BULLETIN OF THE UNITED STATES NATIONAL MUSEUM

CONTRIBUTIONS FROM THE UNITED STATES NATIONAL HERBARIUM

VOLUME 34, PART 7 (END OF VOLUME)

# THE LICHEN GENERA CETRELIA AND PLATISMATIA (PARMELIACEAE)

By WILLIAM LOUIS CULBERSON
and CHICITA F. CULBERSON

SMITHSONIAN INSTITUTION PRESS • WASHINGTON, D.C. • 1968

# Contents

# THE LICHEN GENERA CETRELIA AND PLATISMATIA (PARMELIACEAE)

By WILLIAM LOUIS CULBERSON
and CHICITA F. CULBERSON

## Introduction

In 1960 we undertook a monographic study of the old genus *Cetraria* in the traditionally broad sense that it was understood in Zahlbruckner's *Catalogus Lichenum Universalis*. It soon became obvious that this assemblage contained several major constellations of species and that these species groups were not particularly closely related to each other. One of these major groups is of course *Cetraria* itself, and this genus will be the subject of a future publication. A small, homogeneous, arctic-alpine segregate genus named *Asahinea* has already been treated (Culberson and Culberson, 1965). Two groups remain—the new segregate genera *Platismatia* and *Cetrelia*. The aim of the present study is to describe and delimit these genera and to present a comprehensive treatment of the species which belong to them.

This study has the additional objective of examining the nature of chemical variation in morphologically well defined species groups. It was obvious early in our research that the plants under study showed chemical variations strikingly correlated with morphologic ones. Moreover, the chemical compounds themselves seemed to have closer relationships to each other than those previously noted in other genera of approximately the same size. We decided, therefore, to treat chemistry and morphology in equal detail in our study. Of course, the use of chemistry in lichen taxonomy is now so commonplace that it is impossible to imagine a serious treatment of any group showing chemical diversity in which this aspect of the variation was left unstudied. Few lichenologists, however, have tried to integrate chemical and morphological data or to place chemical variation in the same evolutionary frame of reference in which critical taxonomy places morphological variation. But if we are to involve chemistry in taxonomy, an attempt, however crude, must be made to delineate the nature of chemical variation in lichens. In this monograph we present two genera to serve as subjects for the kind of theoretical speculation that will lead eventually to the structuring of a framework of principles upon which practical taxonomic judgments can rest.

## Historical Background

From the very beginning, generic concepts have been one of the most unsatisfactory aspects of the taxonomy of lichenized fungi. Linnaeus, in his *Species Plantarum* of 1753, considered all the species as members of the single genus *Lichen* and, to the detriment of lichenology, the insensitive Linnaean treatment was selected as the starting point for the nomenclature of the whole group. Even Acharius, the first botanist to see the lichens with a discerning and critical eye, began by keeping all the species in the genus *Lichen* (Acharius, 1798), obviously simply in deference to tradition. A few years later though, in 1803, he divided the lichens into some two dozen genera, one of them being *Cetraria*.

As originally described, the genus *Cetraria* contained eight species, namely:

*C. islandica* (L.) Ach.
*C. cucullata* (Bell.) Ach.
*C. nivalis* (L.) Ach.
*C. lacunosa* Ach.
*C. fallax* (L.) Ach.
*C. glauca* (L.) Ach.
*C. sepincola* (Ehrh.) Ach.
*C. juniperina* (L.) Ach.

The genus soon became a general repository for all parmeliaceous plants with marginal or submarginal apothecia. It was used in its Acharian sense for the species listed above and for related species by most of the major lichenological authors of the nineteenth century, for example, Schaerer, Fries, Tuckerman, Körber, and Massalongo. Nylander alone among the leading lichen students of the time arranged the species differently. He took up the almost forgotten genus *Platisma* described by Hoffmann in 1790—although he changed the spelling to "*Platysma*"—and used it to classify all but one of Acharius' *Cetrariae* (Nylander, 1855). In so doing, he effectively typified the genus *Cetraria* Ach. with *Lichen islandicus* L. by leaving only that species in it (Culberson, 1966b). Nylander's revival of *Platysma* reflected his belief that *Cetraria*, as conceived by other botanists of the time, was not homogeneous.

Although all these species had marginal or submarginal apothecia and pycnidia, it was difficult to find any other major traits shared by even the restricted list of species that Acharius originally put into the genus. In the original complement of species listed above, Nylander saw the erect, linear-lobed, subfruticose, soil-inhabiting *Cetraria islandica* as an element too foreign from the other more distinctly foliose species to be classified in the same genus with them. Nylander, however, apparently did not question the generic affinity of all the foliose species that he recognized in *Platysma*. He saw no obstacle to classifying the broad-lobed, *Parmelia*-like *Cetraria glauca* and the narrow-lobed, erect, soil-inhabiting species such as the familiar *C. cucullata* and *C. nivalis* in the same genus.

As time passed, other workers described many more species in *Cetraria*, and the generic concept became more nebulous still. There were species with marginal, reflexed apothecia, such as *Cetraria stracheyi* Bab., that in some later classifications were transferred to the genus *Nephromopsis* Müll. Arg. There was also a whole array of very broad-lobed forms, most of them foreign to Europe and superficially resembling the *Amphigymnia* Parmelias, for example *Cetraria sanguinea*, *C. collata*, and *C. japonica* from the Orient. In addition, a few particularly anomalous species, such as *C. chrysantha* Tuck. and *C. thomsonii* Stirt., were put in *Cetraria* in spite of their lacking any connection whatever with the bulk of the species already classified there, except for having marginal apothecia.

The *Catalogus Lichenum Universalis* (Zahlbruckner, 1930) took a particularly broad view of *Cetraria* and included all the plants mentioned above and most of their obvious relatives, excluding only a few of the species as members of the genus *Nephromopsis*. Zahlbruckner's *Catalogus* had the effect of rigidly formalizing these generic concepts. With the exception of this study, subsequent treatments have either followed him in recognizing *Cetraria* and *Nephromopsis* (Räsänen, 1952) or have taken a still more conservative position and recognized only *Cetraria* (Rassadina, 1950). Only Eilif Dahl tried to evaluate the major variations among the plants that had been referred to *Cetraria* and to define the major natural groups in an assemblage of species that years of casual taxonomy had left biologically meaningless.

## The "Parmelioid" *Cetrariae*

Dahl challenged the monophyletic nature of *Cetraria* sens. lat. He pointed out that *Cetraria glauca* (L.) Ach., *C. norvegica* (Lynge) Du Rietz, *C. collata* Müll. Arg., and *C. chrysantha* Tuck. differed from the true Cetrarias both morphologically and chemically. The cortex in these species, he demonstrated, is composed of densely agglutinated hyphae with tiny lumina, a type of cortex that he called "platysmoid" but which is more commonly called prosoplectenchymatous (Ozenda, 1963). The upper cortex of true Cetrarias, on the other hand, is composed of thin-walled hyphae with inflated lumina, a type generally termed paraplectenchymatous. These anatomical differences were correlated with the distribution of some lichen substances. The dozen true Cetrarias that Dahl analyzed chemically were characterized by a predominance of usnic acid and fatty acids while the species with a prosoplectenchymatous cortex were characterized by a predominance of atranorin. On the basis of this morphological and chemical information, Dahl postulated that *Cetraria* sens. lat. was polyphyletic. He segregated the species with the prosoplectenchymatous upper cortex and the presence of the substance atranorin from the true Cetrarias and used the old genus *Platisma* Hoffm. to accommodate them.

When we started our study of the lichens traditionally assigned to *Cetraria*, we made a preliminary survey to determine the general range of the morphological and the chemical variation. It was soon obvious that the difference that Dahl had pointed out between the "true" Cetrarias and the members of the *Cetraria glauca* group was indeed a basic one, and it held up as even more and more species were considered. We thereupon decided to put aside the true Cetrarias and to study first the broad-lobed species that had traditionally been classified with them, a group which for convenient reference we can call the "parmelioid" *Cetrariae*.

The "parmelioid" *Cetrariae* include the *Cetraria glauca* group as well as such species as *C. sanguinea, C. japonica*, and *C. collata*. These latter Asiatic species all have pseudocyphellae, a trait present in some but not all members of the *C. glauca* group. Although the position of *C. sanguinea* and *C. japonica*, for example, had never been seriously disputed, apparently no one had noticed that these species were extremely closely related to other species that have always been considered Parmelias, for example *Parmelia cetrarioides* and *P. olivetorum*. (But the superficial similarity of *P. cetrarioides* Del. to the Cetrarias was pointed out from the very beginning by Delise in his choice of the specific epithet.) A species which several years ago was (erroneously) being called *Cetraria collata* in North America is so similar to *Parmelia cetrarioides* that the two species can be separated from each other with certainty only by chemical tests. Although we were unsure of the taxonomic disposition which should be made of all these species, it was clear that *P. cetrarioides* and *P. olivetorum* were very closely related to at least some of the "parmelioid" *Cetrariae* and that they should be classified with them and not among the true *Parmeliae*.

Our knowledge of the "parmelioid" *Cetrariae* was summed up when we compared these plants, the true Cetrarias, and the *Amphigymnia* Parmelias to three very peculiar, distinctive, and closely related species which had been classified in *Cetraria* and which we defined as the new genus *Asahinea* (Culberson and Culberson, 1965). The traits of the "parmelioid" *Cetrariae* and the three other species groups were summarized then in a form which we present here with only slight modifications (Table 1).

But the "parmelioid" *Cetrariae* are themselves not a homogeneous group. From the outset it was clear that the bulk of the "parmelioid" *Cetrariae* really consists of two distinct constellations of species rather than of a single spectrum of forms. Although from Dahl's treatment we might have expected these species to be characterized by the presence of fatty acids as the medullary lichen substances, only some of the

TABLE 1.—*A comparison of the Major traits in* Parmelia *sect.* Amphigymnia, Asahinea, *the "parmelioid"* Cetrariae (=Cetrelia+Platismatia), *and* Cetraria *sens. str.*

| | *Parmelia* sect. *Amphigymnia* (106 species) | *Asahinea* (3 species) | "Parmelioid" *Cetrariae* (24 species) | *Cetraria* sens. str. (about 75 species) |
|---|---|---|---|---|
| Cortex | prosoplectenchymatous | prosoplectenchymatous | prosoplectenchymatous | paraplectenchymatous |
| Rhizines | present | absent | present | present in most |
| Marginal ciliae | present in many | absent | absent | present in some |
| Pycnidia | laminal | laminal or marginal | marginal | marginal |
| Apothecia | laminal | laminal or marginal | laminal or submarginal | marginal |
| Disc | perforate in many | imperforate | perforate in most | imperforate |
| Lichen substances | many; aromatic and aliphatic | 4 aromatic | many; aromatic and aliphatic | many; aromatic and aliphatic |
| Distribution | nearly worldwide | Northern Hemisphere, arctic-montane | Northern Hemisphere, mainly temperate | Northern Hemisphere, arctic-temperate |

species were actually found to contain fatty acids. More than half the species produced (as medullary constituents) one or more aromatic compounds, orcinol-type depsides (anziaic, imbricaric, microphyllinic, olivetoric, and perlatolic acids), or orcinol-type depsidones (alectoronic and $\alpha$-collatolic acids). All the species producing aromatic compounds exclusively as the medullary substances belong to the "*Parmelia cetrarioides*" group while those producing a fatty acid (invariably caperatic acid) as the medullary constituent all belong to the "*Cetraria glauca*" group. The chemistry of the species of the two groups is summarized in Table 2. An analysis of the chemical relationships of the compounds in each group is given in a discussion farther on.

The two groups into which the species fall by similarity of general habit as well as by chemistry of the medullary substances are marked by suites of additional morphological and chemical traits (Table 3). Internally, each of the two groups of the "parmelioid" *Cetrariae* is extremely uniform and yet each is so distinct from the other that they cannot be considered congeneric. We propose the genus *Platismatia* for the 10 members of the *Cetraria glauca* group and *Cetrelia* for the 14 members of the *Parmelia cetrarioides* group.

As characterized here, the genera *Cetrelia* and *Platismatia* both show relatively conservative variation and extremely high levels of internal homogeneity. The chemical variation here is far more precisely cor-

TABLE 2.—*The distribution of the constant chemical substances in the species of* Cetrelia *and* Platismatia *and the number of specimens tested of each species. The few unidentified "accessory" substances found are not tabulated*

| | atranorin | caperatic | alectoronic | anziaic | α-collatolic | fumarprotocetraric | imbricaric | microphyllinic | olivetoric | perlatolic | Number tested |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *CETRELIA* | | | | | | | | | | | |
| *alaskana* | + | | | | | | + | | | | 14 |
| *braunsiana* | + | | + | | + | | | | | | 32 |
| *cetrarioides* sens. str. | + | | | | | | | | | + | 35 |
| *cetrarioides* sens. lat. | + | | | | | | + | | | | 34 |
| *chicitae* | + | | + | | + | | | | | | 24 |
| *collata* | + | | | | | | + | | | | 17 |
| *davidiana* | + | | | | | | | | + | | 7 |
| *delavayana* | + | | | | | | | | | + | 8 |
| *isidiata* | + | | | + | | | | | | | 4 |
| *japonica* | + | | | | | | | + | | | 22 |
| *nuda* | + | | + | | + | | | | | | 22 |
| *olivetorum* | + | | | | | | | | + | | 19 |
| *pseudolivetorum* | + | | | | | | | | + | | 31 |
| *sanguinea* | + | | | + | | | | | | | 67 |
| *sinensis* | + | | | | | | + | | | | 6 |
| *PLATISMATIA* | | | | | | | | | | | |
| *erosa* | + | + | | | | | | | | | 17 |
| *formosana* | + | + | | | | | | | | | 2 |
| *glauca* | + | + | | | | | | | | | 11 |
| *herrei* | + | + | | | | | | | | | 5 |
| *interrupta* | + | + | | | | | | | | | 20 |
| *lacunosa* | + | + | | | | + | | | | | 8 |
| *norvegica* | + | + | | | | | | | | | 7 |
| *regenerans* | + | + | | | | | | | | | 4 |
| *stenophylla* | + | + | | | | | | | | | 5 |
| *tuckermanii* | + | + | | | | | | | | | 7 |

related with visible traits (Table 3) than in most genera of the macrolichens. All the species of *Platismatia* produce the aliphatic fatty acid caperatic acid as the medullary constituent and only one species produces a β-orcinol-type depsidone (fumarprotocetraric acid) in addition to the aliphatic substance. The species of *Cetrelia*, on the other hand, never produce fatty acids as the medullary constituents but only aromatic substances—orcinol-type depsides and depsidones, substances all rather closely related to each other chemically.

One might wonder whether the genera *Cetrelia* and *Platismatia*, as

**TABLE 3.**—*A comparison of the major traits in* Platismatia *and* Cetrelia, *the two genera constituting the "parmelioid"* Cetrariae

| *Cetrelia*<br>(=the *Parmelia cetrarioides* group) | *Platismatia*<br>(=the *Cetraria glauca* group) |
|---|---|
| Upper surface always pseudocyphellate | Upper surface usually pseudocyphellate |
| Soredia rare | Soredia common |
| Isidia common | Isidia rare |
| Lobulae absent | Lobulae common |
| Upper cortex always IKI− | Upper cortex often IKI+ |
| Subhymenium thick, IKI− | Subhymenium thin, IKI+ |
| Thick zone of algae usually present immediately below subhymenium | Algae usually absent from immediately below subhymenium |
| Spores large, ellipsoid, 11–22 × 6–12μ | Spores small, subspherical, 5–8 × 3–5μ |
| Pycnidia common in most species | Pycnidia rare in most species |
| Pycnoconidia with inflated ends | Pycnoconidia without inflated ends |
| Medullarly chemistry: substances all aromatic orcinol-type depsides and and depsidones | Medullary chemistry: the aliphatic substance caperatic acid in every species (one species also with a depsidone) |
| 14 species | 10 species |
| Greatest species concentration in eastern and southeastern Asia | Greatest species concentration in the amphi-North Pacific |

delimited by the morphological and chemical criteria explained above, show phytogeographically meaningful distributional patterns, since such distributions are expected in monophyletic genera. While many parts of the world remain inadequately explored lichenologically, the plants that we are concerned with here are large and conspicuous and have often been collected, even by amateur plant hunters. Their general conspicuousness and the frequency of their collection give one a confidence in the significance of maps of their distribution that one would not have for smaller, less noticeable cryptogams. In Figure 1 the number of species of *Cetrelia* and of *Platismatia* in floras in various parts of the world is plotted. It is obvious from these maps that the genera have very different centers of maximum species numbers although both genera are circumpolar. *Platismatia* is represented most abundantly in the amphi-North Pacific, especially western North America. *Cetrelia*, on the other hand, is most richly represented in East and Southeast Asia. From this phytogeographic evidence it would seem indisputable that *Cetrelia* and *Platismatia* had different centers of origin. It is also noteworthy that neither genus is represented in Australia or New Zealand. *Cetrelia* is not present in Africa, and *Platismatia* is represented there only by a few isolated mountain stations for the ubiquitous *Platismatia glauca*. The genus *Cetraria* (in the strict sense) likewise does not exist in Africa but *Parmelia* sect. *Amphigymnia* (Hale, 1965) is richly represented there. *Cetrelia* is also absent from South America, and *Platismatia* is repre-

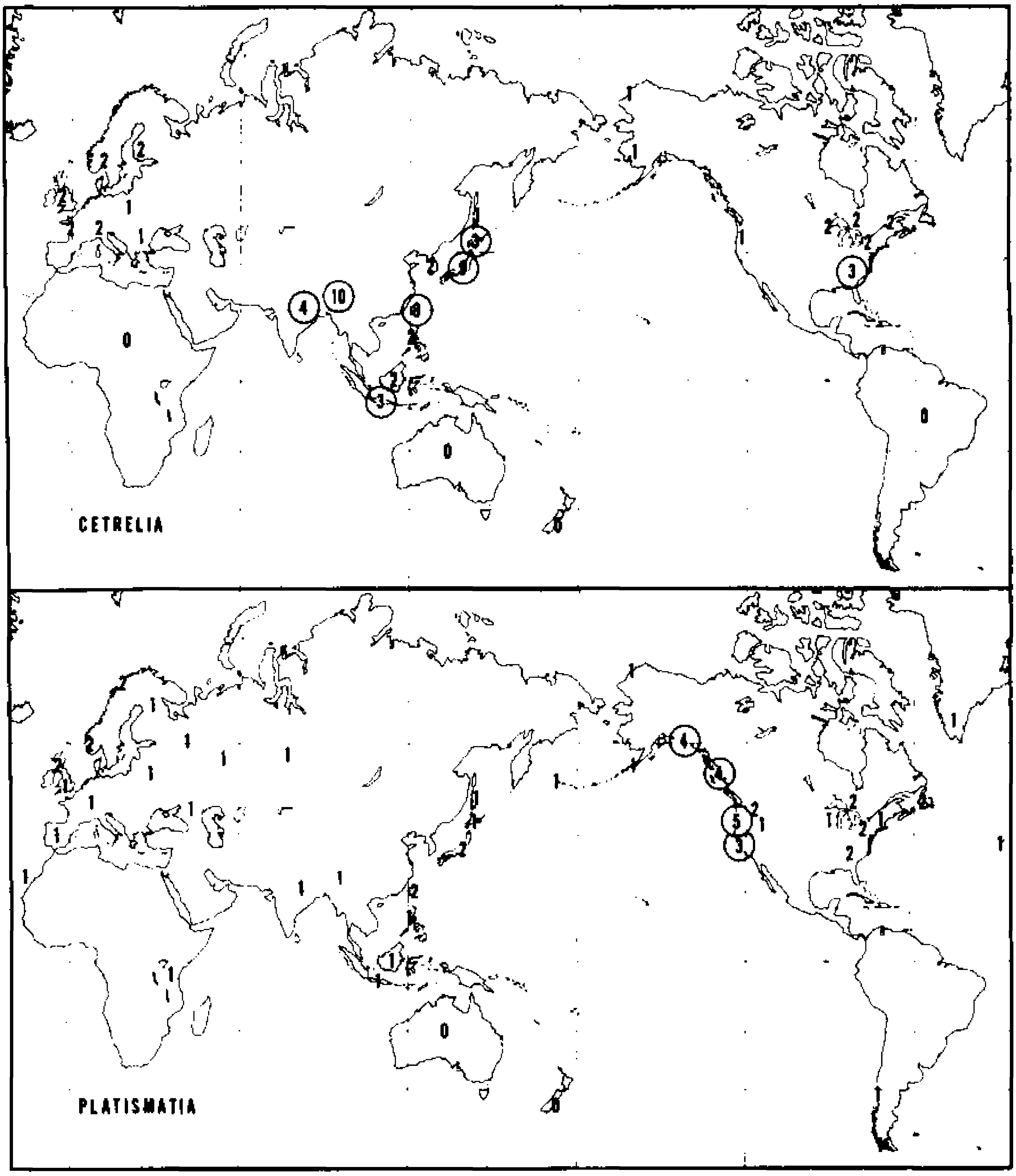


FIGURE 1. The distribution of the genera *Cetrelia* (above) and *Platismatia* (below) by numbers of species in floras in various parts of the world.

sented only in the southern part of that continent and there again by *P. glauca* alone. Both *Cetrelia* and *Platismatia* are temperate, Northern Hemisphere genera, but their different centers of origin and overall ranges clearly indicate that the distinctive morphological and chemical traits that characterize them are the product of different and independent evolutionary histories.

## Morphology

The following morphological characteristics have proved to be the most useful in the study of the species of the genera *Cetrelia* and *Platismatia:*

## CORTEX

The genera of macrolichens, with a few exceptions such as *Collema*, have a true cortex. The cortex is recognizable as the outermost part of the thallus and shows a greater range of anatomical variation than any other vegetative tissue. It may consist of hyphae that are essentially free, erect, and at right angles to the surface of the thallus (e.g., *Roccella*), or interwoven and parallel to the surface of the thallus (e.g., *Anaptychia*), or densely agglutinated throughout. If the hyphae are agglutinated, they may be either inflated and have large lumina (paraplectenchyma)—as in *Peltigera*, *Leptogium*, or *Sticta*—or they may be very little if at all inflated and have tiny lumina (prosoplectenchyma)—as in *Ramalina* and *Parmelia*. The various cortex types have been summarized by Ozenda (1963). In general the major cortex variations closely follow generic lines and the members of a single genus generally all tend to show the same cortex type.

Dahl (1952) pointed out that the species of true *Cetrariae* which he studied have a paraplectenchymatous cortex and that the species which he assigned to the genus *Platysma* have a prosoplectenchymatous cortex. This distinction between the true *Cetrariae* and the so-called "parmelioid" *Cetrariae* has held up even after all the known species have been examined. It is a basic difference of fundamental importance between the "parmelioid" *Cetrariae*—the genera *Platismatia* (Plate 8, Figures 43–44), *Cetrelia* (Plate 8, Figure 42), and *Asahinea* (Plate 7, Figure 40)—and the true *Cetrariae* (Plate 7, Figures 37–38). In its anatomy, the upper cortex of *Cetrelia* and *Platismatia* is very similar to that of the species of *Parmelia* sect. *Amphigymnia* (Plate 7, Figure 39) and indeed to that of the whole genus *Parmelia*, it would seem, although a detailed study of cortex structure throughout *Parmelia* has never been made. The importance of cortex anatomy in defining the "parmelioid" *Cetrariae* as distinct from *Cetraria* is so great that these species would be considered isolated from *Cetraria* even without the accompanying, correlated evidence based upon morphology and chemistry (Table 1). But the fact that *Cetrelia* and *Platismatia* actually have a large series of other traits separating them from the true *Cetrariae* merely underlines the basic and deep-seated nature of their taxonomic isolation from *Cetraria*.

Although cortex structure clearly separates *Cetraria* sens. str. from *Platismatia*, *Cetrelia*, and *Asahinea*, it shows no variations of major consequence among these three genera. The upper cortex in *Platismatia* and *Cetrelia* ranges from about 15 to 30μ thick and the lower cortex from about 10 to 30μ thick. The lower cortex of these genera bears rhizines here and there although naked areas may be extensive. In producing rhizines from the lower cortex these genera differ strikingly from *Asahinea* which does not (Culberson and Culberson, 1965). In addition, although not strictly a cortex trait, a reddish-purple pigment is also generally produced in the lower part of the medulla in *Asahinea*, especially in moribund zones near the lower cortex. It is notable that such pigmentation never occurs in *Cetrelia* or *Platismatia*.

## PSEUDOCYPHELLAE

Pseudocyphellae are small pores in the cortex through which, if they are big enough, the medulla is directly visible. The upper cortex of all the species of *Cetrelia* and of about half the species of *Platismatia* is pseudocyphellate.

In *Cetrelia* there are two kinds of pseudocyphellae, the small type (Plate 12, Figure 52) and the large type (Plate 12, Figure 73). Most species have pseudocyphellae of the small type. These little apertures are less than a millimeter wide and punctiform or irregular in shape. *Cetrelia cetrarioides*, *C. chicitae*, and *C. braunsiana*, for example, all have small pseudocyphellae. Large pseudocyphellae, found in *C. nuda* and *C. collata*, exceed one millimeter in width and often appear to result from the confluence of smaller pores. In the species producing large pseudocyphellae, many specimens show at least some pseudocyphellae of the small type as well.

The distinction between small and large pseudocyphellae was especially valuable in distinguishing *Cetrelia chicitae* and *C. nuda* in Japan. Table 5, under the treatment for *C. braunsiana* (p. 495), shows the distribution of pseudocyphellae of these two types as compared to the distribution of other morphological traits among these three related species in Japan.

## PUNCTA

Perforations found in the lower cortex of some of the species may have distinct taxonomic significance. These pores may not all be of similar origin, and those in *Platismatia* appear to be somewhat different from those in *Cetrelia*. To stress the fact that the exact nature of these peculiar pores or spots in the lower cortex is not clear, we call them puncta rather than pseudocyphellae.

Puncta are best developed in the lower cortex of *Platismatia erosa* (Plate 11, Figure 51) and *P. formosana* where they furnish a valuable trait for distinguishing the former species from the closely related *P. interrupta* and the latter species from the morphologically somewhat similar species *P. lacunosa*. Other members of *Platismatia* lack these conspicuous interruptions in the lower cortex altogether.

A number of species of *Cetrelia* also shows similar spotlike modifications of the lower cortex. The species of *Cetrelia* which produce puncta do not do so invariably, however, and in this genus the tendency to produce a punctate lower cortex has little taxonomic value. *Cetrelia cetrarioides, C. collata, C. davidiana,* and *C. isidiata* all consist of individuals that show at least some puncta in the lower cortex and others that do not, and the occurrence or absence of the trait does not seem to be correlated with any other variations. On the other hand, some *Cetrelia* species—for example *C. alaskana, C. braunsiana,* and *C. sanguinea*—never produce a punctate lower cortex.

In *Cetrelia* some of the puncta are actual pores in the lower cortex and are apparently equivalent to the well developed ones seen in some species of *Platismatia.* But in *Cetrelia* the lower cortex may also show pale flecklike spots and every intergradation between these spots and the true punctate pores. It may be that puncta originate as spots and finally become an actual hole in the lower cortex. In general, though, the abundance of the spots is greater in individuals of such species as *Cetrelia cetrarioides* than is the abundance of true perforations.

In examining the lower cortex of *Cetrelia* species for puncta, one often sees tiny holes in the cortex that are wounds which were made when the specimen was removed from its substrate. Careful observation will distinguish such irregular, sharp-edged wounds from the punctate pores and the associated spotting discussed above, both of which are entirely natural attributes of the plants. Puncta in the lower cortex of *Parmelia* (=*Cetrelia*) *olivetorum* and *P. cetrarioides* were observed by Gyelnik (1933), who was so impressed by these "pseudocyphellae" that he described two new species, *Pseudoparmelia aradensis* and *P. pseudofallax,* based upon them. A year later he (Gyelnik, 1934) reduced *Pseudoparmelia pseudofallax* to a form of *Parmelia* (=*Cetrelia*) *cetrarioides* after he discovered that these "pseudocyphellae" were common and widespread in the latter species. Later still, in a study of the putative genus *Pseudoparmelia,* Santesson (1942) showed that the "pseudocyphellae" in *Pseudoparmelia cyphellata* Lynge, the only species in the genus prior to Gyelnik's two additions, were nothing but wounds where the lower cortex had been pulled off with the rhizines at the time of collection. Santesson assumed that the "pseudocyphellae" in the lower cortex of specimens assigned to this genus by Gyelnik were analogous to those which he described and illustrated in the South American species *P. cyphellata.* But from Gyelnik's descriptions it is clear that the "pseudocyphellae" which he saw in the European plants that he studied were puncta, as defined in the present study, and not wounds of casual origin.

### ISIDIA

Isidia are rare in *Cetrelia* but relatively common in *Platismatia.* In *Cetrelia* only *C. braunsiana* (Plate 13, Figure 55) and *C. isidiata* are truly isidiate. In both these species, however, some individuals are almost devoid of isidia altogether.

In an occasional plant of some ordinarily lobulate species, such as *C. pseudolivetorum* or *C. sinensis*, some of the thallus appendages or lobulae along the margins of the lobes may be so reduced in size that they do not show the dorsiventrality typical of lobulae but resemble isidia instead. These species should properly not be considered isidiate.

In the genus *Platismatia* the species *P. norvegica*, *P. erosa*, and *P. herrei* are regularly isidiate as are many individuals of the polymorphic *P. glauca*. Even in the habitually isidiate species, nonisidiate individuals are sufficiently common to be found with some regularity and, as one would guess, the extent of isidia production in isidiate individuals varies greatly. Also, in some sorediate species the soredia become consolidated into structures that are distinctly isidioid. *Platismatia interrupta* is a particularly variable species in which the soredia may become isidioid; some populations of *P. glauca* also show this tendency.

## SOREDIA

Soredia are common in *Cetrelia* but relatively rare in *Platismatia*—essentially the reverse of the situation for isidia in these genera. The members of the *Cetrelia cetrarioides* group, with the single exception of *C. alaskana*, are all sorediate. The soredia are very fine and powdery and are produced, usually in abundance, at the edge of the lobes in continuous marginal soralia (Plate 13, Figure 54). The soralia are often so small that they can be seen easily only with some magnification.

In *Platismatia* there are no species in which soredia production is an invariable diagnostic trait. Soredia are produced, however, in some specimens of *P. glauca* and in many of *P. interrupta*. In these species the soredia often become isidioid, especially in the older parts of the thallus. In *Platismatia* the soredia are granular and laminal rather than minute and marginal as in *Cetrelia*.

It should be mentioned that an occasional specimen of certain species of *Platismatia*, such as *P. norvegica*, shows the development of conspicuous, capitate soralia on the upper surface of the lobes. Soralia of this sort are so infrequent yet so different from the ordinary soredia in both *Platismatia* and *Cetrelia* that they do not seem to be a normal thallus development at all. They are so anomalous that we regard them as a pathological abnormality and give them no taxonomic significance.

## LOBULAE

Lobulae are minute, dorsiventral lobes on the upper surface and the margins of the thallus. In some specimens they are produced in such abundance on the surface of the thallus that the plants appear to be cristate while in others they are more prominent on the margins so that the thallus appears to be elegantly fringed with tiny lobes. As we characterize them, lobulae are found in the genus *Cetrelia* but not in *Platismatia*. In *Cetrelia* they are restricted to the *C. japonica* complex of species, which includes *C. sinensis* and *C. pseudolivetorum* as well as *C. japonica* (Plate 17, Figure 63). Since both lobulae and isidia are similar in that they are entirely corticate and have an algal zone and a medulla, it is not surprising that they seem to intergrade in form in some specimens. In *C. pseudolivetorum*, for example, many of the lobulae produced are so small and narrow that they no longer show a distinct dorsiventrality and consequently closely resemble isidia. Since no entirely and truly isidiate race of *C. pseudolivetorum* is known, however, it would seem that the isidialike structures sometimes encountered in this species would better be interpreted as extremely reduced lobulae.

In *Platismatia* there are no structures analogous to the lobulae of *Cetrelia*. In fact, the only modified appendages produced at all are the special, branched, coralloid structures that develop from the expanded thallus lobes in some specimens of *Platismatia glauca* (Plate 21, Figure 70) and, more rarely, in *P. herrei*. These fruticose structures, however, are quite different from the tiny foliose lobulae produced by the species of *Cetrelia* discussed above.

## APOTHECIA

In both *Cetrelia* and *Platismatia* the apothecia (Plate 10) are usually produced on the upper surface of the lobes and appear less frequently at the margins. In the position of the apothecia, both genera differ sharply from *Cetraria* in which the apothecia are strictly marginal.

With the exception of a few species, apothecial production in *Platismatia* is very infrequent. In *Cetrelia*, too, apothecia are very rare, except in the *C. collata* group. In both genera the infrequency of apothecial production contrasts strongly with the situation in *Cetraria* where apothecia are generally very common. The rarity of apothecia in the genera studied herein, however, recalls the *Amphigymnia* Parmelias in which the total lack or at least high infrequency of apothecia is typical of many species.

The only species of *Cetrelia* in which apothecia are produced with high regularity is the *collata* group—the species *C. sanguinea*, *C. davidiana*, *C. delavayana*, and *C. nuda*, in addition to *C. collata*. In Japan, 83 percent of the herbarium specimens of *C. nuda* were found to bear apothecia, and *C. sanguinea* in Java also often fruits. *Cetrelia collata*, *C. davidiana*, and *C. delavayana* are known in fruit, but these Chinese species have rarely been collected and the overall frequency of apothecia in them is impossible to assess.

In the *Cetrelia cetrarioides* complex—including *C. cetrarioides*, *C. alaskana*, *C. isidiata*, *C. chicitae*, *C. olivetorum*, and perhaps *C. braunsiana*—only *C. chicitae* has been found in fruit with anything approaching commonness. In Japan about 17 percent of the plants are fertile, but in North America apothecial production in this species is much rarer. Although apothecia are known for *C. cetrarioides*, *C. olivetorum*, and *C. braunsiana*, they are very uncommon. In *C. cetrarioides*, in fact, only a single specimen bearing apothecia with apparently mature spores was seen in this study; and in *C. alaskana* and *C. isidiata* apothecia have never been observed at all.

In the *C. japonica* group, *C. japonica* and *C. pseudolivetorum* are very rarely known to fruit, while the other member of the complex, *C. sinensis*, has never been found with apothecia.

In *Platismatia*, apothecia are also very rarely produced, with two notable exceptions. The two North American species *P. tuckermanii* and *P. stenophylla* commonly fruit and almost every well developed specimen has apothecia. Two species, however, have never been found in fruit—*P. interrupta*, a common species in Japan, and *P. regenerans*, an apparent endemic of North Borneo. Apothecia in all the remaining six species of *Platismatia*—*P. erosa*, *P. formosana*, *P. glauca*, *P. herrei*, *P. lacunosa*, and *P. norvegica*—are known, but their occurrence is rare.

Many of the apothecia of both *Cetrelia* (Plate 11, Figure 50) and *Platismatia* become perforate, especially with age. In this trait they recall the species of *Parmelia* sect. *Amphigymnia* in which perforate apothecia are common. The true *Cetrariae*, however, have imperforate apothecia.

Internally, the apothecia of *Platismatia* and *Cetrelia* differ in a number of ways. In most species of *Platismatia* the subhymenium is in direct contact with the medulla while in *Cetrelia* a thick layer of algae separates the subhymenium from the medulla. The subhymenium of *Platismatia* and that of *Cetrelia* seem to differ markedly with regard to the products which make up the hyphal cell walls and, as a result, they also differ with regard to the color reactions that they exhibit with the IKI reagent. In *Cetrelia* the subhymenium remains uncolored in the presence of IKI, but in *Platismatia* it becomes some shade of purple, violet, lavender, or blue. There is, incidentally, no exception to this general difference. These reactions of the subhymenium, however, should not be confused with the dark blue reaction with IKI of the asci in the hymenium. This latter reaction is very widespread, probably universal, in both genera.

## ASCOSPORES

Spores in the Parmeliaceae generally have been of very little systematic use. In *Platismatia* and *Cetrelia*, however, there is a very clear distinction in the spores at the generic level. In *Platismatia* (Plate 9, Figure 46) the spores are small and short-ellipsoid, ranging in length from 5 to 8μ and in width from 3 to 5μ, with many of the spores being essentially subglobose. In *Cetrelia* (Plate 9, Figure 45), however, the spores are twice as large as those of *Platismatia* and range in length from 11 to 22μ and in width from 6 to 12μ. The large, more or less thick-walled spores of *Cetrelia* are very similar to those of the *Amphigymnia* Parmelias and less like the much smaller spores of the true Cetrarias.

## PYCNIDIA

Like the apothecia, the pycnidia in the two genera are infrequent in general, only a very few species producing them with appreciable regularity. In *Cetrelia*, in fact, pycnidia are unknown altogether in five species, namely, *C. alaskana*, *C. cetrarioides*, *C. isidiata*, *C. olivetorum*, and *C. pseudolivetorum*. Pycnidia are known, but are infrequent to rare, in *C. braunsiana*, *C. chicitae*, *C. japonica*, and *C. sinensis*. Only in the *C. collata* complex do they appear to be common, although some of the Chinese species in this group—*C. collata*, *C. davidiana*, and *C. delavayana*—have been collected too infrequently to permit generalizations. *Cetrelia nuda* (Plate 10, Figure 49), the commonest member of this group in Japan, showed pycnidia in 100 percent of the specimens examined in Japanese herbaria. It will be recalled that it is precisely the *C. collata* complex, of which *C. nuda* is a member, which is the only segment of the genus *Cetrelia* regularly bearing apothecia. A high production of apothecia and a high production of pycnidia are very closely correlated in this group. Of course, the explanation could simply be that these species have a natural tendency to produce both these structures. Nevertheless, one is tempted to assume an intimate relationship in the close correlation of apothecia and pycnidia. If pycnidia and conidia (the pycniospores) which they produce were functioning here in sexual reproduction, then the high frequency of pycnidia in plants also bearing apothecia would be explained.

In *Platismatia* the situation is the same. The only two species in which pycnidial production is frequent are *Platismatia stenophylla* and *P. tuckermanii*. These are also the only two species of the entire genus which produce apothecia with great regularity. In *P. erosa*, *P. regenerans*, and *P. interrupta*, pycnidia are unknown altogether. *Platismatia interrupta* is noteworthy in this regard since it also has never been found with apothecia in spite of its being common in many parts of Japan. The other five species of *Platismatia*—*P. formosana*, *P. herrei*, *P. lacunosa*, *P. norvegica*, and *P. glauca*—all produce pycnidia very infrequently. Pycnidia are so rare in *P. glauca*, in fact, that none was seen in the hundreds of specimens of this common species examined in this study.

In both *Cetrelia* and *Platismatia* the pycnidia are produced on the margins of the lobes and not on the upper surface. In position, then, the pycnidia of both genera are similar to those of *Cetraria*.

The conidia in both genera are rod-shaped and small and measure about 1 by 4 to 5μ. Conidia in *Cetrelia* seem to be produced in the pycnidia with a higher frequency and in greater abundance than in *Platismatia* where pycnidia, seemingly without conidia, are more common. It also appears to be a consistent difference between the two genera that mature conidia in *Cetrelia* have inflated ends while those in *Platismatia* do not.

## Chemistry

Of the ten substances identified in the species studied, a fatty acid (caperatic acid) and a β-orcinol-type depsidone (fumarprotocetraric acid) occur only in *Platismatia*, seven orcinol-type depsides and depsidones occur only in *Cetrelia*, and a β-orcinol-type depside (atranorin) is found in all species of both genera (Table 2). In this section an attempt will be made to suggest how these substances are related to each other. The discussion will be based primarily upon a comparison of the structures of these compounds in the light of what is known about biosynthetic pathways.

All the compounds involved here are derived from acetate and malonate units. An early branching point in the biosynthetic pathway (Figure 2) leads either to aliphatic compounds like the fatty acids or to aromatic substances like the phenolic acids. Phenolic acids may be

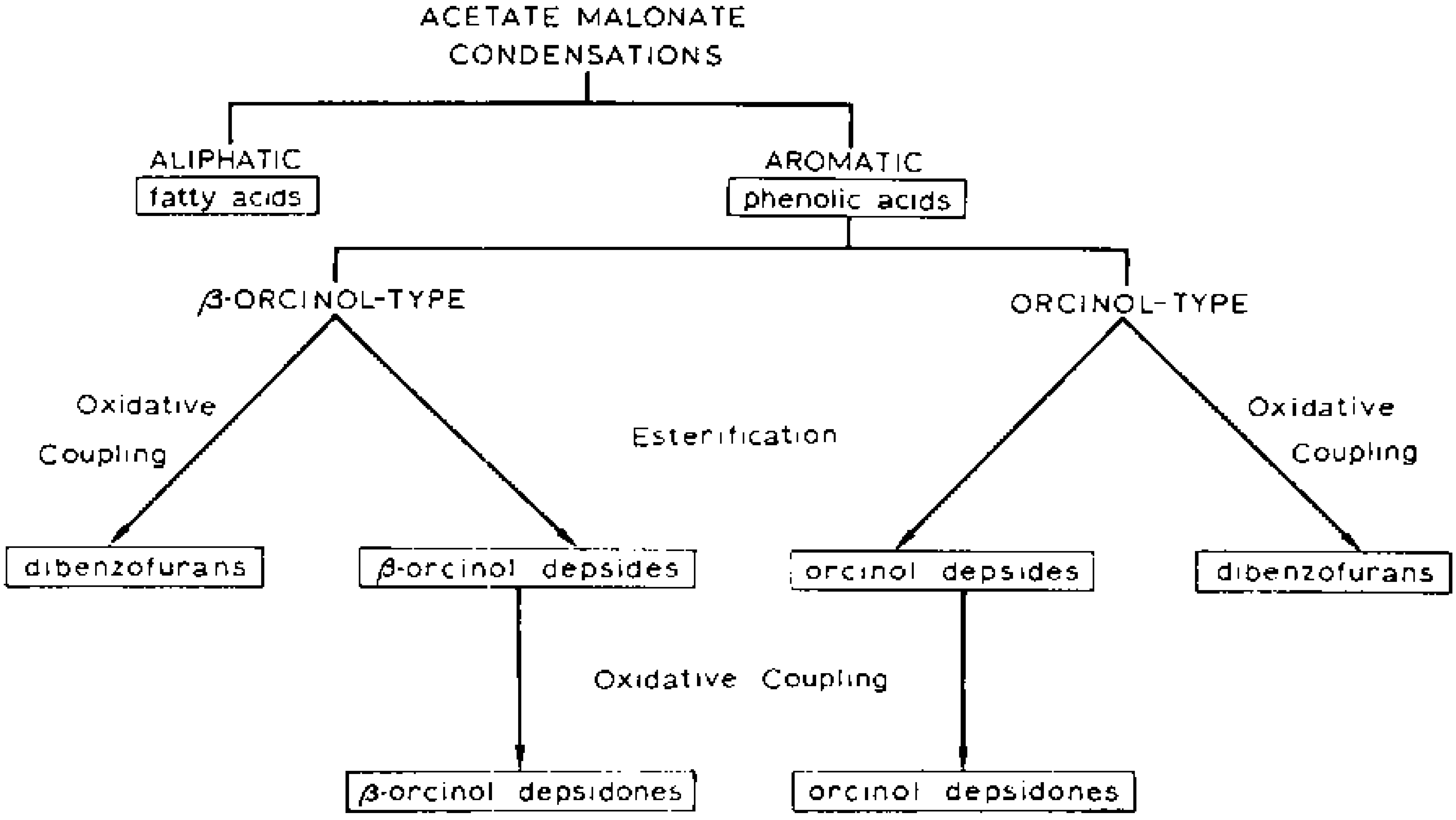


FIGURE 2. A generalized diagram showing postulated biosynthetic pathways in the elaboration of several major categories of taxonomically important lichen substances.

substituted by one of two patterns: namely, orcinol-type compounds like the medullary substances in *Cetrelia* or β-orcinol-type compounds like atranorin and fumarprotocetraric acid in *Platismatia*. Simple orcinol- and β-orcinol-type phenolic acids are esterified to depsides, and some depsides are cyclized to depsidones by oxidative coupling. They may also be methylated, chlorinated, hydroxylated, or decarboxylated (not shown in Figure 2). Various combinations of these relatively few reactions lead to most of the known lichen depsides and depsidones. Direct oxidative coupling of the phenolic acids can give dibenzofuran derivatives known from some species of lichens.

