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A Monograph of the Lichen Genus *Parmelia* Acharius sensu stricto (Ascomycotina: Parmeliaceae)

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ABSTRACT

Hale, Mason E., Jr. A Monograph of the Lichen Genus *Parmelia* Acharius sensu stricto (Ascomycotina: Parmeliaceae). *Smithsonian Contributions to Botany,* number 66, 55 pages, 25 figures, 1987.—The 38 species of *Parmelia* Acharius sensu stricto are revised at the world level. The genus is characterized by punctate or effigurate pseudocyphellae, a black lower surface with simple, furcate or squarrose rhizines, simple hyaline spores, and cylindrical to weakly bifusiform conidia. The most frequent secondary metabolites are salazinic acid and protocetraric acid. *Parmelia* is an extremely conservative genus, most common in temperate-boreal and austral regions, with a low level of vegetative morph formation and speciation. The greatest concentrations of species are found in Japan and New Zealand. Seven new species are described: *P. neodiscordans* Hale, *P. norcrambidiocarpa* Hale, *P. novae-zelandiae* Hale, *P. queenslandensis* Hale, *P. salcrambidiocarpa* Hale, *P. skultii* Hale, and *P. subtestacea* Hale.

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Contents

A Monograph of the Lichen Genus *Parmelia* Acharius sensu stricto (Ascomycotina: Parmeliaceae)

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Introduction

The genus *Parmelia* was proposed by Acharius in 1803. His circumscription was very broad and encompassed a large number of foliose species with lecanorine apothecia, species now recognized in such diverse genera as *Cetraria, Heterodermia, Hypogymnia, Lobaria, Pannaria, Parmelia* sensu lato, *Parmeliella, Parmeliopsis, Physcia, Physconia,* and *Xanthoria.* Early 19th century authors continued to use the name in this broad sense for almost any lichen with a thalline apothecial rim, from *Lecanora* to *Usnea.*

By the end of the 19th century *Parmelia* had begun to assume its more modern and familiar circumscription as a foliose rhizinate genus with laminal apothecia and simple spores (Fries, 1871–1874). At the same time, recognizing clear morphological discontinuities, lichenologists began to describe a number of segregate genera. Early ones, with their dates of publication, included *Menegazzia* Massalongo (1854), *Parmotrema* Massalongo (1860), *Anzia* Stizenberger (1861), *Parmeliopsis* (Nylander) Nylander (1869), *Hypogymnia* (Nylander) Nylander (1896), *Pseudevernia* Zopf (1903), *Pannoparmelia* (Müller Argoviensis) Darbishire (1912), and *Pseudoparmelia* Lynge (1914). Of these genera only *Anzia* and *Parmeliopsis* were ultimately adopted by Zahlbruckner in his catalogue (1929), the others being synonymized under *Parmelia.* However, since 1950, many workers have adopted *Hypogymnia, Menegazzia, Pannoparmelia,* and *Pseudevernia.*

I recently subdivided *Parmelia* sensu lato into two groups on the basis of cortical structure newly discovered with the scanning electron microscope (Hale, 1973), resurrecting some of the old, neglected segregates as well as describing several new genera. One group is represented by the epicorticate species found in *Arctoparmelia* Hale, *Bulbothrix* Hale, *Canoparmelia* Elix and Hale, *Cetrariastrum* Sipman, *Concamerella* Culberson, *Everniastrum* Hale ex Sipman, *Flavoparmelia* Hale, *Hypotrachyna* (Vainio) Hale, *Neofuscelia* Esslinger, *Paraparmelia* Elix and Johnston, *Parmelina* Hale, *Parmotrema* Massalongo, *Pseudoparmelia* Lynge, *Relicina* (Hale and Kurokawa) Hale, *Relicinopsis* Elix and Verdon, *Xanthomaculina* Hale, and *Xanthoparmelia* (Vainio) Hale.

A second group consists of the pseudocyphellate species of *Parmelia* (Hale, 1975, 1976a, 1981). This group has been further subdivided into *Flavopunctelia* (Krog) Hale (the *P. flaventior* group) (Hale, 1980, 1984), *Melanelia* Esslinger (the brown *Parmeliae*) (Esslinger, 1978), and *Punctelia* Krog (Krog, 1982) (the *P. borreri* group), now leaving in *Parmelia* a small, apparently irreducible assemblage of 38 species typified by *P. saxatilis.*

The following characters may be used to delimit *Parmelia:* adnate, sublinear to subirregular lobes without cilia; upper surface effigurate-pseudo-cyphellate, less commonly punctate-pseudocyphellate (in three Asian species); lower surface black, rhizinate, the rhizines simple, furcate, or squarrosely branched; microconidia cylindrical or weakly bifusiform, less than 8.0 µm long; spores simple, 8 per ascus. Chemically it is distinguished by the presence of atranorin and chloroatranorin and lack of usnic acid in the cortex. The closest relative in the family is *Punctelia,* which Krog (1982) characterizes by punctate pseudocyphellae and cylindrical, filiform, or unciform microconidia. I am excluding from *Punctelia* and *Parmelia* the unique usnic acid-containing American endemic *P. sphaerosporella* Müller Argoviensis, now recognized as the monotypic genus *Ahtiana* Goward (Goward, 1985), closer to *Cetraria* Acharius than to *Parmelia.*

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Cortical and Internal Structure

Parmelia has a typical paraplectenchymatous cortex (Hale, 1973, 1981). It consists of densely packed cells forming a layer 4–6 cells thick (20–30 μm). Anglesea et al. (1982) recently discovered a technique of digesting the intracellular polysaccharides, giving new insights into cortical organization. The cortical layer consists of densely packed hyphae that branch in a coralloid pattern, forming 3–5 short branches lying in the same plane. The lower cortex is thinner, less than 20 μm thick. The algal layer and the medulla occupy 100–200 μm of the total thallus thickness.

The upper cortex of *Parmelia* species is perforated by pseudocyphellae. These pores originate as the cortex disintegrates to form a narrow tube about 10 μm in diameter, which enlarges and becomes filled with medullary hyphae (Figure 1*a*) (Hale, 1981). This structure is quite different from the epicortex, which is a pored polysaccharide sheet overlaying a more or less loosely packed, continuous palisade parenchymatous layer (Hale, 1973, 1981). These two structures differ considerably in size: pseudocyphellae are essentially macroscopic and visible with low power magnification (0.1–2 mm long), but the pores in the epicortex can be seen only with SEM, being of the order of 15–40 μm in diameter.

Each species of *Parmelia* has a characteristic orientation of pseudocyphellae as illustrated in Figures 2–8. The most frequent type appears as an irregular effigurate white marking under low power. These so-called maculate markings are marginal and laminal and often fuse into a loose reticulate network as they grow beyond 1 mm in length (Figure 1*c*). At maturity the cortex tends to crack open along the pseudocyphellae, which may then serve as points of origin for isidia and soredia.

Under SEM the maculate appearance can be explained as a thin persistent, densely pored polysaccharide layer acting as a roof over the disintegrating pore area below. This layer is part of the polysaccharide layer covering the rest of the surface. This roof may persist (Figure 1*d*) or soon disintegrate, leaving an open pore (Figure 1*b*) (see Hale (1981) for additional figures).

Pseudocyphellae may also originate exclusively along the lobe margins, just back from the edge. In these cases they form a continuous white line, a rim around the lobes, as in *P. neodiscordans, P. niitakana* (Figure 1*e*), *P. pseudoshinanoana, P. sectilis, P. shinanoana, P. ricasolioides,* and in part *P. cochleata, P. crambidiocarpa, P. norcrambidiocarpa, P. salcrambidiocarpa, P. subtestacea,* and *P. testacea,* and some narrow-lobed forms of *P. discordans* and *P. omphalodes,* and in *P. skultii.*

Two Asian species, *P. meiophora* and *P. submutata,* are distinctive in having very small effigurate pseudocyphellae not much more than 0.1–0.2 mm in size (Figure 1*b*), so small that neither Hue, Nylander, nor Zahlbruckner noticed them when describing the species involved. As far as I can tell, they are identical in origin with the larger pseudocyphellae described above.

A third type of pseudocyphella is characteristic of a small group of three Asian species, *P. isidioclada, P. laevior,* and *P. pseudolaevior.* The pores form along the lobe edge as round, widely spaced, and rather inconspicuous white spots (Figure 1*f*). These pores do not have the persistent roof of other pseudocyphellae in the genus and in fact appear to be identical with the punctiform pores of *Punctelia.* The lobe surface itself is continuous and has neither pseudocyphellae nor reticulated markings. These species are placed more appropriately in *Parmelia* rather than *Punctelia,* because of the presence of salazinic acid and the furcate to squarrosely branched rhizines.

Vegetative Structures

Most *Parmelia* species have rather narrow, sublinear, adnate lobes. They grow on rocks and trees in forested areas and on rocks and humus or mosses in arctic-alpine areas, forming adnate colonies 4–20 cm broad (up to 60 cm in *P. tenuirima!*). All of the species are whitish or greenish mineral gray but some, such as *P. discordans, P. omphalodes, P. signifera,* and *P. skultii,* have a tendency to turn brown to nearly black in exposed habitats.

SURFACE FEATURES.—The surface features of several *Parmelia* species have been studied by Hale (1973) using the scanning electron microscope (SEM). The genus is characterized by a smooth and featureless or nodular surface, typical of lichens with a paraplectenchymatous cortex (Figure 9*a*).

Many species have a hoary white pruina on the surface. Under SEM this pruina is revealed as masses of crystals. I have not investigated the chemical composition of these crystals, but they are reported to consist of oxalates (Wilson et al., 1980), often weddelite (calcium oxalate tetragonal dihydrate) ($CaC_2O_4(2+x)\cdot H_2O$), and less commonly whewellite (calcium oxalate monoclinic monohydrate, $CaC_2O_4\cdot H_2O$) (Jackson, 1981; Wadsten and Moberg, 1985).

The crystals fall into three general shapes: bi-pyramidal weddelite (*P. cochleata, P. cunninghamii, P. fraudans* (Figure 9*c*), *P. kerguelensis, P. meiophora, P. omphalodes, P. pseudoshinanoana, P. saxatilis, P. sulcata, P. squarrosa, P. testacea* (Figure 9*b*)); cubic or parallelepiped shapes, also probably weddelite (*P. cunninghamii, P. hygrophila* (Figure 9*d*), *P. protosulcata,* and *P. sulcata* (Figure 9*f*)); and flat hexagons of whewellite (*P. adaugescens, P. discordans, P. erumpens, P. fraudans* (Figure 9*e*), *P. isidioclada, P. kerguelensis, P. novae-zelandiae, P. pseudoshinanoana, P. saxatilis, P. tenuirima*). There seems to be little if any

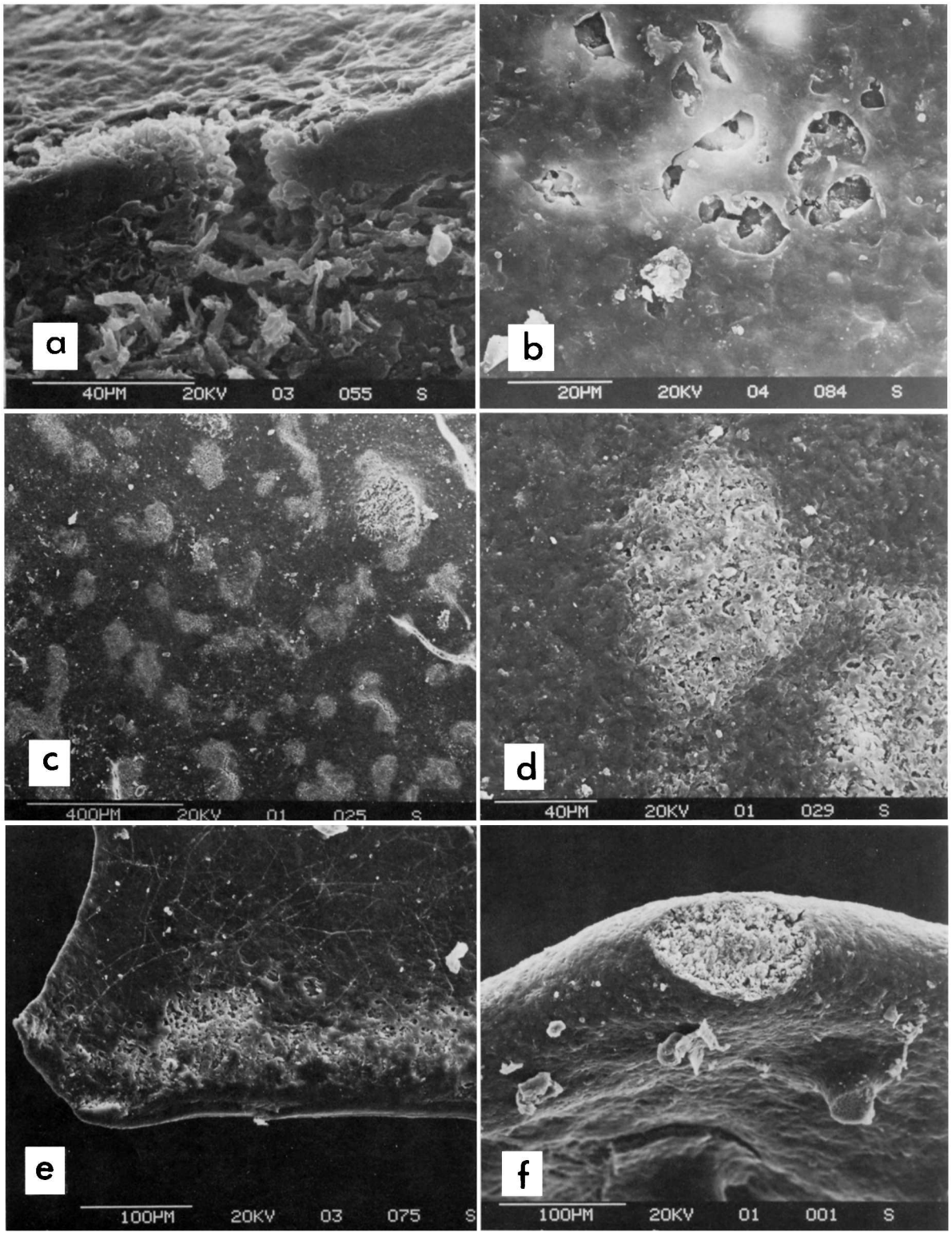

FIGURE 1.—Pseudocyphellae in *Parmelia*: *a*, pore in upper cortex of *P. adaugescens* (*Lai* 7809); *b*, pseudocyphellae of *P. submutata* (*Poelt* L-142); *c*, pseudocyphellae of *P. marmariza* (*Kurokawa* 63056); *d*, pseudocyphellae of *P. marmariza* to show pored "roof" (*Kurokawa* 63056); *e*, submarginal pseudocyphellae of *P. niitakana* (*Hsu* 1374); *f*, marginal pseudocyphellae of *P. laevior* (*Kurokawa* 58255).

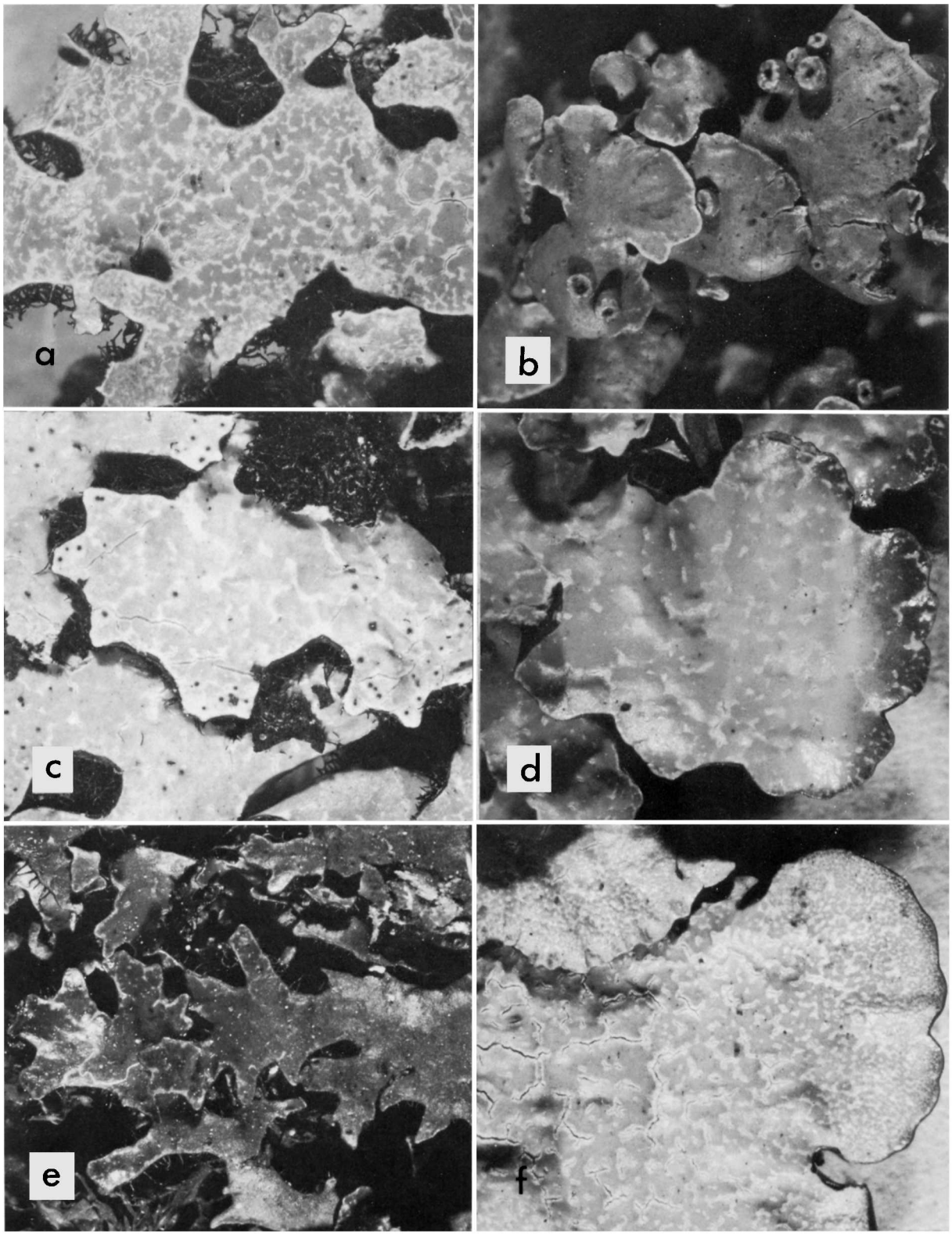

FIGURE 2.—Orientation of pseudocyphellae in *Parmelia* species: *a, P. adaugescens* (*Asahina* s.n.); *b, P. cochleata* (isolectotype in US); *c, P. crambidiocarpa* (*Hale,* 65541); *d, P. cunninghamii* (*Santesson* 6792); *e, P. discordans* (*Issin* s.n.); *f, P. erumpens* (*Hale* 43876). (All ×8.5.)

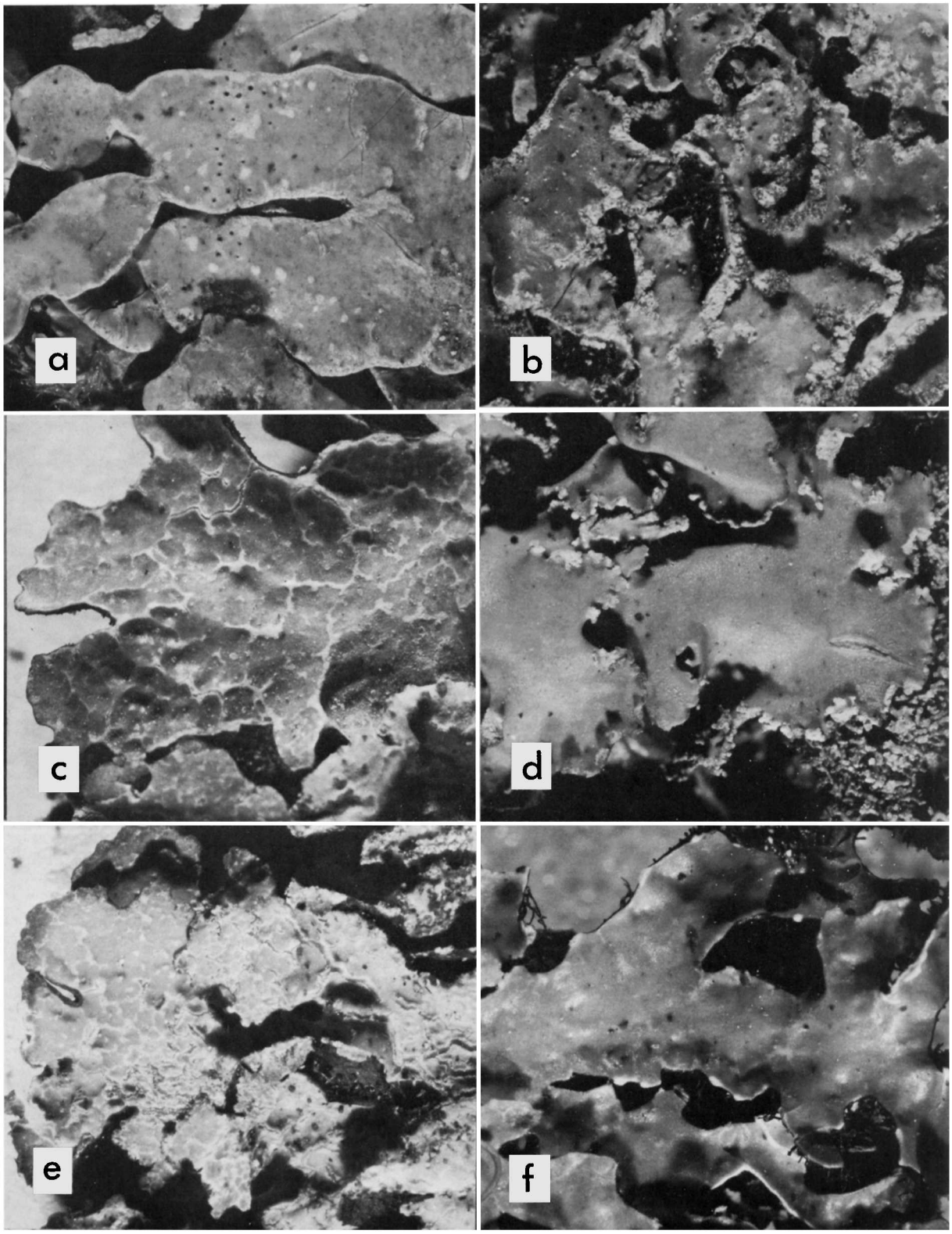

FIGURE 3.—Orientation of pseudocyphellae in *Parmelia* species: *a, P. fertilis* (*Tagawa* s.n.); *b, P. fraudans* (*Hale* 49870); *c, P. hygrophila* (*Noble* 6448); *d, P. isidioclada* (*Kurokawa* 58010); *e, P. kerguelensis* (*Harris* 5670); *f, P. laevior* (*Culberson* 11104). (All ×8.5.)

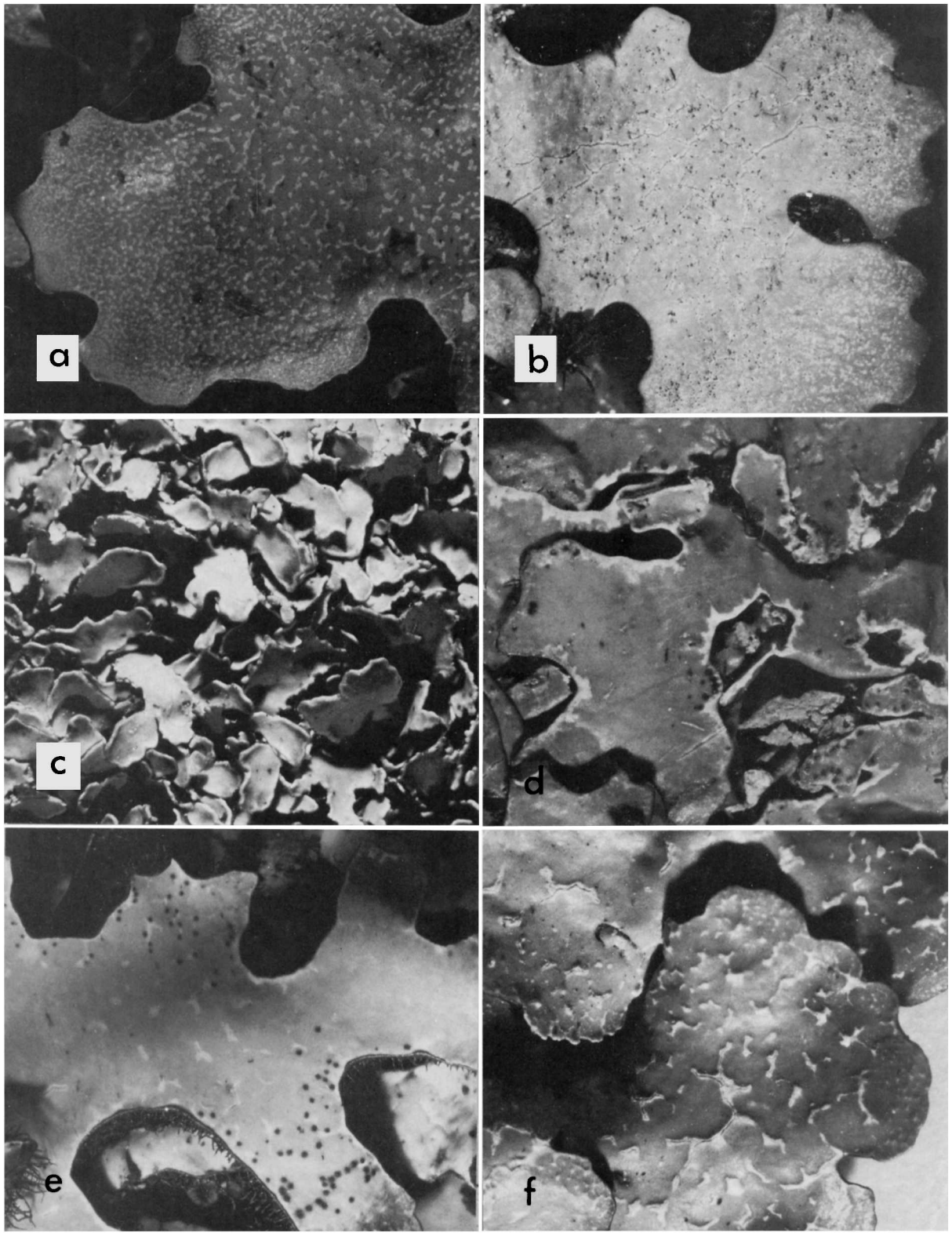

FIGURE 4.—Orientation of pseudocyphellae in *Parmelia* species: *a, P. marmariza* (*Kurokawa* 58062); *b, P. meiophora* (*Poelt* L-151); *c, P. neodiscordans* (holotype in US); *d, P. niitakana* (*Hsu* 1374); *e, P. norcrambidiocarpa* (holotype in US); *f, P. novae-zelandiae* (*Hale* 66232). (All ×8.5.)

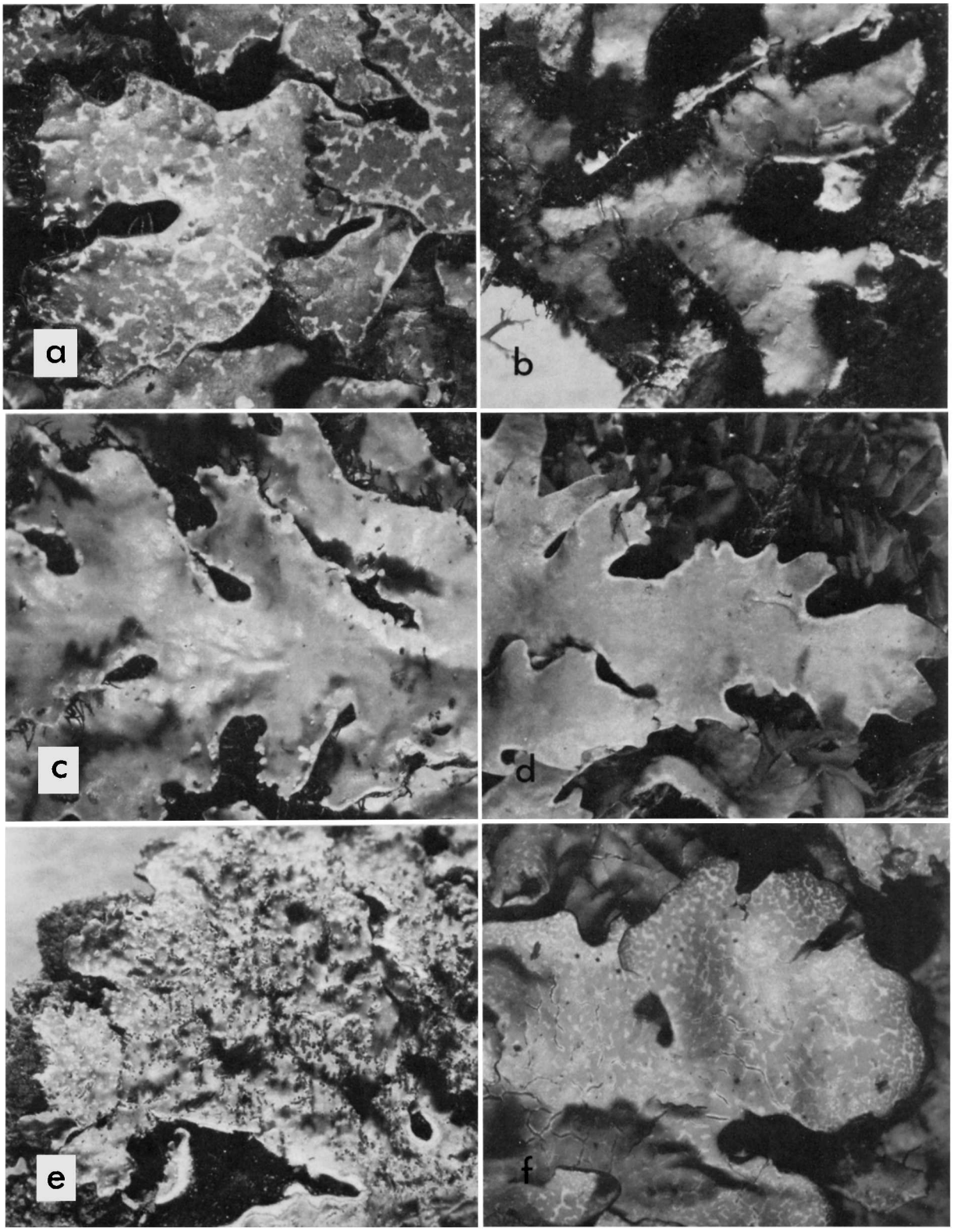

FIGURE 5.—Orientation of pseudocyphellae in *Parmelia* species: *a, P. omphalodes* (*Santesson* 12918); *b, P. protosulcata* (*Santesson* 2953); *c, P. pseudolaevior* (*Kurokawa* 59205); *d, P. pseudoshinanoana* (*Kurokawa* 59206); *e, P. pseudotenuirima* (*Hale* 58276); *f, P. queenslandensis* (holotype in US). (All ×8.5.)

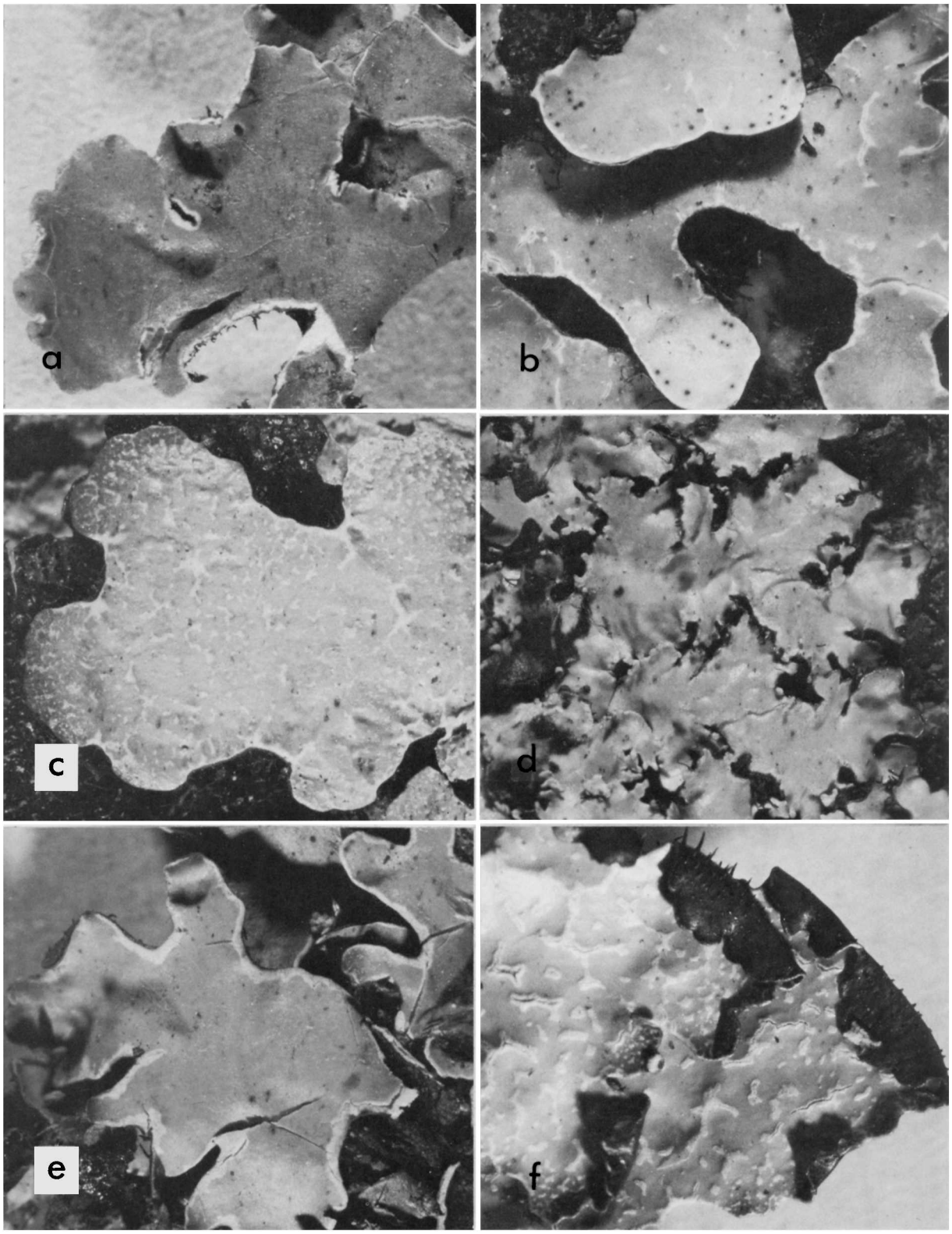

FIGURE 6.—Orientation of pseudocyphellae in *Parmelia* species: *a, P. ricasolioides* (isotype of *P. daliensis* in US); *b, P. salcrambidiocarpa* (holotype in US); *c, P. saxatilis* (*Hale* 48453); *d, P. sectilis* (holotype in US); *e, P. shinanoana* (isolectotype in US); *f, P. signifera* (*Hale* 66435). (All ×8.5.)

