasta*
1. Thallus whitish to ashy gray.
  4. Medulla uniformly yellow .....34. *H. isidiocera*
  4. Medulla white.
    5. Isidia mostly laminal on the lobe surface.
      6. Isidia inflated and hollow (pustules). See dichotomy 17 in the sorediate key above.
      6. Isidia cylindrical, solid, not strongly inflated.
        7. Medulla K+ yellow turning red .....65. *H. rhabdiformis*
        7. Medulla K- or slowly pale yellowish.
          8. Medulla C+ (and KC+) orange (barbatic acid group).
            9. Lobes narrow and appressed, 1-2 mm wide; isidia ciliate. ....  
.....70. *H. steyermarkii*
            9. Lobes 2-5 mm wide, isidia eciliate.
              10. Medulla P- .....31. *H. imbricatula*



10. Medulla P+ red .....17. *H. dentella*
8. Medulla C+ rose or red or C-.
11. Medulla C+ rose or red (anziaic or gyrophoric acids).
12. Isidia cylindrical, erect .....44. *H. neodissecta*
12. Isidia not cylindrical.
13. Isidia becoming lobulate, procumbent .....51. *H. partita*
13. Isidia club-shaped, crumbling apically .....48. *H. osorioi*
11. Medulla C- or faint C+ rose (lecanoric acid).
14. Isidia hollow (pustules) .....14. *H. dactylifera*
14. Isidia solid, not pustulate.
15. Medulla P+ red (protocetraric acid).
16. Lobes sublinear, 1-3 mm wide .....10. *H. consimilis*
16. Lobes subirregular, 3-7 mm wide .....35. *H. koyaensis*
15. Medulla P-.
17. Isidia cylindrical, erect; fatty acids present .....12. *H. costaricensis*
17. Isidia becoming lobulate, procumbent.
18. Aleatoronic acid present (strongly white fluorescent under UV) .....22. *H. ensifolia*
18. Evernic and lecanoric acids present (weak to negative fluorescence) .....3. *H. bogotensis*
5. Isidia marginal toward lobe tips (Figure 4d).
19. Anziaic acid present .....62. *H. rachista*
19. Unknown C+ substance present; known only from Haiti .....57. *H. prolongata*

### Key to Species with Thallus Lacking Soredia, Isidia, and Pustules

1. Thallus greenish yellow (usnic acid present).
2. Lobes long and little branched, divaricate; thallus loosely attached.
3. Medulla K- .....54. *H. physodalica*
3. Medulla K+ yellow turning red.
4. Stictic acid present .....39. *H. lopezii*
4. Salazinic acid present .....7. *H. caraccensis*
2. Lobes shorter, moderately branched; thallus generally adnate.
5. Medulla K+ yellow turning red.
6. Thallus corticolous .....63. *H. reducens*
6. Thallus saxicolous .....20. *H. enderythraea*
5. Medulla K- or K+ very pale yellow.
7. Thallus corticolous; medulla C+ orange .....59. *H. protoboliviana*
7. Thallus saxicolous; medulla C- .....25. *H. flavida*
1. Thallus whitish to ashy gray.
8. All or most of the medulla pigmented yellow or red.
9. Thallus saxicolous.
10. Medulla C+ deep red (olivetric acid) .....49. *H. osteoleuca*
10. Medulla C- .....23. *H. erythrodes*
9. Thallus corticolous.
11. Margins of lobes densely lobulate (Figure 4e) .....9. *H. chlorina*
11. Margins of lobes sparsely lobulate or lacking lobules.
12. Pigment pale yellow, throughout the medulla .....52. *H. peruwiana*
12. Pigment red, occurring in the lower half of the medulla .....67. *H. silvatica*
8. Medulla white throughout.
13. Lobes long and little branched; thallus loosely attached.
14. Medulla C+ orange (barbatic acid group) .....43. *H. monilifera*
14. Medulla C+ rose or red or C-.
15. Medulla C+ deep red (anziaic acid) .....18. *H. ducalis*
15. Medulla C+ rose or C- (aleatoronic acid).
16. Thallus small, 3-6 cm broad .....37. *H. lineariloba*
16. Thallus larger, more than 8 cm broad .....28. *H. gigas*
13. Lobes shorter and moderately branched; thallus adnate.

17. Thallus collected on rocks.
18. Medulla K+ yellow turning red (salazinic acid) .....75. *H. subsaxatilis*
18. Medulla K- or K+ pale yellow.
19. Medulla C+ orange or red.
20. Medulla C+ orange (barbatic acid) .....53. *H. physcioides*
20. Medulla C+ red or rose.
21. Lower part of medulla pigmented orange .....49. *H. osteoleuca*
21. Medulla all white.
22. Medulla C+ deep red (anziaic acid) .....19. *H. eitenii*
22. Medulla C+ rose or C- .....8. *H. chicitae*
19. Medulla C-.
23. Medulla P+ red (protocetraric acid).
24. Lichexanthone present in the cortex (UV+ orange).
25. Lobes sublinear-elongate, coriaceous .....5. *H. brasiliana*
25. Lobes short, brittle and fragile .....42. *H. minima*
24. Lichexanthone absent (UV-).
26. Thallus dark gray; lobes about 1 mm wide, short .....46. *H. obscurella*
26. Thallus whitish gray; lobes 2-4 mm wide .....11. *H. contradicta*
23. Medulla P-.
27. Lichexanthone present in cortex (UV+ orange) .....23. *H. erythrodes*
27. Lichexanthone absent.
28. Lividic acid group present .....38. *H. livida*
28. Lividic acid group absent.
29. Alectoronic acid present .....58. *H. protenta*
29. "Gracilescens" unknown present .....30. *H. gracilescens*
17. Thallus collected on trees.
30. Medulla K+ yellow turning red (salazinic acid).
31. Norstictic acid present .....72. *H. sublaevigata*
31. Norstictic acid absent .....4. *H. boquetensis*
30. Medulla K- or K+ pale yellow.
32. Medulla P+ red (protocetraric acid) .....2. *H. bahiana*
32. Medulla P-.
33. Medulla C+ orange, red, or rose.
34. Medulla C+ orange (barbatic acid group).
35. Apothecia strongly stalked .....52. *H. peruviana*
35. Apothecia adnate.
36. Maculae absent to weakly developed .....53. *H. physcioides*
36. Maculae strongly developed (Figure 4f) .....74. *H. subplumbeata*
34. Medulla C+ red or rose.
37. Lobes subirregular, broadly canaliculate; C+ rose (gyrophoric acid) .....55. *H. pluriformis*
37. Lobes sublinear, not canaliculate.
38. Maculae usually conspicuous; evernic and lecanoric acids present .....61. *H. pulvinata*
38. Maculae absent; olivetoric acid present .....33. *H. intercalanda*
33. Medulla C-.
39. Lobe margins distinctly lobulate .....68. *H. singularis*
39. Lobe margins without lobulae.
40. Lichexanthone present in cortex (UV+ orange) .....45. *H. novella*
40. Lichexanthone absent.
41. Alectoronic acid present .....15. *H. degelii*
41. Alectoronic acid absent.
42. Lividic acid present .....38. *H. livida*
42. "Palmarum" unknown present .....50. *H. palmarum*

## Species Treatment

The species are arranged in alphabetic order. Standard herbarium acronyms are given to show the location of specimens cited except for collections by Hale, all of which are in US.

### 1. *Hypotrachyna andensis*, new species

FIGURE 7a

Thallus arcte adnatus vel adnatus, fragilis, 4–7 cm latus, viridi-flavicans, lobis sublinearibus, separatis, 1–3 mm latis; superne isidiatus, isidiis lobulatis; cortex superior 12 $\mu$ –14 $\mu$  crassus, stratum gonidiale 24 $\mu$ –28 $\mu$  crassum, medulla alba, 120 $\mu$ –130 $\mu$  crassa, cortex inferior 12 $\mu$ –14 $\mu$  crassus; subtus niger, dense rhizinosus. Apothecia substipitata, sporis simplicibus, 10 $\mu$   $\times$  14 $\mu$ .

Thallus closely adnate on twigs or on soil, fragile, 4–7 cm broad, yellowish green; lobes sublinear, rather elongate, mostly separate, 1–3 mm wide; upper surface plane, continuous, becoming isidiate, the isidia at length lobulate, the lobules dorsiventral, about 0.5 mm long, often with short cilia; lower surface densely rhizinate, the rhizines moderately dichotomously branched. Apothecia substipitate, 1–3 mm in diameter; spores 10 $\mu$   $\times$  14 $\mu$ .

CHEMISTRY.—Cortex K–, medulla K+ yellow turning red, C–, P+ orange (usnic acid, norstictic acid, and salazinic acid (holotype); or more rarely norstictic acid, stictic acid, and constictic acid).

TYPE COLLECTION.—San Martín, Peru, *Holligan* L 128 (BM, holotype).

DISTRIBUTION.—Central America, Colombia, Venezuela, and Peru.

HABITAT.—On branches of small shrubs in the paramo or on road banks at 2800–3700 m elevation.

REMARKS.—This paramo species usually is densely isidiate-lobulate. The presumptive progenitor is *H. reducens*. The chemical variation parallels that in *H. sinuosa*, the soreidiate morph.

SPECIMENS EXAMINED.—Costa Rica: Cartago, *Almeda* 2457 (DUKE). Colombia: Cundinamarca, *Cuatrecasas* 27068b (US). Venezuela: Mérida, *Hale* 42658a, 43072, 43146. Peru: *Bryan* 596 (WIS).

### 2. *Hypotrachyna bahiana*, new combination

FIGURE 7b

*Parmelia bahiana* Nylander, 1885: 612. [Type collection: Bahia, Brazil, *Blanchet* (H, lectotype; M, P, isolectotypes).]

*Parmelia insinuans* Nylander, 1885:612. [Type collection: Tropical America, *Bonpland* (H, lectotype; P, isolectotype).]

*Parmelia flava* f. *albescens* Krempelhuber, 1873:10. [Type collection: Serra da Mantiqueira, Brazil, *Warming* (M, lectotype).]

Thallus adnate, mineral gray, 3–6 cm broad; lobes sublinear, short, 1–2 mm wide; upper surface plane, continuous, soredia and isidia lacking; lower surface moderately to densely rhizinate, the rhizines densely dichotomously branched. Apothecia common, adnate, 2–4 mm in diameter; spores 6 $\mu$ –8 $\mu$   $\times$  10 $\mu$ –13 $\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, P+ orange-red (atranorin, protocetraric acid, and, if pigmented in the lower medulla, rhodophyscin).

DISTRIBUTION.—West Indies, Brazil.

HABITAT.—On trees in open forest at 1000–2000 m elevation.

REMARKS.—*Hypotrachyna bahiana* is externally similar to *H. physcioides* but differs in chemistry. It is common only in Brazil. The isidiate morph is *H. consimilis*.

SPECIMENS EXAMINED.—Haiti: Sud, *Imshaug* 23229, *Wetmore* 3364 (MSC). Brazil: Minas Gerais, *Warming* 280 (M); Rio de Janeiro, *Eiten* 6433, 7502 (US), *Glaziou* 1119 (G,H,P).

### 3. *Hypotrachyna bogotensis*, new combination

FIGURE 7c

*Parmelia bogotensis* Vainio, 1899: (122). [Type collection: Bogotá, Colombia, *Weir* 53 (TUR, lectotype; BM, isolectotype).]

*Parmelia culmigena* Zahlbruckner, 1905:81. [Type collection: El Altar, Ecuador, *Meyer* 381 (W, lectotype).]

Thallus adnate to loosely attached, 6–12 cm broad; lobes sublinear, dichotomously branched, 1–6 mm wide; upper surface plane, shiny, white-maculate, densely isidiate, the isidia cylindrical or at length procumbent and dorsiventral; lower surface densely rhizinate, the rhizines finely branched and forming a woolly mat. Apothecia very rare, adnate, to 5 mm in diameter; spores 6 $\mu$   $\times$  12 $\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+, KC+ rose to red, P– (atranorin, evernic acid, and lecanoric acid).

DISTRIBUTION AND HABITAT.—Mexico, Central America, West Indies, South America south to

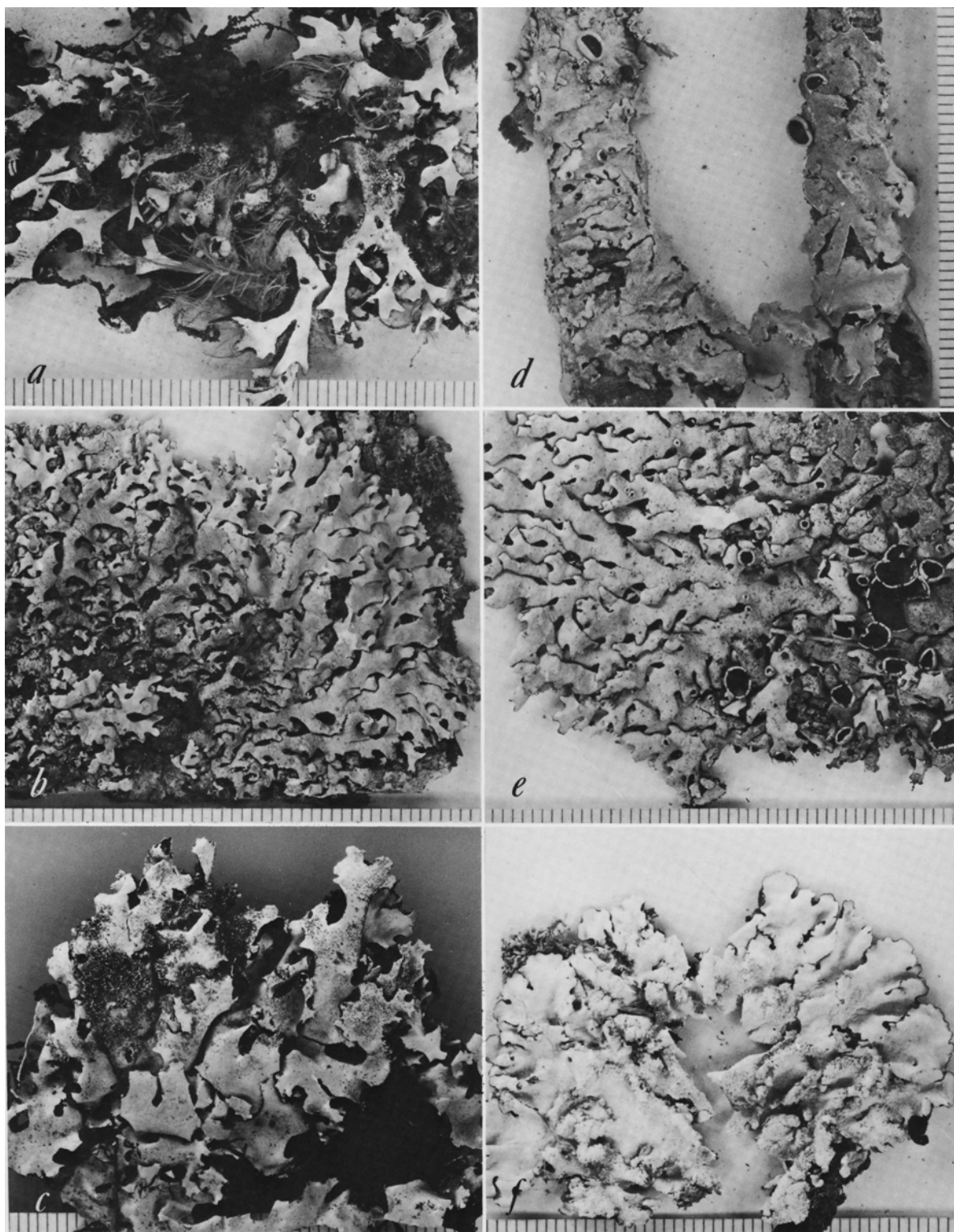


FIGURE 7.—Species of *Hypotrachyna*: a, *H. andensis* (Holligan L128); b, *H. bahiana* (Eiten 7502); c, *H. bogotensis* (Oberwinkler and Poelt 7544); d, *H. boquetensis* (Hale 38878) e, *H. brasiliana* (Reitz and Klein 10187); f, *H. brevirhiza* (Hale 42532). (Scale in mm.)

Chile on trees in secondary and primary forests (oak, pine, *Drimys*), shrubs, fence posts, rocks, and soil on road banks at 1800–4100 m elevation.

REMARKS.—This is an extremely variable and widespread species. The isidia may be quite sparse and merely papillate or even subsorediate but can eventually enlarge and grow procumbent (Figure 4c), almost as narrow lobules, as Vainio (1899) has noted. *Parmelia culmigena* represents this extreme form. It is closely related to both *H. pulvinata*, the presumptive progenitor, and *H. rockii*, a sorediate morph. Care must be taken to distinguish it from *H. ensifolia* (alectoronic acid present) when, as is often the case, both species occur in the same habitat, especially on roadsides.

REPRESENTATIVE SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 20266, 20541, 20542; Oaxaca, *Hale* 20684, 20788; Sinaloa, *Culberson* 13384, 13421 (DUKE). Costa Rica: Alajuela, *Culberson* 12369 (DUKE). Jamaica: *Imshaug* 13044, 15442, 15465 (MSC, US), *Plitt* 129 (US). Haiti: Ouest, *Imshaug* 22959 (MSC, US), 22958 (MSC); Sud, *Imshaug* 23232 (MSC), *Wetmore* 3294, 3369 (MSC). Dominican Republic: La Vega, *Imshaug* 23371, 23402, 23406 (MSC, US), 23537, 23548 (MSC), *Wetmore* 3481, 3613, 3620 (MSC, US), 3522, 3627, 3662 (MSC). Colombia: Boyacá, *Cuatrecasas* 1364a (US); Santander, *Killip and Smith* 18942 (NY), 18594 (US). Venezuela: Mérida, *Hale* 42387, 42607, 43120, 43200, 43277, 43350, *Poelt and Oberwinkler* 13172b, 14427c (M). Peru: *Bryan* 399 (F). Ecuador: *Jameson* 144 (BM). Chile: Aysén, *Santesson* 4309, 4345, 4488, 6943, 6945 (S); Chiloe, *Santesson* 4192 (S); Juan Fernandez, *Skottsberg* 87 (NY, S, US), 198 (BM), *Imshaug* 37384 (MSC); Valdivia, *Santesson* 3274, 3521 (S, US), 3272, 3387, 3404, 3475, 3556, 3710, 7149 (S).

#### 4. *Hypotrachyna boquetensis*, new combination

FIGURE 7d

*Parmelia boquetensis* Hale, 1974b:265. [Type collection: Boquete, Chiriquí, Panama, *Hale* 38878 (US).]

Thallus closely adnate on branches, 8–12 cm broad, greenish ashy gray; lobes subirregular, 3–4 mm wide, the margins toward the center becoming lobulate; upper surface smooth, cracked with age and with conspicuous marginal pycnidia;

lower surface black, sparsely to moderately rhizinate. Apothecia common, adnate, 2–3 mm in diameter; spores  $6\mu \times 12\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K+ red, P+ orange (atranorin and salazinic acid).

DISTRIBUTION.—Panama.

HABITAT.—On trunks and branches of hardwood trees in open pastures at about 1500 m elevation.

REMARKS.—This species is still known only from Panama, where it is rather common in the Chiriquí area. While at first sight similar to *H. sublaevigata*, the lobes are larger and more irregular, pruina does not develop, and the chemistry is different.

SPECIMENS EXAMINED.—Panama: Chiriquí, *Hale* 38811, 38831, 38848, 38902.

#### 5. *Hypotrachyna brasiliana*, new combination

FIGURE 7e

*Parmelia brasiliana* Nylander, 1885:611. [Type collection: Organ Mountains, Brazil, *Weddell* (H, lectotype; P, isotype).]

*Parmelia glaziovii* Müller Argau, 1889:354. [Type collection: Rio de Janeiro, Brazil, *Glaziou* 16670 (G, lectotype).]

Thallus loosely adnate on rocks, coriaceous, ashy white, 6–20 cm in diameter; lobe sublinear, divaricate, 1–4 mm wide; upper surface plane, continuous, irregularly wrinkled and cracked with age; lower surface sparsely to moderately rhizinate, rhizines sparsely dichotomously branched. Apothecia common, adnate, 2–5 mm in diameter; spores  $4\mu\text{--}6\mu \times 8\mu\text{--}10\mu$ .

CHEMISTRY.—Cortex K–, medulla K–, C–, P+ red (lichexanthone and protocetraric acid).

DISTRIBUTION.—Southeastern Brazil.

HABITAT.—On rocks at open rocky slopes at 1000–2300 m elevation.

REMARKS.—*Hypotrachyna brasiliana* is one of the more conspicuous and commonly collected saxicolous lichens in the Rio area. It grows loosely, often on sandstone, forming large whitish colonies that are easily detached. Two related species in the same habitats, *H. contradicta* (lichexanthone absent) and *H. eitenii* (medulla C+ red), would have to be distinguished by chemical tests.

SPECIMENS EXAMINED.—Brazil: Mato Grosso, *Malme* 309, 312, 321B, 2246B (S); Minas Gerais,

*Eiten* 7028, 7031 (US), *Malme* 312A (UPS), *Mosen* 2319bis (UPS), *Vainio* 1184 (BM, M, TUR, UPS), 1189 (M, TUR), 1249 (TUR), 1280 (BM, TUR, UPS); Rio de Janeiro, *Eiten* 6594A (US); Santa Catarina, *Reitz and Klein* 10187 (US), *Ule* 155 (G); São Paulo, *Schiffner* (W).

### 6. *Hypotrachyna brevirhiza*, new combination

FIGURE 7f

*Parmelia brevirhiza* Kurokawa in Hale and Kurokawa, 1964: 166. [Type collection: Isla Riesco, Magallanes, Chile, *Santesson* 2066 (S, holotype; US, isotype).]

Thallus closely adnate, ashy white, 3–6 cm broad; lobes subirregular and short, 1–5 mm wide; upper surface plane to rugulose, dull, frequently white-pruinose, sorediate toward the lobe tips and in part laminally, the soredia coarse and rather diffuse; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia very rare, adnate, to 5 mm in diameter; spores poorly developed,  $3\mu\text{--}4\mu \times 6\mu\text{--}8\mu$ .

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

DISTRIBUTION.—Pantropical in equatorial regions and in southern Chile and Argentina.

HABITAT.—On trees in mist forest, secondary forest, and on rocks at 2000–3800 m elevation (but near sea level in Chile).

REMARKS.—Additional collections of this species were made in the Pacific region and Africa after it was described from Chile. It is essentially pantropical in montane regions. The rather diffuse soralia, very dense rhizine mat, and tendency to form coarse pruina are characteristic features. Closely related *H. majoris* (Vainio) Hale, known from Madagascar and eastern Asia, consistently produces zeorine in addition to salazinic acid. A negative KOH test would separate *H. pseudo-sinuosa* from *H. brevirhiza*.

SPECIMENS EXAMINED.—Venezuela: Mérida, *Hale* 42377; Táchira, *Hale* 42532. Ecuador: Pinchincha, *Knight* 1084B (WIS). Chile: Santiago, *Mahu* 2133 (US). Other records from Chile and Argentina are listed in Hale and Kurokawa (1964:167).

### 7. *Hypotrachyna caraccensis*, new combination

FIGURE 8a

*Parmelia caraccensis* Taylor, 1847:163. [Type collection: Caracas, Venezuela, *Linden* 576 (FH-TAYL, lectotype; BM, G, isolectotypes).]

*Parmelia sinuosa* var. *caraccensis* (Taylor) Lindsay, 1859:218. *Parmelia caraccensis* var. *guatemalensis* Steiner, 1903:234. [Type collection: Guatemala, *Friedrichsthal* (W, lectotype).]

*Parmelia caraccensis* var. *guatemalensis* f. *adspersa* Zahlbruckner, 1905:82. [Type collection: El Altar, Ecuador, *Meyer* 341 (W, lectotype).]

*Parmelia endorubra* Gyelnik, 1934:154. [Type collection: Peru, *Lillie* 1040 (BP, holotype).]

Thallus loosely attached, massicot yellow, 6–30 cm in diameter; lobes long-linear, separate, 2–6 mm wide; upper surface plane, continuous, lacking soredia and isidia; lower surface densely rhizinate, the rhizines densely dichotomously branched, forming a projecting mat along the lobes. Apothecia adnate, 3–9 mm in diameter; spores  $6\mu\text{--}8\mu \times 11\mu\text{--}13\mu$ .

CHEMISTRY.—Cortex K–, medulla K+ red, P+ orange (usnic acid, galbinic acid, norstictic acid, and salazinic acid).

DISTRIBUTION.—Central America southward in the Andes to Bolivia and in southeastern Brazil.

HABITAT.—On hardwood trees, humus, and mosses at 1500–4200 m elevation.

REMARKS.—This must be regarded as the most conspicuous and typical of all the *Hypotrachyna* in the paramo region. It grows in large mats on exposed humus or among grass tussocks. When pressed and dried it tends to fragment. It could only be confused with unusually large or loosely adnate specimens of *H. enderythraea*, which has imbricate, smaller lobes, or with *H. lopezii*, which contains stictic acid.

The syntype from Quito, Ecuador (*Jameson* 1845), is this species. The spores of var. *guatemalensis* are given as  $14\mu\text{--}20\mu$  long, larger than in other material examined, but I doubt that this difference justifies varietal rank.

SPECIMENS EXAMINED.—Costa Rica: Cartago, *Almeda* 737e (DUKE), *Brenes* 34 (US), *Dodge* (US), *Standley* 35221 (US); San José, *Crosby* 3928 (DUKE). Panama: Chiriquí, *Kozlousky and Sawyer* 178 (WIS), *Scholander* (US). Colombia: Boyacá: *Grubb and Guymer* L85b (BM); Cundinamarca, *Barclay* 6107 (US), *Lindig* 2594 (BM, M,



FIGURE 8.—Species of *Hypotrachyna*: a, *H. caraccensis* (Hale 42446); b, *H. chicitae* (Culberson 13210); c, *H. chlorina* (Eiten 7671b); d, *H. consimilis* (Eiten 7293); e, *H. contradicta* (Reitz and Klein 15727); f, *H. costaricensis* (Hale 42139). (Scale in mm.)

P), *Soderstrom* 1305 (US), *Weir* 17 (BM); Santander, *Ariste* (US), *Killip and Smith* 17562 (US). Venezuela: Mérida, *Dennis* 1925 (BM, US), *Hale* 42446, 42676, 42862, 43063, *Nilson* 1523 (UPS), *Oberwinkler* 13171b (M), *Vareschi* 946, 1472 (US). Peru: *Holligan* 60B (BM), *Lechler* 2728 (G, H, M). Ecuador: *Jameson* 137 (BM, US). Bolivia: La Paz: *Julio* 416 (US). Brazil: Minas Gerais, *Damazio* 13 (TUR); Rio de Janeiro, *Lobb* (BM).