## BIOSYNTHETIC DICHOTOMY LEADING TO AROMATIC AND ALIPHATIC SUBSTANCES

All the substances involved in this study appear to be of acetate-malonate origin (Shibata, 1965). Biosynthesis of fatty acids from acetate and malonate units has been the subject of very extensive studies showing formation of straight-chain aliphatic acids by linear condensations of malonate units after an initial condensation with an acetate unit (Richards and Hendrickson, 1964). Figure 3 presents a simplified version of the condensation of acetate and malonate units with reduction of the carbonyl groups to give a simple, saturated, fatty acid (left side of the figure). Caperatic acid has a slightly more complex structure, with three carboxyl groups (one as a methyl ester) and at least a superficial resemblance to citric acid.

Mosbach (1961, 1964) recently described the biosynthesis of the aromatic substance orsellinic acid from acetate and malonate units, but in this process an oxidized form of the chain of condensed units must undergo cyclization to produce the aromatic-ring system. Figure 3 also shows how one acetate and three malonate units could cyclize to orsellinic acid (right side of the figure). The carbonyl groups which are reduced during fatty-acid synthesis are required in aromatic synthesis to provide the double bonds in the aromatic ring—one of them by the loss of water in the cyclization step and two of them by enolization. Since the carbonyls are on alternate carbon atoms in acetate-malonate-derived carbon chains, *meta* orientation of phenolic groups is observed in the aromatic products.

## ORCINOL- AND β-ORCINOL-TYPE SUBSTITUTIONS

An aromatic ring substituted with one alkyl group and two phenolic groups, such as orsellinic acid, is related to orcinol, and a ring with an additional carbon substituent *para* to the first is related to β-orcinol (Figure 4). Phenolic units in lichen substances are generally substituted according to one of these two systems. The biosnythetic origin

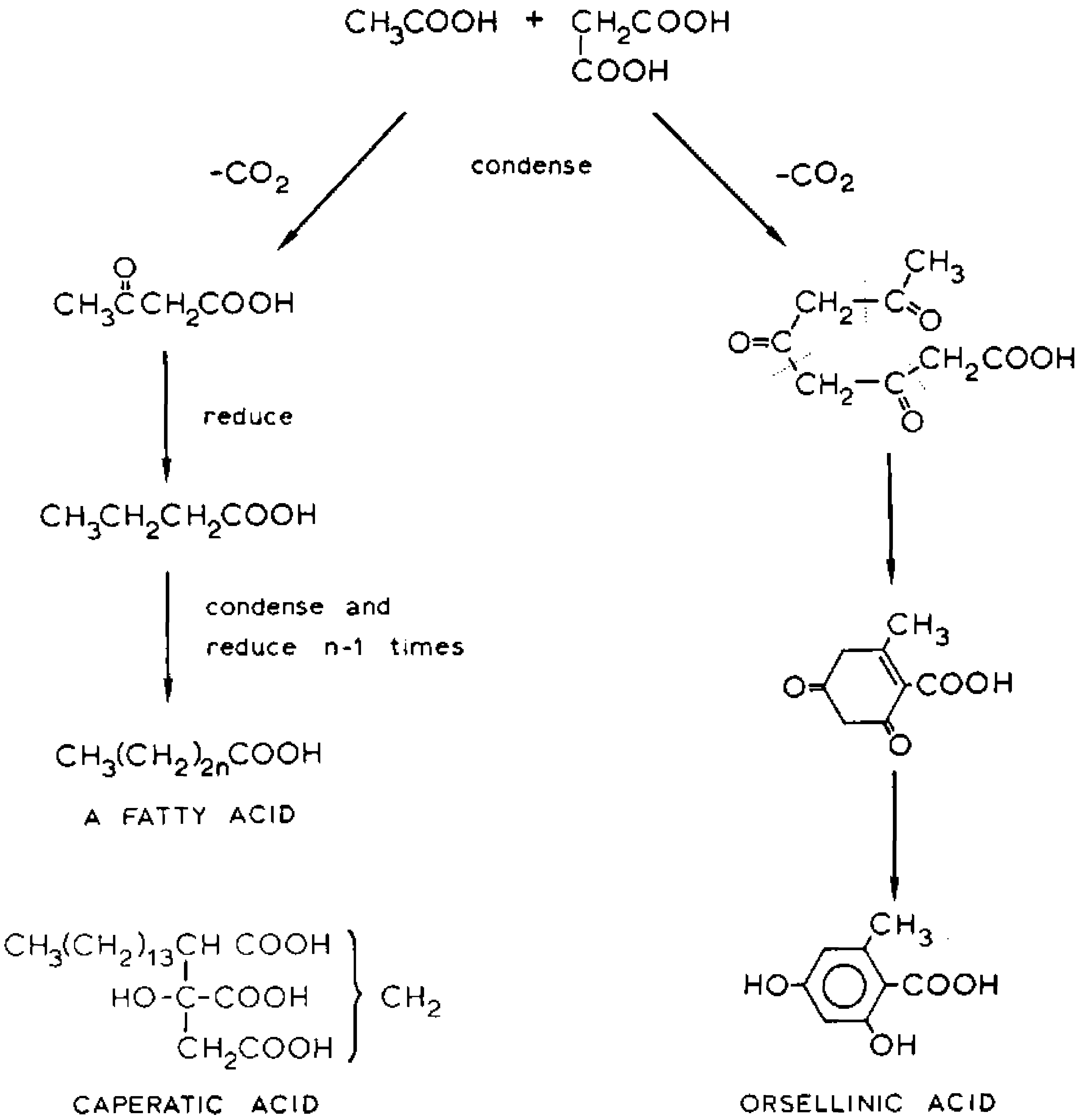


FIGURE 3. A comparison of the biosynthesis of aliphatic acids (on the left) and aromatic phenolic acids (on the right) from acetate and malonate units. (Caperatic acid, the medullary constituent of all species of *Platismatia*, is an example of a typical lichen fatty acid.)

of the extra carbon between the hydroxyl groups in β-orcinol systems is unknown.

If the β-orcinol ring arises by direct carbon substitution onto a preformed orcinol-type ring, then β-orcinol substances would be derived from orsellinic acid by pathway "1" in Figure 4. For the complete synthesis of a depside such as atranorin, several more steps would be required including oxidation to an aldehyde and two esterification reactions. It is also possible to imagine a branched carbon chain which would produce the β-orcinol unit directly by cyclization (Figure 4, pathway "2"). Such a branched chain could form if a propionic acid unit replaced a malonic acid unit in the original condensation. Similar suggestions have been advanced to explain the synthesis of certain aromatic compounds occurring in other groups of plants (for

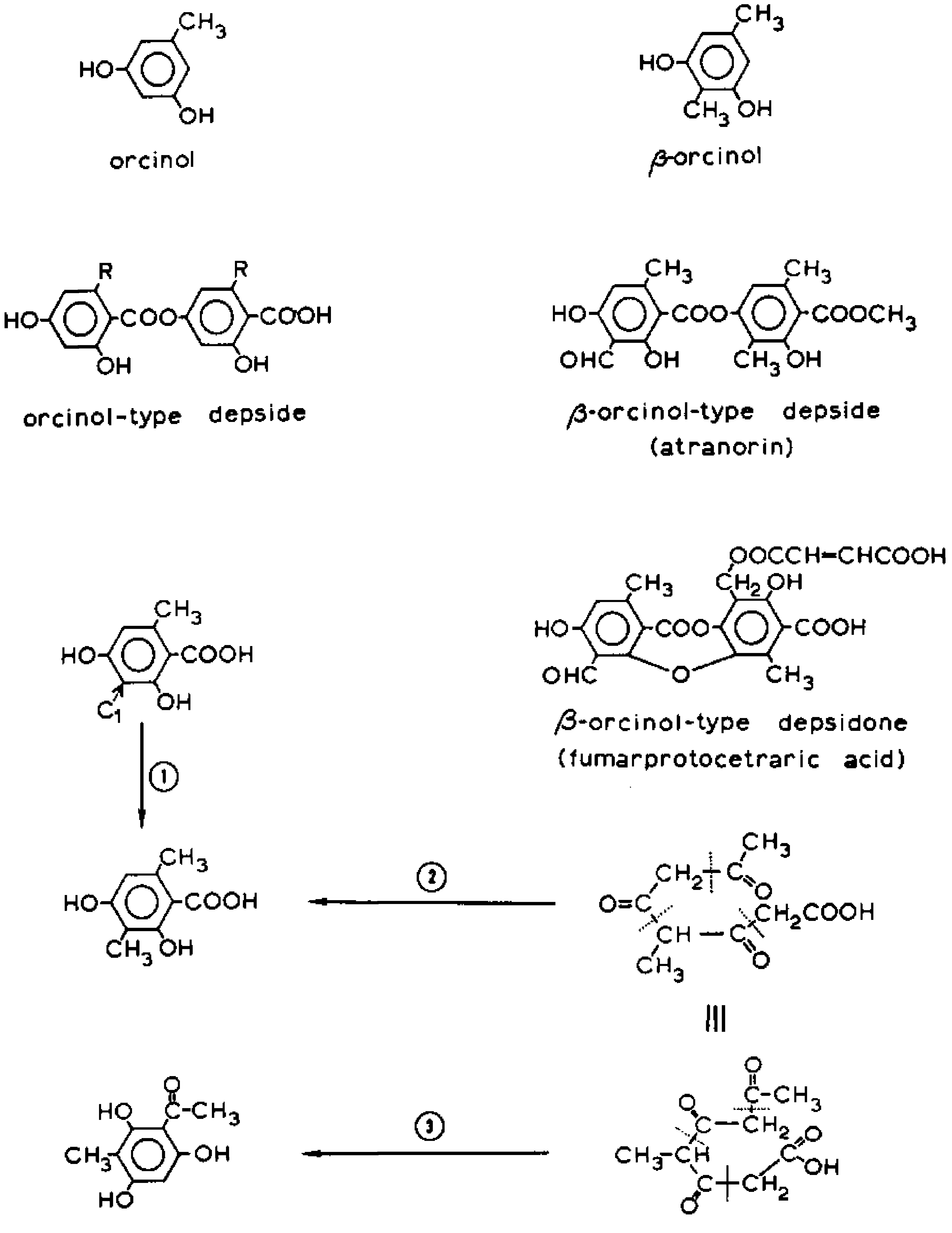


FIGURE 4. A comparison of the structures of orcinol- and β-orcinol-type compounds and two possible biosynthetic pathways (numbered "1" and "2") leading to β-orcinol units. The precursor in pathway "2" could cyclize by pathway "3" to the phenolic unit from which usnic acid is derived.

a discussion, see Whalley, 1963). Perhaps it is not just a coincidence that the same branched carbon chain, cyclizing by a different mechanism, would yield the phenolic ketone required for the synthesis of usnic acid (Figure 4, pathway "3"). Usnic acid and atranorin are by far the two most common lichen substances. Both are found mainly in the upper cortex rather than in the medulla where most of the depsides and depsidones accumulate. The production of a depside or a depsidone in the medulla and either atranorin or usnic acid in the cortex is the most striking pattern observed in the histological distribution of chemical compounds in the macrolichens. Yet the chemical structures of atranorin and usnic acid are so distinct that the possibility of their synthesis from similar starting materials was not immediately obvious.[1]

The production of β-orcinol-type *versus* orcinol-type substances may have distinct taxonomic significance since many groups of lichens show a strong tendency toward the production of one type of compound or the other. In the genera studied here, the medullary constituents of *Cetrelia* are all orcinol-type depsides and depsidones while a β-orcinol depsidone occurs in *Platismatia*. Atranorin, a β-orcinol depside, is found in the upper cortex of all the species of both genera.

## LENGTH AND OXIDATION STATE OF THE SIDE CHAIN IN ORCINOL-TYPE PHENOLIC ACIDS

Figure 3 shows how one acetate and three malonate units could condense to form orsellinic acid, a precursor of many lichen and fungal products. Starting with more than four units would give similar ring systems with a longer side chain. Since each malonate unit contributes two carbons to the final product, the side chain will increase in length in two-carbon steps. Side chains known in lichen substances are $C_1$, $C_3$, $C_5$, and $C_7$. Figure 5 shows the basic phenolic units of the orcinol-type compounds. In the *Cetrelia* compounds, side chains contain five or seven carbons except in ring B of imbricaric acid, which has a three-carbon substituent. In these species there is a tendency toward production of substances with longer side chains than are typical for lichens in general. The orsellinic acid ring, so common in the sub-

---

[1] After this section was written, three studies relating to the biosynthesis of atranorin and usnic acid appeared. Taguchi, Sankawa, and Shibata (1966) elegantly demonstrated that acetate-malonate-derived methylphloroglucinol self-condenses to give usnic acid and that the extra methyl group is indeed incorporated before the aromatic ring is formed. Yamazaki, Matsuo, and Shibata (1965) studied the labeling of lecanoric acid, atranorin, and chloroatranorin in *Parmelia tinctorum* fed with $^{14}C$-labeled acetate and formate. They found incorporation of $^{14}C$ in all three substances when the lichen was fed with labeled acetate, but only in atranorin and chloroatranorin, which are the β-orcinol-type depsides, when the lichen was fed with labeled formate. The results indicate that the extra $C_1$ substituents are supplied by formate. In a second study, Yamazaki and Shibata (1966) showed that $^3H$-labeled orsellinic acid and β-orcinolcarboxylic acid are incorporated exclusively into lecanoric acid and atranorin, respectively, proving that the extra $C_1$ substituent is added before aromatization during the biosynthesis of atranorin.

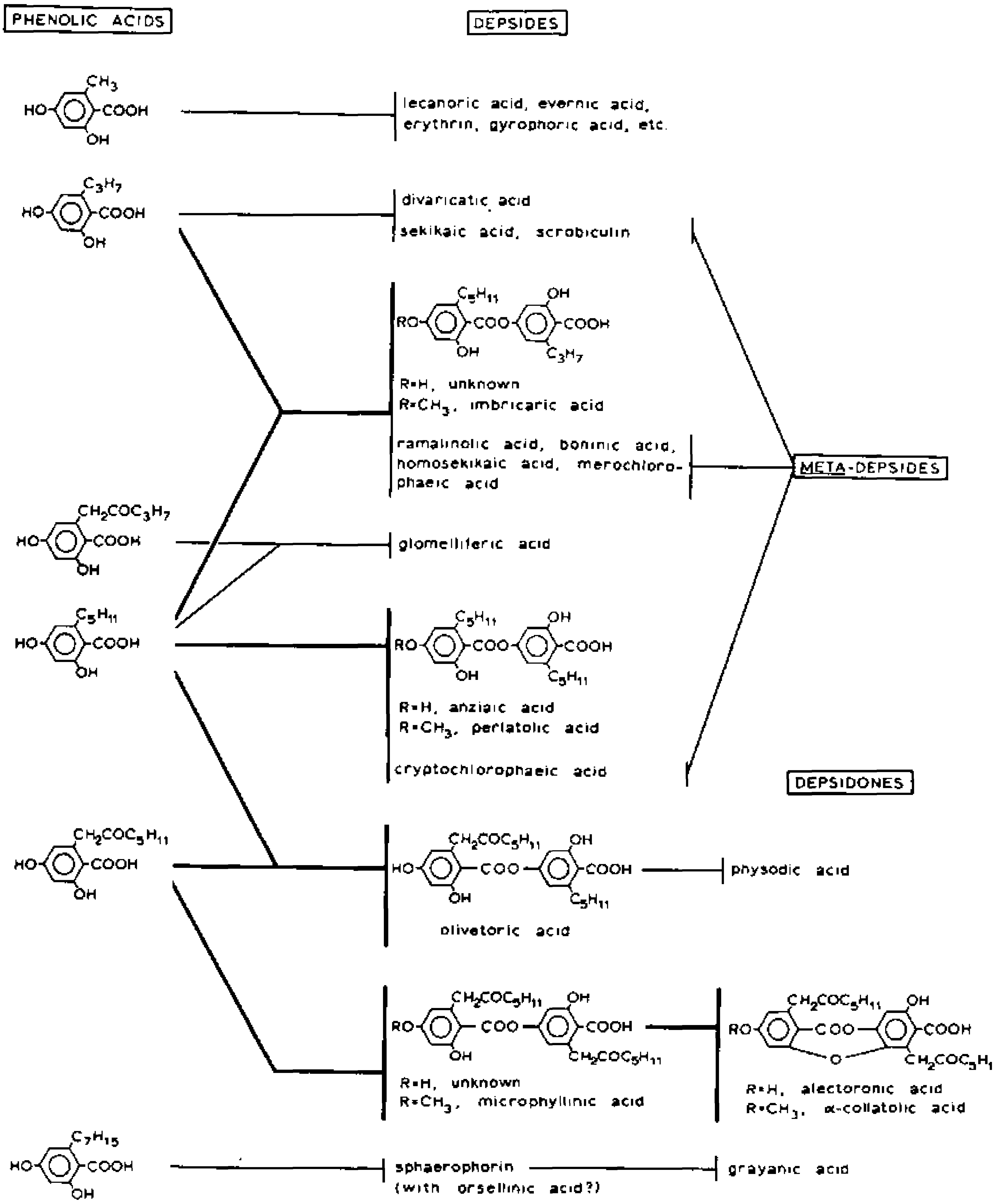


FIGURE 5. Chart showing the phenolic units (left column) incorporated in depsides (middle column) and depsidones (right column). The heavier lines lead to substances found in *Cetrelia* and the chemical structures of these compounds are given. The thinner lines lead to related substances known from other genera of lichens and are indicated for purposes of comparison. The phenolic units are arranged from top to bottom in order of increasing side chain length. Where two phenolic units have side chains of the same length, the less derived (the β-keto type) is given first. This arrangement shows that most of the medullary compounds in *Cetrelia* are both closely related to each other and also more highly derived within the framework of chemical variation shown by orcinol-type depsides and depsidones.

stances in many groups of lichens, is not involved in any known medullary constituents of *Cetrelia.*

Some orcinol-type phenolic rings in lichen substances retain a carbonyl group at the β-carbon of the alkyl side chain. The position of this carbonyl group corresponds to that of one of the original malonate carboxyls, and it seems probable that the β-keto groups result when there is no reduction at this position rather than by a new oxidation step. Lobaric acid and norlobaridone each have an α-keto group which probably forms by oxidation of a previously reduced side chain. Thus compounds with α-keto side chains may be more derived than compounds with fully reduced side chains, which in turn may require more steps for synthesis than a substance with a chain of equal length which retains a β-keto carbon.

In the orcinol-type depsides and depsidones of *Cetrelia*, the $C_7$ side chains retain a β-keto group while the $C_3$ and $C_5$ side chains are fully reduced (Figure 5). Except for the one $C_3$-substituted compound (imbricaric acid), biosynthesis of every phenolic unit in the *Cetrelia* compounds must involve reduction of two carbonyls, either to the $-C_5H_{11}$ group or to the $-CH_2COC_5H_{11}$ group. Oxidized $C_3$ alkyl groups are unknown in lichen substances, and a β-keto $C_5$ substituent is known only in glomelliferic acid.

Thus the biosynthesis of the KC+ compound microphyllinic acid may proceed through exactly the same steps required to synthesize perlatolic acid (KC—) except that the initial condensation leading to the phenolic rings in microphyllinic acid includes one extra malonate unit. In olivetoric acid, one ring is substituted as in perlatolic acid and the other as in microphyllinic acid.

## DEPSIDES AND DEPSIDONES

For many years it was supposed that depsides were converted to depsidones by the loss of water from phenolic groups properly placed on each ring. There was, however, no known lichen depside with a structure suitable to give a known lichen depsidone by this route. It is now generally accepted that depsidones form from depsides by a loss of hydrogen in an oxidative-cyclization process (Figure 6) (Erdtman, 1962; Erdtman and Wachtmeister, 1957). A number of depside-depsidone pairs are known which show very similar ring substituents. In *Cetraria ciliaris* sens. lat. and in some individuals of *Pseudevernia furfuracea* (=*Parmelia furfuracea*), the depside-depsidone pair olivetoric acid and physodic acid occur together (C. F. Culberson 1964, 1965).

If the mechanism shown in Figure 6 is correct, then methylation of any phenolic hydroxyl or even the carboxylic acid group would disrupt

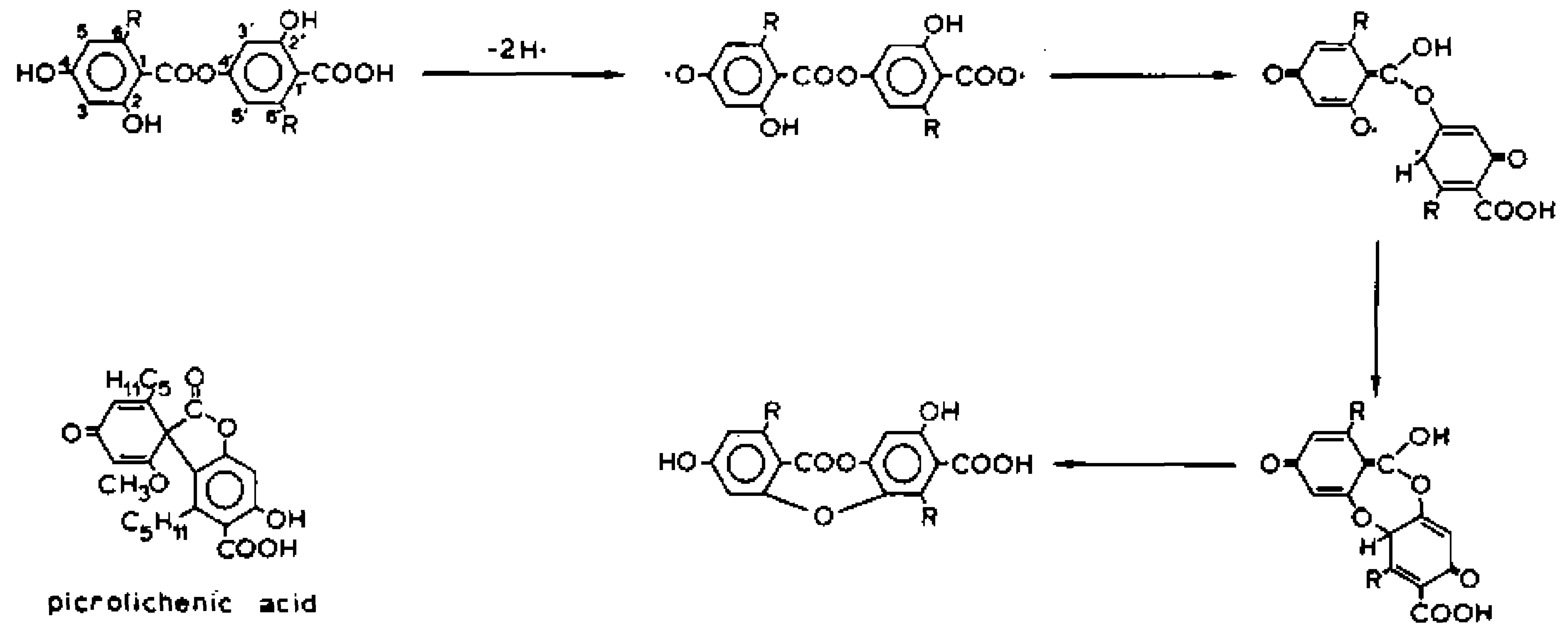


Figure 6. A possible biosynthetic route from depsides to depsidones. Picrolichenic acid is formed when oxidative coupling is blocked by 2-O-methylation. (See the text for fuller explanation.)

the formation of a depsidone from a depside. It has been pointed out (Erdtman and Wachtmeister, 1957) that methylation of the phenolic group *ortho* to the ester linkage can explain the formation of picrolichenic acid (Figure 6) by a mechanism similar to depsidone formation. But methylation at either the 4- or the 2′-hydroxyl may block cyclization altogether. Microphyllinic acid, which occurs in *Cetrelia*, is a depside closely related to alectoronic acid and α-collatolic acid, but it is methylated at the 4-hydroxyl. The related unmethylated depside is not yet known from lichens, but it would be the immediate precursor of the common lichen substance alectoronic acid. The latter substance could then be converted to α-collatolic acid by 4-O-methylation (Figure 5).

Blocking oxidative-cyclization reactions by methylation of hydroxyls that would pass through a quinoid structure during the cyclization is known in the biosynthesis of certain alkaloids where "it seems probable that methylation precedes and controls the direction of oxidative coupling. . ." (Scott, 1965).

## O-METHYLATION

Methylation on oxygen is a very common and simple cause of chemical variation in lichen depsides and depsidones. All the phenolic groups in the molecule as well as the carboxylic acid group of ring B of orcinol-type depsides are subject to methylation, but methyl substitution at the 4-hydroxyl is most frequently observed. Examples among the *Cetrelia* compounds (Figure 5) are perlatolic acid, which is 4-O-methylanziaic acid, and α-collatolic acid, which is 4-O-methylalectoronic acid.

As yet there is no experimental evidence to indicate when methylation occurs, but the biosynthesis of picrolichenic acid requires 2-O-methylation before oxidative cyclization. On the other hand, if 4-O-methylation or 2′-O-methylation can block depsidone formation as suggested above, then depsidones must be methylated at these positions after oxidative cyclization.

It seems that the order of methylation may vary and perhaps the taxonomic significance of substances which differ by methylation alone will also vary. In *Cetrelia*, for example, anziaic acid and perlatolic acid do not seem to occur together and the species in which they occur appear to be very distinct, while alectoronic acid and α-collatolic acid are always found together and seem to be more closely related biosynthetically.

## RELATIONSHIP OF *CETRELIA* COMPOUNDS TO OTHER LICHEN SUBSTANCES

Figure 5 shows the orcinol depsides in *Cetrelia* and some closely related substances from other lichens. The chart is arranged to show, in a very general way, the relationships among these substances and the extreme uniformity of the structures involved. All seven medullary compounds in *Cetrelia* may be derived from three phenolic-acid units and six of the substances from only two such units. Reactions probably required in the biosynthesis of these compounds are (1) esterification of the phenolic units, (2) 4-O-methylation (in imbricaric acid, perlatolic acid, α-collatolic acid), and (3) oxidative cyclization to a depsidone (in alectoronic acid and α-collatolic acid). (See the caption of Figure 5 for additional explanation.)

The *Cetrelia* substances do not show some of the variations observed in other orcinol-type depsides and depsidones. O-Methylation occurs only at the 4-hydroxyl, for example, and more highly methylated substances, such as planaic acid (a methyl ether of perlatolic acid) and confluentic acid (a trimethyl ether of olivetoric acid), are not found in *Cetrelia*. Nor are *meta* depsides found, although many of the known *meta* depsides could be derived from the same phenolic acid units involved in the *Cetrelia* compounds. Perhaps some of the minor constituents not identified in the present study will represent modifications of chemical structure.

While the *Cetrelia* substances seem to be uniform, the synthesis of α-collatolic acid, a monomethyl ether depsidone, represents a certain degree of advancement over, say, the production of simple depsides such as lecanoric acid. The production of relatively advanced but highly uniform chemical substances would substantiate the concept of these species as evolved from ancestors which produced such complex compounds as alectoronic acid and α-collatolic acid. If this is true, the other substances found here might have resulted from a retrogressive evolution in which reactions leading to alectoronic acid and α-collatolic acid became blocked or modified.

Considering the complete lack of direct evidence, other plausible theories to account for the production of these substances could be advanced, but the route suggested here is the simplest one in the light of present knowledge. This hypothesis would support the concept of the origin of *Cetrelia* from an *Amphigymnia*-type ancestor producing alectoronic acid and α-collatolic acid. Hale (1965) found that alectoronic acid (usually with α-collatolic acid) is indeed the most common medullary substance in *Parmelia* subgenus *Amphigymnia*. As in *Cetrelia*, all of these species also produce atranorin in the cortex, but unlike *Cetrelia* the other species of *Amphigymnia* Parmelias produce a wide variety of chemical substances including fatty acids, *meta* depsides, orsellinic acid-derived depsides, and β-orcinol depsidones. It is significant that the common cortex substance usnic acid is produced in *Parmelia* subgenus *Amphigymnia* but not in *Cetrelia*, and it is further noteworthy that usnic acid never occurs in those *Amphigymnia* Parmelias which produce alectoronic acid or olivetoric acid.

## Methods for the Microchemical Identification of Lichen Substances in *Cetrelia* and *Platismatia*

The aim of this section is to give a complete description of the most reliable and convenient tests for determining the constituents of the species treated in this monograph. The usual microcrystal tests (Asahina, 1936–1940) and paper-chromatographic methods (Wachtmeister, 1959) have been used to identify the lichen substances in herbarium specimens in this study, although in the time since the research reported here was done thin-layer chromatography has become the major chromatographic technique in lichen microchemistry. The descriptions here are intended to give the taxonomist enough information for reliable, practical identifications of the nine substances involved in *Cetrelia* and *Platismatia* and are not meant as a complete treatment of all the microcrystal or chromatographic tests which might conceivably be used for these substances. The methods described are sufficient to distinguish these substances from each other as they occur in our genera, but alone they might not be sufficient to identify the same substances in all the other lichens for which additional constituents might introduce complications. In the research described here, many other tests were actually used. These studies were necessary to establish the data reported, but they are not required for routine identifications in specimens of *Cetrelia* and *Plastismatia* now that the major constituents are known.

## SOLUTIONS

The following solutions are used in the microchemical procedures to be described:

1. GE solution. A mixture of three parts of acetic acid and one part of glycerin.
2. GAW solution. A mixture of equal volumes of ethyl alcohol, water, and glycerin.
3. GA*o*-T solution. A mixture of one part *o*-toluidine, two parts alcohol, and two parts glycerin. The solution should be discarded when it turns red. A nearly colorless solution can be prepared if the *o*-toluidine is first distilled from zinc powder.
4. 5 percent NaOH. A solution of 5 grams of sodium hydroxide in 95 ml. of water.
5. Ammonium hydroxide-saturated n-butanol. Concentrated ammonium hydroxide is added to n-butanol and the mixture is shaken thoroughly in a separatory funnel or bottle (the gas pressure frequently being released). Sufficient ammonium hydroxide is added so that, after shaking, two layers will separate. The upper layer and a smaller amount of the lower layer are placed in the chromatographic tank.
6. Pyridine-ethyl acetate-water. A mixture of one part pyridine, two parts ethyl acetate, and one part water.
7. Diazotized benzidine. Dissolve 1.7 grams of benzidine dihydrochloride in 250 ml. of water and add 3 ml. of concentrated hydrochloric acid. Prepare a separate solution of 25 grams of sodium nitrite in 250 ml. of water. Just before use, one part of the sodium nitrite solution is added, by drops, to one part of the benzidine solution.
8. Stable PD. A solution of 10 grams of sodium sulfite and 1 gram of *p*-phenylenediamine in 100 ml. of water to which is added 0.5 ml. or less of a wetting agent (such as "Photoflo").
9. 0.1 M $Na_3PO_4$. A solution of 3.8 grams of trisodium phosphate dodecahydrate in 100 ml. of water.
10. 1 N $H_2SO_4$. A solution prepared by adding 3 ml. of concentrated sulfuric acid to 97 ml. of water with stirring.

In addition to these solutions, acetone, benzene, ethyl alcohol, and ethyl ether, and the usual spot test reagents are used in the microcrystal and paper chromatographic procedures to be described.

## MICROEXTRACTION

Thallus fragments equivalent to approximately one square centimeter are placed in a shell vial (1.2 by 3.5 cm.) and enough benzene is added to cover the sample. After about 5 minutes the benzene is decanted onto a microscope slide on a slide-warming tray (about 55°C). The extraction with benzene at room temperature is repeated twice more, and the solutions are evaporated on the same heated slide. Then the vial is placed on the warming tray and just enough acetone is added to cover the sample. The fragments are extracted for 5 to 10 minutes and the solution is then evaporated on another heated slide. This procedure is repeated twice more, as was done for the benzene extraction. The lichen sample is discarded, and then the two slides with the residues are ready for use.

## MICROCRYSTAL TESTS

The microcrystal tests are performed on portions of the residues from the acetone and benzene extracts. Small amounts of residue are removed with a razor blade and transferred to another slide. The amount of solid residue needed for a test depends primarily upon (1) the solubility of the crystals in the test solution, (2) the volume of test solution used, and (3) the concentration of the substance in the residue being tested. Using a very small cover slip reduces the volume of test solution applied and consequently the amount of solid residue required for a crystal test. If the crystal test fails the first time, a second test with more (or sometimes less) of the residue often gives better results.

Solutions for the crystal tests described below are the GE, GAW, and GA*o*-T solutions and a 5-percent aqueous NaOH solution. A drop of the test solution is applied to a cover slip which is gently placed on the residue so that the liquid covers the solid. Tests with the GA*o*-T solution and with 5 percent NaOH usually do not require heat. Tests with the GE and GAW solutions depend upon a recrystallization process and the slides should be warmed, preferably over a microflame. Many of the substances treated here are more soluble in the GE solution than in the GAW solution, and usually less heat is needed for tests in the GE solution. The solutions should not be allowed to boil, and heating should be stopped at once if the solid seems to dissolve rapidly. Most preparations are now ready for microscopic examination. If crystals have not formed, the slides are reexamined later.

## PAPER CHROMATOGRAPHY

Paper chromatograms are generally prepared on Whatman No. 1 paper although other types of paper (e.g., Whatman No. 3 MM and

Toyo Roshi No. 50) are equally satisfactory. The chromatograms are developed by the ascending method, which is simpler than the descending method and requires less elaborate equipment. Any chromatographic tank is satisfactory, but ideally it should be tall enough for development of the chromatograms to 15 to 20 cm. and still not so large that it becomes difficult to saturate the atmosphere in it with the developing solvent. A filter-paper lining around the inside of the tank helps to keep the atmosphere saturated.

The spots of the extracts are applied 1.5 cm. apart along a line 3 cm. from the bottom of the paper. A small amount of the residue on the slide is treated with a drop of acetone, and a portion of this solution is drawn by capillarity into a narrow glass tube with an inside diameter of about 1 mm. (thin-walled capillary tubing which has been pulled out in a flame to a point). The tip of the tube is then touched several times to a marked point on the starting line. With care, the spots can be kept 3 to 5 mm. in diameter, thereby producing better results with less material than larger spots would. The amount of substance needed for the chromatogram depends largely on how its constituents separate and the sensitivity of the spray reagent. The reagents used in the present study are extremely sensitive, and the spots are easily overloaded. The optimum quantity of material to be applied to a spot can be judged easily after a few trials.

Paper chromatograms of all substances described here except fumarprotocetraric acid are developed in ammonium hydroxide-saturated n-butanol. With this solvent there are two liquid layers. The upper layer is ammonium hydroxide-saturated n-butanol and the chromatogram should be adjusted so that it dips into only this layer. For paper chromatograms of fumarprotocetraric acid, the single-phase solvent pyridine-ethyl acetate-water (1:2:1) is used.

When the chromatogram has developed to a height of 15 to 20 cm., it is dried and then viewed with ultraviolet light. Both long- (366 mμ) and short-wave (254 mμ) lamps were used in the present study. The short-wave light was superior largely because it delivered much less visible light than the particular long-wave lamp available, and the fluorescent spots are more easily distinguished in darkness. The spots are encircled in pencil and labeled for color of fluorescence.

Chromatograms run in ammonium hydroxide-saturated n-butanol are sprayed with a freshly prepared diazotized benzidine solution, and after a few minutes the paper is washed with cold water and dried. Chromatograms of fumarprotocetraric acid developed in pyridine-ethyl acetate-water are sprayed with the stable PD solution. The chromatograms should be sprayed in a hood or in some way so that the mist of the reagents is not inhaled.

All paper chromatograms should be saved. Chromatograms sprayed with stable PD can be kept for some time in a large plastic envelope.

## HYDROLYSIS OF DEPSIDES

The depsides imbricaric acid and perlatolic acid can be confirmed by chromatography of the hydrolyzed residues, and this procedure is also particularly useful in distinguishing olivetoric acid from anziaic acid. The methods described here are slightly modified from those suggested by Wachtmeister (1956) and have been presented in detail elsewhere for imbricaric acid and perlatolic acid (C. F. Culberson and W. L. Culberson, 1965).

A portion of the extract containing the unknown substance is removed from the residue slide with a razor blade and transferred to a vial. The amount required is usually about two to four times as much as is needed for a microcrystal test. The residue is covered with three or four drops of 0.1 M $Na_3PO_4$. The tube is kept stoppered at room temperature or very gently warmed for 15 to 24 hours. After this time most substances produce yellow, orange, pink, or red colors. A little ether is added, and after a few minutes the tube is closed and shaken sufficiently to mix the two layers. When the layers separate, the upper (ether) solution is drawn off carefully to avoid including any of the lower (aqueous) one. The ether solution is evaporated on a warmed slide and the extraction is repeated twice. This extract will usually contain phenolic substances and possibly excess starting material. Next, the aqueous layer is acidified with two drops of 1 N $H_2SO_4$ and extracted with ether as before, evaporating the ether extracts on a second slide. Both extracts are chromatographed in the ammonium hydroxide-saturated n-butanol solvent and the chromatogram is viewed with UV light and sprayed with diazotized benzidine.

Residues may also be hydrolyzed with concentrated sulfuric acid. The solid is placed in a vial and covered with two or three drops of the acid. After ten minutes at room temperature or (better) in a refrigerator, the tube is filled with crushed ice. When the ice melts the solution is extracted with ether three times as described above; the ether solutions are evaporated on a slide; and the aqueous layer is discarded. The residue is chromatographed as described above.

The appearance of the chromatograms from hydrolyzed extracts will vary with the degree of decarboxylation and other side reactions depending upon the particular conditions of the extraction, but the results from this simple test can be particularly valuable.

## THIN-LAYER CHROMATOGRAPHY

After the completion of the microchemical studies for this monograph, the technique of thin-layer chromatography was developed

(Stahl, 1965) and has subsequently been applied successfully to the determination of many lichen substances. Thin-layer chromatography was employed briefly using samples of *Cetrelia* previously studied by the conventional microchemical methods, and in general good results were obtained. For some species, additional spots could be observed which were not found by paper chromatography, but these constituents, present in minute quantities, could not be identified. Table 4 gives the $R_f$ values found for the eight substances known from *Cetrelia*. The chromatograms were run on air-dried silica gel-G plates developed with n-hexane-ethyl ether-formic acid and sprayed with 10 percent $H_2SO_4$. The plates were dried in an oven at 70°C and the color of the spots varied somewhat with the duration and conditions of drying. On the same chromatograms, extracts of *Platismatia lacunosa* containing fumarprotocetraric acid showed a black spot at the origin.

TABLE 4.—*$R_f$ values in thin-layer chromatograms for compounds known in* Cetrelia. *The chromatograms were made on air-dried silica gel-G plates, developed with n-hexane-ethyl ether-formic acid to a height of 10 cm., sprayed with 10 percent $H_2SO_4$, and then dried at 70°C.*

| Substance | $R_f$ | Color After Spraying |
|---|---|---|
| Alectoronic acid | 0.22 | brown |
| Anziaic acid | 0.50 | yellow |
| Atranorin | 0.73 | yellow-brown |
| α-Collatolic acid | 0.28 | brown |
| Imbricaric acid | 0.66 | yellow |
| Microphyllinic acid | 0.35 | red-brown |
| Olivetoric acid | 0.35 | yellow-brown |
| Perlatolic acid | 0.73 | yellow |

## Identification of Specific Substances

### ALECTORONIC ACID AND α-COLLATOLIC ACID

PLATE 1, FIGURES 1–3

The medulla of samples containing alectoronic acid or alectoronic acid and α-collatolic acid shows a strong KC+ reaction and a brilliant white fluorescence in UV light. Neither substance gives a color test with K, C, or PD. The microchemical tests used to identify these compounds in the present study have recently been described elsewhere (W. L. Culberson and C. F. Culberson, 1965).

Benzene at room temperature dissolves some alectoronic acid and α-collatolic acid. Since α-collatolic acid is slightly more soluble in this solvent than alectoronic acid is, small quantities of α-collatolic acid in the mixture can often be detected better in the benzene extract than would be possible using a single acetone extraction.

Plate 1, Figures 1–2, shows examples of the variable crystal form of alectoronic acid and α-collatolic acid cocrystallized from the GE solution. Crystal morphology in the GAW solution is also variable and a common crystal type is illustrated (Plate 1, Figure 3). The final identification of these substances must be made by chromatography. In ammonium hydroxide-saturated n-butanol, alectoronic acid shows a spot at $R_f$ 0.24 which appears bluish in UV light and turns deep red with diazotized benzidine. On the same chromatogram, α-collatolic acid produces a long spot at about $R_f$ 0.56 which shows a pale fluorescence in UV light and turns dark red with diazotized benzidine. The spot for atranorin runs between that for alectoronic acid and that for α-collatolic acid.

### ANZIAIC ACID

### PLATE 1, FIGURES 4–5

All *Cetreliae* showing a C+ medullary reaction contain either anziaic acid or olivetoric acid. Anziaic acid is less common. Like olivetoric acid, it shows no color reactions with K or PD. Anziaic acid is slightly more soluble in benzene than is olivetoric acid, which is only scarcely soluble. The benzene extract contains atranorin along with anziaic acid, and the subsequent acetone extract contains more anziaic acid, often accompanied by more atranorin.

Frequently no crystals of anziaic acid form in the GE solution because the compound is very soluble there, but when recrystallization does occur, there are clusters of small, curved needles (Plate 1, Figure 4). Anziaic acid recrystallizes more dependably from the GAW solution, but the curvature and size of the needles which form (Plate 1, Figure 5) are variable. Unlike olivetoric acid, anziaic acid does not produce very persisting crystals in the GA*o*-T solution. Colorless needles which may be present in a fresh GA*o*-T preparation soon dissolve.

Anziaic acid chromatographs well in ammonium hydroxide-saturated n-butanol giving a spot at $R_f$ 0.67 which is blue in UV light and bright red with diazotized benzidine. While there may be a slight red coloration with diazotized benzidine just above the spot for anziaic acid, the chromatogram is distinguishable from the typical double spot produced by olivetoric acid near the same $R_f$ value. Determination of anziaic acid can be confirmed by hydrolysis since chromatographic analysis then shows a single spot for olivetol-2-carboxylic acid near $R_f$ 0.60.