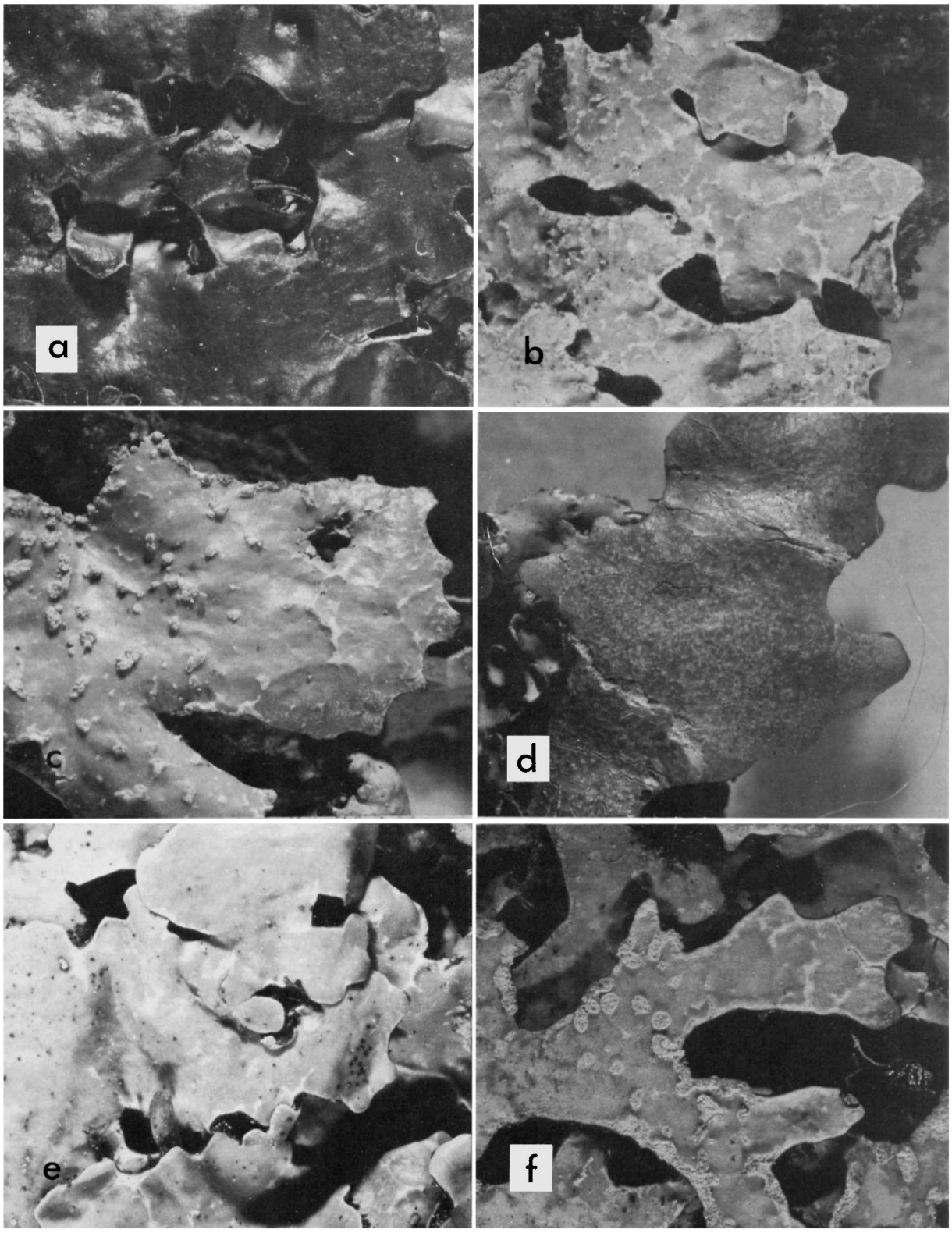

FIGURE 7.—Orientation of pseudocyphellae in *Parmelia* species: *a, P. skultii* (holotype in US); *b, P. squarrosa* (*Hale* 18170); *c, P. submontana* (*Vězda* 845); *d, P. submutata* (*Poelt* L-142); *e, P. subtestacea* (*Hale* 58771); *f, P. sulcata* (*Kjellmert* s.n.). (All ×8.5.)

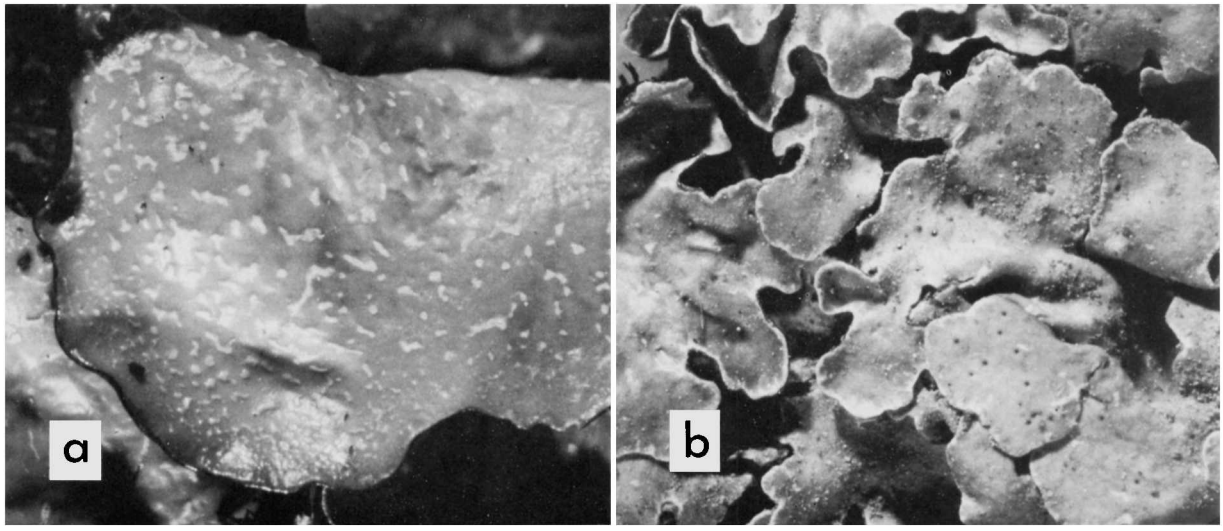

FIGURE 8.—Orientation of pseudocyphellae in *Parmelia* species: *a, P. tenuirima* (*James* 488 pp.): *b, P. testacea* (*Hale* 65112). (All ×8.5.)

correlation with taxonomic features. For example, the crystal shapes of two specimens of *P. fraudans* (Figure 9*c,e*), are significantly different, whereas common *P. sulcata* shows three types among five specimens examined (three flat and one each pyramidal and cubic). It is obvious that many more specimens will have to be examined with SEM before any definite conclusion can be reached on the usefulness of crystal shape in taxonomy.

The lower surface of all species of *Parmelia* is black and more or less continuously vested with rhizines. Broader-lobed species such as *P. tenuirima* may also have a rather conspicuous brown, bare to papillate marginal zone. The rhizines are black and shiny, 0.5–2 mm long, and either simple to sparsely furcate (Figure 10*a,b*), simple with a few weakly squarrosely branched (Figure 10*c*), or mostly strongly squarrosely branched (Figure 10*d*). The following species have simple to furcate rhizines: *P. adaugescens* (Figure 10*a*), *P. cochleata, P. discordans, P. fraudans, P. hygrophila, P. isidioclada, P. marmariza* (Figure 10*b*), *P. neodiscordans, P. niitakana, P. omphalodes, P. pseudolaevior, P. saxatilis, P. sectilis, P. shinanoana, P. skultii,* and *P. submontana.* The following species have simple rhizines and at least some (often densely) squarrosely branched: *P. cunninghamii, P. erumpens, P. fertilis, P. kerguelensis, P. laevior, P. meiophora, P. norcrambidiocarpa, P. novae-zelandiae, P. protosulcata, P. pseudoshinanoana, P. pseudotenuirima, P. queenslandensis, P. ricasolioides, P. salcrambidiocarpa, P. signifera, P. squarrosa, P. submutata, P. sulcata* (Figure 10*c*), *P. subtestacea, P. tenuirima* (Figure 10*d*), and *P. testacea.*

SOREDIA.—Soredia appear to originate from pseudocyphellae in most species and become aggregated into orbicular or linear soralia. In *P. cunninghamii* they originate from marginal fissures not associated with pseudocyphellae, as well as from laminal pseudocyphellae. They are predominantly marginal in *P. cunninghamii, P. fraudans* (Figure 11*a*), and *P. protosulcata;* laminal and marginal in *P. sulcata* (Figure 11*b*); and mostly laminal in *P. submontana. Parmelia erumpens* is unique in having mostly laminal pustular soralia.

ISIDIA.—Although isidia are one of the most easily recognized vegetative propagules in lichens, their origin, development, and structure are not well known. The few SEM pictures published to date (see Hale, 1975, 1976b, for *Hypotrachyna* and 1976a for *Parmelina*) show in general a clearly defined radial structure. There is a more or less continuous polysaccharide layer over the surface, a rather loosely organized paraplectenchymatous cortical layer 20–30 μm thick, which is continuous with the thallus cortex at the base. The interior is filled with loose medullary hyphae, the algae occupying the periphery (Figure 11*f*).

Five species of *Parmelia* have typical shiny, corticate cylindrical isidia: *P. kerguelensis* (Figure 11*c,e*), *P. novae-zelandiae, P. pseudotenuirima, P. saxatilis,* and *P. squarrosa.* The isidia of *P. meiophora* are rather short and basally constricted (Figure 10*d*) in comparison with the other isidiate species. In *P. isidioclada* the isidia become densely coralloid branched and subsorediate. In *P. hygrophila* the isidia are initially corticate but appear to break down apically at maturity, becoming scurfy or subsorediate, an appearance that is enhanced by the dense production of pruina on the isidia.

LOBULES.—Lobules in *Parmelia* are dorsiventral and usually originate along lobe margins; they are very narrow, suberect, and almost isidia-like in appearance. There are three lobulate species here in a strict definition: *P. pseudolaevior, P. pseudoshinanoana,* and *P. sectilis. Parmelia pseudolaevior* seems to be a well-matched morph of non-lobulate *P. laevior; P. pseudoshinanoana* differs from its presumptive parent *P. shinanoana* in lacking gyrophoric acid in the cortex. *Parmelia sectilis* has no extant parent morph.

Parmelia discordans, P. neodiscordans, and *P. omphalodes* often produce lobulate morphotypes, although these lobules

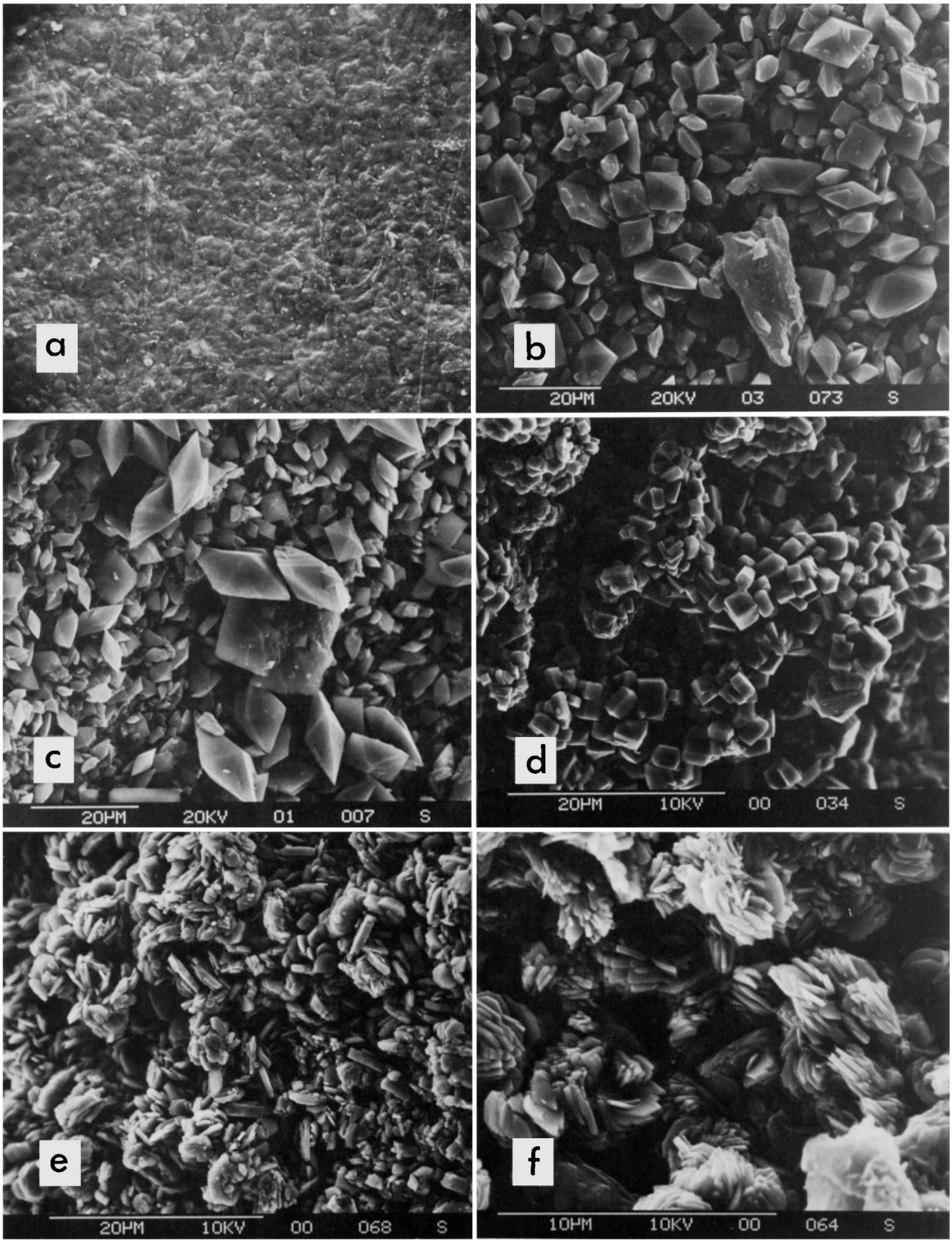

FIGURE 9.—Surface features in *Parmelia*: *a*, surface of *P. squarrosa* (*Hale* 18922, ×425); *b*, pruina of *P. testacea* (*Hale* 58741); *c*, pruina of *P. fraudans* (*Hale* 36414); *d*, pruina of *P. hygrophila* (*Noble*, 6448); *e*, pruina of *P. fraudans* (*Hale*, s.n.); *f*, pruina of *P. sulcata* (*Wetmore* 38229).

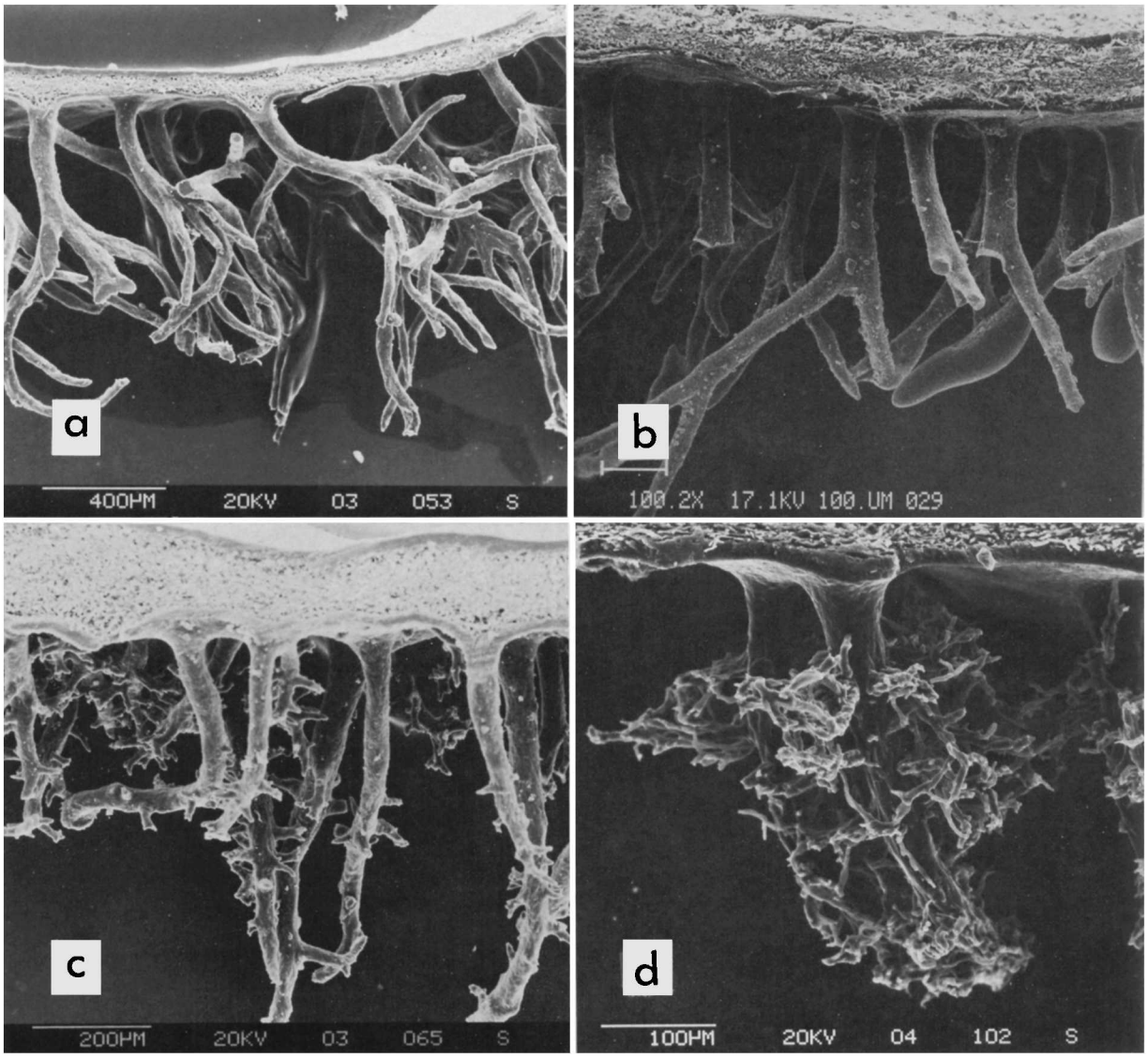

FIGURE 10.—Rhizines of *Parmelia*: *a*, *P. adaugescens* (*Lai* 7809); *b*, *P. marmariza* (*Kurokawa* 63056); *c*, *P. sulcata* (*Hale* 14415); *d*, *P. tenuirima* (*James* 488 pp.).

may be better defined as narrow secondary laciniae. *Parmelia subtestacea* and *P. testacea* often have roundish marginal lobulate secondary lobes. In these cases the lobules should be considered as secondary lobes.

Reproductive Structures

PYCNIDIA.—Vobis (1980) discussed the ontogeny and morphology of pycnidia in many different lichens, but he did not include in his study any species of *Parmelia* sensu stricto. However, he studied *Melanelia acetabulum* (Necker) Esslinger, which has *Umbilicaria*-type ontogeny and Type IV conidiophores, characteristic features of the family Parmeliaceae and apparently encompassing *Parmelia*.

Pycnidia are typically immersed and laminal (Figure 4*e*), 90–110 µm in diameter, with a tendency to group toward the lobe margins in some species. They have been observed in most species but not in *P. hygrophila, P. isidioclada, P. kerguelensis, P. meiophora, P. novae-zelandiae, P. protosulcata, P. pseudolaevior, P. pseudoshinanoana, P. shinanoana,* and *P. submontana.* Most of these species are isidiate or sorediate and often lack apothecia.

The first lichenologist to examine pycnidia and conidia carefully was Lindsay (1859). By today's standards his drawings are rather crude and difficult to interpret. Even with better techniques, however, Hillmann (1936), Krog (1982), and other workers who have examined *Parmelia* species have not been able to describe the conidia of the genus with absolute clarity. Vague and often conflicting descriptions range from cylindrical and straight to somewhat bent or subbifusiform to bifusiform.

It is indeed extremely difficult to see lichen conidia clearly

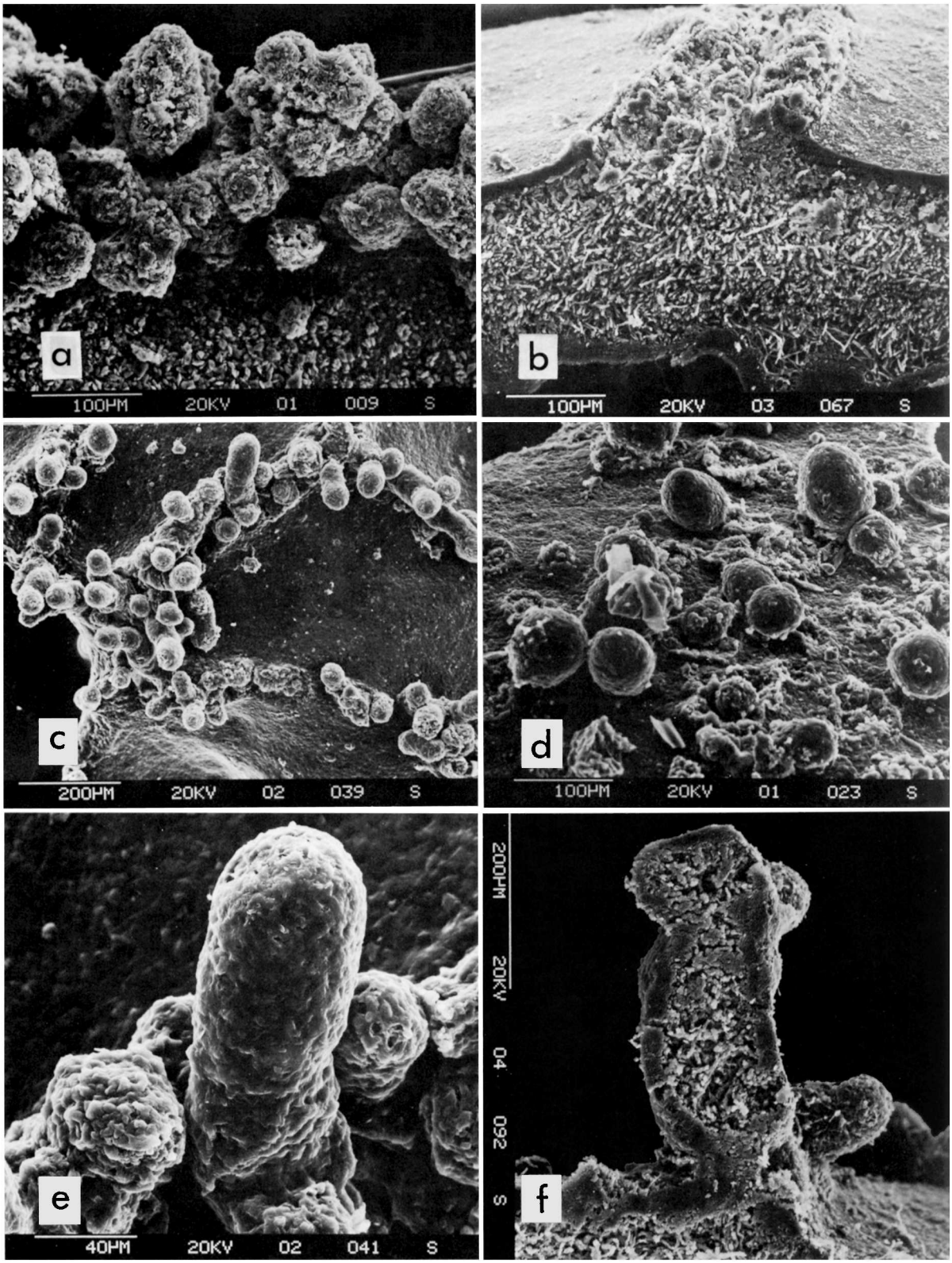

FIGURE 11.—Soredia and isidia of *Parmelia: a*, soralia of *P. fraudans* (*Hale* 36414); *b*, soralia of *P. sulcata* (*Hale* 14415); *c*, isidia of *P. kerguelensis* (*Brodo* 11506); *d*, isidia of *P. meiophora* (*Togashi* s.n.); *e*, isidium of *P. kerguelensis* (*Brodo* 11506); *f*, longitudinal cross section of isidium of *P. saxatilis* (*Hale* 36387).

with an ordinary light microscope. One should ideally use oil immersion, but even then some of the best photographs are rather fuzzy (Vobis, 1980). Enhancement with Nomarski lenses or phase contrast can improve clarity of images but the results are still far from perfect. In my own studies I have mounted freehand sections of pycnidia in glycerin-water and observed the conidia released under a Nomarski microscope.

The conidia of *Parmelia* fall within a very narrow range of length and shape (Figure 12). They are either uniformly cylindrical, straight to slightly bent, slightly inflated at the center, or slighty bifusiform. The only species with strongly, unmistakably bifusiform conidia is *P. signifera*. Most conidia are between 5 and 7 µm long, and only in *P. adaugescens, P. laevior, P. marmariza, P. omphalodes, P. submutata,* and *P. sulcata* do they consistently reach 8.0 µm. There is no dimorphism such as has been reported for *Punctelia* (Culberson and Culberson, 1980; Krog, 1982).

APOTHECIA.—Henssen (1981) includes the Parmeliaceae among families in the Lecanorales with zeorine apothecia. I have not investigated the ontogeny of apothecia in *Parmelia* but assume it follows a pattern similar to that reported by Henssen for *Melanelia exasperata* (De Notaris) Esslinger.

Mature apothecia are usually substipitate and may be rather large, up to 20 mm, as the disc flattens out and splits radially. The amphithecium is well developed, pseudocyphellate, and rugose or even sublobulate with age. The hymenium, which stains deep blue with IKI, is 50–90 µm high. The asci are poorly developed in a few species and lack spores.

SPORES.—All species of *Parmelia,* except for *P. neodiscordans, P. novae-zelandiae, P. skultii,* and *P. submontana,* have been found with apothecia and spores. Spores fall into four size classes with relatively little overlap. One sharply defined group has large spores (range for the group 9–18 × 20–33 µm) with a thick episporium 2–3 µm wide. This group includes *P. adaugescens, P. isidioclada, P. niitakana, P. ricasolioides,* and *P. sectilis,* all Asian endemics. None of these species, it should be noted, are closely related.

The remaining species have spores less than 21 µm long with a thinner episporium 1–2 µm thick. They fall into three groups: one with very small spores, 3–6 × 6–9 µm (closely related *P. meiophora* and *P. submutata*); a second with large spores, 18–21 µm long (*P. crambidiocarpa* and *P. kerguelensis*); and the remainder with spores in the range 11–15 µm long.

Chemistry

When first studied systematically with microcrystal tests (Krog, 1951), *Parmelia* was thought to produce atranorin in the cortex and only two major medullary substances, salazinic acid and protocetraric acid, with accessory lobaric acid and protolichesterinic acid. Although these depsidones do indeed predominate as secondary metabolites, a number of additional products have been identifed with thin layer chromatography and more will probably be discovered. The genus has a distinct chemical profile, with predominantly β-orcinol depsidones, there being no representatives of the para- and meta-depsides (barbatic acid and lecanoric acid groups) in the medulla.

The substances discovered so far are classified as follows. I have analyzed acetone extracts of all specimens in two solvent systems (toluene-dioxane-acetic acid and toluene-ethyl acetate-formic acid), using Merck pre-coated, aluminum-backed TLC plates.

Higher aliphatic acids: Protolichesterinic acid, unidentified acids
Orcinol series:
  Tridepsides: Gyrophoric acid, 4-O-methylgyrophoric acid
  Depsidones: Lobaric acid
β-Orcinol series:
  Para-depsides: Atranorin and chloroatranorin
  Depsidones: Consalazinic acid, fumarprotocetraric acid, galbinic acid, norstictic acid, protocetraric acid, salazinic acid
Dibenzofurans: Usnic acid
Anthraquinones: Skyrin
Undetermined:
  Echinocarpic acid (and associated secondary metabolites) (probably related to alectorialic acid according to J.A. Elix)
  Parmelia testacea unknown #27 (probably a fatty acid according to C.F. Culberson)

These substances occur in the following major combinations. Further details on their occurrence will be found in the species discussions.

Cortical substances:
  Atranorin (probably always with chloroatranorin): All species in the genus
  Gyrophoric acid (with 4-O-methylgyrophoric acid): *P. shinanoana*
  Usnic acid: Soredia of *P. fraudans*
Medullary substances:
  Echinocarpic acid (± conechinocarpic acid): *P. crambidiocarpa, P. norcrambidiocarpa, P. protosulcata, P. subtestacea*
  Fumarprotocetraric acid: *P. neodiscordans, P. protosulcata*
  Lobaric acid: *P. discordans, P. kerguelensis, P. omphalodes, P. protosulcata, P. pseudotenuirima, P. saxatilis*
  Norstictic acid: *P. omphalodes, P. submutata*
  Protocetraric acid: *P. crambidiocarpa, P. discordans, P. kerguelensis, P. protosulcata, P. signifera*
  Protolichesterinic acid: *P. discordans, P. omphalodes*
  Salazinic acid (often with consalazinic acid): *P. adaugescens, P. cochleata, P. cunninghamii, P. erumpens, P. fertilis, P. fraudans, P. hygrophila, P. isidioclada, P. laevior, P. marmariza, P. meiophora, P. novae-zelandiae, P. niitakana, P. norcrambidiocarpa, P. omphalodes, P. pseudolaevior, P. pseudoshinanoana, P. pseudotenuirima, P. queenslandensis, P. ricasolioides, P. salcrambidiocarpa, P. saxatilis, P. sectilis, P. shinanoana, P. signifera, P. skultii, P. squarrosa, P. submontana, P. submutata, P. sulcata, P. tenuirima, P. testacea*
  Stictic acid: *P. skultii*
  Unknown fatty acid (unknown #27): *P. testacea, P. subtestacea* (chemotype)

Chemotypes

The question of "chemical species" arises in *Parmelia* as it does in most parmelioid groups. Lichenologists have still not agreed on the proper treatment of chemical variation, even though it is a fundamental species character in many other fungal groups. An overview by Hawksworth (1976) is the most recent summary of this topic. An objective solution to

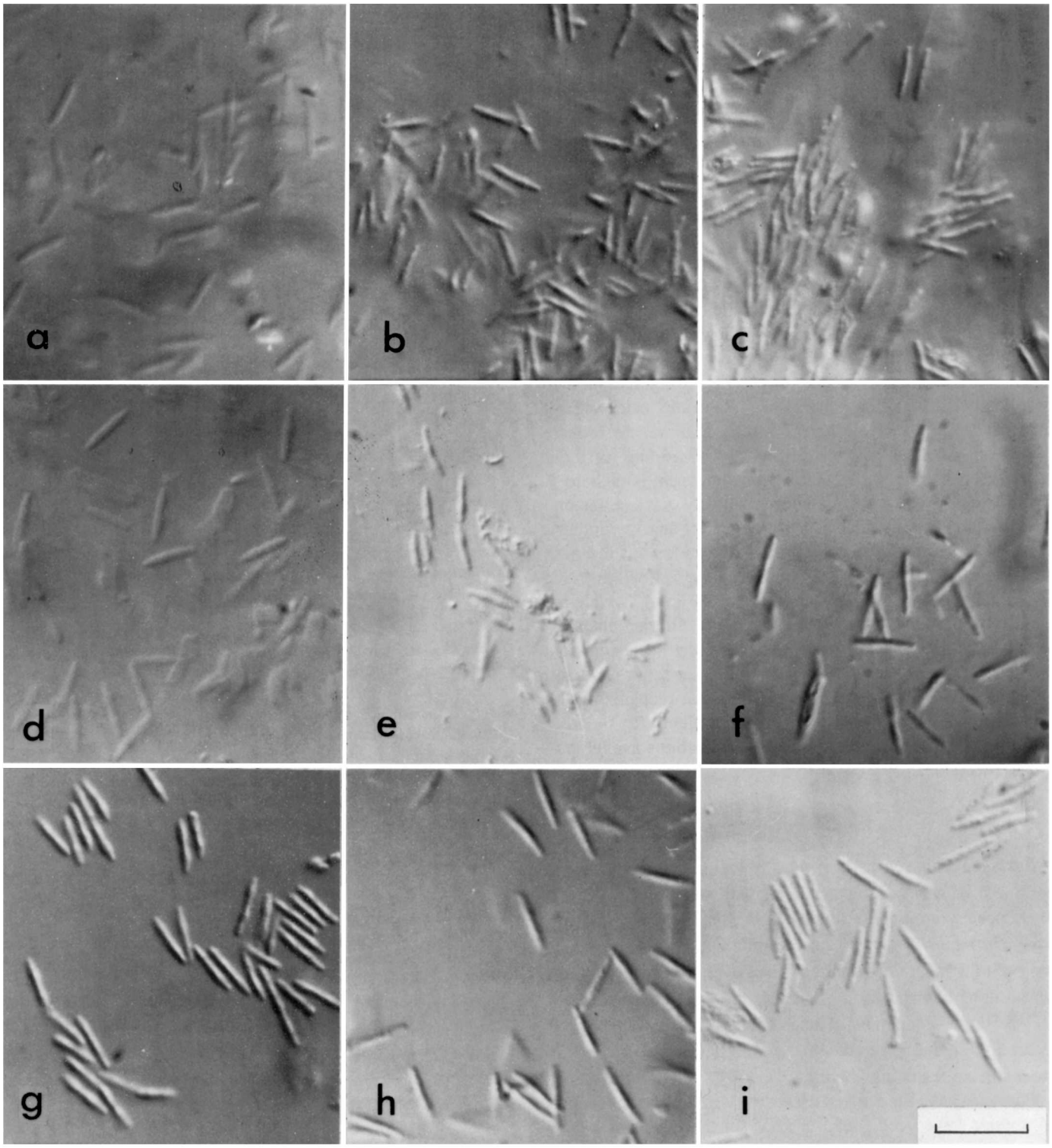

FIGURE 12.—Conidia of *Parmelia* species: *a, P. cochleata* (isolectotype in US); *b, P. cunninghamii* (*Santesson* 7814); *c, P. discordans* (*Kjellmert* s.n.); *d, P. testacea* (*James* 561); *e, P. erumpens* (*Hale* 43657); *f, P. marmariza* (*Nakanishi* 2811); *g, P. omphalodes* (*Hale* 18851); *h, P. saxatilis* (*Hale* 49288); *i, P. sulcata* (*Hale* 49675a). (Scale in *i* = 10 μm.)

this controversial problem will probably not be reached until more experiments, such as those begun by C.F. Culberson (Culberson and Ahmadjian, 1980), are completed.