### 8. *Hypotrachyna chicitae*, new combination

FIGURE 8b

*Parmelia chicitae* Hale, 1971:30. [Type collection: Asunción, Costa Rica, *Culberson* 13210 (US, holotype; DUKE, TNS, isotypes).]

Thallus loosely to closely adnate, fragile, often forming a thick, cushion-like mass, ashy white or blackening toward the center, 4–10 cm broad; lobes sublinear, elongate, often crowded, 1.5–4 mm wide; upper surface plane, shiny, lacking soredia and isidia but with numerous pycnidia; lower surface densely rhizinate, the rhizines sparsely dichotomously branched. Apothecia rare, adnate, 3–6 mm in diameter; spores  $5\mu \times 6\mu$ – $7\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C– (or C+ faint rose), KC+ rose, P– (atranorin, evernic acid, lecanoric acid, obtusatic acid, and norobtusatic acid).

DISTRIBUTION.—Costa Rica, Venezuela, and Peru.

HABITAT.—On rocks, soil, or mosses in paramo at 3300–3600 m elevation.

REMARKS.—The saxicolous habitat at high elevations and unusual chemistry set this species apart from other members of the evernic acid constellation. As *Culberson* and *Hale* (1973) discovered, it falls midway in chemical evolution in the group. Chromatography of the complex mixture of acids is difficult. It could be confused with only one other paramo species, *H. protenta*, which contains alectoronic acid (C–).

SPECIMENS EXAMINED.—Venezuela: Mérida, *Hanselmann* 50 (DUKE, US). Other records from Costa Rica, Venezuela, and Peru are listed by *Hale* (1971b:31).

### 9. *Hypotrachyna chlorina*, new combination

FIGURE 8c

*Parmelia chlorina* Müller Argau, 1880:267. [Type collection: Petrópolis, Brazil, *Deventer* (G, lectotype).]

Thallus adnate to loosely adnate, quite fragile, greenish or yellowish gray, to 8 cm broad; lobes short, crowded, sublinear, 2–5 mm wide; upper surface plane, shiny, becoming densely lobulate toward and at the margins, the lobules delicate, elongate, simple or furcate; lower surface moderately rhizinate. Apothecia rare, substipitate, 3–7 mm in diameter; spores  $7\mu \times 17\mu$ , the asci turning blue with IKI.

CHEMISTRY.—Cortex K+ yellow, medulla K+, C+ yellowish, P– (atranorin, barbatic acid, obtusatic acid, enthothein, and unidentified pigments).

DISTRIBUTION.—West Indies, Panama, Venezuela, Peru, and Brazil.

HABITAT.—On trees, mossy logs, or rocks in cloud forest or secondary forest at 900–2500 m elevation.

REMARKS.—The yellow medulla and production of dense lobules (Figure 4e) are characteristic of this species. The lobules have the same pored epicortical structure as the main thallus, as revealed with the scanning-electron microscope. The chemistry places it in the *H. physcioides* complex but there are no close relatives, although on hasty examination it might be misidentified as *H. isidiocera*, a clearly isidiate species, on account of the similar yellow medulla.

SPECIMENS EXAMINED.—Haiti: Ouest, *Imshaug* 22740 (MSC, US). Panama: Chiriquí, *Hale* 38754, 38770. Venezuela: Mérida, *Hale* 42735, 43014. Peru: Cuzco, *Herrera* 3466a (US). Brazil: Minas Gerais, *Eiten* 6940, 7052 (US); Rio de Janeiro, *Eiten* 6573, 751 9 (US).

### 10. *Hypotrachyna consimilis*, new combination

FIGURE 8d

*Parmelia consimilis* Vainio, 1890:58. [Type collection: Carassa, Minas Gerais, Brazil, *Vainio* 1295 (TUR, lectotype; BM, isotype).]

Thallus adnate on bark, 3–6 cm broad, light mineral gray but turning light tan in the her-



barium; lobes sublinear, becoming crowded, 1–3 mm wide; upper surface plane, continuous, becoming densely isidiate, isidia mostly simple; lower surface moderately rhizinate, the rhizines densely dichotomously branched. Apothecia rare, adnate, 3–5 mm in diameter, the amphithecium isidiate; spores  $5\mu\text{--}8\mu \times 8\mu\text{--}11\mu$ .

CHEMISTRY.—Cortex K+ yellow; medulla K–, C–, P+ orange (atranorin, protocetraric acid, and, if pigmented in lower medulla, rhodophyscin).

DISTRIBUTION.—Mexico, West Indies, Venezuela, Brazil.

HABITAT.—On hardwoods and conifers in open woods at 800–1600 m.

REMARKS.—*Hypotrachyna consimilis* is as rare in the American tropics as its presumptive progenitor *H. bahiana*. It is smaller and more compact than *H. imbricatula* (P–).

SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 20375. Puerto Rico: *Horne* 1162 (US). Dominican Republic: La Vega, *Allard* 17469 (US). Venezuela: Valencia, *Mägdefrau* 493 (M). Brazil: Minas Gerais, *Vainio* 1133 (BM, K, M, TUR, UPS); Rio de Janeiro, *Eiten* 7293 (US).

### 11. *Hypotrachyna contradicta*, new combination

FIGURE 8e

*Parmelia contradicta* Hale, 1974b:265. [Type collection: Teresópolis, Rio de Janeiro, Brazil, *Watson* 521 (BM, holotype; US, isotype).]

Thallus loosely attached on rock, rather coriaceous, whitish mineral gray; lobes linear and elongate, dichotomously branched, 1.5–2.0 mm wide, lacking soredia and isidia; upper surface plane and shiny; lower surface black, sparingly rhizinate, the rhizines coarse, sparsely dichotomously branched. Apothecia abundant, adnate, 2–4 mm in diameter; spores  $4\mu \times 6\mu$ .

CHEMISTRY.—Medulla K–, P+ orange-red (atranorin and protocetraric acid).

DISTRIBUTION.—Southeastern Brazil.

HABITAT.—On open sandstone outcrops at about 1000 m elevation.

REMARKS.—The absence of yellow-fluorescing lichexanthone in the cortex separates this species from the more widespread *H. brasiliensis*; otherwise, the two species are very close. A possible relative occurs in South Africa: *H. fissicarpa* (Kurokawa) Hale, which has large, radially split

apothecia and more imbricate, sublinear lobes.

SPECIMENS EXAMINED.—Brazil: Santa Catarina, *Reitz and Klein* 15727 (US).

### 12. *Hypotrachyna costaricensis*, new combination

FIGURE 8f

*Parmelia costaricensis* Nylander in Polakowsky, 1877:225. [Type collection: Angostura, Costa Rica, *Polakowsky* (H, lectotype).]

*Parmelia hypotrachyna* Nylander, 1860:405. [Type collection: Tolima, Colombia, *Goudot* (P, lectotype).]

*Parmelia sublaevigata* f. *isidiosa* Müller Argau, 1880:267.

*Parmelia tropica* Vainio, 1896:33.

*Parmelia tropica* var. *deformis* Vainio, 1896:33.

*Parmelia deformis* (Vainio) Vainio, 1907:169.

*Parmelia amoena* Zahlbruckner, 1908:464. [For full citations, see Hale, 1971a:11.]

Thallus adnate to loosely adnate, growing on rocks or trees, whitish to greenish mineral gray, 6–10 cm in diameter; lobes sublinear to irregular, often imbricate, 2–6 mm wide; upper surface plane, usually strongly maculate, moderately isidiate, the isidia cylindrical, erect, simple to branched; lower surface moderately to densely rhizinate, forming a thick mat visible along the margins from above, the rhizines densely dichotomously branched. Apothecia rare, adnate, 2–7 mm in diameter; spores  $4\mu\text{--}6\mu \times 8\mu\text{--}10\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla negative with all reagents (atranorin and protolichesterinic and possibly caperatic acids).

DISTRIBUTION.—Mexico, Central America, West Indies, Andean region from Venezuela to Bolivia, Brazil, and Southeast Asia.

HABITAT.—On deciduous trees, conifers, palm, rocks, and (rarely) soil, in scrub forests, secondary cloud forests, and coffee plantations at 1000–3500 m elevation.

REMARKS.—*Hypotrachyna costaricensis* is the second most common species in the genus after *H. imbricatula* in tropical America. It can be recognized by the uniformly isidiate surface, often with strong white maculation, dense rhizine mat, and negative chemical reactions. It occurs over a wide range of habitats and elevation. The fatty acid constituent has not been precisely identified. According to Dr. Chicita Culberson, it probably is near caperatic acid but has a different  $R_F$  value.

The oldest name, *Parmelia hypotrachyna*, is

invalid in *Hypotrachyna* as a tautonym. It is represented by a rather unusual specimen containing traces of gyrophoric acid along with a fatty acid, but no other specimens contain this acid. Zahlbruckner (1929) transferred it to *Anzia* without seeing the type, apparently since Nylander mentioned its affinity with *Anzia colpodes*, presumably because of the dense hypothallus-like rhizine mat. Zahlbruckner also described *P. amoena* in 1908 without having checked the type of *P. tropica*, another synonym, which he guessed was close.

**SPECIMENS EXAMINED.**—Mexico: Chiapas, *Hale* 20036, 20046, 20479; Mexico, *Cain* 27597 (TNT, US); Michoacán, *Hale* 20860, 20966; Veracruz, *Liebmann* 7562d (TUR). Guatemala: Alta Verapaz, *Johnson* 787 (US), *Standley* 70064, 70347 (US); Baja Verapaz, *Hale* 38358, 38617. Costa Rica: Cartago, *Standley* 34985 (US), *Stone* (DUKE); San José, *Standley* 47329 (US). Panama: Chiriquí, *Hale* 38728, 38732, 38783, 38814, 38851, 38928, *Scholander* (US), *Wagner* 42 (M). Cuba: Las Villas, *Imshaug* 24619, 24633A (MSC); Oriente, *Imshaug* 24711 (MSC, US). Jamaica: *Imshaug* 13926 (MSC, US), 14368, 14650, 14912, 16225 (MSC), *Orcutt* 5657 (US). Haiti: Ouest, *Imshaug* 22596 (MSC). Dominican Republic: La Vega, *Imshaug* 23814 (MSC). Dominica: *Elliott* 276 (lectotype of *P. tropica* Vainio) (BM, TUR), 12 (lectotype of *P. tropica* var. *deformis* Vainio) (BM, TUR), *Hale* 35596a. Martinique: *Degelius* (DEGEL). St. Vincent: *Elliott* (TUR). Grenada: *Imshaug* 16235 (MSC, US), 16260, 16271 (MSC). Colombia: Santander, *Cuatrecasas* et al. 12470 (US), *Killip and Smith* 19385 (US), *Lindig* 2531 (UPS); Tolima, *Quimby* (US). Venezuela: Federal, *Santesson* 6678b (S). Mérida, *Hale* 42201, 42242, 42271, 42738, 43301, *Oberwinkler and Poelt* (US). Peru: Amazonas, *Wurdack* 483 (US); Cuzco, *Thomasson* (UPS). Bolivia: La Paz, *Eyerdam* 25139 (F). Brazil: Minas Gerais, *Damazio* 1453 (lectotype of *P. amoena* Zahlbruckner) (WU, BM, H), *Eiten* 6954 (US); Rio de Janeiro, *Ainsworth* 557 (BM, US), *Deventer* 49 (lectotype of *P. sublaevigata* f. *isidiosa* Müller Argau) (G), *Eiten* 7671 (US).

### 13. *Hypotrachyna croceopustulata*, new combination

FIGURE 9a

*Parmelia croceopustulata* Kurokawa in Hale and Kurokawa, 1964:169. [Type collection: Grandfather Mountain, Avery County, North Carolina, *Imshaug* 22275 (MSC, holotype; US, isotype).]

Thallus closely adnate to bark, whitish mineral gray, 4–8 cm in diameter; lobes sublinear, becoming crowded, 1.5–3.5 mm in width; upper surface plane to rugulose, sorediate-pustulate, the soralia coarse and coalescing, mostly laminal, the medulla below often yellow ochre in color; lower surface moderately rhizinate. Apothecia rare, adnate, 1–6 mm in diameter; mature spores lacking.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C–, P+ orange-red (atranorin, protocetraric acid, and rhodophyscin).

**DISTRIBUTION.**—Southeastern United States, Mexico, West Indies.

**HABITAT.**—On conifers (*Abies*, *Picea*, *Pinus*) in open forests at 1400–2000 m elevation.

**REMARKS.**—When first described, *Parmelia croceopustulata* was based in part on *Hypotrachyna gondylophora*, which is also P+ red but contains fumarprotocetraric acid but which, more significantly, has strictly subterminal soralia. This error was later corrected (Hale, 1967) and *H. croceopustulata* was typified as including only laminally pustulate-sorediate plants (Figure 2c) with protocetraric acid. It is a relatively rare species, perhaps most common on conifers in the southern Appalachian Mountains but absent from South America.

**SPECIMENS EXAMINED.**—Mexico: Tamaulipas, *Nakanishi* 179 (US). Haiti: Ouest, *Wetmore* 3213 (MSC, US); Sud, *Imshaug* 23229 (MSC, US).

### 14. *Hypotrachyna dactylifera*, new combination

FIGURE 9b

*Parmelia dactylifera* Vainio, 1890:57. [Type collection: Lafayette, Minas Gerais, Brazil, *Vainio* 363 (TUR, lectotype; BM, FH, M, P, UPS, isoelectotypes).]

*Parmelia tilacea* var. *leucina* Müller Argau, 1880:267. [Type collection: Petrópolis, Brazil, *Deventer* (G, lectotype).]

Thallus closely adnate, tannish mineral gray, 3–8 cm broad; lobes sublinear, often crowded, 1–4 mm wide; upper surface plane, continuous, with age becoming rugulose, becoming densely isidiate, the isidia very large, about 1 mm high, fragile and usually breaking open and pustulate apically without formation of soredia; lower sur-

face moderately rhizinate, the rhizines densely dichotomously branched. Apothecia rare, adnate to substipitate, 1–4 mm in diameter; spores  $5\mu\text{--}7\mu \times 9\mu\text{--}13\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, KC+ rose, P– (atranorin, colensoinic acid, norcolensoinic acid, 4-O-demethylphysodic acid, physodic acid, lividic acid, and associated unknowns, and, if pigmented in the lower medulla, rhodophyscin).

DISTRIBUTION.—Mexico, Costa Rica, Panama, Venezuela, Chile, Brazil, Uruguay, and Africa.

HABITAT.—On trees (hardwoods and conifers) and rarely on rocks, in open secondary forest or cloud forest at 1000–2800 m elevation.

REMARKS.—The isidia of this species are very large and inflated and probably are correctly interpreted as pustules. They are exceedingly variable and the range of variation is still unsettled in spite of the fair number of collections available. The chemistry is identical with that of the presumptive progenitor *H. livida*. Vainio (1890) surmised that *Parmelia sublaevigata* f. *isidiosa* Müller Argau might belong here, but it is a synonym of *H. costaricensis*.

SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 20288, 20375; Durango, *Weber* 33708 (COLO); Veracruz, *Hale* 19520. Costa Rica: Cartago, *Torres* 156 (F). Panama: Chiriquí, *Hale* 38722, 38927, *Scholander* (US). Venezuela: Federal, *Santesson* 6677a (S); Mérida: *Hale* 42042, 43252, *Poelt* 7525 (US). Brazil: Rio de Janeiro, *Dusén* 11 (S), *Eiten* 6529, 6534, 7126 (US); São Paulo, *Sampaio* (P). Uruguay: *Osorio* 5925 (MVM). Chile: Chiloe, *Lobb* (BM).

### 15. *Hypotrachyna degelii*, new combination

FIGURE 9c

*Parmelia degelii* Hale in Hale and Kurokawa, 1964:170. [Type collection: Angola, Mexico, *Degelius* (Degelius herbarium, holotype; US, isotype).]

Thallus rather closely adnate, coriaceous, tanish mineral gray in the herbarium, 4–8 cm broad; lobes short, crowded, sublinear, 1–2.5 mm wide; upper surface plane to rugulose, shiny, faintly white-maculate, lacking soredia and isidia; lower surface moderately rhizinate. Apothecia common, adnate to substipitate, 3–8 mm in diameter,

the amphithecium white-maculate, incised; spores  $4\mu\text{--}5\mu \times 8\mu\text{--}11\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, KC+ rose, P– (atranorin, alectoronic acid, and  $\alpha$ -collatolic acid).

DISTRIBUTION.—Colombia, Peru, Brazil, and Africa.

HABITAT.—On trees, rarely rocks, in open forest at 1000–3500 m elevation.

REMARKS.—*Hypotrachyna degelii* resembles other short-lobed species such as *H. bahiana* (protocetraric acid present) and *H. physcioides* (barbatic acid group present) and must be identified with a chemical test. It is biogenetically unrelated to these species and probably falls closer to the *H. livida* group. The sorediate morph is *H. exsplendens*.

SPECIMENS EXAMINED.—Colombia: Cundinamarca, *King* 505 (US). Peru: Bryan 703 (S, US, WIS). Brazil: Mato Grosso, *Malme* 2545\* (S); Rio Grande do Sul, *Malme* 941 (S).

### 16. *Hypotrachyna densirhizinata*, new combination

FIGURE 9d

*Parmelia densirhizinata* Kurokawa in Hale and Kurokawa, 1964:171. [Type collection: Volcán, Chiriquí, Panama, *Scholander* (US, holotype).]

Thallus loosely attached, whitish mineral gray, 6–20 cm broad; lobes linear-elongate, often divaricate, separate, 2–6 mm wide; upper surface plane, continuous, sorediate-pustulate near the tips, the soralia subcapitate; lower surface densely rhizinate, the rhizines projecting as a mat along the margins, densely dichotomously branched. Apothecia very rare, substipitate, to 10 mm in diameter; spores  $10\mu \times 17\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, KC+ rose, P– (atranorin, alectoronic acid, and  $\alpha$ -collatolic acid).

DISTRIBUTION.—Southeastern United States, Mexico, Central America, West Indies, Colombia, Venezuela, Ecuador, Peru, Bolivia, Chile, Argentina, and Africa.

HABITAT.—On trees (open pine forests, *Drimys*, *Baccharis*), rocks, and mossy humus in open areas and on roadside banks at 2000–3700 m elevation.

REMARKS.—The lobes of this species are not as elongate on the average as those of its presumptive progenitor *H. gigas*. It has a much wider

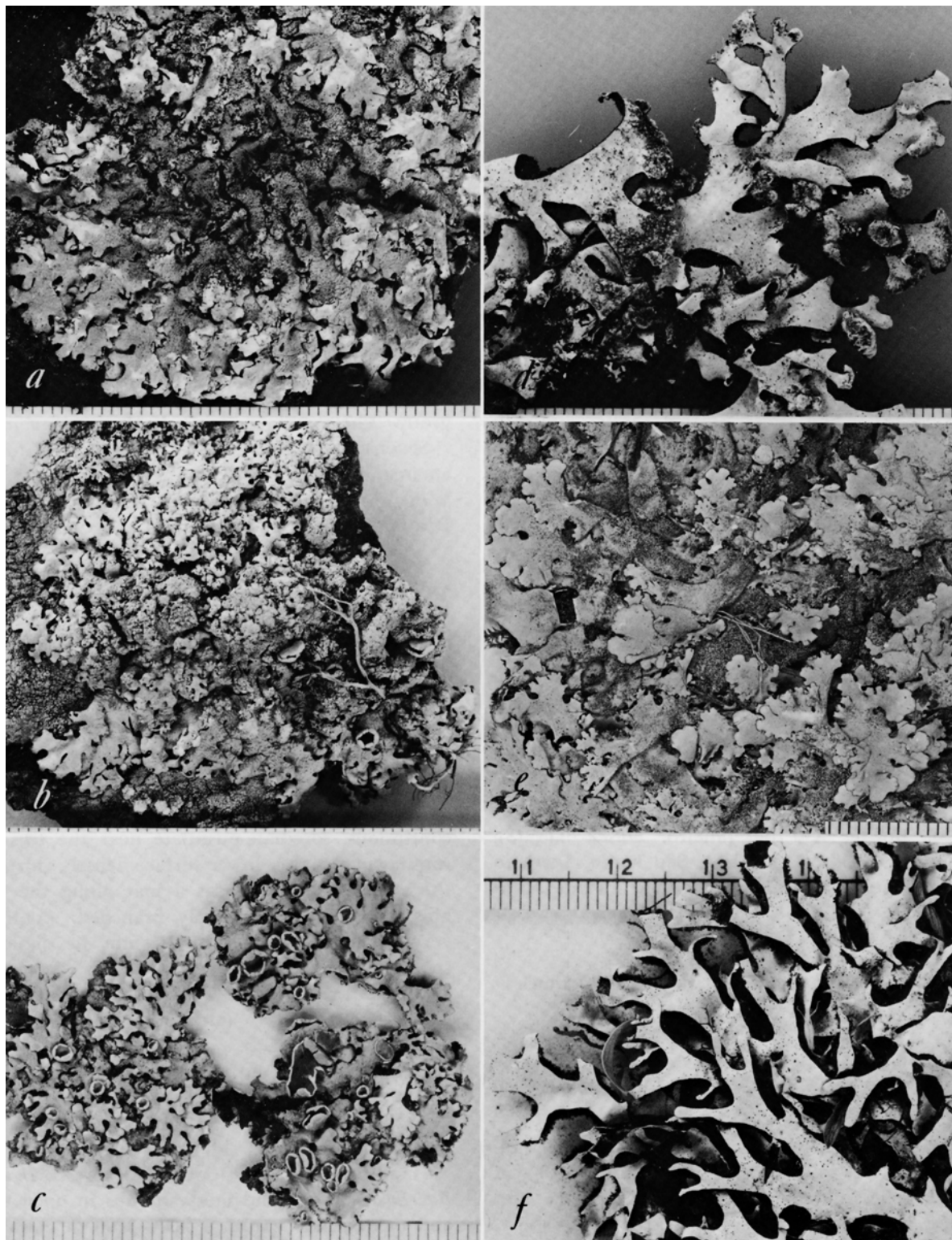


FIGURE 9.—Species of *Hypotrachyna*: a, *H. croceopustulata* (Imshaug 22383); b, *H. dactylifera* (Hale 42075); c, *H. degelii* (Bryan 703); d, *H. densirhizinata* (Hale 43194); e, *H. dentella* (McCullough 570); f, *H. ducalis* (Holligan L59B). (Scale in mm.)

geographic range than *H. gigas*—as we might expect for a sorediate morph—from the cold temperate mountains of the southern Appalachians to southern Chile. The chemistry is uniform, and no specimens contain gyrophoric acid, strongly suggesting that *H. densirhizinata* originated before *H. gigas* interbred with a gyrophoric acid-containing population. Without a chemical test *H. densirhizinata* could be confused with any of the species in the chemical complex including *H. laevigata*, *H. oostingii*, and *H. thysanota*.

**SPECIMENS EXAMINED.**—Mexico: Oaxaca, Sharp et al. 2684 (NICH). Guatemala: Solola, Kellerman (OSU, US). Costa Rica: Cartago, Culberson 12416 (DUKE). Colombia: Tolima, Quimby (US). Venezuela: Mérida, Hale 42389, 42695, 42808, 43194, Hanselmann 62 (DUKE, US). Chile: Juan Fernandez, Imshaug 37469 (MSC); Valdivia, Santesson 3604 (S, US). Argentina: Lamb 6003 (UPS). For additional records from Guatemala, Panama, Haiti, Dominican Republic, Colombia, Peru, Ecuador, Bolivia, and Chile see Hale and Kurokawa (1964:171–172).

### 17. *Hypotrachyna dentella*, new combination

FIGURE 9e

*Parmelia dentella* Hale and Kurokawa, 1964:172. [Type collection: Cheaha State Park, Clay County, Alabama, McCullough 570 (US, holotype; TNS, isotype).]

*Parmelia laevigata* var. *ceratina* Müller Argau, 1880:267. [Type collection: Petrópolis, Brazil, Deventer (G, lectotype).]

Thallus loosely adnate on rocks, 3–8 cm broad, greenish mineral gray; lobes subirregular to linear, short, 2–6 mm wide; upper surface plane, continuous, often quite white-maculate, densely isidiate, the isidia simple to branched, up to 0.7 mm high; lower surface sparsely to moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia rare, adnate, 1–2 mm in diameter; spores  $4\mu\text{--}6\mu \times 8\mu\text{--}10\mu$ .

**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow, C– or C+ pale yellow, P+ orange (atranorin, barbatic acid, echinocarpic acid, 4-O-demethylbarbatic acid, obtusatic acid, and norobtusatic acid).

**DISTRIBUTION.**—Southeastern United States, Mexico, Venezuela, and Brazil.

**HABITAT.**—On rocks in open woods and pastures at about 1000 m elevation.

**REMARKS.**—This species is closely related to *H. imbricatula* but differs in being smaller and in producing P+ echinocarpic acid.

**SPECIMENS EXAMINED.**—Mexico: Tamaulipas, Nakanishi 111 (US). Venezuela: Mérida; Hale 42727. Brazil: Rio de Janeiro, Eiten 6532 (US).

### 18. *Hypotrachyna ducalis*, new combination

FIGURE 9f

*Parmelia ducalis* Jatta, 1908:407. [Type collection: Mobuku Valley, Nabitava verso Kirchuchu, and Duroni W of Valle dei Laghi, Ruwenzori, Apruti (not seen).]

Thallus loosely adnate, whitish mineral gray, about 10 cm broad; lobes linear-elongate, separate to divaricate, 2–5 mm wide; upper surface plane, shiny, soredia and isidia lacking; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia seen only in African material:  $3\mu\text{--}4\mu \times 8\mu\text{--}9\mu$ .

**CHEMISTRY.**—Cortex K+ yellow, medulla K– C+ red, P– (atranorin and anziaic acid).

**DISTRIBUTION.**—Venezuela, Peru, and Africa.

**HABITAT.**—Over mosses and humus at the base of trees in thickets in open areas and paramo at 3000–3800 m elevation.

**REMARKS.**—The type of *H. ducalis* has not yet been found, but Jatta's description clearly refers to a nonsorediate linear-lobed species similar to other collections made in the mountains of Kenya and Uganda. In any event, in chemistry and morphology the population in South America is identical to the population in Africa. Externally, *H. ducalis* is close to *H. gigas*, which contains alectoronic acid. Vegetative morphs include *H. producta* (sorediate), *H. partita* (isidiate-lobulate), and *H. rachista* (lobulate).