## ATRANORIN

PLATE 1, FIGURE 6; PLATE 2, FIGURES 7–10

A number of papers describe the microchemical identification of atranorin. This compound turns yellow with K and pale yellow with PD, although the latter reaction is rarely observed on the thallus. Atranorin is somewhat soluble in benzene at room temperature but is usually found in the subsequent acetone extract as well unless it is present in the thallus in only very small concentration. Colorless prisms in the GE solution (Plate 1, Figure 6) and yellow needles in the GA*o*-T solution (Plate 2, Figures 7–8) are used to identify this substance. The crystal test in GA*o*-T is very sensitive (C. F. Culberson, 1963), and it is usually successful even in the presence of other compounds. Large concentrations of alectoronic acid, α-collatolic acid, and especially microphyllinic acid, however, may inhibit the crystal formation of atranorin in the GA*o*-T solution and also sometimes may decrease the size or alter the appearance of the prisms in the GE solution. The shade of yellow of the crystals in the GA*o*-T solution is somewhat variable, perhaps due to the presence of chloroatranorin or other compounds in the samples. Two types of atranorin crystals in the GA*o*-T solution are shown (Plate 2, Figure 9). The smaller, finer, more sharply curved needles are also a somewhat deeper yellow color. Atranorin is sparingly soluble in alcohol and does not recrystallize from the GAW solution.

Chromatography in ammonium hydroxide-saturated n-butanol gives a good spot ($R_f$ 0.53) which is yellow in the ammonia atmosphere of the developing tank, fluoresces yellow in UV light, and turns yellow with diazotized benzidine. In the pyridine-ethyl acetate-water developing solvent, atranorin travels with the solvent front ($R_f = 1$).

## CAPERATIC ACID

PLATE 2, FIGURES 11–12; PLATE 3, FIGURES 13–18

The only fatty acid definitely proved to occur in the genera studied here is caperatic acid, but microcrystal tests are not a good method for identifying fatty acids, and it is certain that other constituents will be found when better techniques are perfected.

Caperatic acid shows no thallus spot tests. It is sparingly soluble in benzene at room temperature while protolichesterinic acid, another common fatty acid of lichens, dissolves readily. By extracting the thallus fragment first with benzene and then with acetone, these two fatty acids would be separated from each other. This solubility difference is fortunate since experiments with pure caperatic acid extracted from *Parmelia cryptochlorophaea* Hale (C. F. Culberson, 1965) show that under certain conditions this compound produces crystals in the GE solution which are similar to those of protolichesterinic acid.

Normally, caperatic acid crystallizes from the GE solution as circular or cloud-shaped clumps appearing somewhat similar to drops of oil (Plate 3, Figures 13–14). These crystals are very distinctive and easily recognizable. But many GE preparations show plate-like crystals, singly or in radiating clusters (Plate 3, Figures 15–16), similar to those typical of protolichesterinic acid. Sometimes plate-like crystals seem to emerge from the circular ones (Plate 3, Figures 17–18). At first this gives the impression of a mixture of protolichesterinic acid and caperatic acid. But, since the lichen fragment was extracted first with benzene and this extract showed no protolichesterinic acid, the presence of protolichesterinic acid in the second residue is not likely.

Chemical transformation of caperatic acid into protolichesterinic acid under the influence of acetic acid in the GE solution is extremely unlikely. A careful comparison of the crystal shapes indicates two possible explanations: (1) either caperatic acid has two crystal forms or (2) caperatic acid here is sometimes converted to some substance other than protolichesterinic acid. The most obvious reaction which might occur in the GE solution is the hydrolysis of the methyl ester of caperatic acid, giving norcaperatic acid. A sample of pure norcaperatic acid showed crystals (Plate 4, Figure 19) in the GE solution that were very similar to, but probably not identical with, the cloud-type crystals of caperatic acid. The crystals of norcaperatic acid in the GAW solution (Plate 4, Figure 20) are indistinguishable from those of caperatic acid.

Crystals of caperatic acid in GAW solution are very small circular plates usually clustered into large radiating aggregates (Plate 2, Figure 12). In some preparations there are curly crystals, especially at the center of the aggregates of caperatic acid (Plate 2, Figure 11), perhaps of an unidentified fatty acid.

Caperatic acid shows small, fuzzy, colorless balls in the GA*o*-T solution, and it distorts the yellow crystals produced by atranorin when the latter substance is also present (Plate 2, Figure 10).

When samples containing caperatic acid are chromatographed in ammonium hydroxide-saturated n-butanol, a weakly fluorescing, trailing spot may be found near $R_f$ 0.75. When the chromatogram is sprayed with diazotized benzidine to reveal atranorin or other compounds, the spot for caperatic acid turns very pale yellow and, while the chromatogram is still wet, is barely visible. This is not, of course, a reliable method for identifying caperatic acid.

### FUMARPROTOCETRARIC ACID

In this study one species, *Plastismatia lacunosa*, gave a positive test with PD and contained fumarprotocetraric acid. This substance is not removed from the thallus by extraction with benzene at room temperature. Fumarprotocetraric acid dissolves in warm acetone but in this species it is accompanied by atranorin and usually also caperatic acid. From residues also containing caperatic acid, crystals of the *o*-toluidine derivative of fumarprotocetraric acid are not readily identifiable in the GA*o*-T solution, and all determinations of this substance were made by chromatography.

Paper chromatograms developed with ammonium hydroxide-saturated n-butanol show fumarprotocetraric acid as a dense streak near the origin. The spot turns dark red with diazotized benzidine and differs little in appearance from that of several other PD+ depsidones. Extracts from specimens showing such a spot were rechromatographed in pyridine-ethyl acetate-water (1:2:1). With this solvent, fumarprotocetraric acid shows a distinctive spot ($R_f$ 0.39) which quenches UV light and turns yellow after spraying with the stable PD reagent.

## IMBRICARIC ACID

PLATE 4, FIGURES 21–23

The microchemical methods used to identify imbricaric acid are described in detail elsewhere (C. F. Culberson and W. L. Culberson, 1966). A pure sample of this substance extracted from *Cetrelia sinensis* was used to check the microchemical tests used on crude extracts from thallus fragments. Imbricaric acid is negative with K, C, KC, and PD, but the KC+ reaction of the thallus of many samples containing imbricaric acid requires that the latter substance be distinguished from both KC+ and KC− compounds—in this study perlatolic acid, alectoronic acid, α-collatolic acid, and microphyllinic acid.

Imbricaric acid is somewhat soluble in benzene at room temperature. The subsequent acetone extract is often gummy and less satisfactory for the microcrystal tests. The large needles formed in the GE solution (Plate 4, Figure 21) show oblique extinction ($\phi=45°$) in polarized light and in this respect differ from those of all other substances encountered here. The needles in the GAW solution (Plate 4, Figure 22) also show oblique extinction ($\phi=45°$). In the GA*o*-T solution, imbricaric acid forms colorless needles (Plate 4, Figure 23), probably its *o*-toluidine salt. In the crude extracts where atranorin is also present, fuzzy yellow crystals form (Plate 4, Figure 24). These crystals may result from cocrystallization since very similar crystals were observed when a mixture of pure imbricaric acid and pure atranorin was treated with the GA*o*-T solution.

By chromatography in ammonium hydroxide-saturated n-butanol, imbricaric acid undergoes slow hydrolysis giving a spot at $R_f$ 0.78, blue-white in UV light and orange-red with diazotized benzidine, which trails down from the spot to about $R_f$ 0.38 to 0.43 due to the degradation product divaric acid. Imbricaric acid can be definitely distinguished from perlatolic acid by hydrolysis with acid or base and by observing the strong spot at $R_f$ 0.38 for divaric acid. In most cases, however, the observation of crystals with oblique extinction in the GE and GAW solutions and chromatography of the unhydrolyzed material are sufficient to identify imbricaric acid.

### MICROPHYLLINIC ACID

PLATE 5, FIGURES 25–27

Microphyllinic acid is negative with K, C, and PD but gives a strong red coloration with KC. In at least one report in the literature, microphyllinic acid was mistaken for alectoronic acid because both substances give a positive KC test and needles in the GE solution. But microphyllinic acid can be definitely identified by microcrystal tests and chromatography.

Some microphyllinic acid is removed from the thallus fragment by extraction with benzene at room temperature. Some atranorin is also extracted then. The subsequent acetone extract contains less microphyllinic acid and is often a dark gum that is difficult to work. The microcrystal tests usually give best results with the benzene extract. In the GE solution, straight radiating needles form (Plate 5, Figure 25) with an extinction angle of zero. Atranorin often crystallizes in the same preparation, although the microcrystal test for atranorin in the GA*o*-T solution is inhibited by microphyllinic acid. In the GAW solution, microphyllinic acid recrystallizes as long, fine, sparsely clustered needles with an extinction angle of zero (Plate 5, Figure 26). These crystals are most similar to those of perlatolic acid but do not resemble those of alectoronic acid. The most rapid method for distinguishing microphyllinic acid from the other KC+ substances in *Cetrelia* is by the crystals of the sodium salt (Plate 5, Figure 27) which precipitate from 5 percent aqueous sodium hydroxide.

Microphyllinic acid hydrolyzes completely during chromatography in ammonium hydroxide-saturated n-butanol, and two characteristic spots are observed. The upper one, ($R_f$ 0.93), which shows a bright blue-white fluorescence in UV light and turns orange with diazotized benzidine, is due to the ring A fragment (Figure 5). The lower spot ($R_f$ 0.49), which interferes with the chromatographic determination of atranorin, appears blue in UV light, turns dark red with diazotized benzidine, and is due to the ring B fragment. The same spots are observed after base hydrolysis.

## OLIVETORIC ACID

PLATE 5, FIGURES 28–30; PLATE 6, FIGURE 31

Samples showing a positive thallus reaction with C may contain either anziaic acid or olivetoric acid. Olivetoric acid gives no coloration with K or PD, but turns red with C, and the color is still more intense with KC. Olivetoric acid is reported to give a green color with aqueous $Ba(OH)_2$ (Asahina, 1936) while anziaic acid does not give such coloration, but this reaction was not used in the present study. Olivetoric acid is only slightly soluble in benzene and less soluble in it than anziaic acid is. The benzene extract of thallus fragments with olivetoric acid and atranorin encountered in this study is usually a small, colorless crust which contains only a trace of olivetoric acid. The subsequent acetone extract contains more atranorin and abundant olivetoric acid.

In the GE solution, olivetoric acid is quite soluble and it crystallizes slowly as small, fine, curved needles forming a dense mat (Plate 5, Figure 28). Olivetoric acid is less soluble in the GAW solution, and it usually produces beautiful, curved needles (Plate 5, Figure 29), which are larger and thicker than those in the GE solution. The crystals of anziaic acid in the GE and GAW solutions (Plate 1, Figures 4–5) are sufficiently similar to those of olivetoric acid that tests using these crystallizing reagents may require confirmation. Olivetoric acid also produces crystals in the GA*o*-T solution without heating. These clusters of straight, colorless needles or needle plates (Plate 5, Figure 30; Plate 6, Figure 31) form rapidly and are usually mixed with the yellow crystals formed by atranorin. Although anziaic acid may show small colorless needles under the same conditions, these soon dissolve.

Olivetoric acid hydrolyzes during chromatography in ammonium hydroxide-saturated n-butanol producing a double spot—one center ($R_f$ 0.73) turns dark bluish-red with diazotized benzidine and the other ($R_f$ 0.60) turns dark red with the same spray. These spots correspond closely to those produced by base hydrolysis which gives a spot for olivetol-2-carboxylic acid that is blue in UV light and turns dark red with diazotized benzidine ($R_f$ 0.59) and a second spot, from ring A, that is blue in UV light and dark bluish-red with diazotized benzidine ($R_f$ 0.76). Anziaic acid also gives olivetol-2-carboxylic acid by hydrolysis but not the second spot at $R_f$ 0.76.

## PERLATOLIC ACID

PLATE 6, FIGURES 32–34

Perlatolic acid gives no color reactions with the usual reagents, but some specimens containing this substance show a positive reaction with KC due to the presence of a still unidentified compound. This situation is also encountered with samples containing imbricaric acid. Because of the spurious KC+ reaction observed with perlatolic and imbricaric acid-containing samples, the microchemical tests must distinguish these substances from each other and from the known KC+ substances occurring in *Cetrelia.*

Extraction of the thallus fragment with benzene at room temperature removes a portion of the perlatolic acid along with atranorin. The benzene extract is usually cleaner and more easily crystallized with the microcrystal solutions than is the subsequent gummy acetone extract.

When either extract is treated with the GE solution, perlatolic acid recrystallizes as clumps of needles (Plate 6, Figure 32) with straight extinction. Atranorin is usually observed in the same slide. In the GAW solution, perlatolic acid forms needles (Plate 6, Figure 33) which are usually shorter than those of imbricaric acid and their angle of extinction is zero. Many residues containing perlatolic acid show large colorless crystals (Plate 6, Figure 34) in the GA*o*-T solution when a test is made for atranorin. These crystals are very different from those of imbricaric acid in the same solution, but they have not been observed regularly enough to provide a good test for perlatolic acid.

Perlatolic acid chromatographs in ammonium hydroxide-saturated n-butanol with an $R_f$ of about 0.83 which is slightly higher than the $R_f$ value for imbricaric acid. When the developing solvent is fresh, perlatolic acid hydrolyzes slightly and trails to an $R_f$ of about 0.59 due to the formation of olivetol carboxylic acid. The spot for perlatolic acid appears blue-white in UV light and turns orange-red with diazotized benzidine. Chromatographic confirmation of the presence of perlatolic acid is obtained by acid or base hydrolysis and chromatography of the products. The spot for olivetol carboxylic acid is at $R_f$ 0.59 as compared to that for divaric acid at $R_f$ 0.38, which would be found by hydrolysis of imbricaric acid. This procedure has been described in detail (C. F. Culberson and W. L. Culberson, 1966).

## AN UNIDENTIFIED SUBSTANCE

### PLATE 6, FIGURES 35–36

An unidentified substance in several species of *Cetrelia* gives yellow crystal clusters (Plate 6, Figure 35) in the GE solution. Many of the same specimens showed fine yellowish-tan needles (Plate 6, Figure 36) in the GA*o*-T solution, and it is possible that the crystals in these two solutions are caused by the same compound. The yellow crystals in the GE solution usually form near the edge of the slide, and the solution in the center of the preparation does not appear yellow. This suggests that the unidentified substance might not be a yellow pigment in the lichen but rather a colorless substance which turns yellow and deposits crystals in the GE solution where it is exposed to the air.

## Chemical Criteria in the Taxonomy of *Cetrelia* and *Platismatia*

In the previous discussion of the generic traits of *Cetrelia* and *Platismatia,* the high level of chemical uniformity within each genus was pointed out, an internal homogeneity all the more notable considering the great magnitude of the chemical difference between the two genera (Table 2). Chemistry here offers a striking correlation with the other characteristics that define the genera. The use of chemistry in the study of *Cetrelia* and *Platismatia* has considerable theoretical interest for taxonomy because it shows (1) the value of chemistry in an instance where it becomes a major characteristic defining genera, (2) the usefulness at the species level of chemical variations that are highly correlated with morphological variations in a genus which has undergone evolutionary diversification in both chemistry and morphology (*Cetrelia*), and (3) an example of a chemically conservative genus (*Platismatia*).

The involvement of chemistry in addition to morphology in the formulation of taxonomic judgments in lichenology has had a limited but nonetheless distinguished history, some of the most refined examples of its use being the elegant taxonomic systems constructed by Yasuhiko Asahina in Japan and by the late Alexander Evans in this country. Although today an increasing number of biochemists are becoming interested in the unique natural products of the lichens, lichen taxonomists by and large continue to ignore chemical variation. The major objection that most lichenologists raise to chemical considerations in lichenology is that chemistry, especially at the species level, is not used in most other groups of plants and that consequently it should not be used in lichenology either. The slight taxonomic usefulness of corolla pigmentation in the flowering plants is regularly pointed to as proof of the inconsequential significance of chemical variation as an indication of the natural relationships of plants at the species level. In rejecting chemistry from taxonomic considerations, Almborn (1965) probably summed up most present-day lichenologists' views when he wrote: "It is essential that lichen taxonomy be founded on firm principles not deviating too much from those generally accepted in other plant groups."

While Almborn's view may appear to reflect the commendable caution that characterizes responsible scientific judgment, most taxonomists recognize that the taxonomic characters valuable in one group of plants may be of absolutely no value whatever in another. In speaking of vascular plants, Cronquist (1964) remarked: "We have found, to our sorrow, that individual morphologic characters do not have a fixed, inherent taxonomic importance wherever they occur. Instead, they are only as important as they prove to be, in any individual instance, in marking groups that have been perceived on the basis of all the available evidence." This observation is no less true for the cryptogamic plants than for the vascular plants, and it is no less true for chemical characters than for morphologic characters. The best taxonomy is always eclectic. A blind rejection of a whole category of information—in this case chemical information—is as extreme and as philosophically unsound as the diametrically opposed view would be—namely, to insist upon reflecting in the taxonomic system every minute variation that a diligent chemist could find. In the actual practice of classification, the taxonomist needs considerably more latitude and freedom than either of these extreme positions would permit since the different types of chemical variation to be found in the lichens do not all seem to be equally important.

In order to explain how the chemical information found in the present study was actually applied to the formulation of the taxonomic judgments, it is necessary to recall what sort of chemical data were actually found—although there is nothing unique about the chemical information here. The nature of the chemical variation in *Cetrelia* and *Platismatia* is essentially like that found in all the rest of the macrolichens. The chemistry of the species of these genera can be characterized as the production of two histological categories of substances, the cortex constituent and the medullary constituent (or constituents).

Individuals of *Cetrelia* and *Platismatia* all produce atranorin as the upper-cortex constituent. No other lichen substance is produced in this tissue and apparently every individual of every species produces this constituent. The only other common upper-cortex substance, usnic acid, a very widespread constituent in *Parmelia* for example, is never produced in the two new genera. Since it shows no variation, upper-cortex chemistry in *Cetrelia* and *Platismatia* is of no taxonomic value.

The chemistry of the medulla is more variable, at least in *Cetrelia;* the individual produces one substance (or occasionally two), and the production of a given substance or of a given pair of substances precludes the production of other medullary compounds. If morphologically uniform or highly similar specimens show any qualitative variation in medullary chemistry, it is a variation of the typical replacement type in which one compound is substituted for another, usually with the chemically different populations showing different geographic ranges—for example, *Cetrelia japonica* with microphyllinic acid in Japan and *C. sinensis* with imbricaric acid in Formosa and China.

In interpreting chemical data in lichen species, one is faced with two questions: (1) To what extent are the data on the nonoccurrence of given substances in specimens and in species really due to true absence and to what extent are they due merely to the failure of technique to reveal their presence? (2) What is the biological significance (and consequent taxonomic significance) of the chemical variations that are found?

The pattern of chemical variation in which every specimen produces one medullary compound (or occasionally one pair of compounds) and in which morphologically similar plants exist in one or several of "chemical races" is so well known that it is now clear that it is the major type of chemical variation in all the lichens. In the present study every species matches this chemical pattern in that every one has at least one distinct and constant medullary constituent. There are no specimens without medullary compounds. In the present study the constant medullary compounds are given high taxonomic significance. Morphologically similar or identical populations with different but constant medullary constituents are considered distinct species. (*Cetrelia collata* with imbricaric acid is considered distinct from *C. nuda* with $\alpha$-collatolic and alectoronic acids.) The constant constituents of the species are listed in Table 2.

In addition to the constant constituent medullary compound, some populations show an additional substance (or additional substances) in some specimens but not in others. For example *Platismatia erosa*, *P. interrupta*, *P. formosana*, and *P. regenerans* all produce caperatic acid as the constant medullary constituent. In addition, in some individuals of all these species, an unidentified substance could be demonstrated. We do not know whether this substance occurred in all the specimens and was not detected because of the limitations of our chemical techniques or whether the compound is merely present in only part of the populations. Since it occurs in addition to another substance (caperatic acid) that is invariably present and since its real distribution is unknown, this and the few other "accessory" substances found have not been considered in the delimitation of species. Likewise, in *Cetrelia cetrarioides* we are not sure whether some specimens contain both perlatolic and imbricaric acids although it is certain that most specimens contain only one substance or the other. Therefore, in this instance we have not used chemistry in the taxonomy because we feel that the chemical variation in this widespread species is still too inadequately explained.

The above examples demonstrate how the apparent absence of chemical constituents in individuals and in species has been evaluated.

The second problem, interpreting for taxonomic purposes the level of biological significance of chemical variation, is far more difficult. Since little has been definitively proved concerning the biosynthesis of the substances involved, we cannot estimate how different biologically the chemical races of morphologically similar lichens really are. Five main categories of evidence, however, lead to the inevitable conclusion that in morphologically similar or identical populations the largest chemical variations (those based on the constant chemical components) reflect major genetic differences; namely: (1) the orderly, nonrandom replacement series that the major medullary compounds regularly display; (2) the fact that chemically different populations usually show different geographic distributions; (3) the observation, noted repeatedly in many genera, that where geographic ranges overlap and where chemically different populations become sympatric—and where consequently chemically different plants may even grow side by side—no chemically intermediate individuals are found; (4) the fact that in localities where the chemical races are sympatric and where some chemically different plants do exist side by side, the chemical races as a whole select different habitats (W. L. Culberson and C. F. Culberson, 1967); and (5) the lack of any indication whatever that environment has anything to do with the qualitative presence of the major medullary constituents.

For a few lichen substances, there is some biosynthetic information which helps in taxonomic evaluations. For example, it is believed that stictic acid is derived from norstictic acid by a simple, one-step methylation reaction. In a recent study of the *Ramalina siliquosa* group (W. L. Culberson, 1967), no taxonomic importance was attached to the demonstration of norstictic acid in some of the stictic acid-producing individuals because norstictic acid is the biochemically expected precursor of stictic acid. Unfortunately, much of our knowledge of the biosynthesis of the substances produced in the genus *Cetrelia* is less precise, but it should be pointed out that in the present study we have not involved in the defining of species limits any pairs of substances believed to have such an intimate biosynthetic relationship as that of norstictic and stictic acids. It is precisely in the area of interpreting the biological significance of chemical variation that the lichenologist of the future, with a more precise knowledge of the chemical relationships of the compounds, will hopefully be able to distinguish significant from inconsequential chemical differences just as we hope today to distinguish significant from inconsequential morphological differences.

## Acknowledgments

This research was supported by National Science Foundation Grant GB-1239 and by U. S. Public Health Service Research Grant GM-08345 from the Division of General Medical Sciences, National Institutes of Health. We also wish to thank Professor Emeritus Dr. Yasuhiko Asahina for the many kindnesses extended to us during the months that we worked in his laboratory in Tokyo. The photographs of anatomical sections were taken by Miss Barbara Fox and those of herbarium specimens by Mr. Charles Racine.

## Taxonomic Treatment

### ***Cetrelia*** **Culb. et Culb., gen. nov.**

Thallus (5–)7–24(–26) cm. latus; laciniae 0.5–2.0(–2.5) cm. latae. Superficies superior pallide cinerea, albida, vel apud exemplaria vetera herbarii pallide citrella, pseudocyphellata, isidiata vel sorediata. Superficies inferior picea, rhizinata, saepe punctata. Cortex superior 15–30(–34)μ crassus, prosoplectenchymatosus; medulla 85–230(–264)μ crassa, alba; cortex inferior (10–)12–25(–31)μ crassus. Apothecia (0.1–)0.5–2.0(–4.2) cm. lata, submarginalia, vulgo perforata; hymenium (53–)62–110(–124)μ crassum, asci IKI+ caerulescentes; strata subhymenialia (35–)40–78(–84)μ, IKI–, stratum conspicuum algarum fere tegentia. Sporae 8-nae, ellipsoideae, 11–22(–25)×6–12μ. Pycnidia marginalia; conidia 1–1.5×(3–)4–6μ, recta, extremis nonnihil inflatis. Typus generis *C. cetrarioides* est.

Thallus (5–)7–24(–26) cm. broad; lobes 0.5–2.0(–2.5) cm. broad. Upper surface ashy white or tan, pseudocyphellate, isidiate or sorediate. Lower surface black, rhizinate, punctate in some species. Upper cortex 15–30(–34)μ thick, prosoplectenchymatous; medulla 85–230(–264)μ, white; lower cortex (10)12–25(–31)μ thick. Apothecia (0.1–) 0.5–2.0(–4.2) cm. broad, submarginal, usually perforate; hymenium (53–)62–110(–124)μ, the asci IKI+ blue; subhymenial layers (35–) 40–78(–84)μ, IKI–, usually underlain by a conspicuous layer of algae. Spores 8, ellipsoid, 11–22(–25)×6–12μ. Pycnidia marginal; conidia 1–1.5×(3–)4–6μ, rod-shaped, the ends slightly inflated.

Constituents: atranorin and alectoronic, anziaic, α-collatolic, imbricaric, microphyllinic, olivetoric, or perlatolic acids.

None of the species of the *Parmelia cetrarioides* group, recognized here as the genus *Cetrelia*, is the type of a validly described genus which could be used for them. Although *Cetraria sanguinea* Schaer., a member of the new genus, was included along with a *Parmelia* in the genus *Aspidelia* Stirt., that generic name is invalid (W. L. Culberson, 1966a). The name *Cetrelia* is a fanciful concoction from *Cetraria* and *Parmelia*, the genera in which most of the species had previously been placed.

## Artificial Key to the Species of *Cetrelia*

1. Thallus sorediate or isidiate or both.
  2. Thallus sorediate, primarily along the margins of the lobes, not isidiate.
    3. Medulla C+ pink or pinkish-orange, olivetoric acid present; widely distributed . . . . . . . . . . . . . . . . . . . . **11. C. olivetorum**
    3. Medulla C−, olivetoric acid absent; widely distributed.
      4. Medulla KC− or KC+ dirty pinkish, alectoronic acid and $\alpha$-collatolic acids absent; widely distributed, common in Europe but rare in North America.
        5. Medulla usually KC−, perlatolic acid present. **3. C. cetrarioides** sens. str.
        5. Medulla usually KC+ dirty pinkish or rarely KC−, imbricaric acid present . . . . . . . . . . . . . . **3. C. cetrarioides** sens. lat.
      4. Medulla KC+ bright pink or red, alectoronic and $\alpha$-collatolic acids present; widely distributed, common locally in eastern North America but rare in Europe . . . . . . . . . . . . . . **4. C. chicitae**
  2. Thallus isidiate, not sorediate.
    6. Isidia accompanied by conspicuous dorsiventral lobulae in tufts on the thallus surface or as a fringe along the margins of the thallus lobes . . 9
    6. Isidiate plants without dorsiventral lobulae.
      7. Medulla C+ red, anziaic acid present; isidia often poorly developed; Formosa and Japan . . . . . . . . . . . . . . **8. C. isidiata**
      7. Medulla C−, KC+ pink or red, alectoronic and $\alpha$-collatolic acids present; isidia well developed and not at all sorediose through most of the range but granular, poorly developed and sorediose in the southern part (Philippines); Asia . . . . . . . . . . . **2. C. braunsiana**
1. Thallus neither sorediate nor isidiate.
  8. Thallus with dorsiventral lobulae in tufts or clusters on the upper surface or as a fringe along the margins of the lobes.
    9. Medulla C− ; lobulae well developed and abundant.
      10. Microphyllinic acid present; Japan and southeastern Asia. **9. C. japonica**
      10. Imbricaric acid present; China and Formosa . . **14. C. sinensis**
    9. Medulla C+ pink or red; lobulae well developed or poorly developed, infrequent, granular, and isidioid.
      11. Olivetoric acid present; Japan, Formosa, China, and the Himalayas. **12. C. pseudolivetorum**
      11. Anziaic acid present; mountains of southern and southeastern Asia and Japan . . . . . . . . . . . . . . . . . . **13. C. sanguinea**
  8. Thallus without lobulae.
    12. Pseudocyphellae very small, rarely reaching 1 mm. long, simple and punctiform (Plate 12, Figure 52).
      13. Medulla C+ pink or red.
        14. Olivetoric acid present; mountains of southwestern China. **6. C. davidiana**
        14. Anziaic acid present; mountains of southern and southeastern Asia and Japan. . . . . . . . . . . **13. C. sanguinea** (some forms)
      13. Medulla C− ; perlatolic or imbricaric acid present.

15. Lobes relatively thick and uniformly colored; pycnidia conspicuously distributed along margins of the lobes; on trees, southwestern China. **7. C. delavayana**

15. Lobes relatively thin, the margins darker than the center; pycnidia unknown; on tundra soil in Alaska . . . . . . **1. C. alaskana**

12. Pseudocyphellae very large, some more than 1 mm. long, compound and irregular (Plate 12, Figure 53).

16. Medulla KC+ pink, alectoronic and α-collatolic acid present; Japan, Formosa, and southwestern China . . . . . . . . **10. C. nuda**

16. Medulla KC−, imbricaric acid present; southwestern China and Nepal. **5. C. collata**

**1. Cetrelia alaskana** (Culb. & Culb.) Culb. & Culb., comb. nov. PLATE 14

*Cetraria alaskana* Culb. & Culb., Bryologist 69:200. 1966. Type: U.S.A., Alaska, Cape Sabine, *Thomson, Lich. Arct.* 13 (DUKE, holotype; COLO, LD, MSC, WIS, WIS-Herb. Thomson, isotypes).

Thallus medium, 5–7 cm. broad, pale, yellowish-tan, or brownish, often mottled with black, the margins distinctly brown. Lobes 1–1.5 cm. broad, smooth, not pruinose, esorediate, pseudocyphellate, the pores minute. Lower surface jet-black throughout or the margins chestnut brown, smooth, not punctate, rhizines few, often very short and papilliform. Upper cortex 16–29μ thick; medulla 86–135μ thick; lower cortex 16–23μ thick. Apothecia and pycnidia unknown.

MEDULLARY REACTIONS.—K−, C−, KC− or KC+ pale pink, PD−.

CONSTITUENTS.—Imbricaric acid and atranorin.

DISTRIBUTION (Map, Figure 10).—The west coast of Alaska on the Bering Sea and Arctic Ocean; in the tundra.

*Cetrelia alaskana* is a conspicuous, large-lobed lichen inhabiting plant debris in the Alaskan tundra. It has doubtless been collected more frequently than the present records indicate and has consistently been mistaken for other species. The fact that it may be locally abundant is clearly shown by the fact that at Cape Sabine, the type locality, Thomson collected enough of the species to issue in his exsiccat series, *Lichenes Arctici*.

*Cetrelia alaskana* resembles *C. cetrarioides* more than it does any other species. Both have characteristic, minute, easily overlooked pseudocyphellae in the upper cortex. *Cetrelia alaskana*, however, can easily be distinguished from *C. cetrarioides* by its lack of soredia.

*Cetrelia alaskana* has also been mistaken for *Asahinea chrysantha* (Tuck.) Culb. & Culb. which occurs in the same region and the two species can probably be found together in the field. *Cetrelia alaskana* always has some rhizines on the lower surface even though they may not be produced in abundance while the lower surface of *A. chrysantha* is invariably naked. *Asahinea chrysantha* also contains usnic acid in the upper cortex and is consequently yellow-colored in contrast to the usnic acid-lacking, tan-colored upper cortex of *C. alaskana*. The medulla of *A. chrysantha* contains alectoronic acid and is consequently strongly fluorescent in ultraviolet light while the medulla of *C. alaskana* contains imbricaric acid and is not fluorescent. A detailed account of *Asahinea* and its relationships to other groups in the Parmeliaceae has already been given (W. L. Culberson and C. F. Culberson, 1965).

CHEMICAL ANALYSIS.—All 14 samples of *C. alaskana* tested microchemically contained atranorin and imbricaric acid. The identity of imbricaric acid was definitely established by the extraction and detailed analysis of a small sample (C. F. Culberson and W. L. Culberson, 1966). The substance responsible for the KC+ reaction observed on the thallus could not be identified.

ADDITIONAL SPECIMENS EXAMINED:

U.S.A.: ALASKA: Pitmegea River, 15 mi. upstream from Cape Sabine, 68°48′N, 154°20′W, *Thomson, Lich. Arct.* 13. (Type collection, see above.) Ogotoruk Creek Drainage, 68°05′N, 165°32–47′W, *Johnson et al.* 21 (COLO). 40 mi. east of Cape Lisburne, *Cantlon & Gillis* 57–136A (MSC). Kuskakwin, Goodnews Bay, *Geist*, 1933 (Herb. Degelius, LD). Lower Telephone Creek, *Palmer* 585 (US, WIS). Peace River, *Palmer* 614 (US, WIS).

2. **Cetrelia braunsiana** (Müll. Arg.) Culb. & Culb., comb. nov. PLATE 15

*Parmelia braunsiana* Müll. Arg., Flora 64:506. 1881. Type: Japan, Tokyo, *Brauns* 2 (*pro parte*) (G, holotype).

*Platysma braunsianum* (Müll. Arg.) Hue, Nouv. Arch. Mus., IV, 1:210. 1899.

*Cetraria braunsiana* (Müll. Arg.) Zahlbr., Bot. Mag. [Tokyo] 41:353. 1927.

*Parmelia braunsiana* f. *isidiosa* Müll. Arg., Flora 64:506. 1881. Type: Japan, Tokyo, *Brauns* 2 (*pro parte*) (G, holotype).

*Platysma braunsianum* f. *isidiosum* (Müll. Arg.) Hue, Nouv. Arch. Mus., IV, 1:210. 1899.

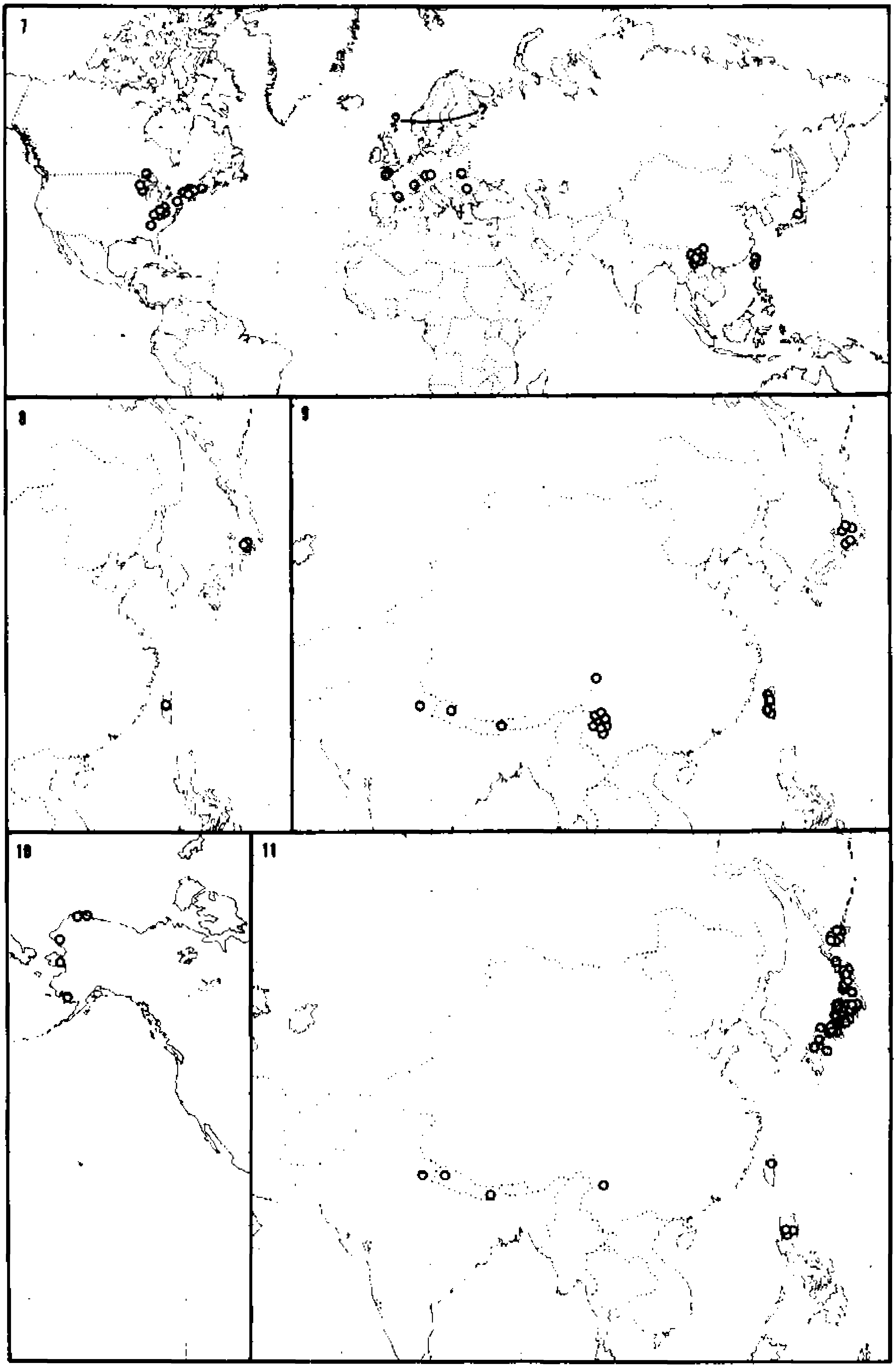
*Cetraria braunsiana* f. *isidiosa* (Müll. Arg.) Zahlbr., Catal. Lich. Univ. 6:284. 1930.

*C. collata* f. *isidiata* Asah., Journ. Jap. Bot. 10:475. 1934. Type: Japan, Musashi Prov., Mt. Buko, *Asahina* 71b (TNS, lectotype).

Thallus medium to large, 12–24 cm. broad; lobes 0.5–1.7 cm. broad. Upper surface gray or ashy-white, uniformly brownish or tan in old herbarium specimens, the margins ± ascendent and commonly isidiate, at least in part, the tips pruinose, pseudocyphellate, the pores small, punctiform to irregular, rarely more than 1 mm. broad, often associated with tiny, granular, delicately coralloid isidia. Lower surface black, the margins brown or grayish like the color of the upper surface, not punctate; rhizines black. Upper cortex 19–25$\mu$ thick; medulla 109–264$\mu$ thick; lower cortex 16–22$\mu$ thick. Apothecia rare, submarginal, perforate, about 0.5 mm. broad; hymenium 93–109$\mu$ thick; subhymenial layers 40–53$\mu$ thick, underlain by a dense layer of algae. Spores 8, ovoid, 12–15$\times$8–9$\mu$. Pycnidia rare, marginal, black, pruinose; conidia 1$\times$4–6$\mu$, rod-shaped, the ends slightly enlarged.

MEDULLARY REACTIONS.—K−, C−, KC+ pink, PD−.

CONSTITUENTS.—Alectoronic and $\alpha$-collatolic acids and atranorin.



Figures 7–11. Distributions. 7. *Cetrelia olivetorum* (Nyl.) Culb. & Culb. 8. *Cetrelia isidiata* (Asah.) Culb. & Culb. 9. *Cetrelia pseudolivetorum* (Asah.) Culb. & Culb. 10. *Cetrelia alaskana* (Culb. & Culb.) Culb. & Culb. 11. *Cetrelia braunsiana* (Müll. Arg.) Culb. & Culb.

DISTRIBUTION (Map, Fig. 11).—Widespread in Hokkaido and Honshu, Japan, in the high mountains of Formosa, Luzon, Philippines, Yunnan, China, and in the Himalayas; on tree trunks and over boulders.

*Cetrelia braunsiana*, *C. chicitae*, and *C. nuda* have been recognized in recent years by Japanese botanists as *Cetraria collata* f. *isidiata* Asah., *C. collata* sens. str. (=f. *collata*), and *C. collata* f. *nuda* Hue respectively. They are, however, quite distinct morphologically, although chemically all produce atranorin and alectoronic and α-collatolic acids. *Cetrelia braunsiana* is isidiate, *C. chicitae* is sorediate, and *C. nuda* produces neither soredia nor isidia, but it has pseudocyphellae different from those of the other two species.

The differences among these three species, and the consequent justification for regarding them as distinct and of specific rank are summarized in Table 5.

TABLE 5.—*The percentages of Japanese specimens of* Cetrelia braunsiana, C. chicitae, *and* C. nuda *showing various morphological traits and the geographic distribution of the species*

| | *braunsiana* | *chicitae* | *nuda* |
|---|---|---|---|
| Total number of specimens examined | 74 | 35 | 51 |
| Small pseudocyphellae (less than 1 mm.) | 93 | 100 | 10 |
| Large pseudocyphellae (more than 1 mm.) | 7 | 0 | 90 |
| Isidia | 100 | 0 | 0 |
| Soredia | 0 | 100 | 0 |
| Apothecia | 4 | 17 | 83 |
| Pycnidia | 7 | 14 | 100 |
| Pycnidia pruinose | 0 | 0 | 24 |
| Lobes pruinose (at least in part) | 69 | 43 | 14 |
| Lower surface punctate | 1 | 6 | 59 |
| Japanese range | Hokkaido, Honshu | Hokkaido, Honshu | Southern Honshu, Shikoku, Kyushu |

Japanese specimens belonging to this group never produce both isidia and soredia and most (90%) of the specimens with neither isidia nor soredia have large pseudocyphellae rather than the small ones characteristic of the other two species. It should be pointed out, however, that the isidia in *Cetrelia braunsiana* are often produced in very small numbers. Invariably, however, if Japanese specimens belonging to this group and having small pseudocyphellae and no soredia are examined carefully under the dissecting microscope, at least a few delicate marginal isidia will be found. The type specimen itself of *C. braunsiana* has very few isidia.

It is apparent from Table 5 that *Cetrelia braunsiana* and *C. chicitae* are more similar to each other than they are to *C. nuda*. The nonisidiate, esorediate *C. nuda* always produces pycnidia, which are often pruinose, and commonly has apothecia and a punctate lower cortex. It actually belongs to the *Cetrelia sanguinea* group and is not particularly closely related to *C. braunsiana* and *C. chicitae* at all, although its taxonomy has been confused with theirs.

As pointed out above, it is generally possible to distinguish Japanese specimens of *Cetrelia braunsiana* from those of *C. chicitae* by careful examination of the plants for isidia. Farther south, and especially in the Philippines, the distinctions may become more difficult. In some Philippine specimens the margins of the lobes are densely covered with soredia-like structures that become isidioid and granular, apparently by compaction and the formation of a cortexlike surface. These anomalous specimens are otherwise well developed and may represent a unique local race even though essentially typical specimens of both *C. braunsiana* and *C. chicitae* are also known from the Philippines. This local problem in distinguishing between some specimens of *C. braunsiana* and *C. chicitae,* however, should not be taken to indicate that these two species differ only slightly because in reality they differ quantitatively in the expression of many traits (Table 5). Nevertheless, the identification of certain isolated specimens from the Philippines may depend entirely upon the presence of isidia as opposed to soredia.

The type specimen of *Parmelia braunsiana* Müll. Arg. is isidiate and the type of *P. braunsiana* f. *isidiosa* Müll. Arg., really part of the same collection, is somewhat more isidiate. In view of the great variation in the production of isidia in the Japanese population of this species, there is no basis for recognizing the forma.

*Cetrelia braunsiana* is part of the Sino-Japanese floristic element with a range extension into Formosa and the Philippines. In spite of its relatively close relationship to the very widespread species *C. chicitae,* no specimens of it from outside the Orient are known. In Japan *C. braunsiana* is widely distributed and is found at lower elevations as well as in the mountains. Its broader amplitude of ecologic tolerance, as compared to that of most of the Japanese species of *Cetrelia,* is also seen in its general abundance in Japan as well as in its more extensive vertical geographic range there.

CHEMICAL ANALYSIS.—Alectoronic acid, $\alpha$-collatolic acid, and atranorin were identified in the 32 samples tested. The tests were made without difficulty and, in most cases, directly on the acetone extract, the concentration of $\alpha$-collatolic acid being sufficient to give a good chromatogram. Although many of the residues were yellow, no known pigment could be identified and all tests for usnic acid were negative.