Ultimately some "chemical species" will be found on closer study to have subtle morphological differences, obviating any decision as to their validity. Others will stand as good species, especially when strong correlating geographical or habitat differences are found. Finally some will be rejected as ever more refined analytical tests show them to be artifacts of earlier, imperfect tests, which were incapable of detecting minor metabolites (Elix, 1982). Another obstacle to an orderly solution is that very few "chemical species" have been adequately sampled and studied in the field.

There are several species pairs in *Parmelia* that may be considered nearly identical except for chemistry and which I am recognizing at the species level in this monograph. The best known pair is *P. omphalodes* (salazinic acid) and *P. discordans* (protocetraric acid). Although these are broadly sympatric, Skult (1984) found that *P. discordans* is more strongly oceanic in distribution. A second pair is isidiate *P. saxatilis* (salazinic acid), which is mostly saxicolous and boreal, and *P. kerguelensis* (protocetraric acid), which is corticolous in North America and mainly saxicolous in South Africa. A third pair is *P. norcrambidiocarpa* (echinocarpic acid) and *P. salcrambidiocarpa* (salazinic acid), which are allopatric in Australia and New Zealand. Similar chemical variation is used in part to separate *P. testacea* (salazinic acid and unknown #27) and *P. subtestacea* (echinocarpic acid and unknown #27). On the other hand, I am not recognizing the protocetraric acid chemotype of Australian *P. signifera* (unnamed), because there are too few collections available to make a decision.

Phytogeography

Parmelia behaves as a typical boreal-temperate genus in North America and Europe. It is a small, well collected group of 9 species familiar to all lichenologists. Africa has a very small *Parmelia* flora with no endemic species. Eastern Asia has been the most important center of evolution for the genus. Japan alone has at least 12 species, and Asia as a whole 17, 10 of them endemics. Three species, *P. meiophora, P. ricasolioides,* and *P. submutata,* seem to have originated in the mountains of southern China.

Parmelia has also evolved extensively in Australasia, where 14 species have been found. Twelve of these, *P. crambidiocarpa, P. cunninghamii* and *P. protosulcata* (both also in austral South America), *P. norcrambidiocarpa, P. novaezelandiae, P. pseudotenuirima, P. queenslandensis, P. salcrambidiocarpa, P. signifera, P. subtestacea, P. tenuirima,* and *P. testacea,* occur only in the southern hemisphere. The remaining two, *P. kerguelensis* and *P. sulcata,* occur in both hemispheres.

The 38 species of *Parmelia* are distributed as follows in the major geopolitical units of the world:

NORTH AMERICA

Canada: *P. fertilis, P. fraudans, P. hygrophila, P. kerguelensis, P. omphalodes, P. saxatilis, P. skultii, P. squarrosa, P. sulcata.*

USA: *P. discordans, P. fraudans, P. hygrophila, P. kerguelensis, P. neodiscordans, P. omphalodes, P. saxatilis, P. skultii, P. squarrosa, P. sulcata.*

SOUTH AMERICA

Argentina: *P. cunninghamii, P. protosulcata, P. saxatilis, P. sulcata.*

Chile: *P. cunninghamii, P. protosulcata, P. saxatilis, P. sulcata.*

Falkland (Malvinas) Islands: *P. cunninghamii, P. saxatilis, P. sulcata.*

EUROPE

Greenland/Iceland: *P. fraudans, P. omphalodes, P. saxatilis, P. sulcata.*

Europe (including Turkey): *P. discordans, P. fraudans, P. omphalodes, P. saxatilis, P. skultii, P. submontana, P. sulcata.*

AFRICA

Tunisia: *P. submontana.*

East Africa (Ethiopia, Kenya): *P. saxatilis, P. sulcata.*

South Africa: *P. erumpens, P. kerguelensis.*

ASIA

Japan: *P. adaugescens, P. cochleata, P. erumpens, P. fertilis, P. isidioclada, P. laevior, P. marmariza, P. pseudolaevior, P. pseudoshinanoana, P. shinanoana, P. squarrosa, P. sulcata.*

Korea: *P. cochleata, P. fertilis, P. squarrosa.*

Mongolia: *P. cochleata, P. omphalodes.*

China: *P. fertilis, P. laevior, P. marmariza, P. meiophora, P. ricasolioides, P. squarrosa, P. submutata, P. sulcata.*

Himalayan region (northern India, Nepal, Sikkim, Pakistan): *P. adaugescens, P. marmariza, P. meiophora, P. omphalodes, P. ricasolioides, P. squarrosa, P. submutata, P. sulcata.*

Southern India: *P. erumpens.*

SOUTHEAST ASIA

Taiwan: *P. adaugescens, P. erumpens, P. fertilis, P. laevior, P. marmariza, P. niitakana, P. submutata.*

Philippines: *P. isidioclada, P. sectilis.*

Sabah: *P. erumpens, P. sectilis.*

Indonesia: *P. erumpens.*

AUSTRALASIA

Australia: *P. cunninghamii, P. erumpens, P. norcrambidiocarpa, P. pseudotenuirima, P. queenslandensis, P. salcrambidiocarpa, P. signifera, P. sulcata, P. tenuirima, P. testacea.*

New Zealand: *P. crambidiocarpa, P. cunninghamii, P. kerguelensis, P. norcrambidiocarpa, P. novae-zelandiae, P. protosulcata, P. salcrambidiocarpa, P. saxatilis, P. signifera, P. subtestacea, P. sulcata, P. tenuirima, P. testacea.*

Key to the Species of *Parmelia*

1. Thallus with powdery, granular, pustulate or subisidiate soredia (under high magnification the isidia-like soredia of *P. fraudans* and *P. isidioclada* may be mistaken for true isidia).
   2. Pseudocyphellae punctiform, occurring only on lobe edges . . . . . ***P. isidioclada***
   2. Pseudocyphellae predominantly effigurate, on lobe surface and/or margins.

3. Soredia pustular, mostly laminal; cortex deeply fissured . . . . . *P. erumpens*
3. Soredia powdery, marginal or along ridges on surface; cortex not deeply cracked.
4. Medulla K- (protocetraric acid) . . . . . *P. protosulcata*
4. Medulla K+ yellow turning red (salazinic acid).
5. Soralia mostly laminal along ridges.
6. Rhizines strongly squarrosely branched; pantemperate-panboreal . . . . . *P. sulcata*
6. Rhizines simple; Mediterranean region . . . . . *P. submontana*
5. Soralia mostly marginal.
7. Soredia yellowish; boreal regions . . . . . *P. fraudans*
7. Soredia greenish or whitish gray; austral regions . . . . . *P. cunninghamii*

1. Thallus lacking soredia.
8. Thallus with dense suberect, marginal (or in part laminal) dorsiventral lobules or isidiate lobules.
9. Pseudocyphellae round, punctiform, only on lobe edges . . . . . *P. pseudolaevior*
9. Pseudocyphellae elongate, mostly marginal.
10. Pseudocyphellae conspicuous as a broad white rim; Japan . . . . . *P. pseudoshinanoana*
10. Pseudocyphellae inconspicuous; southeastern Asia . . . . . *P. sectilis*
8. Thallus without conspicuous suberect lobules (*P. discordans, P. neodiscordans, P. omphalodes, P. subtestacea,* and *P. testacea* may have dense appressed secondary lobules); if isidiate, the isidia mostly laminal.
11. Thallus isidiate.
12. Medulla K– (protocetraric acid) . . . . . *P. kerguelensis*
12. Medulla K+ yellow turning red (salazinic acid).
13. Isidia produced only along lobe margins . . . . . *P. isidioclada*
13. Isidia produced mostly on lobe surface or along ridges on lobe surface.
14. Upper surface finely white-maculate pseudocyphellate, the pseudocyphellae less than 0.5 mm long; China and Taiwan . . . . . *P. meiophora*
14. Upper surface with larger effigurate pseudocyphellae more than 0.5 mm long.
15. Isidia dull, decomposing and becoming subsorediate; Pacific Northwest . . . . . *P. hygrophila*
15. Isidia usually shiny, corticate, not becoming sorediate.
16. Thallus small, 3–5 cm broad, closely attached; isidia very dense; Australia . . *P. pseudotenuirima*
16. Thallus larger, 5–20 cm broad, adnate to loosely attached; not occurring in Australia.
17. Lobes broad and apically rotund, 4–10 mm wide . . . . . *P. novae-zelandiae*
17. Lobes narrower, sublinear, 1–5 mm wide.
18. Rhizines simple to furcate . . . . . *P. saxatilis*
18. Rhizines squarrosely branched . . . . . *P. squarrosa*
11. Thallus lacking isidia.
19. Medulla K– (fumarprotocetraric acid, protocetraric acid or unknown #27).
20. Thallus corticolous; New Zealand.
21. Lobes subirregular, contiguous; pseudocyphellae mostly marginal . . . . . *P. subtestacea* (chemotype)
21. Lobes sublinear, separate; pseudocyphellae mostly laminal . . . . . *P. crambidiocarpa*
20. Thallus saxicolous; Europe and North America.
22. Fumarprotocetraric acid present; North America . . . . . *P. neodiscordans*
22. Protocetraric acid present; Europe . . . . . *P. discordans*
19. Medulla K+ yellow or yellow turning red (salazinic acid or echinocarpic acid).
23. Pseudocyphellae punctate, on lobe edges . . . . . *P. laevior*
23. Pseudocyphellae effigurate, laminal and/or marginal.
24. Pseudocyphellae marginal as a white rim around lobes; Japan and East Asia only.
25. Saxicolous; cortex C+ rose (gyrophoric acid) . . . . . *P. shinanoana*
25. Corticolous; cortex C– (atranorin only).
26. Lobes subirregular, apically rotund; Japan . . . . . *P. cochleata*
26. Lobes sublinear, apically obtuse; Taiwan . . . . . *P. niitakana*
24. Pseudocyphellae laminal and marginal, not forming a conspicuous marginal rim (except in *P. subtestacea* and *P. testacea* from New Zealand).
27. Rhizines squarrosely branched.
28. Pseudocyphellae less than 0.3 mm long, appearing as fine white maculae; Taiwan and China . . . . . *P. submutata*

28. Pseudocyphellae distinct, effigurate, up to 1 mm long.
    29. Lobes broad and rotund, to 10 mm wide; pseudocyphellae separate, laminal . . . ***P. tenuirima***
    29. Lobes sublinear, 1–5 mm wide; pseudocyphellae marginal and/or laminal, often fusing.
        30. Lobes subirregular; pseudocyphellae mostly marginal.
            31. Salazinic acid present . . . . . ***P. testacea***
            31. Echinocarpic acid present . . . . . ***P. subtestacea***
        30. Lobes sublinear; pseudocyphellae mostly laminal.
            32. Collected in Japan, East Asia and Canada . . . . . ***P. fertilis***
            32. Collected in Australasia.
                33. Echinocarpic acid present.
                    34. Spores more than 16 µm long . . . . . ***P. crambidiocarpa***
                    34. Spores less than 16 µm long . . . . . ***P. norcrambidiocarpa***
                33. Salazinic acid present.
                    35. Rhizines forming a dense, projecting mat; lobes sublinear, separate; Tasmania and New Zealand . . . . . ***P. salcrambidiocarpa***
                    35. Rhizines sparse to moderate, not projecting; lobes sublinear but short and crowded; Queensland and northern N.S.W., Australia . . . ***P. queenslandensis***

27. Rhizines simple to furcate.
    36. Pseudocyphellae mostly marginal.
        37. Apothecia numerous, to 2 mm in diameter; Himalayan region . . . . . ***P. ricasolioides***
        37. Apothecia, if present, larger, to 15 mm in diameter; boreal areas or New Zealand.
            38. Thallus greenish mineral gray; Australasia.
                39. Salazinic acid present . . . . . ***P. testacea***
                39. Echinocarpic acid present . . . . . ***P. subtestacea***
            38. Thallus whitish to brownish gray or blackening; boreal regions.
                40. Salazinic acid present (without norstictic acid) . . . . . ***P. omphalodes***
                40. Salazinic and norstictic acids present . . . . . ***P. skultii***
    36. Pseudocyphellae mostly laminal.
        41. Collected on rocks or soil; thallus often turning brownish.
            42. Pseudocyphellae laminal; upper surface becoming fissured; Australasia . . . . ***P. signifera***
            42. Pseudocyphellae laminal and marginal; upper surface continuous; boreal regions . . . . . ***P. omphalodes***
        41. Collected on trees; thallus greenish or whitish mineral gray.
            43. Pseudocyphellae separate, less than 0.5 mm long . . . . . ***P. marmariza***
            43. Pseudocyphellae separate or fusing into a network, to 1 mm long.
                44. Collected in Australasia (see 32).
                44. Collected in Japan and eastern Asia.
                    45. Upper surface conspicuously cracked with age; pseudocyphellae mostly laminal . . . . . ***P. adaugescens***
                    45. Upper surface not cracking conspicuously; pseudocyphellae marginal, forming a nearly continuous rim.
                        46. Spores about 30 µm long; Taiwan . . . . . ***P. niitakana***
                        46. Spores about 15 µm long; Japan, East Asia . . . . . ***P. cochleata***

Taxonomic Treatment

The 38 species of *Parmelia* are arranged below in alphabetical order. Locations of specimens cited in synonymies and "Specimen Examined" sections are indicated by standard herbarium acronyms.

Parmelia

Parmelia Acharius, 1803:153 [nomen conservandum].
Lichen L., 1753:1140. [Lectotype species: *Lichen saxatilis* L.]
Aspidelia Stirton, 1900:81. [Lectotype species *Aspidelia beckettii* Stirton (= *Parmelia tenuirima*, see Culberson, 1966).]

DESCRIPTION.—Thallus foliose, 4–60 cm broad, greenish to whitish mineral gray; lobes sublinear to more rarely subirregular, 1.5–10 mm wide; upper surface plane to foveolate, isidiate, sorediate, or lacking soredia and isidia, pseudocyphellate, the pseudocyphellae usually effigurate, rarely punctiform; lower surface black, moderately to densely rhizinate, the rhizines simple, furcate or squarrosely branched. Pycnidia common, immersed, laminal; conidia cylindrical to slightly

bifusiform, straight or slightly bent, 5.5–8.0 µm long. Apothecia adnate to substipitate, 1–20 mm in diameter, the disc pale brown, the amphithecium usually pseudocyphellate; spores 8/ascus, simple, colorless, 3–18 × 6–33 µm long, the episporium 1–4 µm thick.

CHEMISTRY.—Atranorin and chloroatranorin (rarely gyrophoric acid) in the cortex; salazinic acid, consalazinic acid, protocetraric acid, fumarprotocetraric acid, echinocarpic acid, or unidentified substances and as accessory or trace substances conechinocarpic acid, galbinic acid, lobaric acid, norstictic acid, protolichesterinic or related fatty acids, or stictic acid in the medulla.

Parmelia adaugescens

FIGURES 2*a*, 13*a*

Parmelia adaugescens Nylander, 1890:28. [Type collection: Ichigome, Japan, *Almquist* (H, Nyl. herb. no. 34876, lectotype).]

Parmelia pseudomarmariza Awasthi, 1976:186. [Type collection: Mervakhola Valley, Nepal, *Awasthi* 2305 (AWAS).]

DESCRIPTION.—Thallus adnate on bark, rather firm, 8–15 cm broad, greenish to whitish mineral gray (brownish in the herbarium); lobes sublinear, long, contiguous, 2–5 mm wide; upper surface shiny, plane, rugose-foveolate with age, transversely cracked in older parts, pseudocyphellae effigurate, conspicuous, 0.5–1.5 mm long, marginal and laminal, mostly separate or forming a loose network; lower surface black, densely rhizinate, the rhizines simple to furcate or dichotomously branched, 1–2 mm long. Pycnidia common but poorly developed; conidia cylindrical, straight, 7–8 µm long. Apothecia common, substipitate, urceolate and inrolled when young, 4–8 mm in diameter, the amphithecium rugose, pseudocyphellate; hymenium 65–70 µm; spores 13–15 × 21–27 µm, the episporium distinct, 2–3 µm thick.

CHEMISTRY.—Atranorin and salazinic acid (Asahina, 1951b) and consalazinic acid.

REMARKS.—This widespread Asian species is characterized by the large spores and large, uniformly dispersed pseudocyphellae. It is most common in Japan and Taiwan but extends as far west as Pakistan in Asia. It seems rather isolated from other large-spored species such as *P. isidioclada* and *P. sectilis*, which have different orientation of the pseudocyphellae. There is some intergradation with *P. cochleata*, which has small spores, as well as with *P. fertilis*, which also has small spores and richly branched rhizines.

Parmelia pseudomarmariza, described from Nepal, has similarly large spores and slightly smaller but comparable pseudocyphellae. It does not seem sufficiently different from *P. adaugescens* to be kept as a distinct species.

Specimens Examined

Pakistan: *Iqbal* 742 (US). Sikkim: *Hara et al.* s.n. (TNS, US). India: West Bengal, *Hara et al.* s.n. (TNS, US). China: Prov. Heiho, *Takahashi* 2928 (TNS). Japan: Prov. Awa, *Fujikawa* (TNS); Prov. Inaba, *Nakanishi* 24 (TNS); Prov. Ishikari, *Asahina* s.n. (TNS); Prov. Iwashiro, *Kurokawa* 58169 (TNS, US); Prov. Iyo, *Nakanishi* 56 (US); Prov. Kii, *Numajiri* s.n. (TNS); Prov. Kozuke, *Asahina* s.n. (TNS); Prov. Musashi, *Asahina* s.n. (TNS); Prov. Mutsu, *Hale* 29301, 29302, 29306, 29312, 29355 (US); Prov. Shimotsuke, *Kurokawa* 56530A (TNS); Prov. Tosa, *Fujikawa* s.n. (TNS). Taiwan: *Kurokawa* 1209 (TNS, US); Miaoli County, *Lai* 6874, 7795, 7809, 7813 (US); Nantou County, *Suzuki* 10901 (US); Taichung County, *Lai* 6876, 6875 (US).

Parmelia cochleata

FIGURES 2*b*, 13*b*

Parmelia cochleata Zahlbruckner, 1927b:350. [Type collection: Mt. Fuji, Japan, *Asahina* 27 (W, holotype; TNS, US, isotypes).]

Parmelia marmariza var. *physcioides* Zahlbruckner, 1927b:352. [Type collection: Mt. Buko, Musashi, Japan, *Asahina* 24 (W, holotype, TNS, isotype).]

Parmelia pseudosaxatilis Asahina, 1951b:354. [Type collection: based on *P. marmariza* var. *physcioides* Zahlbruckner.]

DESCRIPTION.—Thallus loosely adnate on bark, firm, greenish mineral gray, 6–20 cm broad; lobes sublinear to subirregular, crowded, 1–5 mm wide, the margins lobulate, lobules rotund, 1–2 mm wide, more or less concave or hood-shaped, becoming suberect; upper surface plane to very weakly foveolate, continuous, shiny, becoming pruinose at the lobe tips, pseudocyphellae marginal, forming a nearly continuous narrow white rim, only sparsely developed on the lobe surface, separate; lower surface black, moderately to densely rhizinate, the rhizines simple to furcate, 1–2 mm long. Pycnidia numerous; conidia (Figure 12*a*) cylindrical to weakly bifusiform, slightly bent, 5.5–7.0 µm long. Apothecia numerous, substipitate, 3–8 mm in diameter, the rim somewhat inrolled, finely crenate, the amphithecium sparsely pseudocyphellate; hymenium 60–70 µm; spores poorly developed, about 6 × 10 µm, the episporium 1 µm thick (Asahina reports 6–8 × 12–13 µm in type description).

CHEMISTRY.—Atranorin and salazinic acid (consalazinic acid lacking). Protolichesterinic acid also reported by Kurokawa and Nakanishi (1971) in 2 of 5 specimens tested.

REMARKS.—*Parmelia cochleata* is widespread but not especially common in Japan. In the typical form it has strongly cochleate lobes but at other times the lobes are quite flat and appressed and the species lacks other distinguishing features except the generally marginal pseudocyphellae, similar to those in *P. rudior* and *P. testacea* from New Zealand.

Specimens Examined

Korea: *Kimura* s.n. (TNS). Japan: Prov. Buzen, *Kurokawa* 62481 (TNS); Prov. Inaba, *Ikoma* 2179 (TNS), *Nakanishi* 12167 (KOBE); Prov. Iyo, *Ogata* 159 (TNS); Prov. Kii, *Kurokawa* 60235, *Numajiri* 24 (TNS); Prov. Musashi, *Kurokawa* 64288 (TNS); Prov. Shinano, *Hiratsuka* s.n. (TNS); Prov. Suruga, *Asahina* 27 (TNS); Prov. Totomi, *Nakanishi* 51 (TNS). Golubkova (1981) reports the species from Mongolia.

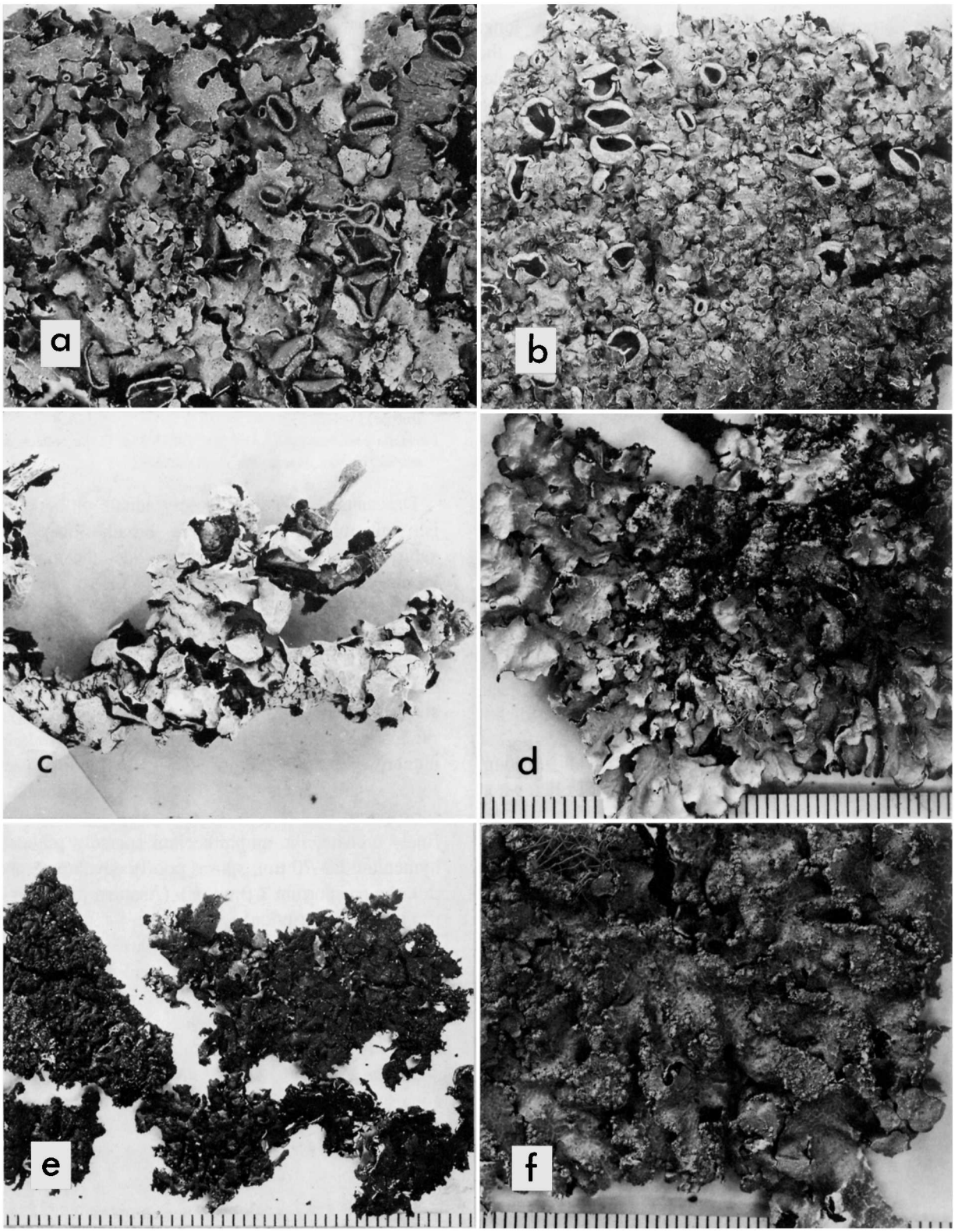

FIGURE 13.—Species of *Parmelia*: *a*, *P. adaugescens* (lectotype in H); *b*, *P. cochleata* (type of *P. marmariza* var. *physcioides* Zahlbruckner in W); *c*, *P. crambidiocarpa* (lectotype in W); *d*, *P. cunninghamii* (*Santesson* 6792); *e*, *P. discordans* (*Laurila* in *Lichenes Fennici Exsiccati* 195); *f*, *P. erumpens* (*Hale* 59471). (Scales in mm.)

Parmelia crambidiocarpa

FIGURES 2c, 13c, 14

Parmelia crambidiocarpa Zahlbruckner, 1941:109. [Type collection: Wilkes Pools, Mt. Egmont National Park, North Island, New Zealand, *Cranwell* ZA205 (W, lectotype; CHR, isolectotype).]

DESCRIPTION.—Thallus adnate to loosely adnate on bark, firm, whitish or pale greenish gray, 6–15 cm broad; lobes sublinear, often little branched, subdivaricate, browning at the tips, 1–4 mm wide; upper surface shiny, continuous or cracking transversely with age, plane, pseudocyphellae forming an irregular but nearly continuous rim around the lobe margins, 0.1–0.3 mm wide, also laminal and effigurate, 0.2–0.8 mm long, separate, fissuring with age; lower surface black, moderately to densely rhizinate, the rhizines simple to furcate or squarrosely branched, 1–2 mm long and often projecting as a mat around the lobe margins. Pycnidia common, 90–110 µm in diameter; conidia cylindrical, rod-shaped, 5.5–6.0 µm long. Apothecia common, becoming stipitate and cupuliform, splitting radially with age, to 20 mm in diameter, the disc pale tan to very dark brown, the amphithecium rugose and effigurate-pseudocyphellate; hymenium 80–90 µm high; spores 10–15 × 17–21 µm, the episporium about 2 µm thick.

CHEMISTRY.—Atranorin, chloroatronorin, and protocetraric acid or echinocarpic acid (and associated unknowns) or protocetraric and echinocarpic acids together in nearly equal concentration.

REMARKS.—*Parmelia crambidiocarpa* is a member of the *P. testacea* complex, closely related to *P. norcrambidiocarpa* and *P. salcrambidiocarpa*. Although Galloway and Elix (1983) synonymized it with *P. testacea*, I have concluded from my own field studies in New Zealand that it is a distinct species, separated by a series of highly correlated morphological and chemical characters.

The morphological characters are quite distinctive. The thallus is typically loosely adnate, rather large, and with narrow, sublinear lobes. The pseudocyphellae are both marginal and laminal and usually fissure with age. The rhizines form a dense mat below and often project out from the margins. The apothecia tend to be strongly stipitate and nearly urceolate, although very large apothecia become flattened and radially split. Disc color ranges from very pale tan (11% of 37 fertile specimens examined) to light brown (59%) or very dark brown (30%).

The spores of *P. crambidiocarpa* are consistently large. The average maximum length is 18.4 µm (range 15–21 µm) and width 11.4 µm (9–12 µm) (29 measurements). The episporium is about 2 µm thick. For the other two externally similar species in this group, *P. norcrambidiocarpa* and *P. salcrambidiocarpa*, spores do not exceed 15 µm in length and the episporium is only 1–1.5 µm thick.

The chemistry is also distinctive. The type specimen from the Dawson Falls area at Mt. Egmont contains a mixture of echinocarpic and protocetraric acids. I visited this locality and made a random sample of 69 specimens in the subalpine scrub zone at 1000–1200 m elevation. The sample consisted of 39% with echinocarpic and protocetraric acids, 45% with echinocarpic acid (and associated unknowns)—although traces of protocetraric acid might have been missed on the TLC plates—and 16% with protocetraric acid alone. Unknown #27, so typical of the *P. testacea* group, was not detected in any specimens.

Taking the whole range of *P. crambidiocarpa*, one finds a complex pattern for combinations of the acids. At Tongariro National Park, another isolated volcanic peak about 150 km east of Mt. Egmont, specimens with protocetraric acid alone made up an overwhelming 98% of the population (54 specimens tested), the remainder containing both echinocarpic and protocetraric acids. A similar proportion appears to hold for the Urewera area farther to the east although the sample size (5) is too small to be sure. On the South Island, where the species is far less abundant and largely replaced by *P. norcrambidiocarpa*, all specimens (21 tested) contained protocetraric acid except for one collection in beech forest near Tuatapere and one (sterile) from Lewis Pass with both echinocarpic and protocetraric acids present.

Parmelia crambidiocarpa has strong ecological requirements. On North Island of New Zealand it is abundantly developed—and in fact the only member of the *P. testacea* group except for rare *P. salcrambidiocarpa*—at 1000–1300 m elevation in the subalpine zone on a variety of trees and shrubs (*Nothofagus, Dracophyllum, Nothopanax, Pseudopanax*, etc.). I did not collect it below 600 m elevation. On South Island it occurs above 600 m in the highest passes but also grows near sea level at high latitudes in the extreme south, where it occurs with *P. norcrambidiocarpa* (Figure 14). In random samples made at 71 localities in New Zealand, I collected 149 specimens (23%) of *P. crambidiocarpa* out of a total of 715 collections in the *P. testacea* complex. A similar percentage (17% or 14 of 88 collections) was found in the herbarium collections at CHR.

Representative Specimens Examined
(protocetraric acid)

New Zealand: North Island, *Elix* 8195, 8208 (ANUC), *Hale* 65108, 65527, 65572 (US), *Hayward* H112.70 (US); South Island, *Elix* 7702 (ANUC), 8527 (CHR), *Hale* 65146, 65236, 65497, 65782 (US), *Imshaug* 47879, 55985 (MSC), *Molloy* CHR266952 (CHR).

Representative Specimens Examined
(echinocarpic acid)

New Zealand: North Island, *Davey* CHR160226 (CHR), *Hale* 65296, 65533 (US).