**SPECIMENS EXAMINED.**—Venezuela: Mérida, Hale 43059. Peru: San Martin, Holligan L59B (BM).

### 19. *Hypotrachyna eitenii*, new combination

FIGURE 10a

*Parmelia eitenii* Hale, 1974b:266. [Type collection: Serra dos Orgãos, Rio de Janeiro, Brazil, G. and L. Eiten 7125 (US).]

Thallus loosely attached to rocks, brittle, min-

eral gray, about 6 cm in diameter; lobes sublinear, dichotomously branched, about 3 mm wide; upper surface plane, without soredia or isidia; lower surface sparsely to moderately rhizinate, the rhizines long. Apothecia abundant, adnate, to 4 mm in diameter; spores  $5\mu \times 7\mu-8\mu$ .

CHEMISTRY.—Cortex K+ yellowish, medulla K-, C+ red, P- (trace atranorin, lichexanthone, and anziaic acid).

DISTRIBUTION.—Southeastern Brazil.

HABITAT.—Rocks in scrubby forest at about 1800 m elevation.

REMARKS.—This saxicolous species is very close to *H. brasiliensis* in external appearance and in habitat. As a possible recent derivative of the *H. brasiliensis* group, it diverges very significantly in chemical biogenesis.

## 20. *Hypotrachyna enderythraea*, new combination

FIGURE 10b

*Parmelia enderythraea* Zahlbruckner, 1929:136. [Type collection: Based on *P. erythrocardia* Zahlbruckner.]

*Parmelia erythrocardia* Zahlbruckner, 1908, p. 466. [Type collection: Camarinhas, Brazil, Damazio 1761 (W, lectotype). Not *P. erythrocardia* (Müller Argau) Vainio, 1900:7.]

Thallus adnate to loosely adnate on rock or soil, massicot yellow, 4–8 cm in diameter; lobes variable, linear-elongate, often crowded, 1–3 mm wide; upper surface plane, continuous, sometimes pruinose at the tips; lower surface moderately rhizinate, the rhizines often projecting beyond the margins. Apothecia rare, adnate, 2–15 mm in diameter; spores  $7\mu-8\mu \times 13\mu-15\mu$ .

CHEMISTRY.—Cortex K-; medulla K+, P+ orange to red (galbinic, norstictic, salazinic, and usnic acids).

DISTRIBUTION.—Panama, Jamaica, Andean region from Venezuela to Bolivia, and southeastern Brazil.

HABITAT.—On soil and rocks in open forests and in the paramo at 2200–3700 m elevation.

REMARKS.—Degree of lobe adnation and width are rather variable in this species. The lobes may be separate and elongate to imbricate and short, variation that may result from environmental modification, for it grows in exposed paramo areas. The chemistry places this species close to *H. microblastia*, a closely related isidiate morph.

*Hypotrachyna caraccensis* is a good candidate for the sexual morph because of the identical chemistry, but it is much larger and divaricate.

SPECIMENS EXAMINED.—Jamaica: *Culberson and Culberson* 13730, 13733 (DUKE, US). Venezuela: Mérida, *Hale* 42464, 42898, 43150, 43218, 43324, 43340 (US), *Hanselmann* 33 (DUKE, US), *Oberwinkler and Poelt* 7542, 7547 (M, US). Peru: Chachapoyas, *Matthews* (US), *Wurdack* 484 (US); Cuzco, *Iltis* 3313 (WIS), *Thomasson* (UPS). Bolivia: *Julio* 414 (US). Ecuador: *Fiske* (US).

## 21. *Hypotrachyna endochlora*, new combination

FIGURE 10c

*Parmelia endochlora* Leighton, 1871:140. [Type collection: Askev Wood, Kerry, Ireland, *Taylor* (BM, lectotype).]

*Parmelia millaniana* Stirton, 1874:79. [Type collection: Loch Long, Argyleshire, Scotland, *Macmillan* (BM, lectotype).]

*Parmelia xanthomyela* Nylander, 1874:306. [Type collection: Fontainebleau, France, *Nylander* (H, lectotype).]

*Parmelia pittieri* Müller Argau in Durand and Pittier, 1891: 53. [Type collection: Rancho Rotundo, Costa Rica, *Pittier* 5050 (G, lectotype).]

*Parmelia madagascariensis* Vainio, 1898: (33). [Type collection: Tanala, Ambohitombo, Madagascar, *Forsyth* 562 (TUR, lectotype; BM, isolectotype).]

*Parmelia xanthomyela* f. *sorediosa* Hue, 1899:146. [Type collection: Mafate, Bourbon, *Rodriguez* (P, lectotype).]

*Parmelia endochlora* f. *sorediosa* (Hue) Zahlbruckner, 1929: 166.

*Parmelia gallicana* Gyelnik, 1931:288. [Type collection: Based on *Parmelia xanthomyela* f. *sorediosa* Hue.]

Thallus loosely adnate, greenish mineral gray, 8–13 cm broad; lobes sublinear, margins sometimes dissected with age, 2–6 mm wide; upper surface shiny, plane, continuous, faintly to strongly white-maculate, pustulate, the pustules mainly subterminal, soon turning granular-sorediate; medulla pale cendre green; lower surface moderately to densely rhizinate, the rhizines densely dichotomously branched. Apothecia rare, adnate, 4–14 mm in diameter; spores  $9\mu-14\mu \times 18\mu-22\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K-, C+ orange, P- (atranorin, barbatic acid, obtusatic acid, norobtusatic acid, entothoin, undetermined pigments, rarely echinocarpic acid).

DISTRIBUTION.—Mexico, Central America, Colombia, Venezuela, Brazil, western Europe, South Africa, Madagascar, St. Helena, Hawaii.

HABITAT.—On trees, rarely rocks, and over mos-

ses in mature forests, primary cloud forest, and scrubby areas at 1700–3500 m elevation.

REMARKS.—This widespread species is very similar to *H. laevigata* except for the yellowish medulla. It occurs over a broader range, however, including Africa and the Pacific. The pigmentation is apparently the same as that in *H. chlorina* and *H. isidiocera* but the results with TLC are unsatisfactory for resolution. Actually the chemistry is variable, with one or two of the minor constituents and echinocarpic acid sometimes absent.

SPECIMENS EXAMINED.—Mexico: Michoacán, *Hale* 20973. Costa Rica: San José, *Culberson* 12572 (DUKE). Panama: Chiriquí, *Hale* 38931, *Scholar* (US). Dominican Republic: La Vega, *Wetmore* 3509 (MSC). Colombia: Tolima, *Quimby* 37 (US). Venezuela: Mérida, *Hale* 43261. Brazil: Rio de Janeiro, *Eiten* 6577, 7093, 7709 (US). Uruguay: *Higgins* (BM).

## 22. *Hypotrachyna ensifolia*, new combination

FIGURE 10d

*Parmelia ensifolia* Kurokawa in Hale and Kurokawa, 1964:172.

[Type collection: Alto de la Bandera, La Vega, Dominican Republic, *Imshaug* 23430 (MSC, holotype; US, isotype).]

*Parmelia lobulifera* var. *insensitiva* Degelius, 1941:63. [Type collection: Forney Ridge, Swain County, North Carolina, *Degelius* (Degelius herbarium, lectotype).]

Thallus adnate, whitish mineral gray, 5–11 cm broad; lobes sublinear, dichotomously branched, 1–5 mm wide; upper surface shiny, continuous, becoming densely isidiate-lobulate on the surface and along the margins, the lobules up to 1.5 mm long, often ciliate; lower surface moderately rhizinate, the rhizines densely dichotomously branched. Apothecia rare, adnate, 3–4 mm in diameter; spores  $8\mu\text{--}10\mu \times 14\mu\text{--}18\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, KC+ rose, P– (atranorin, alectoronic acid, and  $\alpha$ -collatolic acid or with  $\alpha$ -collatolic present in trace amounts or lacking).

DISTRIBUTION.—Costa Rica, Panama, West Indies, Colombia, Venezuela, and New Zealand.

HABITAT.—On trees or boulders in cloud forest or on soil banks at 2000–3700 m elevation.

REMARKS.—*Hypotrachyna ensifolia* is characterized by abundant lobulate isidia, often becoming ciliate. It may represent the isidiate morph of *H.*

*gigas* although the lobes are shorter. It often occurs with morphologically similar *H. bogotensis*, which can be distinguished by a C+ rose color test or absence of white fluorescence in ultraviolet.

SPECIMENS EXAMINED.—Costa Rica: Cartago, *Culberson* 12360 (DUKE, US). Colombia: Santander, *Killip and Smith* 20281 (US). Venezuela: Mérida, *Hale* 42390, 42455, 42897, 43131, *Oberwinkler and Poelt* 7511 (M, US). Additional records from Mexico, Panama, Jamaica, Haiti, Dominican Republic, and Venezuela are listed in Hale and Kurokawa (1964:173).

## 23. *Hypotrachyna erythrodes*, new combination

FIGURE 10e

*Parmelia erythrodes* (Zahlbruckner) Hale and Kurokawa, 1964:173.

*Parmelia brasiliiana* var. *erythrodes* Zahlbruckner, 1909:169.

[Type collection: Mt. Itatiaya, Minas Gerais, Brazil, *Schiffner* (WU, lectotype).]

Thallus adnate to closely adnate on rock, often brittle and forming fragile mats, whitish ivory or very pale yellowish ashy gray, 4–8 cm broad; lobes sublinear, becoming crowded and imbricate, 1–3 mm wide; upper surface plane, continuous, without soredia or isidia; medulla white or turning dull salmon; lower surface moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia common, adnate, 2–6 mm in diameter; spores  $5\mu\text{--}6\mu \times 9\mu\text{--}12\mu$ .

CHEMISTRY.—Cortex K–, medulla K–, C–, P– (lichexanthone, 4-O-demethylphysodic acid, and physodic acid, with or without lividic acid and colensoinic acid, and rhodophyscin with associated unknowns).

DISTRIBUTION.—Venezuela, Peru, and Brazil.

HABITAT.—On rocks and stone walls in sparsely forested areas and in the paramo at 1600–3500 m elevation.

REMARKS.—This is one of the commonest saxicolous lichens in the paramo along with *H. osteoleuca*, which contains olivetoric acid. Both of these species contain lichexanthone in the cortex and have a distinctive whitish to pale cream color. *Hypotrachyna erythrodes* is differentiated by the presence of the lividic acid complex and frequent production of a pale salmon or orange pigment in the medulla. Almost half of the specimens from Venezuela were found to lack lividic acid

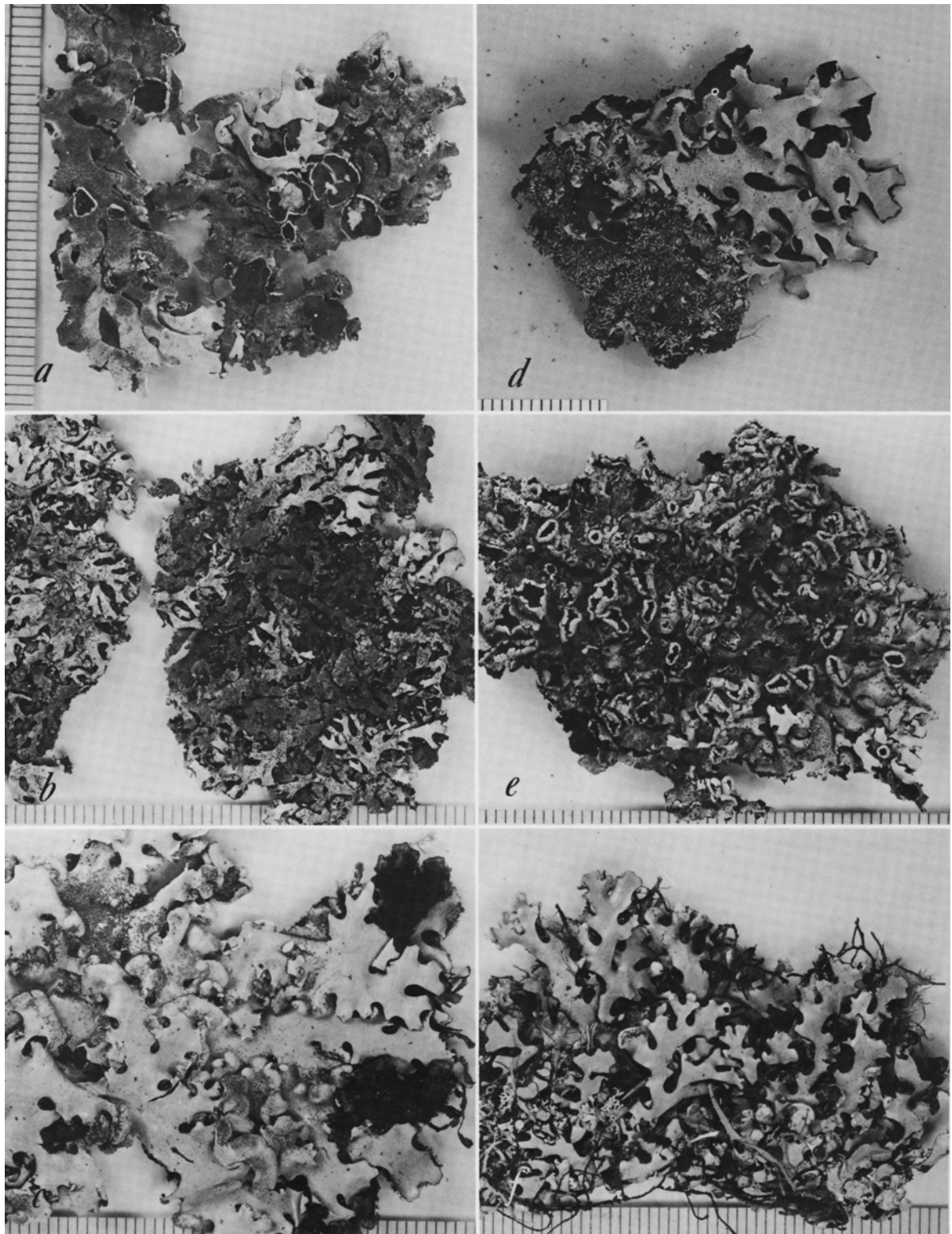


FIGURE 10.—Species of *Hypotrachyna*: a, *H. eitenii* (Eiten 7125); b, *H. enderythraea* (Hale 42464); c, *H. endochlora* (Hale 43261); d, *H. ensifolia* (Imshaug 23430); e, *H. erythrodes* (Hale 43321); f, *H. exspendens* (Standley). (Scale in mm.)



and to produce almost random assortments of the remaining components. TLC cannot adequately resolve these substances, and a final analysis of the chemical variation will have to come with high-pressure liquid chromatography.

**SPECIMENS EXAMINED.**—Venezuela: Mérida, *Den- nis* 2370 (BM), *Hale* 42469, 42472, 42488, 42619, 42791, 42792, 42798, 42809, 42825, 42863, 43147, 43186A, 43321, 43329; Táchira, *Hale* 42556. Peru: *Lobb* (BM). Brazil: Minas Gerais, *Eiten* 7030 (US).

#### 24. *Hypotrachyna exsplendens*, new combination

FIGURE 10f

*Parmelia exsplendens* Hale in Hale and Kurokawa, 1964:174. [Type collection: Murdock's Gap, Blue Mountains, Jamaica, *Imshaug* 15306 (MSC, holotype; US, isotype).]

Thallus adnate on bark, tannish mineral gray, 4–8 cm broad; lobes short, sublinear, 1.5–2.5 mm wide; upper surface plane, shiny, strongly white-maculate, sorediate, the soralia subterminal, capitate; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia not seen.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, P–, C–, KC+ rose (atranorin, alectoronic acid, and  $\alpha$ -collatolic acid).

**DISTRIBUTION.**—Mexico, West Indies, Guatemala, Costa Rica, South Africa.

**HABITAT.**—On trees in evergreen forests at 900–1200 m elevation.

**REMARKS.**—The diagnostic characters are sub-terminal capitate soralia, distinct white maculae, and presence of alectoronic acid. This species is much smaller and has more imbricate, adnate lobes than *H. densirhizinata*, another species with alectoronic acid. The presumptive progenitor is *H. degelii*, which also is known from Africa.

**SPECIMENS EXAMINED.**—Costa Rica: *Brenes* 47 (US). Jamaica: *Culbertson* 13509 (DUKE). Other records from Mexico, Guatemala, and Jamaica are listed in Hale and Kurokawa (1964:175).

#### 25. *Hypotrachyna flavida*, new combination

FIGURE 11a

*Parmelia flavida* Zahlbruckner, 1929:137. [Type collection:

Based on *P. flava* Krempelhuber not *P. flava* Rebentisch, 1804:303.]

*Parmelia flava* Krempelhuber, 1873:10. [Type collection: Serra de Piedade, Brazil, *Warming* 294 (M, lectotype; G, UPS, isolectotypes).]

*Parmelia flava* var. *stellata* Lynge, 1914:150. [Type collection: São João d'el Rey, Minas Gerais, *Malme* 311 (S, lectotype).]

*Parmelia flava* var. *subdichotoma* Lynge, 1914:149. [Type collection: São João d'el Rey, Minas Gerais, Brazil, *Malme* 310 (S, lectotype).]

Thallus adnate to loosely attached, coriaceous, sea-foam green, 3–5 cm broad; lobes sublinear, separate, 0.5–2 mm wide; upper surface plane to convex, continuous or irregularly cracked on older lobes; lower surface moderately rhizinate, the rhizines long, sparsely dichotomously branched, often projecting beyond the lobe margins. Apothecia adnate, 1–3.5 mm in diameter; spores  $5\mu$ – $6\mu \times 10\mu$ – $12\mu$ .

**CHEMISTRY.**—Cortex K–, medulla K–, C–, or KC+ rose, P+ orange-red (usnic acid and protocetraric acid).

**DISTRIBUTION.**—Colombia, Venezuela, Peru, and Brazil.

**HABITAT.**—On open sandstone outcrops or (rarely) on soil at 1200–4100 m elevation.

**REMARKS.**—This saxicolous species has a fairly restricted distribution in northern South America. Vainio (1890) noted the branched rhizines in his descriptions and classified the species in section *Xanthoparmelia* because of the yellow color of the thallus. Krempelhuber (1873) reported the type on tree bark, but the actual specimens appear to be saxicolous. The great variability in lobe width led Lynge (1914) to describe two new varieties, both narrow-lobed.

**SPECIMENS EXAMINED.**—Colombia: Santander, *Killip and Smith* 15186 (NY, US), 17527 (US). Venezuela: Mérida, *Hale* 42121a, *Oberwinkler and Poelt* (M, US). Peru: *Lobb* (BM). Brazil: Bahia, *Blanchet* (M); Minas Gerais, *Damazio* 959 (W), 1402 (G), *Eiten* 7003, 7027 (US), *Henschen* (UPS, US), *Vainio* 1163 (BM, TUR, UPS), 1522 (BM, M, TUR); Rio de Janeiro, *Gaudichaud* 9 (H).

#### 26. *Hypotrachyna flavovirens*, new combination

FIGURE 11b

*Parmelia flavovirens* Kurokawa in Hale and Kurokawa, 1964:

176. [Type collection: 50 km SE Natales, Magallanes, Chile, *Santesson* 5681 (S, holotype; US, isotype).]

Thallus adnate, sea-foam green, 3–6 cm in diameter; lobes sublinear, short and sometimes imbricate, 1–2.5 mm wide; upper surface plane, shiny, becoming rugulose with age, lobulate toward the center, sorediate, the soralia mainly subterminal, capitate; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia adnate, 2–4 mm in diameter, the amphithecium rugose; spores  $7\mu\text{--}10\mu \times 11\mu\text{--}15\mu$ .

CHEMISTRY.—Cortex K–, medulla K–, C–, P+ orange-red (usnic acid and protocetraric acid).

DISTRIBUTION.—Southern Chile.

HABITAT.—On trees (*Nothofagus*) and on rocks at low elevation.

REMARKS.—This species is essentially indistinguishable from the typical form of *H. sinuosa*, a pantemperate-pantropical montane species also common in the range of *H. flavovirens*. The chemical pattern (protocetraric or protocetraric with norstictic and salazinic acids) suggests a backcrossing between the progenitor of *H. flavovirens* (extinct?) and that of *H. sinuosa* (*H. reducens*).

SPECIMENS EXAMINED.—Chile: Magallanes, *Santesson* 8191 (S, US); Tierra del Fuego, *Santesson* 7460 (S). Other records from Chile are listed in Hale and Kurokawa (1964:176).

## 27. *Hypotrachyna formosana*, new combination

FIGURE 11c

*Parmelia formosana* Zahlbruckner, 1934:57. [Type collection: Mt. Arisan, Nimandaira, Taiwan, *Asahina* 70 (W, lectotype; TNS, isolectotype).]

Thallus adnate to closely adnate, whitish mineral gray, 3–8 cm in diameter; lobes sublinear, crowded, 1–3 mm wide; upper surface plane to rugulose, continuous, moderately to densely pustulate over most of the surface, the pustules breaking open apically but not becoming sorediate; medulla white or ochre below the pustules; lower surface moderately rhizinate. Apothecia rare, adnate, the amphithecium pustulate, 3–5 mm in diameter; spores  $4\mu\text{--}6\mu \times 7\mu\text{--}11\mu$ .

CHEMISTRY.—Cortex K–, medulla K+ reddish, C–, P– or P+ orange (lichexanthone, colensoinic acid, norcolensoinic acid, 4-O-demethyl-

physodic acid, physodic acid, lividic acid, and associated unknowns, rarely protocetraric acid, and, if pigmented, rhodophyscin).

DISTRIBUTION.—Eastern United States, Mexico, Central America, West Indies, Venezuela, Peru, Brazil, Africa, India, southeastern Asia, and Japan.

HABITAT.—On trees (hardwoods and conifers) in upland cloud forest, secondary forests, and pine forests and on rocks in open areas at 900–3000 m in tropical regions and down to sea level in temperate areas.

REMARKS.—*Hypotrachyna formosana* is pantropical with wide ecological amplitude, occurring on both trees and rocks. The dense pustules and positive orange fluorescence under ultraviolet instantly identify it. It belongs to the *H. livida* complex and the sexual morph seems to be rare *H. novella*. The chemistry is very uniform and identical with that of *H. livida* except for the rare occurrence of protocetraric acid. The second syntype of *Parmelia formosana* (*Asahina* 60 from Taiwan) can be identified with *H. exsecta* (Taylor) Hale, an Asian species with barbatic acid.

SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 19942, 20110, 20417, 20469, 20806; Michoacán, *Hale* 20852. Guatemala: Alta Verapaz, *Standley* 71865 (US); Baja Verapaz, *Hale* 38370, 38384; Huehuetenango, *Standley* 82325 (US). Panama: Chiriquí, *Scholander* (US). Cuba: Oriente, *Imshaug* 24757, 24760 (MSC). Haiti: Ouest, *Imshaug* 22546 (MSC). Venezuela: Mérida, *Hale* 42069, 42570. Peru: San Martín, *Allard* 22578b (US). Brazil: Rio de Janeiro, *Eiten* 6460, 7671a (US). Chile: Chiloe, *Santesson* 4107 (S); Valdivia, *Santesson* 7261 (S).

## 28. *Hypotrachyna gigas*, new combination

FIGURE 11d

*Parmelia gigas* Kurokawa in Hale and Kurokawa, 1964:177.

[Type collection: Bogotá, Colombia, *Joseph* B70 (US, holotype; DUKE, LD, MSC, REN, S, TNS, UPS, WIS, isotypes).]

*Parmelia exporrecta* Kurokawa in Hale and Kurokawa, 1964: 174. [Type collection: Cerro San Felipe, Oaxaca, Mexico, *Hale* 20722 (US, holotype).]

Thallus loosely attached and divaricate, rarely pendulous, 8–40 cm broad; lobes elongate, linear, separate, 3–10 mm wide; upper surface plane, continuous, without soredia or isidia; lower surface

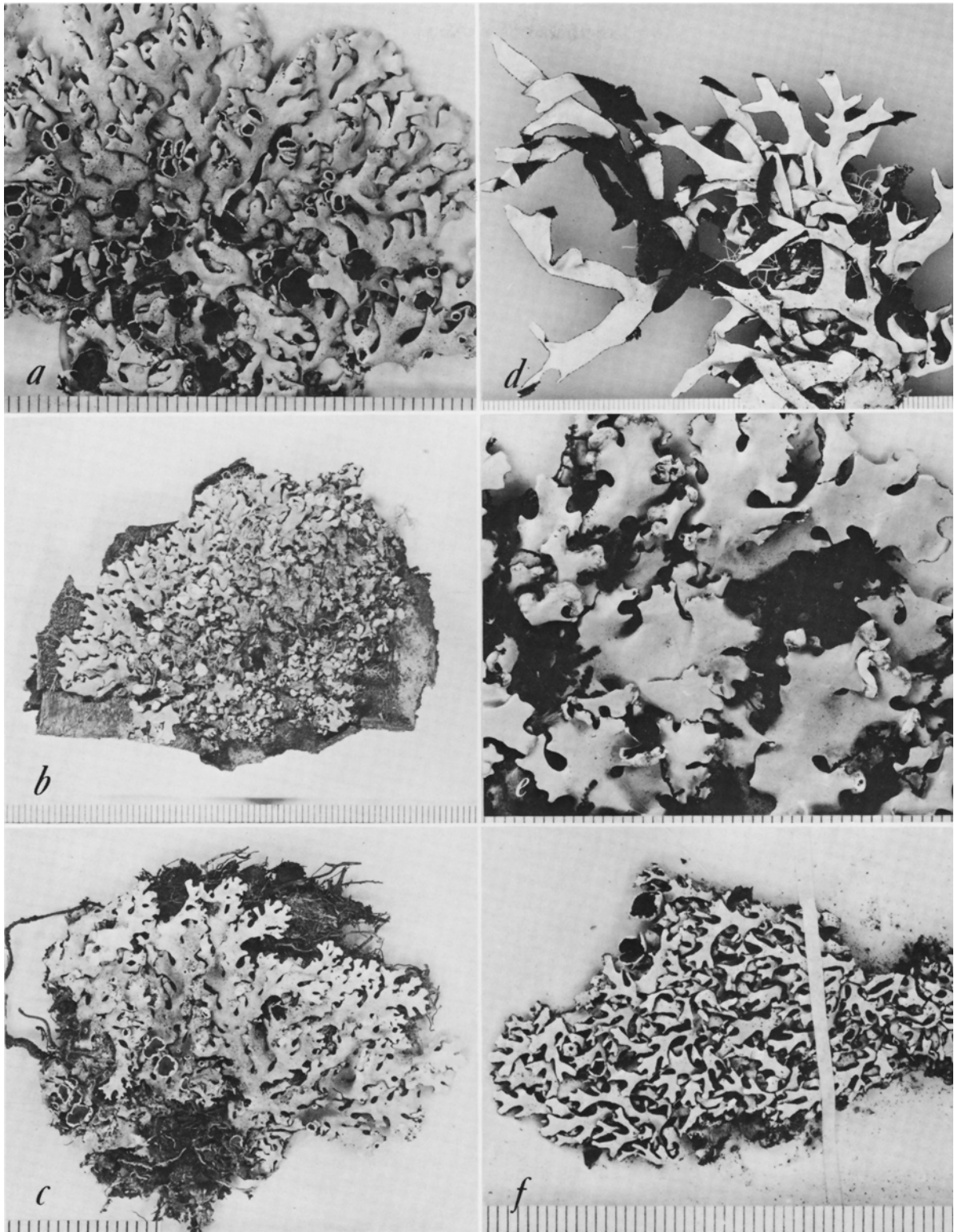


FIGURE 11.—Species of *Hypotrachyna*: a, *H. flavida* (Eiten 7003); b, *H. flavovirens* (Santesson 5681); c, *H. formosana* (Asahina F70); d, *H. gigas* (Hale 42375); e, *H. gondylophora* (Hale 20879); f, *H. gracilescens* (Vainio 1917 in BM). (Scale in mm.)

moderately to densely rhizinate, the rhizines conspicuous as a mat along the lobe margins, densely dichotomously branched. Apothecia very rare, substipitate, up to 15 mm in diameter, the amphithecium rugose; spores  $8\mu\text{--}10\mu \times 16\mu\text{--}18\mu$ , the epispodium  $1.5\mu$  thick.