NOMENCLATURE.—In the Japanese botanical literature the name *Cetraria braunsiana* (Müll. Arg.) Zahlbr. has been used consistently to refer to the species treated here as *Platismatia interrupta* Culb. & Culb. A simple but widespread misunderstanding of the application of the name apparently accounts for this.

This species was named for David Brauns (1827–1893), Professor of Geology at the University of Halle, who made the original collection near Tokyo in 1881.

REPRESENTATIVE SPECIMENS EXAMINED:

JAPAN: HOKKAIDO: Sapporo, *Faurie* 9212 (PC). Prov. Ishikari: Daisetsu, Kuro-dake, *Asahina*, 1937 (TNS, two collections); Hot Spring Matsuyama, *Asahina*, 1935 (TNS). Prov. Kitami: Lake Abashiri, *Asahina & Togashi*, 1953 (TNS). Prov. Kushiro: Lake Akan, *Asahina*, 1953 (TNS).

HONSHU: Hirosaki, *Faurie* 196 (PC). Prov. Bingo: Sera-gun, Kamiyama-mura, *Sato*, 1932 (TNS). Prov. Echigo: Iwafune-gun, Arakawa-cho, *Togashi*, 1956 (TNS). Prov. Echizen: Imadate-gun, Okamoto-mura, *Hosoi & Ui*, 1935 (TNS). Prov. Ettyu: Magawa Pass, *Asahina*, 1936 (TNS, two collections). Prov. Harima: Shiso-gun, Mikawa-mura, Funakoshi, *Utsumi*, 1951 (TNS). Prov. Inaba: Karo, *Ikoma*, 1953 (TNS). Prov. Iwaki: Matsukawa-ura, *Kurokawa* 58086, 58087 (TNS). Prov. Iwashiro: Ura-bandai, *Asahina*, 1954 (TNS). Prov. Izu: Nirayama, Honryu-ji Temple, *Asahina*, 1956 (TNS). Prov. Kaga: Enuma-gun, Hot Spring Yamanaka, *Togashi*, 1959 (TNS). Prov. Kai: Mt. Minobu, *Togashi*, 1961 (TNS, three collections). Prov. Kii: Mt. Koya, *Numajiri* 699 (TNS). Prov. Kozuke: Tano-gun, Ueno-mura, Shio-no-sawa Pass, *Togashi*, 1956 (TNS). Prov. Mikawa: Mt. Horaiji, *Asahina*, 1956 (TNS, two collections). Prov. Mino: Seki-ga-hara, *Asahina*, 1938 (TNS). Prov. Musashi: Chichibu, Ryogami-mura, Hyugaotani, *Kurokawa* 550534 (TNS); Mt. Buko, *Asahina* 71b (TNS). Prov. Owari: Inuyama, *Asahina*, 1938 (TNS). Prov. Rikuchu: Isawa, Mt. Shishihana, *Suzuki* 491 (TNS). Prov. Rikuzen: Tamatsukuri-gun, Naruko-cho, *Asahina & Togashi* (TNS). Prov. Sagami: Odawara, Mt. Daiyuzan, Saijo Temple, *Togashi*, 1956 (TNS). Prov. Settsu: Arima-gun, Dojo-mura, *Togashi*, 1952 (TNS). Prov. Shimotsuke: Nikko, Lake Yuno-ko, *Asahina*, 1931 (TNS, two collections). Prov. Shinano: Lake Shirakaba, *Asahina & Togashi*, 1958 (DUKE); Mt. Kimpu, *Asahina, Togashi & Nuno* (TNS, 2 collections); Suwa-gun, Izumino-cho, *Asahina & Togashi*, 1958 (TNS); Mt. Yatsu-ga-take, Hot Spring Shibu-no-yu, *Kurokawa* 58198 (TNS) and 58199 (DUKE); Mt. Tadeshina, *Kurokawa* 51746, 71864, 58374, 58375 (TNS) and 58375 (MSC); Mt. Norikura, *Asahina*, 1952 (TNS). Prov. Suo: Hikarishi, Murozumi, *Asahina & Togashi*, 1959 (TNS). Prov. Suruga: Lake Saiko (Nishi-no-umi) near Mt. Fuji, *Culberson & Culberson* 10684 (DUKE). Prov. Tango: Miyazu-shi, Nariai Temple, *Togashi*, 1956 (TNS). Prov. Uzen: Goshiki-numa, *Suzuki*, 1954 (TNS). Prov. Wakasa: Mt. Aoba, *Togashi*, 1956 (TNS). Prov. Yamashiro: Atago-gun, Hanaze-mura, Mt. Taihi, *Togashi*, 1955 (TNS).

SHIKOKU: Prov. Tosa: Hata-gun, Okata-cho, *Kurokawa* 550231, 550232 (TNS); Mt. Yokogura, *Fujikawa*, 1931 (TNS).

FORMOSA: Mt. Ali, 2,200 m., *Kurokawa* 13 (TNS). Mt. Ba-Hsen, 2,180 m., *Jen-rong Wang* 133 (DUKE). Piyanan Pass, 1,600–1,900 m., *Kurokawa* 821 (TNS).

PHILIPPINES: LUZON: Benguet Prov.: Mt. Pulog, *McGregor*, 1909 (TUR). Mountain Prov.: Mt. Data, *Hale* 26019, 26150, 26401 (US).

CHINA: YUNNAN: Kou-toui, above Mo-so-yn,[2] *Delavay* 3009 (PC).

NEPAL: Mewakhola Valley, 11,000 ft., *Awasthi* 2265 (UPS). Above Sauwala Khola, 10,500 ft., *Stainton et al.* 4379b (*pro parte*) (BM).

INDIA: Northwestern Himalayas: Kamaon, Almora District, Dhakuri Ridge, 9,500 ft., *Awasthi & Awasthi* 633 (UPS).

**3. Cetrelia cetrarioides** (Del. ex Duby) Culb. & Culb., comb. nov. PLATE 15

*Parmelia perlata* β *cetrarioides* Del. ex Duby, Bot. Gall., ed. 2, 601. 1830. Type: France, Mont d'Or, *Delise*, 1828 (STR, lectotype). The lectotype, designated by Hale (1960), was not seen, but an extract of a fragment of it prepared by Hale was studied microchemically by us (see below).

*P. cetrarioides* (Del. ex Duby) Nyl., Flora 52:289. 1869.

*P. monochorum* Zahlbr., Symb. Sin. 3:191. 1930. Type: China, Szechwan, Döko Pass southwest of Muli, *Mazzetti* 7399 (WU, holotype).

*P. cetrarioides* f. *bisoralifera* Laven, Repert. Spec. Nov. Fedde 50:294. 1941. Type: Bavaria, prope lacum Lautersee, *Laven* (not seen).

Thallus medium to large, 7–16 cm. broad; lobes (0.5–)1–1.5 cm. broad. Upper surface uniformly tan or pale, pseudocyphellate, the pores very small, rarely reaching 0.5 mm., the margins of the lobes finely and usually abundantly sorediate. Lower surface jet-black, the margins brown, usually punctate with many small pores; rhizines few, black, rarely pale. Upper cortex (16–)19–28(–31)μ thick; medulla (62–)90–155(–171)μ thick; lower cortex 16–25(–28)μ thick. Apothecia extremely rare, 1–2 mm. broad (immature, the only ones seen *in situ*). Spores ovoid, 12–14×19–24μ (seen in a single apothecial fragment). Pycnidia unknown.

MEDULLARY REACTIONS.—K−, C−, KC− or KC+ pinkish, PD−.

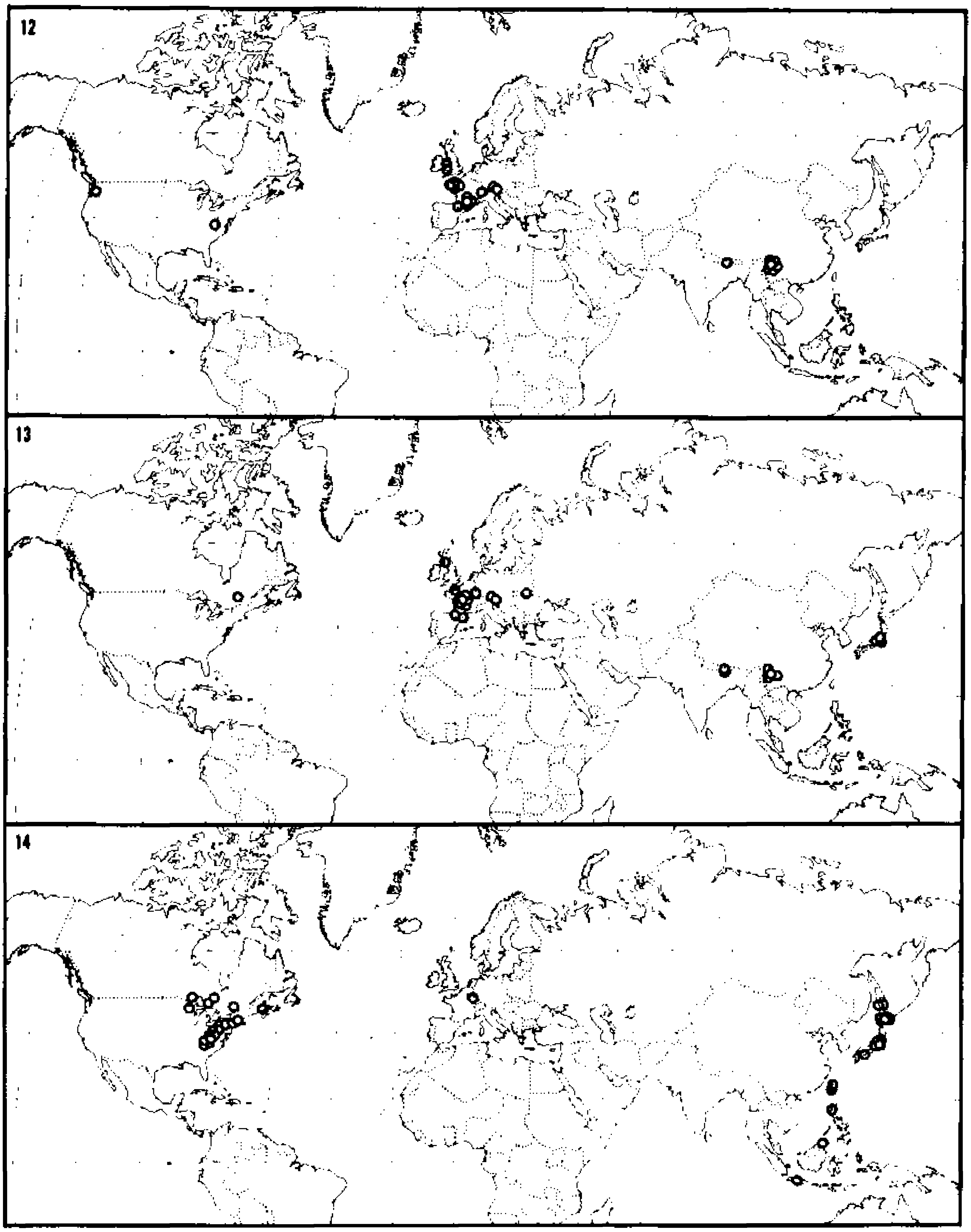
CONSTITUENTS.—Perlatolic or imbricaric acid and atranorin.

DISTRIBUTION (Maps, Figures 12–13).—Eastern North America, Japan, the mountains of southern Asia, and western Europe; usually in shady places, on the bark of trees, rock faces, and over boulders.

The *Cetrelia cetrarioides* complex includes four chemically distinct populations. The population producing atranorin and olivetoric acid in the medulla is slightly but distinctly different morphologically from the other three and clearly represents a different taxon, here treated as the species *Cetrelia olivetorum* (see page 515). The remaining three chemical types consist of plants which produce atranorin and (1) perlatolic acid, (2) imbricaric acid, or (3) alectoronic and α-collatolic acids. In examining a large series of herbarium specimens one may be tempted to see subtle morphological "tendencies" among the chemical races, but the accurate identification of individual specimens ultimately depends upon chemical analysis.

---

[2] The spelling of Chinese place names in the citation of specimens taken by Delavay follows Bretschneider's (1898) excellent summary of Delavay's botanical work. Our only modification of Bretschneider's spellings has been to hyphenate compound names.



FIGURES 12–14. Distributions. 12–13. *Cetrelia cetrarioides* (Del. ex Duby) Culb. & Culb. (two chemical strains). 12. *Cetrelia cetrarioides* (Del. ex Duby) Culb. & Culb. sens. str., the strain with perlatolic acid. 13. *Cetrelia cetrarioides* (Del. ex Duby) Culb. & Culb. sens. lat., the strain with imbricaric acid. 14. *Cetrelia chicitae* (Culb.) Culb. & Culb.

In the present study the plants containing alectoronic and α-collatolic acids are assigned to *Cetrelia chicitae* and the perlatolic and imbricaric acid-containing plants to *C. cetrarioides* sens. lat. It may be thought arbitrary and untenable, in the absence of a unique morphology, to consider the plants that produce alectoronic and α-collatolic acids to represent a distinct species while keeping together taxonomically those that produce perlatolic acid and those that produce imbricaric acid. As pointed out in a previous study of the chemistry and geographic distribution of the components of the *cetrarioides* complex (Culberson, 1958), plants assigned to *C. chicitae* represent the bulk of the *P. cetrarioides* complex in North America, while in Europe the complex is made up almost entirely of perlatolic and imbricaric acid-producing populations. While the three chemical races might be nearly sympatric purely from the point of view of qualitative range (although the worldwide distribution here is poorly known), the quantitative distributions are clearly different. For this reason and since the production of the two compounds alectoronic acid and α-collatolic acid seems to be a relatively large departure from the chemistry of the other chemical types, this type is regarded as a distinct species.

The retention of the remaining two types, the perlatolic acid-containing plants and the imbricaric acid-containing ones, within the single species *Cetrelia cetrarioides* is less satisfactory. Unlike the chemical species *C. chicitae*, these two races do not seem to be significantly more abundant in one part of their range than in other parts. Although by proper chemical analyses it is possible to identify which of the acids is present in a given specimen, there are a few imbricaric acid-containing specimens in which our microchemical and chromatographic tests cannot assure with absolute certainty the absence of perlatolic acid (although an alternate explanation is possible; see the chemical discussion below). In view of the essentially sympatric distribution of these two chemical types and the possibility at least that some individuals may actually produce both perlatolic and imbricaric acids, it does not seem desirable at present to try to accommodate the chemical variation in the taxonomy.

Some nonchemical aspects of the taxonomy in the *Cetrelia cetrarioides* complex are also still not completely explored. For example, two anomalous, well developed, imbricaric acid-producing specimens from Sikkim in the Himalayas, where the genus *Cetrelia* is exceptionally well represented, lacked soredia altogether. The plants are relatively small-lobed and by habit alone are obviously closely allied to *C. cetrarioides*. Since typical specimens of the imbricaric acid-producing race of *C. cetrarioides* are found in the same Himalayan region, these specimens have provisionally been assigned to *C. cetrarioides* in spite of their lack of soredia. They are pointed out here only to call attention to the fact that additional studies on new collections of the *C. cetrarioides* complex from the Himalayas might necessitate additional modifications in the taxonomy.

The tundra-inhabiting species *Cetrelia alaskana* might be mistaken for *C. cetrarioides* because superficially it looks similar. Like many individuals of *C. cetrarioides*, *C. alaskana* produces imbricaric acid, but it is never sorediate while soredia are usually well developed in most specimens of *C. cetrarioides.* The two species also have strikingly different ecologies, and their geographic ranges are widely separated.

The soredia in *Cetrelia cetrarioides* are typically confined to the margins of the lobes in long soralia. An anomalous form with conspicuous capitate soralia has been named as an infraspecific variation (Laven, 1941). An analogous form bearing capitate soredial masses has also been described for *Platismatia norvegica.* These rare, peculiar forms are not considered taxonomically in this study because they seem to represent pathological rather than natural growths.

In its broad sense, including both the chemical races that compose it, *Cetrelia cetrarioides* is the most widely ranging species in the genus. It is, of course, the very fact of this broad range and the accompanying internal chemical variation that would speak against considering *C. cetrarioides* a single species as it is regarded in the present study.

*Cetrelia cetrarioides,* like the closely related species *C. olivetorum* and *C. chicitae,* is generally restricted to places with relatively moist, cool climates. It is probably most abundant and best developed in the British Isles and in other oceanic parts of western Europe. As would be expected, the southernmost stations of its range on all continents are in mountains.

Throughout much of its range *Cetrelia cetrarioides* is very infrequent. Its extreme rarity in North America has already been reported (Culberson, 1958), a rarity all the more noteworthy in view of the extreme local abundance of the closely related species *C. chicitae* (see the discussion for that species). In parts of Europe *C. cetrarioides* is also very rare. For example, in the southern parts of Norway (Lynge, 1921), Sweden (Du Rietz, 1924), and Finland (Hakulinen, 1963)—regions which have been intensively explored by lichenologists—it has been found in only a few localities.[3] In Asia too the records are widely scattered. The extreme rarity of the species of course means that it has often gone unnoticed by collectors. The distribution maps given here (Figures 12–13) are consequently only roughly approximate.

CHEMICAL ANALYSIS.—Sixty-nine samples of this species were tested; 35 contained atranorin and perlatolic acid and 34 contained atranorin and imbricaric acid mixed with at least one unidentified phenolic substance. Perlatolic acid was identified by the crystals observed in the

---

[3] No Scandinavian specimens of *Cetrelia cetrarioides* were seen in this study. Although the species unquestionably occurs in southern Scandinavia, no localities are given on the maps (Figures 12–13) because the chemical race to which such specimens belong is unknown. The presence of *C. cetrarioides* sens. lat. in Scandinavia is acknowledged on the map in Figure 1 which shows the geographic distribution of species numbers in the genus *Cetrelia.* The two species recorded there for Scandinavia are *C. cetrarioides* and *C. olivetorum.*

GE and GAW solutions and by the straight extinction of these crystals with crossed Nicols. Imbricaric acid crystals show oblique extinction and a somewhat different morphology in these solutions.

All residues were chromatographed in $NH_4OH$-n-butanol, and many of them were hydrolyzed with 0.1 N $Na_2HPO_4$ to detect imbricaric acid. While perlatolic acid-containing samples were always KC− (with the possible exception of one specimen), a definite to pale KC+ red reaction was observed on many imbricaric acid-containing thalli. Imbricaric acid was identified by comparison with imbricaric acid in *Cetrelia alaskana* (C. F. Culberson and W. L. Culberson, 1966). A KC+ reaction which has also been observed with *C. alaskana* is due to an unidentified KC+ substance or to a low concentration of some C+ substance. Further studies are necessary to identify this material.

Asahina and Fuzikawa (1935) have suggested that imbricaric acid and perlatolic acid may occur together, but their evidence is not conclusive. Hydrolysis of several imbricaric acid-containing residues showed a spot by chromatography at an $R_f$ corresponding to that for olivetol-2-carboxylic acid. This could be explained if perlatolic acid were also present, but such a mixture would still not be KC+. Either the samples containing imbricaric acid may also contain perlatolic acid and still a third constituent to give the KC+ reaction, or these samples contain imbricaric acid and a KC+ substance that produces olivetol-2-carboxylic acid upon hydrolysis.

NOMENCLATURE.—After a careful study of the appropriate specimens from Delise's herbarium, Hale (1960) was able to typify *Parmelia perlata β cetrarioides* Del. ex Duby in the sense that the binomial *P. cetrarioides* (Del. ex Duby) Nyl. has generally been used. Although we were not able to examine the lectotype, Hale's (1960) photograph of it is unmistakable. From a microextract that he had made from it at the time of his study and which he subsequently gave to us for testing, we confirmed his report that this specimen contains perlatolic acid. In the quite possible eventuality that a future interpretation based on additional evidence should recognize the imbricaric acid-producing race as a distinct species, it should be noted that *P. monachorum* Zahlbr. offers apparently the oldest specific epithet for this variation; we have identified imbricaric acid and atranorin in the holotype.

Santesson (1942) noted that *Pseudoparmelia pseudofallax* Gyeln. is also a synonym of "*Parmelia cetrarioides,*" but we have not seen the type specimen and do not know to which chemical race it belongs. Even if it belongs to the variant producing imbricaric acid, it could not be used, since the epithet *monachorum* is older.

ADDITIONAL SPECIMENS EXAMINED:

Specimens of *C. cetrarioides*, the perlatolic acid-producing race:

U.S.A.: West Virginia: Pendleton Co.: Panther Knob, *Hale* 14264 (DUKE). Washington: Snohomish Co.: Marysville, *Grant*, 1926 (MICH), 1927 (MICH).

CHINA: Yunnan: Kou-toui, above Mo-so-yn (Lan-kong), 3,000 m., *Delavay* 1887 (PC); Yen-tze-hay, 300 m., *Delavay*, 1887 (PC); Yen-tze-hay, Lan-kong. *Delavay*, s.d. (PC); Koua-la-po, *Delavay* 1595 (*pro parte*) (PC); Koua-la-po, Ko-kin, 3,000 m., *Delavay*, 1885 (PC, 2 collections).

SIKKIM: Tonglo, 10,000 ft., *Hooker* 2083 (K).

POLAND: Mont. Carphatica, Mont. Gorganae, near Skole, *Aasamaa* Cet-302 (DUKE).

AUSTRIA: Hallstadt, *ex herb. Bory de St-Vincent*, 1805–1806 (PC).

GERMANY: Bayern: Obere Hochebene, Wornbrunn, *Schwind*, 1925 (BP).

SWITZERLAND: Vaugeron, near Genève, *Schleicher* 80 (DUKE). Ticino: Fusio, Maggia Valley, *Barkman* 4290 (DUKE).

FRANCE: Côtes-du-Nord: Forêt de Lorges, *des Abbayes*, 1929, 1930 (Herb. des Abbayes, 2 collections).

Finistère: Forêt de Coatloc'h, *Piquenard*, 1900 (PC); the same, *des Abbayes*, 1930, 1933 (Herb. des Abbayes, 2 collections).

Aveyron: Forêt de Serre, *Barreau*, 1831 (PC, 3 collections).

Sarthe: Forêt de Perseigne, *des Abbayes*, 1936 (Herb. des Abbayes).

Vosges: Docelles, *Harmand, Lich. Loth.* 288 (*pro parte*) (PC).

Puy-de-Dôme: Bois de Job, near Ambert, *Gasilien*, 1883 (Herb. des Abbayes).

Hautes-Pyrénées: Pauze, near Cauterets, collector unknown (PC).

WALES: Merionethshire: Penmaenpool, *Culberson & Culberson* 11564 (DUKE).

Specimens of *C. cetrarioides* sens. lat., the imbricaric acid-producing race:

CANADA: Québec: Labelle Co.: North of La Conception, *Hermann* 15783 (DUKE).

JAPAN: Fujiyama; Ityigome-Magajisi, *Almquist*, 1879 (S); the same, Umagayeshi, *Almquist*, 1879 (S). Togakushi, *Faurie* 777 (PC).

CHINA: Yunnan: Hee-chan-men, *Delavay*, 1887 (PC); Santo-ha-ho, 3,000 m., *Delavay*, 1888 (PC, 2 collections); Lenago Pass between Mekong and Yangtse, 27°43'N, *Gebauer*, 1914 (W). Szechwan: Döko Pass SW of Muli, *Handel-Mazzetti* 7399 (UW).

SIKKIM: Lachan, 13,000 ft., *Hooker* 2086 (K). Wallanchoon 13,000 ft., *Hooker* 1814, 2082 (K).

POLAND: Mont. Carphatica, Mont. Gorganae, near Skole, *Aasamaa* Cet-301 (DUKE).

GERMANY: München, *Arnold, Lich. Monac. Exs.* 324a, (*pro parte*), 324b, (*pro parte*) (PC).

CZECHOSLOVAKIA: Nízke Poloniny, Nová Sedlica, *Pišút, Lich. Slovak. Exs.* 13 (DUKE).

FRANCE: Calvados: Forêt de St-Tever, collector unknown, 1890 (PC).

Seine-et-Marne: Fontainebleau, *Nylander*, s.d. (PC).

Puy-de-Dôme: Besse, *des Abbayes*, 1933, 1935 (Herb. des Abbayes, 2 collections).

Haute-Vienne: Montagnes de Goullet, *Lamy de la Chapelle*, 1874 (PC); Goullet, bei St. Sylvestre, *Lamy de la Chapelle*, as *Arnold, Lich. Exs.* 582 (PC).

Pyrénées-Orientales: La Massane, *des Abbayes*, 1933 (Herb. des Abbayes).

Hautes-Pyrénées: Pauze, near Cauterets, collector unknown, s.d. (PC).

SCOTLAND: Argyllshire: Ardnamurchan Peninsula, Salen, *Culberson & Culberson* 11816 (DUKE).

4. **Cetrelia chicitae** (Culb.) Culb. & Culb., comb. nov. PLATE 14
*Cetraria chicitae* Culb., Bryologist 68:95. 1965. Type: U.S.A., West Virginia, *Hale, Lich. Amer. Exs.* 56 (DUKE, holotype).

Thallus medium to large, 10–16 cm. broad; lobes 0.7–1.7 cm. broad. Upper surface light gray or ashy, uniformly brown or tan in old herbarium specimens, smooth, often pruinose at the tips, the margins erupting with fine soredia, pseudocyphellate, the pores small, rarely exceeding 1 mm. Lower surface jet-black, the margins brown or colored like the upper surface and in some specimens wrinkled, the crests of the folds becoming punctate. Upper cortex 16–26(–31)μ thick; medulla 85–186(–260)μ; lower cortex, 10–26μ thick. Apothecia very uncommon, perforate, 4–5 mm. broad; hymenium 62–78μ thick; subhymenial layers 62–78μ thick. Mature spores unknown. Pycnidia rare, marginal; conidia 1×5–6μ, rod-shaped, the ends somewhat enlarged.

MEDULLARY REACTIONS.—K−, C−, KC+ pink, PD−.

CONSTITUENTS.— Alectoronic acid and α-collatolic acid and atranorin.

DISTRIBUTION (Map, Figure 14).—Southern Ontario and New Brunswick, Canada, and the adjacent United States, south in the Appalachian Mountains to North Carolina; southern Sakhalin and Japan, and the mountains of Formosa, Luzon (Philippines), Sabah (Borneo), and Java; on the trunks of trees and on rocks and over boulders. A discussion of the range of this species is included in the treatment for *C. cetrarioides* (p. 501).

*Cetrelia chicitae* is essentially indistinguishable morphologically from *C. cetrarioides,* although the species differ in chemical constituents and in their geographic distributions. For a full discussion of the relationship of *C. chicitae* to *C. cetrarioides* and to *C. olivetorum,* see the treatment of *C. cetrarioides* (p. 498). The relationship of *C. chicitae* to other species of the same chemistry for which it might be mistaken is explained in the taxonomic discussion of *C. braunsiana* (pp. 495–496).

CHEMICAL ANALYSIS.—The 24 samples tested all contained atranorin, alectoronic acid, and α-collatolic acid. Early in the study, 14 of these specimens were tested by means of a single acetone extraction, but later the method of double extractions with benzene and then acetone was employed. Microcrystal tests in the GE, GAW, and GA*o*-T solutions were always confirmed by chromatography to prove the presence of α-collatolic acid. In the fragments tested the concentrations of all three substances were always sufficient to give a good test without the difficulties sometimes encountered in other species in demonstrating small concentrations of α-collatolic acid or atranorin in the presence of alectoronic acid.

ADDITIONAL SPECIMENS EXAMINED:

U.S.A. AND CANADA: For a long list of selected specimens examined, see the original description of this species (W. L. Culberson, 1965).

U.S.S.R.: SAKHALIN ISLAND: Takinosawa, *Asahina*, 1932 (TNS, 2 collections); Aikawa, *Asahina*, 1932 (TNS).

KOREA: Locality unknown, *Asahina*, 1934 (TNS).

JAPAN: For a complete list of the Japanese specimens examined at the time that the species was described, see W. L. Culberson (1965).

FORMOSA: Mt. Ali, 2,200 m., *Kurokawa* 12, 38 (TNS); Mt. Shin-Kao-San, Mt. Chien-San, 3,100–3,300 m., *Kurokawa* 251 (TNS).

SABAH: Kinabalu National Park, near East Mesilau River, 1,700 m., *Hale* 28431 (US).

PHILIPPINES: MOUNTAIN PROV.: Mt. Data, 2,312 m., *Hale* 26358 (US).

JAVA: Res. Pasoeroean, Goenoeng Ardjoena, Tretes-Lalidjiwa-track, *Du Rietz* 95:15 (UPSV).

FRANCE: VOSGES: Docelles, l'Encerf, *Harmand, Lich. Loth.* 288 (DUKE, PC).

5. **Cetrelia collata** (Nyl.) Culb. & Culb., comb. nov.

*Platysma collatum* Nyl., Flora 70:134. 1887. Type: China, Yunnan, *Delavay* 1590 (H-Herb. Nyl. No. 36116a, holotype).

*Cetraria collata* (Nyl.) Müll. Arg., Nouv. Giorn. Bot. Ital. 24:192. 1892.

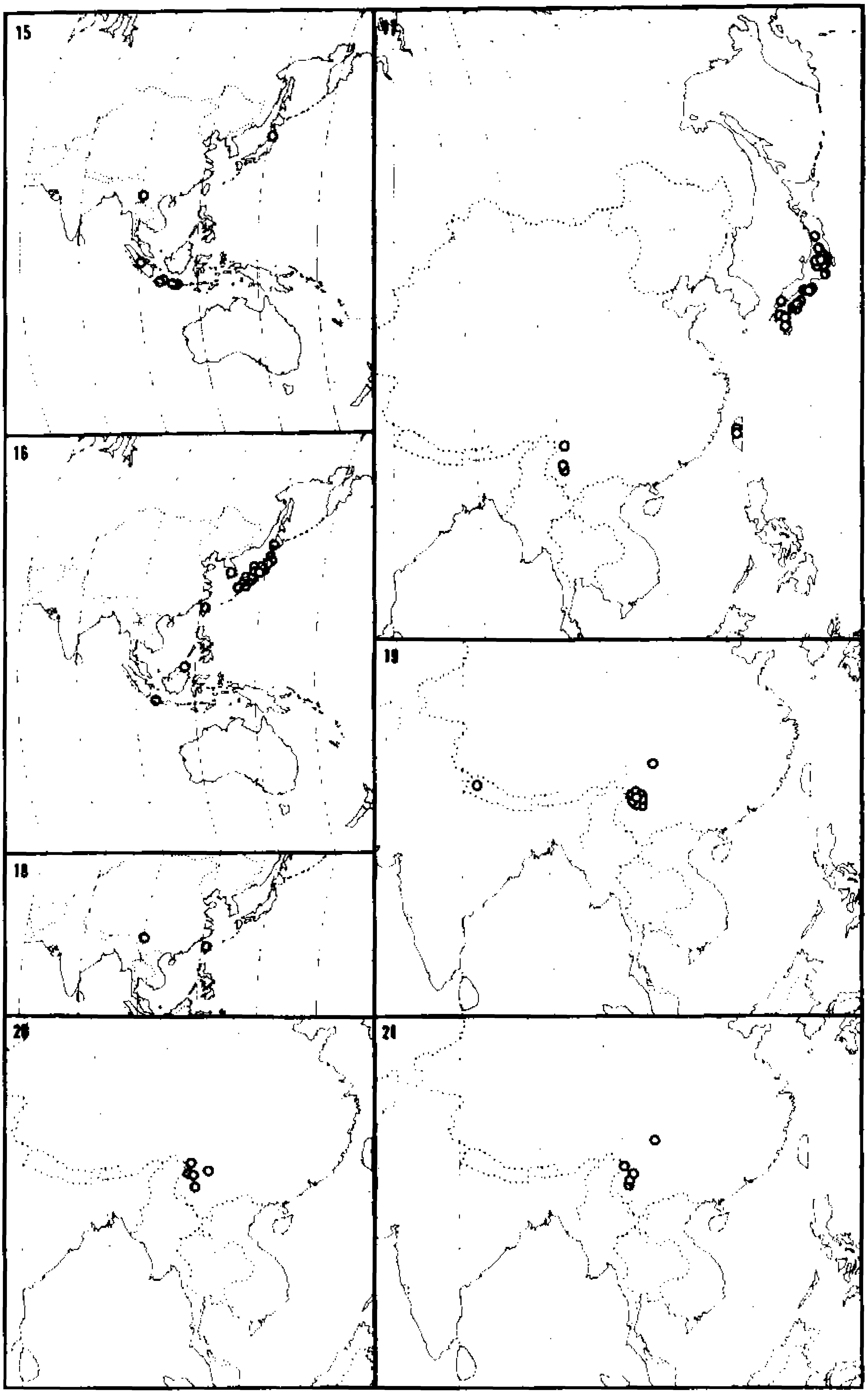
Thallus medium, to 15.0 cm. broad; lobes 0.8–2.5 cm. broad. Upper surface pale brownish in old herbarium specimens (whitish when fresh?), smooth, pseudocyphellate, the pores large, many becoming confluent and exceeding 1 mm. Lower surface jet-black, punctate in some specimens, the margins dark brown or colored like the upper surface, relatively smooth, ascendent; rhizines few. Upper cortex 16–34μ thick; medulla 109–264μ thick; lower cortex 16–25μ thick. Apothecia 0.7–2.0 cm. broad, cup-shaped at first and expanded with age, perforate or entire, the thalloid exciple wrinkled and abundantly pseudocyphellate; hymenium 99–124μ thick, subhymenial layers 35–56μ thick. Spores 8, ellipsoid, 15–20×7–12μ, the spore wall about 1.5μ thick. Pycnidia large, marginal, unstalked; conidia about 1.5×6.0μ, rod-shaped, the ends often somewhat inflated.

MEDULLARY REACTIONS.—K−, C−, KC− or KC+ pinkish, P−, UV−.

CONSTITUENTS.—Imbricaric acid and atranorin.

DISTRIBUTION (Map, Figure 19).—The high mountains of Szechwan and Yunnan, China, and Nepal; on the trunks and stems of trees and shrubs.

*Cetrelia collata* might be mistaken for *C. davidiana*, *C. delavayana*, *C. nuda*, or *C. sanguinea*. It differs from all these species, however, in producing imbricaric acid rather than some other substance in the medulla. It can easily be distinguished by its C− medullary reaction from *C. davidiana* (with olivetoric acid) and *C. sanguinea* (with anziaic acid), both of which are C+ pink or red in the medulla. From *C. nuda* (with alectoronic and α-collatolic acid) and *C. delavayana* (with perla-



FIGURES 15–21. Distributions. 15. *Cetrelia sanguinea* (Schaer.) Culb. & Culb. 16. *C. japonica* (Zahlbr.) Culb. & Culb. 17. *C. nuda* (Hue) Culb. & Culb. 18. *C. sinensis* Culb. & Culb. 19. *C. collata* (Nyl.) Culb. & Culb. 20. *C. davidiana* Culb. & Culb. 21. *C. delavayana* Culb. & Culb.

tolic acid) it is best distinguished by the appropriate microchemical tests.

CHEMICAL ANALYSIS.—All 17 samples tested contained imbricaric acid and the residue from extracts gave straight needles of oblique extinction in the GE and GAW solutions. Atranorin was easily identified by microcrystal tests. Most extracts were chromatographed before and after base hydrolysis. The hydrolyzed residues frequently showed an additional weak spot at an $R_f$ corresponding to olivetol-2-carboxylic acid and most samples tested showed a definite KC+ pink reaction apparently due to the presence of at least one unidentified substance.

ADDITIONAL SPECIMENS EXAMINED:

CHINA: SZECHWAN: Mt. Lose-chan, south of Ningyüen, 3,950 m., *Handel-Mazzetti* 1441 (WU).

YUNNAN: Lidjiang, Mt. Ndaza Ko, 4,000 m., *Rock*, as *Zahlbr.*, *Lich. Rar. Exs.* 322 (S, UPS, W); Snow Range, 4,300–12,000 ft., *Rock*, 1931 (W); Mt. Yülung-schan, *Handel-Mazzetti* 4254 (WU); between Dali (Talifu) and Hodjing, above Hsiang-schuiho, 26°10′N, 3,400 m., *Handel-Mazzetti* 7398 (*pro parte*) (W); Lopin-chan Pass, above Lan-Kong, *Delavay*, 1888 (PC, 2 collections); Mt. Tsang-chan, above Tali, 400 m., *Delavay*, 1885 (PC), 4,000 m., *Delavay*, 1885 (PC, 2 collections), *Delavay*, 1887 (PC); Fang-Yang-Tschang, above Mo-so-yn, *Delavay*, 1887 (WU); Koua-la-po, 3,000 m., *Delavay*, 1885 (H-Herb. Nylander, PC).

NEPAL: Above Sauwala Khola, 10,500 ft., *Stainton et al.* 4379b (*pro parte*) (BM).

**6. Cetrelia davidiana** Culb. & Culb., sp. nov. PLATE 16

Thallus mediocris, 9–14 cm. latus; laciniae 0.7–2.2 cm. latae. Superficies superior sordide citrella (albida apud plantas vivas?), levis, pseudocyphellata, pseudocyphellis parvis, ca. 0.5 mm. crassis vel confluentibus et ad 1 mm. Superficies inferior picea, marginibus castanea vel pallida, levis vel subrugosa, fere punctata. Cortex superior 19–31μ crassus, medulla 115–226μ crassa; cortex inferior 12–22μ crassus. Apothecia 0.5–2.0 cm. lata, perforata, primum cupuliformia deinde expansa et radiatofissa, excipulo thallino rugoso et pseudocyphellatissimo; hymenium 71–115μ crassum; subhymenium hyalinum vel subluteum, 40–81μ crassum, stratum crassum algarum tegens. Sporae 8-nae, ellipsoideae, 14–19×7–11μ. Pycnidia numerosa, marginalia, raro in superficie superiore ad margines laciniarum; conidia 1×3–5μ recta, extremis nonnihil inflatis.

Thallus medium, 9–14 cm. broad; lobes 0.7–2.2 cm. broad. Upper surface uniformly light tan (whitish when fresh?), smooth, pseudocyphellate, the pores small, about 0.5 mm. in diameter, or becoming confluent and reaching 1 mm. Lower surface jet-black, the margins brown or colored like the upper surface, smooth or somewhat wrinkled, especially at the ascendent margins of the lobes, if punctate, the puncta restricted to the crests of the ridges. Upper cortex 19–31μ thick;

medulla 115–226μ thick; lower cortex 12–22μ thick. Apothecia 0.5–2.0 cm. in diameter, perforate, cup-shaped at first then expanded and split longitudinally, the thalloid exciple much wrinkled and abundantly pseudocyphellate; hymenium 71–115μ thick; subhymenial layers colorless or pale yellowish, 40–81μ thick, immediately underlain by a thick zone of algae. Spores 8, ellipsoid, 14–19×7–11μ, the spore wall relatively thick, 1.0–1.7μ. Pycnidia abundant, marginal or a few laminal toward the margin of the lobes; conidia 1×3–5μ, rod-shaped, the ends of some somewhat enlarged.

TYPE.—"In montis Yülung-schan prope urbem Lidjiang ["Likiang"], Yunnan," China, *Handel-Mazzetti* 4254 (W, holotype).

MEDULLARY REACTIONS.—K−, C+ pink, PD−.

CONSTITUENTS.—Olivetoric acid and atranorin.

DISTRIBUTION (Map, Figure 20).—Mountains of Szechwan and Yunnan, China; on the bark of trees.

*Cetrelia davidiana* is a Chinese species without soredia, isidia, or lobulae. It is similar to *C. olivetorum* chemically and in that it has minute pseudocyphellae, but differs in that it is esorediate. It is also similar to *C. pseudolivetorum* but differs in that it lacks the marginal lobulae.

*Cetrelia davidiana* must be distinguished chemically from similar esorediate and nonisidiate species most closely related to it. The positive reaction of the medulla with C will suffice to separate it from *C. collata* and *C. nuda* and even from *C. alaskana* and *C. delavayana*, the latter two of which also differ morphologically in possessing small and inconspicuous pseudocyphellae rather than large and obvious ones. The medullary reaction of *C. davidiana* with C is generally a pink or rose due to the presence of olivetoric acid while that of *C. sanguinea*, containing anziaic acid, is usually bright red. But definitive microchemical tests are obviously preferable here to the thallus spot tests.

CHEMICAL ANALYSIS.—The extracts from fragments of seven samples were tested. Atranorin was usually determined by crystals in the GE and GA*o*-T solution and by chromatography. Olivetoric acid was crystallized from the GE, GAW, and GA*o*-T solutions and was confirmed by chromatography to distinguish it definitely from anziaic acid. Physodic acid did not occur with olivetoric acid in any of the samples tested.

SPECIMENS EXAMINED:

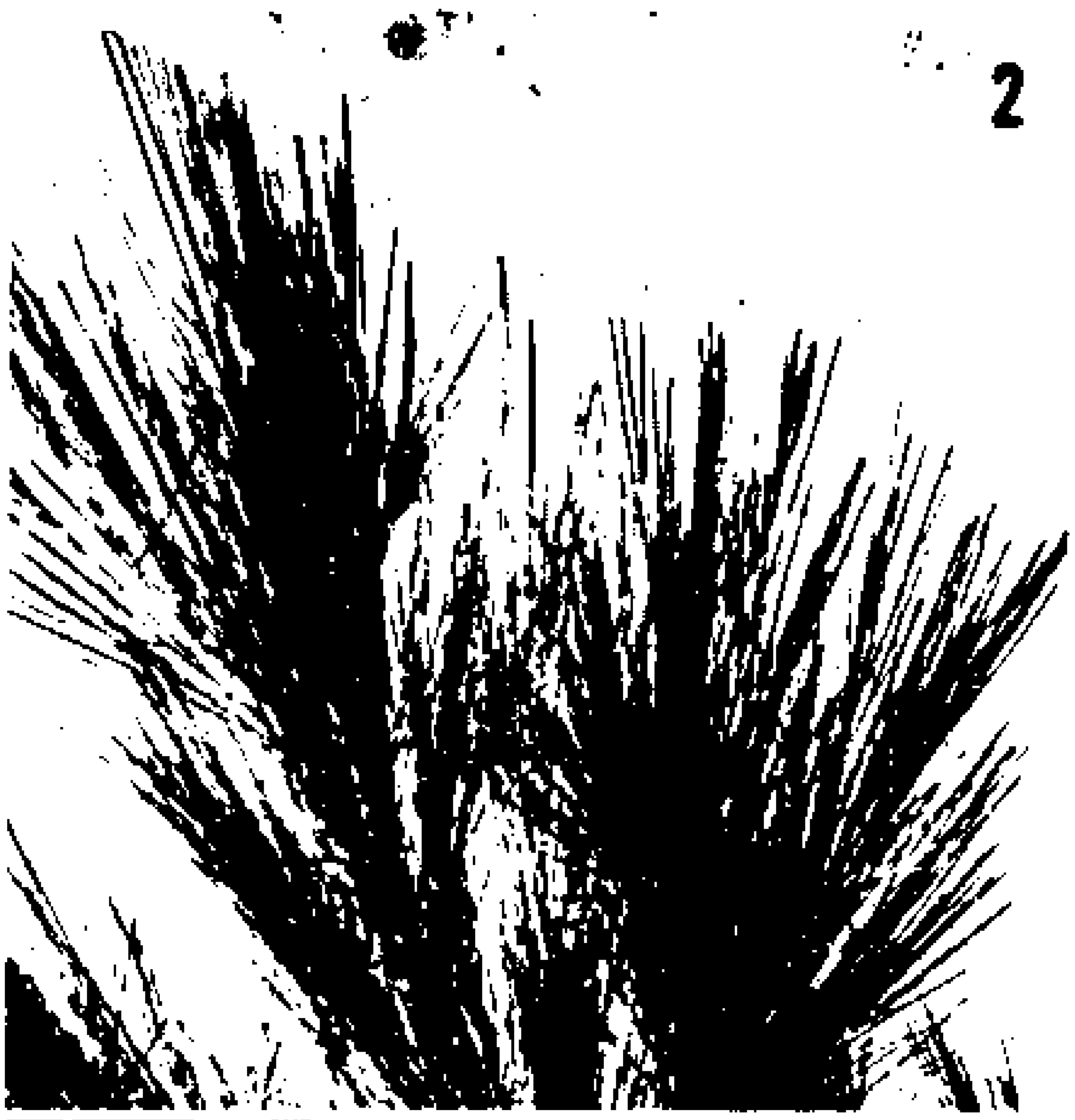
CHINA: SZECHWAN: Above Fumadi, Wolo-ho River between Yenyüen and Yungning, ca. 3,300 m., *Handel-Mazzetti* 3039 (WU).