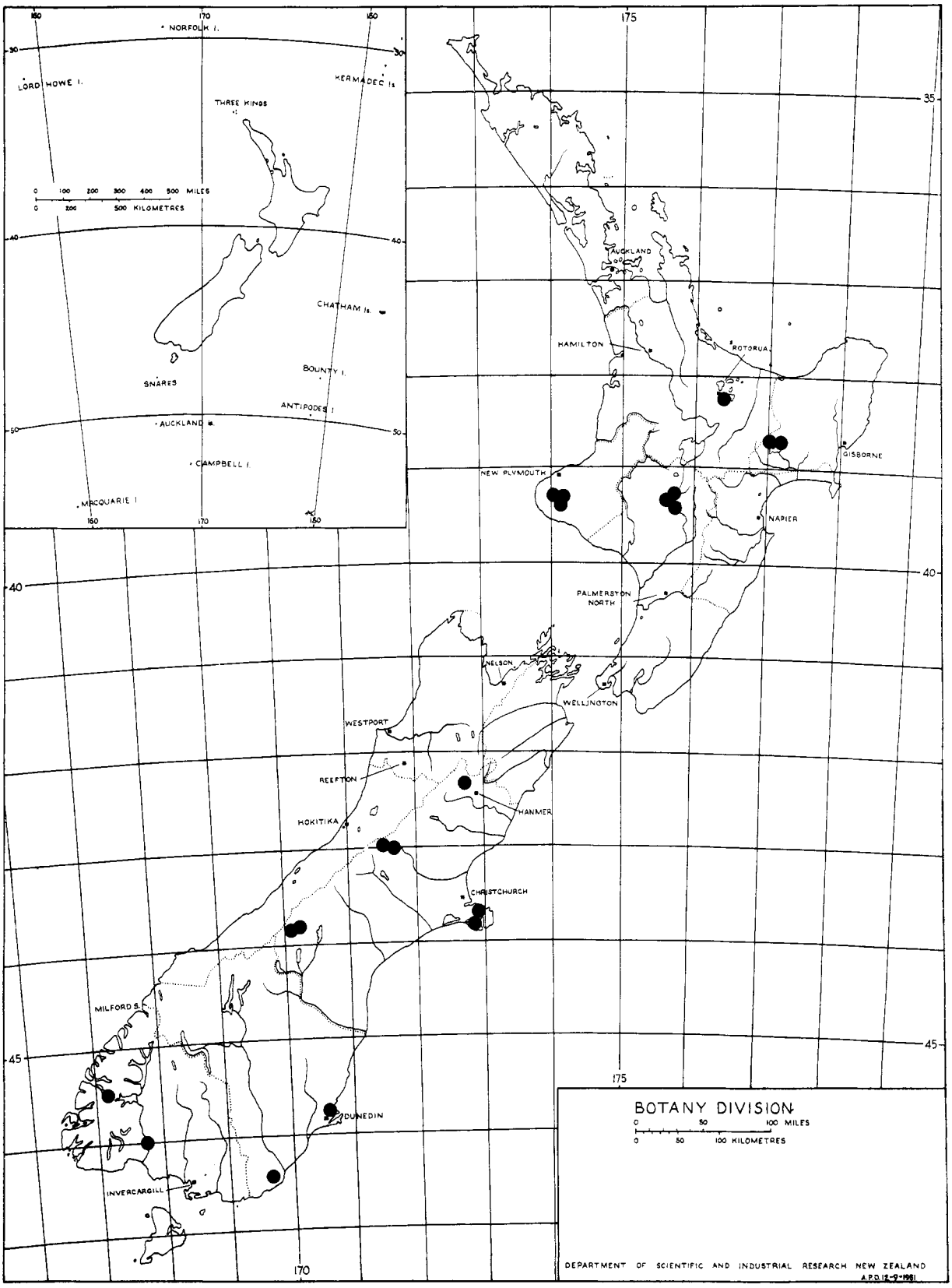

FIGURE 14.—Distribution of *Parmelia crambidiocarpa* in New Zealand.

Representative Specimens Examined (echinocarpic and protocetraric acids)

New Zealand: North Island, *Hale* 65279, 65537, 65783 (US); South Island, *Elix* 7507 (CHR), *Hale* 65779 (US).

Parmelia cunninghamii

FIGURES 2*d*, 13*d*

Parmelia cunninghamii Crombie, 1876:228. [Type collection: Island Harbour, Falkland Islands, 18 April 1868, *Cunningham* (BM, lectotype; H, isotype).]
Parmelia brownii Dodge, 1970:449. [Type collection: Camp Hill, Macquarie Island, *Brown* 69 (FH-Dodge).]

DESCRIPTION.—Thallus adnate on bark, more rarely on rocks, very firm, pale greenish to brownish mineral gray, 8–12 cm broad; lobes subirregular, apically subrotund, contiguous, usually turning up at the margins, 3–7 mm wide; upper surface shiny, becoming white pruinose at the tips, plane to rugose-foveolate with age, reticulately fissured only in older parts, sorediate, the soralia linear along the margins, orbicular when laminal, pseudocyphellae effigurate, 0.3–1 mm long, rather sparsely developed to well developed, marginal and laminal, separate, sinuous; lower surface black, moderately to densely rhizinate, the rhizines simple to squarrosely branched, 1–2 mm long. Pycnidia rare, marginal; conidia (Figure 12*b*) cylindrical, straight to slightly bent, 5.5–7.0 µm long. Apothecia rare, substipitate, 4–15 mm in diameter, the amphithecium arugose, pseudocyphellate, the disc brown; hymenium 65–70 µm; spores 8–9 × 10–12 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin and chloroatranorin, salazinic acid (Galloway and Elix, 1983), consalazinic acid, and accessory lobaric acid.

REMARKS.—This widespread austral species can be recognized by the firm, shiny thallus and well-developed marginal soralia. It differs from closely related *P. sulcata*, with which it occurs in austral regions, in several respects. For example, the surface is not strongly foveolate-ridged, the soralia are chiefly marginal, and the rhizines are not so densely squarrosely branched. *Parmelia protosulcata*, a narrow-lobed species with protocetraric acid, has sparser, often orbicular soralia. When these are better developed they become linear and approach *P. cunninghamii* very closely.

Parmelia cunninghamii is preeminently a species of the moist forests of austral South America and New Zealand. Farther west in Australia it occurs in temperate rain forest.

Specimens Examined

Argentina: Prov. Chubut, *Lamb* 5860 (US); Cerro Mazo, *James* 1644 (BM); SW Patagonia, *James* 579 (BM); Tierra del Fuego, *Santesson* 1145 (S, US). Falkland Islands: *Imshaug* 40162 (US). Chile: Prov. Chiloe, *Redon* 03575 (US); Prov. Malleco, *Eyerdam* 10860 (COLO, US), *Mahu* 2537 (US); Terr. Magallanes, *Imshaug* 44566 (MSC), *Santesson* 7814 (US), 8012, 8188 (S); Tierra del Fuego, *Santesson* 5910, 6013, 6792, 7385, 7396 (S, US), 5812, 6005, 7497 (S); Valdivia, *Mahu* 1699 (US). New Zealand: Antipodes Island, *Du Rietz* 2598:3 (UPS, US); South Island Fiord District, *Du Rietz* 1856a (UPS, US); South Island–Eastern Botany District, *Du Rietz* 1462:26 (UPS, US); Otago, *James* 611/2 (BM), *Martin* 1116 (BM), *Murray* 1273 (BM), *James* 1623 (BM, US), *Thomson* Z.136 (CHR); Canterbury, *Elix* 8570 (CHR), *Galloway* s. n. (CHR), *Tibell* 9232, 9439, 9682 (UPS); Auckland Islands, *Imshaug* 56283 (MSC), *James* 1345 (BM), 1378 (FH, US). Australia: New South Wales, *Hale* 66605 (US), South Australia, *Elix* 4901 (ANUC); Tasmania, *Elix* 5593 (ANUC); Victoria, *Bastow* (US), *Elix57* (ANUC), *James* Au2136, Au2138 (BM); Marion Island, *Huntley* 971 (US).

Parmelia discordans

FIGURES 2*e*, 13*e*

Parmelia discordans Nylander in Brenner, 1886:40. [Type collection: Hogland, Finland, *Brenner* s.n. (H, Nyl. herb. no 34916, lectotype).]
Parmelia omphalodes f. *insensitiva* Magnusson, 1919:89. [Type collection: Vestrogothia, Göteborg, Sweden, *Magnusson* s.n. (UPS, lectotype (not seen); FLAS, isolectotype).]
Parmelia omphalodes var. *discordans* (Nylander) Magnusson, 1929:89.
Parmelia insensitiva (Magnusson) Anders, 1928:152.
Parmelia omphalodes subsp. *discordans* (Nylander) Skult, 1984:138.

DESCRIPTION.—Thallus adnate to loosely adnate, very fragile and brittle, dark to blackish brown, 4–8 cm broad; lobes sublinear, short and imbricate, 1–3 mm wide, usually developing small secondary lobes with age; upper surface plane to weakly foveolate, shiny, continuous, sparsely cracked with age, pseudocyphellae mostly marginal but a few also laminal on older lobes, small, 0.2–0.5 mm long, effigurate and coalescing at times to form a loose, mostly marginal reticulate network; lower surface black, sparsely to moderately rhizinate, the rhizines simple to furcate, 1–1.5 mm long. Pycnidia not common; conidia cylindrical, straight to slightly bent, 5.5–6.5 µm long (Figure 12*c*). Apothecia rather rare (25% frequency in Finland (Skult, 1984)), adnate to substipitate, 2–5 mm in diameter, the amphithecium pseudocyphellate-reticulate, the disc plane; hymenium 55–60 µm; spores 8–10 × 14–16 µm, the episporium 1.5–2 µm thick.

CHEMISTRY.—Atranorin, protocetraric acid, and lobaric acid (Culberson, 1970) with accessory substances galbinic acid, fumarprotocetraric acid and unidentified fatty acids (Skult, 1984).

REMARKS.—Lichenologists are not in agreement on the status of *Parmelia discordans*, as it appears to be a "chemical species." Many Europeans (e.g., Degelius, 1931; Krog et al., 1980; Santesson, 1984) consider it to be at most a variety (var. *discordans* (Nylander) Magnusson) of *P. omphalodes*. Skult (1984) calls it a subspecies of *P. omphalodes*. Anders (1928), Culberson (1970), and Kurokawa (1976) used specific rank.

Morphologically *P. discordans* seems to be consistently smaller, with slightly narrower lobes. *Parmelia omphalodes* itself, however, has a very great range of variation, overlapping this character and almost any other morphological character one might want to designate as unique to *P. discordans*. Nylander himself compared it originally to *"P. prolixa* var. *panniformis,"* a brown *Parmelia*. The apothecial and pycnidial characters are essentially identical for the two species.

Parmelia discordans appears to be a relatively rare species in Europe, at least in comparison with *P. omphalodes*. Degelius (1931, 1944), however, found it to be more common on the basis of a KOH test in Ångermanland and Gotland, Sweden, and in Westland, Norway (1934). Skult (1984) collected it intensively in Finland, where it behaves as an oceanic species in the southwestern part of the country.

Specimens Examined

Europe. Great Britain: Scotland, *Denison* 251, *Dixon*, s.n. (US). Finland: Satakunta, *Laurila* in *Lichenes Fenniae Exsiccati* 195 (US). Sweden: Bohuslän, *Magnusson* in *Lichenes Selecti Exsiccati* 106 (FLAS) and *Kryptogamae Exsiccatae* 2571 (US); Småland, *Zetterstedt* s.n. (US); Västmanland, *Kjellmert* s.n. (US); Vestrogothia, *Magnusson*, s.n. (US). Belgium: Prov. Luxembourg, *Lambinon* in *Vězda, Lichenes Selecti Exsiccati* 916 (US). France: Sarthe, *Monguillon* in *des Abbayes, Lichenes Gallici* 39 (BM). Spain: Asturias, *Vasquez* s.n. (US).

Parmelia erumpens

FIGURES 2*f*, 13*f*, 15

Parmelia erumpens Kurokawa, 1969, no. 74. [Based on *Parmelia tenuirima* f. *corallina* Müller Argoviensis.]

Parmelia tenuirima f. *corallina* Müller Argoviensis, 1883:46. [Type collection: Gippsland, Australia, *Stirling* s.n. (G, lectotype; UPS, US, isolectotypes).]

DESCRIPTION.—Thallus adnate to loosely adnate on rocks and trees, fairly firm, pale greenish to whitish mineral gray, 8–20 cm broad; lobes short, subirregular to apically rotund, imbricate, 2–8 mm wide; upper surface shiny, plane, soon becoming conspicuously reticulately cracked, pseudocyphellae effigurate, 0.2–1.0 mm long, somewhat raised, dense, fusing into a reticulate network over the whole surface, sorediate, the soredia coarse and isidioid, often bursting apically, forming dense marginal and laminal soralia; lower surface black, moderately rhizinate, the rhizines simple or squarrosely branched at maturity, 1–2 mm long. Pycnidia rather rare; conidia (Figure 12*e*) cylindrical to weakly bifusiform, straight, 5.5–7.0 µm long. Apothecia rarne, stipitate, the rim inrolled but the disc flattening and splitting radially at maturity, 4–15 mm in diameter, the amphithecium reticulately cracked, pseudocyphellate, sorediate; hymenium 65–70 µm; spores 6–8 × 10–12 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin and chloroatranorin, salazinic acid (Galloway and Elix, 1983), and consalazinic acid.

REMARKS.—This is one of the more widespread Asian-African species (Figure 15), easily recognized by the deeply reticulately fissured cortex and abundant coarse pustular soredia. In Australia it is collected most commonly on sandstone outcrops in sclerophyll forests but in other areas it is usually corticolous. In India, for example, it occurs at 1400–2200 m elevation in open montane forests. In New Zealand it grows in mature, moist *Nothofagus* forests, and in South Africa it is found in the wet coastal forests in the Tsitsikama area. It seems to lack any recognizable parent morph, although *P. signifera* would have to be considered very closely related. *Parmelia signifera* has larger spores (13–15 µm) and greater chemical variation. Another parent morph proposed by Galloway and Elix (1983), *P. tenuirima*, is a much larger lichen with separate pseudocyphellae and larger spores (12–15 µm long).

Specimens Examined

Australia: Lord Howe Island, *Watts* (US); Australian Capital Territory, *Streimann* 4452, 7893 (US); New South Wales, *Cheel and Borman* 1045 (BM, US), *Craigie* L1692 (NSW), *Degelius* A-77 (US), *Du Rietz* 60a, 546h (UPS, US), *Flockton* 725 (US), *Hale* 58450, 58835, 59011, 59257, 59262, 59471 (US), *Kurokawa* 5151, 6542 (TNS, US), *Staer* L1720 (NSW), *Streimann* 9518 (US), *Weber and McVean* L47307, L49615, L49912 (US); Victoria, *Hale* 58254, 28258 (US), *Streimann* 2335 (US); Western Australia, *Weber* L50111 (COLO, US). New Zealand: North Island, *Galloway* s.n. (CHR), *Hale* 59503, 59499 (US), *James* 111 (BM, US), *Tibell* 13203 (UPS); South Island, *Hale* 66234 (US). South Africa: Cape Province, *Hale* 72001, 72002 (US). India: Tamil Nadu, *Hale* 40245, 40250, 43578, 43657, 43813, 43815, 43876 (US). Sabah: *Hale* 29017 (US). Kurokawa (1969) has published additional records from Japan, Taiwan, and Indonesia.

Parmelia fertilis

FIGURES 3*a*, 16*a*

Parmelia fertilis Müller Argoviensis, 1887:316. [Type collection: Siberia, USSR, *comm. Lahm*, no. 7 (G, lectotype).]

Parmelia subdivaricata Asahina, 1951b:356. [Type collection: Mt. Arisan, Nimandaira, Taiwan, *Asahina* F.71 (TNS, lectoptype).]

DESCRIPTION.—Thallus adnate on bark, firm, pale greenish to whitish mineral gray, 6–12 cm broad; lobes sublinear, fairly long and divaricate to contiguous (shorter and more adnate in Canadian specimens), 1.5–5 mm wide; upper surface plane to weakly foveolate, transversely cracked with age, pseudocyphellae effigurate, conspicuous, 0.5–1 mm long, marginal and laminal, sometimes forming a discontinuous white rim, fusing with age to form a coarse reticulate network; lower surface black, densely rhizinate, the rhizines simple to densely squarrosely branched, 0.5–2 mm long. Pycnidia common; conidia cylindrical to weakly bifusiform, straight to slightly bent, 5.5–6.5 µm long. Apothecia common, substipitate, the rim inrolled, 2–7 mm in diameter, the disc dark brown, the amphithecium finely reticulate-pseudocyphellate; hymenium 55–60 µm; spores usually lacking or very poorly developed, 6–8 × 12–14 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin and salazinic acid (Asahina, 1951b, in type of *P. subdivaricata*) along with consalazinic acid.

REMARKS.—Asahina (1951b) described this as a new species, *P. subdivaricata*, unaware that Müller Argoviensis had earlier published *P. fertilis* on the basis of a single rather poor specimen from Siberia. He noted the squarrosely branched rhizines, an important diagnostic character for the species. Asahina found bifusiform conidia, but material that I have examined has mostly cylindrical ones.

Parmelia fertilis is very common in Japan on maples, oaks, and other trees in open forests along with its probable isidiate morphotype *P. squarrosa*. The probable sorediate morphotype

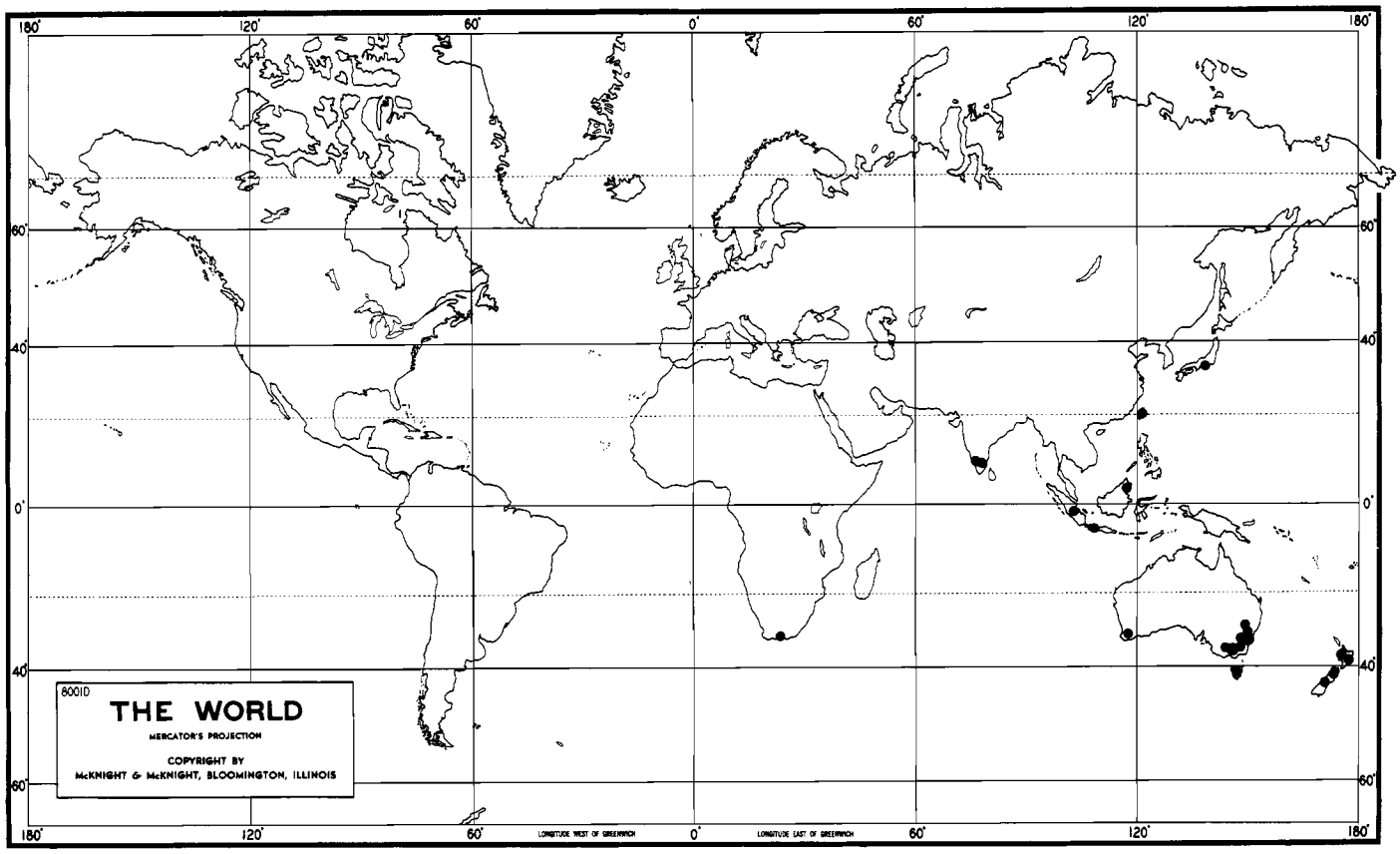

FIGURE 15.—Distribution of *Parmelia erumpens*.

is *P. sulcata*, a very rare species in the range of *P. fertilis*, which differs in having larger microconidia (6–8 μm long).

Sharon Gowan and colleagues recently discovered the species in New Brunswick and Nova Scotia, where it is rare. The specimens are more crowded and adnate than the Japanese material but spore size and rhizine branching are identical.

Specimens Examined

Canada: New Brunswick, *Gowan* 3332-4 (CAN, US). Korea: Chosen, *Asahina* s.n. (TNS), *Fujikawa* (TNS). Japan: Prov. Awa, *Fujikawa* (TNS); Prov. Bingo, *Sato* 60 (TNS); Prov. Bungo, *Kurokawa* 62356 (TNS), 63194 in *Lichenes Critici et Selecti* 27 (US); Prov. Buzen, *Asahina* s.n. (TNS); Prov. Etchu, *Nishijima* 18 (TNS); Prov. Hoki, *Asahina* s.n. (TNS); Prov. Inaba, *Nakanishi* 12076 (KOBE); Prov. Ishikari, *Endo* 216 (TNS); Prov. Iwaki, *Kurokawa* 58083 (TNS), 78009 in *Lichenes Selecti et Critici* 426 (US); Prov. Iyo, *Nakanishi* 90 (KOBE), *Yanagisawa* 1484 (TNS), *Kurokawa* 60050 in *Lichenes Rariores Critici Exsiccati* 85 (as *P. subdivaricata*) (US); Prov. Kii, *Numajiri* s.n. (TNS); Prov. Mutsu, *Asahina* 46 (TNS), *Hale* 29333, 29342 (US), *Kurokawa* 56218 (TNS); Prov. Rikuchu, *Nakanishi* B92 (KOBE); Prov. Sagami, *Kurokawa* 58050 (US); Prov. Shimotsuke, *Hale* 63138 (US), *Ogata* 1815 (TNS); Saghalin, *Asahina* s.n. (TNS); Prov. Yamato, *Tagawa* s.n. (US). Taiwan: Chia-yi County, *Koponen* 17314 (US); Taichung County, *Lai* 6866 (US); Taitung *Kurokawa* 2586 (US). Zhao et al. (1982) reported it from Anhui, Chekiang, and Kiangsi provinces in China (as *P. subdivaricata*).

Parmelia fraudans

FIGURES 3*b*, 16*b*

Parmelia saxatilis (L.) Acharius **fraudans* Nylander, 1861:100. [Type collection: Savolaxia, Finland, *Nylander* (H, Nyl. Herb. no. 34869, lectotype. A syntype (*Malmgren*: Kajana) was not located at H).]
Parmelia fraudans (Nylander) Nylander, 1890:28.

DESCRIPTION.—Thallus adnate on rock, rather brittle, greenish to brownish mineral gray with a yellowish cast, 8–16 cm broad; lobes sublinear, short, contiguous to imbricate, 1–4 mm wide; upper surface shiny or dull and white pruinose, plane to rugose-foveolate, transversely cracked with age, pseudocyphellae effigurate, small, to 0.5 mm long, mostly marginal and soon becoming densely sorediate, the soralia sinuous along lobe margins with a few isolated orbicular laminal soralia, the soredia coarse to almost subisidiose at maturity; lower surface dark brown and shiny at the margin, black at the center, densely rhizinate, the rhizines simple to furcate, 1–1.5 mm long. Pycnidia rather rare and often poorly developed; conidia iciylindrical to weakly bitusiform, straight to slightly bent, 5.5–6.5 μm long. Apothecia rare, adnate, 2–3 mm in diameter; hymenium 45 μm; spores 5–6 × 10–12 μm, the episporium 1 μm thick.

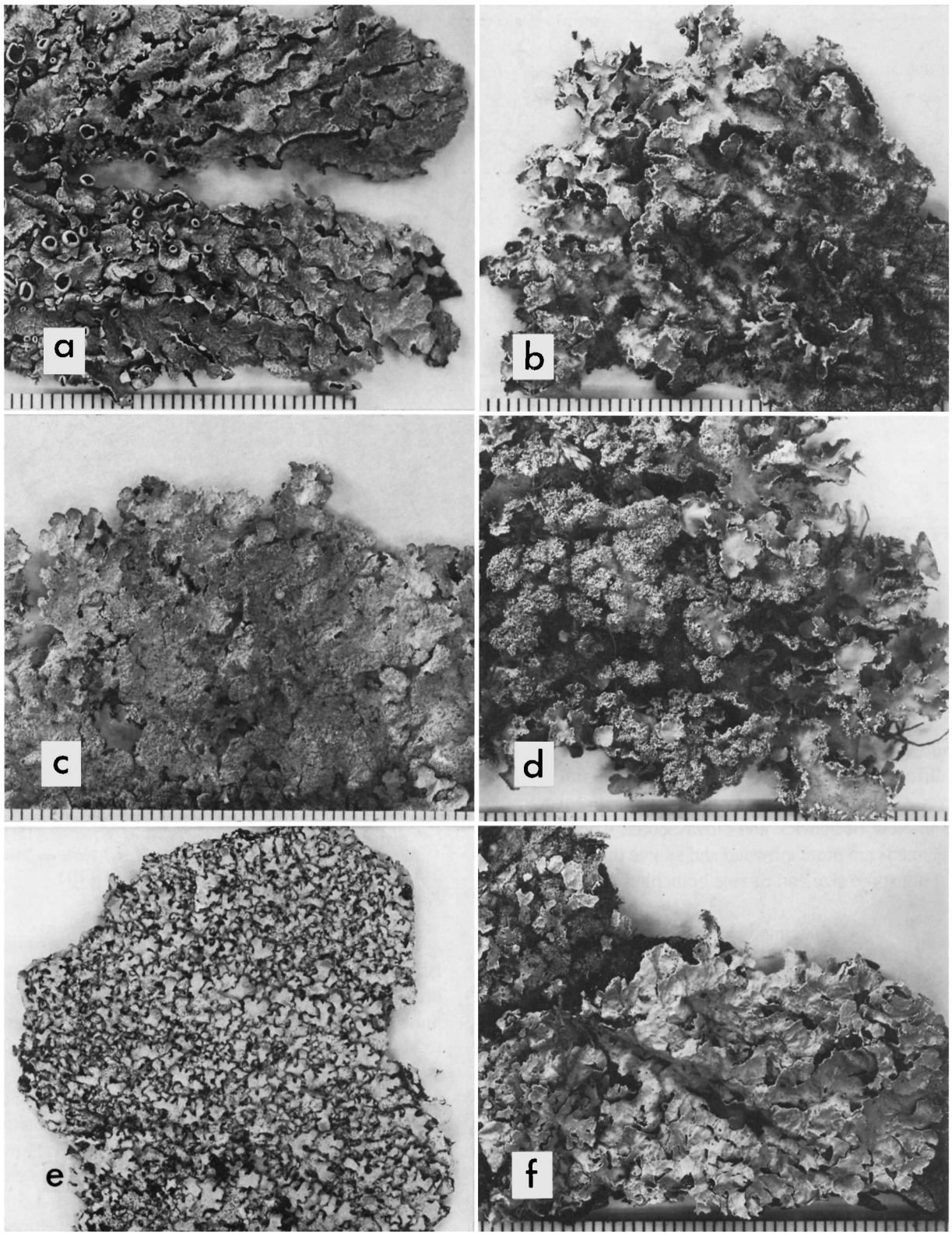

FIGURE 16.—Species of *Parmelia*: *a*, *P. fertilis* (*Hale* 29333); *b*, *P. fraudans* (*Hale* 49870); *c*, *P. hygrophila* (*Noble* 6448); *d*, *P. isidioclada* (*Kurokawa* 58010); *e*, *P. kerguelensis* (lectotype in BM); *f*, *P. kerguelensis* (*Brodo* 11506). (Scales in mm.)

CHEMISTRY.—Atranorin, usnic acid (in the soralia), salazinic acid, and protolichesterinic acid (Dahl, 1952; Krog, 1968).

REMARKS.—*Parmelia fraudans* is a well-known boreal European species that also occurs in North America. The presence of small quantities of usnic acid in the soralia is unique in the genus. The orientation of soralia is similar to that in *P. sulcata,* which often occurs in the same habitat but has densely squarrosely branched rhizines and lacks usnic acid.

In North America *P. fraudans* is collected most often on rocks just above the high water mark in large lakes in the boreal zones but has also been found as far south as Arizona. Thomson (1984:302) has plotted the distribution of this species in arctic America.

Representative Specimens Examined

Canada: Northwest Territories, *Ahti* 14441 (US), *Scotter* 1953, 2588, *Thomson* 11873 (WIS), 14047 (US, WIS); Manitoba, *Scotter* 3007 (WIS). Ontario: *Cain* 26998, *Hale,* 36414, 36510, 36665, 49852 (US). USA: Arizona, *Nash* 22636 (ASU); Michigan, *Hale* 33890, 34998 (US); Minnesota, *Hale* 33325, *Wetmore* 34882 (US); Colorado, *Anderson* 2416, *Shushan* 1139 (COLO, US); Montana, *Standley* 18567 (US). Greenland: *Gelting* in *Lichenes Groenlandici Exsiccati* 121 (US). Norway: *Erickson* 355, *Hasselrot* s.n., *Lynge* 5147 (US). Sweden: *Hasselrot* s.n., *Österlind* s.n., *Santesson* 13415 (US). Finland: *Ahlner* s.n. (US), *Lång* in *Kryptogamae exsiccatae* 1970 (US), *Räsänen* in *Lichenes Fenniae Exsiccati* 45 (US).

Parmelia hygrophila

FIGURES 3*c,* 16*c*

Parmelia hygrophila Goward and Ahti, 1983:9. [Type collections: 17 km E of Nelson, Kokanee Creek Park, BC, Canada, *Goward* 81-1601 (UBC, holotype; US, isotype).]

DESCRIPTION.—Thallus adnate on bark, whitish gray, often becoming densely pruinose, 4–10 cm in diameter; lobes sublinear, 3–5 mm wide; surface plane to weakly ridged, pseudocyphellae effigurate, 0.1–0.3 mm long, forming a network in the marginal area, erupting at maturity with the formation of coarse, granular, subsorediate isidia, the isidia very weakly corticate with pale tips, densely clumped and branched with age, 0.1–0.15 mm in diameter and 0.5–1.5 mm high; lower surface jet black, moderately rhizinate, the rhizines simple to sparsely furcate. Pycnidia not seen. Apothecia rare, substipitate, about 2 mm in diameter; hymenium 50–60 μm; spores 8, simple, 9–12 × 14–16 μm (from original description).

CHEMISTRY.—Atranorin and salazinic acid.

REMARKS.—This species was only recently discovered in the Pacific Northwest. It is close to *P. saxatilis,* differing primarily in the "ecorticate soredioid isidia." Another difference is that *P. hygrophila* is primarly a corticolous lichen in humid, oceanic forests, whereas *P. saxatilis* is saxicolous.

Specimens Examined

Canada: British Columbia, *Noble* 6448 (US). Other records are given in Goward and Ahti (1983).

Parmelia isidioclada

FIGURES 3*d,* 16*d*

Parmelia isidioclada Vainio, 1921:48. [Type collection: Prov. Mimasaka, Japan, *Yasuda* 210 (TUR, lectotype).]

Parmelia yasudae Räsänen, 1940:84. [Type collection: Prov. Iyo, Japan, *Yasuda* 656 (H, lectotype).]

Parmelia psoromoides Räsänen, 1949:79. [Type collection: Mt. Panai, Prov. Benguet, Luzon, Philippines, *Copeland* 1378 (H, lectotype).]

DESCRIPTION.—Thallus loosely adnate on bark or rock, rather firm, greenish mineral gray (turning brownish in the herbarium), 8–12 cm broad; lobes sublinear, elongate, contiguous, 2–4 mm wide, the margins rolled upward, punctate-pseudocyphellate along the edges, the pseudocyphellae soon becoming granular and giving rise to dense, branched, cylindrical to somewhat lobulate, eventually coralloid-isidioid growths along the length of the lobes, to 1 mm high, apically crumbling and subsorediate with age; upper surface plane, shiny, continuous; lower surface brown to whitish in a narrow marginal zone, black at the center, densely rhizinate, the rhizines simple to furcate, 1–1.5 mm long. Pycnidia not seen. Apothecia rare, substipitate, less than 5 mm wide; hymenium about 60 μm high; spores 13–16 × 23–30 μm (from description of *P. psoromoides*).

CHEMISTRY.—Atranorin and salazinic acid (Asahina, 1951a; Krog, 1968) and consalazinic acid.

REMARKS.—This rare, montane-tropical, temperate species appears to be relatooed too *P. laevior* because of the lateral punctate pseudocyphellae. It is unusual, however, in having very large spores, as well as marginal granular isidia.

Specimens Examined

Japan: Prov. Idzu, *Kurokawa* 58010 (TNS, US); Prov. Ohmi, *Hale* 29467a (US). China: Kiangsi, *Hämet-Ahti* 3322 (H). Krog (1968) tentatively identified a specimen from Alaska.

Parmelia kerguelensis

FIGURES 3*e,* 16*e, f*

Parmelia kerguelensis Wilson, 1900:87. [Type collection: Royal Sound, Kerguelen Island, *Robert Hall* s.n. (MEL, lectotype).]

Parmelia pseudosulcata Gyelnik, 1934:282. [Type collection: Mary's Peak, Oregon, *Sipe* 684 (BP, holotype; MICH, isotype).]

DESCRIPTION.—Thallus adnate to loosely adnate on bark or rock, fairly firm, greenish to light brownish mineral gray, 6–10 cm broad; lobes sublinear, contiguous, sometimes short and more crowded, 1–2.5 mm wide, brownish towards the tips, at times white pruinose; upper surface dull, plane to weakly foveolate, continuous but becoming fissured with age, pseudocyphellae irregularly effigurate, 0.2–0.5 mm long, sparse and inconspicuous to fairly well developed, marginal and laminal, isidiate, the isidia developing mostly on the surface, scattered initially but at maturity clumped along faint ridges, cylindrical, little branched, 0.04–0.06 × 0.1–0.3 mm; lower surface black, moderately rhizinate, the rhizines simple

to furcate, rarely weakly squarrosely branched, 0.5–1.5 mm long. Pycnidia not seen. Apothecia rare, substipitate, 10–15 mm in diameter, flat with a radially split disc at maturity; hymenium 65–70 µm; spores 9–12 × 14–18 µm, the episporium 1–2 µm wide.