CHEMISTRY.—Cortex K+ yellow, medulla K-, C- or C+ rose, KC+ red, P- (atranorin, alecortonic acid, and  $\alpha$ -collatolic acid with gyrophoric acid as an accessory substance).

DISTRIBUTION.—Mexico, Panama, Colombia, Venezuela, Ecuador, Peru, and Bolivia.

HABITAT.—On small trees, humus, soil along road banks, and rarely rocks in high-elevation, humid forest and in the paramo at 2600–3900 m elevation.

REMARKS.—This is one of the lichen spectaculars of the paramo region along with *H. caracensis*. It grows loosely on humus and festoons small shrubs in the paramo. Individual lobes may be up to 20 cm long. At lower elevations it forms extensive suberect colonies on exposed tree trunks. The two chemical populations are morphologically identical and appear to be sympatric, at least in Venezuela. I am regarding these as one species for the present. The holotype of *Parmelia exportrecta* contains gyrophoric acid in addition to alecortonic acid and  $\alpha$ -collatolic acid; the holotype of *P. gigas* lacks gyrophoric acid.

SPECIMENS EXAMINED.—Mexico: Oaxaca, *Hale* 20723 (DUKE, US), *Skorepa* 5559 (US); Veracruz, *Liebmann* 116 (UPS). Colombia: Boyacá, *Cuatrecasas* 1348 (US); Cundinamarca, *Lindig* 2573 (P), *Ariate* (UPS). Venezuela: Mérida, *Hale* 42360, 42367, 42376, 42673, 43158, 43187, 43231, *Linden* 1088 (BM), 1089 (P), *Nilsson* 1508 (UPS), *Oberwinkler and Poelt* 7519 (M, US). Peru: Cuzco, *Gómez* 631 (US), *Holligan* 38 (BM). Bolivia: Bang 1853 (H, NY), *Spruce* 174 (BM). Argentina: Patagonia, *Dusén* 122 (S). Additional localities for Mexico, Panama, Venezuela, Colombia, and Ecuador are listed in *Hale* and *Kurokawa* (1964:177, 178).

### 29. *Hypotrachyna gondylophora*, new combination

FIGURE 11e

*Parmelia gondylophora* *Hale*, 1967:420. [Type collection: Clingmans Dome, Swain County, North Carolina, *Hale* 33570 (US, holotype; DUKE, FH, UPS, isotypes).]

Thallus loosely attached, whitish mineral gray, 8–15 cm broad; upper surface plane, smooth, sometimes faintly white-maculate, sorediate toward the tips, the soralia capitate; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia not seen.

CHEMISTRY.—Cortex K+ yellow, medulla K-, C-, P+ orange-red (atranorin, fumarprotocetraric acid, and succinprotocetraric acid along with rhodophyscin (under soralia) if pigment present).

DISTRIBUTION.—Southeastern United States, Mexico, Costa Rica, Dominican Republic, Venezuela, Bolivia, and Africa.

HABITAT.—On trees (hardwoods and conifers), rarely on rocks, in cloud forests at 1000–2200 m elevation.

REMARKS.—The most unusual feature of this species is the chemistry; no other *Hypotrachyna* is known to contain fumarprotocetraric acid (*Hale*, 1967). Otherwise it is externally similar to *H. densirhizinata* or robust forms of *H. laevigata*.

SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 19920; Oaxaca, *Nakanishi* 349 (US); Veracruz, *Hale* 20867, 20879. Costa Rica: San José, *Stone* (DUKE). Dominican Republic: La Vega, *Imshaug* 23470 (MSC, US). Venezuela: Mérida, *Oberwinkler and Poelt* 7530 (M, US). Bolivia: Inquisive, *Overbeck* 5455 (US).

### 30. *Hypotrachyna gracilescens*, new combination

FIGURE 11f

*Parmelia gracilescens* *Vainio*, 1890:53. [Type collection: Carrasa, Minas Gerais, Brazil, *Vainio* 1517 (TUR, lectotype).]

Thallus loosely adnate on rock, buff mineral gray, 3–5 cm in diameter; lobes sublinear, dichotomously branched, more or less divaricate-imbricate, 1–2 mm wide; upper surface plane, shiny, without maculae, soredia, or isidia; lower surface moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia adnate, 1–2 mm in diameter; spores  $7\mu \times 11\mu$ .

CHEMISTRY.—Cortex K+ yellow, K-, C-, P- (atranorin and one or two unidentified substances).

DISTRIBUTION.—Southeastern Brazil.

HABITAT.—On open rock outcrops at 1400–1500 m elevation.

REMARKS.—This very rare saxicolous species is externally close to *H. livida* but has an unusual chemistry. Without knowing the molecular structure of the “gracilescens” unknown, however, we cannot speculate on its relation to species containing lividic acid. Vainio (1890) differentiated the species from *Parmelia chilena*, *P. bahiana*, and *P. subsinuosa* (all KC+ red) by the negative KC reaction.

SPECIMENS EXAMINED.—Brazil: Minas Gerais, Damazio 934 (G), Vainio 1218, 1532 (BM, TUR).

### 31. *Hypotrachyna imbricatula*, new combination

FIGURE 12a

*Parmelia imbricatula* Zahlbruckner, 1909:168. [Type collection: Itapeirica, São Paulo, Brazil, Schiffner (W, lectotype; MICH, isotype).]

*Parmelia lobulifera* var. *luteoreagens* Degelius, 1941:61. [Type collection: Myrtle Point, Mt. LeConte, Tennessee, U.S.A., Degelius (DEGEL, lectotype).] For additional synonymy see Hale, 1971a:16.

Thallus adnate, 5–10 cm in diameter, whitish mineral gray but often turning pale tannish in the herbarium; lobes sublinear, often crowded, 2–4 mm wide; upper surface plane, shiny, usually strongly white-maculate, moderately isidiate, the isidia thin, cylindrical, simple to branched, sometimes darkening at the tips; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia infrequently developed, 2–10 mm in diameter; spores  $7\mu\text{--}10\mu \times 11\mu\text{--}16\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+ orange, P– (atranorin, barbatic acid, 4-O-demethylbarbatic acid, obtusatic acid, and norobtusatic acid).

DISTRIBUTION.—Southeastern United States southward to Chile.

HABITAT.—On trees (oaks, pine, juniper, *Araucaria*, *Arbutus*, coconut palm, citrus), stumps, rocks, and (rarely) soil, in primary and secondary forests at 200–2600 m elevation.

REMARKS.—*Hypotrachyna imbricatula* is the commonest and most widely distributed species in the genus. It also has wide ecological amplitude. The isidia usually are well developed and may rarely become in part lobulate or procumbent. In the herbarium it often turns light brownish with age. The presumptive progenitor is *H. physcioides* and

the sorediate morph *H. laevigata*. A very similar species, *H. bogotensis*, is separated by the C+ rose (rather than orange) reaction caused by evernic and lecanoric acids. The very common *H. costaricensis* has broader lobes and a uniformly dense rhizine mat below, as well as completely negative color tests.

REPRESENTATIVE SPECIMENS EXAMINED.—Mexico: Chiapas, Hale 20021, 20197, 20365, 20455, 21202; Michoacán, Arsène 8032, 8245 (US), Darrow 5155 (Darrow herbarium), Kiener 18456 (DUKE); Oaxaca, Hale 20652; Sinaloa, Breedlove 16758d (US); Veracruz, Hale 21059, 21146. Guatemala: Baja Verapaz, Hale 38322, 38341; Jalapa, Standley 76825 (F, US); Totonicapán, Standley 84542 (F, US); Zacapá, Steyermark (US). Honduras: Morazán, Standley and Molina 4320 (F). Costa Rica: Cartago, Culberson 13219 (DUKE); San José, Culberson 12403, 12628 (DUKE), Standley 43033, Standley and Valerio 43174, 43479 (US). Panama: Chiriquí, Almeda 1025A (DUKE), Hale 38720, 38820, 38884, 38911, Maxon 4989 (US), Scholander (US). Cuba: Oriente, Imshaug 25030 (MSC); Pinar del Rio, Imshaug 25221, 25225 (MSC, US). Jamaica: Imshaug 12950, 13382, 13417 (MSC, US), 15278, 15531 (MSC), Orcutt 5626 (US), Plitt (US). Haiti: Ouest, Imshaug 22958, 22980, 23069 (MSC, US), Wetmore 3001, 3044, 3121, 3151 (MSC, US); Sud, Imshaug 23235 (MSC, US). Dominican Republic: La Vega, Allard 17695, 17709, 17715 (US), Imshaug 23628, 23683 (MSC, US), Wetmore 3428, 3513 (MSC, US). Guadeloupe: Hale 38280. Dominica: Hale 35345. Trinidad: Hale 38212, 38294. Colombia: Santander, Cuatrecasas 12470 (US), Charetier 211 (US), Killip and Smith 18942 (US). Venezuela: Bolívar, Steyermark and Dunsterville 92981 (US); Federal, Jahn 249 (US); Mérida, Hale 42185, 42761, 43302. Peru: Cuzco, Herrera 3461a (US), Worthley (US). Guyana: Lillie 47 (BM). Brazil: Bahia, Willey (US); Minas Gerais, Mosén 2319 (UPS), Vainio 1085 (TUR); Rio de Janeiro, Eiten 6512 (US); Santa Catarina, Reitz and Klein 11991, 15501 (US). Chile: Valdivia, Santesson 3785 (S, US).

### 32. *Hypotrachyna immaculata*, new combination

FIGURE 12b

*Parmelia immaculata* Kurokawa in Hale and Kurokawa, 1964:

178. [Type collection: Zoutpansberg, Union of South Africa, *Almborn* 6551 (LD, holotype; US, isotype).]

Thallus loosely adnate to adnate, very fragile, whitish mineral gray, 5–7 cm broad; lobes sublinear, contiguous, 1.5–3 mm wide; upper surface plane, shiny, sorediate, the soralia mostly subterminal, large and capitate, often pigmented ochre below, 1–2 mm in diameter; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia rare, adnate, 2–3 mm in diameter; spores  $6\mu \times 11\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K– or K+ reddish, P– or P+ dull reddish, C (atranorin, colensoinic acid, 4-O-demethylphysodic acid, lividic acid, and associated unknown substances).

DISTRIBUTION.—Venezuela, Brazil, and South Africa.

HABITAT.—On trees, rarely on soil, in open forest and along roadbanks at 2000–3000 m elevation.

REMARKS.—The South American material of this poorly known species is variable in size and lobation but compares with the African population in overall morphology and chemistry. Additional collections are needed to settle any doubt. In any event, it would be considered as the sorediate morph of *H. livida*. On reexamining the type of *H. immaculata* I found that it consists of a mixture of two species, one (apparently new) with lichexanthone in the cortex and one (lectotype) with atranorin.

SPECIMENS EXAMINED.—Venezuela: Mérida, *Hale* 42900, 42969. Brazil: Minas Gerais, *Warming* 281 (M).

### 33. *Hypotrachyna intercalanda*, new combination

FIGURE 12c

*Parmelia intercalanda* Vainio, 1890:53. [Type collection: Sitio, Minas Gerais, Brazil, *Vainio* 899 (TUR, Vainio herbarium number 3014, lectotype; BM, M, UPS, isolectotypes).]

*Parmelia fragilis* Lynge, 1914, p. 123. [Type collection: Santa Anna da Chapada, Mato Grosso, Brazil, *Malme* 2365\* (S, lectotype).]

Thallus adnate to closely adnate on bark, tannish mineral gray, 3–6 cm broad; lobes sublinear, crowded to separate, 0.5–2 mm wide; upper surface plane to rugulose, continuous, faintly maculate, without soredia or isidia; medulla white;

lower surface moderately rhizinate, the rhizines densely dichotomously branched. Apothecia common, adnate to substipitate, the disc light brown, 2–4 mm in diameter; spores  $5\mu\text{--}6\mu \times 8\mu\text{--}10\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+ red (atranorin and olivetoric acid).

DISTRIBUTION.—Southeastern Brazil and Argentina.

HABITAT.—On trees, rarely on humus over rocks, in open woods at about 500–1200 m elevation.

REMARKS.—The C+ red test caused by olivetoric acid was first noted by Vainio (1890) in the original description. *Hypotrachyna osteoleuca* also produces this rare acid, along with lichexanthone, but the two species have different geographic distribution and ecology. According to C. Culberson's scheme (Culberson and Hale, 1973), a species such as this one could have originated from progenitors containing microphyllinic acid or perlatolic acid. Further biochemical transformations of *H. osteoleuca* itself might have produced 4-O-methylphysodic-physodic acid progenitors of the *H. livida* complex.

SPECIMENS EXAMINED.—Brazil: Mato Grosso, *Malme* in *Lichenes Austroamericani* 88 (G, LD, UPS); Minas Gerais, *Henschen* (UPS, US), *Vainio* 936 (TUR, UPS) (syntype of *P. intercalanda*); Paraná, *Montes* 10116 (DUKE, LD, MVM, US); São Paulo, *Puiggari* (G); Santa Catarina, *Reitz and Klein* 15985 (US). Argentina: Misiones, *Montes* 10106 (MVM, US), *Osorio* 4297 (MVM, US).

### 34. *Hypotrachyna isidiocera*, new combination

FIGURE 12d

*Parmelia isidiocera* Nylander, 1860:382. [Type collection: Cape Krusenstern, American Arctic, *Beechey* (BM, lectotype; H, isolectotype).]

Thallus loosely adnate, fragile, greenish mineral gray, 5–15 cm broad; lobes sublinear, short, often crowded; upper surface shiny, strongly white-maculate, becoming densely isidiate toward the margins, the isidia tall, erect, easily breaking off at the tips to reveal the yellow medulla; medulla sulphur yellow; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia rare, substipitate, 2–8 mm in diameter, the rim isidiate, rugose; spores  $7\mu\text{--}8\mu \times 12\mu\text{--}16\mu$ .

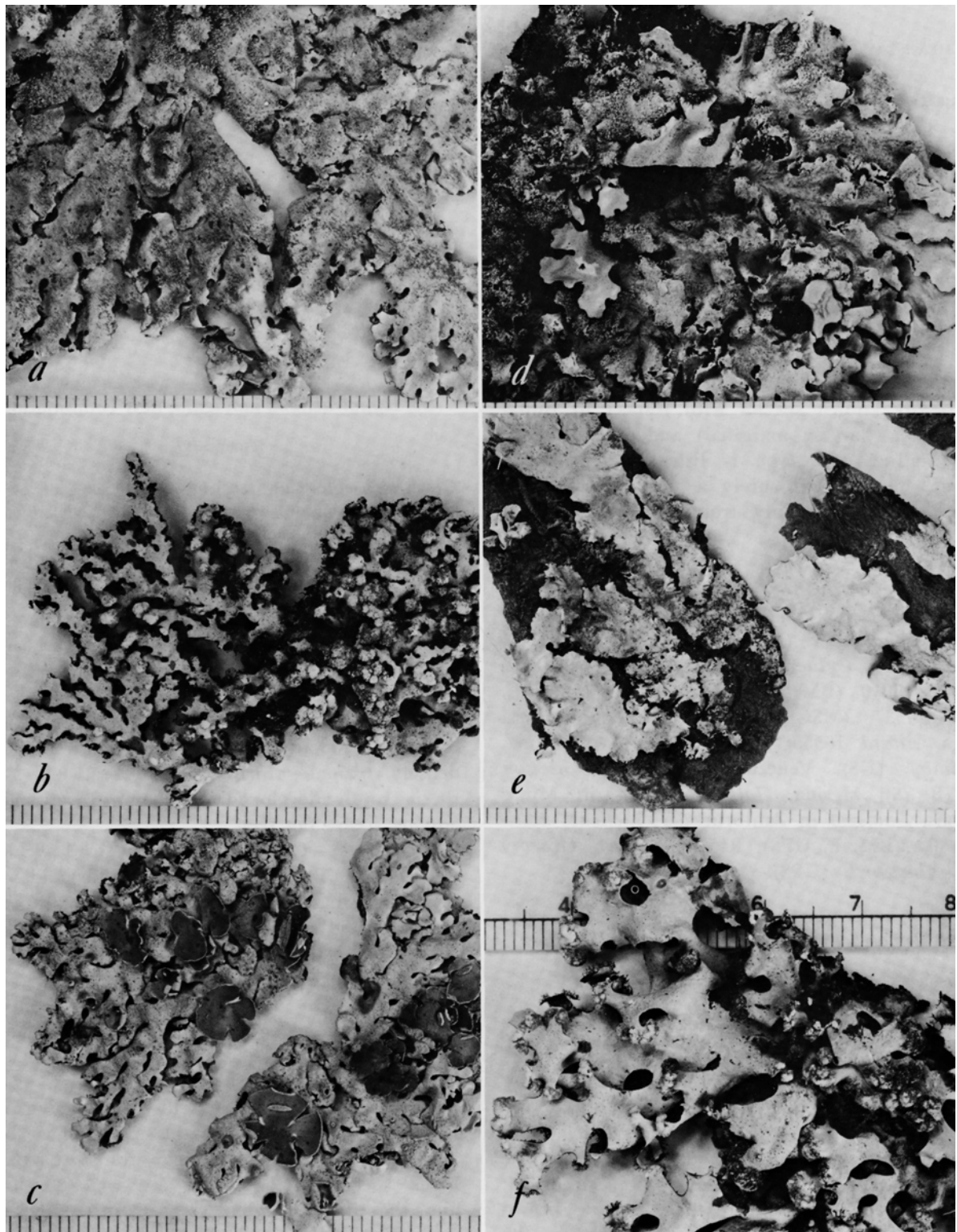


FIGURE 12.—Species of *Hypotrachyna*: a, *H. imbricatula* (Hale 21059); b, *H. immaculata* (Hale 42900); c, *H. intercalanda* (Osorio 4297); d, *H. isidiocera* (Hale 20219); e, *H. koyaensis* (Nakanishi 284); f, *H. laevigata* (Hale 43106). (Scale in mm.)

CHEMISTRY.—Cortex K+ yellow, medulla K+, C+ yellowish, P- (atranorin, barbatic acid, obtusatic acid, entothecin, undetermined pigments, and other substances, rarely echinocarpic acid and a trace of norobtusatic acid).

DISTRIBUTION.—Mexico, Central America, West Indies, Colombia, Venezuela, Brazil, Hawaii.

HABITAT.—On trees (oak, pine) in virgin pine forests, cloud forests, and on rocks in open woods at 1000–3000 m elevation.

REMARKS.—This robust lichen is easily recognized by the bright yellow medulla exposed as the large isidia break away. While obviously a member of the *H. physcioides* group, it is distant from any known species with respect to isidial formation (largely marginal) and brittleness of the thallus. The type is listed as "American Arctic" but this is surely a mistake since the species is known only from montane tropical regions.

SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 20219 (DUKE, US). Guatemala: Alta Verapaz, *Johnson* 171g (US). Panama: Chiriquí, *Hale* 38690, *Scholander* (US). Jamaica: *Britton* 1110, 1121 (FH), *Culberson* 13502, 13894 (DUKE), *Harris* 10010 (BM, FH), *Imshaug* 12993 (MSC, US), 14937 (MSC). Dominican Republic: La Vega, *Allard* 16555G (US). Colombia: Tolima, *Quimby* (US). Venezuela: Federal, *Santesson* 6677B (S); Mérida, *Hale* 43289. Brazil: Minas Gerais, *Damazio* in *Zahlbruckner*, *Lichenes Rariores* 93 (BM, P, UPS); Rio de Janeiro, *Gregory and Ainsworth* (UPS).

### 35. *Hypotrachyna koyaensis*, new combination

FIGURE 12e

*Parmelia koyaensis* Asahina, 1953:67. [Type collection: Mt. Koya, Kishu, Japan, *Asahina* 52101 (TNS, lectotype).]

Thallus adnate, membranaceous, ashy white, up to 10 cm broad; lobes irregular, subrotund apically, with crenate margins, 4–10 mm wide; upper surface plane, continuous, moderately isidiate, the isidia simple to rarely branching, cylindrical; lower surface black but with a narrow brown zone at the margins, moderately rhizinate, the rhizines moderately dichotomously branched. Apothecia rare, stipitate, 1–3 mm in diameter; spores  $8\mu \times 16\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K-, C-, P+ orange-red (atranorin, protocetraric acid, and an unidentified fatty acid).

DISTRIBUTION.—Japan, Southeast Asia, Mexico.

HABITAT.—On trees (*Pinus*) at 2100 m elevation.

REMARKS.—This species has the subirregular rotund lobation so typical of Asian species. The isidia are sparse and the rhizines sparsely to moderately branched. Its occurrence in the New World is difficult to explain.

SPECIMENS EXAMINED.—Mexico: Oaxaca, *Nakanishi* 284 (US).

### 36. *Hypotrachyna laevigata*, new combination

FIGURE 12f

*Lichen laevigatus* Smith, 1808:1852. [Type collection: Anglesey, Caernarvonshire, England, *Davies* (LINN, lectotype).]

*Parmelia laevigata* (Smith) Acharius, 1814:212.

*Parmelia boliviana* var. *cephalota* Zahlbruckner, 1926:16. [Type collection: Loma Frei Jorge, Coquimbo, Chile, *Skottsberg* 448 (W, lectotype; S, isolectotype).]

Thallus adnate to loosely adnate, greenish to whitish mineral gray, 3–10 cm broad; lobes linear, 1.5–6.0 mm wide; upper surface plane, shiny, usually strongly white-maculate, pustulate-sorediate toward the lobe tips, soralia capitate; lower surface densely rhizinate, rhizines densely branched. Apothecia rarely developed, to 5 mm in diameter, adnate; spores not seen.

CHEMISTRY.—Cortex K+ yellow, medulla K-, C+ orange, P- (atranorin, barbatic acid, 4-O-demethylbarbatic acid, obtusatic acid, and norobtusatic acid).

DISTRIBUTION.—United States southward to Chile, Europe.

HABITAT.—On trees (hardwoods, conifers, *Drimys*, *Nothofagus*) and rocks in open cloud or rain forests at 600–3700 m elevation.

REMARKS.—This was one of the first *Hypotrachyna* species to be described on the basis of European material, but the name has been applied in floristic lists to many different narrow-lobed species. The soredia are well developed and the maculae often very distinct. The presumptive progenitor is *H. physcioides*, and the parallel isidiate morph is *H. imbricatula*. According to *Culberson and Hale* (1973), the obtusatic acid originated from a cross between a progenitor



containing evernic acid (*H. pulvinata*) and a progenitor containing barbatic acid (extinct or now represented by *H. massartii* (Hue) Hale in Asia). The species evolved parallel with *H. rockii*, the sorediate morph of *H. pulvinata*, and the two are very similar externally.

**SPECIMENS EXAMINED.**—Mexico: Chiapas, *Hale* 19885; Oaxaca, *Yoshimura* 650533 (NISH). Costa Rica: Cartago, *Culberson* 12419, 13221 (DUKE); San José, *Ream* (WIS). Jamaica: *Plitt* (US). Dominican Republic: La Vega, *Imshaug* 23386, 23561 (MSC, US). Guadeloupe: *Culberson* 14503 (DUKE). Dominica: *Elliott* 1321, 1556, 1559 (TUR), *Hale* (see data in Hale, 1971a:17). Colombia: Cundinamarca, *Killip* 11900 (US), *Nee and Mori* 4219 (US), *Weir* 53 (BM); Santander, *Charetier* 189 (US); Tolima, *King* 506 (US). Venezuela: Mérida, *Hale* 42214, 42647, 43106, 43206. Guyana: *McConnell and Quelch* 503 (BM). Brazil: Rio de Janeiro, *Eiten* 7093 (US). Chile: Aysén, *Santesson* 6948 (S, US); Coquimbo, *Munoz* 1257 (S), *Sparre* 2933 (S); Juan Fernandez, *Skottsberg* 285 (UPS); Valdivia, *Santesson* 3273, 3277, 3464, 3786, 3698, 7571 (S).

### 37. *Hypotrachyna lineariloba*, new combination

FIGURE 13a

*Parmelia lineariloba* Kurokawa in Hale and Kurokawa, 1964: 180. [Type collection: Alto de la Bandera, La Vega, Dominican Republic, *Weimore* 3475 (MSC, holotype; US, isotype).]

Thallus loosely attached to bark, rather fragile, ashy white, 3–6 cm broad; lobes elongate, linear, dichotomously branched, subdivaricate, 0.5–2 mm wide; upper surface plane, shiny, continuous, lacking soredia and isidia; lower surface moderately rhizinate, the rhizines about 1 mm long, sparsely dichotomously branched. Apothecia not seen.

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

**DISTRIBUTION.**—Dominican Republic.

**HABITAT.**—On trunks of *Pinus* in open forests on ridges at 2400–2800 m elevation.

**REMARKS.**—No new collections of this species have been made and it may indeed be endemic to the pine forests of the West Indies. It resembles *H. gigas*, a larger species which always contains  $\alpha$ -collatolic acid along with alectoronic acid.