YUNNAN: Between Dali (Talifu) and Hodjing, above Hsiang-schuiho, 26°15′N, ca. 3,400 m., *Handel-Mazzetti* 7398 (*pro parte*) (W, 2 collections); Mt. Yülung-schan near Lidjiang, *Handel-Mazzetti* 4254 (W, WU); Ti-ou-ze Pass, above Ta-pin-tze, *Delavay*, 1888 (PC); Koua-la-po (Ho Kin), 3,000 m., *Delavay*, 1885 (PC).

# PLATES

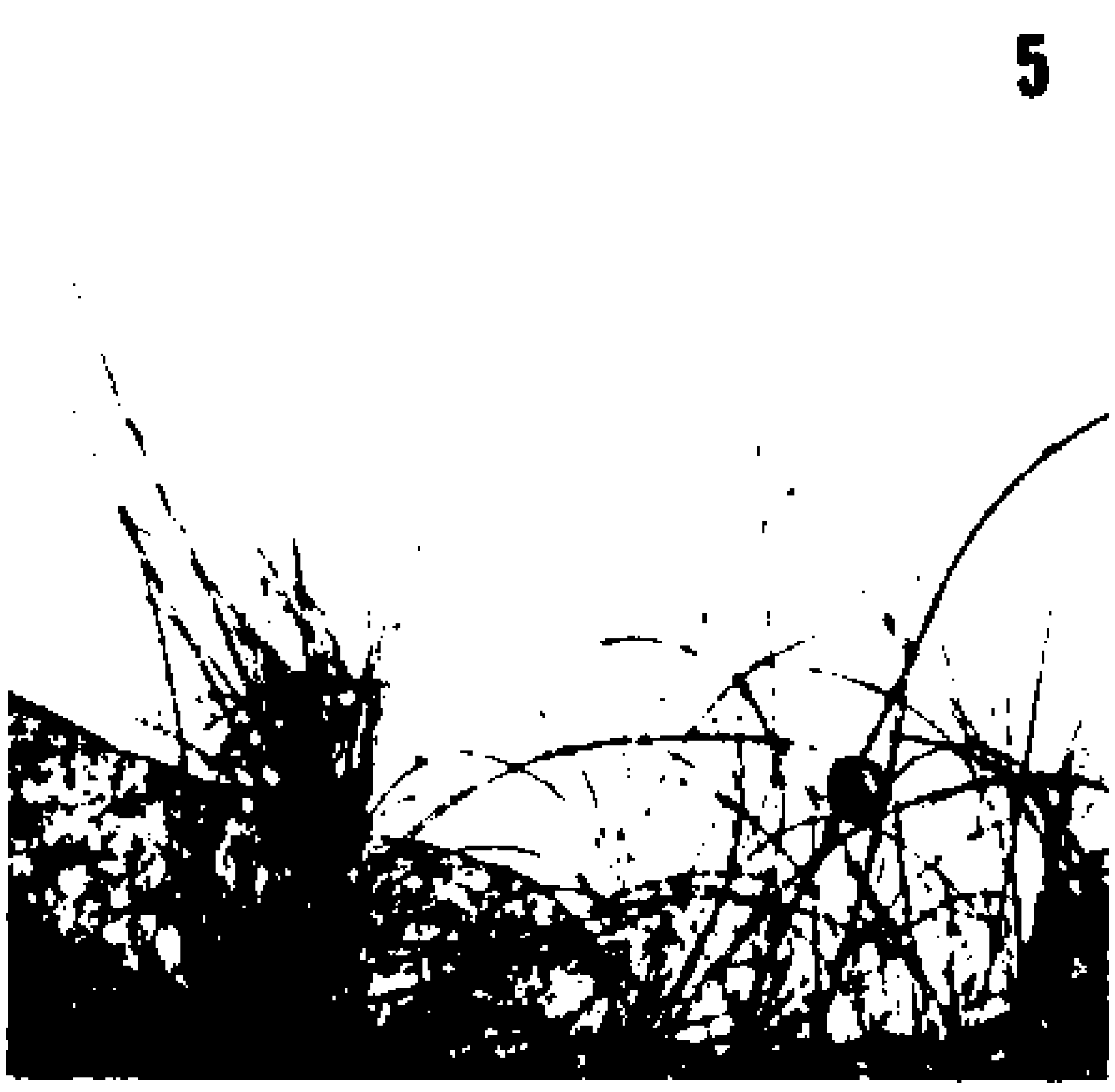
## PLATE 1

Crystals produced by substances in the microcrystal-test solutions: 1. Alectoronic acid and α-collatolic acid cocrystallized in GE. The smaller crystals are atranorin. Prepared from the acetone extract after benzene extraction of *Cetrelia chicitae* (× 125). 2. Alectoronic acid and α-collatolic acid cocrystallized in GE. Prepared from the acetone extract after benzene extraction of *Cetrelia braunsiana* (× 110). 3. Alectoronic acid and α-collatolic acid cocrystallized in GAW. Prepared from the acetone extract after benzene extraction of *Cetrelia chicitae* (× 200). 4. Anziaic acid recrystallized in GE. Prepared from the acetone extract after benzene extraction of *Cetrelia isidiata* (× 450). 5. Anziaic acid recrystallized in GAW. Prepared from the acetone extract after benzene extraction of *Cetrelia isidiata* (× 165). 6. Atranorin recrystallized in GE. Prepared from the acetone extract after benzene extraction of *Cetrelia sanguinea* (× 140).



2

3



5

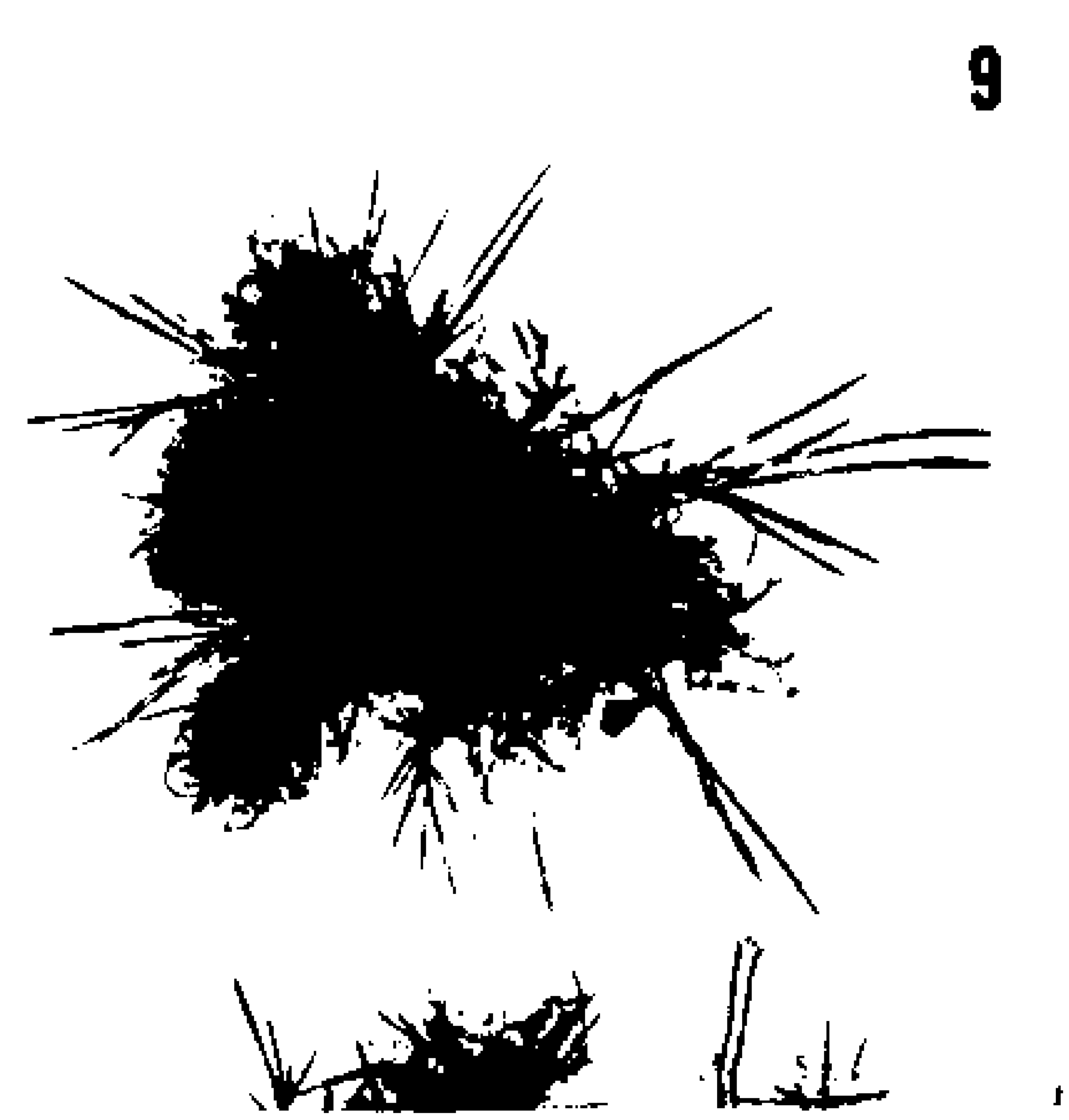
6

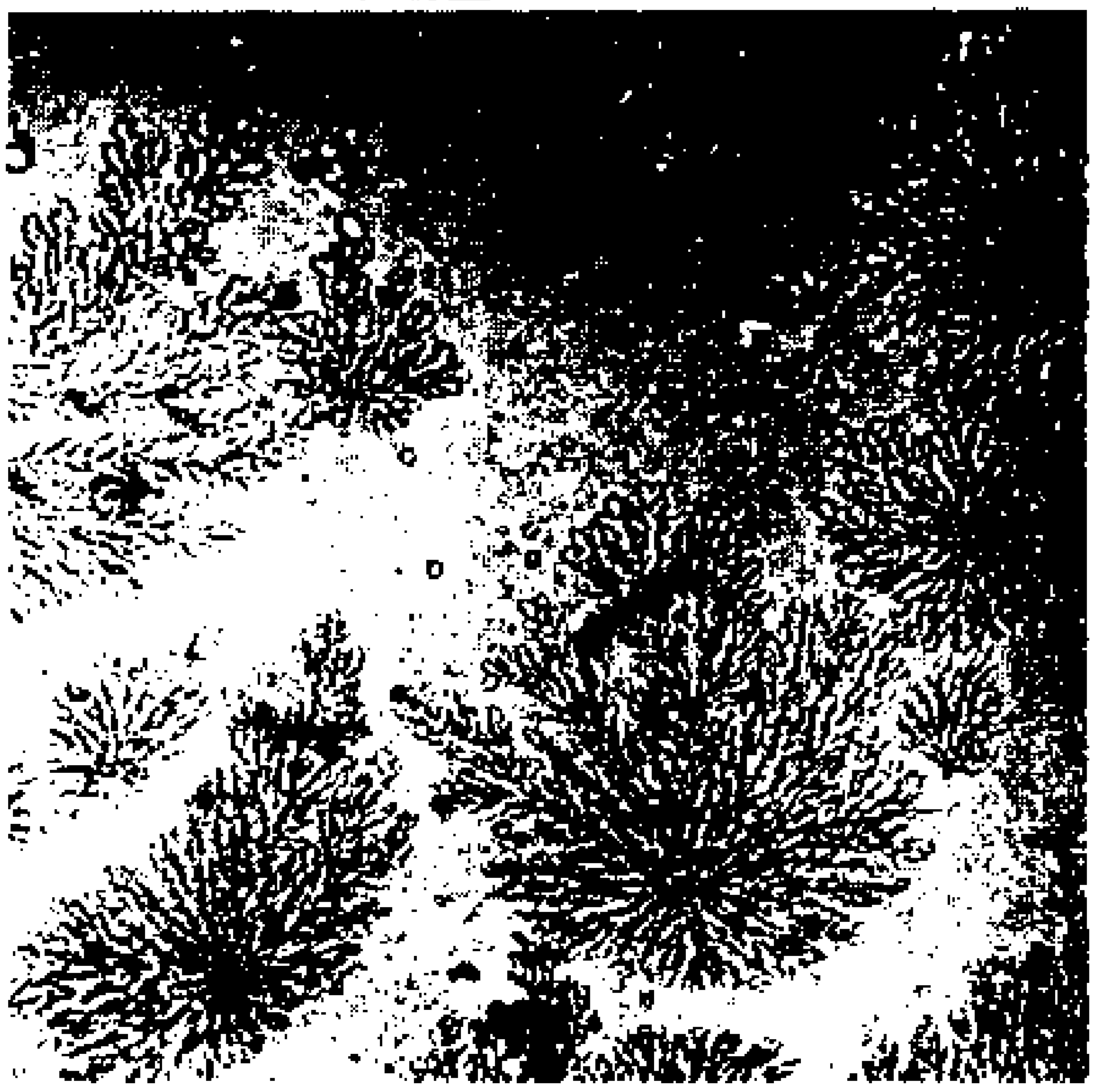
PLATE 2

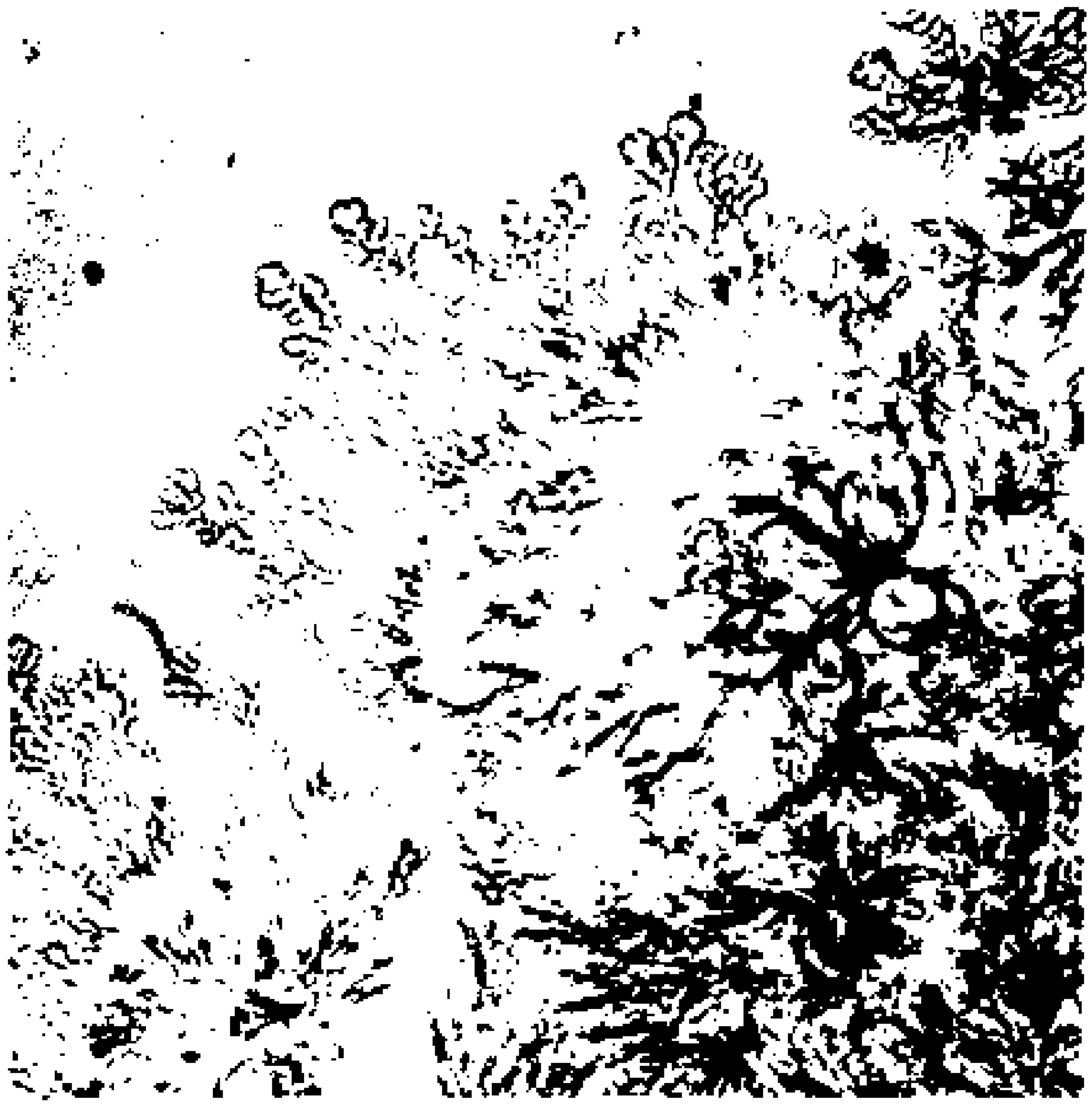
Crystals produced by substances in the microcrystal-test solutions: 7. The yellow atranorin condensation product with GA*o*-T. Prepared from the benzene extract of *Platismatia erosa* (×120). 8. The yellow atranorin condensation product with *o*-toluidine in GA*o*-T. Prepared from the benzene extract of *Platismatia tuckermanii* (×110). 9. The yellow atranorin condensation product with *o*-toluidine in GA*o*-T showing two crystal types, the larger needles typical of the atranorin derivative. The smaller, more densely clustered needles may be due to an unidentified substance. Prepared from the benzene extract of *Platismatia interrupta* (×130). 10. Yellow crystals of the condensation product of atranorin and *o*-toluidine in GA*o*-T distorted by the accompanying colorless caperatic acid. Prepared from the acetone extract after benzene extraction of *Platismatia tuckermanii* (×135). 11. Caperatic acid recrystallized in GAW. Prepared from the acetone extract of benzene-extracted *Platismatia erosa* (×115). 12. Caperatic acid recrystallized in GAW showing typical crystals and abnormal curly plates toward the center of the clusters. Prepared from the acetone extract of benzene-extracted *Platismatia interrupta* (×100).


7


8

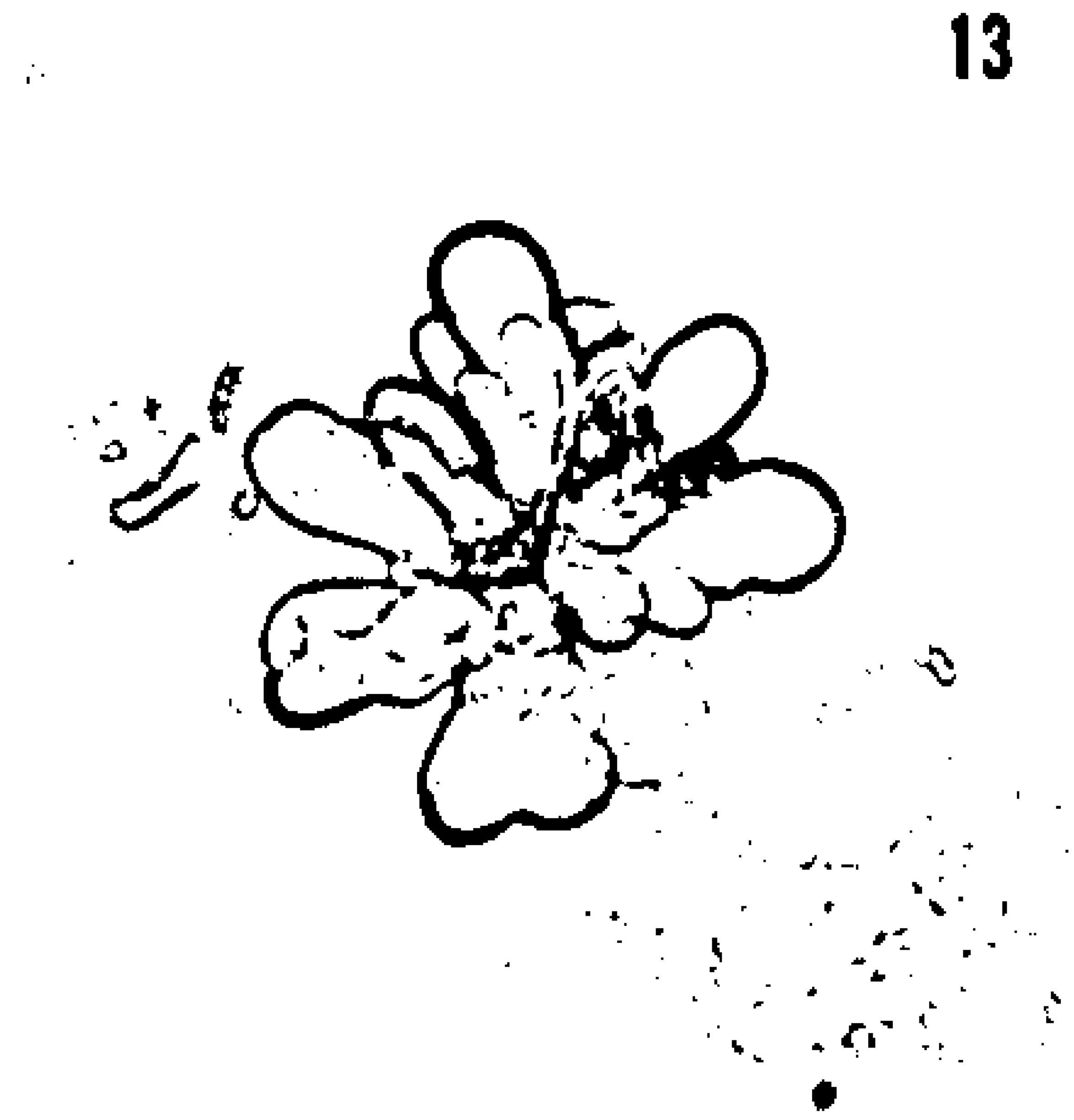

9





## PLATE 3

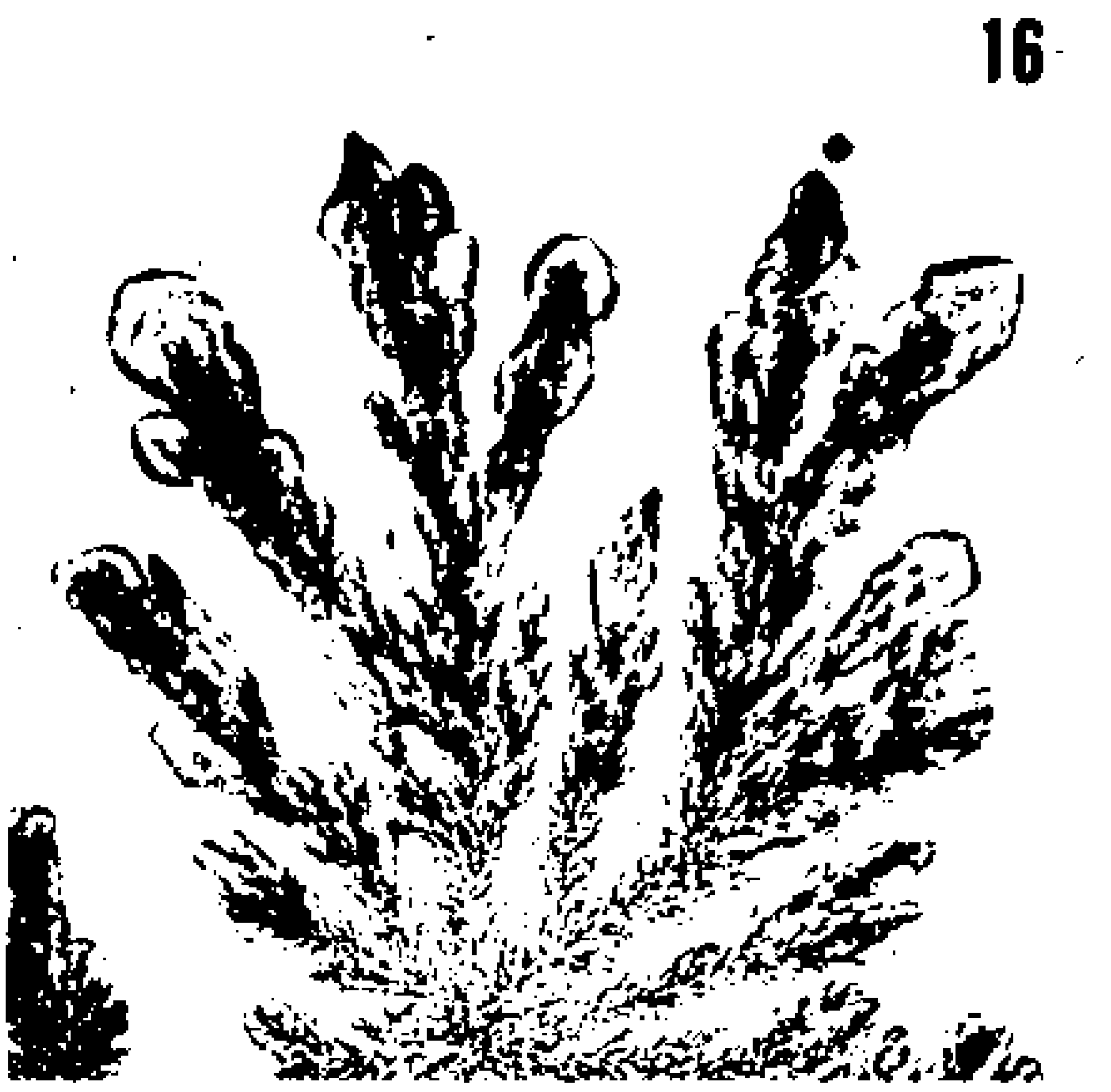
Crystals of caperatic acid in the microcrystal-test solutions: 13. The "cloud" form of caperatic acid from recrystallization in GE. Prepared from caperatic acid isolated from *Parmelia cryptochlorophaea* (×240). 14. The "cloud" form of caperatic acid from recrystallization in GE. Prepared from the acetone extract of benzene-extracted *Platismatia glauca* (×140). 15. The "plate" form of caperatic acid from recrystallization in GE. Prepared from a pure sample of caperatic acid isolated from *Parmelia cryptochlorophaea* (×120). 16. The "plate" form of caperatic acid from recrystallization in GE. Prepared from the acetone extract of benzene-extracted *Platismatia glauca* (×130). 17. Mixed crystal forms of caperatic acid from recrystallization in GE. Prepared from pure caperatic acid isolated from *Parmelia cryptochlorophaea* (×120). 18. Mixed crystal forms of caperatic acid from recrystallization in GE. Needles and prisms of atranorin are also present. Prepared from the acetone extract of benzene-extracted *Platismatia erosa* (×110).



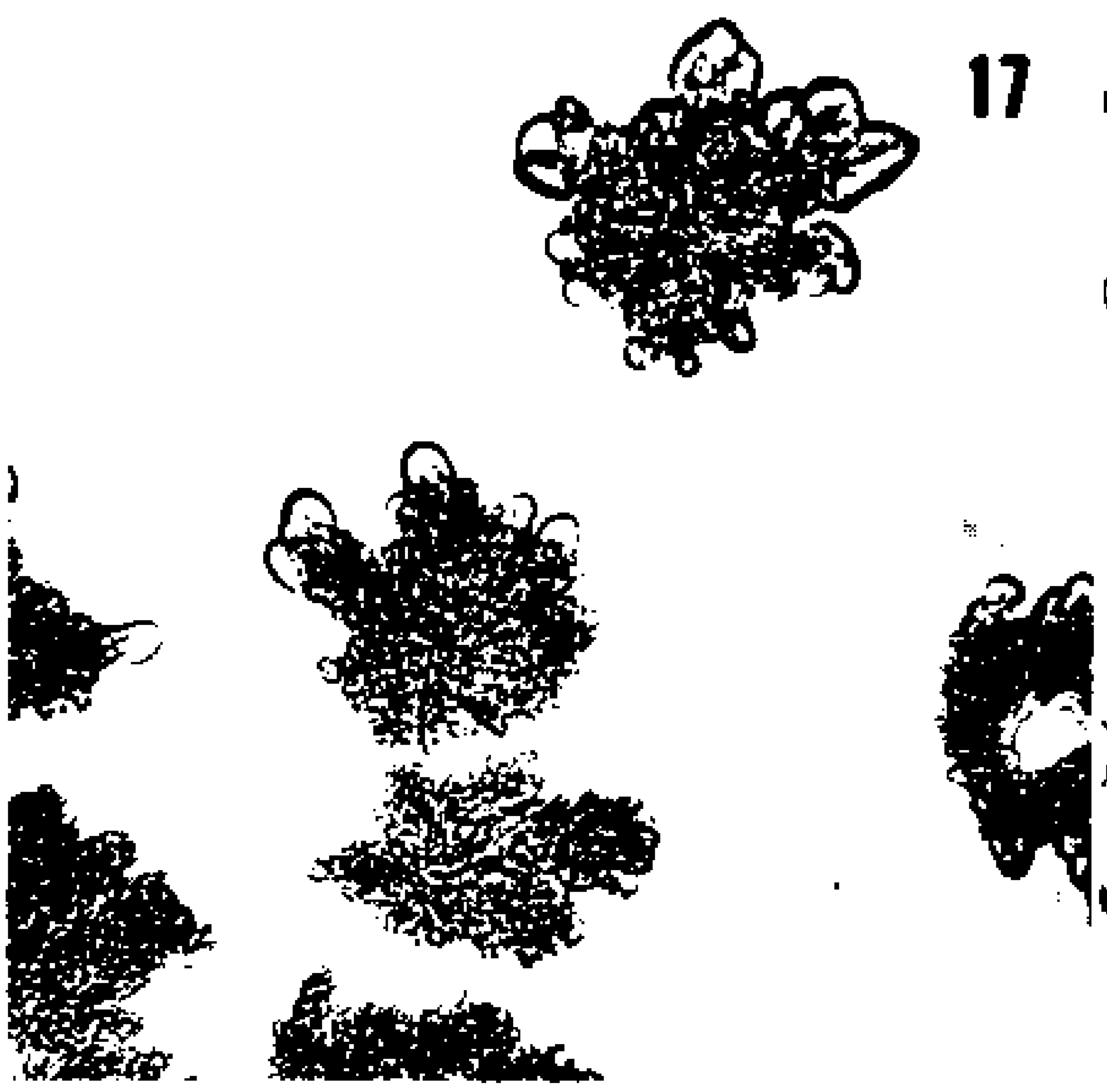
13

14

15



16

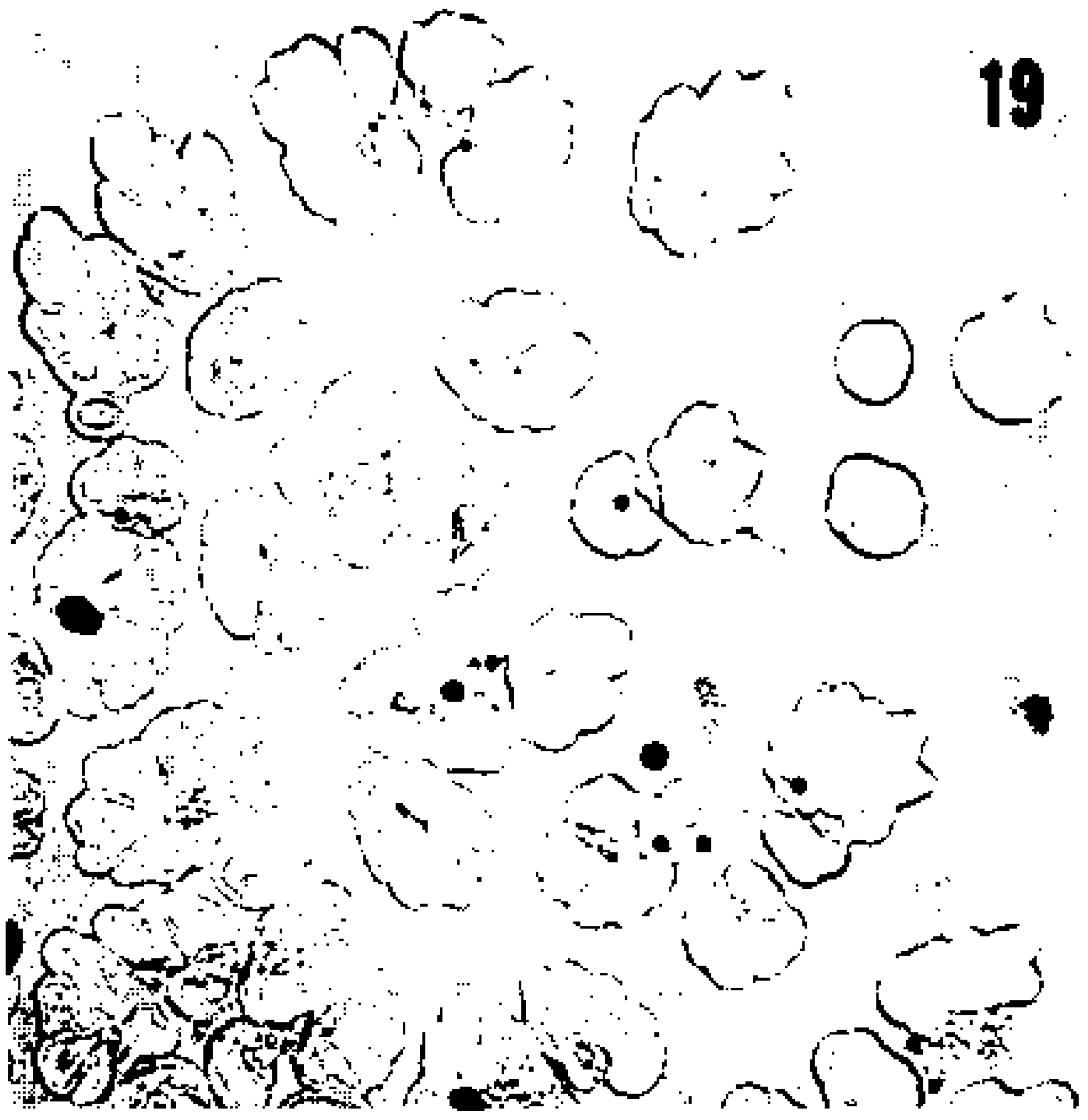


17

18

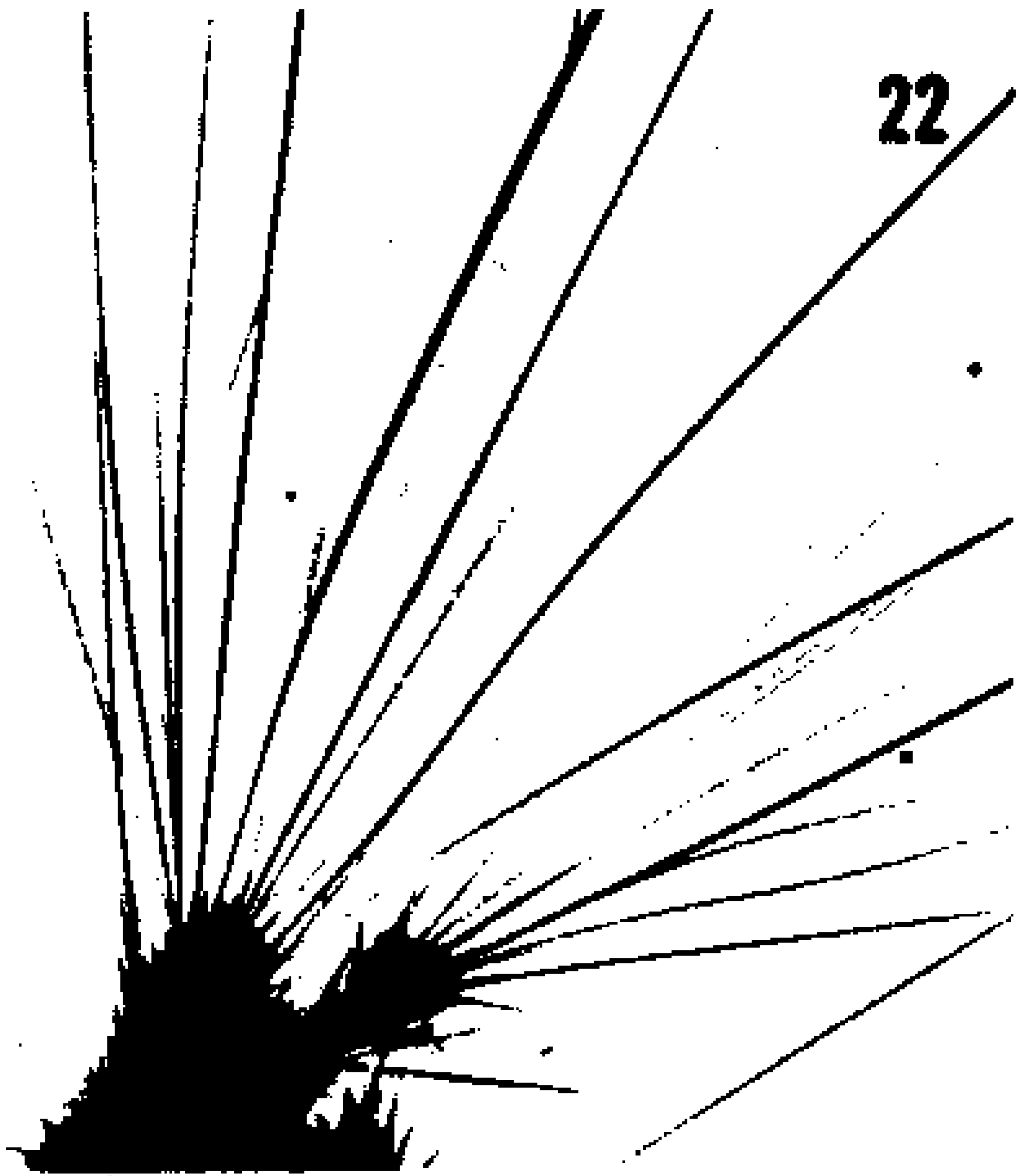
## PLATE 4

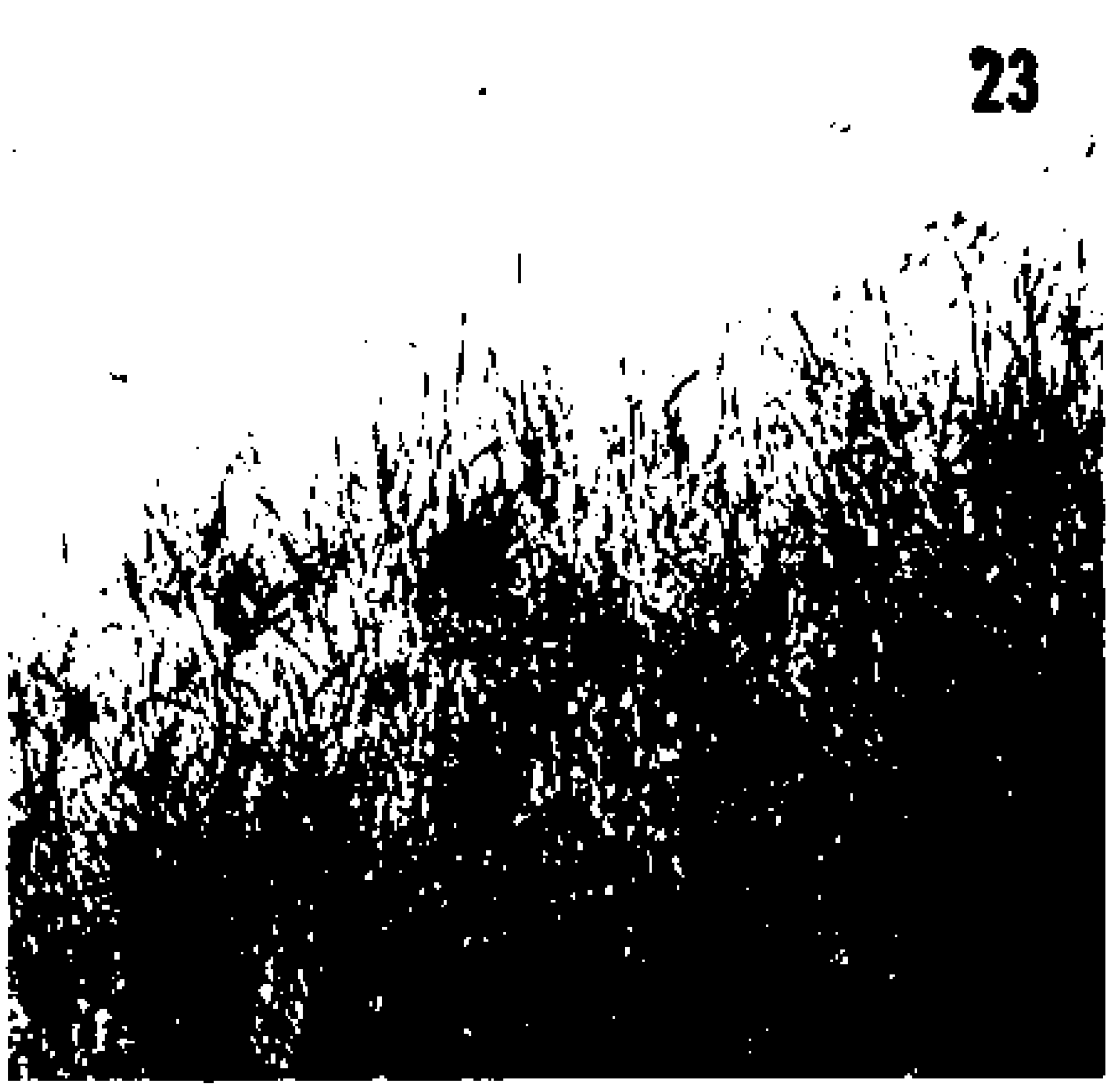
Crystals produced by substances in the microcrystal-test solutions: 19. Pure norcaperatic acid recrystallized in GE (×165). 20. Pure norcaperatic acid recrystallized in GAW (×110). 21. Imbricaric acid (large needles) and atranorin (small prisms) recrystallized in GE. Prepared from the benzene extract of *Cetrelia cetrarioides* (×110). 22. Imbricaric acid recrystallized in GAW. Prepared from the benzene extract of *Cetrelia cetrarioides* (×115). 23. The *o*-toluidine salt of imbricaric acid (colorless needles) in GA*o*-T. The fuzzy crystals barely visible are yellow and may be a cocrystallization with the atranorin condensation product with *o*-toluidine. Prepared from the benzene extract of *Cetrelia sinensis* (×130). 24. Small yellow crystals beside the atranorin condensation product with *o*-toluidine in GA*o*-T; commonly observed in samples containing imbricaric acid. Such crystals may be due to cocrystallization or to an unidentified substance. Prepared from the benzene extract of *Cetrelia cetrarioides* containing imbricaric acid (×130).