CHEMISTRY.—Atranorin, protocetraric acid, and lobaric acid.

REMARKS.—*Parmelia kerguelensis* has the same northern hemisphere–southern hemisphere distribution pattern as *P. saxatilis* and *P. sulcata* but is much less common. It is the only *Parmelia* species in South Africa. In the northern hemisphere it is known only from the moist coastal forests of the Pacific Northwest, where it was first recognized as *P. pseudosulcata* by Gyelnik. Although the specific epithet implies a close relationship with sorediate *P. sulcata,* this species is actually very close to *P. saxatilis,* as both have mostly simple rhizines and isidia. Without careful examination, in fact, *P. kerguelensis* would be identified as *P. saxatilis*. Aside from the clear chemical distinction (K– in the medulla), it lacks the conspicuous reticulate network of pseudocyphellae on the lobe surfaces and has a tendency for squarrose rhizines. In Canada at least *P. kerguelensis* is found on tree bark, *P. saxatilis* on rocks, a basic habitat difference. In South Africa, however, where trees are rare, it is found on sheltered sandstone outcrops as well as on trees in forested areas.

Specimens Examined

Canada: British Columbia, *Ohlsson* 1638, 2410, 2446 (CAN), *Brodo* 11506 (CAN). USA: California, *Hale* 57877 (US). Republic of South Africa: Cape Province, *Almborn* 5090, *Hale* 72142 (US), *Maas Geesteranus* 6820 (LD, US). New Zealand: South Island, *Hale* 66266 (US); Campbell Island, *Harris* 4358, 4488, 5644, 5670 (US).

Parmelia laevior

FIGURES 3*f*, 17*a*

Parmelia laevior Nylander, 1890:28. [Type collection: Ichigome, Japan, *Almquist* s.n. (H, Nyl. herb. no. 34857, lectotype; S, isolectotype).]

Parmelia laevior f. *denigrata* Hue, 1899:166. [Type collection: Onikobe, Japan, *Faurie* 305 (PC, lectotype).]

Parmelia petrophila Vainio, 1921:48. [Type collection: Prov. Kii, Japan, *Yasuda* 193 (TUR, Vain. herb. no. 2933, lectotype).]

Parmelia hakonensis Zahlbruckner, 1927b:348. [Type collection: Hakone, Prov. Sagami, Japan, *Yamashita* 13 (TNS, isolectotype).]

Parmelia laevior f. *hakonensis* (Zahlbruckner) Asahina, 1952:112.

Parmelia ontakensis Asahina, 1954:323. [Type collection: Mt. Ontake, Hidaguchi 6-gome, Prov. Hida, Japan, *Asahina* 54819 (TNS, lectotype; US, isolectotype).]

DESCRIPTION.—Thallus loosely adnate on bark, firm, pale greenish to brownish mineral gray, 6–15 cm broad; lobes sublinear, contiguous, 1.5–4 mm wide, somewhat lobulate; upper surface shiny, plane to weakly rugose, sparsely transversely cracked with age, pseudocyphellae on lateral edges of the lobes, round to elongate, about 0.2 mm long; lower surface black moderately rhizinate, the rhizines simple to furcate to sparsely squarrosely branched at maturity, 1–2 mm long. Pycnidia common; conidia cylindrical, straight to slightly bent, 6–8 µm long. Apothecia common stipitate and urceolate, flaring at maturity with an open, radially split disc, 5–10 mm in diameter, the rim and amphithecium warty pseudocyphellate; hymenium 60–65 µm; spores 8–9 × 14–16 µm, the episporium distinct, about 1 µm thick.

CHEMISTRY.—Atranorin, salazinic acid (Asahina, 1951a), and consalazinic acid.

REMARKS.—*Parmelia laevior* is a representative of a small isolated group of *Parmeliae* with lateral, punctate pseudocyphellae. This group includes *P. pseudolaevior,* a very close lobulate morphotype, and *P. isidioclada,* a large-spored temperate-tropical species. It is rather common in Japan on conifers and hardwoods; there are few collections elsewhere.

Specimens Examined

Japan: Prov. Aki, *Hale* 29551 (US); Prov. Bungo, *Kurokawa* 63192 (TNS); Prov. Buzen, *Kurokawa* 62479 (TNS); Prov. Hida, *Kurokawa* 64072 (TNS); Prov. Higo, *Kurokawa* 63121 (TNS); Prov. Hitachi, *Asahina* 12b (TNS); Prov. Hizen, *Kurokawa* 52599 (TNS); Prov. Hoki, *Yasuda* s.n. (TNS); Prov. Hyuga, *Hale* 29640, 29688 (US); Prov. Inaba, *Yasuda* s.n. (TNS); Prov. Ishikari, *Asahina* s.n. (TNS); Prov. Iyo, *Kurokawa* 550149 (US); Prov. Kii, *Numajiri,* s.n. (TNS); Prov. Oita, *Omura* 707 (US); Prov. Osumi, *Kurokawa* 63055 (TNS); Prov. Musashi, *Shibuichi* 4546 (US); Prov. Shimotsuke, *Culberson* 10641 (US), *Hale* 63134 (US), *Ogata* 80c (TNS); Prov. Shinano, *Asahina* 547, 2627 (TNS), *Kurokawa* 58200, 58255 (US); Prov. Suruga, *Culberson* 10691, 11104, *Iishiba* 64, 69, 72 (US). Taiwan: Nantou, *Lai* 2355 (US). USSR: Primorsk, *Vasileve* 10 (US). Zhao et al. (1982) report it from Chekiang Province in China.

Parmelia marmariza

FIGURES 4*a*, 17*b*

Parmelia marmariza Nylander, 1890:28. [Type collection: Ichigome, Japan, *Almquist,* s.n. (H, Nyl. herb. no. 34879, lectotype).]

Parmelia marmariza f. *angustifolia* Asahina, 1951b:353. [Type collection: Shimoda, Prov. Idzu, Japan, *Asahina* s.n. (TNS, lectotype).]

Parmelia submarmariza Asahina, 1953:65. [Type collection: Mt. Kenzan, Prov. Awa, Shikoku, Japan, *Fujikawa,* s.n. (TNS, lectotype).]

DESCRIPTION.—Thallus adnate on bark, quite firm, whitish to greenish mineral gray, 8–12 cm broad; lobes subirregular to sublinear, rather short, contiguous, 2–8 mm wide; upper surface shiny, plane to weakly foveolate, continuous, black-rimmed, coarsely lobulate with age, pseudocyphellae effigurate, raised, small, 0.2–0.5 mm long, numerous and conspicuous, marginal and laminal, in part fusing into a weak reticulate network; lower surface black, densely rhizinate, the rhizines simple to furcate, 1–2 mm long. Pycnidia common; conidia (Figure 12*f*) cylindrical, straight to slightly bent, 6–8 µm long. Apothecia common, substipitate, the rim remaining inrolled but the disc splitting with age, 5–12 mm in diameter, the amphithecium coarsely rugose with pseudocyphellae on the ridges; hymenium 55–60 µm; spores 8–9 × 12–14 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin, chloroatranorin, and salazinic acid (Asahina, 1951b), and consalazinic acid.

REMARKS.—The most important feature of this Asian species

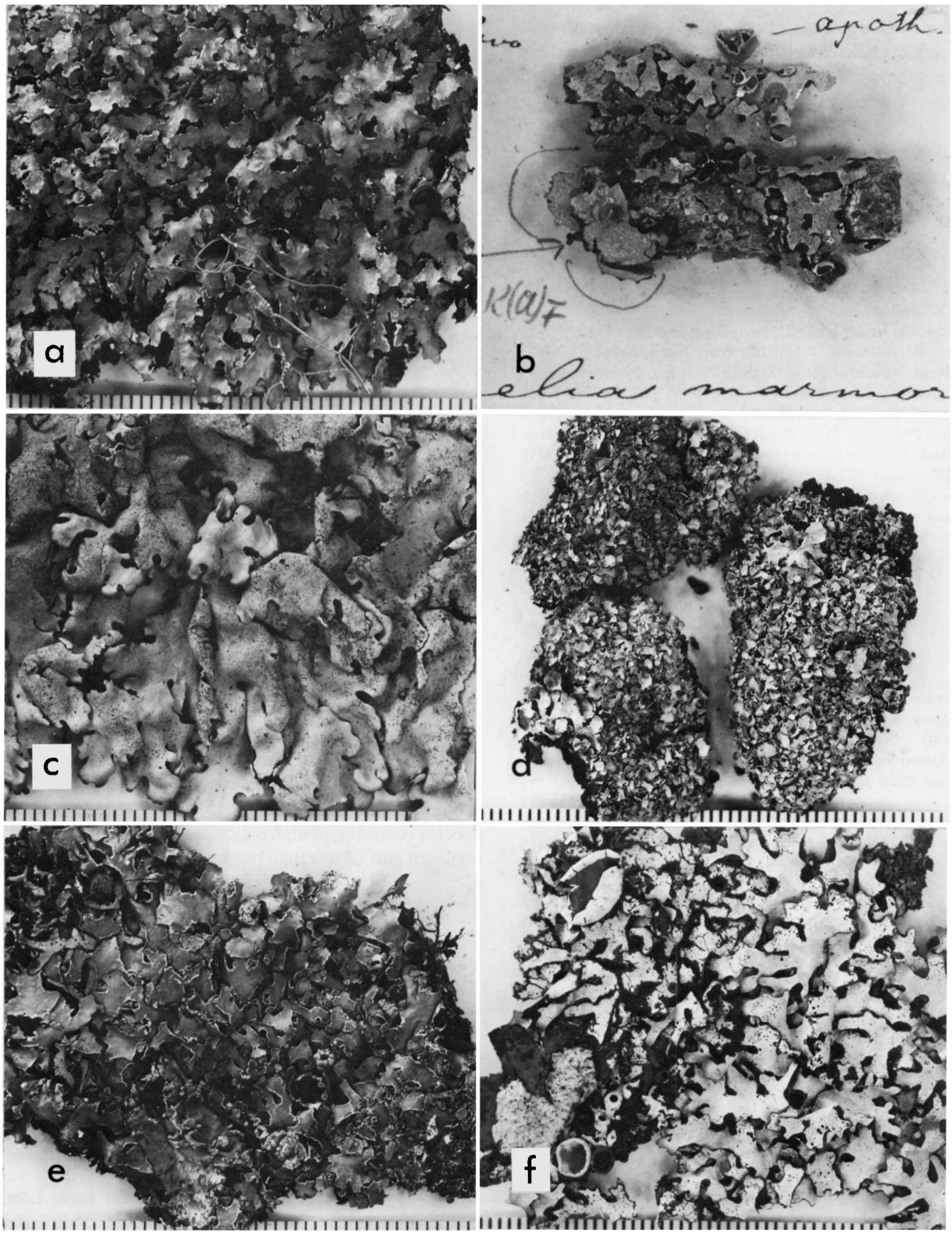

FIGURE 17.—Species of *Parmelia*: *a*, *P. laevior* (*Hale* 29357); *b*, *P. marmariza* (lectotype in H); *c*, *P. meiophora* (*Poelt* L-151); *d*, *P. neodiscordans* (holotype in US); *e*, *P. niitakana* (*Hsu* 1374); *f*, *P. norcrambidiocarpa* (holotype in US). (Scales in mm.)

is the distinct and numerous but comparatively small and crowded pseudocyphellae. This is in contrast to the larger, less numerous pseudocyphellae of *P. adaugescens*, another common Asian species, with mostly simple rhizines but much larger spores.

Asahina described *P. submarmariza* to accommodate some specimens with smaller spores (8–11 µm long)—in my opinion not significantly smaller—and a less strongly rugose amphithecium.

Specimens Examined

Japan: Prov. Awa, *Fujikawa* s.n. (TNS); Prov. Higo, *Kurokawa* 63120 (TNS); Hiroshima Pref., *M. Nakanishi* 2811 (US); Prov. Hizen, *Kurokawa* 62597 (TNS); Prov. Inaba, *Nakanishi* 12157 (KOBE); Prov. Iyo, *Ogata*, s.n. (TNS), *Nakanishi* 72 (KOBE), *Yoshimura* 1675 (US); Prov. Izu, *Asahina* 30825 (TNS), *Kurokawa* 57038 (US); Prov. Kii, *Kurokawa* 71099 in *Lichenes Critici Selecti Exsiccati* 234 (US); Prov. Kozuke, *Kurokawa* 55480 (US); Prov. Ohsumi, *Kurokawa* 63056 in *Lichenes Critici Selecti Exsiccati* 29 (TNS, US); Prov. Sagami, *Kurokawa* 58062 (US); Prov. SuPruga, *Asaahaaina* 538 (US); Yakushoima, *Fujikawa*, s.n. (TNS); Prov. Yamato, *Nakanishi* 50 (KOBE). Taiwan: *Asahina*, s.n. (US). India: *Awasthi* 644 (AWAS), *Watt* 5391 (BM). Nepal: Lingalelah, *Watt* 7087 (BM). Zhao et al. (1982) report it from Anhui and Shensi provinces in China.

Parmelia meiophora

FIGURES 4*b*, 17*c*

Parmelia meiophora Nylander, 1889:45. [Type collection: Song-pin, Yunnan, China, *Delavay* s.n. (H, Nyl. Herb. no. 35201, lectotype; US, W, isolecto-types.]

Parmelia meiophora var. *isidiata* Chao [Zhao], 1964:156. [Type collection: Yunnan, China, *Chao* 1002 (not seen).]

DESCRIPTION.—Thallus loosely adnate on bark, firm, greenish mineral gray (turning brownish in the herbarium), 8–15 cm broad; lobes subirregular, contiguous to imbricate, 3–5 mm wide; upper surface shiny, plane, continuous to finely cracked with age, pseudocyphellae numerous and small, 0.2–0.3 mm long, separate, isidiate, the isidia bullate, short, about 0.1 mm thick and 0.1–0.2 mm high, unbranched, the tips often darkening; lower surface black, densely rhizinate, the rhizines richly squarrosely branched, 1–2 mm long. Pycnidia not found. Apothecia rare, adnate, 3–5 mm in diameter; hymenium 55–60 µm; spores 5–6 × 7–8 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin and salazinic acid (Misra et al., 1976) and consalazinic acid.

REMARKS.—*Parmelia meiophora* is unquestionably the isidiate morphotype of *P. submutata*. Together they make up an anomalous element in the genus, because of the numerous small pseudocyphellae, too small to be seen with the naked eye. In his original description Nylander did not mention the presence of pseudocyphellae at all.

Very little is known of the habitat and ecology of the species, except to note that it occurs at high elevation (3000–4000 m) in conifer-*Rhododendron* cloud forests.

Specimens Examined

China: Prov. Setschwan, *Handel-Mazzetti* 2856 (US, W). Nepal: Gola, *Togashi* s.n. (US); Khumbu, *Poelt* 151 (M, US). Zhao et al. (1982) report specimens from Yunnan.

Parmelia neodiscordans Hale, new species

FIGURES 4*c*, 17*d*

DESCRIPTION.—Thallus *P. discordantis* similis sed colore albicanti et substantiis chimicis aliis differt.

Thallus adnate to loosely attached on rock, whitish gray but sometimes brownish with age, 5–8 cm broad; lobes sublinear, crowded and imbricate, 1–2 mm wide; surface plane, marginally and in part laminally lobulate, the lobules 1–2 mm wide and 0.5–3.0 mm long, suberect; pseudocyphellae inconspicuous along the lobe margins as a whitish raised rim; lower surface jet black, sparsely to moderately rhizinate, the rhizines coarse, simple, up to 1 mm long. Pycnidia rather rare, about 90 µm in diameter; conidia cylindrical, straight to slightly bent, 6–7 µm long. Apothecia not seen.

CHEMISTRY.—Atranorin and fumarprotocetraric acid, with accessory unidentified fatty acids.

HOLOTYPE.—Deer Mountain, Acadia National Park, Washington Co., Maine, USA, *M.E. Hale* 37496 (US).

REMARKS.—The few specimens of this unusual species were first identified as *P. discordans* on the basis of a mistaken chemical test for protocetraric acid. Dr. Richard Harris brought to my attention the correct chemistry. Although similar to *P. discordans*, it has a whitish cast and never turns so dark brown. It differs from *P. omphalodes*, which is also whitish in the Appalachian region, in the smaller size and dense, uniform lobules. *Parmelia neodiscordans* is a strictly Appalachian species occurring at high elevations (more than 1500 m) in the southern part of its range but near sea level in New England.

Specimens Examined

USA: New York, *Anderson* s.n. (NY), *Brodo* 2901 (US), *Harris* 16579 (US); West Virginia: *Hale* 10112, 14957 (US).

Parmelia niitakana

FIGURES 4*d*, 17*e*

Parmelia niitakana Asahina, 1951a:332. [Type collection: Sokei, Mt. Niitaka, Taiwan, *Kumada* 23712 (TNS, lectotype).]

Parmelia shinanoana f. *calvescens* Zahlbruckner, 1934:56. [Type collection: Mt. Morrison, Taiwan, *Sasaki* s.n. (W, lectotype; TNS, isolectotype).]

DESCRIPTION.—Thallus loosely adnate on bark, firm, pale greenish mineral gray, 6–10 cm broad; lobes sublinear, contiguous, 1.5–3 mm wide; upper surface shiny, plane, continuous, pseudocyphellae effigurate, marginal, forming a continous white rim 0.1–0.2 mm wide around the lobes; lower surface black, densely rhizinate, the rhizines simple to furcate, 1–2 mm long. Pycnidia common; microconidia cylindrical to a few vaguely bifusiform, 5.5–6.5 µm long. Apothecia

common, substipitate, urceolate, 2–4 mm in diameter, the amphithecium rugose-sublobulate with pseudocyphellae on the ridges; hymenium 65–70 μm; spores 13–15 × 27–30 μm, the episporium distinct, 3 μm thick.

CHEMISTRY.—Atranorin and salazinic acid (Asahina, 1951a) and consalazinic acid.

REMARKS.—This Taiwan endemic has lobes with a conspicuous white marginal rim formed by the continuous linear pseudocyphellae. It is also characterized by the large spores and the curiously sublobulate ridging on the amphithecium so well depicted by Asahina. It is most closely related to the Philippine species *P. sectilis* because of the very large spores. It occurs at high elevations in Taiwan, probably on most major mountains above 3000 m high.

Specimens Examined

Taiwan: Hattsukan, *Suzuki* s.n. (TNS), Chiayi County, *Hsu* 1374 (US), Mt. Nan-Fu-Ta-San, *Kurokawa* 1211 (US).

Parmelia norcrambidiocarpa Hale, new species

FIGURES 4*e*, 17*f*, 18

DESCRIPTION.—Thallus ut in *P. crambidiocarpa* sed sporis parvis (6–8 × 11–13 um) differt.

Thallus adnate to loosely attached on bark, fairly firm, whitish gray, 6–12 cm broad; lobes subirregular to sublinear, little branched, becoming divaricate, browning at the tips, 1–4 mm wide; upper surface shiny, continuous to transversely cracked with age, plane, pseudocyphellae forming a very narrow, nearly continuous marginal rim, 0.1–0.2 mm wide, also laminal and effigurate, 0.2–0.6 mm long, separate, fissuring with age; lower surface densely rhizinate, the rhizines simple to strongly squarrosely branched, 0.5–2 mm long, usually projecting as a mat around the lobe margins. Pycnidia common, 90–110 μm in diameter; conidia cylindrical, rod-shaped, 5.5–6.0 μm long. Apothecia common, substipitate and cupuliform, splitting radially with age, to 20 mm in diameter, the disc brown to dark brown, the amphithecium rugose, effigurate-pseudocyphellate; hymenium 60–70 μm high; spores 7–10 × 10–15 μm, the episporium 1 μm thick.

CHEMISTRY.—Atranorin, chloroatranorin, and echinocarpic acid (and associated unknowns).

HOLOTYPE.—St. James Walkway, Tarn Nature Trail, Lewis Pass road, South Island, New Zealand, elev. 850 m, *M.E. Hale* 65352 (US; isotypes in ANUC, BM, CHR, UPS).

REMARKS.—This new species is a member of the *P. testacea* complex. It is closely related to *P. crambidiocarpa* and *P. salcrambidiocarpa*, the thallus of these three species being essentially identical with sublinear lobes, marginal and laminal pseudocyphellae splitting open with age, and a dense mat of rhizines below. However, there are significant differences in chemistry, distribution, and, in part, spores.

The apothecia of *P. norcrambidiocarpa* are typical for the group except that the disc is even darker than in *P. crambidiocarpa*. Of 34 specimens examined, none had a pale tan disc, 56% were light to medium brown, and 44% were dark brown. Spore differences are more significant: average maximum length is 13.4 μm (25 measurements) with a range of 12–15 μm, and average width 8.8 μm (range 7–10 μm). There is no overlap with the larger spores of *P. crambidiocarpa* and in fact a highly statistically significant value of P = .005 was calculated for spore length differences between the two species. *Parmelia salcrambidiocarpa* has identical small spores.

Chemistry is extremely uniform: atranorin and echinocarpic acid and associated unknowns. Some specimens of *P. crambidiocarpa* on North Island also contain only echinocarpic acid (and were identified by spore size); the only two from South Island with echinocarpic acid also contained protocetraric acid. *Parmelia salcrambidiocarpa* contains only salazinic acid.

Parmelia norcrambidiocarpa is by far the most common foliose lichen in the subalpine scrub zone on the major mountain chains running the length of the South Island (Figure 18). I collected 161 specimens at 32 localities, the bulk (85%) between 300 m and 910 m elevation. It comprised 23% of the 715 specimens I collected at random in New Zealand and 30% of the 88 collections in CHR. It has yet to be collected on North Island or in Tasmania.

Representative Specimens Examined

New Zealand: South Island, *Allan* CHR160255 (CHR), *Child* 1556 (CHR), *Elix* 8675 (ANUC), *Hale* 65118, 65325, 65391, 65472, 65659, 65670, 65719, 65789, 65841 (US).

Parmelia novae-zelandiae Hale, new species

FIGURES 4*f*, 19*a*

DESCRIPTION.—Thallus ut in *P. tenuirima* sed isidiis munitis differt.

Thallus loosely adnate on bark, rather fragile, pale greenish straw colored, 6–15 cm broad; lobes broad and rotund, 4–10 mm wide; upper surface plane, the pseudocyphellae mostly laminal, uniformly dispersed, angular, 0.3–1.0 mm long, simple or branched, splitting open with the formation of coarse isidia, the isidia somewhat inflated, branching with age; lower surface black and shiny, the rhizines coarse, sparsely developed, 1–2 mm long. Pycnidia and apothecia not seen.

CHEMISTRY.—Atranorin and salazinic acid.

HOLOTYPE.—5 Mile stream trail, Rimutaka State Forest, E of Lower Hutt, North Island, New Zealand, *M.E. Hale* 58809 (US).

REMARKS.—This New Zealand endemic was identified as *P. pseudotenuirima* by Galloway and Elix (1983), although they subsequently recognized the variation in the New Zealand collections (Galloway and Elix, 1984). It is amply distinct because of the much larger thallus, large separate pseudocyphellae (as in *P. tenuirima*), and coarse, irregularly inflated

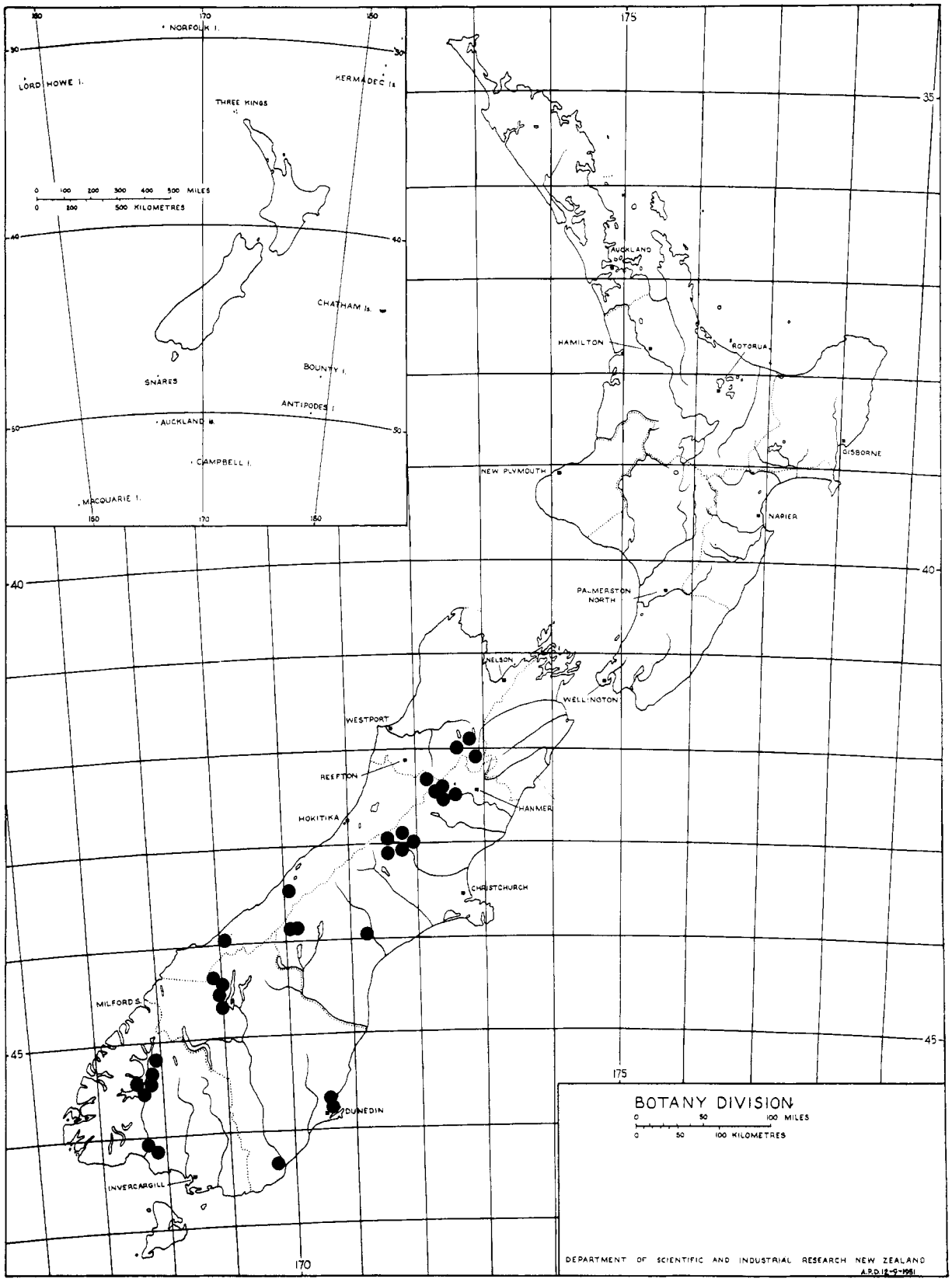

FIGURE 18.—Distribution of *Parmelia norcrambidiocarpa* in New Zealand.

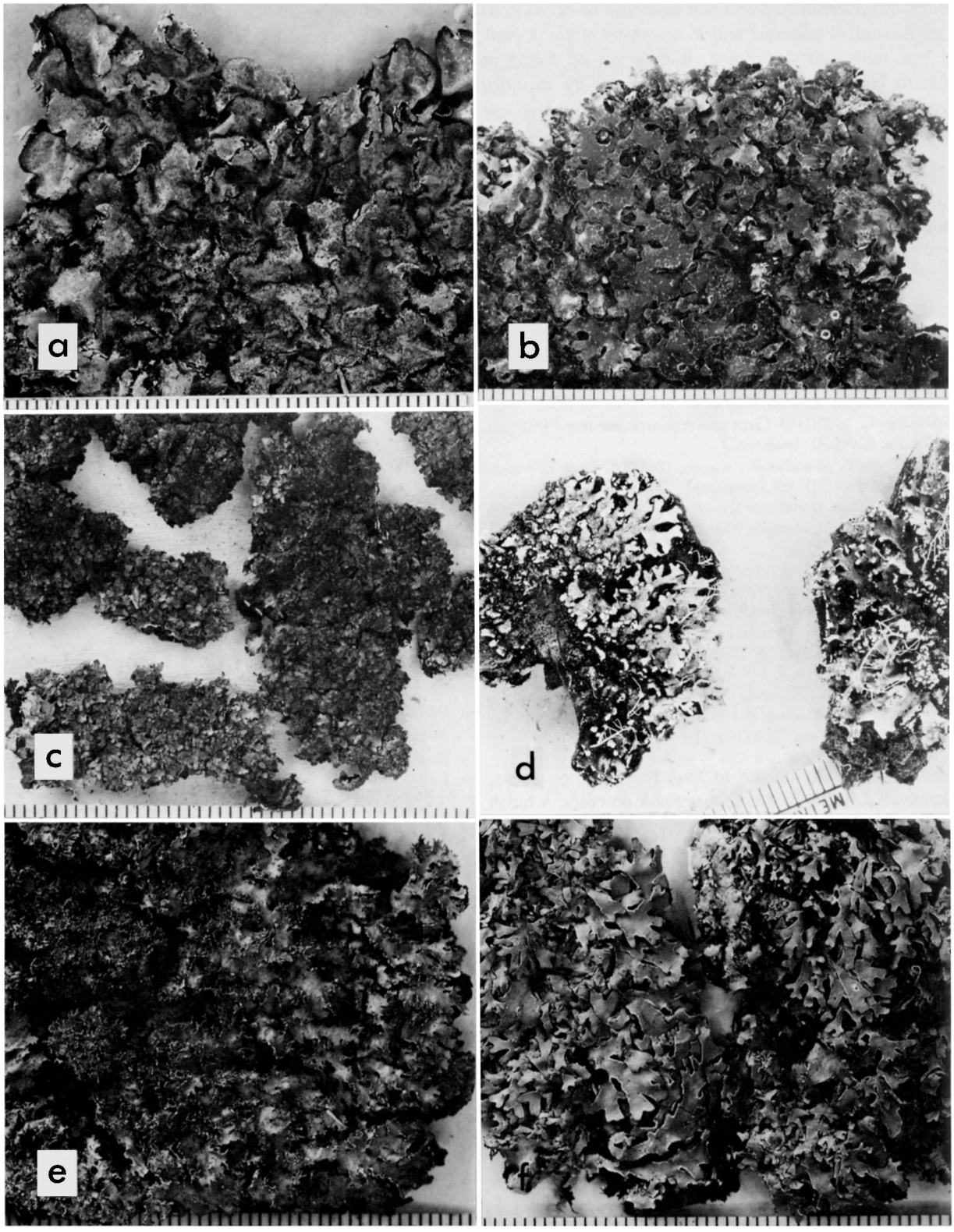

FIGURE 19.—Species of *Parmelia*: *a*, *P. novae-zelandiae* (holotype in US); *b*, *P. omphalodes* (*Santesson* 23706); *c*, *P. omphalodes* (*pinnatifida* form) (*Vězda* in *Lichenes Selecti Exsiccati* 1735); *d*, *P. protosulcata* (holotype in US); *e*, *P. pseudolaevior* (*Kurokawa* 59205); *f*, *P. pseudoshinanoana* (*Nakanishi* 5172). (Scales in mm.)

isidia. *Parmelia pseudotenuirima* can therefore be considered as a strict Australian endemic and *P. novae-zelandiae* a New Zealand one, although, of course, it may yet be found in Tasmania. In New Zealand it occurs rather rarely in moist *Nothofagus* forests or even on large trees in pastures at low elevation.

Specimens Examined

New Zealand: North Island, *Hale* 58809 (US); South Island, *Hale* 65443, 66232 (US). Three additional records are listed under *P. tenuirima* in Galloway and Elix (1983), of which I have checked *Bartlett* s.n. from Pandora.

Parmelia omphalodes

FIGURES 5*a*, 19*b,c*

Parmelia omphalodes (L.) Acharius, 1803:204.

Lichen omphalodes L., 1753:1143. [Type collection: specimens and Dillenius, 1742, pl. 24: fig. 80A (OXF, lectotype).]

Parmelia omphalodes β. *panniformis* Acharius, 1803:204. [Type collection: Helvetia, *Schleicher* 257 (H-Ach, lectotype).]

Parmelia omphalodes var. *panniformis* f. *subconcentrica* Crombie, 1872:306. [Type collection: Braemar, Marrone, Aberdeen, Great Britain, *Crombie* s.n. (BM, lectotype).]

Parmelia sulcata var. *laevis* f. *hirsuta* Crombie, 1875:140. [Type collection: Ben Lawers, Perth, Great Britain, *Crombie* s.n. (BM, lectotype).]

Parmelia omphalodes var. *herminica* Tavares, 1945:120. [Type collection: Serra da Estrela, *Tavares* s.n. (LISU) (not seen).]

Parmelia pimnnatifida Kurokawa, 1976:378. [Based on *Parmelia omphalodes* β. *panniformis* Acharius.]

Parmelia omphalodes subsp. *pinnatifida* (Kurokawa) Skult, 1984:138.

[Additional varieties and forms, which I consider to be synonyms, will be found in Hillmann (1936) and Skult (1984).]