**SPECIMENS EXAMINED.**—Additional records for the Dominican Republic are listed in Hale and Kurokawa (1964:181).

### 38. *Hypotrachyna livida*, new combination

FIGURE 13b

*Parmelia livida* Taylor, 1847:171. [Type collection: New Orleans, Louisiana, *Hooker Herbarium* (FH-TAYL, lectotype; BM, H, isolectotypes).]

*Parmelia osseoalbida* Lynge, 1914:133. [Type collection: Porto Alegre, Rio Grande do Sul, Brazil, *Malme* 595 (S, lectotype; UC, UPS, isolectotypes).]

Thallus closely adnate, rather coriaceous (on bark) to fragile (on rock), whitish mineral gray, 4–9 cm broad; lobes sublinear, dichotomously branched, contiguous, 1–2 mm wide; upper surface shiny, plane to rugulose, lacking soredia and isidia; lower surface moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia numerous, adnate to substipitate, 1–5 mm in diameter; spores  $5\mu \times 10\mu$ – $12\mu$ .

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C–, KC+ rose, P– (atranorin, colensoinic acid, norcolensoinic acid, 4-O-demethylphysodic acid, physodic acid, lividic acid, and associated unknowns).

**DISTRIBUTION.**—Southeastern United States, Bahamas, Venezuela, southeastern Brazil southward to Argentina).

**HABITAT.**—On tree trunks and branches or (more rarely) on rocks, in open forests and gallery forests at 500–2800 m elevation (to near sea level in the United States).

**REMARKS.**—*Hypotrachyna livida* is characterized by the adnate thallus, lack of diaspores, and complex chemistry. While we still do not know the structure of lividic acid, the presence of at least colensoinic and physodic acids would place the species on a high evolutionary scale in the genus (*Culberson and Hale*, 1973). Some specimens (in Brazil) appear to lack lividic acid and contain colensoinic acid and related compounds. These may represent a newly evolving species but careful studies with high-pressure liquid chromatography are needed to settle the chemistry.

The species is by far most common in the deciduous forests of southeastern United States (*W. Culberson*, 1961) and then reappears in a climatically similar zone in southern Brazil to

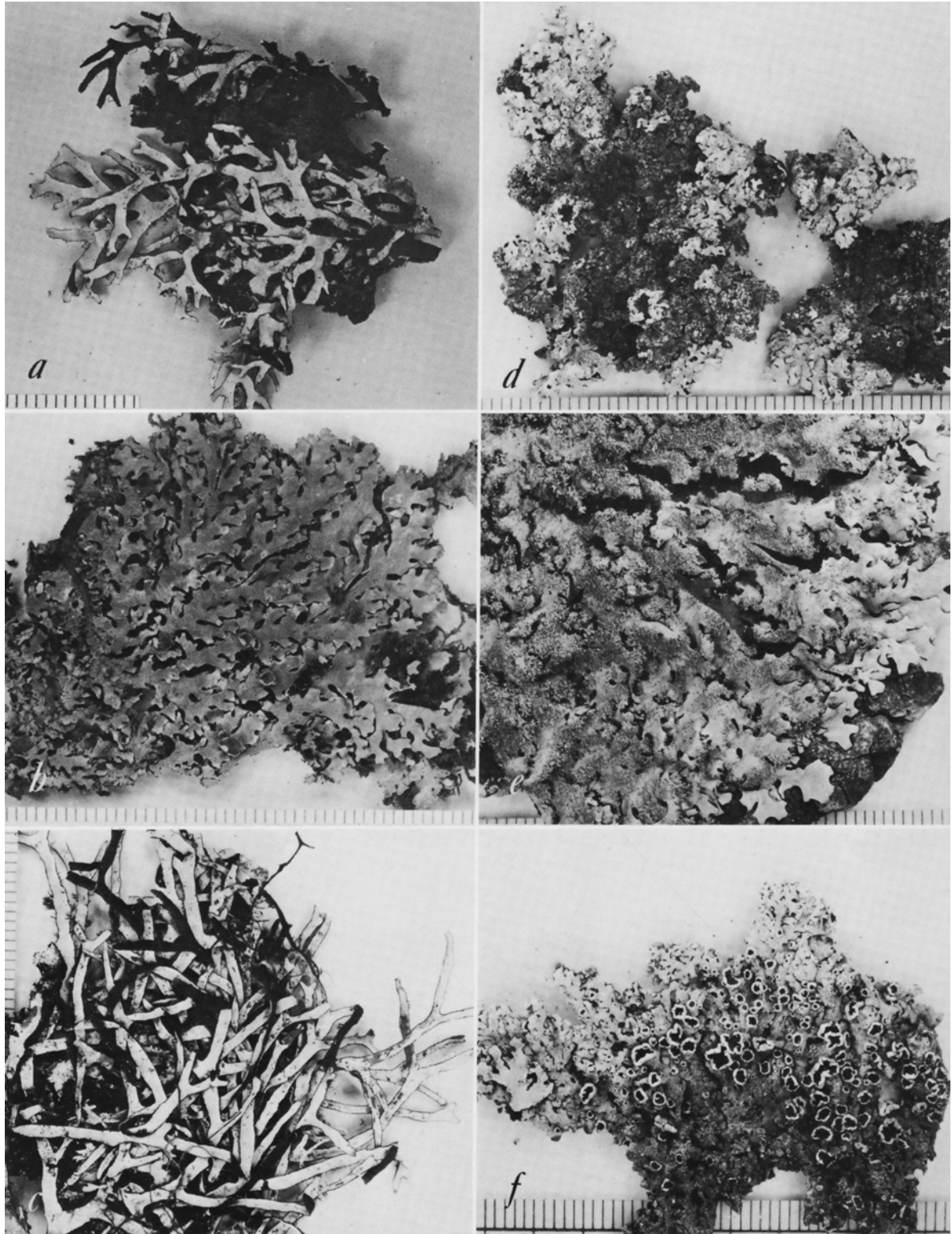


FIGURE 13.—Species of *Hypotrachyna*: a, *H. lineariloba* (Wetmore 3425); b, *H. livida* (Reitz and Klein 15150); c, *H. lopezii* (Hale 42463); d, *H. malmei* (Malme 2750); e, *H. microblasta* (Hale 42031); f, *H. minima* (Malme 2747B in S). (Scale in mm.)

Argentina. The rock form described by Lynge as *Parmelia osseoalbida* is somewhat more fragile than corticolous forms.

*Hypotrachyna livida* is the progenitor of several vegetative morphs: *H. immaculata* (sorediate), *H. dactylifera* (isidiate-pustulate), and *H. pustulata* (pustulate). This whole complex has evolved parallel with *H. novella* (a species containing lichexanthone), as discussed below.

**SPECIMENS EXAMINED.**—Venezuela: Federal, *San-tesson* 6682 (S, US); Mérida, *Hale* 42833; Valencia, *Mägdefrau* 389 (M). Brazil: Minas Gerais, *Vainio* 1400 (BM, TUR, as *P. gracilis*); Rio de Janeiro, *Eiten and Eiten* 6598, 7396, 7403, 7468 (US), *Glaziou* (G); Rio Grande do Sul, *Malme* 1330B (S); São Paulo, *Düsen* 11 (S); Santa Catarina, *Reitz and Klein* 13213, 15185, 15809, 16002 (US). Uruguay: Lavalleya, *Hosseus* 45 (H), *Osorio* 6480 (MVM, US); Maldonado, *Hosseus* 93457a (H), *Osorio* 5040 (MVM); Rocha, *Hosseus* 43, 47 (H, M); Treinta y Tres, *Osorio* 6000 (MVM, US). Argentina: Without collector (M).

### 39. *Hypotrachyna lopezii*, new species

FIGURE 13c

Thallus laxe adnatus, viridi-flavicans, lobis lineari-elongatis, divaricatis, nigromarginatis, 1.5–2 mm latis; cortex superior 14 $\mu$ –16 $\mu$  crassus, stratum gonidiale 24 $\mu$ –18 $\mu$  crassum, medulla alba, 130 $\mu$  crassa, cortex inferior 18 $\mu$ –20 $\mu$  crassus; subtus niger, sparse rhizinosus vel papillatus, rhizinis longis. Apothecia rara, substipitata, sporis simplicibus, 7 $\mu$   $\times$  14 $\mu$ .

Thallus loosely attached, greenish yellow, to 12 cm broad; lobes linear-elongate, sparsely dichotomously branched, divaricate and almost appearing subfruticose, black rimmed, 1.5–2 mm wide; upper surface plane to concave, shiny, lacking isidia and soredia; lower surface in part bare and papillate, otherwise sparsely rhizinate, the rhizines long, sparsely dichotomously branched. Apothecia rare, substipitate, 8–11 mm in diameter, the amphithecium rugose; spores 7 $\mu$   $\times$  14 $\mu$ .

**CHEMISTRY.**—Cortex K–, medulla K+ yellow turning red, C–, P+ orange (usnic acid, norstictic acid, stictic acid, and constictic acid).

**TYPE COLLECTION.**—La Aguada, Mérida, Venezuela, *Hale* 43208, 6 February 1974 (US, holotype).

**DISTRIBUTION.**—Venezuela.

**HABITAT.**—On base of shrubs and twigs in open rocky paramo at 2800–3500 m elevation.

**REMARKS.**—This paramo species might be confused initially with *H. caraccensis*, but the lobes are narrower, usually black rimmed, and the rhizines very sparse. The chemistry is unusual, stictic acid being rare in *Hypotrachyna*. The species is named in honor of Prof. Manuel Lopez Figueiras.

**SPECIMENS EXAMINED.**—Venezuela: Mérida, *Hale* 42463, 43142, 43195.

### 40. *Hypotrachyna malmei*, new combination

FIGURE 13d

*Parmelia malmei* Lynge, 1914:116. [Type collection: Bocca da Serra, Mato Grosso, Brazil, *Malme* 2750 (S, lectotype; W, isolectotype).]

Thallus loosely adnate on rocks, very fragile, 3–5 cm in diameter, ashy white; lobes sublinear, short, crowded, 0.5–1.5 mm wide; upper surface plane, dull, pustulate, the pustules entire or bursting open apically, without forming soredia; medulla in part yellow-ochre below; lower surface moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia adnate, the amphithecium pustulate, 0.5–2 mm in diameter; spores 6 $\mu$ –8 $\mu$   $\times$  8 $\mu$ –12 $\mu$ .

**CHEMISTRY.**—Cortex K–, medulla K– or K+ reddish, P+ orange (lichexanthone, protocetraric acid, alecortonic acid, and rhodophyscin).

**DISTRIBUTION.**—Southeastern Brazil.

**HABITAT.**—On open sandstone outcrops.

**REMARKS.**—This rare saxicolous species is characterized by the pustules and unusual combination of chemicals. It will undoubtedly be found again in southeastern Brazil with more intensive collecting. I had originally synonymized it with *H. minima* (Hale, 1960) and compared it with *H. formosana*. It is, however, morphologically and chemically distinct from both of these.

### 41. *Hypotrachyna microblasta*, new combination

FIGURE 13e

*Parmelia microblasta* Vainio, 1890:57. [Type collection: Carrassa, Minas Gerais, Brazil, *Vainio* 1214 (TUR, lectotype; BM, M, P, UPS, isolectotypes).]

*Parmelia revoluta* f. *isidiosa* Müller Argau, 1891:378.  
*Parmelia propagulifera* Vainio, 1899: (123).  
*Parmelia jamaicensis* Vainio, 1915:23.  
*Parmelia pseudorevoluta* Gyelnik, 1931:289.  
*Parmelia neopropagulifera* Gyelnik, 1938a:39.  
*Parmelia endorubra* f. *imbricatiformis* Gyelnik, 1938b:277.  
*Parmelia norstictica* Hale, 1959:128.  
 [For full synonymy, see Hale, 1971a:18.]

Thallus adnate to loosely attached, 5–15 cm in diameter, pale yellowish green, turning reddish in the herbarium if improperly curated; lobes sublinear, 1–4 mm wide; upper surface plane, shiny, without maculae, moderately to densely isidiate, the isidia cylindrical, tall, simple or coralloid-branched; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia 2–6 mm in diameter, adnate, the amphithecium isidiate; spores  $6\mu\text{--}8\mu \times 10\mu\text{--}13\mu$ .

CHEMISTRY.—Cortex K–, medulla K+ red, P+ orange (atranorin (traces), usnic acid, norstictic acid, salazinic acid, and galbinic acid).

DISTRIBUTION.—Mexico, Central America, West Indies, Andean region from Venezuela to Peru, southeastern Brazil, Hawaii, and Southeast Asia.

HABITAT.—On trees (hardwoods and conifers), rocks, and soil in open secondary forests, pastures, and road banks at 900–3100 m elevation.

REMARKS.—*Hypotrachyna microblasta* is common in a wide range of habitats throughout tropical America. The extensive synonymy is difficult to understand in view of the general uniformity of the species. The thallus frequently discolors red when improperly pressed and dried. The chemistry relates it to *H. enderythraea*, the presumptive nonisidiate sexual morph or a population derived from it.

REPRESENTATIVE SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 20038, 20210, 20221, 20353, 20385, 20553; Michoacán, *Arsène* (US). Guatemala: Quetzaltenango, *Standley* 86085 (US). Costa Rica: Alajuela, *Standley and Torres* 47471 (US); Cartago, *Standley and Valerio* 46807 (US). Panama: Chiriquí, *Hale* 38799, 38842, 38912, 38925, *Scholander* (US). Cuba: Oriente, *Imshaug* 25141, 25179 (MSC), *Morton* 9595, 9596 (US). Jamaica: *Cummings* (FH), *Hart* 54 (NY), *Imshaug* 12943, 13057, 13308, 13313 (MSC), 13327 (LD, MSC), 13857, 13923, 14815, 14898, 15452 (MSC, US), *Maxon* 8634 (US), *Plitt* (US). Haiti: Ouest, *Imshaug* 23088, *Wetmore* 2993 (MSC, US). Dominican Republic: La Vega, *Allard* 17726A (US),

*Imshaug* 23389 (MSC), 23573 (MSC, US). Guadeloupe: *Duss* 676 (NY). Dominica: *Hale* 35450. Colombia: Cundinamarca, *Cuatrecasas* 231, 27068a (US), *Weir* 78 (BM); Santander, *Killip and Smith* 18942a (US). Venezuela: Bolívar, *Steyermark* 59817 (US); Federal, *Santesson* 6683 (S) Mérida, *Hale* 42146, 42192, 42773, 43028, *Oberwinkler and Poelt* (M, US), *Vareschi* 883 (US). Peru: Cuzco, *Marin* 21916 (F). Ecuador: Imbabura, *Wiggins* 38941 (COLO). Brazil: *Sowerby* (lectotype of *P. revoluta* f. *isidiosa* Müller Argau) (G); Minas Gerais, *Vainio* 1160 (BM, M, TUR, UPS).

#### 42. *Hypotrachyna minima*, new combination

FIGURE 13f

*Parmelia minima* Lyngé, 1914:139. [Type collection: Bocca da Serra, Mato Grosso, Brazil, *Malme* 2747 bis (S, lectotype).]

Thallus adnate on rocks, fragile and breaking apart, creamy whitish gray and darkening toward the center, 6–8 cm broad; lobes sublinear, crowded and imbricate, 0.5–1.5 mm wide; upper surface plane to rugulose, continuous to cracked with age, pycnidia and papillate apothecial initials abundant; medulla orange-red in the lower part; lower surface sparsely to moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia common, adnate, 1–2.5 mm in diameter, the amphithecium crenate and bullate; spores  $7\mu \times 10\mu$ .

CHEMISTRY.—Cortex K–, medulla K–, C–, KC+ reddish, P+ orange (lichexanthone and protocetraric acid).

DISTRIBUTION.—Southeastern Brazil.

HABITAT.—On open sandstone rocks at about 1000 m elevation.

REMARKS.—This saxicolous species is as rare as its close relative *H. malmei* in Brazil. The pustules, which I originally described (Hale, 1960), are entire and confined to the amphithecium. This difference, in addition to chemistry (lack of alectoronic acid), clearly separates *H. minima* from *H. malmei*.

#### 43. *Hypotrachyna monilifera*, new combination

FIGURE 14a

*Parmelia monilifera* Kurokawa in Hale and Kurokawa, 1964:

182. [Type collection: La Aguada, Mérida, Venezuela, *Mägdefrau* 651 (M, holotype; US, isotype).]

Thallus loosely adnate on bark, 10–15 cm broad, whitish mineral gray; lobes linear-divaricate, 2–6 mm wide; upper surface plane, continuous; lower surface densely rhizinate, the rhizines moderately branched, conspicuously moniliform-segmented, projecting as a mat beyond the lobe margins. Apothecia not present.

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+ orange, P– (atranorin, barbatic acid, 4-O-demethylbarbatic acid, possibly traces of obtusatic and norobtusatic acids).

DISTRIBUTION.—Venezuela.

HABITAT.—On bark of small trees in lower paramo region at about 2800 m elevation.

REMARKS.—While superficially close to *H. gigas*, this species has a stiffer thallus and peculiar moniliform rhizines easily detected with a hand lens. I was fortunate in being able to re-collect it at the type locality where, apparently, it is very rare in comparison with *H. gigas* and corticolous. The chemistry relates it to the *H. physcioides* group, but the elongate lobes and the rhizines put it in an isolated position in the genus.

SPECIMENS EXAMINED.—Venezuela: Mérida, *Hale* 43085.

#### 44. *Hypotrachyna neodissecta*, new combination

FIGURE 14b

*Parmelia neodissecta* Hale, 1971c:94. [Type collection: 6 km SE of Zouépo, N'Zérékoré, Guinea, *Santesson* 10597d (UPS, holotype; US, isotype).]

Thallus loosely attached, rather fragile, pale greenish ashy gray, 3–7 cm broad; lobes sublinear to subirregular, in part subascending, becoming subcaniculate, 1–3 mm wide; upper surface shiny, continuous, becoming densely isidiate, isidia cylindrical, mostly simple; lower surface densely rhizinate, the rhizines moderately dichotomously branched. Apothecia adnate, the amphithecium isidiate, 2–3 mm in diameter; spores not found (in African material,  $6\mu\text{--}8\mu \times 12\mu\text{--}14\mu$ ).

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

DISTRIBUTION.—Venezuela, Africa, and India.

HABITAT.—On trees in secondary forest at 2000–2200 m elevation.

REMARKS.—*Hypotrachyna neodissecta* was first discovered in Guinea and subsequently collected in other African localities and in India. I would not have expected to find it in the New World. It is distinguished from *Parmelina dissecta* (Nylander) Hale, for which it would almost certainly be mistaken, by the branched rather than simple rhizines, lack of cilia, and overall canaliculate-revolute pattern of lobation.

SPECIMENS EXAMINED.—Venezuela: Mérida, *Hale* 42973.

#### 45. *Hypotrachyna novella*, new combination

FIGURE 14c

*Parmelia novella* Vainio, 1890:56. [Type collection: Sitio, Minas Gerais, Brazil, *Vainio* 1028 (TUR, lectotype; BM, FH, M, isolectotypes).]

*Parmelia brasiliensis* var. *novella* (Vainio) Lyngé, 1914:115.

*Parmelia regis* Lyngé, 1914:126. [Type collection: São Paulo d'el Rey, Minas Gerais, Brazil, *Malme* 178 (S, lectotype; UPS, isolectotype).]

Thallus closely adnate on bark, tannish mineral gray, 2–4 cm broad; lobes sublinear, crowded, 1–2.5 mm wide; upper surface plane, continuous, darkening toward the center; lower surface black, densely rhizinate, the rhizines densely dichotomously branched. Apothecia common, adnate, 2–7 mm in diameter, the amphithecium crenulate; spores  $6\mu \times 12\mu$ .

CHEMISTRY.—Cortex K–, medulla K–, C+ rose or C–, P– (lichexanthone, colensoinic acid, norcolensoinic acid, 4-O-demethylphysodic acid, lividic acid, physodic acid, and associated unknown substances).

DISTRIBUTION.—Venezuela and southeastern Brazil.

HABITAT.—On trees in open forests at 1000–2000 m elevation.

REMARKS.—*Hypotrachyna novella* is essentially identical to *H. livida* except for the replacement of atranorin by lichexanthone. It also has a much more restricted distribution. Chemically identical *H. formosana* could be considered as the pustulate vegetative morph.

SPECIMENS EXAMINED.—Venezuela: Valencia, *Mägdefrau* 398 (M). Brazil: Mato Grosso, *Malme* (S, UPS, US); Rio de Janeiro, *Eiten* 7724a (US); São Paulo, *Hemmendorf* (S).

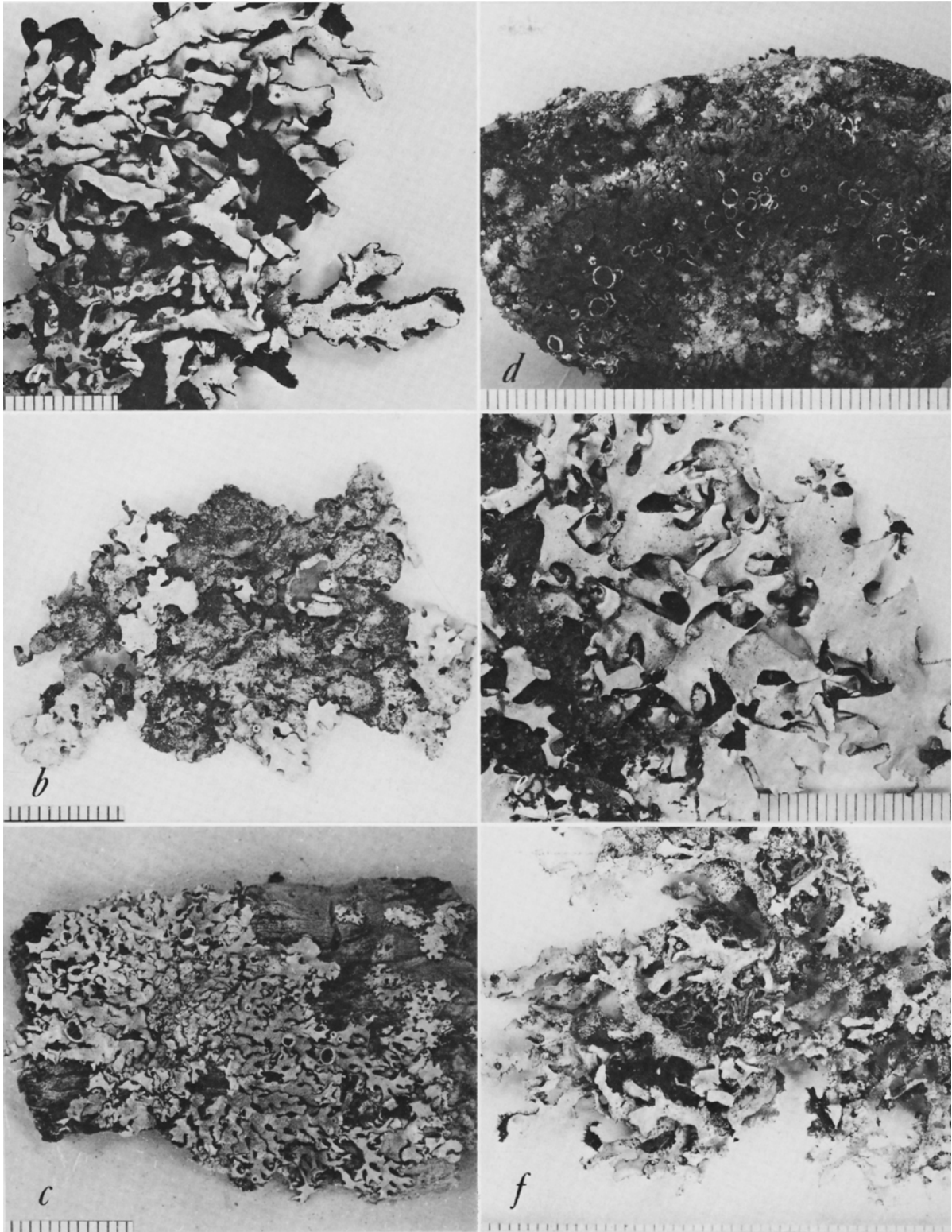


FIGURE 14.—Species of *Hypotrachyna*: a, *H. monilifera* (Mägdefrau 651); b, *H. neodissecta* (Santesson 10597d); c, *H. novella* (Malme 178 in S); d, *H. obscurella* (Hale 43342); e, *H. oostingii* (Dey 2403); f, *H. osorioi* (Osorio 6507). (Scale in mm.)

**46. *Hypotrachyna obscurella*, new combination**

FIGURE 14d

*Parmelia gracilescens* f. *obscurella* Vainio, 1890:54. [Type collection: Carassa, Minas Gerais, Brazil, *Vainio* 1180 (TUR, lectotype; BM, isolectotype).]

Thallus very closely adnate to rocks, dark mineral gray, 4–6 cm broad; lobes sublinear, short, crowded, 1–1.5 mm wide; upper surface plane, shiny, cracked transversely with age, pycnidia numerous, isidia and soredia lacking; lower surface moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia common, adnate, 1–2.5 mm in diameter; spores  $6\mu \times 8\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, KC– or KC+ reddish, P+ orange (atranorin and protocetraric acid).

DISTRIBUTION.—Venezuela and Brazil.

HABITAT.—On exposed rocks in open areas and in the paramo at 1500–3500 m elevation.

REMARKS.—This dark, small, saxicolous lichen blends in with the background igneous rock substratum and is difficult to collect because of the close adnation. It is very common on boulders in the paramo regions of Venezuela and probably occurs throughout the Andes. There are no close relatives in the genus.

SPECIMENS EXAMINED.—Venezuela: Mérida, *Hale* 43188A 43322, 43342. Brazil: Minas Gerais, *Vainio* 1431 (BM, TUR).

**47. *Hypotrachyna oostingii*, new combination**

FIGURE 14e

*Parmelia oostingii* Dey, 1974:362. [Type collection: Balsam Cone, Yancey County, North Carolina, *Dey* 1236 (DUKE, holotype; US, isotype).]

Thallus loosely attached, firm, whitish mineral gray, 8–12 cm broad; lobes sublinear, dichotomously branched, more or less separate, 2–5 mm wide; upper surface plane, shiny, pustulate, the pustules subterminal, becoming coarsely sorediate or remaining as open pits; lower surface moderately to densely rhizinate, the rhizines moderately dichotomously branched. Apothecia not seen.

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+ red, P– (atranorin, gyrophoric acid, and weakly UV+ fluorescent unknown substances).

DISTRIBUTION.—Southeastern United States and southern Chile.

HABITAT.—On trees (conifers, *Nothofagus*) in open woods at lower elevations in Chile, at 2000 m in southeastern United States.