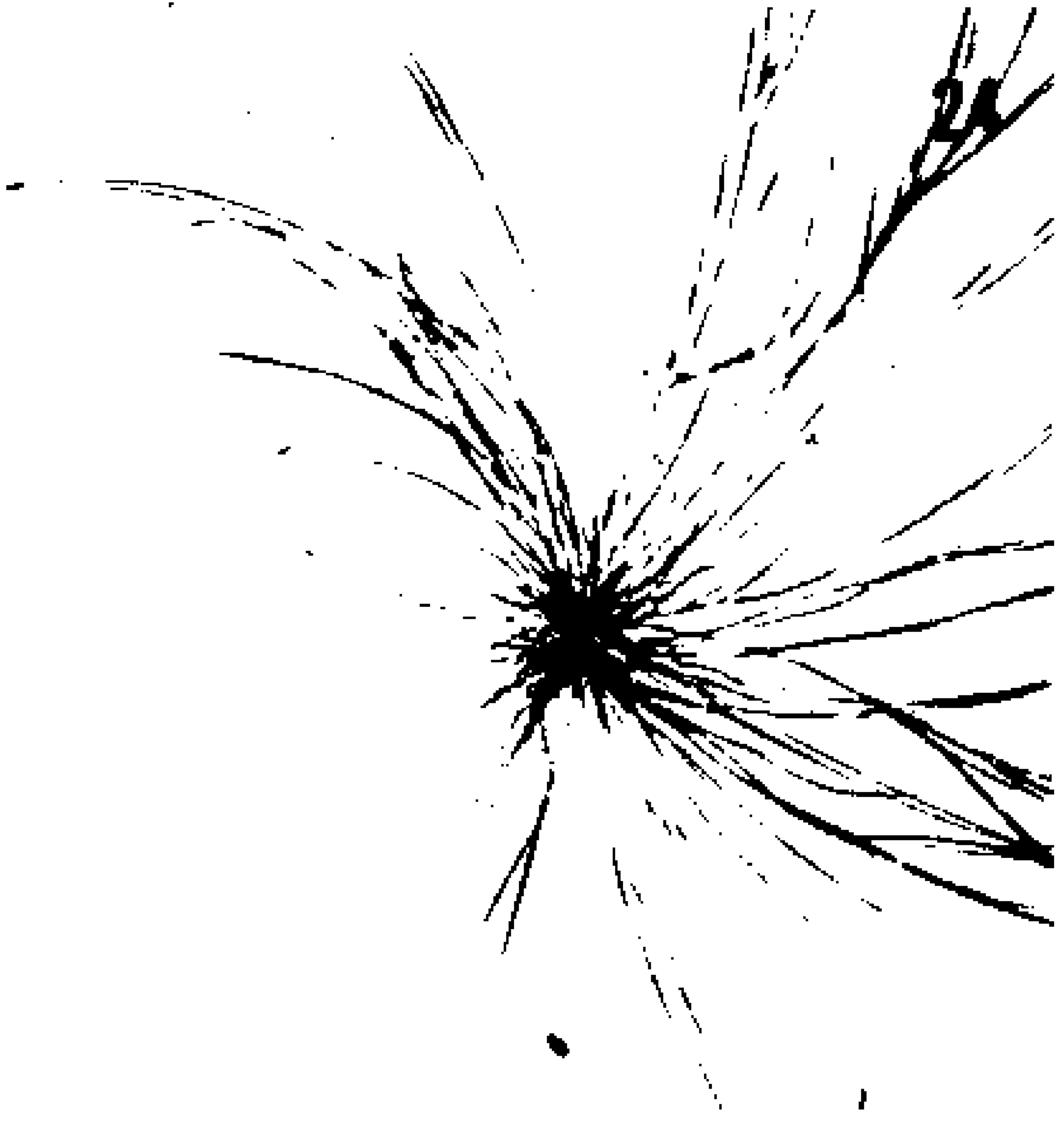

19


20


21


22

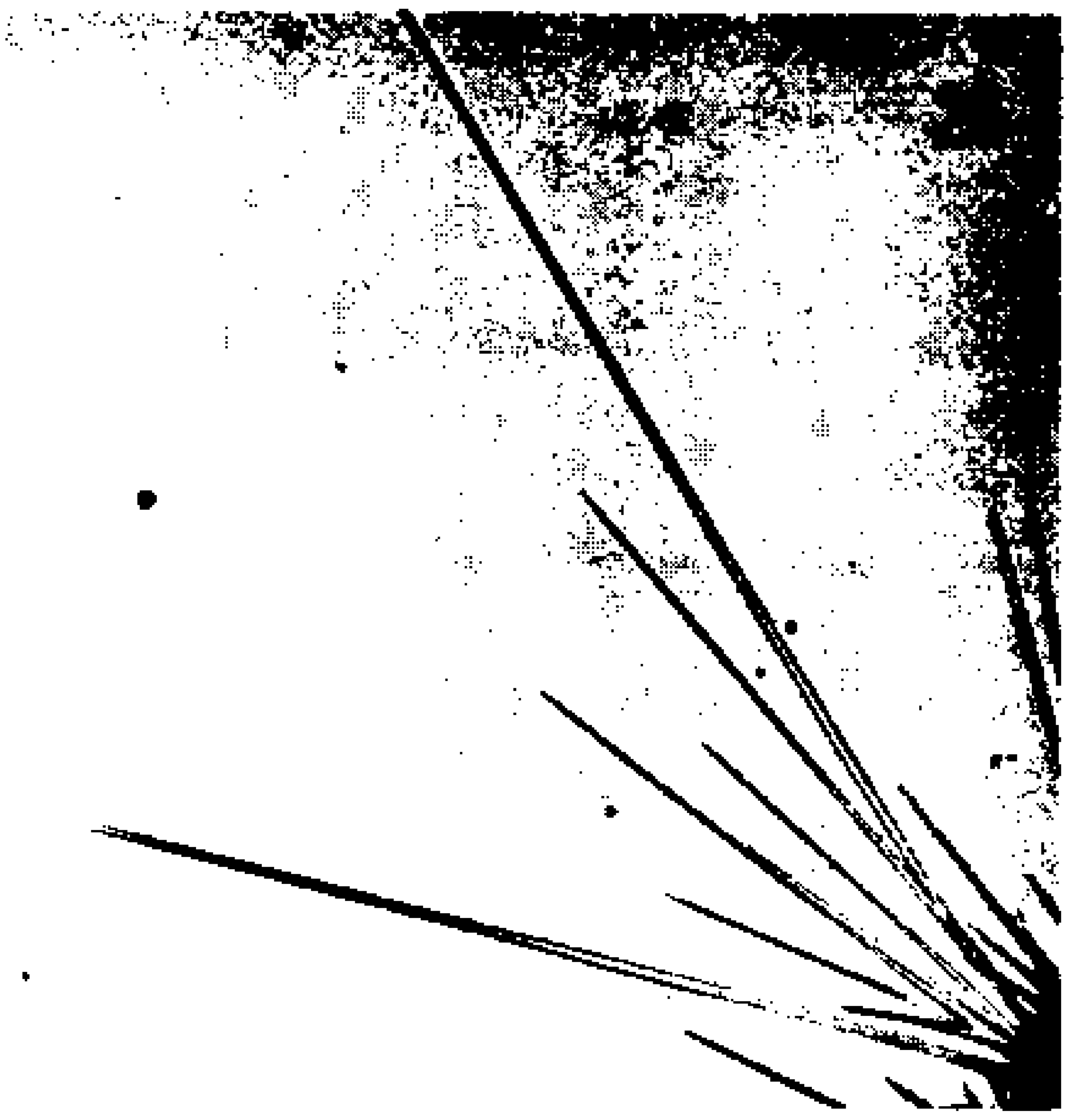

23


24

## PLATE 5

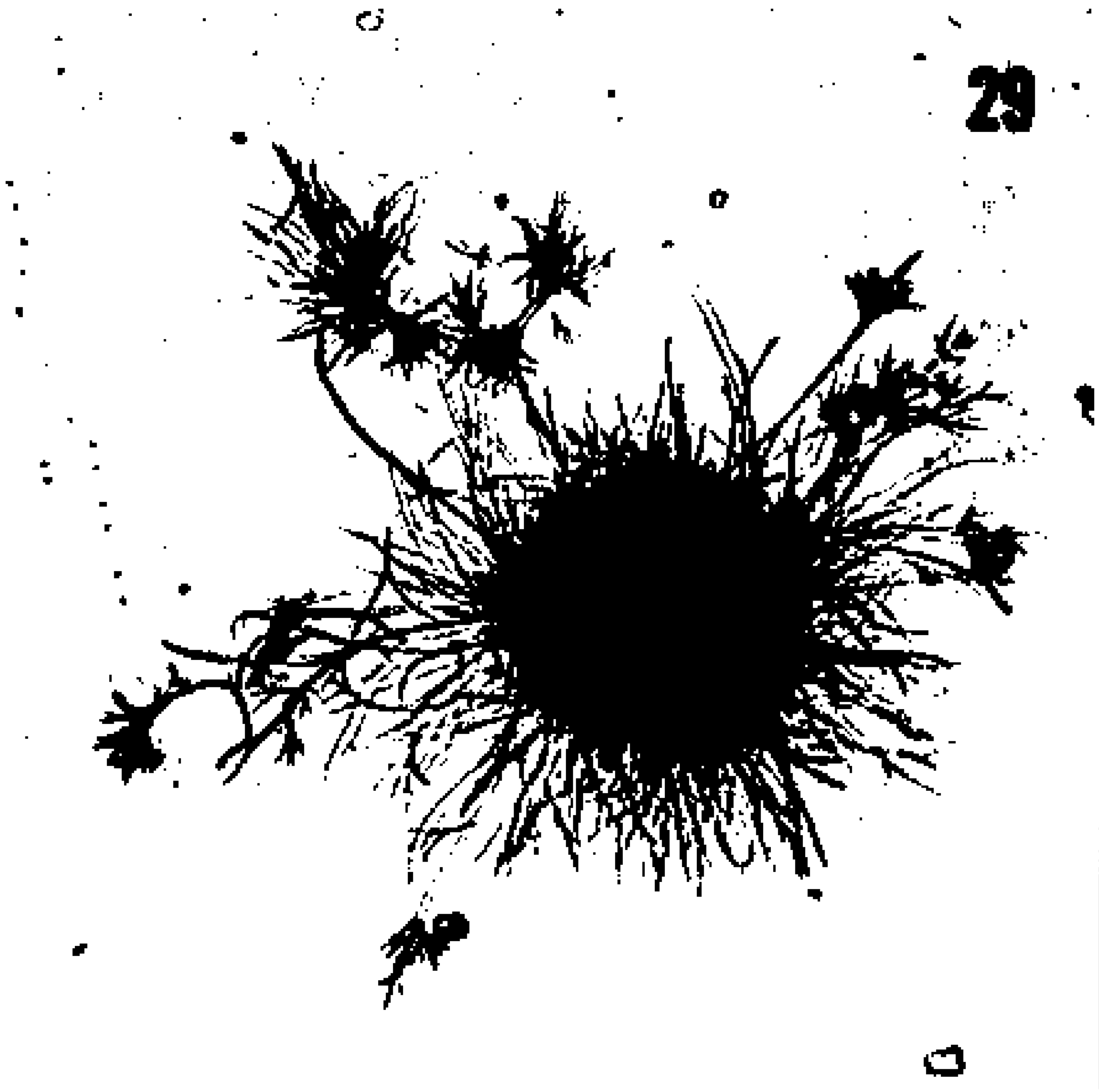
Crystals produced by substances in the microcrystal-test solutions: 25. Microphyllinic acid recrystallized in GE. Prepared from the benzene extract of *Cetrelia japonica* (× 120). 26. Microphyllinic acid recrystallized in GAW. Prepared from the benzene extract of *Cetrelia japonica* (× 135). 27. The sodium salt of microphyllinic acid precipitated in 5% aqueous sodium hydroxide. Prepared from the benzene extract of *Cetrelia japonica* (× 110). 28. Olivetoric acid recrystallized in GE. Prepared from the acetone extract of benzene-extracted *Cetrelia olivetorum* (× 490). 29. Olivetoric acid recrystallized in GAW. Prepared from the acetone extract of benzene-extracted *Cetrelia davidiana* (× 120). 30. The colorless *o*-toluidine salt of olivetoric acid in GA*o*-T. Prepared from the acetone extract of benzene-extracted *Cetrelia olivetorum* (× 110)


25




27

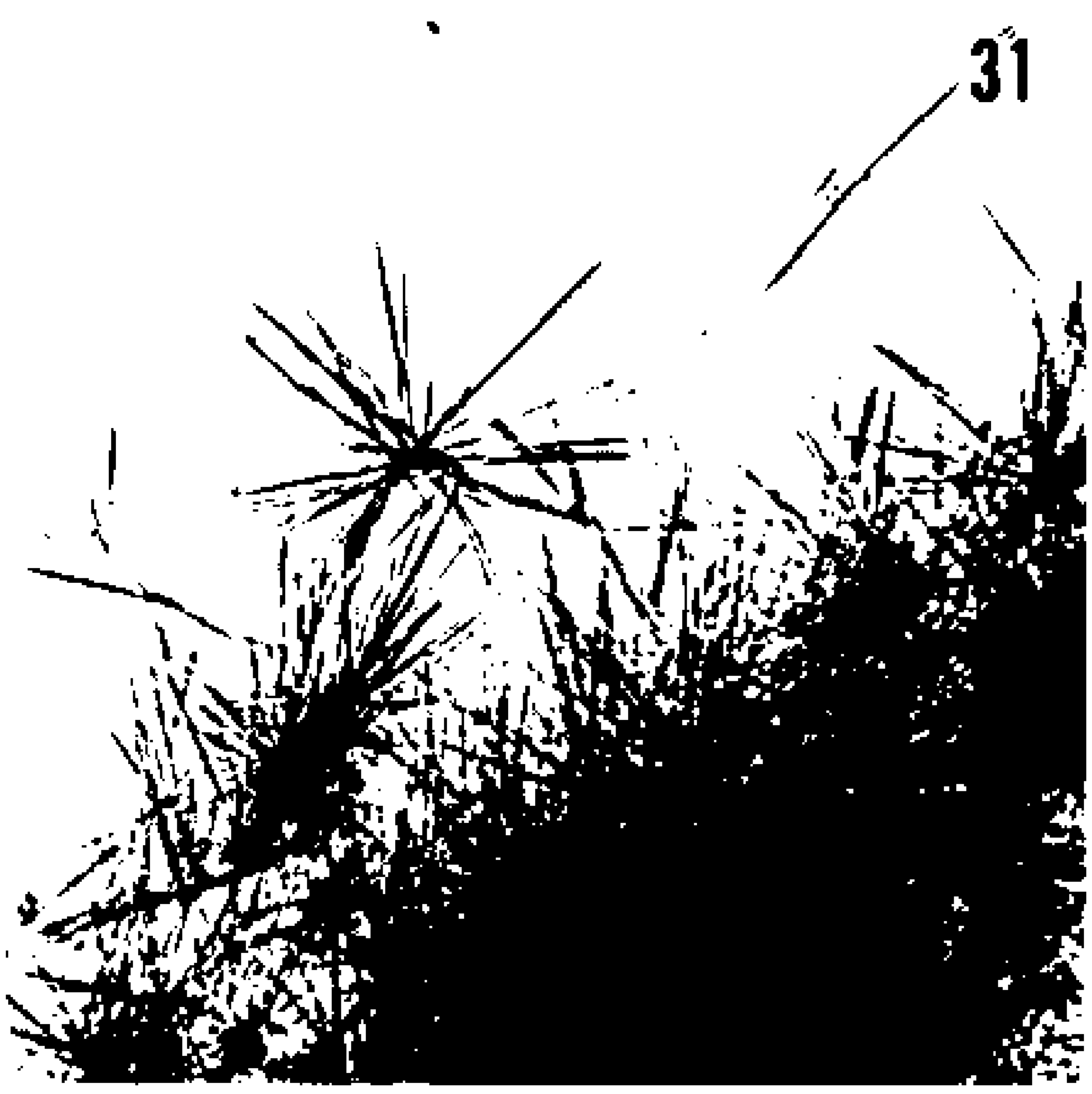

28


29

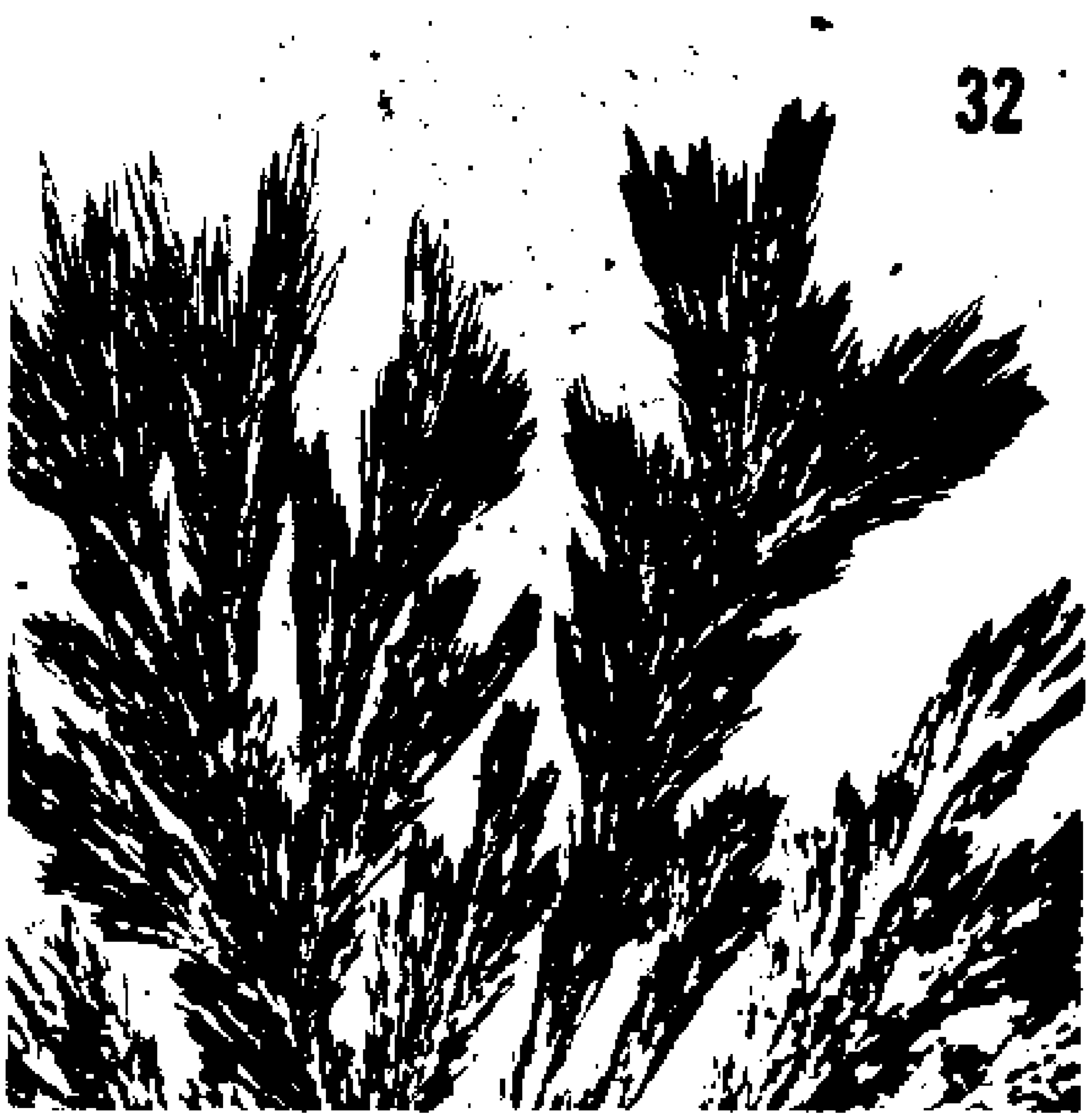

30

## PLATE 6

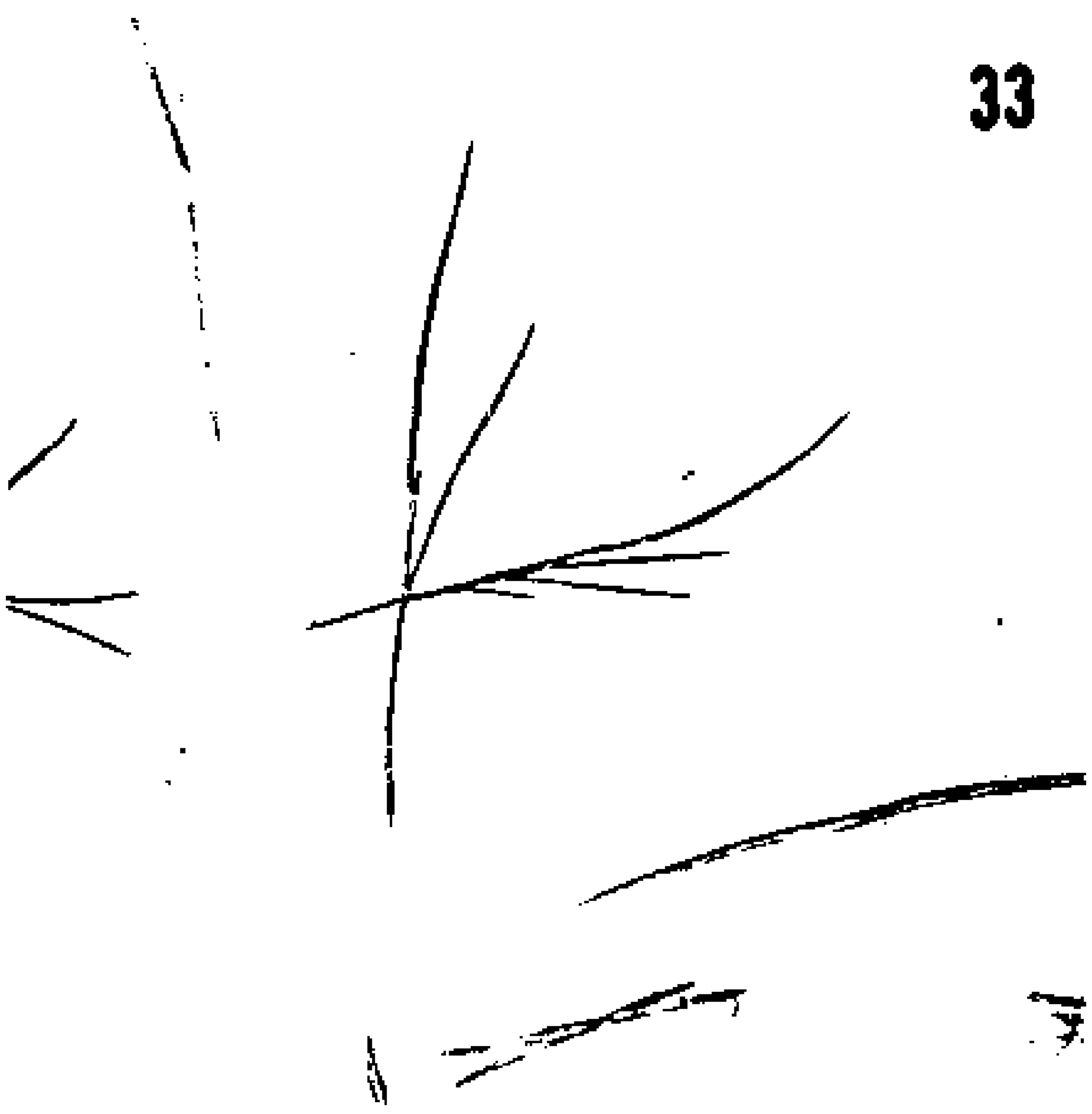
**Crystals produced by substances in the microcrystal-test solutions:** 31. The colorless *o*-toluidine salt of olivetoric acid in GA*o*-T. Prepared from the acetone extract of benzene-extracted *Cetrelia pseudolivetorum* (× 140). 32. Perlatolic acid recrystallized in GE. Prepared from the benzene extract of *Cetrelia cetrarioides* (× 115). 33. Perlatolic acid recrystallized from GAW. Prepared from the benzene extract of *Cetrelia delavayana* (× 115). 34. The *o*-toluidine salt of perlatolic acid (large colorless crystals) and atranorin (small yellow clusters) in GA*o*-T. Prepared from the benzene extract of *Cetrelia delavayana* (× 170). 35. Yellow crystals of an unidentified substance crystallized in GE. Prepared from an extract of *Platismatia erosa* (× 380). 36. Unidentified yellowish-tan crystals formed in GA*o*-T from an extract of *Platismatia interrupta* (× 100).



31



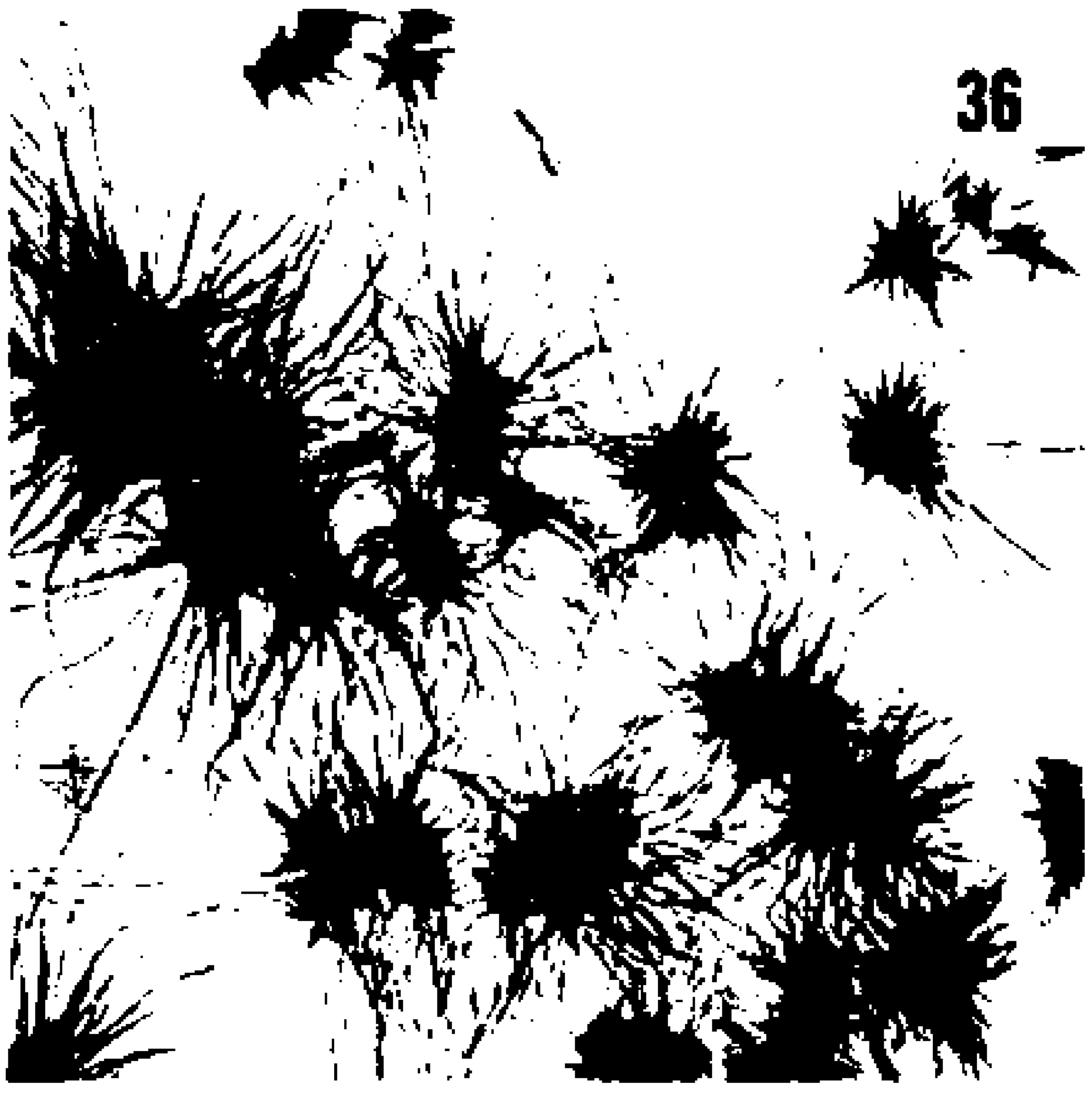
32



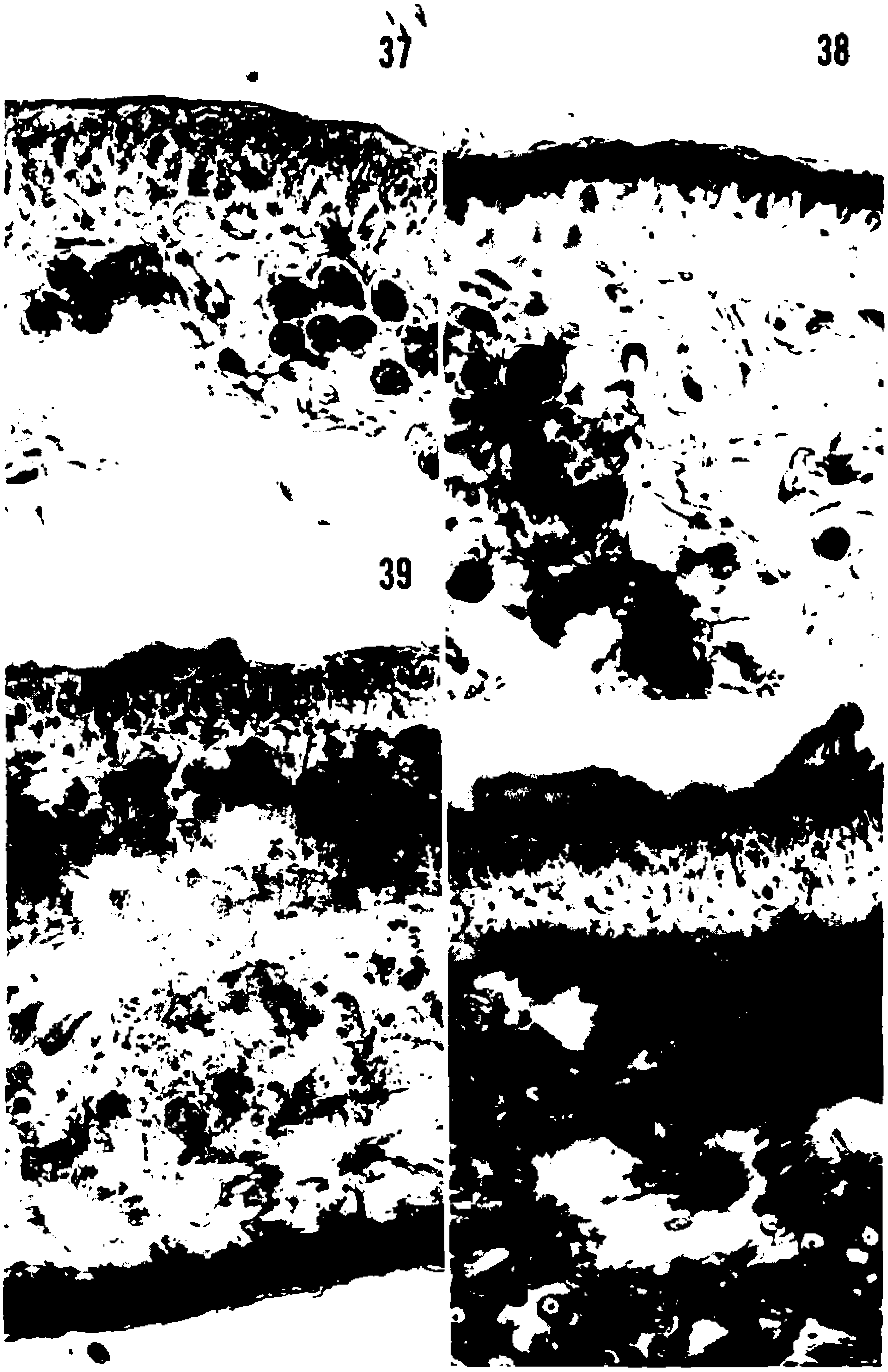
33

34

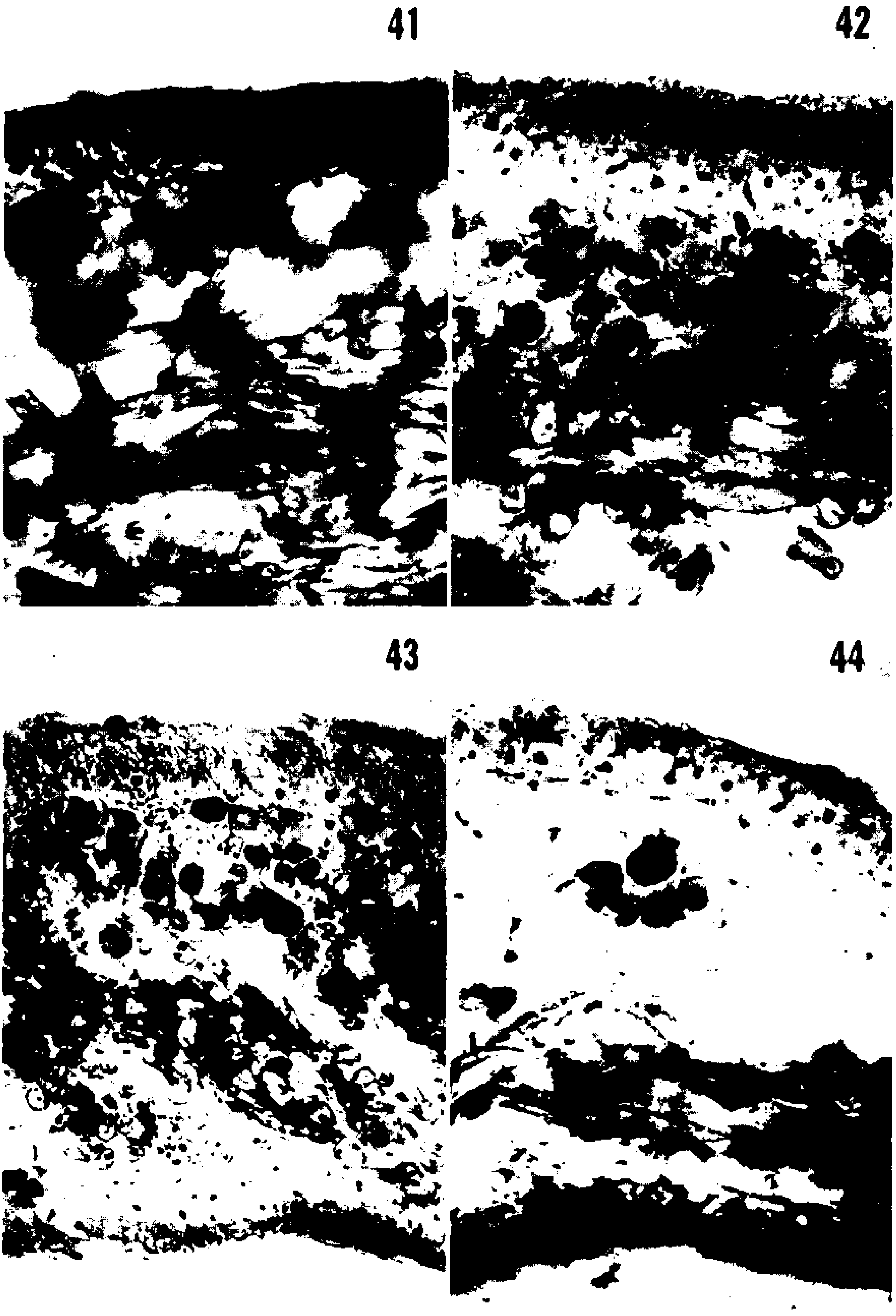
35



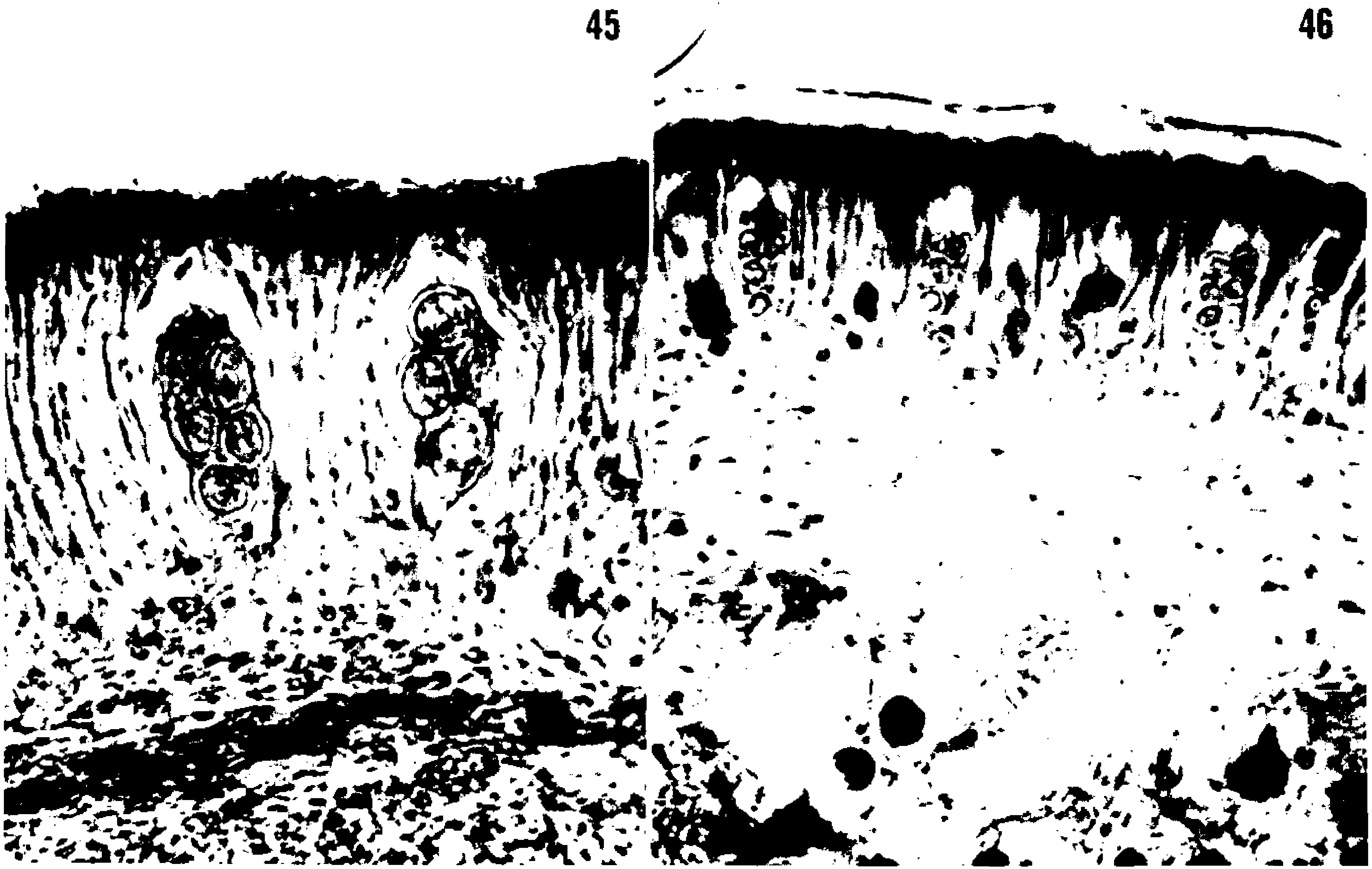
36



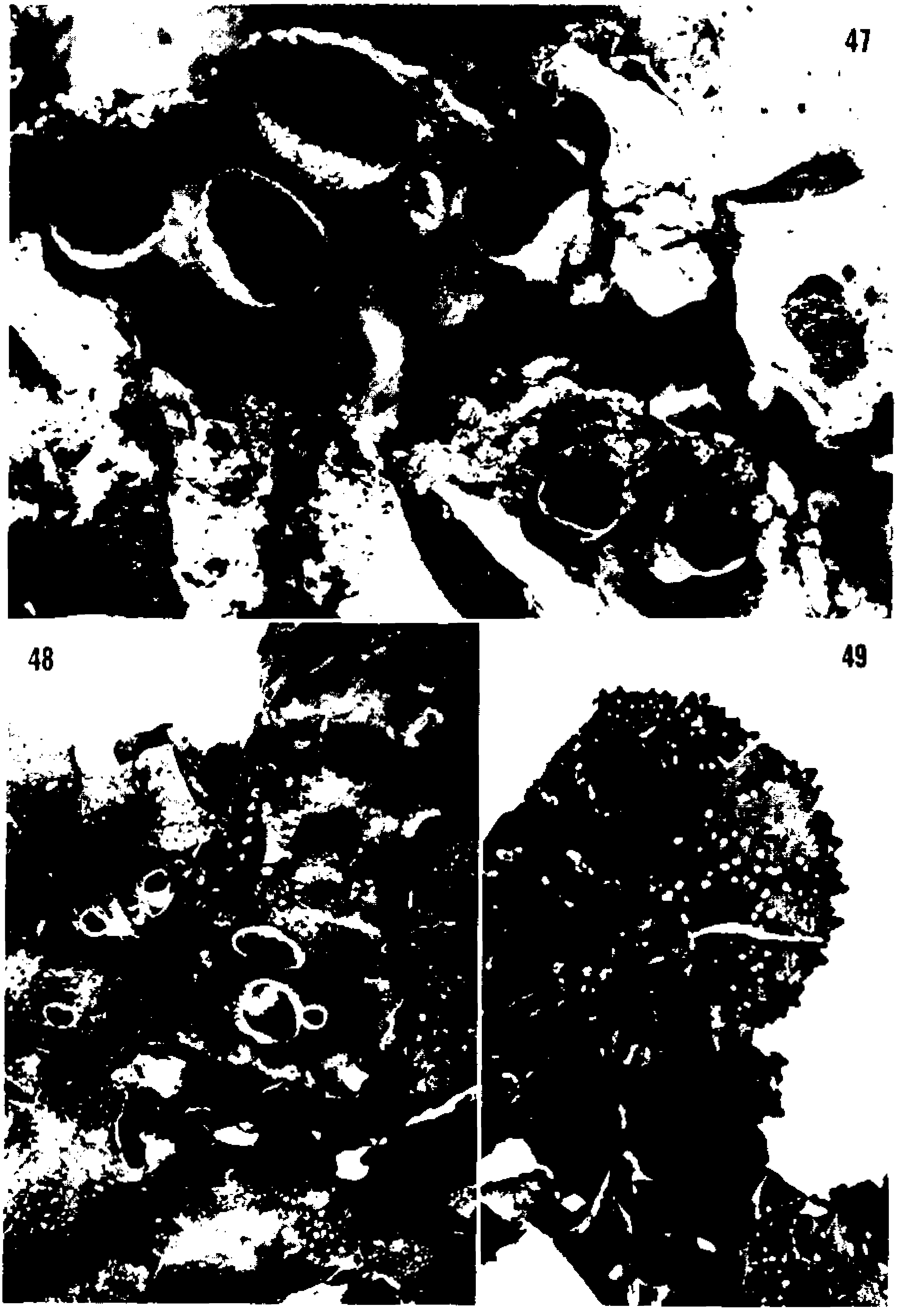
Anatomical structure of the upper cortex in *Cetraria*, *Parmelia*, and *Asahinea*: 37. Paraplectenchymatous cortex of *C. oakesiana* Tuck. 38. Same, *C. ericetorum* Opiz. 39. Prosoplectenchymatous cortex of *P.* (*Amphigymnia*) *stuppea* Tayl. 40. Same, *A. chrysantha* (Tuck.) Culb & Culb. All photographs ×300.