DESCRIPTION.—Thallus adnate to loosely adnate on rocks, firm to somewhat brittle, extremely variable in color, whitish mineral gray to dark chestnut brown or even black, 6–20 cm broad; lobes sublinear, short, becoming crowded and imbricate, often becoming laciniate with dense marginal secondary lobes, 1–4 mm wide; upper surface shiny, plane to weakly foveolate, continuous or becoming cracked along older pseudocyphellae, pseudocyphellae effigurate, variable, to 0.5 mm long, mostly marginal as a nearly continuous rim (especially in *"P. pinnatifida"*), becoming more numerous on the lobe surface with age and forming a distinct network; lower surface black and shiny, moderately rhizinate, the rhizines simple to furcate, 1–1.5 mm long. Pycnidia common; conidia cylindrical, straight or a few bent or very weakly bifusiform, 5.5–6.5 μm long (Figure 12*g*) (Hillmann (1936) reports 1 × 5–6 μm). Apothecia not common, substipitate and urceolate but at maturity open the disc splitting somewhat, 3–12 mm in diameter, the amphithecium rugose; hymenium 60–80 μm; spores often poorly developed, 7–9 × 10–15 μm, the episporium 1–2 μm thick.

CHEMISTRY.—Atranorin, lobaric acid (lacking in *"P. pinnatifida"*), salazinic acid (Culberson, 1970; Krog, 1968; Kurokawa, 1976; Thomson, 1979), consalazinic acid, protolichesterinic acid (Skult, 1984), rarely also with traces of accessory galbinic acid (Culberson in Vězda, 1980), fumarprotocetraric acid, or protocetraric acid (Skult, 1984) and several unidentified fatty acids (Dey, 1978; Kurokawa, 1976; Skult, 1984).

REMARKS.—The Swedish specimen (Flora Suecica 947) cited by Linnaeus is not in the Linnean Herbarium. I have selected the Dillenian sheet at OXF as the lectotype (see Crombie, 1880).

As might be expected for a widespread boreal-arctic lichen, *P. omphalodes* exhibits a great range of variation in thallus color (from whitish mineral gray to blackish brown), development of pseudocyphellae (from sparse and marginal to well developed as a laminal network) and secondary lobation (some specimens without secondary lobes, others heavily lobulate), in large part variations that are modified by the harsh, exposed habitats it frequently occupies. Poelt (1974) does not recognize any of the numerous varieties and forms based on habitat modifications described from Europe.

Skult (1984) has made an especially thorough study of the species in Finland, recognizing three taxa: *P. omphalodes* subsp. *discordans*, *P. omphalodes* subsp. *omphalodes*, and *P. omphalodes* subsp. *pinnatifida*. Subspecies *discordans* was separated by the presence of protocetraric acid and subsp. *pinnatifida* by the absence of lobaric acid in salazinic acid-containing specimens. All specimens with lobaric and salazinic acids were called subsp. *omphalodes*. Relatively few intermediates were found in Fennoscandia.

Parmelia pinnatifida, long recognized by European lichenologists as *P. omphalodes* var. *panniformis*, is also differentiated from typical *P. omphalodes* by a number of subtle, intergrading morphological characters. Kurokawa (1976) emphasized the predominance of marginal pseudocyphellae. It also has somewhat narrower lobes (Skult, 1984), which are repeatedly branched, and a congested, nearly pulvinate thallus.

The populations of *P. omphalodes* in North America, however, although almost always lacking lobaric acid (96% of 84 specimens tested), are not like the European ones. Their morphology is much closer to typical European *P. omphalodes*, and after studying a small sample Skult (1984) considered them to be intermediate between his subsp. *omphalodes* and subsp. *pinnatifida*. I am inclined not to make any taxonomic divisions in the group at this time.

An unnamed chemotype first recognized by Skult is distinguished by several subtle morphological characters and by the presence of norstictic acid in equal concentration with salazinic acid. I am calling this a new species, *P. skultii* (see below).

In the United States *Parmelia omphalodes* is locally common on rocks at the highest elevations in the Appalachian Mountains (Dey, 1978; Hale 1959) but is very rare in the western states. Imshaug (1957:249) found it only on Mt. Rainier in Washington in his intensive study of alpine lichens, and I have collected it only in Montana. It is, however, a very common tundra lichen in the arctic-boreal regions of Canada, Alaska (Krog, 1968), and Europe (see map in Thomson, 1984:308).

Representative Specimens Examined
(salazinic acid with or without lobaric acid).

Canada: Northwest Territories, *Ahti* 14496, *Hale* 236, *Thomson and Larsen* 5859, 11066 (US); Quebec, *Gallo* 3055, *Morton* 11922 (US); Ontario, *Brodo* 5974, *Cain* 26407, *Garton* 5451, *Hale* 36547, *Wetmore* 28431 (US); British Columbia, *Macoun* 243 (US). USA: Maine, *Parlin* 11699 (US); New York, *Hale* 23570, *Shushan* 3479 (US); West Virginia, *Hale* 14293 (US); Virginia, *Egan* 3947, *Hale* 18851, *Luttrell* 3318 (US); North Carolina, *Esslinger* 3489 in *Lichenes Selecti Exsiccati* 1093 (US), *Hale* 18047 (US); Tennessee, *Hale* 37594; Michigan, *Imshaug* 4249 (MSC), *Thomson* 17191 (US); Montana, *Hale* 49973 (US), *Imshaug* 8249 (MSC); Alaska, *Croasdale* 89b, *Llano* 396g, 511b, *Nash* 13119, *Palmer* 1342, *Shushan and Maher* 10, *Thomson* 5463, *Thomson and Ahti* 18428, *Weber and Viereck* 7060 (US). Greenland: *Andersen and Hansen* in *Lichenes Groenlandici* 291 (US). Iceland: *Kristinsson* 9114, 16489 (US). Great Britain: Caernarvon, *Holl* s.n. (BM); Cornwall, *Culberson and Culberson* 11738 (US); Devon, *Davis* s.n. (BM); Devonshire, *Hebden* 1942 (US); Kincardine, *Crombie* s.n. (BM); Scotland, *Vickery* s.n. (US). Norway: *Norman* 5156 (US). Sweden: *Kjellmert* s.n., *Santesson* 23706 (US), *Vrang* in *Cryptogamae Exsiccatae* 4846 (US). Finland: *Hakulinen* s.n., *Räsänen* in *Lichenes Fenniae Exsiccati* 706 (US). Denmark: *Christiansen* 1121 (US). Austria: Tirol, *Steiner* in *Cryptogamae Exsiccatae* 4731, *Herre* 32 (US). Switzerland: *Schleicher* 86 (US). Czechoslovakia: Moravia occ., *Černohorský* 1245 (PRC), *Vězda* in *Lichenes Selecti Exsiccati* 23 (US); Slovakia, *Vězda* in *Lichenes Bohemoslovakiae Exsiccati* 49 (US). Hungary: Magas Tátra, *Fóriss* 3280 (US). Bulgaria: *Szatala* s.n. (US). France: Finistère, *Culberson* 10483 in *Vězda, Lichenes Selecti Exsiccati* 1740 (US). Portugal: Beira Alta, *Tavares* 4640 (US); Braga, *Sampaio* in *Lichenes de Portugal* 260 (US). Faroes: Torshavnd, *Černohorský* 1909 (PRC). USSR: Siberia, *Elias, et al.* L-68228, *Laurow* 2301 (US). Mongolia: *Schubert* M600 (US). Nepal: Khumbu, *Poelt* 130, 133 (M).

Parmelia protosulcata

FIGURES 5*b*, 19*d*

Parmelia protosulcata Hale, 1982:162. [Type collection: Lago Fagnano, Tierra del Fugeo, Argentina, *Santesson* 7955 (S, holotype; US, isotype).]

DESCRIPTION.—Thallus adnate to loosely adnate on bark, pale greenish to brownish mineral gray, 2–6 cm broad; lobes sublinear, short, contiguous, 2–3 mm wide; upper surface plane to weakly foveolate, becoming white pruinose at the tips, deeply reticulately fissured in older parts, pseudocyphellae effigurate, small and rather sparsely developed, mostly on the lobe tips or margins, sorediate, the soralia developing on lobe tips and margins, usually orbicular but fusing and becoming linear or densely aggregated with age, the soredia coarse; lower surface black, moderately rhizinate, the rhizines simple to sparsely furcate or squarrosely branched, 0.5–1 mm long. Pycnidia not seen. Apothecia rare, substipitate, 4–5 mm in diameter, the amphithecium rugose, pseudocyphellate; hymenium 60–65 µm; spores 7–9 × 11–13 µm (spore data from *Imshaug and Ohlsson* 45613).

CHEMISTRY.—Atranorin, chloroatranorin, protocetraric acid, accessory lobaric acid, echinocarpic acid, and conechinocarpic acid (Galloway and Elix, 1984) or rarely fumarprotocetraric acid.

REMARKS.—This austral species occurs in South America and on some of the subantarctic islands, as well as in Australia and New Zealand (Galloway and Elix, 1984). It may be accompanied by *P. sulcata,* which would be distinguished by the different chemistry, a more foveolate surface, laminal soralia, large fissurine pseudocyphellae, and densely squarrosely branched rhizines. It is most closely related to another austral species, *P. cunninghamii,* which has broader lobes, linear soralia, and salazinic acid.

Specimens Examined

New Zealand: Campbell Island, *Harris* 5455 (MSC, NY). Falkland Islands: *Howkins* 2964 (FH). Chile: Prov. Magallanes, *Imshaug and Ohlsson* 43842, 43896, 44401, 44568, 45155, 45613 (MSC), 45613 (MSC, US), *Santesson* 1843 (S, US); Prov. Osorno, *Imshaug* 42961 (MSC); Brunswick Peninsula, *Imshaug and Harris* 39095, 39260, 39328, 39329, 39404 (MSC).

Parmelia pseudolaevior

FIGURES 5*c*, 19*e*

Parmelia pseudolaevior Asahina, 1951a:331. [Type collection: Sengenjunja, Prov. Suruga, Japan, *Asahina* s.n. (TNS, lectotype; US, isolectotype).]

DESCRIPTION.—Thallus adnate on bark or rock, rather brittle, pale greenish to brownish mineral gray, 8–12 cm broad; lobes sublinear, contiguous to imbricate, 1–3 mm wide, the margins becoming densely lobulate, the lobules suberect to erect, 0.1–0.3 mm wide, 1–2 mm long, the lower surface whitish; upper surface shiny, plane to weakly rugose-foveolate, continuous, pseudocyphellae punctate, round, lateral on lobe edges, rarely submarginal, 0.1–0.2 mm long; lower surface black, shiny moderately rhizinate, the rhizines simple to sparsely furcate, 0.5–1 mm long. Pycnidia not seen. Apothecia rare, substipitate, 2–10 mm in diameter, at first urceolate, then expanded, flat and radially split, the amphithecium sparsely punctate-pseudocyphellate; hymenium 60–65 µm; spores 6–9 × 10–15 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin, salazinic acid (Asahina, 1951a), and consalazinic acid.

REMARKS.—*Parmelia pseudolaevior* is clearly the lobulate morphotype of *P. laevior,* both having lateral punctate pseudocyphellae. It is rather common in Japan and apparently restricted there. A synonym cited by Asahina, *P. laevior* f. *microphyllina* Hue, is actually better identified with *P. pseudoshinanoana.*

Specimens Examined

Japan: Prov. Aki, *Hale* 29363, 29377, 29505 (US); Prov. Bungo, *Kurokawa* 63193 (TNS); Prov. Izu, *Asahina,* s.n. (TNS); Prov. Kii, *Kurokawa* 56061, 57281 (US), 60262 (TNS); Prov. Ishikari, *Yoshimura* 12235b in *Lichenes Japonici Exsiccati* 41 (US); Prov. Rikutyu, *Kurokawa* 59277 (US); Prov. Shimotsuke, *Hale* 63127 (US); Prov. Shinano, *Kurokawa* 59205 in *Lichenes Critici Selecti Exsiccati* 34 (US); Prov. Suruga, *Asahina* 92 (TNS).

Parmelia pseudoshinanoana

FIGURES 5*d*, 19*f*

Parmelia pseudoshinanoana Asahina, 1951a:334. [Type collection: Omiyaguchi, 2-gome, Mt. Fuji, Prov. Suruga, Japan, *Asahina* 52 (TNS, lectotype; US, isolectotype).]

Parmelia laevior f. *microphyllina* Hue, 1899:166. [Type collection: Japan, *Faurie* 518 (PC, lectotype).]

DESCRIPTION.—Thallus adnate on bark, fragile, pale greenish to brownish mineral gray, 6–12 cm broad; lobes sublinear, contiguous, 1.5–3 mm wide, the margins becoming densely lobulate, the lobules 0.2–0.3 mm wide, 1–2 mm long, suberect; upper surface plane, shiny, white pruinose at the tips, continuous, pseudocyphellae marginal, appearing as a more or less continuous white rim 0.5–1 mm wide; lower surface black, densely rhizinate, the rhizines shiny, becoming densely squarrosely branched, 1–3 mm long. Pycnidia not seen. Apothecia not common, barely substipitate, 2–4 mm in diameter, the rim finely crenate, pseudocyphellate; hymenium 55–60 µm; spores 6 × 10–12 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin and salazinic acid (Asahina, 1951a).

REMARKS.—Asahina considered this Japanese species to be a lobulate relative of *P. shinanoana*. Although they share continuous rim-forming pseudocyphellae, *P. shinanoana* has mostly simple rhizines and produces gyrophoric acid in the cortex. *Parmelia pseudoshinanoana* is widespread in Japan but not especially common.

Specimens Examined

Japan: Prov. Iyo, *Kurokawa* 60048 (TNS); Prov. Kii, *Koizumi* (TNS); Prov. Musashi, *Kurokawa* 550574, 59153, 70156 in *Lichenes Critici Selecti Exsiccati* 129 (US); Saitama Pref., *Omura* 332 (US); Prov. Shinano, *Asahina* 33 (TNS), *Kurokawa* 520639, 58554, 59206 in *Lichenes Critici Selecti Exsiccati* 35, 59207 (US); Prov. Shimotsuke, *Kurokawa* 64059 (TNS); Shizuoka Pref., *M. Nakanishi* 5172 (US); Prov. Suruga, *Faurie* 512 (TNS).

Parmelia pseudotenuirima

FIGURES 5*e*, 20*a*

Parmelia pseudotenuirima Gyelnik, 1931:289. [Type collection: based on *P. tenuirima* f. *isidiosa* Müller Argoviensis.]

Parmelia tenuirima f. *isidiosa* Müller Argoviensis, 1896:90. [Type collection: Victoria, Australia, *Wilson* 83 (G, lectotype). Collector on the label is Knight.]

DESCRIPTION.—Thallus closely adnate on bark, firm, pale greenish to whitish mineral gray (brownish in the herbarium), 3–5 cm broad; lobes sublinear to subirregular, short, contiguous, 1–2 mm wide; upper surface shiny, finely foveolate, reticulately cracked with age, pseudocyphellae small, 0.2–0.3 mm long, effigurate in outline, numerous, mostly laminal, isidiate, the isidia cylindrical, 0.05–0.07 × 0.1–0.3 mm, simple to branched, very dense on older parts of the thallus and obscuring the lobes; lower surface black, moderately rhizinate, the rhizines simple to squarrosely branched, 0.5–1 mm long. Pycnidia rare, about 100 µm in diameter; conidia cylindrical, rod-shaped, 5.5–6.0 µm long. Apothecia very rare, substipitate, 3–6 mm in diameter, the amphithecium warty, isidiate, the disc brown; hymenium 45–55 µm; spores poorly developed, 7–9 × 11–13 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin and chloroatranorin, lobaric acid and salazinic acid (Galloway and Elix, 1983).

REMARKS.—This small lichen is known only from Australia (see distribution map in Galloway and Elix, 1983:403). It is not related to any other species in the genus. Literature reports of *P. saxatilis* from Australia probably represent this species. New Zealand records cited by Galloway and Elix (1983) are all *P. novae-zelandiae*. A typical habitat is the base and lower trunks of *Callitris endlicheri* and *Casuarina* in open eucalypt forest and especially on old burned stumps.

Specimens Examined

Australia: New South Wales, *Hale* 58276, *Weber* 365 in *Lichenes Exsiccati* 365 (US), *Weber and McVean* L-49416, L-50060 (US); Victoria, *James* Au2139, *Streimann* HS3223 (US). Filson (1982:555) gives additional records for Australian Capital Territory and South Australia.

Parmelia queenslandensis Hale, new species

FIGURES 6*a*, 20*b*

DESCRIPTION.—Thallus similis *P. signifera* sed thallo persistenti albo-cinereo, corticola, et sporis minoribus differt.

Thallus corticolous, adnate to closely adnate, leathery, whitish to pale greenish mineral gray, 5–8 cm broad; lobes broadly sublinear, rather short and becoming imbricate, 2–5 mm wide; upper surface shiny, smooth, the pseudocyphellae effigurate, dense and small in a marginal zone but larger and more or less separate toward the center, 0.2–1.0 mm long, becoming fissured with age; lower surface sparsely to moderately rhizinate, the rhizines rather coarse, simple to weakly squarrosely branched with age. Pycnidia common, 90–110 µm in diameter; conidia weakly bifusiform, 6–7 µm. Apothecia common, substipitate, radially split with the rim folded upward with age, 5–10 mm in diameter, the disc light brown; hymenium 50–60 µm; spores 6–9 × 11–12 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin, chloroatranorin, and salazinic acid.

HOLOTYPE.—Near the north exit, Mt. Bunya National Park, Queensland, Australia, elev. ~600 m, *M.E. Hale* 65970 (US; isotypes in BM, MEL).

REMARKS.—I first identified this lichen as *P. signifera* in spite of the unusual substrate, canopy branches in rain forest. *Parmelia queenslandensis* is strictly corticolous, persistently whitish or greenish gray and occurs at elevations of 400 to 1100 m from extreme northern New South Wales to the Atherton Tablelands in northern Queensland, well north of the range of *P. signifera*. *Parmelia signifera* is almost always saxicolous in rather exposed habitats and usually turns pale to dark brown. In Australia it occurs from northern New South Wales to Tasmania with no reports yet from Queensland (Galloway and Elix, 1983). Spore differences, which I have not tested statistically, are minor but consistent: 11–12 µm

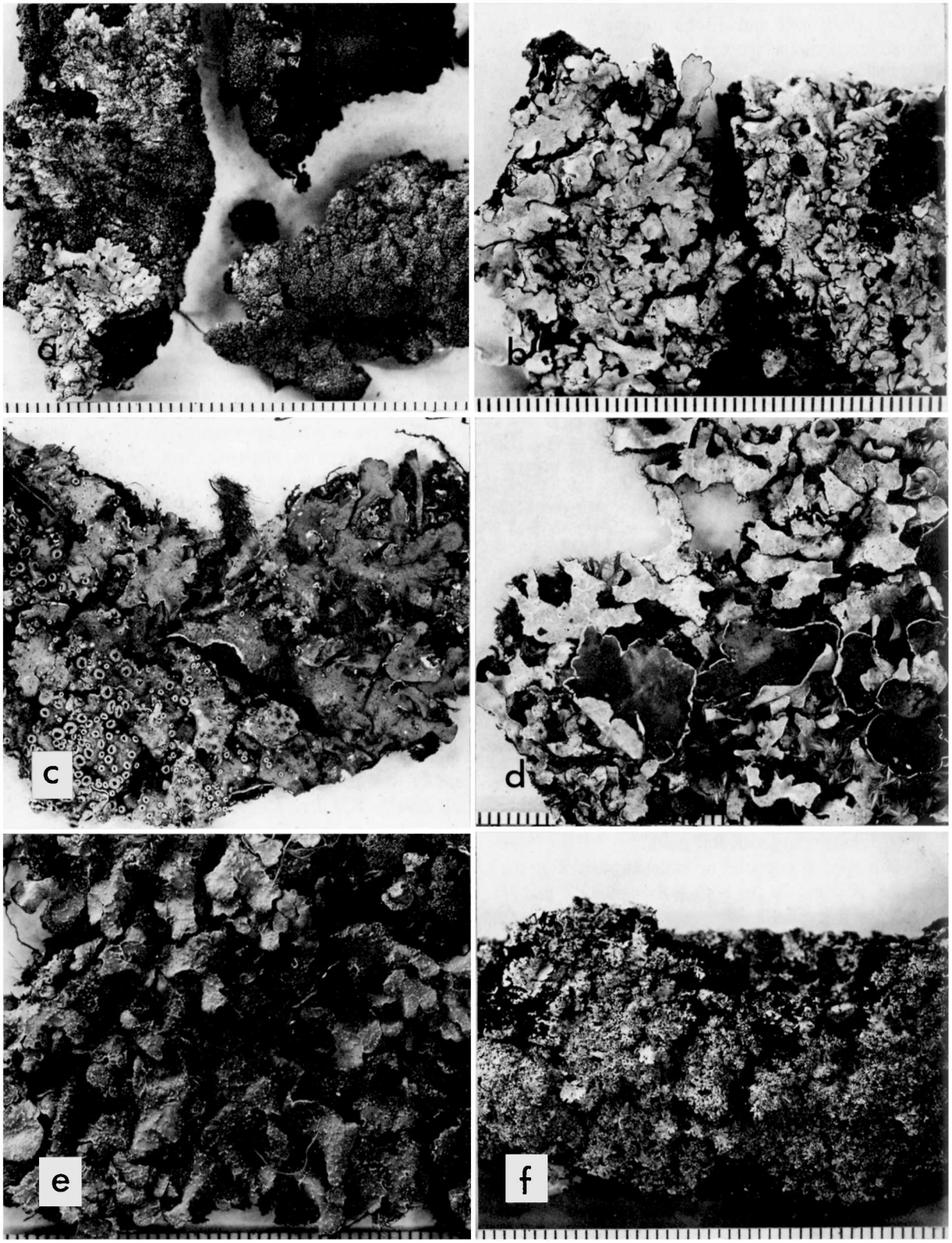

FIGURE 20.—Species of *Parmelia*: *a*, *P. pseudotenuirima* (*Hale* 58276); *b*, *P. queenslandensis* (holotype in US); *c*, *P. ricasolioides* lectotype in H); *d*, *P. salcrambidiocarpa* (holotype in US); *e*, *P. saxatilis* (*Arnold* in *Lichenes Universalis* 9); *f*, *P. sectilis* (*Hale* 26536). (Scales in mm.)

long in *P. queenslandensis* and 13–15 µm in *P. signifera*. Another related corticolous species, *P. tenuirima*, also has larger spores (12–15 µm long), brown rotund lobes (4–10 mm wide), and rather small, separate pseudocyphellae. It is common in New Zealand, much less so in Australia and represented by only one record as far north as Queensland.

Specimens Examined

Australia: Queensland, *Hale* 59480, 64001, 64128, 65971, 65972 (US); New South Wales, *Hale* 66686 (US).

Parmelia ricasolioides

FIGURES 6*a*, 20*c*

Parmelia ricasolioides Nylander, 1887:135. [Type collection: Yunnan, China, s.c. (H, Nyl. Herb. no. 35283, lectotype; PC, TUR, isolectotypes).]
Parmelia daliensis Zahlbruckner, 1930:183. [Type collection: between Dali and Hodjing, Yunnan, China, *Handel-Mazzet2ti* S658t,2 (W, lectotype; TNS, US, isolectotypes).]
Parmelia daliensis f. *tardiva* Zahlbruckner, 1930:184. [Type collection: Muli, Yunnan, China, *Handel-Mazzetti* 7368 (W, lectotype; WU, isolectotype).]

DESCRIPTION.—Thallus adnate to loosely adnate on bark, brittle, brownish mineral gray in the herbarium, 6–8 cm broad; lobes subirregular, short and crowded, contiguous, 2–3 mm wide; upper surface shiny, plane to weakly rugose, continuous, pseudocyphellae inconspicuous, entirely marginal, elongate; lower surface black, densely rhizinate, the rhizines simple to furcate, 0.5–1 mm long. Pycnidia common; conidia cylindrical, straight 5–6 µm long (Nylander, 1887). Apothecia numerous, substipitate, 1–2 mm in diameter, the rim inrolled, crenate; hymenium 55 µm; spores 9–13 × 20–24 µm, the episporium about 2 µm thick.

CHEMISTRY.—Atranorin and salazinic acid.

REMARKS.—This species occupies an isolated position in the genus. Nylander likened it to both *"P. perlata"* and *P. tenuirima*. The pseudocyphellae are very weakly developed along the lobe margins and the surface is continuous. It occurs at high elevations (to 3700 m), probably in *Rhododendron* forests.

Specimens Examined

Nepal: Okhaldunga, *Poelt* L715 (US). India: NEFA, *Panigrahi* 16079A (AWAS). Zhao et al. (1982) reported it from Yunnan Province in China.

Parmelia salcrambidiocarpa Hale, new species

FIGURES 6*b*, 20*d*, 21

DESCRIPTION.—Similis *P. crambidiocarpae* sed sporis parvis (7–10 × 12–15 µm) et thallo acidum salazinicum continenti differt.

Thallus corticolous, adnate to loosely attached, nearly pulvinate with age, firm, whitish mineral gray, 4–12 cm broad; lobes sublinear, little branched, becoming divaricately branched, 1.5–4 mm wide; upper surface shiny, plane, smooth to rugose, continuous or transversely cracked with age, the pseudocyphellae forming a nearly continuous narrow rim around the margins, 0.1–0.2 mm wide, also laminal and effigurate, 0.2–1 mm long, separate, fissuring with age; lower surface moderately to densely rhizinate, the rhizines simple to moderately squarrosely branched, 1–3 mm long, usually projecting as a mat around the lobe margins. Pycnidia numerous, 90–110 µm in diameter; conidia cylindrical to weakly bifusiform, 5–6 µm long. Apothecia common, stipitate, 5–18 mm in diameter, the disc sometimes flat and radially splitting, light to dark brown; hymenium 55–65 µm; spores 7–10 × 12–15 µm, the episporium 1.0–1.5 µm thick.

CHEMISTRY.—Atranorin, chloroatranorin, and salazinic acid with or without consalazinic acid (one collection, *Kantvilas and James* 633/81, also contains lobaric acid).

HOLOTYPE.—Whakapapanui Walk Trail Head near the Chateau, Tongariro National Park, North Island, New Zealand, elev. 1180 m, *M.E. Hale* 65558 (US).

REMARKS.—This species is in the *P. testacea* complex, closely related to both *P. crambidiocarpa* and *P. norcrambidiocarpa* (see discussions under these species). It is easily distinguished from *P. crambidiocarpa* by the smaller spores and chemistry. The average maximum spore size, 8.9 × 13.4 µm (range 7–10 × 12–15 µm for 17 collections), is the same as in *P. norcrambidiocarpa*. As in *P. crambidiocarpa* the apothecial disc ranges from very pale brown (29%) to brown (23%) or dark brown (47%) (17 collections examined).

Parmelia salcrambidiocarpa differs from morphologically identical *P. norcrambidiocarpa* in containing salazinic acid rather than echinocarpic acid. In addition the two species are allopatric, *P. salcrambidiocarpa* occurring in Tasmania and the Tongariro-Urewera region of North Island of New Zealand (Figure 21). *Parmelia norcrambidiocarpa* occurs only on South Island of New Zealand. I collected *P. salcrambidiocarpa* at 8 localities in Tasmania, a total of 28 specimens out of 186, the remainder being *P. testacea*.

Ecologically *P. salcrambidiocarpa* behaves much as the other species in this group. It is usually collected on *Nothofagus cunninghamii* in Tasmania at 600–1200 m elevation and in New Zealand on *Dracophyllum* and other subalpine shrubs up to 1300 m elevation.

Specimens Examined

Australia: Tasmania, *Hale* 68654, 68656, 68695-698, 68821-828, 68690, 68768-772, 68785, 68786 (US), *Kantvilas* 192/82 (ANUC), *Kantvilas and James* 633/81 (ANUC). New Zealand: North Island, *Hale* 65114-116, 65372, 65551, 65556, 65557, 65567-569 (US).

Parmelia saxatilis

FIGURES 6*c*, 20*e*

Parmelia saxatilis (L.) Acharius, 1803:204.
Lichen saxatilis L., 1753:1142. [Type collection: Sweden, sheet 1273.61 (LINN, lectotype).]

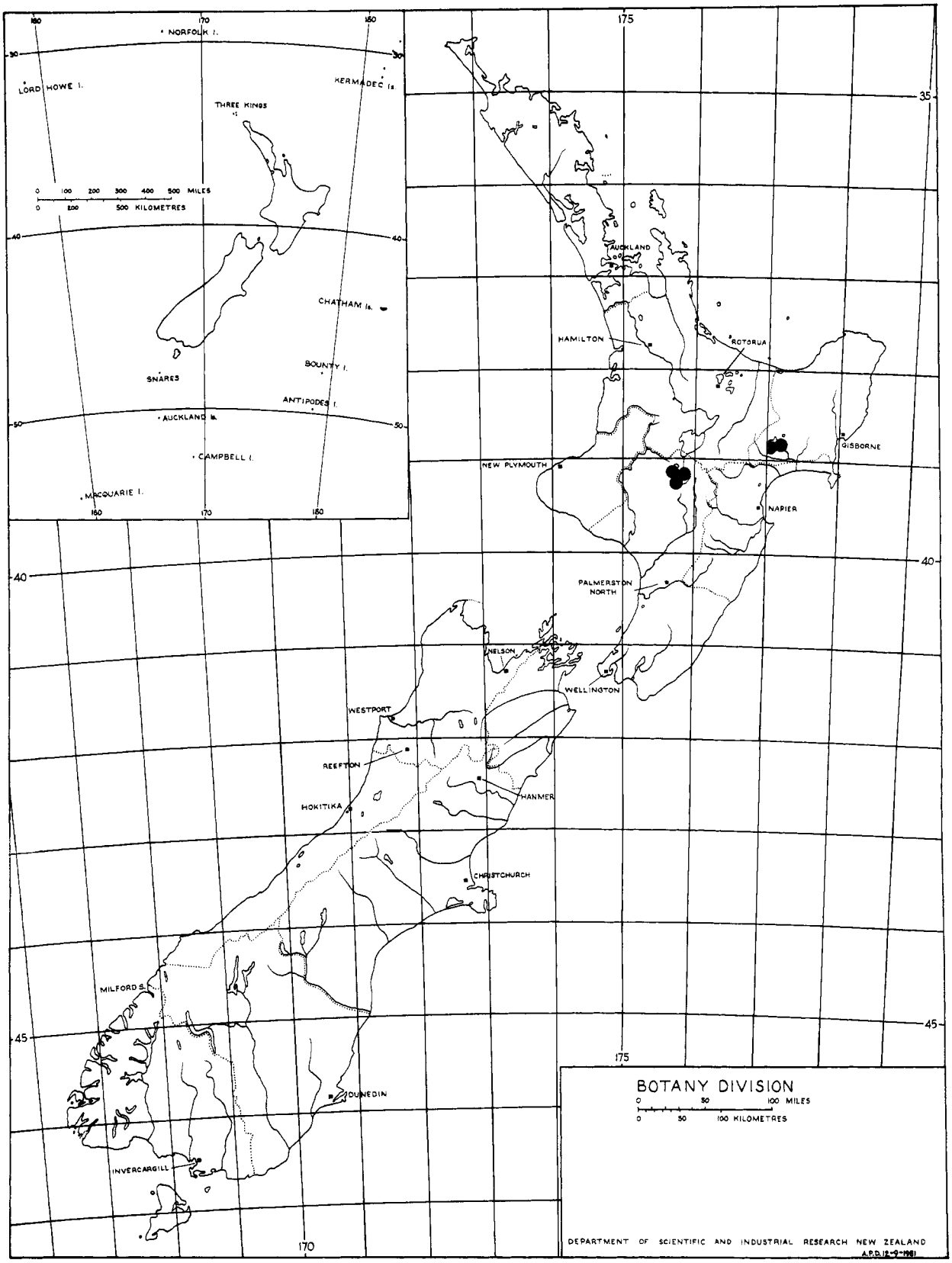

FIGURE 21.—Distribution of *Parmelia salcrambidiocarpa* in New Zealand.

Parmelia saxatilis var. *laevis* Nylander, 1860:389. [Type collection: Pyrenees central, *Nylander* s.n. (H, Nyl. herb. no. 34863, lectotype).]

Parmelia saxatilis f. *rubricosa* Steiner, 1904:399. [Type collection: Cumbre Nueva, La Palma, Canary Islands, *Bornmüller* 3256 (WU, lectotype).]

Parmelia acervata Hue, 1915:43. [Type collection: Cape Tuxen, Graham Land s.c. 190 (PC, lectotype; see Lamb, 1948:241).]

Parmelia saxatilis f. *squamigera* Gyelnik, 1931a:152. [Type collection: Helsinki, Finland, *Gyelnik* s.n. (BP, lectotype).]

Parmelia saxatilis f. *corallicola* Gyelnik, 1931a:152. [Type collection Domos, Mt. Vadallokovek, Pest, Hungary, *Gyelnik* s.n. (BP, lectotype).]

Parmelia saxatilis f. *prima* Gyelnik, 1931b:284. [Type collection: Magas Tatra, Koprova Valley, Hungary, *Timkó* s.n. (BP, lectotype).]

Parmelia saxatilis var. *imbricatoides* Gyelnik, 1932:450. [Type collection: Artukainen, Finland, *Linkola* s.n. (BP, lectotype).]

Parmelia saxatilis var. *pseudoviridis* Gyelnik, 1932:448. [Type collection: St. Gilgen, Austria, *Gyelnik* s.n. (BP, lectotype).]

Parmelia saxatilis f. *acervata* (Hue) Lamb, 1948:241.

[See Hillmann (1936) for additional subspecific taxa, all of which appear to be synonyms of *P. saxatilis*.]