REMARKS.—Externally this species is very close to *H. laevigata* and *H. thysanota*. Specimens from Chile had been misidentified as *H. densirhizinata*. Chemistry places it closest to *H. thysanota*, which would react both C+ red (gyrophoric acid) and P+ red (echinocarpic acid).

SPECIMENS EXAMINED.—Chile: Tierra del Fuego, *Santesson* 6799 (S, US).

**48. *Hypotrachyna osorioi*, new combination**

FIGURE 14f

*Parmelia osorioi* Hale, 1974b:266. [Type collection: Abra de Cotto, Lavalleja, Uruguay, *Osorio* 6507 (MVM, holotype; US, isotype).]

Thallus loosely adnate on rock, fragile, light tannish mineral gray, about 8 cm in diameter; lobes sublinear, about 2 mm wide; upper surface plane, continuous, coarsely isidiate, isidia simple and cylindrical to coralloid-branched, apically breaking down and almost pustulate or sorediate, dense with age; lower surface moderately rhizinate, rhizines moderately dichotomously branched. Apothecia rare, adnate, 3–7 mm in diameter; spores  $6\mu \times 12\mu$ .

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

DISTRIBUTION.—Uruguay.

HABITAT.—On stones in open forest at less than 1000 m elevation.

REMARKS.—The isidia of this rather fragile species are well developed and tend to enlarge apically and crumble, unlike any other in the genus. It may be related to *H. pluriformis*-*H. revoluta*, although the lobes are more regularly linear.

SPECIMENS EXAMINED.—Uruguay: Rocha, *Hosseus* 48 (H); San José, *Osorio* 6178 (MVM).

**49. *Hypotrachyna osteoleuca*, new combination**

FIGURE 15a

*Parmelia osteoleuca* Nylander, 1863:439. [Type collection:

Bogotá, Colombia, *Lindig* 2528 (H, lectotype; BM, FH, G, H, M, P, W, isolectotypes.)]

Thallus closely adnate or becoming loosely attached as thick thallus mats form, ashy white or darkening, 5–10 cm broad; lobes sublinear, often imbricate and crowded, 1–3 mm wide; upper surface plane, smooth, continuous, lacking soredia and isidia but usually heavily pycnidiate; medulla white to pale salmon; lower surface sparsely to densely rhizinate, the rhizines densely dichotomously branched. Apothecia common, adnate to substipitate, the disc dark brown, 1–4 mm in diameter; spores  $5\mu\text{--}6\mu \times 7\mu\text{--}9\mu$ .

CHEMISTRY.—Cortex K–, medulla K–, C+ red, P– (lichexanthone, olivetoric acid, rhodophyscin (in lower medulla), and unidentified substances).

DISTRIBUTION.—Colombia and Venezuela.

HABITAT.—On exposed rocks in the paramo at 2800–3000 m elevation.

REMARKS.—The positive C test was first noted by Vainio (1890), who also noted the superficial resemblance to *H. brasiliensis*. In Venezuela this species occurs intermixed on boulders in the paramo with *H. erythrodes*, which reacts C–.

SPECIMENS EXAMINED.—Colombia: Santander, *Killip and Smith* 15186 (US). Venezuela: Mérida, *Hale* 42680, 42853, 42864, 43311, 43323, 43336.

### 50. *Hypotrachyna palmarum*, new combination

FIGURE 15b

*Parmelia palmarum* Lyngé, 1914:136. [Type collection: Buriti, Serra da Chapada, Mato Grosso, Brazil, *Malme* 2243C\* (S, lectotype).]

*Parmelia zahlbruckneri* Lyngé, 1914:125. [Type collection: Bocca da Serra, Serra da Chapada, Mato Grosso, Brazil, *Malme* S, lectotype].]

Thallus adnate, turning cream or cinnamon-buff in the herbarium, rather fragile, 3–8 cm broad; lobes sublinear, crowded, more or less imbricate, short, 1–3 mm wide; upper surface shiny, plane to rugose and cracked on older lobes, isidia and soredia lacking; medulla white to very pale yellow; lower surface moderately rhizinate, the rhizines rather sparsely dichotomously branched. Apothecia common, adnate, the amphithecium crenate, the disc often split, 2–6 mm in diameter; spores  $5\mu\text{--}7\mu \times 9\mu\text{--}11\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–,

C–, KC+ rose, P– (atranorin, colensoinic acid, the “palmarum” unknown, and other unidentified substances).

DISTRIBUTION.—Southeastern Brazil.

HABITAT.—On trees or sandstone outcrops in open or secondary forests at 600–1500 m elevation.

REMARKS.—This rather rare species is closely related to *H. livida* since they both contain colensoinic acid. Hopefully, the full relationship will be revealed when the molecular structure of the “palmarum” unknown is determined. The rock form, described by Lyngé as *Parmelia zahlbruckneri*, is indistinguishable in chemistry and morphology from the corticolous forms. This parallels the situation with *Hypotrachyna livida*–*Parmelia ossealbida*.

SPECIMENS EXAMINED.—Brazil: Mato Grosso, *Malme* in *Lichenes Austroamericani* 90 (H, UPS), *Malme* 2393\*\*\*\* (S, US), *Richards* 6355 (BM); Minas Gerais, *Warming* 279 (M); Santa Catarina, *Reitz and Klein* 16005 (US); São Paulo, *Eiten and Eiten* 3255, 3256 (US).

### 51. *Hypotrachyna partita*, new species

FIGURE 15c

Thallus laxe adnatus, membranaceus, cinereo-albicans, usque ad 15 cm latus, lobis sublinearibus, 4–7 mm latis, superne isidiatis, mox lobulascensibus, lobulis 0.3 mm latis, 1 mm longis; cortex superior  $16\mu\text{--}18\mu$  crassus, stratum gonidiale  $22\mu\text{--}24\mu$  crassum, medulla alba,  $80\mu\text{--}90\mu$  crassa, cortex inferior  $16\mu\text{--}18\mu$  crassus; subtus niger, dense rhizinosus. Apothecia ignota.

Thallus loosely adnate, rather membranaceous and fragile, greenish mineral gray, to 15 cm broad; lobes sublinear to subirregular, the tips often broadly rotund, 4–7 mm wide; upper surface plane, shiny, initially isidiate, the isidia becoming strongly lobulate, the lobules dorsiventral, about 0.3 mm wide and 1 mm long, simple to palmately divided, developing both laminally and marginally and becoming very dense in older parts; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia not seen.

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+ red, P– (atranorin and anziaic acid rarely accompanied by perlatolic acid).



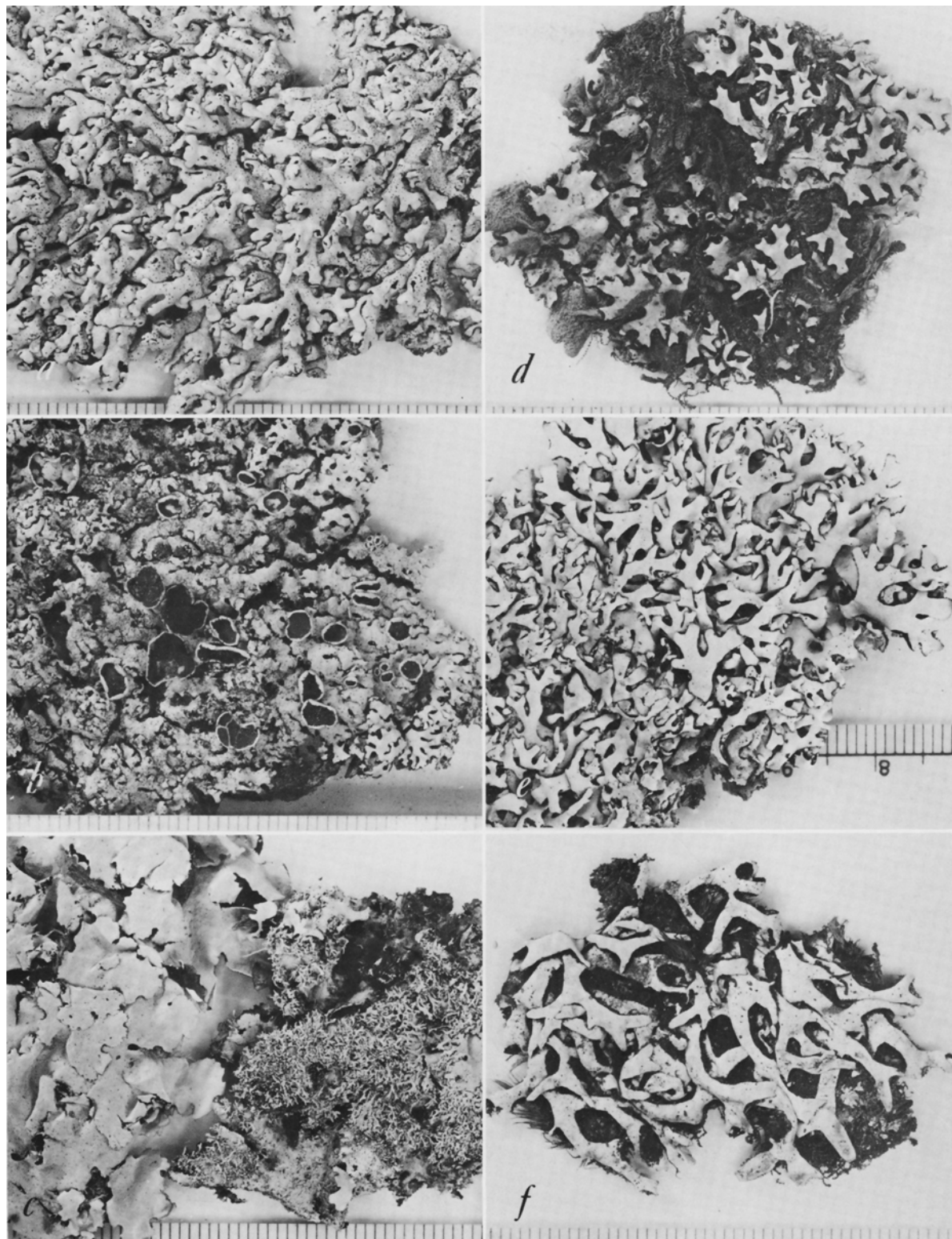


FIGURE 15.—Species of *Hypotrachyna*: a, *H. osteoleuca* (Hale 43332); b, *H. palmarum* (Eiten 3255); c, *H. partita* (Hale 43143); d, *H. peruviana* (Lechler 2727 in G); e, *H. physcioides* (Hale 43354); f, *H. physodalica* (Mora 984). (Scale in mm.)

TYPE COLLECTIONS.—Between La Aguada and La Montaña, Mérida, Venezuela, *Hale* 43143, 6 February 1974 (US, holotype).

DISTRIBUTION.—Central America and Venezuela.

HABITAT.—On trunks of trees in open or cloud forest and on soil at road banks at 2200–3600 m elevation.

REMARKS.—This species is common on stabilized roadsides where superficially morphologically similar *H. bogotensis* and *H. ensifolia* also occur. The lobulate isidia of *H. partita* are extremely variable and often densely developed. Perlatolic acid was detected in only one specimen (*Culbertson* 12395) which has very large, almost palmately divided lobules and had been subjected to recent lava ash fall.

SPECIMENS EXAMINED.—Costa Rica: Cartago, *Nee and Mori* 3540 (US). Panama: Chiriquí, *Hale* 38930. Venezuela: Mérida, *Hale* 42118, 42144, 42852, 43065, 43167, 43191, 43205, 43242.

## 52. *Hypotrachyna peruviana*, new combination

FIGURE 15d

*Parmelia peruviana* Nylander, in Crombie, 1876:228. [Type collection: Tatanara, Peru, *Lechler* 2727 (H, lectotype; BM, G, M, P, S, UPS, isolectotypes).]

Thallus loosely adnate on bark, rather fragile, 4–7 cm in diameter; lobes short, sublinear, 2–6 mm wide; upper surface plane to rugulose, faintly maculate, lacking isidia and soredia; medulla pale chalcedony yellow; lower surface densely rhizinate, the rhizines 1–2 mm long, dichotomously branched. Apothecia conspicuously stipitate to columnar, 3–6 mm high, 2–5 mm in diameter, the amphithecium rugose; spores  $7\mu\text{--}12\mu \times 11\mu\text{--}18\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K+ yellowish, C+ orange (atranorin, barbatic acid, obtusatic acid, entothoin, and unidentified pigments).

DISTRIBUTION.—Peru and Brazil.

HABITAT.—On trees in open forests at 1000–1500 m elevation.

REMARKS.—The coarsely stalked apothecia are distinctive for this species. The yellow pigment is very pale and probably different from that in *H. endochlora*. The species is related to *H. physcioides*, as Nylander (1885) suspected, but has diverged considerably from any presumptive pro-

genitor in this group because of the unusual apothecia and production of pigments.

SPECIMENS EXAMINED.—Brazil: Rio de Janeiro, *Gregory and Ainsworth* 529, 530 (BM, US); Santa Catarina: *Reitz and Klein* 16091 (US).

## 53. *Hypotrachyna physcioides*, new combination

FIGURE 15e

*Parmelia physcioides* Nylander, 1860:385. [Type collection: Silla de Caracas, Venezuela, *Humboldt and Bonpland* (P, lectotype; BM, H, isolectotypes).]

*Parmelia laevigata* var. *gracilis* Müller Argau, 1879:169. [Type collection: Bogotá, Colombia, *André* 923 bis (G, lectotype; BM, US, isolectotypes).]

*Parmelia boliviana* Nylander, 1885:612. [Type collection: Prov. Larecaja and Caupolicán, Bolivia, *Weddell* (P, lectotype).]

*Parmelia gracilis* (Müller Argau) Vainio, 1890:55.

*Parmelia digitata* Lynge, 1914:98. [Type collection: Santa Anna da Chapada, Mato Grosso, Brazil, *Malme* 2545 (S, lectotype; LD, US, W, isolectotypes).]

*Parmelia confusula* Zahlbruckner, 1929:162. [Type collection: Based on *P. gracilis* (Müller Argau) Vainio, not *P. gracilis* Sprengel, 1827:277, or *P. gracilis* Müller Argau, 1887:317].]

Thallus adnate to loosely attached, usually rather coriaceous, 6–15 cm broad, ashy white to tannish mineral gray; lobes sublinear, separate to crowded, 2–6 mm wide; upper surface plane to convex, dull and sometimes white pruinose at the tips to shiny and distinctly white-maculate, rarely becoming sparsely to densely lobulate-laciniate toward the center, isidia and soredia lacking; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia adnate to substipitate, 2–10 mm in diameter; spores  $6\mu\text{--}9\mu \times 12\mu\text{--}16\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C– or C+ orange, KC+ orange, P– (atranorin, barbatic acid, 4-O-demethylbarbatic acid, obtusatic acid, and norobtusatic acid).

DISTRIBUTION.—Mexico, Central America, West Indies, Colombia, Venezuela, Peru, Ecuador, Bolivia, Brazil, and Southeast Asia.

HABITAT.—On trees (conifers and hardwoods) and rocks in open or disturbed forests at 1500–4100 m elevation.

REMARKS.—*Hypotrachyna physcioides* is common in the northern part of its range but apparently lacking in most of Brazil and southward. It is extremely variable. Typical soil- or rock-

inhabiting specimens (as in the type) are almost coriaceous and have dull linear lobes. Some corticolous forms (as in the type of *Parmelia boliviana*) are thinner and have shorter, sub-linear lobes and a shiny surface with white maculae. Many intermediates can be found. The chemistry, however, is uniform in all cases.

A rather densely lobulate population described by Lyngé as *Parmelia digitata* probably is only an extreme form which intergrades with the more normal and abundant nonlobulate population.

This species is the presumptive progenitor of various vegetative morphs, *H. laevigata* (sorediate) and *H. imbricatula* (isidiate), as well as being part of the same constellation that produced *H. chlorina*, *H. endochlora*, *H. isidiocera*, *H. peruviana*, etc. The possible origin of *H. physcioides* from hybridization between evernic-acid-containing *H. pulvinata* and a barbatic-acid-containing progenitor similar to *H. massartii* (Hue) Hale is discussed by Culberson and Hale (1973).

**SPECIMENS EXAMINED.**—Mexico: Puebla, *Arène* 4253 (US). Guatemala: Alta Verapaz, *Standley* 91328 (US). Costa Rica: Alajuela, *Standley and Torres* 47720 (US); Cartago, *Culberson* 12394 (DUKE, US), *Stork* L-38 (US); San José, *Culberson* 13215 (DUKE). Panama: Chiriquí, *Martin* 2751 (US). Haiti: Ouest, *Imshaug* 22990, 22991 (MSC), *Wetmore* 3121 (MSC); Sud, *Imshaug* 23238 (MSC). Dominican Republic: La Vega, *Imshaug* 23459, 23628 (MSC). Colombia: Cundinamarca, *King* 472 (US), *Nee and Mori* (US), *Soderstrom* 1305b, 1305c (US), *Weir* 27 (BM, US); Santander, *Killip and Smith* 15644, 18593 (US). Venezuela: Mérida, *Hale* 42171, 42433, 42485, 42804, 43126, 43224, 43326, *Hanselmann* 168 (DUKE, US), *Mägdefrau* 698 (M, US), *Nash* 2013, 2014 (US).

#### 54. *Hypotrachyna physodolica*, new combination

FIGURE 15f

*Parmelia physodolica* Hale, 1971d:436. [Type collection: Guasca, Cundinamarca, Colombia, *Perez-Arbelaes* 1104 (US, holotype).]

Thallus loosely adnate, often scattered, coriaceous but easily breaking apart, sea-foam yellow, to 8 cm broad; lobes sublinear, elongate, sparsely

dichotomously branched, separate, 1–3 mm wide; upper surface plane, shiny, maculae, soredia, and isidia lacking; lower surface moderately to densely rhizinate, the rhizines dichotomously branched. Apothecia not seen.

**CHEMISTRY.**—Cortex K–, medulla K–, C–, P+ orange-red (usnic acid, physodalic acid, and a trace of protocetraric acid or usnic acid and protocetraric acid only).

**DISTRIBUTION.**—Colombia, Venezuela, and Peru.

**HABITAT.**—On soil and over humus in the paramo at 3700–4100 m elevation.

**REMARKS.**—This paramo species is easily recognized by the deep greenish yellow color and sub-linear divaricate lobes. Both *H. caraccensis*, a much larger species, and *H. lopezii*, which has a nearly bare lower surface, react K+ red or yellow. The type of *H. physodolica* was reported to contain only physodalic acid, but subsequent TLC tests showed traces of protocetraric acid. Specimens collected later contain only protocetraric acid. I am provisionally regarding these chemically variable populations as a single species, at least until we know more about the biogenesis and co-occurrence of these closely related acids.

**SPECIMENS EXAMINED.**—Colombia: Cundinamarca, *Mora* 984 (US); Santander, *Killip and Smith* (17527 (US). Venezuela: Mérida, *Hanselmann* 340 (DUKE, US), *Oberwinkler and Poelt* (M, US). Peru: San Martín, *Holligan* L60A (BM) .

#### 55. *Hypotrachyna pluriformis*, new combination

FIGURE 16a

*Parmelia pluriformis* Nylander, 1860:381. [Type collection: Brazil, *Weddell* (H, lectotype; P, isolectotype).]

*Parmelia pluriformis* var. *chlorocarpa* Müller Argau, 1881:85. [Type collection: Apiahy, Brazil, *Puiggari* 125e (G, lectotype).]

*Parmelia pluriformis* var. *multifida* Müller Argau, 1881:85. [Type collection: Apiahy, Brazil, *Puiggari* 1283 (G, lectotype).]

*Parmelia everniaeformis* Zahlbruckner, 1902:416. [Type collection: Petrópolis, Brazil, *Höhnell* 163 (W, lectotype).]

*Parmelia subpluriformis* Zahlbruckner, 1909:172. [Type collection: Mt. Jaraguá, São Paulo, Brazil, *Schiffner* (W, lectotype).]

Thallus adnate or loosely attached to bark, greenish mineral gray, 5–8 cm broad; lobes sub-linear to subirregular, imbricate, sometimes be-

coming canaliculate, 1–5 mm wide; upper surface plane to convex, continuous, lacking soredia and isidia; lower surface black in the center but with a broad brown zone along the margins, moderately rhizinate. Apothecia common, substipitate, 2–10 mm in diameter, the amphithecium rugulose, the disc often radially split; spores  $8\mu\text{--}11\mu \times 14\mu\text{--}25\mu$ .

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

DISTRIBUTION.—Mexico, Brazil, Uruguay, and Argentina.

HABITAT.—On trees in open forest at 1000–2300 m elevation.

REMARKS.—The lobes of this species are unique in being subirregular and in part canaliculate and revolute. The thallus has a coriaceous texture. Spore size is variable but definitely larger than in most *Hypotrachyna*. Zahlbruckner (1909), in fact, recognized *Parmelia subpluriformis* on the basis of large, thick-walled spores, but I would consider this as merely the extreme on a broad scale of spore size. It has the same chemistry as *H. revoluta* and *H. osorioi*, two vegetative morphs that originated from a sexual morph similar to *H. pluriformis*.

SPECIMENS EXAMINED.—Mexico: Puebla, Hale 19621. Brazil: Minas Gerais, Burchell 1105/68, 2252 (BM), Christina (P), Vainio 794 (M, TUR), 1049, 1052 (BM, TUR); Rio de Janeiro, Glaziou 1832 (UPS); São Paulo, Gehrt (US, W), Lindberg (UPS), Schiffner (BM, G). Uruguay: Canelones, Rosa-Mato 1031 (S); Florida, Imshaug 42406A (MSC). Argentina: Misiones, Montes 10073 (MVM).

### 56. *Hypotrachyna producta*, new species

FIGURE 16b

Thallus laxe adnatus, 6–7 cm diametro, cinereo-albicans, lobis sublinearibus, 2–3 latis, superne sorediatis; cortex superior  $13\mu\text{--}15\mu$  crassus, stratum gonidiale  $14\mu\text{--}16\mu$  crassum, medulla alba,  $65\mu\text{--}90\mu$  crassa, cortex inferior,  $12\mu$  crassus; subtus niger, modice rhizinosus. Apothecia ignota.

Thallus loosely adnate on bark, whitish mineral gray, 6–10 cm in diameter; lobes sublinear, becoming elongate and subdivicinate, 2–4 mm wide; upper surface shiny, plane, sorediate, the soredia subterminal in orbicular soralia, the soredi-

ate lobes becoming subrevolute; lower surface moderately rhizinate, the rhizines moderately to densely dichotomously branched. Apothecia not seen.

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

TYPE COLLECTION.—On *Picea rubens*, Mt. Le Conte, Sevier County, Tennessee, Nakanishi 174, 8 May 1971 (US, holotype; KOBE, isotype).

DISTRIBUTION.—Southeastern United States, Colombia, and Africa.

HABITAT.—On trunks and branches of trees (hardwoods and conifers) in open forest at 2000–3600 m.

REMARKS.—*Hypotrachyna producta* is morphologically similar to other sorediate species such as *H. laevigata* and *H. oostingii*. It would have to be identified with a chemical test. The presumptive progenitor is *H. ducalis*, which is also rarely collected in tropical America.

SPECIMENS EXAMINED.—Colombia: Cundinamarca, Killip 34118 (US); Santander, Killip and Smith 17798 (US).

### 57. *Hypotrachyna prolongata*, new combination

FIGURE 16c

*Parmelia prolongata* Kurokawa in Hale and Kurokawa, 1964: 182. [Type collection: Pic Macaya, Sud, Haiti, Wetmore 3233 (MSC, holotype; US, isotype).]

Thallus adnate to loosely adnate, mineral gray, 5–10 cm in diameter; lobes sublinear, 1.5–4 mm wide; upper surface plane, shiny, faintly maculate, sparsely lobulate-isidiate along the margins, the “isidia” in part lobulate, sometimes branched, 2–3 mm long; lower surface densely rhizinate. Apothecia not seen.

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+ red, P– (atranorin and an unidentified C+ substance).

DISTRIBUTION.—Haiti.

HABITAT.—On pine trees at about 2000 m elevation.

REMARKS.—This rare species is still known only from the type collection in Haiti. Specimens from other localities so identified on the basis of a C+ red reaction were found to contain anziaic acid and to have a different kind of isidial formation. These have been recognized as *H. rachista* (Hale, 1971d). The C+ substance in *H. prolongata*

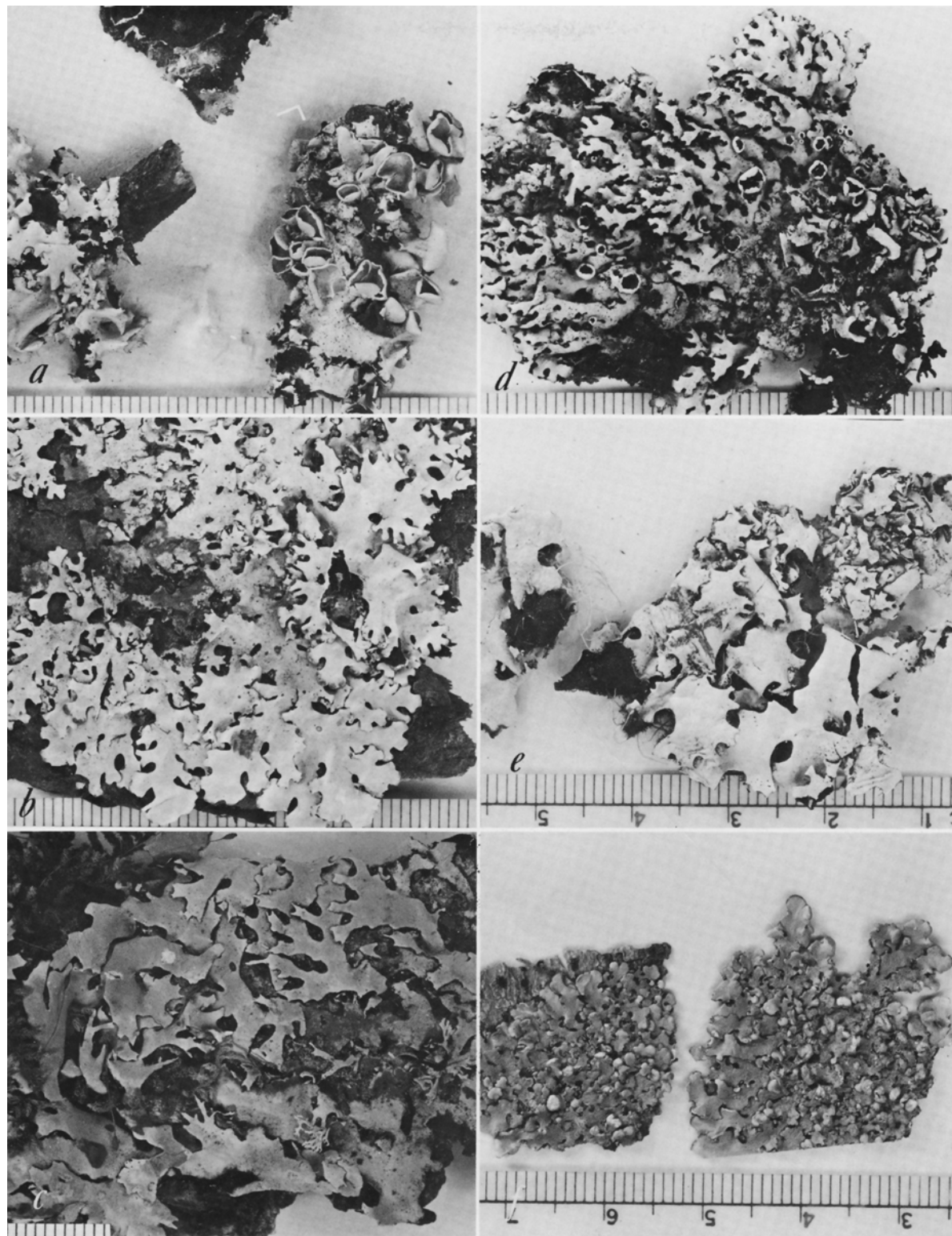


FIGURE 16.—Species of *Hypotrachyna*: a, *H. pluriformis* (Schiffner in W); b, *H. producta* (Nakanishi 174); c, *H. prolongata* (Wetmore 3233); d, *H. protenta* (Hale 43365); e, *H. protoboliviana* (Flenniken 1874); f, *H. pseudosinuosa* (Hale 35450). (Scale in mm.)

does not compare with anziaic acid, gyrophoric acid, lecanoric acid, or olivetoric acid and probably represents a new compound.