Anatomical structure of the upper cortex in *Cetrelia* and *Platismatia*: 41. Prosoplectenchymatous cortex of *C. chicitae* (Culb.) Culb. & Culb. 42. Same, *C. nuda* (Hue) Culb. & Culb. 43. Prosoplectenchymatous upper cortex of *P. glauca* (L.) Culb. & Culb. 44. Same, *P. tuckermanii* (Oakes) Culb. & Culb. All photographs ×300.

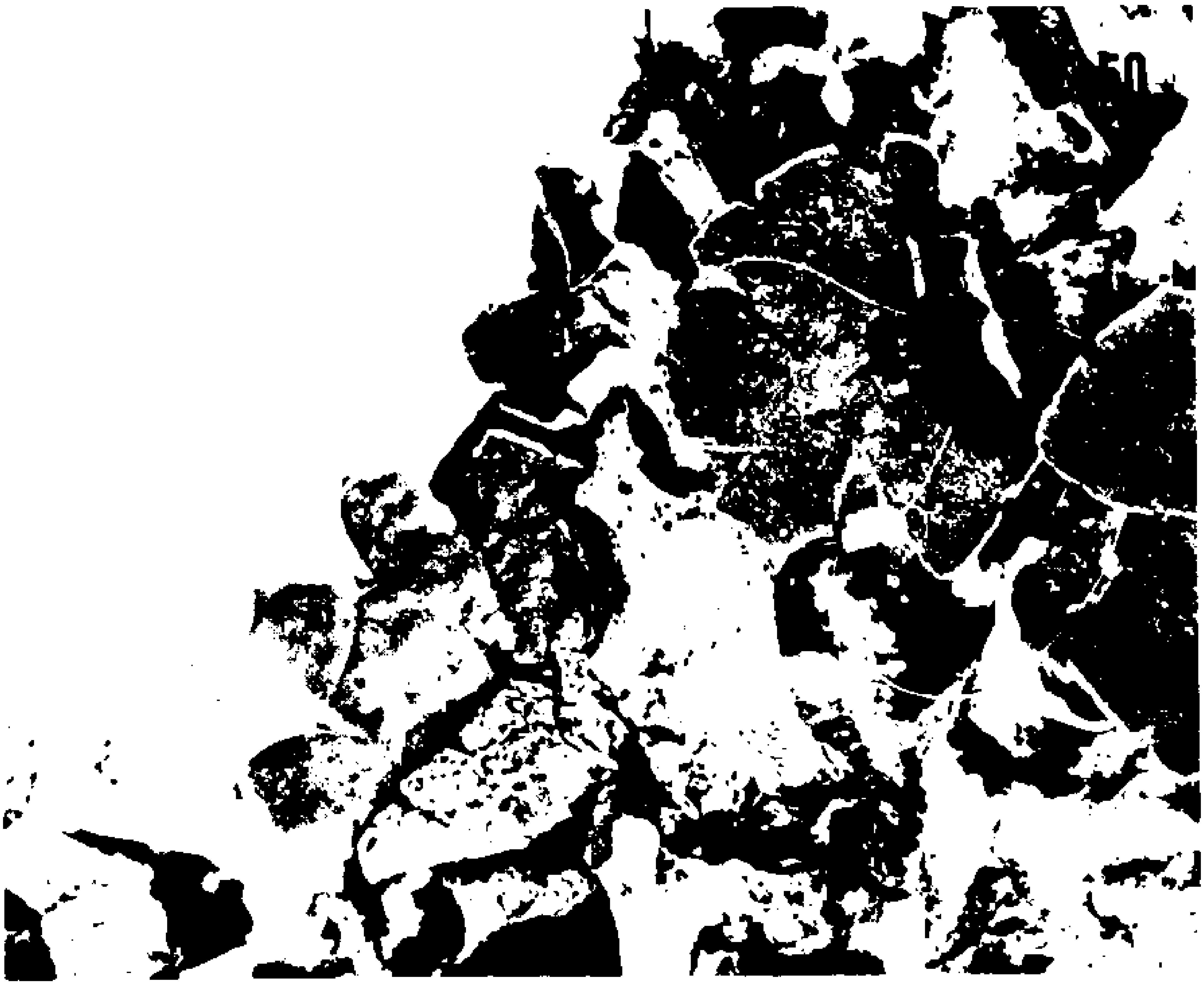


The hymenium, asci, and ascospores of *Cetrelia* and *Platismatia:* 45. *C. nuda* (Hue) Culb. & Culb. showing the large asci with large ascospores



Laminal and submarginal apothecia in *Cetrelia*: 47. Immature apothecia of *C. cetrarioides* (Del. ex Duby) Culb. & Culb. (*Culberson & Culberson* 11563, from Merionethshire, Wales) ×8. 48. Apothecia of *C. nuda* (Hue) Culb. & Culb. (*Asahina*, 1934, from Mt. Fuji, Japan) ×4. 49. Apothecium and marginal pycnidia of *C. nuda* (Hue) Culb. & Culb. (*Togashi*, 1955, from Yamoto Province, Japan) ×6.

50

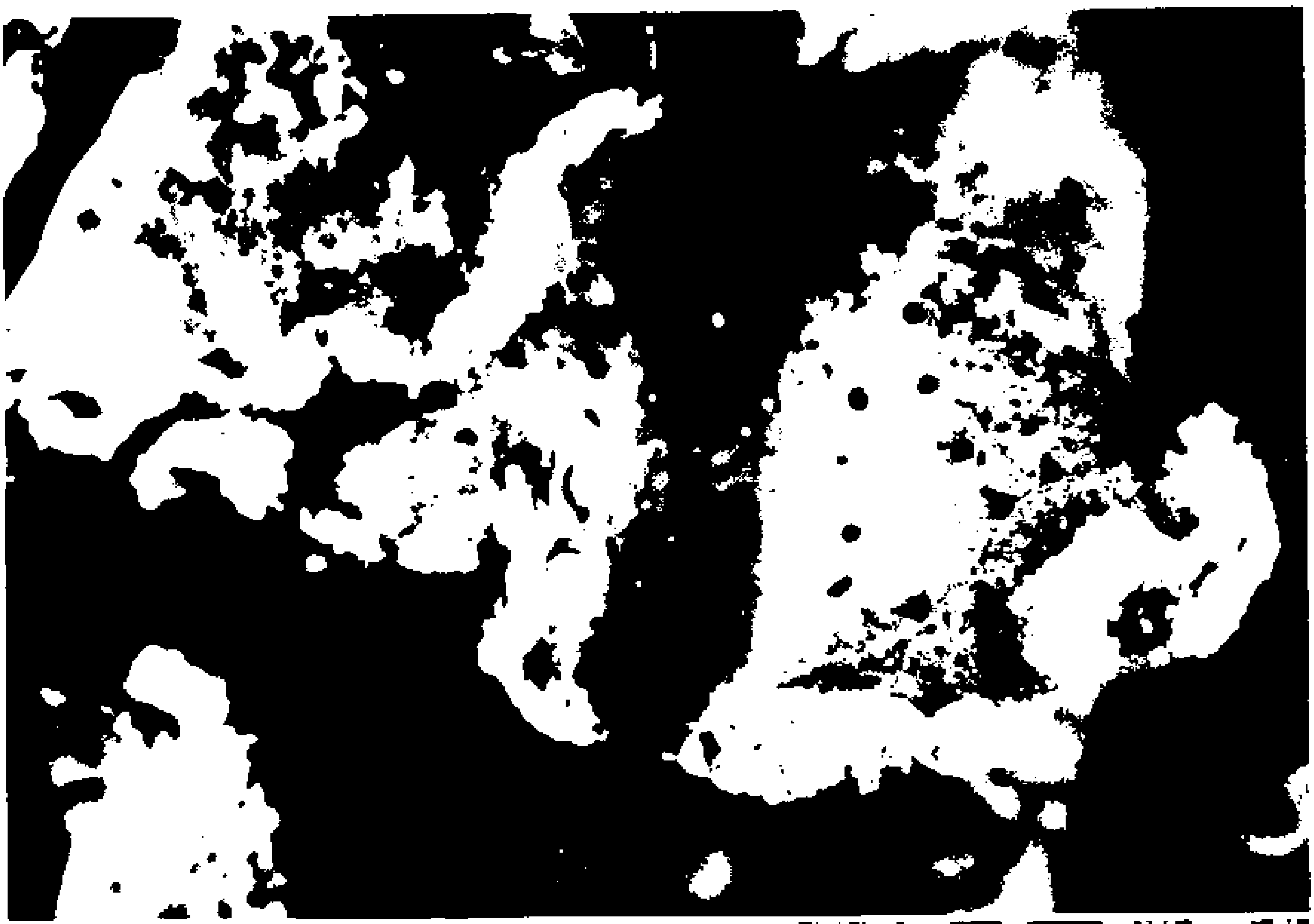


51

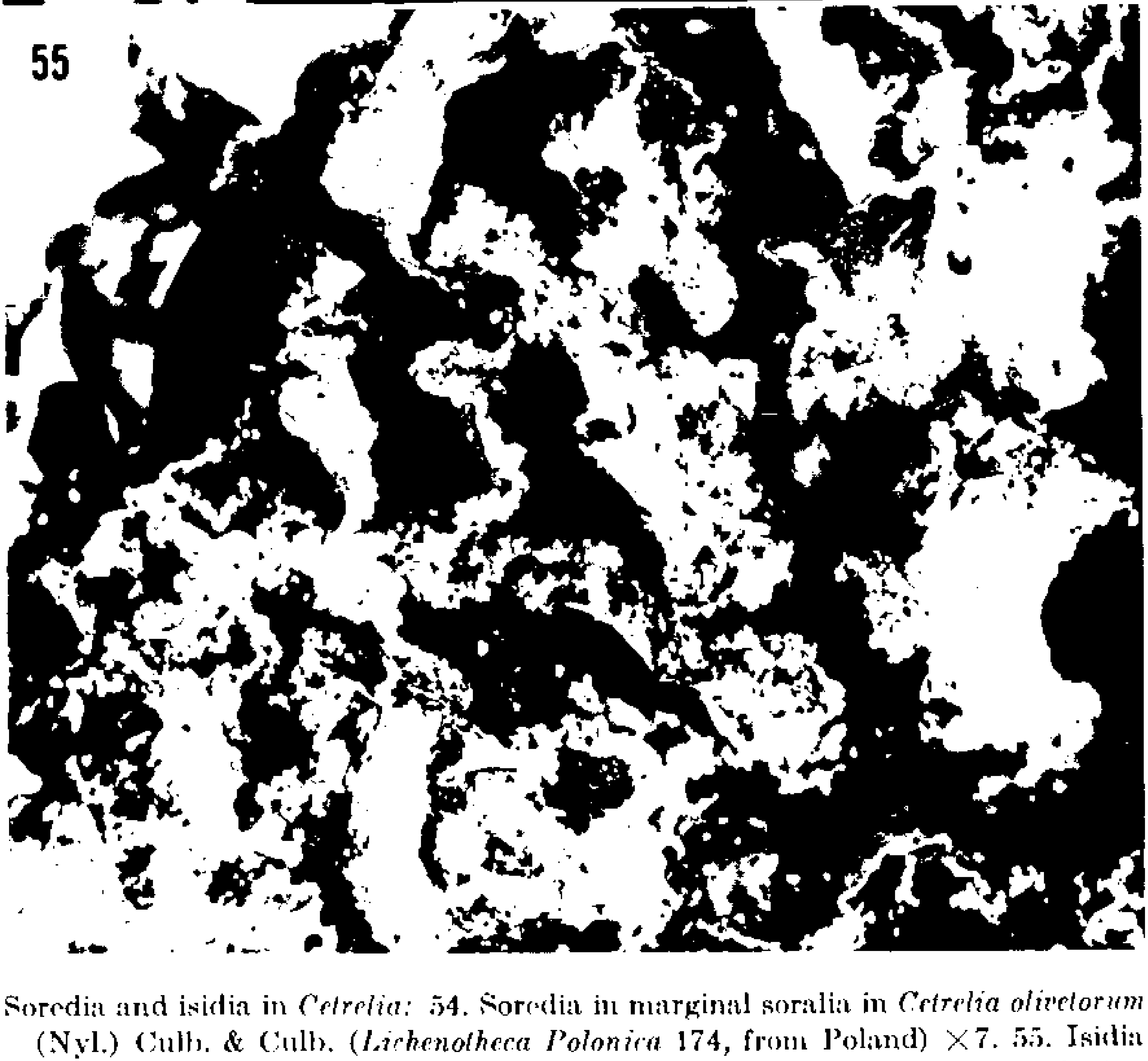
50. Perforate apothecia of *Cetrelia davidiana* Culb. & Culb. (*Handel-Mazzetti* 4254, from Yunnan Province, China) ×3.7. 51. Punctate lower cortex of *Platismatia erosa* Culb. & Culb. (*Awasthi* 2292, from Nepal) ×6.

52

The two types of pseudocyphellae in *Cetrelia:* 52. The small type of pseudocyphellae: *Cetrelia olivetorum* (Nyl.) Culb. & Culb. (*Faxon*, 1882, from New England). 53. The large type of pseudocyphellae: *Cetrelia nuda* (Hue) Culb. & Culb. (*Togashi*, 1955, from Musashi Province, Japan). Both photographs ×3.5.

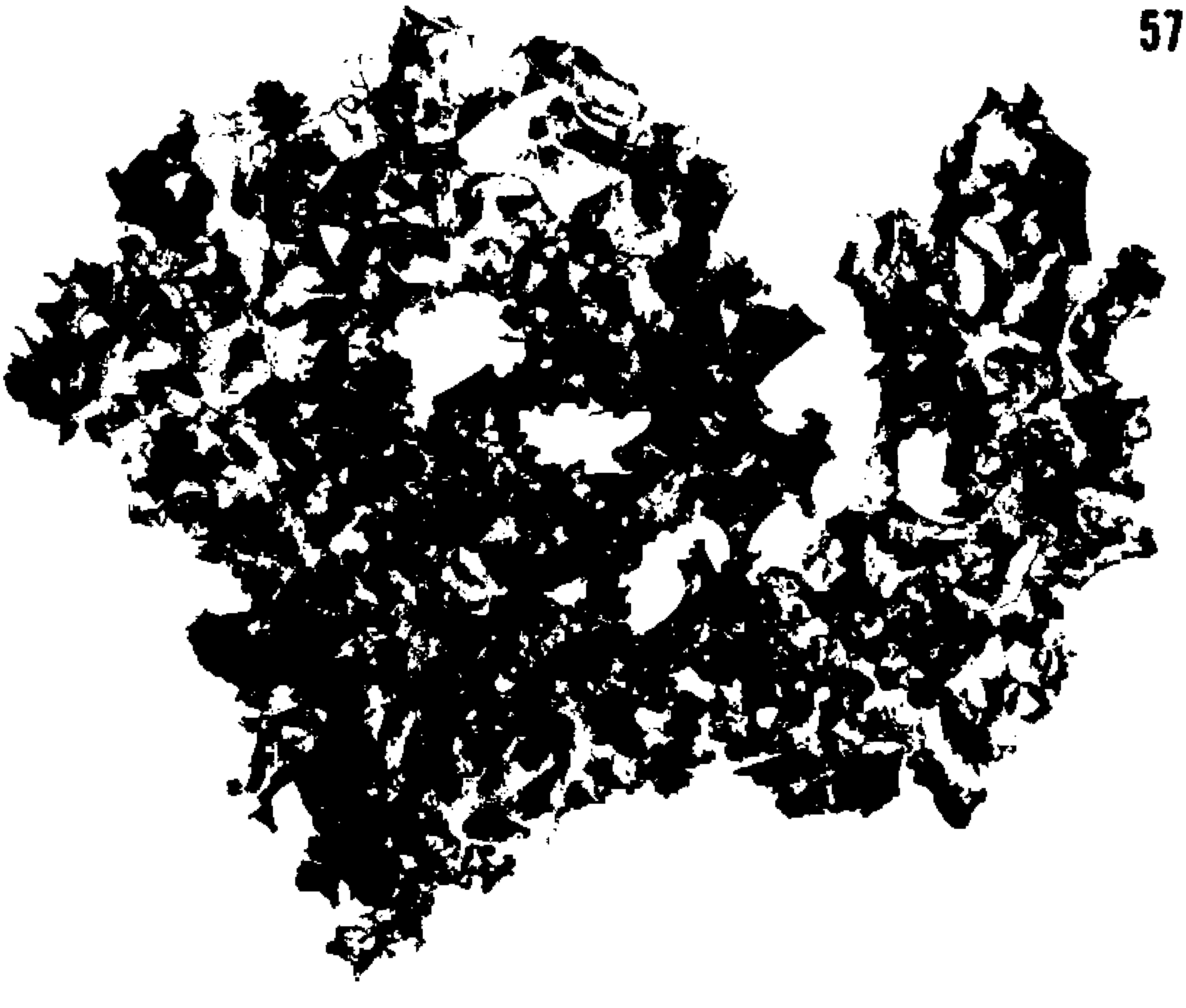


55



Soredia and isidia in *Cetrelia*: 54. Soredia in marginal soralia in *Cetrelia olivetorum* (Nyl.) Culb. & Culb. (*Lichenotheca Polonica* 174, from Poland) ×7. 55. Isidia in *Cetrelia braunsiana* (Müll. Arg.) Culb. & Culb. (*Togashi*, 1956, from Echigo Province, Japan) ×7.

56

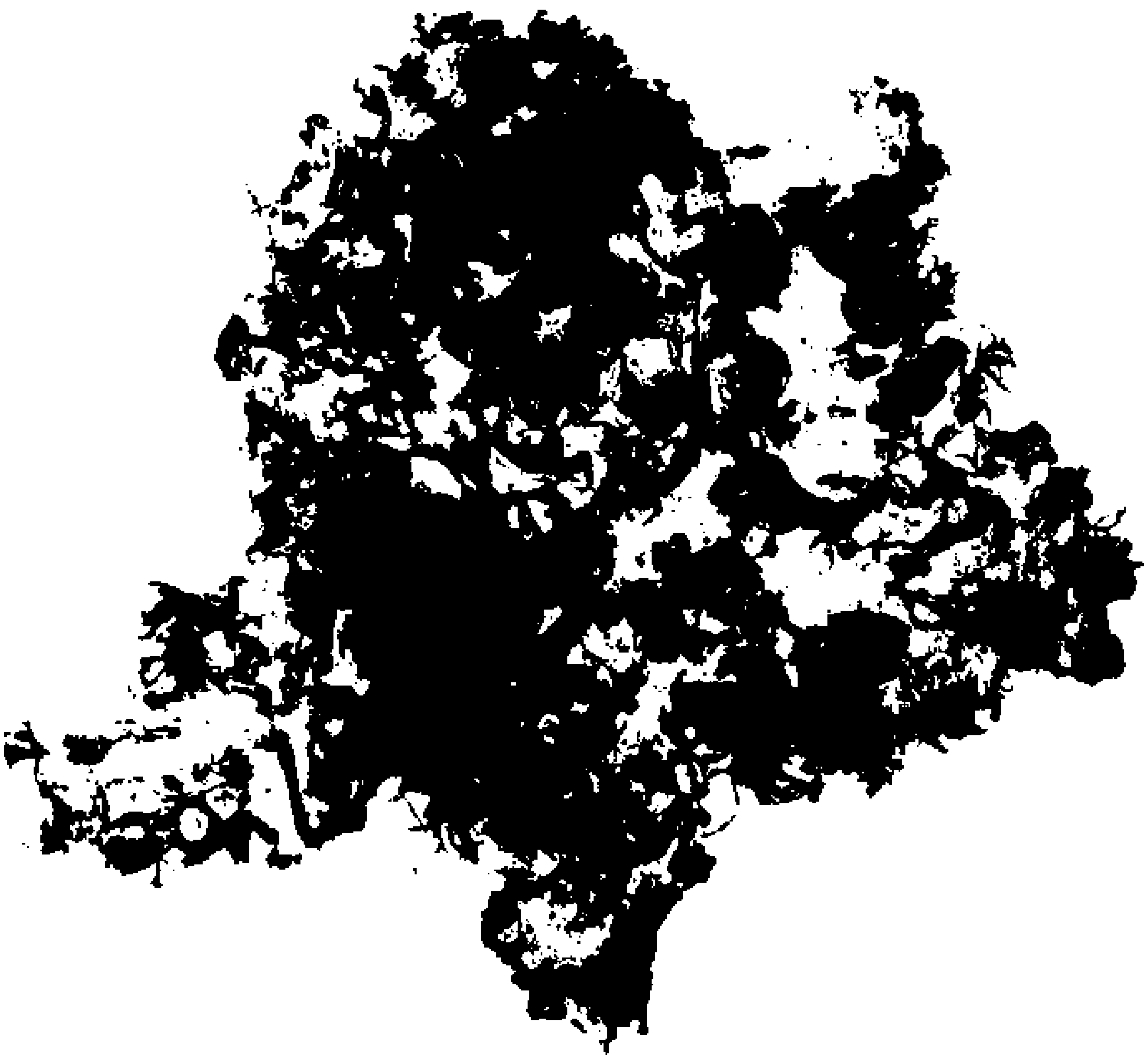


57

56. *Cetrelia alaskana* (Culb. & Culb.) Culb. & Culb. (Holotype, *Thomson, Lichenes Arctici* 13, from Cape Sabine, Alaska) × 1.3. 57. *Cetrelia chicitae* (Culb.) Culb. & Culb. (*Kurokawa* 59222, from Shinano Province, Japan) × 1.

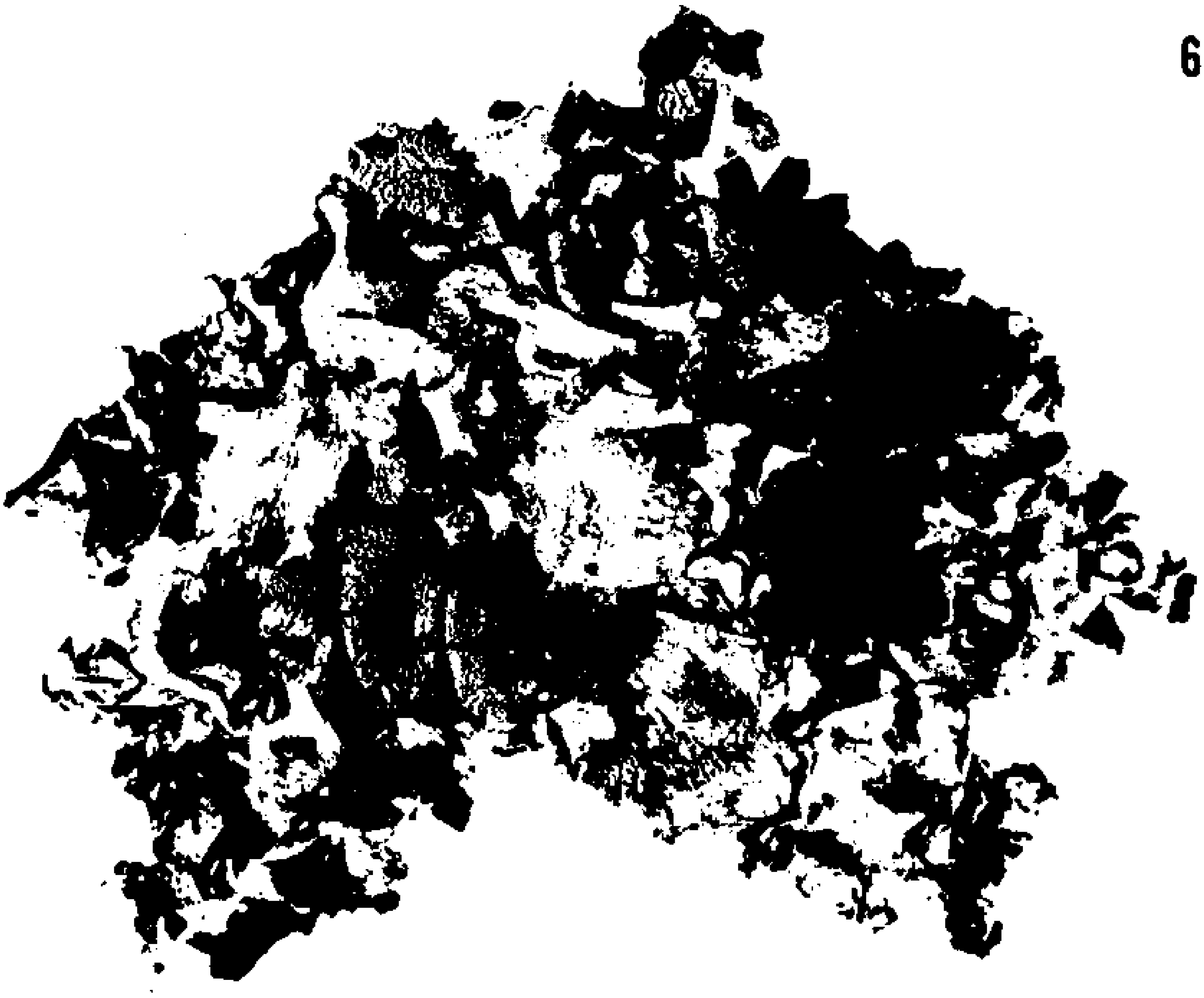
58

59

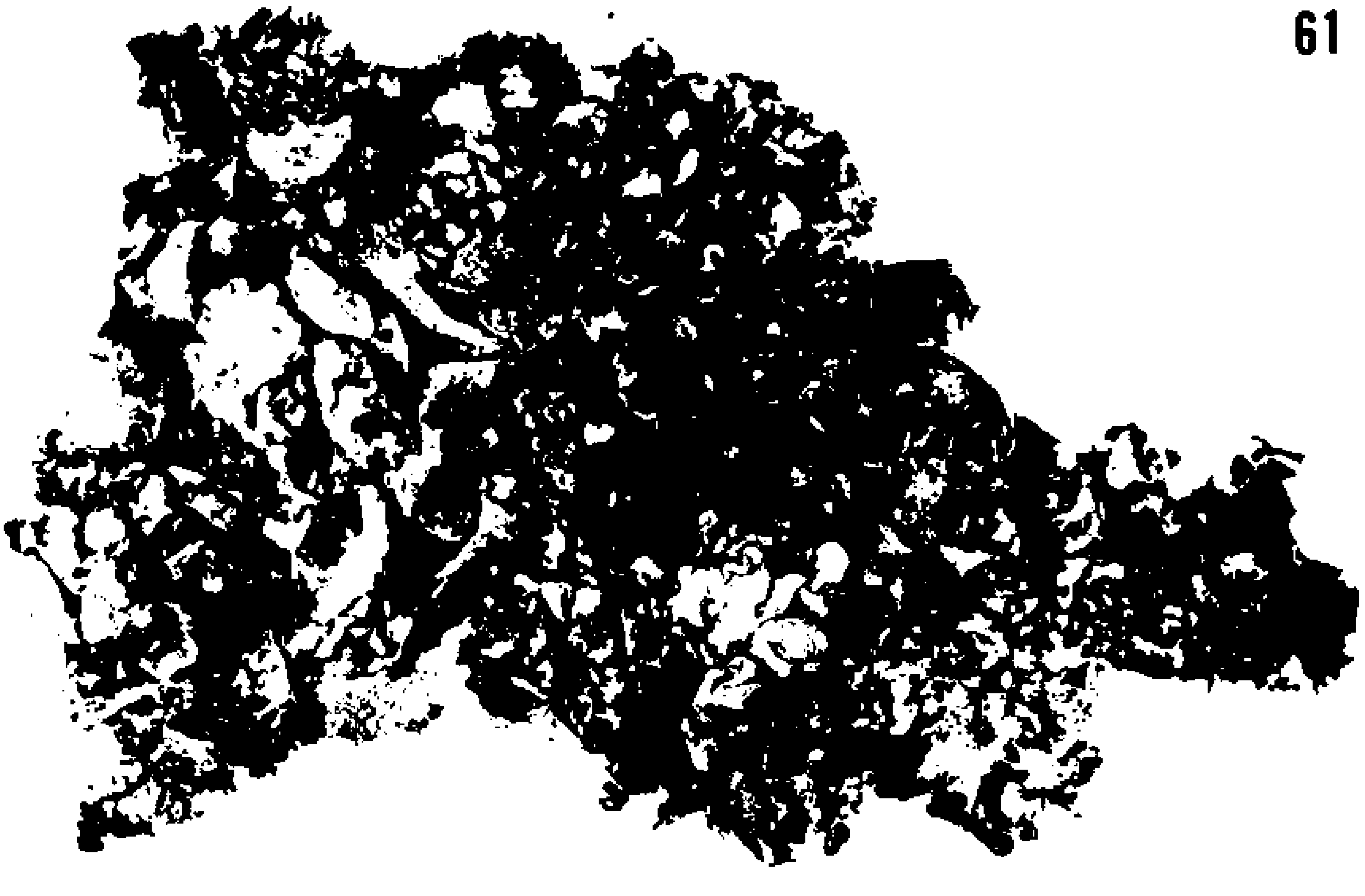


58. *Cetrelia braunsiana* (Müll. Arg.) Culb. & Culb. (*Togashi*, 1956, from Echigo Province, Japan) ×2. 59. *Cetrelia cetrarioides* (Del. ex Duby) Culb. & Culb. (*Culberson & Culberson* 11564, from Merionethshire, Wales) ×0.8.

60

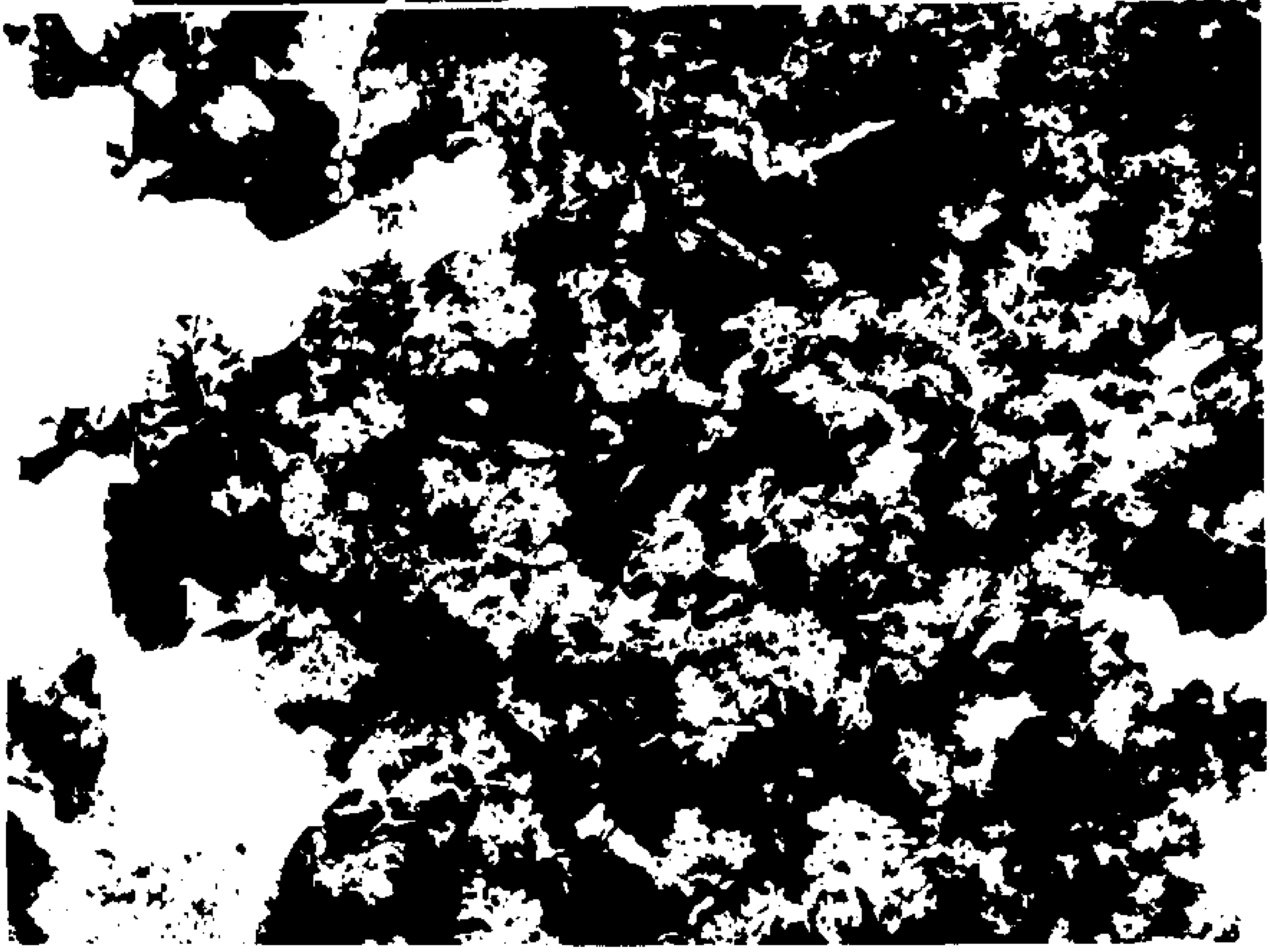


61



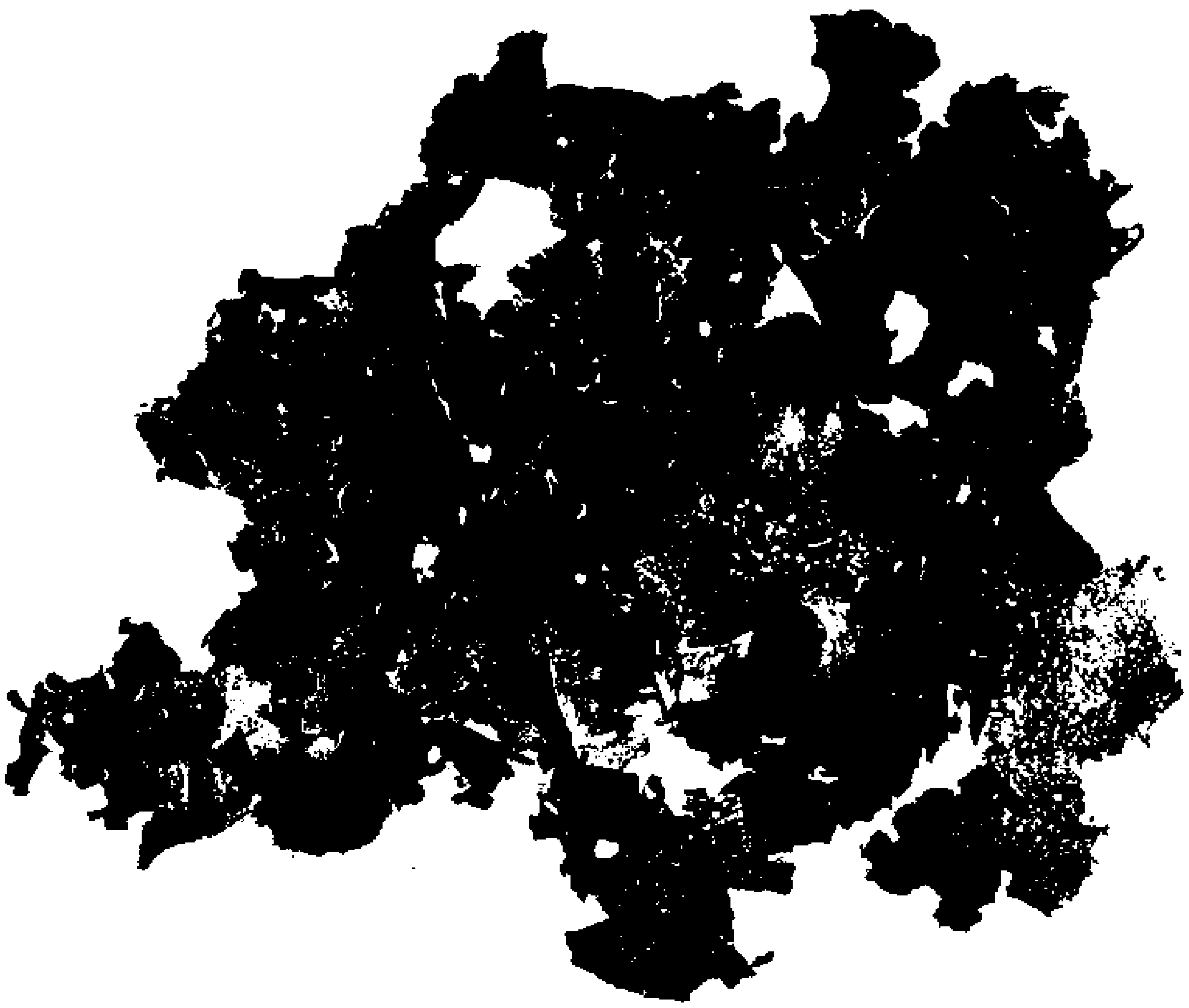
60. *Cetrelia davidiana* Culb. & Culb. (*Handel-Mazzetti* 4254, from Yunnan Province, China) ×1.3. 61. *Cetrelia delavayana* Culb. & Culb. (Isotype, *Delavay*, 1888, from Yunnan Province, China) × 1.5.

62



62. *Cetrelia isidiata* (Asah.) Culb. & Culb. (*Kurokawa* 331, from Formosa) × 1.
63. *Cetrelia japonica* (Zahlbr.) Culb. & Culb. (*Kurokawa* 58374, from Shinano Province, Japan), showing detail of the lobulae × 5.

64



65

64. *Cetrelia nuda* (Hue) Culb. & Culb. (*Asahina*, 1934, from Suruga Province, Japan) × 1.3. 65. *Cetrelia olivetorum* (Nyl.) Culb. & Culb. (*Lichenotheca Polonica* 174, from Poland) × 1.2.

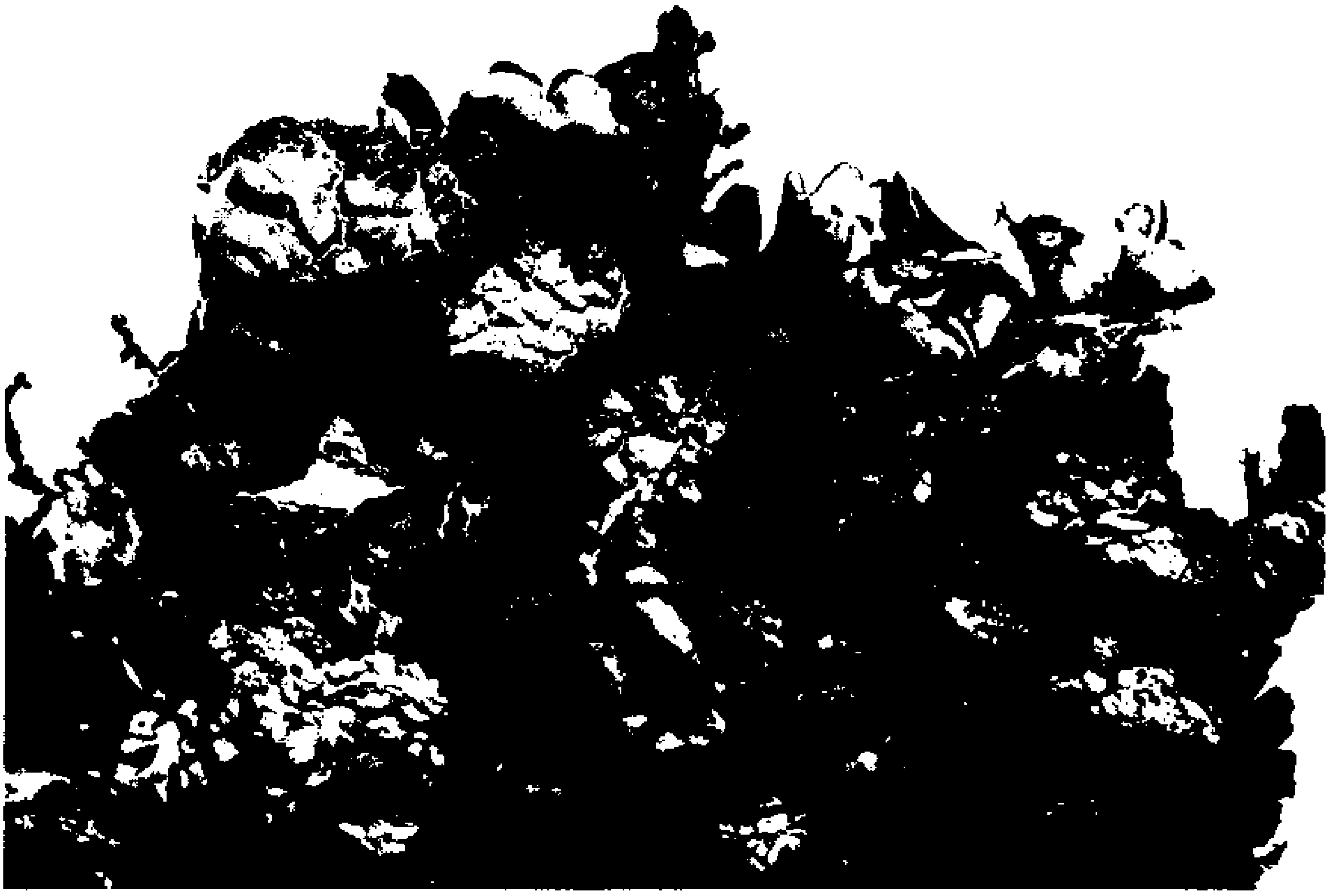
**66**

**67**

66. *Cetrelia pseudolivetorum* (Asah.) Culb. & Culb. (*Kurokawa* 137, from Formosa) ×1. 67. *Cetrelia sanguinea* (Schaer.) Culb. & Culb. (*Du Rietz*, 1927, from Java) ×1.2.

68

69



68. *Cetrelia sinensis* Culb. & Culb. (*Kurokawa* 449, from Formosa) ×1.5. 69. *Platismatia erosa* Culb. & Culb. (*Poelt* L37, from Nepal) ×2.