DESCRIPTION.—Thallus adnate to loosely adnate on rock, more rarely on bark, fairly firm, greenish mineral gray, turning brownish in exposed habitats, sometimes whitish with varying amounts of pruina, 8–20 cm broad; lobes sublinear, contiguous to crowded, 2–4 mm wide; upper surface shiny, continuous or cracking with age along the pseudocyphellae, reticulate-foveolate, the pseudocyphellae effigurate, large, 0.3–1.0 mm long, marginal and laminal, often fusing into a recitulate network and soon becoming isidiate, the isidia cylindrical, simple to sparsely branched, darkening at the apices, 0.06–0.15 mm in diameter, up to 0.5 mm high, becoming very dense on older lobes; lower surface black, densely rhizinate, the rhizines simple to furcate or rarely subsquarrosely branched, 1–2 mm long. Pycnidia uncommon, about 100 µm in diameter; conidia cylindrical, straight to slightly bent, 6–7 µm long (Hillmann (1936) reported 1 × 5–7 µm). Apothecia occasional, substipitate, 2–8 mm in diameter, cupuliform, the amphithecium and rim coarsely rugulose, isidiate; hymenium 80–100 µm; spores 9–11 × 16–18 µm, the episporium 2–3 µm thick.

CHEMISTRY.—Atranorin, chloroatranorin, and salazinic acid (Galloway and Elix, 1983), accessory lobaric acid (Krog, 1951) with or without protolichesterinic acid (Kurokawa and Nakanishi, 1971) or unidentified fatty acids (Dey, 1978).

REMARKS.—This is the most widespread species in the genus, occurring in both hemispheres and known to all lichenologists. For such a common species it has very little morphological and chemical variation. The presence or absence of the accessory substance lobaric acid is loosely correlated with geography. In Europe about a third of the collections (50 tested) have only salazinic acid, the rest having salazinic and lobaric acids. In Alaska and Canada (see map in Thomson, 1984:310) these two chemotypes are nearly equally common, but in western United States and South America most specimens contain only salazinic acid (91% of 75 tested). All specimens in the Appalachian region of eastern North America, where the species occurs on rocks at the highest elevations, seem to have lobaric acid constantly (Dey, 1978). *Parmelia kerguelensis* appears to be a protocetraric acid-containing chemotype.

Most corticolous specimens from Japan, eastern North America, and the west coast of North America, usually identified as *P. saxatilis* in herbaria, have proved to be *P. squarrosa*, a closely related species with densely squarrosely branched rhizines. This probably includes the reports of Zhao et al. (1982) for *P. saxatilis* in China.

Representative Specimens Examined

Canada: Northwest Territories, *Inskip* 11 (BM, US); Newfoundland, *Fernald* 2210 (US); Quebec, *LeGallo* 2943, *Samuel* 62 (US); Ontario, *Hale* 36240, *Imshaug* 4132, *Wetmore* 29481 (US); British Columbia, *Brodo* 10982, *Noble* 6336, *Norris* 2325D (US). USA: Maine, *Egan* 6119, *Hale* 37477, *Merrill* in *Lichenes Exsiccati* 152, *Pike* 4341 (US); New Hampshire, *Rathburn* s.n. (US); New York, *Harris* s.n., *Hermann* 14693 (US); West Virginia, *Hale* 15463 (US); North Carolina, *Hale* 33628 (US); Michigan, *Egan* 3522 (US); Colorado, *Anderson* 2843, *Kiener* 4523, *Shushan* 5033, *Weber and Klockenbrink* in *Lichenes Exsiccati* 538 (US); Montana, *Hale* 49319 (US); Idaho, *Hale* 48533 (USA); Washington, *Imshaug* 1184, *Thomson* 14717 (US); Oregon, *Brown* 857, *Hale* 49288, *Pike* 379 (US); California, *Hale* 51588, 56220, *Herre* 702 (US); Alaska, *R. Hale* 159, *Hermann* 21857, *Llano* 416c, *Schaack* 250, *Thomson and Shushan* 6208, *Viereck* 2292 (US). Chile: Aysen, *Santesson* 4820 (S, US); Cautin, *Redon* 3576 (US); Magallanes, *Santesson* 2158 (S, US); Malleco, *Mahu* 2466 (US); Tierra del Fuego, *Santesson* 1246 (S, US); Juan Fernandez, *Imshaug* 37035, 37410 (MSC). Argentina: Tierra del Fuego, *Dusén* 262 (US), *Santesson* 346, 7532, 8224 (S). Falkland Islands: *Hawkins* 2962 (FH), *Lechler* 76 (BM). Greenland: *Alstrup* in *Lichenes Groenlandici Exsiccati* 195, *Hansen* in *Lichenes Groenlandici Exsiccati* 19, *Lynge* s.n. (US). Iceland: Reykjavik, *Černohorský* 1924 (PRC), *Kristinsson* 18087, 22174 (US); Reydarvatn, *Smarda* 1610 (PRC). Great Britain: Cornwall, *Curnow* s.n. (BM); Merioneth, *James* 2077 (BM). Ireland: W. Galway, *Larbalestier* 211 (BM). Norway: *Lynge* 5165 (US). Sweden: *Magnusson* 8562 (US). Finland: *Lai* 10911, *Räsänen* in *Lichenes Fennicae Exsiccati* 856 (US). Denmark: *Christiansen* 9857 (US). Netherlands: *Maas Geesteranus* 7005 (US). Germany: *Erichsen* 667, *Hillmann* in *Kryptogamae Exsiccatae* 2862 (US). Austria: *Herre* 32 (US). Czechoslovakia: *Černohorský* 589 (PRC), *Matousek* in *Lichenes Slovakiae Exsiccati* 72 (US). Hungary: *Fóriss* 1885, *Timkó* in *Flora Hungarica Exsiccata* 319 (US). France: *Beraud* s.n., *Iltis* 3122 (US). Spain: *Vazquez* s.n. (US). Portugal: *Sampaio* in *Lichenes de Portugal* 259 (US). Teneriffe: *Imshaug* 33860 (MSC). New Zealand: North Island, *Galloway* s.n. (CHR); South Island, *Hale* 63216 (US), *James* 564 (BM), *Martin* A-167 (CHR). There are also reports by Krog (in litt.) from Kenya, by Golubkova (1981) from Mongolia, by Kurokawa (1966) from Nepal, and by Lindsay (1973b) from Adelaide Island in Antarctica.

Parmelia sectilis

FIGURES 6*d*, 20*f*

Parmelia sectilis Hale, 1968:326. [Type collection: summit of Mt. Data, Mountain Prov., Philippines, *Hale* 26536 (US, holotype; TNS, isotype).]

DESCRIPTION.—Thallus adnate to closely adnate on bark, brittle, light greenish mineral gray, 8–12 cm broad; lobes sublinear, contiguous, 1.5–2 mm wide, marginally dissected and densely isidiate-lobulate, the lobules erect, branched, 0.1–0.2 mm wide, to 1 mm long, the tips cylindrical; upper surface shiny, plane to weakly rugose, continuous, pseudocyphellae effigurate, elongate, mostly marginal, forming an

interrupted white rim around the lobes; lower surface black, densely rhizinate, the rhizines simple to furcate, 1–1.5 mm long. Pycnidia rare; conidia cylindrical, straight, 5–6 µm long. Apothecia not common, substipitate, 2–4 mm in diameter, the rim and amphithecium deeply rugose with numerous lobules or isidia-like projections, the disc brown; hymenium 90–100 µm high; spores 15–18 × 28–33 µm, the episporium distinct, 3–4 µm.

CHEMISTRY.—Atranorin, salazinic acid, and consalazinic acid.

REMARKS.—*Parmelia sectilis* occurs at higher elevations (1600–2300 m) in the pine forests of the Philippines and in oak forests in Sabah. It is the only species of *Parmelia* that seems to have evolved and remained in the tropics. It is distantly related to *P. niitakana, P. pseudoshinanoana,* and *P. shinanoana,* which have similar though more strongly developed rim-forming pseudocyphellae. It has the largest spores in the genus.

Specimens Examined

Philippines: Mountain Prov., *Hale* 26104, 26194, 26219, 26397, 26536 (US). Sabah: Kinabalu National Park, *Hale* 28378, 28241, 28507, 28630, 28786, 28935, 29050, 29090 (US).

Parmelia shinanoana

FIGURES 6*e*, 22*a*

Parmelia shinanoana Zahlbruckner, 1927b:349. [Type collection: Mt. Yatsu-gadake, Shinano, Japan, *Asahina* 548 (W, lectotype; US, isolectotype).]

DESCRIPTION.—Thallus adnate on rock, fragile, pale greenish to distinctly brownish mineral gray, 8–20 cm broad; lobes sublinear, contiguous, 1.5–3 mm wide, sparsely lobulate in older parts; upper surface shiny, plane, continuous, pseudocyphellae marginal, linear, forming a conspicuous white rim about 2 mm wide around the lobes; lower surface black, sparsely to moderately rhizinate, the rhizines simple to furcate, 1–2 mm long. Pycnidia not seen. Apothecia rare, adnate and inconspicuous, 1–2 mm in diameter, the rim crenate, pseudocyphellae; hymenium 60–65 µm; spores poorly developed, 5–6 × 9–11 µm, the episporium 1 µm thick (after Asahina, 1952:114).

CHEMISTRY.—Atranorin, gyrophoric acid, and 4-O-methylgyrophoric acid in the cortex, salazinic acid in the medulla (Kurokawa and Takahashi, 1970).

REMARKS.—*Parmelia shinanoana* has very conspicuous rim-forming pseudocyphellae, similar to *P. niitakana* and *P. pseudoshinanoana* and, as the main chemical feature, the production of gyrophoric acid in the cortex, unique in the entire family Parmeliaceae. It is known only from Japan, where it is not commonly collected.

Specimens Examined

Japan: Prov. Awa, *Fujikawa* s.n. (TNS); Prov. Buzen, *Kurokawa* 62477 (TNS); Prov. Iyo, *Kurokawa* 60047 (TNS), *Ochi* s.n. (TNS); Prov. Kozuke, *Kurokawa* 58588 (TNS); Prov. Musashi, *Kurokawa* 56140 (US), 64289 (TNS); Saghalin, *Asahina* s.n. (TNS); Prov. Shinano, *Kurokawa* 58500 (US); Prov. Yamato, *S. Nakanishi* 41 (KOBE).

Parmelia signifera

FIGURES 6*f*, 22*b*

Parmelia signifera Nylander, 1888:25. [Type collection: New Zealand, *Knight* s.n. (H, Nyl. Herb. no. 34828, lectotype; BM, isolectotype).]
Parmelia saxatilis var. *signifera* (Nylander) Müller Argoviensis, 1892:30.

DESCRIPTION.—Thallus adnate to loosely adnate on rock (rarely on bark), sometimes forming dense, pulvinate mats, rather firm to brittle, darkish green to brownish mineral gray, the tips usually distinctly brownish, 8–20 cm or more broad; lobes sublinear, crowded and imbricate, 2–8 mm wide, more or less lobulate with age in the center, the lobules marginal, suberect; upper surface shiny, plane to rugose or foveolate, extensively fissured with age along pseudocyphellae, the pseudocyphellae effigurate, 0.3–1 mm long, separate or in part fusing into a loose white network, appearing raised; lower surface black, the margin shiny and dark brown, densely rhizinate, the rhizines rather dense, about 1 mm long, simple to sparsely squarrosely branched. Pycnidia common; conidia bifusiform, 5.0–56.5 µm long. Apothecia common, adnate to substipitate, 6–12 mm in diameter, the disc brown, flattened, often radially split, the amphithecium heavily effigurate-pseudocyphellate; hymenium 55–60 µm; spores 6–8 × 13–15 µm, the episporium distinct, about 1 µm thick.

CHEMISTRY.—Atranorin and chloroatranorin, salazinic acid (Galloway and Elix, 1983) and consalazinic acid, and accessory lobaric acid; or rarely atranorin and protocetraric acid.

REMARKS.—This is by far the most commonly collected saxicolous *Parmelia* in Australia and New Zealand (see distribution map in Galloway and Elix, 1983:408). In Australia, in particular, it forms large, pulvinate, exfoliating colonies on granite and sandstone outcrops in open sclerophyll forests. In New Zealand the typical habitat is more exposed ridges in open mountainous areas. In a sense it is the austral counterpart of *P. omphalodes,* which has much less conspicuous pseudocyphellae and is, of course, a northern arctic-alpine lichen. A few specimens (*Hale* 58374, *Melville* 2009) containing protocetraric acid instead of salazinic acid are morphologically indistinguishable.

When corticolous, there is rarely confusion with *P. tenuirima,* a large greenish mineral gray lichen that has less dense, separate pseudocyphellae and cylindrical to vaguely bifusiform conidia. However, a few narrow-lobed, usually corticolous specimens may be difficult to name as *P. signifera* or *P. tenuirima* (see also Hillmann, 1939). Filson (1982:565) feels that the two species may prove to be identical, but both morphological and conidial differences seem to preclude this unlikely possibility.

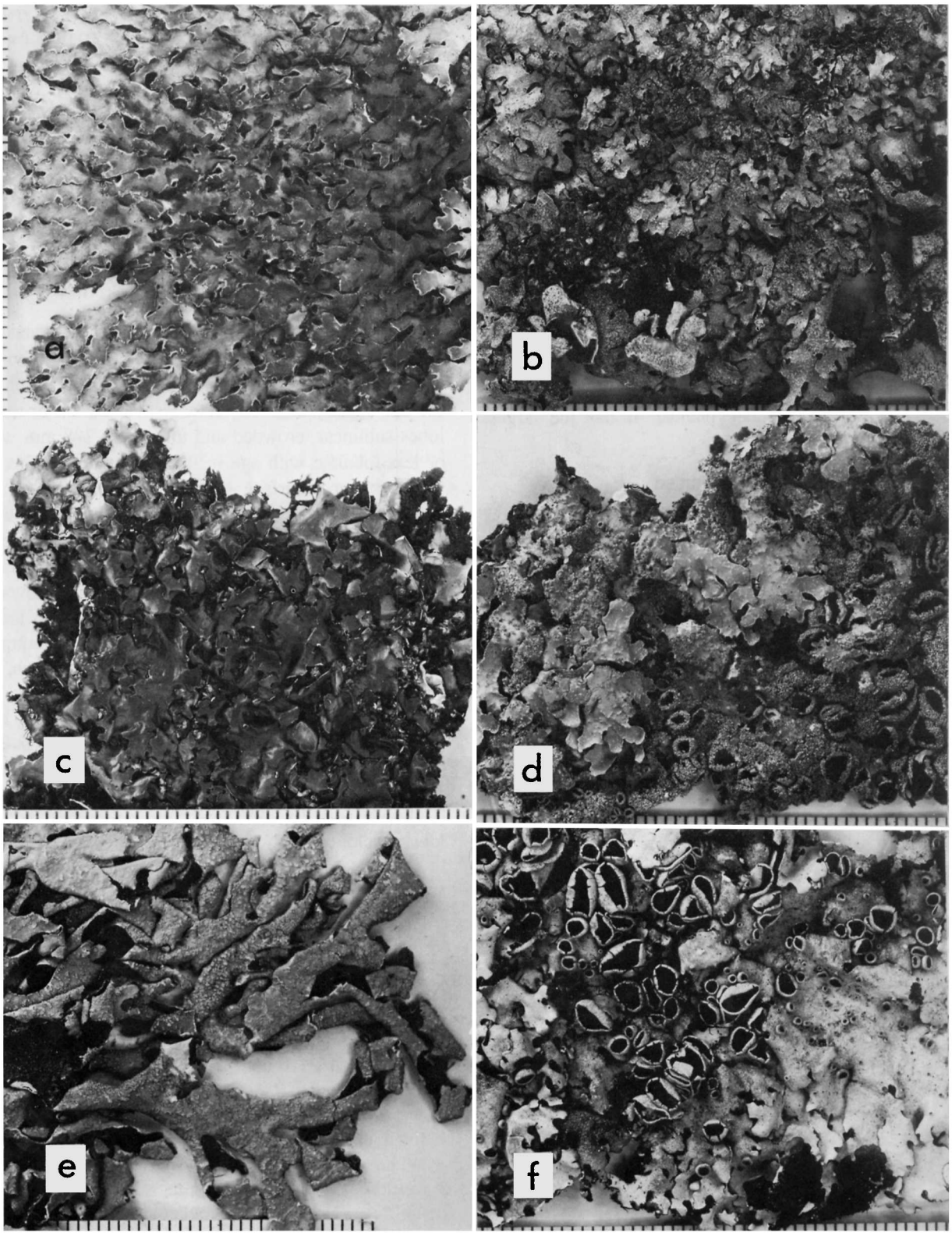

FIGURE 22.—Species of *Parmelia*: *a*, *P. shinanoana* (*Kurokawa* 58588); *b*, *P. signifera* (*Hale* 58289); *c*, *P. skultii* (holotype in US); *d*, *P. squarrosa* (holotype in US); *e*, *P. submontana* (lectotype of *P. contorta* Bory in PC); *f*, *P. submutata* (*Poelt* L-142). (Scales in mm.)

Specimens Examined

Australia: New South Wales, *Du Rietz* 704, 792a (UPS, US), *Flockton* 1443 (US), *Hale* 58289, 58301, 58927, 59106, 59286, 59296, 59443, 66122, 66639 (US), *Streimann* 2496, 4017, 7414, 7473, 9138, 9286 (US), *Verdon* 1364, 1428, 1513, 1587, 1832, 7415 (US); Australian Capital Territory, *Hoogland* 7775, 7779 (US), *Weber* 251 (US); Victoria, *Hale* 58256, 58330, 58326, 58374, 58474, 58977, 59159, 59414, 59541 (US), *Melville* 2009 (BM, US), *Streimann* 2820, 3267, 3410, 3414 (US); Macquarie Island, *Isaird* s.n. (US). New Zealand: South Island, *Du Rietz* 1802a (UPS, US), *Hale* 66177, 66435 (US), *James* 482, 1419, 1471 (BM, US), *Galloway* s.n. (CHR), *Martin* s.n. (BM, US), *Mason* 134 (BM).

Parmelia skultii Hale, new species

FIGURES 7*a*, 22*c*

Parmelia omphalodes subsp. *glacialis* Skult, 1985:201. [Type collection: Mould Bay, Prince Patrick Island, NWT, Canada, *MacDonald* s.n. (CANL, holotype).]

DESCRIPTION.—Subsimilis *Parmelia omphalodi* sed thallo acidum salazinicum continenti differt.

Thallus usually growing on soil among mosses or on rocks, fragile, brown to nearly black at maturity (or whitish with pruina), 6–10 cm broad; lobes sublinear, rather short, 2–4 mm wide, crowded and imbricate with secondary laciniae; upper surface plane, smooth to minutely rugulose, often becoming white pruinose with age, the margins pseudocyphellate, the pseudocyphellae more or less continuous, narrow and inconspicuous, laminal pseudocyphellae rarely seen; lower surface black and shiny, sparsely to moderately rhizinate, the rhizines simple to fucate, 0.5–2 mm long. Pycnidia rare, 90–110 µm in diameter; conidia cylindrical, rod-shaped, 6–8 µm long. Apothecia not seen.

CHEMISTRY.—Atranorin, salazinic acid, norstictic acid (equal or exceeding the concentration of salazinic acid), consalazinic acid (±), protolichesterinic acid (±), fumarprotocetraric acid (±), stictic acid (±), and several unknowns (Skult, 1984).

HOLOTYPE.—West wall of pass, on soil over rocks, Anaktuvuk Pass, 151–52°W, 68°20′N, Alaska, USA, *G.A. Llano* 299a (US).

REMARKS.—Skult (1984) first pointed out the existence of a norstictic acid-containing population of *P. omphalodes* in his broader study of the *P. omphalodes* complex in eastern Fennoscandia. He noted the rather broad, marginally pseudocyphellate lobes and frequent occurrence of pruina, the two most important morphological features that separate it from typical *P. omphalodes*. I believe this combination of characters to recognize it as a distinct species. It appears to be restricted to high latitudes, especially near the ocean, from the Aleutian Islands to Novaya Zemlya.

Specimens Examined

USA. Alaska: St. Matthew Island, *Trelease* 1165 (US); Port Clarence, *Trelease* 1129 (US); Cape Lisburne, *Bean* s.n. (US); Diomede Island, *Palmer* 801 (US); Point Barrow, *Thomson et al.* 25 (US, WIS), *Scholander* s.n. (US); Attu Island, *van Schaak* 205 (US). Canada. Northwest Territories: Bylot Island, *Scotter* 68129 (WIS); Axel Heiberg Island, *Scotter* 46165 (WIS); Kaminceriak Lake, *Scotter* 4316 (WIS). Novaya Zemlya: *Lynge* s.n. (US). Skult (1985) also reports a specimen from Spitsbergen.

Parmelia squarrosa

FIGURES 7*b*, 22*d*

Parmelia squarrosa Hale, 1971:29. [Type collection: Shenandoah National Park, Madison County, Virginia, USA, *M.E. Hale* 36494 (no. 142 in *Lichenes Americani Exsiccati*) (US, holotype).]

Parmelia saxatilis **divaricata* Delise ex Nylander, 1890:27. [Type collection: Itchigomé, Japan, *Almquist* in 1879 (H, Nyl. herb. no. 34853, lectotype).]

DESCRIPTION.—Thallus adnate to loosely adnate on bark, less commonly on rocks, fairly firm, pale greenish to whitish mineral gray, 4–15 cm broad; lobes sublinear, becoming imbricate, 1–5 mm wide; upper surface plane to foveolate, shiny or white pruinose with age, continuous but cracking along pseudocyphellae with age, pseudocypellae angular, 0.5–1 mm long, abundant, marginal and laminal, often forming a reticulate network, isidiate, coarse isidia forming along ridges and pseudocyphellae, cylindrical and barely constricted at the base, 0.10–0.15 × 0.1–0.5 mm high, clustered; lower surface black and shiny, densely rhizinate, the rhizines squarrosely branched, 1–1.5 mm long. Pycnidia rare; conidia cylindrical, straight to slightly bent, 5.5–6.5 µm long. Apothecia rare, substipitate, poorly developed, 1–3 mm in diameter, the amphithecium densely isidiate; hymenium 55–60 µm; spores poorly developed, 8–9 × 13–15 µm, the episporium 2 µm thick.

CHEMISTRY.—Atranorin, salazinic acid, and consalazinic acid.

REMARKS.—*Parmelia squarrosa* is one of the commoner corticolous lichens in both North America (see map in Thomson, 1984:313) and Japan, growing on oak and other deciduous trees in open forests. The sparse population extending from Alaska to California may in fact be a continuation of the Japanese one. It is rare in the Alps in Europe (Hyvonen, 1985). The overlap in range with *P. saxatilis*, with which it was lumped in the past, is extremely limited. In eastern United States, for example, *P. saxatilis* occurs in exposed habitats on the highest mountains (more than 1500 m), above the habitats where *P. squarrosa* normally occurs (Dey, 1978). It does grow with *P. saxatilis* in Maine and along the eastern shore of Lake Superior, but even in these areas where they appear to be sympatric, the two species occupy different habitats, *P. saxatilis* growing on exposed rocks, *P. squarrosa* on less-exposed rocks and trees back from the shorelines.

Representative Specimens Examined

Canada: Nova Scotia, *Maass* 73 (US); Quebec, *Fabius* 7836, *Gallo* 3095 (US); Ontario, *Hale* 33556, 34818, 34945, 36556, 49836 (US), *Sharp* 440 (US); British Columbia, *Brodo* 14257 (US). USA: Maine, *Egan* 5833, *Hale* 37534, *Merrill* in *Lichenes Exsiccati* 35 (US); New Hampshire, *Tuckerman* in *Reliquiae Tuckermanianae* 72; Massachusetts, *Hermann* 14087, *Willey* s.n. (US); Connecticut, *Hale* 33, 14915, 15406 (US); New York, *Brodo* 1213, *Hale* 16661 (US); New Jersey, *Hale* 15288 (US); Pennsylvania, *Hale* 16046, 17217

(US); Maryland, *Hale* 14489, *Plitt* s.n. (US); West Virginia, *Hale* 12501, 14966 (US); Kentucky, *Hale* 13739 (US); Indiana, *Hale* 14191 (US); Missouri, *Hale* 4241 (US); Michigan, *Hale* 34126, 33995 (US); Minnesota, *Fink* 57, *Hale* 23045 (US); Iowa, *Fink* s.n. (US); Virginia, *Hale* 15170, 18170 (US); Tennessee, *Hale*, 18033, Moore 274 (US); South Carolina, *Hale* 7706 (US); Alabama, *Hale* 7072, *McCullough* 535 (US); Georgia, *Hale* 30922 (US); Arkansas, *Hale* 3518 (US); California, *Becking* 610602, *Hale* 49579 (US); Oregon, *Imshaug* 17653b (US); Alaska, *Palmer* 786 (US). China: Manchuria, *Asahina* s.n. (TNS). Nepal: Khumbu, *Poelt* 126, 155, 170 (M); Langtang Himal, *Stainton* 4104 (BM). Sikkim: *Togashi* s.n. (TNS). Korea: *Fujikawa* s.n. (TNS). USSR: Kurile Islands: *Okada* s.n. (TNS). Saghalien: *Fujikawa* s.n. (TNS). Japan: Hokkaido, *M. Nakanishi* 3493 (US); Prov. Honshu, *Kurokawa* 80003 in *Lichenes Rariores Critici Exsiccati* 483 (US); Prov. Ishikari, *Asahina* s.n. (TNS); Prov. Izu, Asahina s.n. (TNS); Prov. Mutsu, *Hale* 29293 (US); Prov. Kai, *Jinzenji* 64016 (TNS); Prov. Omi, *Asahina* s.n. (TNS); Prov. Shimotsuke, *Hashimoto* s.n. (TNS); Prov. Shinano, *Kurokawa* 59242 (US); Prov. Tanba, *Asahina* 71 (TNS); Prov. Tango, *Togashi* s.n. (TNS).

Parmelia submontana, new name

FIGURES 7*c*, 22*e*

Parmelia contorta Bory, 1832:305. [Type collection: Atlas Cedres, *Taygete* 1420 (PC, lectotype). Not *Parmelia contorta* (Hoffmann) Sprengel, 1827:298 (= *Aspicilia contorta* (Hoffmann) Krempelhuber).]

Parmelia saxatilis var. *contorta* (Bory) Zahlbruckner, 1907:68.

Parmelia sulcata f. *contortoides* Zahlbruckner, 1927a:97. [Type collection: Hohenberg, Brennalpe, Austria, *Suza* s.n. and Neuwalde, St. Ägyd, Austria, *Suza* s.n. (W, syntypes; not seen).]

Parmelia bohemica Nádvorník, 1951:244.[Type collection: Planavy, Hlinsko, Bohemia, *Nádvorník* s.n. in 1931 (PRM, lectotype; US, isolectotype). Not *Parmelia bohemica* Gyelnik, 1932a:218 (= *Xanthoparmelia conspersa* (Acharius) Hale).]

Parmelia bohemica f. *contortoides* (Zahlbruckner) Nádvorník, 1951:244.

Parmelia submontana Nádvorník, 1957:72. [Nomen illeg. Basionym not cited in description. Type collection: Based on *P. bohemica* Nádvorník.]

DESCRIPTION.—Thallus loosely attached to bark, trailing in well-developed specimens, firm, greenish mineral gray, 10–15 cm broad; lobes elongate, linear, up to 30 mm long, little branched, divaricate, sometimes weakly canaliculate, 2–5 mm wide; upper surface shiny, plane to rugulose, continuous, pseudocyphellae small, round to effigurate, laminal and marginal, 0.3–1 mm long, soon becoming sorediate, the soralia orbicular to linear with an eroded center with age, the soredia granular to nearly isidioid; lower surface black, sparsely rhizinate, the rhizines simple to sparsely furcate, 1–1.5 mm long. Apothecia and pycnidia not seen.

CHEMISTRY.—Atranorin, salazinic acid, and consalazinic acid.

REMARKS.—This relatively rare European species has not been well understood. Nylander (1860:389), who must have examined the type specimen in Paris, considered it an elongate form of "*P. saxatilis* var. *sulcata*." He said it also occurred in North America but cited no specimens. Zahlbruckner (1907) gave the first modern review (as *P. saxatilis* var. *contorta*), including an excellent figure of the species, stressing the long separate lobes. Recent collections in Austria and Corsica have confirmed in my mind the distinctiveness of the species: long, little branched lobes, numerous orbicular soralia, small pseudocyphellae, and sparse, mostly simple rhizines, as characterized by Poelt (1974:447). Schindler (1975) has written an up-to-date summary of the distribution and ecology of the species in Europe. It is a Mediterranean–South European montane element.

Specimens Examined

France: Corsica, *Lambinon, Rondon and Vězda* in *Lichenes Selecti Exsiccati* 845 (US). Austria: Linz, *Schauer* s.n. (M). Czechoslovakia: Bohemia, *Nádvorník* s.n. (FH); Orlicke, *Nádvorník* s.n. (US). Schindler (1975) cites further collections from Germany, Poland, Russia, Yugoslavia, Italy, Greece, Turkey, and Tunisia.

Parmelia submutata

FIGURES 7*d*, 22*f*

Parmelia submutata Hue, 1899:172. [Type collection: San-tchang-kiou, Yunnan, China, *Delavay* s.n. (PC, lectotype).]

Parmelia rhododendri Zahlbruckner, 1930:187. [Type collection: Hsiang-schuiho, Yunnan, China, *Handel-Mazzetti* 6518 (W, lectotype; TNS, US, isolectotypes).]

Parmelia leiocarpodes Zahlbruckner, 1934b:207. [Type collection: mountains of Kopati, Djago, and Muli, China, *Rock* s.n. (W, lectotype).]

DESCRIPTION.—Thallus adnate to closely adnate, firm, greenish mineral gray (brownish in the herbarium), 8–12 cm broad; lobes subirregular to sublinear, imbricate, 2–5 mm wide; upper surface shiny, plane, becoming finely reticulately cracked, pseudocyphellae numerous and small, 0.1–0.2 mm long, laminal; lower surface black, densely rhizinate, the rhizines simple to densely squarrosely branched, 1–1.5 mm long. Pycnidia poorly developed; conidia cylindrical, straight, 6–8 µm long (after Zahlbruckner for the type of *P. rhododendri*). Apothecia common, adnate to substipitate, 3–5 mm in diameter, the amphithecium smooth, the disc brown; hymenium 45–50 µm; spores 3–5 × 6–9 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin, salazinic acid, and consalazinic acid with or without norstictic acid.

REMARKS.—This is the parent morph of *P. meiophora*. In his descriptions Zahlbruckner recognized the dendroid branched rhizines but not the fine reticulations on the surface representing pseudocyphellae. It is more widesp read than *P. meiophora* but seems to occur in similar habitats, high elevation pine-*Rhododendron* forests. About a third of the specimens tested from Taiwan have relatively high concentrations of norstictic acid.

Representative Specimens Examined

Taiwan: Prov. Ilan, *Kurokawa* 929, 931, 1038 in *Lichenes Critici Selecti Exsiccati* 38 (US); Mt. Chien-San, *Kurokawa* 932 (US); Mt. Arisan, *Ogata* s.n. (TNS); Taichung County, *Chun* s.n. (US). China: Yunnan, *Delavay* s.n. (PC). It has also been reported by Kurokawa (1966:610) from Nepal.

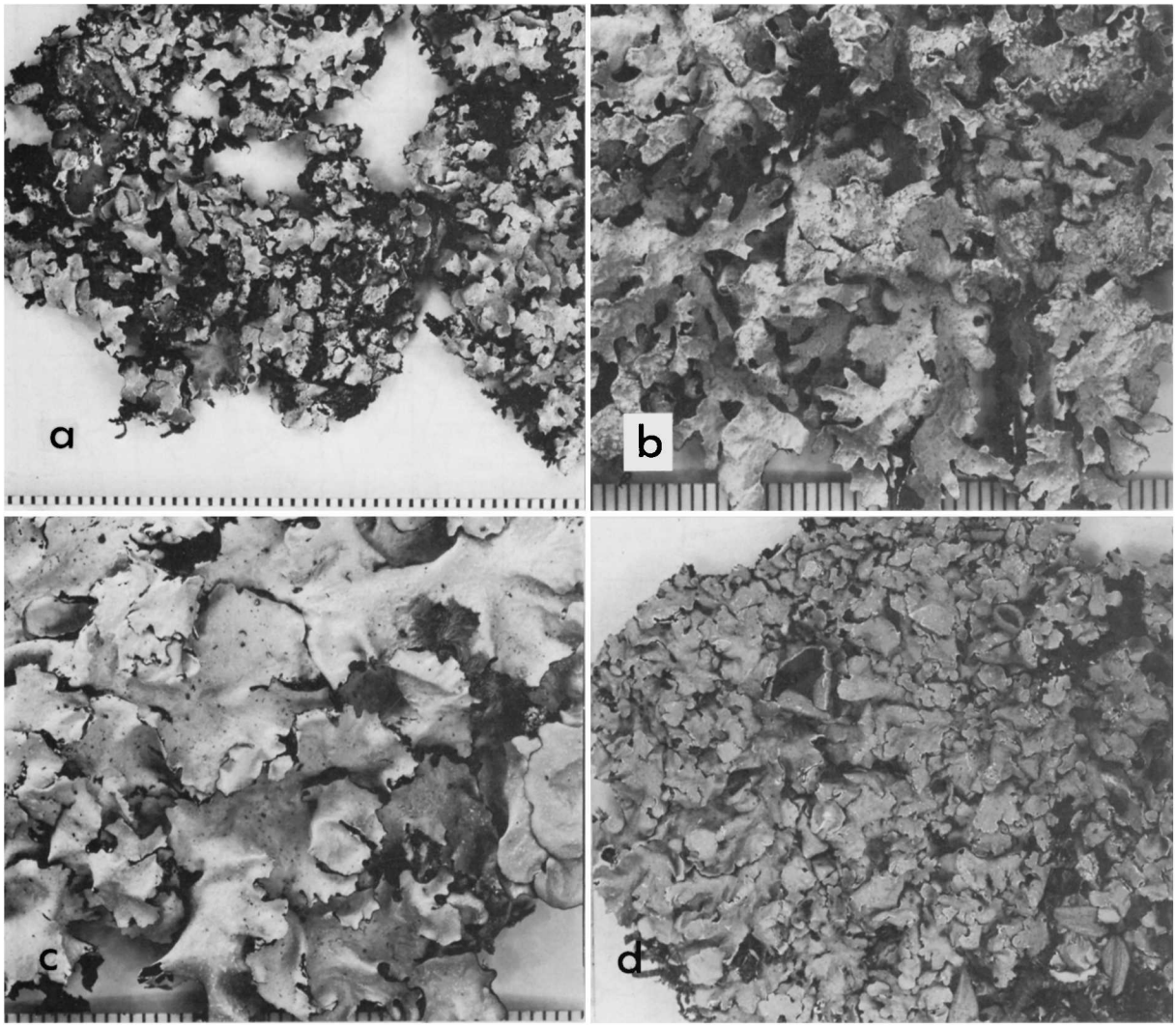

FIGURE 23.—Species of *Parmelia: a, P. subtestacea* (holotype in US); *b, P. sulcata* (*Kjellmert* s.n.); *c, P. tenuirima* (*James* 488 pp.); *d, P. rudior* (type of *P. erimis* in H). (Scales in mm.)