### 58. *Hypotrachyna protenta*, new species

FIGURE 16d

Thallus laxe adnatus, saxicola, 6–10 cm diametro, lobis sublinearibus, imbricatis, 2–4 mm latis; cortex superior 14 $\mu$ –16 $\mu$  crassus, stratum gonidiale 24 $\mu$  crassum, medulla alba, 80 $\mu$ –90 $\mu$  crassa, rare pro parte aurantiaca, cortex inferior 14 $\mu$ –16 $\mu$  crassus; subtus niger, modice rhizinosus. Apothecia numerosa, substipitata, sporis simplicibus, 6 $\mu$   $\times$  12 $\mu$ .

Thallus rather loosely adnate on rocks, the colonies easily breaking apart, whitish ashy, 6–10 cm broad; lobes sublinear, more or less crowded or imbricate, variable, 2–4 mm wide, sometimes becoming densely appressed lobulate toward older parts; upper surface shiny, plane to minutely rugulose, often heavily pycnidiate, soredia and isidia lacking; lower surface densely rhizinate, the rhizines sparsely to moderately dichotomously branched, sometimes projecting as a narrow mat along the margins. Apothecia numerous, adnate, 4–8 mm in diameter; spores 6 $\mu$   $\times$  12 $\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, KC+ red, P– (atranorin, alectoronic acid,  $\alpha$ -collatolic acid, and, if pigmented, rhodophyscin).

TYPE COLLECTION.—Open forest along stream, on rocks, El Valle, Mérida, Venezuela, *Hale* 43365, February 1974 (US, holotype; DUKE, TNS, UPS, isotypes).

DISTRIBUTION.—Central America, Colombia, and Venezuela southward to Peru, and Brazil.

HABITAT.—On rocks in open forests and in the paramo at 1700–4000 m elevation.

REMARKS.—*Hypotrachyna protenta* grows on open boulders or even soil in paramo and subparamo regions. Typically the lobes are densely imbricate and black rimmed but under some conditions they are almost separate and divaricate. The species resembles *H. chicitae* but can be distinguished by the negative C reaction and white fluorescence under ultraviolet. It can also be separated from small, high-elevation forms of *H. physcioides* (C+ orange) by a color test.

SPECIMENS EXAMINED.—Costa Rica: *Stork* (DUKE,

*H. MICH*, US, W). Panama: Chiriquí, *Hale* 38796, *Scholander* (US). Colombia: Cundinamarca, *King* 505 (US). Venezuela: Mérida, *Hale* 42130a, 42193, 42915, 42929, 43030, 43278, 43288, 43339. Peru: Cuzco, *Stafford* 1008 (F, US). Brazil: Santa Catarina, *Reitz and Klein* 17545 (US); São Paulo, *Schiffner* (BM, W).

### 59. *Hypotrachyna protoboliviana*, new combination

FIGURE 16e

*Parmelia protoboliviana* Hale, 1974b:267. [Type collection: Volcán Irazú, Cartago, Costa Rica, *Flenniken* 1874 (US).]

Thallus adnate on bark, rather fragile, about 8 cm in diameter, light yellowish green; lobes more or less sublinear, short, 4–5 mm wide; upper surface smooth, without isidia or soredia; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia poorly developed, about 1 mm in diameter; spores lacking.

CHEMISTRY.—Cortex K–, medulla K–, C+ orange, P– (usnic acid, barbatic acid, 4-O-demethylbarbatic acid, obtusatic acid, and norobtusatic acid).

DISTRIBUTION.—Costa Rica.

HABITAT.—On trees in open forest at about 3200 m elevation.

REMARKS.—Identical to *H. physcioides* except for the replacement of atranorin by usnic acid, *H. protoboliviana* is known only from Costa Rica in an active volcanic region. As a very recently evolved species it has not given rise to any vegetative morphs comparable to those of *H. physcioides*.

SPECIMENS EXAMINED.—Costa Rica: Cartago, *Flenniken* 2358 (US).

### 60. *Hypotrachyna pseudosinuosa*, new combination

FIGURE 16f

*Parmelia pseudosinuosa* Asahina, 1951:329. [Type collection: Shimohirano-mura, Shinano, Japan, *Takahashi* 99 (TNS, lectotype).]

*Parmelia anaptychioides* Kurokawa in Hale and Kurokawa, 1964:165. [Type collection: Pico Trujillo, Dominican Republic, *Wetmore* 3617 (MSC, holotype; US, isotype).]

Thallus closely adnate, light mineral gray, 3–9 cm in diameter; lobes sublinear, short and sometimes crowded, 1–4 mm wide; upper surface

plane, continuous, sorediate, the soralia capitate, mainly subterminal; lower surface moderately rhizinate. Apothecia rare, adnate, 2–4 mm in diameter; spores  $6\mu\text{--}8\mu \times 8\mu\text{--}10\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, P+ orange red (atranorin, protocetraric acid).

DISTRIBUTION.—Mexico, West Indies, Peru, South Africa, Japan, and Southeast Asia.

HABITAT.—On tree trunks and small branches (hardwoods, *Pinus*) in secondary forests at 1800–2200 m elevation.

REMARKS.—The thallus of *H. pseudosinuosa* is often small and closely adnate, as in the type of *Parmelia anaptychioides* (Hale, 1971a). It is one of the few species of *Hypotrachya* first described from Asia and later found to be pantropical. There is no presumptive parent species.

SPECIMENS EXAMINED.—Mexico: Oaxaca, *Nakanishi* 285 (US). Dominica: *Hale* 35358, 35488. Chile: Valparaíso, *Imshaug* 36628, 36642 (MSC). Records from Jamaica and Haiti are listed in Hale and Kurokawa (1964:166).

### 61. *Hypotrachyna pulvinata*, new combination

FIGURE 17a

*Parmelia pulvinata* Fée, 1824:123. [Type collection: Tropical America (G, lectotype).]

*Parmelia subsinuosa* Nylander, 1885:613. [Type collection: Tropical America, *Bonpland* (H, Nylander herbarium number 35169, lectotype; P, isolectotype).]

*P. caraccensis* f. *pulvinata* (Fée) Zahlbruckner, 1929:58.

Thallus adnate to loosely attached, whitish mineral gray, 8–12 cm broad; lobes short and often crowded, sublinear, 2–6 mm wide; upper surface plane, shiny, white-maculate; lower surface densely rhizinate, the rhizines often projecting as a mat beyond the margins, densely dichotomously branched. Apothecia common, adnate, 5–17 mm in diameter, the amphithecium strongly white-maculate; spores  $6\mu\text{--}7\mu \times 10\mu\text{--}13\mu$ .

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

DISTRIBUTION.—Southwestern United States, Mexico, Central America, Jamaica, Andean region from Venezuela to Bolivia, and southeastern Brazil.

HABITAT.—On trees (oak, pine), soil, over

mosses in pine forests, scrubby mist forest, and paramo at 1200–4300 m elevation.

REMARKS.—*Hypotrachyna pulvinata* is easily recognized by the white maculae, dense rhizine mat, and C+ rose or red color test. It is very common in the dry upland oak-pine forests from southern New Mexico-Arizona southward to Guatemala but becomes quite rare in South America. The vegetative morphs, *H. rockii* (sorediate) and *H. bogotensis* (isidiate), are two of the commonest species in tropical America. It is *H. pulvinata* or a progenitor similar to it which probably crossed with a barbatic-acid-containing progenitor such as *H. massartii* (Hue) Hale to give rise to the obtusatic-acid-containing constellation including *H. physcioides* and its vegetative morphs, *H. peruviana*, etc. (Culberson and Hale, 1973).

SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 20330, 20571; Federal, *Kramer* 1817 (US); Mexico, *Hale* 19290; Oaxaca, *Hale* 20672, 20688, 20691, 20700, 20784; Sinaloa, *Culberson* 13356 (DUKE). Guatemala: Quetzaltenango, *Steyermark* 34898 (US); Totonicapán, *Standley* 84507 (US). Costa Rica: San José, *Standley and Valerio* 43750 (US). Panama: Chiriquí, *Scholander* (US). Jamaica: *Imshaug* 15495 (MSC), *Plitt* (US). Colombia: Magdalena, *Flenniken* 2295 (US); Santander, *Killip and Smith* 19560 (US); Tolima, *Killip and Varela* 34678a (US). Venezuela: Mérida, *Dennis* 1940 (BM), *Hale* 42365, 42374, 42460. Ecuador: Pichincha, *Jameson* 145 (BM), *Ugent* (US, WIS). Peru: *Bryan* 579 (US, WIS). Bolivia: Cochabamba, *Ugent* (US, WIS); Larecajá, *Mandon* 1753 (BM, S). Brazil: Minas Gerais, *Henschen* (UPS).

### 62. *Hypotrachyna rachista*, new combination

FIGURE 17b

*Parmelia rachista* Hale, 1971d:436. [Type collection: Clingmans Dome, Swain County, North Carolina, *Kurokawa* 6755 (US; isotype in TNS).]

*Parmelia lobulifera* var. *sanguineoreagens* Degelius, 1941:63. [Type collection: Mt. Kephert, North Carolina, *Degelius* (US, lectotype).]

Thallus adnate to loosely adnate, 6–12 cm broad, whitish mineral gray; lobes linear, dichotomously branched, variable, 1–5 mm wide; upper surface plane, continuous, becoming dactyloid-isidiate at the lobe tips, isidia dorsiventral, often

dissected; lower surface black but sometimes with a narrow white rim below the lobe tips, densely rhizinate, the rhizines densely dichotomously branched. Apothecia not seen.

CHEMISTRY.—Cortex K+ yellow, medulla K-, C+ red, P- (atranorin and anziaic acid).

DISTRIBUTION.—Southeastern United States, Mexico, Panama, Dominican Republic, Colombia, Venezuela, and Peru.

HABITAT.—On trees (hardwoods and conifers), over mosses, and on soil at road banks at 2000–3500 m elevation.

REMARKS.—The isidia of this species are unusual in branching and position on the thallus (Figure 4d) and one might question whether they should be called isidia or lobules. The distinctive chemistry relates *H. rachista* to *H. ducalis* and its sorediate morph *H. producta*. The species is most commonly collected in the southern Appalachian Mountains in the United States and seems rare in tropical America.

SPECIMENS EXAMINED.—Dominican Republic: La Vega, *Imshaug* 23402 (MSC). Venezuela: Mérida, *Hale* 42610, 42648, 42896, 43139, 43239. Peru: Pasco, *Tovar* 397 (BM). For additional records from Mexico, Panama, and Colombia see Hale (1971:437).

### 63. *Hypotrachyna reducens*, new combination

FIGURE 17c

*Parmelia reducens* Nylander, 1968:438. [Type collection: Colombia, *Lindig* 2743 (H, Nylander herbarium number 35100, lectotype).]

Thallus adnate to loosely attached, sea-foam yellow, 2–5 cm in diameter; lobes sublinear, separate, 1–2 mm wide; upper surface plane to rugulose, faintly white-maculate, lacking soredia and isidia; lower surface densely rhizinate, the rhizines sometimes projecting out as a mat along the margins. Apothecia common, substipitate, the disc becoming radially split, 1–5 mm in diameter; spores  $5\mu\text{--}7\mu \times 9\mu\text{--}11\mu$ .

CHEMISTRY.—Cortex K-, medulla K+ yellow turning red, C-, P+ orange-red (usnic acid, norstictic acid, salazinic acid, sometimes a trace of atranorin).

DISTRIBUTION.—Panama, Colombia, Peru, Sabah, and New Guinea.

HABITAT.—On trunk and twigs of hardwood trees in exposed areas at 2800–3500 m elevation.

REMARKS.—While rarely collected, *H. reducens* is easily identified since it is the only nonsorediate, nonisidiate yellow species (outside of rare *H. protoboliviana*) on trees. It is always fertile. The typical habitat seems to be exposed shrubs in the paramo. The presumed sorediate morph, *H. sinuosa*, may occur in similar habitats.

SPECIMENS EXAMINED.—Panama: Chiriquí, *Scholarer* (US). Colombia: *Humbry-Tracy* 313 (BM); *Lindig* 122 (BM, M), 799 (M, P, syntypes of *P. reducens*). Peru: Recuay, *Gómez* 549 (US).

### 64. *Hypotrachyna revoluta*, new combination

FIGURE 17d

*Parmelia revoluta* Floerke, 1815:11. [Type collection: Germany, *Floerke* (FH-Tuck, lectotype).]

Thallus loosely adnate, rather fragile, greenish mineral gray, 3–8 cm broad; lobes sublinear to subirregular, often short and more or less ascending at the tips, subcanaliculate, 1–5 mm wide; upper surface plane, shiny, becoming very coarsely pustulate toward the lobe tips, the pustules becoming coarsely sorediate and sometimes eroding centrally leaving bare blackish areas of medulla, heavily sorediate lobes becoming revolute; lower surface black but with a brownish zone along the margins, sparsely rhizinate, the rhizines sparsely dichotomously branched. Apothecia very rare, adnate to substipitate, 2–6 mm in diameter; spores  $6\mu\text{--}8\mu \times 10\mu\text{--}12\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K-, C+ red, P- (atranorin and gyrophoric acid).

DISTRIBUTION.—Eastern United States, West Indies, Venezuela to Chile in the Andes, Europe, South Africa, Japan, and Indonesia.

HABITAT.—On trees (hardwoods and conifers) in open or cloud forest and on rocks at 1000–4500 m elevation (at sea level in Chile).

REMARKS.—This classical European species (Almborn, 1942) has a montane pantropical distribution. The name, however, has been applied incorrectly to many different species in the tropics. There is a wide and often perplexing range of variation in soredial formation, but in general the soredia are laminal to subterminal, causing the lobes to become broadly revolute, and may even



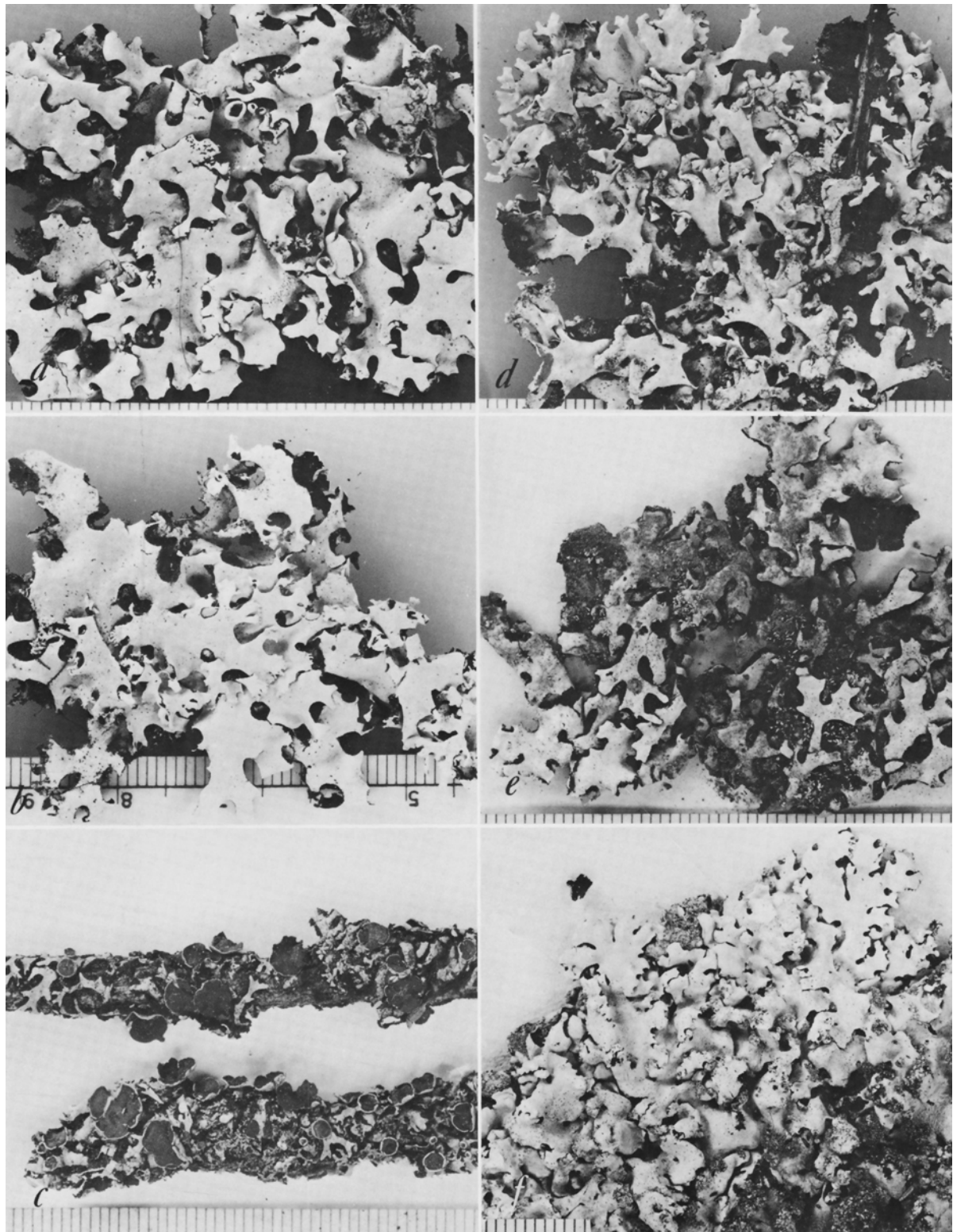


FIGURE 17.—Species of *Hypotrachyna*: a, *H. pulvinata* (Hale 20784); b, *H. rachista* (Hale 43139); c, *H. reducens* (Lindig 122 in M); d, *H. revoluta* (Hale 43293a); e, *H. rhabdiformis* (Wurdack 483); f, *H. rockii* (Rock 7). (Scale in mm.)

erode away leaving large, bare pustule-like areas (Figure 2a). The lobes also vary widely in width and degree of erectness. Spore size for European material was determined by Hillmann (1936) to be up to  $16\mu$  long, somewhat larger than American material. A presumptive progenitor, *H. pluriformis*, has significantly larger spores, up to  $25\mu$  long. Vainio's determination of his number 1140 as *Parmelia revoluta* from Brazil is incorrect; it is *H. rockii*.

**SPECIMENS EXAMINED.**—Dominican Republic: La Vega, *Allard* 16530A (US). Venezuela: Mérida, *Hale* 42995, 43296, 43306. Bolivia: *Brooke* 6819 (US), *Overbeek* 5455 (US). Chile: Chiloe, *Santesson* 4029 (S, US), 4031 (S); Valdivia, *Rabenhorst* (M, US), *Santesson* 2363 (S).

### 65. *Hypotrachyna rhabdiformis*, new combination

FIGURE 17e

*Parmelia rhabdiformis* Kurokawa in Hale and Kurokawa, 1964:183. [Type collection: El Boquete, Chiriquí, Panama, *Maxon* 5128a (US, holotype).]

Thallus adnate, light tannish mineral gray, 5–8 cm broad; lobes sublinear, short, imbricate, 2–6 mm wide; upper surface plane, continuous, moderately isidiate, the isidia mostly simple and cylindrical, to 0.5 mm high or more, becoming club-shaped or lobulate; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia adnate, 1–5 mm in diameter, the amphithecium isidiate; spores  $6\mu$ – $8\mu \times 15\mu$ – $21\mu$ .

**CHEMISTRY.**—Cortex K+ yellow, medulla K+ yellow turning red, C–, P+ orange (atranorin, norstictic acid, and in *Iltis* 3005 and *Wurdack* 483 a trace of stictic acid).

**DISTRIBUTION.**—Panama and Peru, Southeast Asia.

**HABITAT.**—On trees or on soil in cloud forest at 1300–2300 m elevation.

**REMARKS.**—This isidiate species has a unique chemistry. Superficially it resembles *H. costaricensis*, which has very dense rhizines and reacts K–. The collections from Peru are more robust than the type but agree in other features.

**SPECIMENS EXAMINED.**—Peru: Chachapoyas, *Wurdack* 483 (US); Urubamba, *Iltis* 3005 (US, WIS).

### 66. *Hypotrachyna rockii*, new combination

FIGURE 17f

*Parmelia rockii* Zahlbruckner, 1912:379. [Type collection: Kauai, Hawaii, *Rock* 7 (W, lectotype; US, isotype).]

Thallus adnate to loosely attached, 5–12 cm in diameter, whitish mineral gray; lobes sublinear, 1–6 mm wide; upper surface plane, shiny, often distinctly white-maculate, pustulate initially near the lobe tips, usually becoming coarsely sorediate; medulla white except for pale orange spots under the soralia; lower surface black, densely rhizinate. Apothecia rarely developed, adnate, 2–8 mm in diameter; spores  $5\mu$ – $7\mu \times 11\mu$ – $14\mu$ .

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C+ rose, P– (atranorin, evernic acid, and lecanoric acid).

**DISTRIBUTION.**—Southeastern United States to southern Chile, South Africa, Southeast Asia, and Hawaii.

**HABITAT.**—On tree bark (oaks, pine, *Ficus*, *Drimys*) and rocks in open forests at 1000–3300 m elevation.

**REMARKS.**—*Hypotrachyna rockii* is a very common lichen in the highland oak-pine forests of Mexico and Central America as well as in the West Indies. It is very similar externally to *H. laevigata* in having distinct maculae and subterminal soredia but can be distinguished from it by a color test with C. The presumptive progenitor is *H. pulvinata* (Culberson and Hale, 1973).

**REPRESENTATIVE SPECIMENS EXAMINED.**—Mexico: Chiapas, *Hale* 20214, 20242, 20290, 20534, 20561; Michoacán, *Arsène* 3746 (US), *Hale* 20850, 20987; Puebla, *Hale* 21048; Veracruz, *Hale* 21116, 21176. Guatemala: Alta Verapaz, *Standley* 69331 (US); Baja Verapaz, *Hale* 38333; Chimaltenango, *Standley* 60097 (US); Huehuetenango, *Standley* (US); Totonicapán, *Standley* 84522 (F). Costa Rica: San José, *Standley and Valerio* 43898 (US). Panama: Chiriquí, *Hale* 38768, 38819, 38863, *Scholarer* (US). Cuba: Oriente, *Imshaug* 25045 (MSC, US). Jamaica: *Imshaug* 12954, 13802, 15424, 15541 (MSC, US), *Orcutt* 5626c (US), *Plitt* (US). Haiti: Ouest, *Imshaug* 22591 (MSC), 22538 (US), *Wetmore* 2973, (MSC); Sud, *Wetmore* 3365 (MSC). Dominican Republic: Cordillera Central, *Imshaug* 23537 (MSC, US), 23639 (MSC); La Vega, *Allard* 16529a (US). Dominica:

*Hale* 35586. Martinique: Culberson 14555 (DUKE). Colombia: Santander, *Charetier* 202 (US). Venezuela: Federal, *Vareschi* 427c (US); Mérida, *Hale* 42553, 42734, 42974, 43287. Peru: Cuzco, *Iltis* 3004 (US, WIS), *Thomasson* (UPS). Chile: Magallanes, *Santesson* 8010 (S, US); Tierra del Fuego, *Santesson* 6793 (S, US); Valdivia, *Mahu* 1695 (US). Brazil: Minas Gerais, *Vainio* 1140 (BM).

### 67. *Hypotrachyna silvatica*, new combination

FIGURE 18a

*Parmelia silvatica* Lyngé, 1914:118. [Type collection: Santa Anna da Chapada, Mato Grosso, Brazil, *Malme* 2393\* (S, lectotype).]

*Parmelia crustacea* Lyngé, 1914:108. [Type collection: Santa Anna da Chapada, Mato Grosso, Brazil, *Malme* (S, lectotype).]

*Parmelia silvatica* var. *pinnata* Lyngé, 1914:120. [Type collection: Santa Anna da Chapada, Mato Grosso, Brazil, *Malme* 2393\*\*\* (S, lectotype).]

*Parmelia silvatica* var. *radiata* Lyngé, 1914:120. [Type collection: Santa Anna da Chapada, Mato Grosso, Brazil, *Malme* 2393\*\* (S, lectotype).]

Thallus closely adnate on bark, whitish mineral gray, 2–6 cm in diameter; lobes sublinear, often crowded, 0.5–2 mm wide; upper surface plane, shiny, faintly maculate; medulla in the lower half antimony yellow; lower surface moderately rhizinate, the rhizines densely dichotomously branched. Apothecia common, adnate, 1–2 mm in diameter; spores  $5\mu\text{--}6\mu \times 10\mu\text{--}12\mu$ .

CHEMISTRY.—Cortex K–, medulla K–, C–, P+ orange-red (lichexanthone, protocetraric acid, and an unidentified anthraquinone).

DISTRIBUTION.—Southern Brazil.

HABITAT.—On trees in open forests.

REMARKS.—This rare lichen resembles *H. livida* externally but the chemistry is completely different. Some specimens are very closely adnate and have narrow lobes. These were described by Lyngé under the synonyms listed above.

SPECIMENS EXAMINED.—Brazil: Mato Grosso, *Malme* (S, UPS) in *Lichenes Austroamericani* 87 (G, H, LD, UPS), 2271 Ba (S), 2511 Ba (S).

### 68. *Hypotrachyna singularis*, new combination

FIGURE 18b

*Parmelia singularis* Hale, 1974b:267. [Type collection: Cerros Calla Calla, Chachapoyas, Peru, *Hutchinson and Wright* 5704 (US, holotype; UC, isotype).]

Thallus loosely adnate on branches, subcoriaceous, whitish to pale yellowish mineral gray, about 8 cm broad; lobes subirregular to sublinear, 3–5 mm wide, marginally dissected and lobulate, the lobules to 1 mm long, narrow; upper surface smooth and shiny, continuous; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia numerous, adnate, to 5 mm in diameter; spores  $6\mu\text{--}7\mu \times 10\mu\text{--}12\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K–, C–, P– (atranorin and apparently a fatty substance not further identified).

DISTRIBUTION.—Peru.

HABITAT.—On tree in open forest at 3100 m elevation.

REMARKS.—*Hypotrachyna singularis* is characterized by the rather coriaceous thallus and numerous elongate marginal lobules. It is known only from the type collection.

### 69. *Hypotrachyna sinuosa*, new combination

FIGURE 18c

*Lichen sinuosus* Smith, 1809:2050. [Type collection: Dumfriesshire, England, *Burgess* (LINN, lectotype).]

*Parmelia sinuosa* (Smith) Acharius: 1814:207.

*Parmelia despreauxii* Delise ex Duby, 1830:602. [Type collection: Vire, France, *Despreaux and Briquebec* (not seen).]

*Parmelia sinuosa* var. *virescens* Krempelhuber, 1861:131. [Type collection: Mittenwald, Germany, *Krempelhuber* (M, lectotype; UPS, isolectotype).]

*Parmelia meyeri* Zahlbruckner, 1905:82. [Type collection: Chimborazo, Ecuador, *Meyer* 365 (W, lectotype).]

Thallus adnate to loosely adnate on bark and twigs, rarely on rock, sometimes suberect at the periphery, pale greenish yellow, 2–7 cm broad; lobes sublinear, short, 0.7–3 mm wide; upper surface plane, continuous, sorediate, less commonly pustulate-sorediate, the soralia capitate, orbicular to diffuse, subterminal; lower surface densely rhizinate, the rhizines sometimes forming a marginal mat. Apothecia very rare, adnate, 1–4 mm in diameter; spores  $7\mu\text{--}9\mu \times 10\mu\text{--}14\mu$ .

CHEMISTRY.—Cortex K–, medulla K+ yellow turning red, P+ orange (usnic acid and salacinic acid, sometimes with norstictic acid and a trace of stictic acid).

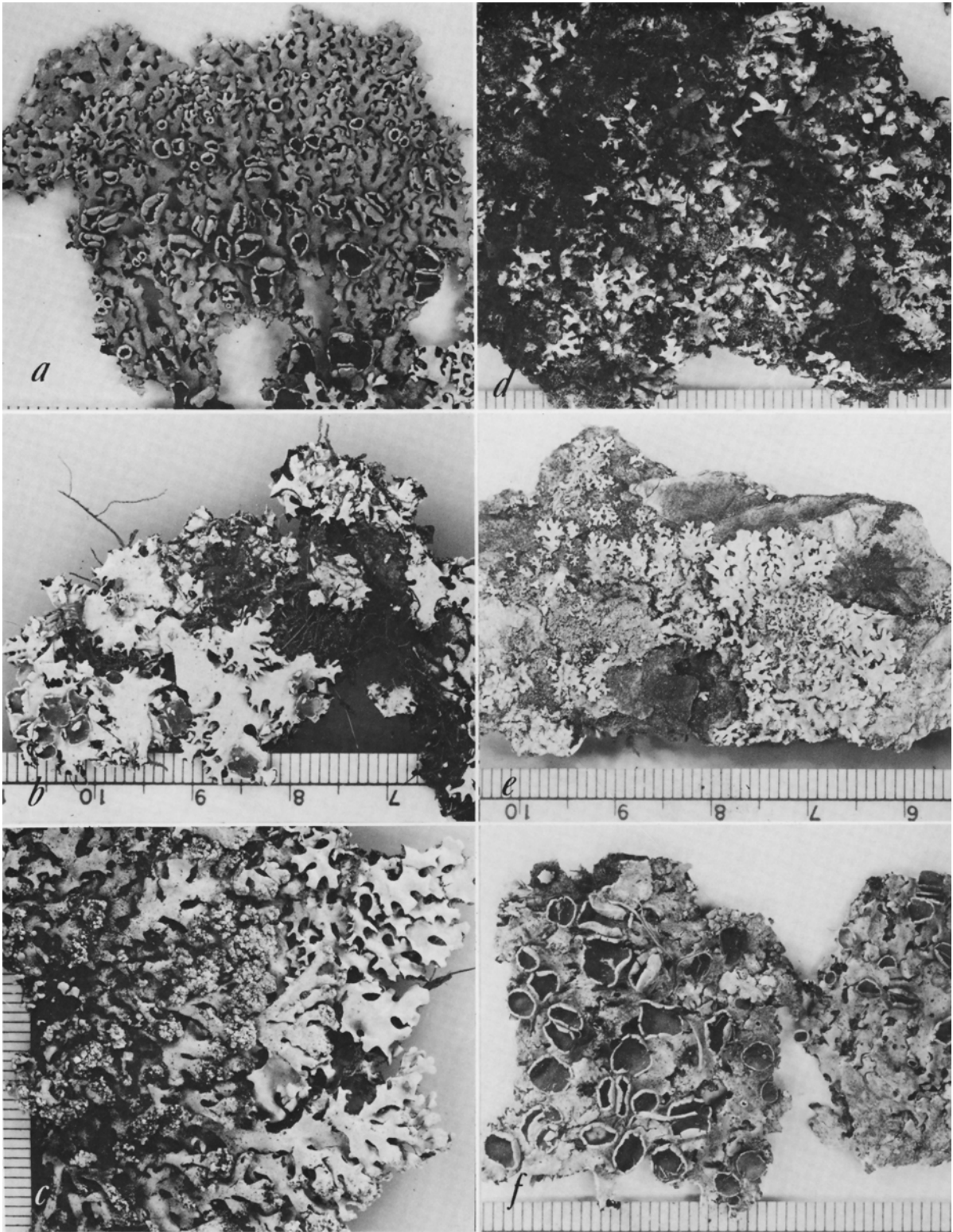


FIGURE 18.—Species of *Hypotrachyna*: a, *H. silvatica* (Malme in S); b, *H. singularis* (Hutchinson and Wright 5704); c, *H. sinuosa* (Hale 43071a); d, *H. steyermarkii* (Steyermark 106123); e, *H. subaffinis* (Imshaug 22531); f, *H. sublaevigata* (Hale 38810). (Scale in mm.)

**DISTRIBUTION.**—Alaska to Oregon, southeastern United States, Mexico, West Indies, Andean region from Venezuela to Chile, Europe, southeastern Asia from southern Japan to Java.

**HABITATS.**—On trees (hardwoods and conifers) and rarely rocks and on small shrubs in the paramo at 2000–3500 m (to near sea level in boreal areas).

**REMARKS.**—The development of soredia in this pantropical-montane, pantemperate species is extremely variable. The type and the bulk of the specimens examined have discrete subterminal soralia and powdery soredia. At the other extreme, the soralia (as in *Parmelia meyeri*) may originate as laminal to subterminal pustules which become coarsely sorediate or rarely remain esorediate. There are various intergradations between these types. Most of the problematic specimens have been collected in the West Indies or in the high Andes. The chemistry also is variable, typically salazinic acid with or without norstictic acid but sometimes with stictic acid or different combinations of these. We may be dealing with several intergrading morphological and chemical populations but for the present they are most conveniently recognized as a single species.

Smith cited three syntypes: the Dumfriesshire lectotype, a Menzies specimen from Nova Scotia (LINN, US) which can be identified as *Parmelia galbina* (Acharius) Hale, and a Turner and Hooker collection from Ballacheulish which I have not located. *Parmelia despreauxii* is represented by collections in BM and G apparently identified by Delise himself, but the most appropriate lectotype probably is housed in Strasbourg (STR). A syntype of *P. meyeri* (Meyer 388) is not a *Parmelia* at all but is a member of the Lecanoraceae.

**SPECIMENS EXAMINED.**—Mexico: Oaxaca, *Nakanishi* 370 (KOBE) 393 (US); Puebla, *Van Horn* 59199 (US); Veracruz, *Hale* 20897. Costa Rica: San José, *Culberson* 12580, 13199 (DUKE); Haiti: Ouest, *Imshaug* 23016 (MSC, US). Dominican Republic: La Vega, *Imshaug* 23392, 23518 (MSC, US), *Wetmore* 3673 (MSC, US). Colombia: Boyacá, *Cuatrecasas* 1787a (US); Cundinamarca, *Lindig* 2548 (P); Santander, *Killip and Smith* 18595 (US). Venezuela: Mérida, *Hale* 42711, 42794, 42820, 43210, *Nash* 1983 (US), *Schwabe* (M). Bolivia: Cochachamba, *Ugent* (US,

WIS). Chile: Aysén: *Santesson* 4603, 8413 (UPS); Juan Fernandez, *Imshaug* 37440 (MSC); Magallanes, *Santesson* 1848, 1994, 6441, 7827 (S), 6586 (UPS); Tierra del Fuego, *Santesson* 404, 420, 7864 (S), 5471 (UPS); Valdivia, *Santesson* 7262 (S).

## 70. *Hypotrachyna steyermarkii*, new combination

FIGURE 18d

*Parmelia steyermarkii* Hale, 1974b:268. [Type collection: Sierra Parima, Amazonas, Venezuela, *Steyermark* 106123 (US).]

Thallus closely adnate on mosses on bark, fragile, light mineral gray, about 8 cm broad; lobes narrow, dichotomously branched, 1–2 mm broad; upper surface plane, shiny, isidiate, the isidia initially simple and cylindrical but soon procumbent and in part lobulate, becoming ciliate; lower surface moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia not seen.

**CHEMISTRY.**—Cortex K+ yellow, medulla K–, C+ orange, P– (atranorin, barbatic acid, 4-O-demethylbarbatic acid, obtusatic acid, and nor-obtusatic acid).

**DISTRIBUTION.**—Venezuela.

**HABITAT.**—On a small tree in forest at 1300 m elevation.

**REMARKS.**—This species is distinguished from chemically identical *H. imbricatula* by the very narrow lobes and the consistently procumbent, ciliate isidia.

## 71. *Hypotrachyna subaffinis*, new combination

FIGURE 18e

*Parmelia subaffinis* Zahlbruckner, 1929:213. [Type collection: Based on *P. affinis* Vainio, not *P. affinis* (Dickson) Acharius, 1803:212 (= *Pannaria*).]

*Parmelia affinis* Vainio, 1890:52. [Type collection: Carassa, Minas Gerais, Brazil, *Vainio* 1331 (TUR, Vainio herbarium number 3010, lectotype; BM, isolectotype).]

Thallus closely adnate on bark, sea-foam yellow, 3–5 cm broad; lobes sublinear, dichotomously branched, 0.4–2 mm wide; upper surface plane, continuous, sorediate, the soralia capitate, mostly laminal; lower surface densely rhizinate, the rhizines often projecting along the margins. Apo-

thecia rare, adnate, 0.7–2.5 mm in diameter; spores  $5\mu\text{--}7\mu \times 8\mu\text{--}11\mu$ .

CHEMISTRY.—Cortex K+ yellowish, medulla K–, C–, P+ pale orange (usnic acid, echinocarpic acid, and associated unknowns).

DISTRIBUTION.—Mexico, Central America, West Indies, Brazil.

HABITAT.—On trees (oaks and pines) in open forests at 1000–2000 m elevation.

REMARKS.—This is a very small, closely adnate species without any close relatives, except perhaps *H. velloziae*. While Vainio's type was collected on hardwood trees, almost all collections from the West Indies, where it is most common, were taken from *Pinus* bark.

SPECIMENS EXAMINED.—Mexico: Chiapas, *Hale* 20352, 20384. Guatemala: Baja Verapaz, *Hale* 38308, 38342. Haiti: Ouest, *Imshaug* 22531 (MSC, US), 22539, 22764, 23081, 23599, 23761 (MSC), *Wetmore* 3203 (MSC, US). Dominican Republic: La Vega, *Allard* 16542, 16544, 16552, 16581, 16589 (US); Santiago, *Wetmore* 3882 (MSC, US). Brazil: Minas Gerais, *Vainio* 771 (BM, M, TUR), 986, 3010 (TUR), 1391 (TUR, UPS).

## 72. *Hypotrachyna sublaevigata*, new combination

FIGURE 18f

*Parmelia tiliacea* var. *sublaevigata* Nylander, 1860:383. [Type collection: South America, *Bonpland* (P, lectotype; H, isotype).]

*Parmelia sublaevigata* (Nylander) Nylander, 1867:306.

*Parmelia chilena* Nylander, 1885:612. [Type collection: Chile, *M. Gay* (P, lectotype).]

*Parmelia canescens* Kurokawa in *Hale* and Kurokawa, 1964:167. [Type collection: Colchagua, Chile, *Dusén* 92 (S, holotype; US, isotype).]

Thallus closely adnate on bark or twigs, 3–8 cm in diameter, dull mineral gray but often turning red in the herbarium because of improper curating; lobes subirregular and short, crowded, 2–5 mm wide; upper surface plane to rugulose, continuous, often becoming whitish pruinose; lower surface densely short rhizinate. Apothecia common, substipitate, 2–5 mm in diameter; spores  $5\mu\text{--}7\mu \times 8\mu\text{--}10\mu$ .

CHEMISTRY.—Medulla K+ yellow turning red, P+ orange (atranorin, norstictic and salazinic acids).

DISTRIBUTION.—Mexico, Panama, and Chile.

HABITAT.—On oaks, pine, *Drimys*, and *Discaria* in open or secondary forests at 1500–2100 m elevation.

REMARKS.—The lobes of *H. sublaevigata* tend to be subrotund, crowded, and closely adnate. Apothecia are usually numerous. In Panama this species could be confused with *H. boquetensis*, which contains only salazinic acid and has longer lobes. Nylander's syntype of *Parmelia tiliacea* var. *sublaevigata* is *Leprieur* 504 (P), an isidiate species in the genus *Bulbothrix* *Hale*. *Parmelia canescens* was differentiated from *H. sublaevigata* only by the presence of norstictic acid, but later tests with thin-layer chromatography showed that salazinic acid also is present.

SPECIMENS EXAMINED.—Mexico: Durango, *Bell* s.n. (DUKE), *Fox* M87 (US); Michoacán, *Arsène* 4046b, 4459b (US); Sinaloa, *Culberson* 13449 (DUKE). Panama: Chiriquí, *Hale* 38810. Chile: Curicó, *Mahu* 3492 (US); Santiago, *Mahu* 28, 2133a (US); Tierra del Fuego, *Santesson* 6004 (S, US); Valdivia, *Santesson* 3719, 3730 (S, US); 3722 (S); Valparaíso, *Mahu* 1140 (US).

## 73. *Hypotrachyna subphysodolica*, new combination

FIGURE 19a

*Parmelia subphysodolica*, *Hale*, 1974b:268. [Type collection: Puerto Ballena, Chile, *Imshaug* 43121A (MSC, holotype; US, isotype).]

Thallus closely adnate on twigs, yellowish green, 6–7 cm broad; lobes sublinear, about 2 mm wide; upper surface plane, shiny, moderately isidiate, the isidia cylindrical, simple, becoming short ciliate, about 0.3 mm high; lower surface moderately rhizinate. Apothecia not seen.

CHEMISTRY.—Cortex K–, medulla K–, P+ orange-red (usnic acid and physodalic acid).

DISTRIBUTION.—Southern Chile.

HABITAT.—On tree in mossy forest near sea level.

REMARKS.—The diagnostic features of this rare species are the yellow color, isidia, and presence of physodalic acid. While it might be mistaken for *H. microblasta*, its range is far south of that species. It is not related to the only other physodalic-acid-containing species in the genus, *H. physodolica*, a paramo lichen in the northern Andes.

**74. *Hypotrachyna subplumbeata*, new combination**

FIGURE 19b

*Parmelia subplumbeata* Dodge, 1959:106. [Type collection: Mt. Karisimbi, Congo, *Derscheid* 2504 (US, lectotype).]

*Parmelia kahusiensis* Dodge, 1959:105. [Type collection: Mt. Kahusi, Congo, *Hendrickx* 4300 (EAH, holotype).]

Thallus loosely adnate, rather coriaceous, 5–10 cm broad; lobes sublinear, crowded, 2–4 mm wide; upper surface smooth, heavily white-maculate,

without soredia or isidia; lower surface densely rhizinate, the rhizines densely dichotomously branched. Apothecia abundant, substipitate, 2–5 mm in diameter; spores not developed.

CHEMISTRY.—Cortex K+ yellow, medulla K–, C+ orange, P– (atranorin, barbatic acid, and 4-O-demethylbarbatic acid).

DISTRIBUTION.—Mexico and Africa.

HABITAT.—On small trees near the tree line at about 3800 m elevation.

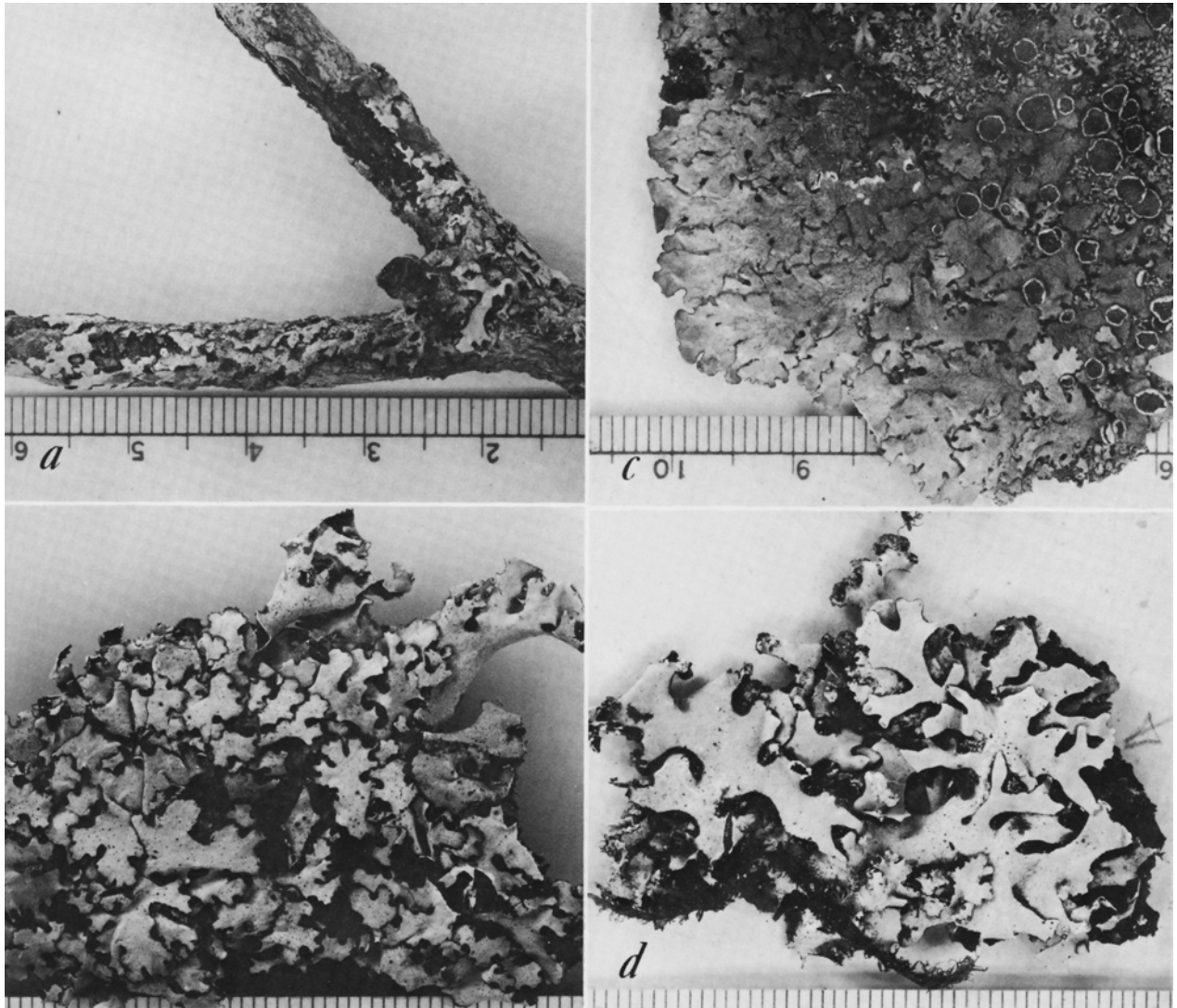


FIGURE 19.—Species of *Hypotrachyna*: a, *H. subphysodolica* (*Imshaug* 43121A); b, *H. subplumbeata* (*Moore and Wood* 4944); c, *H. subsaxatilis* (*Arsène* 3974); d, *H. thysanota* (*Hale* 21118). (Scale in mm.)

REMARKS.—According to Culberson and Hale (1973), *H. subplumbeata* is the remnant of an ancient population (now mostly extinct in the New World but widespread in the Old World) that contains barbatic acid without obtusatic acid. It could be the progenitor species which hybridized with *H. pulvinata* to produce the obtusatic-acid-containing species in the *H. physcioides* constellation. The thallus is rather coriaceous and the maculae strongly developed, just as in the African population.

SPECIMENS EXAMINED.—Mexico: Mexico, *Kiener* 18577 (DUKE), *Moore and Wood* 4944 (US).

### 75. *Hypotrachyna subsaxatilis*, new combination

FIGURE 19c

*Parmelia subsaxatilis* Bouly de Lesdain, 1914:6. [Type collection: Cerro Azul, Michoacán, Mexico, *Arsène* 3973 (P, lectotype).]

Thallus loosely adnate on rock, dark mineral gray, 4–8 cm broad; lobes sublinear, short, crowded, 1–3.5 mm wide; upper surface plane to rugulose and cracked, lacking isidia and soredia; lower surface sparsely to moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia adnate, 1.5–4.5 mm in diameter; spores  $7\mu\text{--}9\mu \times 11\mu\text{--}15\mu$ .

CHEMISTRY.—Cortex K+ yellow, medulla K+ yellow turning red, P+ orange-red (atranorin and salazinic acid).

DISTRIBUTION.—Mexico.

HABITAT.—On rocks and soil over rocks in open areas at about 2200 m elevation.

REMARKS.—While amply distinct and collected in quantity by *Arsène*, this species remains a rarity known only from Mexico. It is unrelated to any other species in the genus.

SPECIMENS EXAMINED.—Mexico: Michoacán, *Arsène* 3974, 3974b (US).

### 76. *Hypotrachyna thysanota*, new combination

FIGURE 19d

*Parmelia thysanota* Kurokawa in Hale and Kurokawa, 1964: 186. [Type collection: 11 km E Las Vigas, Veracruz, Mexico, *Hale* 20943 (US, holotype).]

*Parmelia nakanishii* Hale, 1971d:434. [Type collection: Mt. Leconte, Sevier County, Tennessee, *Nakanishi* 205 (US, holotype; KOBE, DUKE, TNS, isotypes).]

Thallus loosely adnate, whitish mineral gray, to 15 cm broad; lobes linear, dichotomously branched, subdivaricate, 2–5 mm wide; upper surface plane, shiny, becoming pruinose near the tips, sorediate, the soralia mostly subterminal, often protruding, coalescent; lower surface densely rhizinate, the rhizines densely dichotomously branched, often projecting as a mat beyond the margins. Apothecia not seen.

CHEMISTRY.—Cortex K+ yellow, medulla K–, C– red, P+ red (atranorin, echinocarpic acid, gyrophoric acid, and microphyllinic acid).

DISTRIBUTION.—Southeastern United States and Mexico.

HABITAT.—On conifers (*Abies*, *Pinus*) in open forests at about 2000 m elevation.

REMARKS.—Gyrophoric acid was the only constituent identified with microcrystal tests for this species. Dey (1974) has analyzed the type specimen with thin-layer chromatography and discovered the additional substances. This is the only report of microphyllinic acid outside of *Cetraria*, although Culberson and Hale (1973) postulated its possible occurrence in *Hypotrachyna*. Superficially, this species is similar to *H. laevigata* or *H. densirhizinata*; no nonsorediate progenitor has been discovered.

SPECIMENS EXAMINED.—Additional records from the United States and Mexico are listed in Hale and Kurokawa (1964:186), and in Hale (1971d: 434) under *Parmelia nakanishii*.

### 77. *Hypotrachyna velloziae*, new combination

FIGURE 20

*Parmelia velloziae* Vainio, 1890:64. [Type collection: Carassa, Minas Gerais, Brazil, *Vainio* 1455 (TUR, Vainio herbarium number 2892, lectotype; BM, FH, M, UPS, isolectotypes).]

Thallus closely adnate to bark, fragile, pale viridine yellow, 3–7 cm in diameter; lobes sublinear, dichotomously branched, 0.5–2 mm wide; upper surface plane, continuous, sorediate, the soralia mostly laminal, capitate, often coalescing; medulla turning yellow-ochre under the soralia;





FIGURE 20.—*Hypotrachyna velloziae* (Wetmore 307).  
(Scale in mm.)

lower surface moderately rhizinate, the rhizines sparsely dichotomously branched. Apothecia not seen.

CHEMISTRY.—Cortex K—, medulla K—, P+ orange-red (usnic acid, protocetraric acid, and rhodophyscin).

DISTRIBUTION.—West Indies and Brazil.

HABITAT.—On trunk of trees (*Pinus*) in open or virgin pine forests (West Indies) at 1200–1600 m elevation.

REMARKS.—*Hypotrachyna velloziae* parallels *H. subaffinis* in distribution (mainly West Indies) and habitat (pine trees) but differs completely in chemistry. There is no nonsorediate sexual morph.

SPECIMENS EXAMINED.—Haiti: Ouest, *Imshaug* 22535 (MSC, US), *Wetmore* 3071, 3217 (MSC, US). Dominican Republic: La Vega, *Allard* 16541a, 16562d (US).

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