Parmelia subtestacea Hale, new species

FIGURES 7*e*, 23*a*, 24

DESCRIPTION.—Similis *P. testacea* sed thallo acidum echinocarpicum continenti differt.

Thallus adnate on bark, usually thin and rather brittle, pale greenish mineral gray, 5–12 cm broad; lobes sublinear to mostly subirregular, short, imbricate, 1–5 mm wide, usually with marginal secondary lobes 1–2 mm wide, flaring to rounded, developing with age; upper surface shiny, plane to distinctly rugose-foveolate, continuous, pseudocyphellae forming a nearly continuous white rim 0.1–0.2 mm wide around the main and secondary lobes, also laminal on the main or older lobes, separate, sparse, 0.2–0.4 mm long, usually not fissuring with age; lower surface black, sparsely to moderately rhizinate but with a distinct bare to papillate brown zone around the margins, the rhizines simple to furcate to sparsely squarrosely branched, 0.5–1.5 mm long. Pycnidia numerous, 90–100 μm in diameter; conidia cylindrical, rod-shaped to weakly bifusiform, 5.5–6.5 μm long. Apothecia common, substipitate, generally remaining flat but sometimes cupuliform, 4–20 mm in diameter, the disc very pale brown, rarely darkening, splitting radially at maturity, the amphithecium rugose and effigurate-pseudocyphellate; hymenium 60–65 μm; spores 7–10 × 11–15 μm, the episporium 1.0–1.5 μm thick.

CHEMISTRY.—Atranorin, chloroatranorin, echinocarpic acid (and associated unknowns), with or without unknown #27 or rarely with unknown #27 alone. A fatty acid near protolichesterinic acid was detected in several specimens tested by Dr. C.F. Culberson).

HOLOTYPE.—Silver beech forest with understory grazing, near entrance to Mt. Aspiring National Park, Routeburn Road,

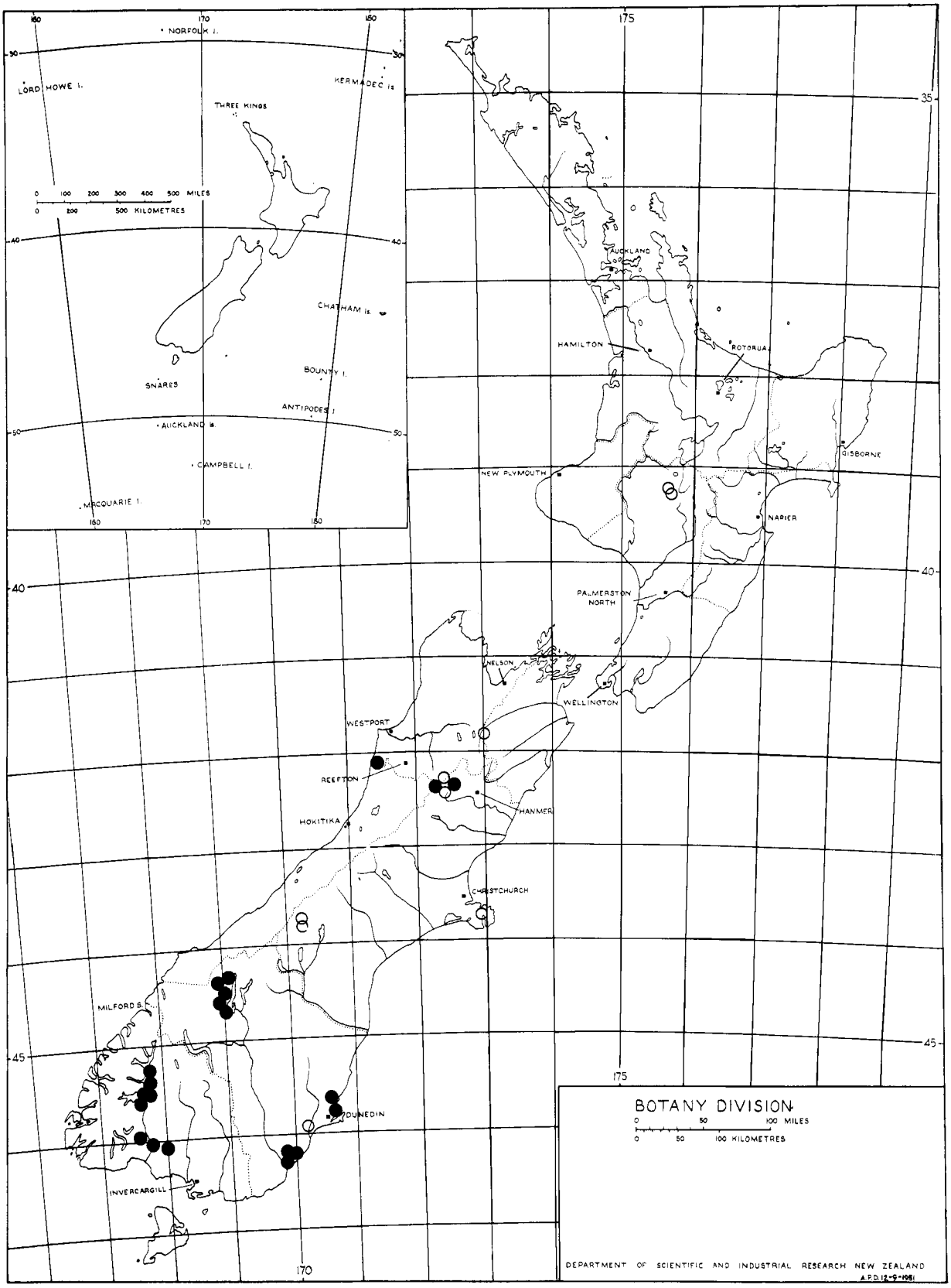

FIGURE 24.—Distribution of *Parmelia subtestacea* in New Zealand. (Circles = unknown #27 chemotype; solid dots = echinocarpic acid and unknown #27 chemotype.)

elev. 350 m, South Island, New Zealand, *M.E. Hale* 65402, 30 Jan 1984 (US; isotypes in CHR, BM).

REMARKS.—Galloway and Elix (1983) recently summarized their knowledge of the intergrading morphologies and diverse chemical patterns that characterize the *P. testacea* complex, corticolous lichens especially common in New Zealand and Tasmania. They concluded from a study of herbarium specimens that this complex represented a single variable species, *P. testacea,* but also stressed the need for more detailed field studies.

Hoping to elucidate this species more fully myself for this monograph, I conducted field studies of several weeks duration in New Zealand and Tasmania in 1984 and 1985, randomly collecting 902 specimens at 86 localities. All of the material was chromatographed and examined for spores and morphology. I concluded that the *P. testacea* complex can be divided into two distinct major groups, the *P. crambidiocarpa* group (*P. crambidiocarpa, P. norcrambidiocarpa* and *P. salcrambidiocarpa*) and the *P. testacea* group (*P. subtestacea* and *P. testacea*).

In terms of gross morphology, the *P. testacea* group is distinguished by the adnate to closely adnate thallus, irregularly lobed thallus with frequent production of roundish to flaring marginal secondary lobes, by the relatively sparse, mostly marginal pseudocyphellae, and by sparse to moderate rhizines. In contrast the *P. crambidiocarpa* group has sublinear lobes, infrequent production of secondary lobes, marginal and laminal pseudocyphellae, and dense rhizines (see *P. crambidiocarpa* for fuller discussions of the differences).

The *Parmelia testacea* group has three different lichen substances produced in four different combinations: echinocarpic acid–unknown #27, salazinic acid, salazinic acid–unknown #27, and unknown #27 alone. Of 381 random collections on North and South islands of New Zealand, the echinocarpic acid–unknown #27 chemotype made up 56% (215 specimens) and unknown #27 alone 7% (26 specimens). These two chemotypes define *P. subtestacea.* The other two combinations with salazinic acid (salazinic acid–unknown #27 in 99 specimens (26%) and salazinic acid alone in 41 (11%)) constitute *P. testacea.*

The chemotypes have strong geographical correlations. *Parmelia subtestacea* with echinocarpic acid–unknown #27 does not occur on North Island at all but predominates on South Island (Figure 24), where it makes up 71% of the group (215 of 302 collections). It is virtually the only member of the group found south of the Mt. Cook region, and north of Mt. Cook it occurs chiefly in the Arthurs Pass and Lewis Pass regions. Salazinic acid-containing *P. testacea* is essentially allopatric, occurring mostly at low elevations north of Lewis Pass, eastern Canterbury, and on North Island. All specimens of the group in Tasmania are *P. testacea.*

The apothecia of *P. subtestacea* are adnate to substipitate, most often with an open pale tan disc (69% of 32 fertile specimens examined) or light to medium brown (28%) or rarely dark brown (3%). Spores are small and thin-walled: Average maximum dimension 8.7 × 12.6 µm (range 7–10 × 11–15 µm for 22 specimens examined). Eight fertile collections of the unknown #27 chemotype have virtually identical apothecia and spore dimensions but 75% of the specimens have a brown or dark brown apothecial disc with only 25% pale tan.

Parmelia subtestacea is especially common on roadside *Nothofagus* and other trees (e.g., *Griselina lucida, Leptospermum ericoides, Metrosideros tomentosa*) in most forested areas of South Island. It is, however, rare at base level in mature, dense forests, where it occurs only on canopy branches. The upper limit of elevatioun is about 600 m, above which the *P. crambidiocarpa* group occurs.

The chemotype unknown #27 alone is considered to be the "acid-free" chemotype of *P. subtestacea.* It is rare and I collected only 27 specimens out of 241 in this group. It occurred with the echinocarpic acid–unknown #27 chemotype at 4 localities, intermixed on the same trees, and alone at 4 other localities. On North Island, where the echinocarpic acid–unknown #27 chemotype is lacking, I collected 13 specimens with unknown #27 at just two localities, 12 of them in a mass sample of a fallen tree near the Tongariro National Park headquarters on Okahune road. No specimens have been collected at the same sites as *P. testacea,* and this is the main justification for recognizing this chemotype as the acid-free chemotype of *P. subtestacea.*

Representative Specimens Examined
(echinocarpic acid and unknown #27)

New Zealand: South Island, *Allan* CHR160348 (CHR), *Galloway* CHR342966 (CHR), *Hale* 63246, 65220, 65466, 65585, 65643, 65758, 65820 (US), *Tihomson* CHR342997 (CHR).

Representative Specimens Examined
(unknown #27 alone)

New Zealand: North Islandn, *Hale* 65552 (US); South Island, *Elix* 6989, 7085, 7138 (ANUC), *Hale* 65505, 65777 (US), *Martin* ZA111 (CHR).

Parmelia sulcata

FIGURES 7*f*, 23*b*

Parmelia sulcata Taylor, 1836:145. [Type collection: Dunkerron, Kerry, Ireland, *Taylor* s.n. (FH-Tayl, lectotype; BM, US, isolectotypes).]

Parmelia saxatilis var. *rosiformis* (*"rosaeformis"*) Acharius, 1810:470. [Type collection: Sweden, s.c. (H-Ach., lectotype).]

Parmelia saxatilis var. *sulcata* (Taylor) Nylander, 1860:389.

Parmelia cruenta Darbishire, 1912:13. [Type collection: Navarino Island, Tierra del Fuego, Chile, *Skottsberg* s.n. (S, lectotype; BM, isolectotype).]

Parmelia rosiformis (Acharius) Gyelnik, 1928:592.

Parmelia sulcata f. *aberrans* Zahlbruckner, 1931:84. [Type collection: Cerro El Roble do Libun, Chile, *Espinosa* s.n. (W, lectotype).]

Parmelia rosiformis f. *cretaceosorediosa* Gyelnik, 1931b:289. [Type collection: between Monor and Pilis, Hungary, *Timkó* s.n. (BP, lectotype).]

Parmelia rosiformis f. *pomazensis* Gyelnik, 1931b:289. [Type collection: near Pomáz, Pest, Hundary, *Gyelnik* s.n. (BP, lectotype).] near Pilisszántó, Pest, Hungary, *Kummerli et al.* s.n. (BP, lectotype).]

Parmelia rosiformis f. *rufescentisorediosa* Gyelnik, 1931b:290. [Type collection: Zlatnó, Hungary, *Vángel* s.n. (BP, lectotype).]

Parmelia rosiformis f. *subnullisorediosa* Gyelnik, 1931b:290. [Type collection: Mt. Paulmauer, St. Aegyd, Austria, *Suza* s.n. (BP, lectotype).]

Parmelia rosiformis f. *turocensis* Gyelnik, 1931b:290. [Type collection: near Stubnyafürdö, Turoc, Hungary, *Margittai* s.n. (BP, lectotype).]

Parmelia rosifomis f. *viridisorediosa* Gyelnik, 1931b:289. [Type collection: Nagyszénás Mountains near Budapest, Hungary, *Gyelnik* s.n. (BP, lectotype).]

Parmelia rosiformis var. *pseudoviridis* Gyelnik, 1932b:448. [Type collection: St. Gilgen, Austria, *Gyelnik* s.n. (BP, lectotype).]

Parmelia rosiformis f. *fagicola* Gyelnik, 1932b:450. [Type collection: near Kudsir, Hungary, *Gyelnik* s.n. (BP, lectotype).]

[See Hillmann (1936) for additional subspecific epithets that I consider to be synonyms.]

DESCRIPTION.—Thallus adnate to loosely adnate on bark and rock, rather firm, greenish to whitish mineral gray, 8–20 cm broad; lobes sublinear but rather short, crowded to imbricate, 2–5 mm wide; upper surface shiny, becoming strongly foveolate, continuous to irregularly cracked with age, pseudocyphellae effigurate, 0.3–1 mm long, laminal and marginal, separate, soon becoming sorediate, the soralia marginal and laminal along the ridges; lower surface black, densely rhizinate, the rhizines becoming densely squarrosely branched. Pycnidia poorly developed; conidia (Figure 12*i*) cylindrical, straight to slightly bent, 6–8 µm long (Hillmann (1939) reports 5–8 µm). Apothecia rare, substipitate, 2–6 mm in diameter, the amphithecium smooth, the rim sorediate, disc dark brown; hymenium 55–60 µm; spores usually poorly developed, 6–8 × 11–14 µm, the episporium 1 µm thick.

CHEMISTRY.—Atranorin and chloroatranorin, salazinic acid (Galloway and Elix, 1983), and consalazinic acid. Dey (1978) also reports accessory lobaric acid.

REMARKS.—*Parmelia sulcata* is easily typified by material in the Taylor herbarium. Gyelnik (1930) chose the name *"rosaeformis"* because it is older (but of a different rank!) than *sulcata*. Although Magnusson (1933) disapproved of this name change for such a long-established species, he need not have worried, because this epithet was never actually used in species rank. Zahlbruckner's (1929:216) reference to *"P. rosaeformis* Röhl." is erroneous. Röhling merely cited *"P. rosaeformis"* as a variety of *P. saxatilis*.

The most important diagnostic characters of *P. sulcata* are the well-developed laminal soralia and the richly squarrosely branched rhizines. Morphological variation in lobe configuration is slight. Most of the numerous varieties and forms have been described on the basis of soredial characters, such as coarseness and color. The chemistry is very uniform. No accessory substances were detected among approximately 100 specimens tested with thin layer chromatography, although Dey (1978) reported specimens from the Appalachian Mountains with lobaric acid.

Parmelia sulcata is very closely related to *P. fertilis*, its probable parent morph, which is less foveolate and has less dense pseudocyphellae and slightly smaller conidia. The two species are largely allopatric. The companion isidiate morph, *P. squarrosa*, is more closely related to *P. fertilis*.

This is a very widespread, even weedy species (see map of the American arctic distribution in Thomson, 1984:318, and of the Australasian distribution in Galloway and Elix, 1983:412), which is more common than *P. saxatilis* in temperate and subboreal regions. The rarity of the species in Japan, however, is remarkable (Kurokawa, 1968). In austral regions it has been collected as far south as Georgia (59°S), where it may in fact have been introduced from whaling ships (Lindsay, 1973a).

Representative Specimens Examined

Canada: Newfoundland, *Waghorne* 116 (US); Quebec, *Bigelow* s.n., *Fabius* 696, 7830 (US); Ontario, *Cain* 26889 (TRT, US), *Hale* 34806, 34912 (US); Alberta, *Hale* 38944, *Turner* 10174 (US); British Columbia, *Macoun* 150 (US); Northwest Territories, *Hale* 329 (US). USA: Maine, *Hale* 37626, *Harris and Bailey* 5855 (US); Vermont, *Drushel* 10581 (US); Massachusetts, *Gates* 2244, *Smith* 12388 (US); Connecticut, *Hale* 158, 14768 (US); New York, *Hale* 16664, *Hermann* 14441, *Ogden* 54109 (US); New Jersey, *Hale* 15315, *Leonard* 6428 (US); Pennsylvania, *Hale* 16058, 19107, *Olday* 356 (US); Maryland, *Hale* 14488, 14506, *Norden* 36 (US); West Virginia, *Allard* 10858, *Hale* 12608, 16647 (US); Michigan, *Hale* 11081 (US), *Imshaug* 25423 (MSC, US); Minnesota, *Fink* 57, *Hale* 23148 (US), *Wetmore* 21759, 22774 (MIN, US); North Dakota, *Trana and Disrud* 71038 (US); South Dakota, *Hale* 49737 (US), *Wetmore* 10352 (MIN, US); Montana, *Hale* 48612, 49201 (US); Idaho, *Hale* 49374 (US); Wyoming, *Hale* 49178 (US); Colorado, *Weber and Shushan* 29132, *Shushan* 5205 (COLO, US); New Mexico, *Hale* 48924, *Imshaug* 10008, *Standley* 13985 (US); Arizona, *Darrow* 1853 (US); Washington, *Ireland* 5997 (US); Oregon, *Hale* 21562, 48499 (US); California, *Brown* 737, *Hale* 51762, *Herre* 450, *Lindsay* 258, *Tucker* 6219 (US). Argentina: Tierra del Fuego, *Imshaug* 54304, 54445 (MSC), *Santesson* 432 (S, US), 410, 611, 1098, 7878 (S). Chile: Magallanes, *Imshaug* 38699, 39310 (MSC), *Santesson* 1844, 6384, 7999, 8189 (S). Greenland: *Hansen* in *Lichenes Groenlandici Exsiccati* 12. Ireland: W. Mayo, *Wattam* s.n. (BM). Great Britain: Cumberland, *Johnson* 69 (BM). Finland: *Fagerstrom* in *Lichenotheca Fennica* 685 (US), *Lai* 10954 (US). Sweden: *Almborn and Hale* 33458, *Kjellmert* s.n. (US). Denmark: *Christiansen* s.n. (US). Germany: *Erichsen* 159 (US). France: *Crozals* s.n. (US). Hungary: *Fóriss* in *Lichenotheca Hungarica* 527. Spain: *Vasquez and Rico* s.n. (US). Portugal: *Sampaio* in *Lichenes de Portugal* 258, *Tavares* in *Lichenes Lusitaniae Selecti Exsiccati* 169 (US). USSR: *Elias et al.* L-67970 (COLO, US). Kenya: *Hedberg* 1846b (UPS, US). Nepal: Khumbu, *Poelt* 124, 137, 201 (M). India: Kashmir, *Awasthi* 2628, 993 (AWAS). New Zealand: South Island, *Du Rietz* 1713:7 (UPS, US), *Hale* 65095, 66429 (US), *Martin* 5373 (BM, US). Australia: New South Wales, *Elix* s.n. (ANUC).

Parmelia tenuirima

FIGURES 8*a*, 23*c*

Parmelia tenuirima Hooker and Taylor, 1844:645. [Type collection: Tasmania, "van Diemens Land," *Gunn* s.n. (FH-Tayl. herb. sheet 1131, lectotype; BM, isolectotype).]

Parmelia tenuiscypha Taylor, 1847:175. [Type collection: Macquarry River, Australia, *Ball herb.* (FH-Tayl, lectotype). See Müller Argoviensis, 1888:203.]

Aspidelia beckettii Stirton, 1900:81. [Type collection: New Zealand, *Beckett*

s.n. (BM, lectotype (not seen); see Culberson, 1966:114).]

Parmelia tenuirima var. *platyna* Zahlbruckner, 1941:108. [Type collection: Mt. Cargill, Dunedin, New Zealand, *Thomson* ZA56 (W, lectotype).]

DESCRIPTION.—Thallus adnate to loosely adnate on bark, rather firm, pale to dark greenish mineral gray, 8–60 cm broad; lobes broad and subirregular, 4–10 mm wide, often clearly black rimmed; upper surface shiny, sometimes coarsely white maculate, plane to foveolate in older parts, continuous but cracking along old pseudocyphellae, the pseudocyphellae effigurate, fairly small but conspicuous, 0.5–1 mm long, marginal and laminal, uniformly scattered, separate; lower surface black except for a brown marginal bare zone, sparsely to moderately rhizinate, the rhizines simple to thickly squarrosely branched, 1–1.5 mm long. Pycnidia common; conidia cylindrical to slightly bent, a few vaguely bifusiform, 5.5–7.0 µm long. Apothecia common, stipitate, 5–15 mm in diameter, the amphithecium rugose, pseudocyphellate, the disc brown, radially split and sometimes perforate with age; hymenium 65–70 µm; spores 8–10 × 12–15 µm, the episporium about 1 µm thick.

CHEMISTRY.—Atranorin and chloroatranorin, salazinic acid (Culberson, 1966; Galloway and Elix, 1983), and consalazinic acid.

REMARKS.—This distinctive species has the broadest lobes of any in the genus, with conspicuous, separate pseudocyphellae. It often has a faintly greenish cast. Closely related *P. signifera*, largely a saxicolous species, has denser, net-forming pseudocyphellae and a brownish cast. *Parmelia tenuirima* is common at higher (and wetter) elevations in southeastern mainland Australia, but reaches its best development at higher latitudes in New Zealand and Tasmania (see distribution map in Galloway and Elix, 1983:415), occurring most often on lower trunks of large *Nothofagus* trees in open mossy forests, where colonies attain enormous size.

Hillmann (1939) examined this species rather carefully and disposed of most of the published subspecific names. He regarded f. *corallina* Müller Argoviensis as a probable distinct species, at least a variety (it is now recognized as *P. erumpens* Kurokawa). A f. *sorediata* Müller Argoviensis (1894:258), based on a Holst specimen from Usambara, is *Parmotrema reticulatum* (Taylor) Choisy. A variety described by Wilson (1893), var. *multifida*, was not found by Hillmann or me. Finally, f. *isidiosa* Müller Argoviensis had already been raised to species level by Gyelnik as *P. pseudotenuirima* over Hillmann's objections ("Von der Anschauung ausgehend, dass jede 'planta isidiosa' eine eigene Species darstellt hat Gyelnik die f. *isidiosa* Müll. Arg. ... zur Art erhoben").

Specimens Examined

New Zealand: North Island, *Hale* 58886, 66468 (US); South Island, *Du Rietz* 1760:1, 1851:b (UPS, US), *Galloway* s.n. (CHR), *Hale* 65086, 65755 (US), *James* 488, 1531 (BM, US), *Martin* 557 (BM), *Thomson* T.522 (CHR), *Wade* 96 (BM). Australia: Australian Capital Territory, *Hale* 59395 (US); New South Wales, *Hale* 59357, 59370 (US), *Weber and McVean* L-49328 (US); Tasmania, *Brown* s.n. (BM), *James* Au2112, Au2116 (BM), *Oldfield* s.n. (US), *Pearcey* s.n. (BM); Victoria, *Degelius* A-218 (US), *Filson* 6508, 7038 (US), *James* Au2115 (BM), *Lam* 7509b (US).

Parmelia testacea

FIGURES 8*b*, 23*d*, 25

Parmelia testacea Stirton, 1877–1878:203. [Type collection: near Wellington, North Island, New Zealand, *Buchanan* s.n. (BM, lectotype; CHR, solectotype).]

Parmelia tenuirima **P. rudior* Nylander, 1888:25. [Type csollection: New Zealand, *Knight* 27 (H, Nyl. herb. no. 35289, lectotype).]

Parmelia tenuirima Hooker and Taylor var. *erimis* Nylander, 1888:25. [Type collection: New Zealand, *Knight* 55 (H, Nyl. herb. no. 35286, lectotype).]

Parmelia rudior (Nylander) Zahlbruckner, 1929:198.

Parmelia erimis (Nylander) Hillmann, 1939:259.

Parmelia signifera f. *pallidior* Zahlbruckner, 1941:107. [Type collection: Dunedin, South Island, New Zealand, *Thomson* ZA249 (W, lectotype). The syntype (Otago Heads, *Thomson* ZA211 in W) is *Parmotrema reticulatum* (Taylor) Choisy.]

DESCRIPTION.—Thallus adnate to closely adnate on bark, thin and rather brittle, pale greenish gray, 5–15 cm broad; lobes sublinear to mostly subirregular, short and imbricate, 1–5 mm wide, usually with marginal secondary lobules 1–2 mm wide, flaring to rounded, becoming dense with age; upper surface shiny, plane to rugose-foveolate, continuous, the pseudocyphellae forming a nearly continuous white rim 0.1–0.2 mm wide around the main and secondary lobes, also sparsely laminal on the main or older lobes, separate, 0.2–0.4 mm long, usually not fissuring with age; lower surface black, sparsely to moderately rhizinate but with a distinct narrow bare to papillate brown zone around the margins, the rhizines simple to furcate to sparsely squarrosely branched, 0.5–1.5 mm long. Pycnidia numerous, 90–100 µm in diameter; conidia cylindrical, rod-shaped to weakly bifusiform, 5.5–6.5 µm long (Hillmann (1939) reported them as bifusiform, 6.0–6.5 µm long for the type of *P. erimis*). Apothecia common, adnate to substipitate, generally remaining flat but sometimes cupuliform, 4–20 mm in diameter, the disc very pale tan (sometimes concolorous with the thallus) to medium brown, rarely darkening, splitting radially at maturity, the amphithecium rugose and effigurate-pseudocyphellate; hymenium 60–65 µm; spores 7–10 × 11–15 µm, the episporium 1–1.5 µm thick.

CHEMISTRY.—Atranorin, chloroatranorin, salazinic acid, and usually consalazinic acid, with or without unknown #27 (all types contain unknown #27).

REMARKS.—*Parmelia testacea* (see under *P. subtestacea* for additional discussions of the *P. testacea* complex) is characterized by the adnate, irregularly lobed, marginally pseudocyphellate thallus with sparse to moderate rhizines, small spores, and the presence of salazinic acid. Externally it is indistinguishable from *P. subtestacea*. Adnation and lobe configuration are the same, as are apothecial characters. The apothecia have an average maximum diameter of 8.4 mm and a range of 4–20 mm (29 specimens examined). The disc tends to be pale tan and rarely darkens to brown. Of 29 specimens scored for color, 52% were classified as pale tan, 45% as light

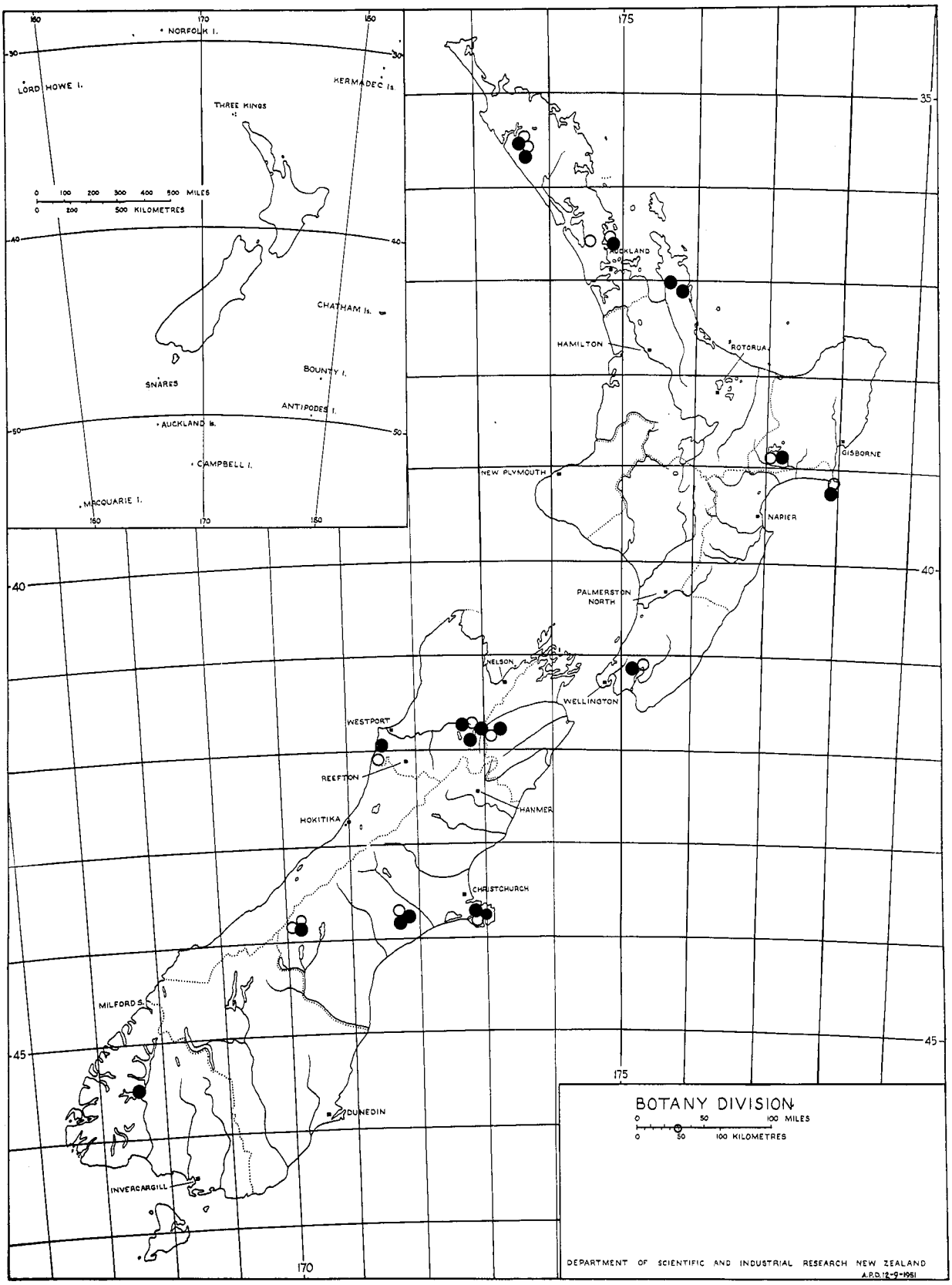

FIGURE 25.—Distribution of *Parmelia testacea* in New Zealand. (Circles = salazinic acid and unknown #27 chemotype; solid dots = salazinic acid chemotype.)

brown, and only 3% as dark brown. Spores are small, the average dimensions being 8.5 × 12.7 μm (range: 7–10 × 11–15 μm for 21 specimens examined), virtually identical with those of *P. subtestacea*.

Parmelia testacea is not chemically uniform. Although the main component is salazinic acid, most specimens (71% or 99 of 140 randomly collected specimens) also contain unknown #27. Specimens containing salazinic acid–unknown #27 were collected at 6 localities, specimens with only salazinic acid at 3 localities, and specimens of both chemotypes at 8 localities, often intermixed on the same trees. In Tasmania, where *P. testacea* was the commonest member of the *P. testacea* complex, all specimens (156 tested) contained salazinic acid and unknown #27.

Parmelia testacea occupies habitats very similar to those of *P. subtestacea,* although the two species are almost completely allopatric, occurring together at only three localities (Tuatapere, Mt. Cook, and Tongariro) (Figure 25). It grows very frequently on *Nothofagus* species in New Zealand and Tasmania, especially on trunks of trees along highways or river banks. In dense forest it grows on canopy branches and is difficult to collect.

Representative Specimens Examined (salazinic acid)

New Zealand: North Island, *Allan* CHR160212 (CHR), *Elix* 8030 (ANUC), *Hale* 58837, 65194, 65763 (US); South Island, *Elix* 7807 (ANUC, CHR), 8171 (ANUC), *Galloway* CHR348312 (CHR), *Hale* 65302, 65377, 65839 (US).

Representative Specimens Examined (salazinic acid and unknown #27)

New Zealand: North Island, *Barton* CHR342984 (CHR), *Elix* 8003 (ANUC), *Hale* 65112, 65196, 65385, 65740, 65775 (US); South Island, *Elix* 6677, 7716 (ANUC), *Galloway* CHR240705 (CHR), *Hale* 65304, 65335, 65769 (US), *Taylor* 8a (CHR). Australia: Tasmania, *Kantvilas* 125/82 (ANUC), *Hale* 68613, 68636-642, 68671, 68688 (US).

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(Synonyms in italics)

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