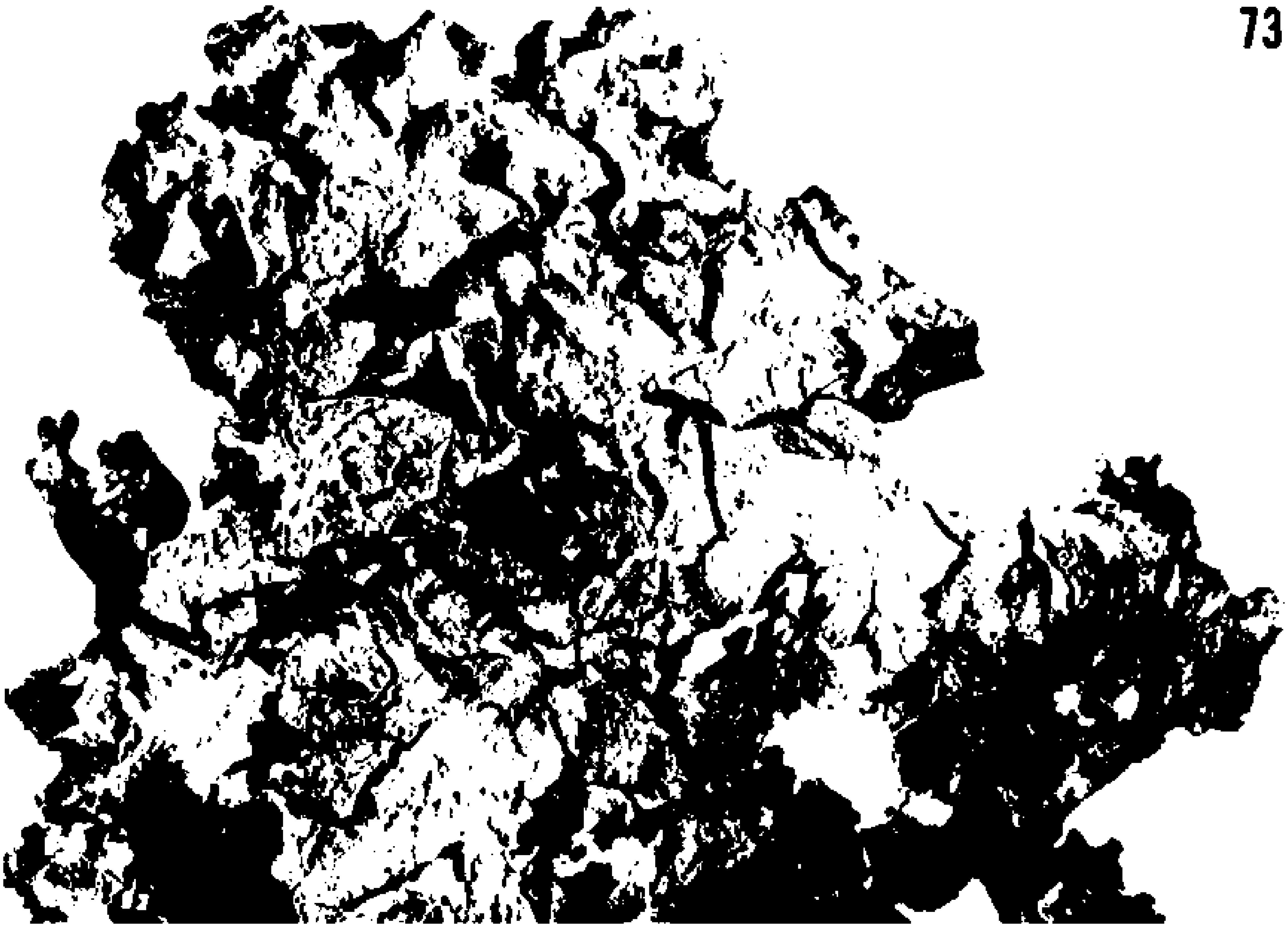
70

71

*Platismatia glauca* (L.) Culb. & Culb. (two forms): 70. With fruticose branchlets (*Stickney* 1005b, from Montana) ×2.5. 71. With sorediate lobes (*Imshaug* 26501, from Quebec Province, Canada) ×1.1.

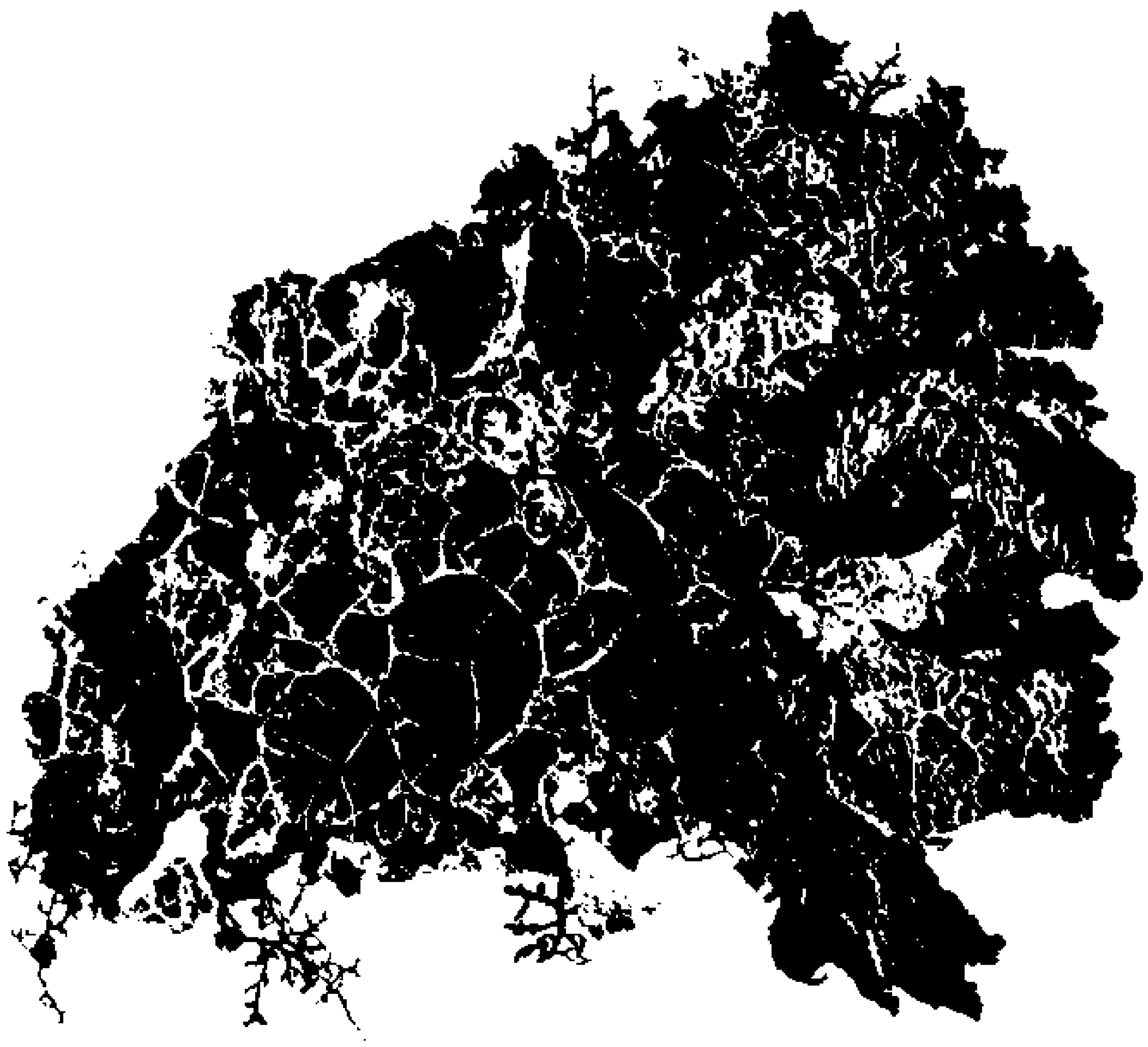
72

73

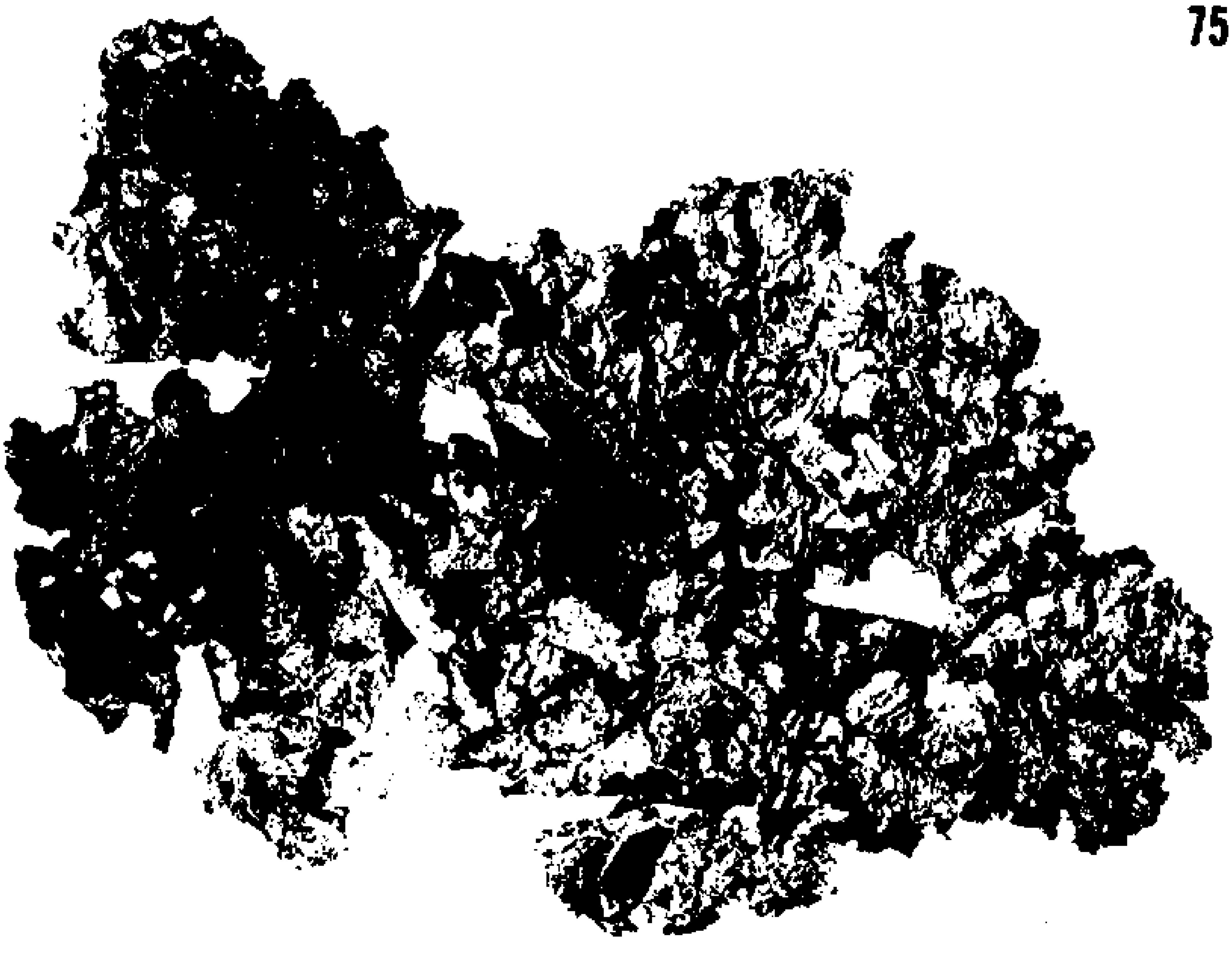


72. *Platismatia herrei* (Imsh.) Culb. & Culb. (Lectotype, *Hall*, 1871, from Oregon) ×1. 73. *Platismatia interrupta* Culb. & Culb. (*Culberson & Culberson* 10669, from Suruga Province, Japan) ×1.5.

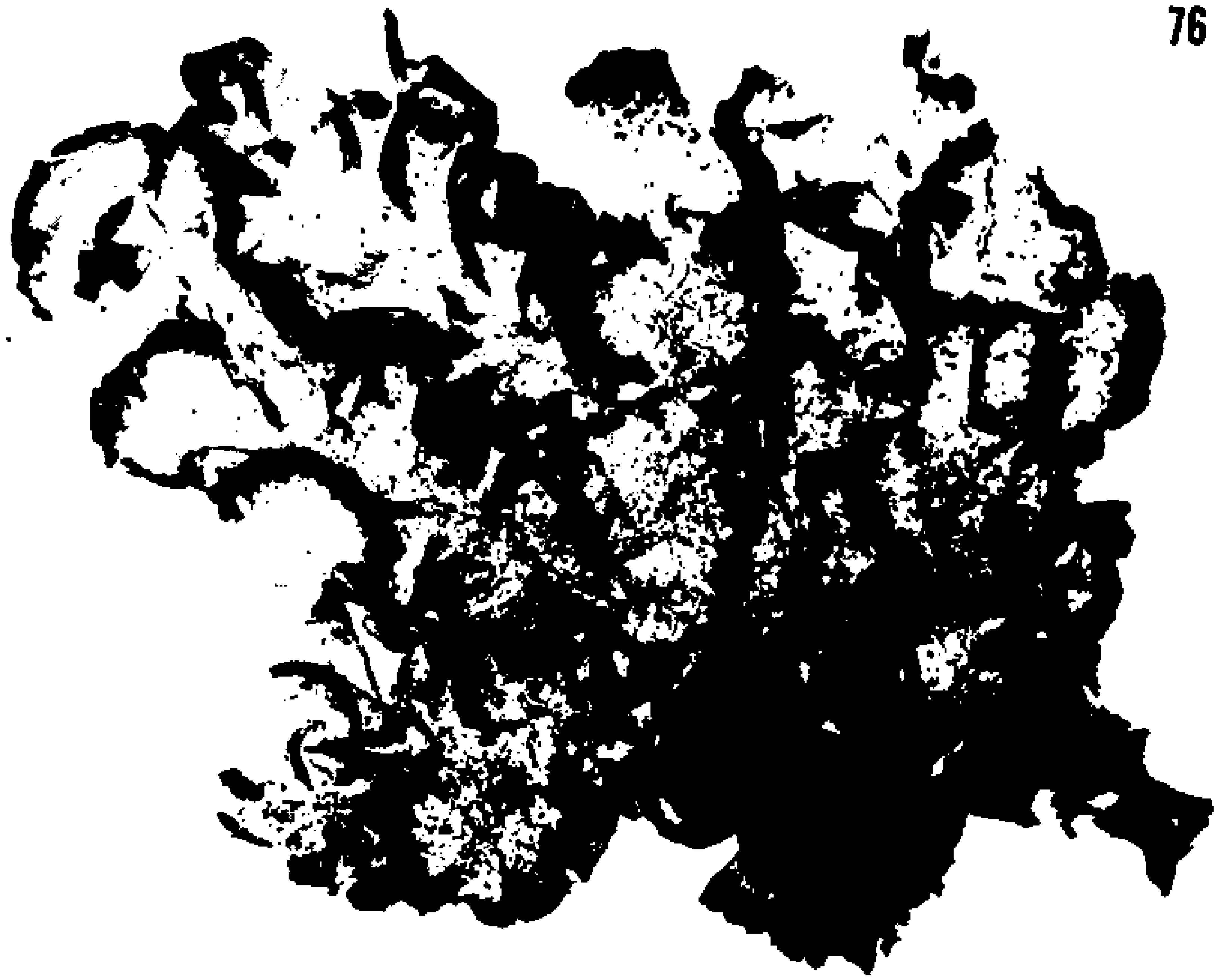
74



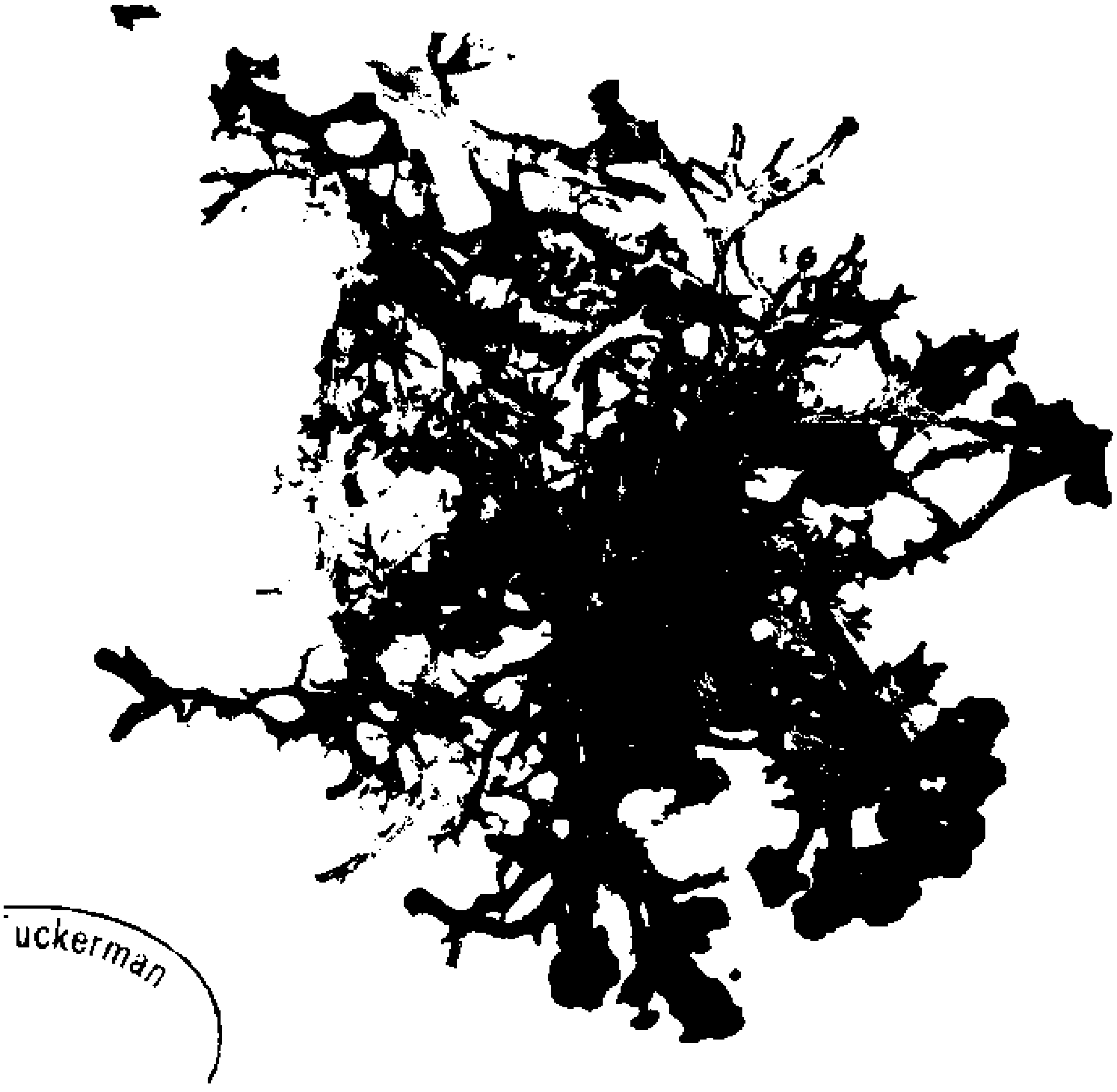
75



74. *Platismatia lacunosa* (Ach.) Culb. & Culb. (*Eyerdam*, 1947, from Alaska) × 1.3. 75. *Platismatia norvegica* (Lynge) Culb. & Culb. (*Szczawinski* V.I./558, from Vancouver Island, British Columbia, Canada) × 1.

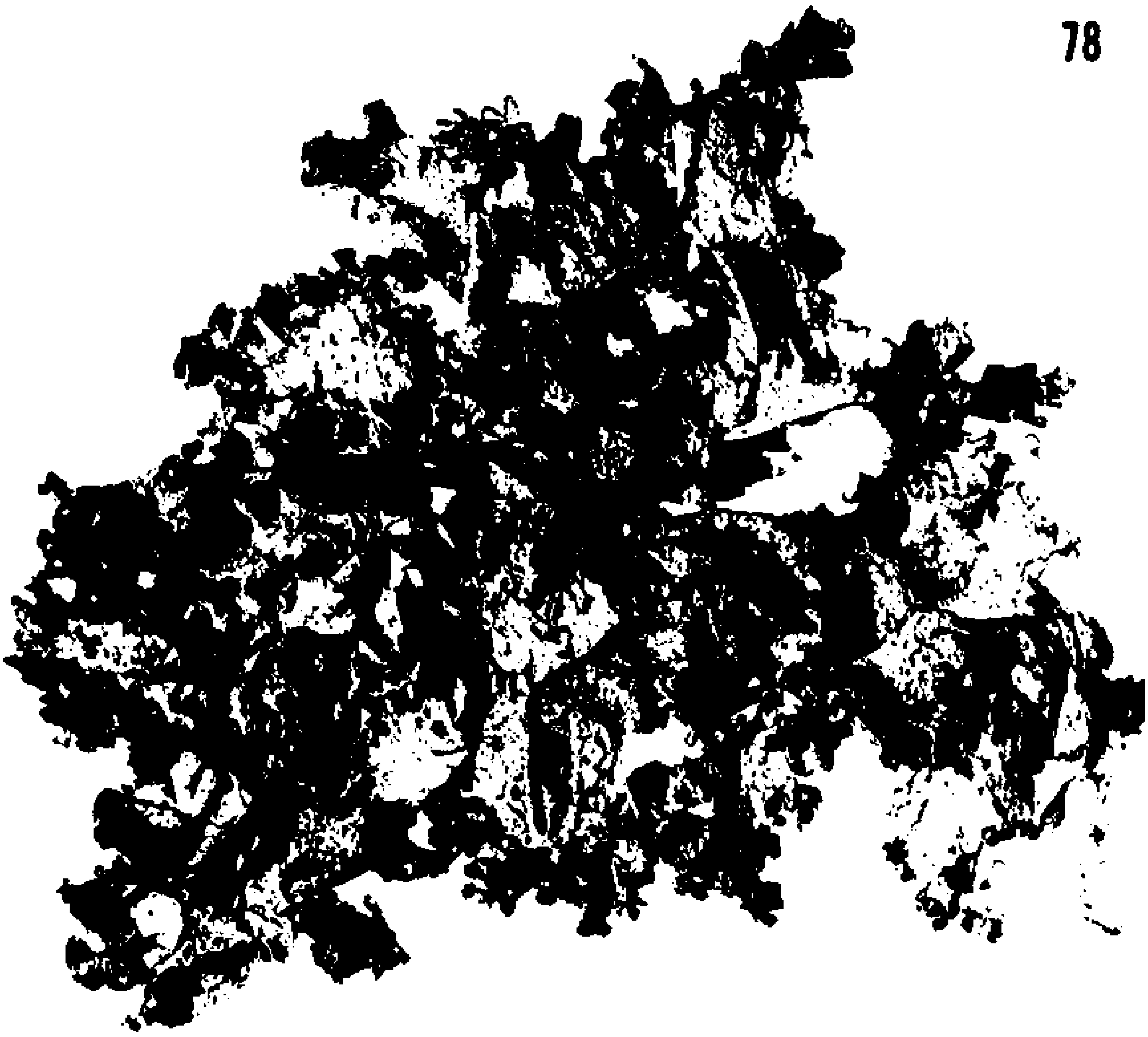


76

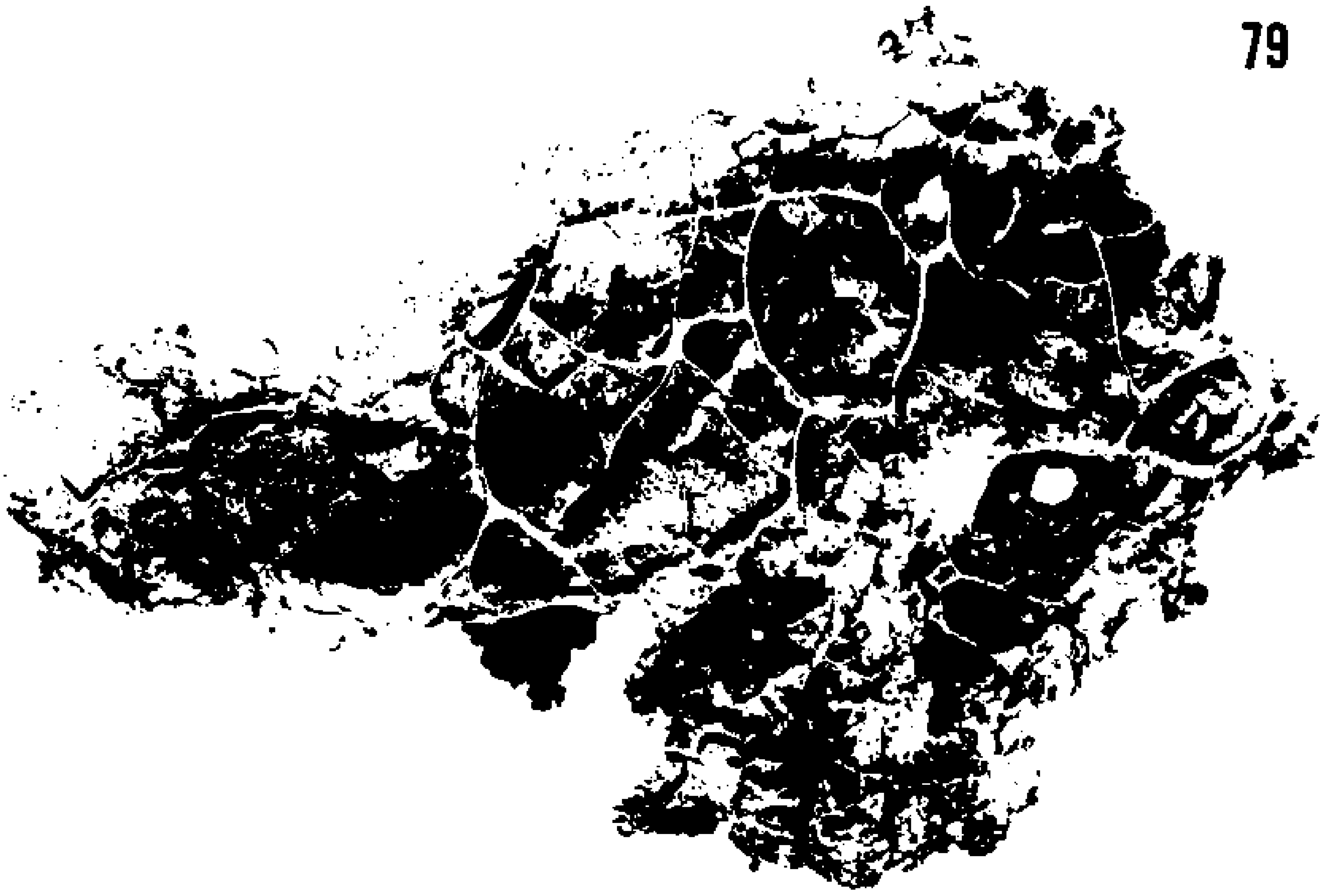


77

76. *Platismatia regenerans* Culb. & Culb. (Holotype, *Hale* 28207, from Sabah) ×2. 77. *Platismatia stenophylla* (Tuck.) Culb. & Culb. (Holotype, *Bolander* 384, from California) ×0.9.



78



79

78. *Platismatia tuckermanii* (Oakes) Culb. & Culb. (*Moore* 1372, from North Carolina) ×1.3. 79. *Platismatia formosana* (Zahlbr.) Culb. & Culb. (*Suzuki*, 1935, from Formosa) ×2.

### 7. **Cetrelia delavayana** Culb. & Culb., sp. nov. PLATE 16

Thallus mediocris, 7–10 cm. latus; laciniae 1.3–1.7 cm. latae. Superficies superior sordide citrella apud exemplaria vetera herbarii (albida apud plantas vivas?), levis, pseudocyphellata, pseudocyphellis punctatis, paucis, parvissimis. Superficies inferior picea, marginibus castanea, nonnihil punctata, leviter rhizinata. Cortex superior 16–22μ crassus; medulla 101–186μ crassa; cortex inferior (12–)16–23μ crassus. Apothecia ad 0.8 cm. lata, perforata, excipulo thallino dense pseudocyphellato; hymenium 62–109μ crassum; strata subhymenialia 43–78μ crassa, supra hyalina et subtus aurea. Sporae 8-nae, ellipsoideae, 16–24×9–12μ. Pycnidia magna, marginalia, non stipitata; conidia ca. 1.5×6.0μ, recta, extremis nonnihil inflatis.

Thallus medium, 7–10 cm. broad; lobes 1.3–1.7 cm. broad. Upper surface pale brownish in old herbarium specimens (whitish when fresh?), smooth, pseudocyphellate, the pores few, very small, rarely reaching 0.5 mm. Lower surface jet-black, the margins dark brown, somewhat punctate in some specimens; rhizines few. Upper cortex 16–22μ thick, medulla 101–186μ thick; lower cortex (12–)16–23μ thick. Apothecia to 0.8 cm. broad, perforate, the thalloid exciple densely pseudocyphellate; hymenium 62–109μ thick; subhymenial layers 43–78μ thick, hyaline above and golden yellow below. Spores 8, ellipsoid, 16–24×9–12μ. Pycnidia large, marginal, unstalked; conidia about 1.5×6.0μ, rod-shaped, the ends often somewhat inflated.

TYPE.—"Au col de Lopin-chan," Yunnan, China, *Delavay*, 1888 (PC, holotype).

MEDULLARY REACTIONS.—K−, C−, KC− or KC+ pinkish, P−.

CONSTITUENTS.—Imbricaric acid and atranorin.

DISTRIBUTION (Map, Figure 21).—In the mountains of Szechwan and Yunnan, China; on the bark of trees and shrubs.

*Cetrelia delavayana* can be distinguished from most other esorediate and nonisidiate species of the genus both morphologically, by the presence of small pseudocyphellae rather than large aggregate ones, and chemically by the presence of perlatolic acid. *Cetrelia collata* produces imbricaric acid and inhabits much the same range but has very large pores exceeding 1 mm. *Cetrelia alaskana* has small pores and imbricaric acid, its habit is completely different, and its range is the western coast of Alaska.

CHEMICAL ANALYSIS.—Eight samples of this species were tested. All showed perlatolic acid and atranorin. Four residues were hydrolyzed and showed no trace of divaric acid, indicating the absence of imbricaric acid, but at least two samples gave a KC+ reaction which could not be associated with identifiable crystals or chromatographic spots. It is possible that this unidentified KC+ accessory compound is the same as that which gives a KC+ reaction in other *Cetrelia* species which contain acid.

SPECIMENS EXAMINED:

CHINA: SZECHWAN: Mt. Lose-chan, south of Ningyüen, 3,950 m., *Handel-Mazzetti* 1441 (WU).

YUNNAN: Yangtze watershed, Likiang, Likiang Snow Range, *Rock* 11775 (W); Lenago Pass between Mekong and Yangtse, 27°43′N, *Gebauer*, 1914 (TNS, W, WU); between Dali (Talifu) and Hodjing, above Hsiang-schuiho, 26°15′N, 3,400 m., *Handel-Mazzetti* 7398 (W); Lopin-chan Pass, *Delavay*, 1888 (PC, 2 collections).

**8. Cetrelia isidiata** (Asah.) Culb. & Culb., comb. nov. PLATE 17

*Cetraria sanguinea* Schaer. f. *isidiata* Asah. *in* Sato, Parmeliales (I), in Nakai & Honda, Nova Fl. Jap. 73. 1939. Type: Japan, Honshu, Titibu [=Chichibu], Mt. Kobushi, *Asahina*, 1933 (TNS, holotype).

Thallus small to large, 5–19 cm. broad; lobes 0.5–1.5 cm.broad. Upper surface grayish or uniformly light brown in old herbarium specimens, pseudocyphellate, the pores tiny and infrequent, isidiate, the isidia mostly marginal, globose to somewhat coralloid or slightly branched, or poorly developed and very infrequent altogether. Lower surface jet-black, the margins brown, punctate or not; rhizines conspicuous but unevenly distributed. Upper cortex 16–31$\mu$ thick; medulla 84–217$\mu$ thick; lower cortex 13–31$\mu$ thick. Apothecia and pycnidia unknown.

MEDULLARY REACTIONS.—K−, C+ red, PD−

CONSTITUENTS.—Anziaic acid and atranorin.

DISTRIBUTION (Map, Figure 8).—Honshu, Japan, and Formosa; on trees.

The only other C+ isidiate species that *Cetrelia isidiata* might be mistaken for is *C. pseudolivetorum* which contains olivetoric acid and reacts to produce a pink color with this reagent. A chemical test is desirable for the identification of these species since the thallus spot tests may be somewhat variable.

The original classification of the present taxon as a variety of the Javanese species *sanguinea* is not tenable even though both produce anziaic acid in the medulla. The Javanese plants lack isidia, have very large pseudocyphellae that become confluent, and usually bear apothecia, while the Japanese and Formosan ones have isidia and minute pseudocyphellae and are unknown in fruit. *Cetrelia isidiata* seems to be a very well defined species, more closely related to *C. chicitae*, for example, than to *C. sanguinea*.

The single Formosan collection examined (Plate 17) is rich and well developed, but it shows a very meager production of isidia as do the Japanese specimens. Since only a few collections of this species are known, it is impossible to give a definitive assessment of the importance of isidia as a diagnostic trait; in fact they may be of little consequence. It is, therefore, with some hesitation that we take up *isidiata* as the specific epithet, a name given by Asahina to the taxon when he considered it a forma of the species treated in this monograph as *Cetrelia sanguinea*. Isidia are much less well developed in the present species than in *C. braunsiana*, for example.

CHEMICAL ANALYSIS.—The four known specimens of this species were tested, and all contained atranorin (proved in the GA*o*-T solution) and anziaic acid (identified by paper chromatography).

ADDITIONAL SPECIMENS EXAMINED:

JAPAN: HONSHU: Chichibu, Mt. Kobushi, *Asahina*, 1933 (TNS, original collection; 3 specimens).

FORMOSA: Mt. Shin-Kao-San, Mt. Shi-San, 3,300–3,600 m., *Kurokawa* 311 (TNS).

**9. Cetrelia japonica** (Zahlbr.) Culb. & Culb., comb. nov. PLATE 17

*Cetraria japonica* Zahlbr., Annal. Mycol. 14:60. 1916. Type: Japan, Prov. Kotsuke, Mt. Akagi, *Yasuda* (W, lectotype).

*Platysma collatum* f. *microphyllinum* Hue, Nouv. Arch. Mus., IV, 1:209. 1899. Type: Japan, Fujiyama, *Faurie* 519 (PC, lectotype).

*Cetraria collata* f. *microphyllina* (Hue) Zahlbr. Catal. Lich. Univ. 6:285. 1930.

Thallus medium to very large, 10–28 cm. broad; lobes 0.5–1.5 cm. broad, the margins densely fringed with multibranched lobulae, narrow and isidioid or more broadly expanded and lobelike, in some specimens becoming so abundantly developed as to make the lichen appear cristate. Upper surface grayish-white or ashy-white (or light brownish in old herbarium specimens), smooth, pseudocyphellae conspicuous, punctiform to elongate but rarely reaching 1 mm. in size. Lower surface jet-black, a marginal zone near the tips of the lobes chestnut brown or even whitish, not punctate; rhizines black. Upper cortex 18–23$\mu$ thick, interspersed with abundant crystals; medulla 83–171$\mu$ thick; lower cortex 16–23$\mu$ thick, without crystals, darkening. Apothecia very rare, submarginal, often perforate, 0.4–1.3 cm. broad; hymenium 65–70$\mu$ thick; subhymenial layers 47–57$\mu$ thick, underlain by a thick continuous zone of algae. Spores 8, ellipsoid, 14–21$\times$8–11$\mu$. Pycnidia very rare, large, black, emergent, about 0.1 mm. broad, restricted to the marginal lobulae, the ostiole prominent; conidia 1.5$\times$5$\mu$, rod-shaped, the ends somewhat enlarged.

MEDULLARY REACTIONS.—K–, C–, KC– or KC+ pink, PD–.

CONSTITUENTS.—Microphyllinic acid and atranorin.

DISTRIBUTION (Map, Figure 16).—The mountains of Hokkaido and Honshu in Japan, South Korea, Formosa, northern Sabah (Borneo), and Java.

*Cetrelia japonica* is chemically distinct from all the other species of the genus in the production of microphyllinic acid. Morphologically, however, it could be mistaken for *C. sinensis* (with imbricaric acid), *C.*

*sanguinea* (with anziaic acid), or *C. pseudolivetorum* (with olivetoric acid). While its distinction from *C. sinensis* is probably purely chemical, the morphology of the whole population of *C. japonica* is apparently somewhat different from that of the populations of *C. sanguinea* and *C. pseudolivetorum*, although it must be admitted that many individual specimens of all these species cannot be identified without chemical tests. As a rule the margins of the lobes of *C. japonica* are moderately to densely fringed with tiny lobulae or dorsiventral isidia. *Cetrelia pseudolivetorum* and *C. sanguinea* also have similar lobulae, but as a rule the lobulae are less well developed, and many thalli, especially in *C. sanguinea*, may lack them altogether.

The population assigned herein to *Cetrelia japonica* may represent two taxa. The only known Javanese specimen has only true isidia rather than lobulae. It may be a rare Javanese endemic, but it is assigned to *C. japonica* provisionally because such isidia can be found (with lobulae) on some specimens of *C. japonica* from Japan, because the Javanese plant produces microphyllinic acid (a rare chemical trait in the genus), and because typical specimens of *C. japonica* are known from nearby Sabah.

CHEMICAL ANALYSIS.—This species contains the rare lichen substance microphyllinic acid. Twenty-two samples were tested, and all but two showed atranorin in either the GE or the GA*o*-T solutions. But microphyllinic acid seems to interfere with the crystal tests for atranorin so that often it is necessary to allow the slides to stand overnight before crystals of atranorin are observable in the GA*o*-T solution. The two samples which seem to give a negative test for atranorin undoubtedly do contain this substance since the GA*o*-T slides became bright yellow, and atranorin should be considered a constant component of this species. Atranorin was not determinable by chromatography in the presence of microphyllinic acid by the methods used in this study because a decomposition product of microphyllinic acid has the same $R_f$ value as atranorin. Microphyllinic acid was proven by its crystals in the GE solution and in 10 percent NaOH solution as well as by chromatography.

REPRESENTATIVE SPECIMENS EXAMINED:

JAPAN: HOKKAIDO: Prov. Ishikari: Mt. Ashibetsu, *Asahina*, 1935 (TNS, 2 collections).

HONSHU: Togakushi, *Faurie* 777, 795 (PC, 2 collections). Towada, *Faurie* 14300, 14304 (PC, 2 collections). Prov. Echigo: Iwafune-gun, Takanosu, *Togashi*, 1959 (TNS). Prov. Hitachi: Tsukuba, *Asahina*, 1924 (TNS). Prov. Inaba: Yazu-gun, Mt. Misumi, *Ikoma* 2512 (TNS). Prov. Iwashiro: Makukawa Hot Spring, *Kurokawa* 58127 (TNS, US). Prov. Kai: Mt. Fuji, Yoshida-guchi, *Hisauchi*, 1928 (TNS). Prov. Kii: Mt. Koya, *Asahina & Togashi*, 1957 (TNS); the same, *Numajiri*, 1926 (TNS, 3 collections). Prov. Kotsuke: Mt. Akagi, *Yasuda* (W). Prov. Mikawa: Mt. Horaiji, Park Iwagoya, *Asahina et al.*, 1960 (TNS). Prov. Musashi:

Mine-no-Yakushi, *Asahina*, 1939 (TNS); Chichibu, Mt. Ryogami, *Kurokawa* 550571 (TNS). Prov. Rikuchu: Mt. Hayachine, Monma-guchi, *Kurokawa* 59275 (TNS). Prov. Sagami: Hakone, Mt. Futago, *Asahina*, 1952 (TNS); Motohakone, *Asahina*, 1924 (TNS). Prov. Settsu: Mt. Myoken, *Ui*, 1935 (TNS). Prov. Shinano: Mt. Yatsu-ga-take, *Kurokawa* 51196, 51197, 51198 (TNS); Pass Kitazawa, Hattyo-zaka, *Asahina*, 1937 (TNS); Mt. Nyugasa, Yoshioka, 1937 (TNS). Prov. Suruga: Mt. Fuji, Omiyama-guchi, 3-2-gome, *Togashi*, 1961 (TNS); Fujiyama, *Faurie* 519 (PC). Prov. Tanba: Minamikuwata-gun, Sogabe-mura, *Togashi*, 1956 (TNS). Prov. Wakasa: Mt. Aoba, *Togashi*, 1956 (TNS, 2 collections). Prov. Yamato: Omine-san, Mt. Sanjo-ga-take, *Togashi*, 1952 (TNS).

Shikoku: Prov. Awa: Mt. Ken-zan, *Fujikawa*, 1934 (TNS). Prov. Tosa: Between Mt. Tsutsujo and Mt. Tebako, *Iwatsuki* 1804 (TNS).

Kyushu: Prov. Bungo: Mt. Urahiko, *Komura*, 1951 (TNS). Prov. Buzen: Mt. Hikosan, *Komura* 984 (TNS). Prov. Higo: Mt. Ichibusa, *Fujikawa*, 1933 (TNS). Prov. Hizen: Mt. Unzen, Nodake, *Asahina & Togashi*, 1958 (TNS). Yakushima, Kosugidani, *Omura*, 1950 (TNS).

KOREA: Prov. Kei-nan: Mt. Chi-san, *Sato* 331a (MSC).

FORMOSA: Prov. Ilan: Piyanan Pass, 1,100–1,300 m., *Kurokawa* 741 (TNS).

SABAH (BORNEO): Kinabalu National Park, from Mesilau River to Kundason, along Mesilau Trail, *Hale* 29269 (US).

JAVA: Res. Pasoeroean, Goenoeng Ardjoena, Tretes-Lalidjiwa-track, *Du Rietz* 95:16 (UPSV).

**10. Cetrelia nuda** (Hue) Culb. & Culb., comb. nov. PLATE 18

*Platysma collatum* f. *nudum* Hue, Nouv. Arch. Mus., IV, 1:208. 1899. Type: Japan, Fujiyama, *Faurie* 569 (PC, lectotype).

*Cetraria collata* f. *nuda* (Hue) Zahlbr., Catal. Lich. Univ. 6:285. 1930.

*Parmelia yunnana* Hue f. *subnuda* Zahlbr., Hedwigia 74:210. 1934. Type: China, Lidjiang Snow Range, 11,300–12,000 ft., *Rock*, 1931 (W, holotype).

Thallus large, 16–24 cm. broad; lobes 0.6–1.8 cm. broad. Upper surface grayish or ashy-white, smooth, pseudocyphellate, the pores large, conspicuous, irregular, becoming confluent, the largest aggregates exceeding 1 mm. Lower surface black, the margins of some lobes similar in color to the upper surface, wrinkled in part and, if very rugose, with puncta on the crests of the folds. Upper cortex 16–31$\mu$ thick; medulla 130–186$\mu$ thick; lower cortex 16–22$\mu$ thick. Apothecia very common, submarginal to superficial, perforate, irregular at maturity, 1.3–1.5 cm. broad. Spores 8, ovoid, 14–16$\times$6–10$\mu$. Pycnidia always present, large, often pruinose, marginal or at times superficial; conidia 1$\times$5–7$\mu$, rod-shaped, the ends slightly inflated.

Medullary reactions.—K−, C−, KC+ pink, PD−.

Constituents.—Alectoronic and $\alpha$-collatolic acids and atranorin.

Distribution (Map, Figure 17).—Widely distributed in the islands Honshu, Shikoku, and Kyushu in Japan and the high mountains of Formosa and Yunnan; locally common on tree trunks and over boulders.

In Japan this species is often conspicuous because of its broad lobes speckled with aggregate pseudocyphellae and its large thallus. The negative reaction of the medulla with C will distinguish it from *Cetrelia* *davidiana* and *C. sanguinea*; from *C. collata*, which contains imbricaric acid, the only certain identification is based upon the microchemical demonstration of the alectoronic and/or α-collatolic acids of *C. nuda*. *Cetrelia alaskana* and *C. delavayana*, which may superficially resemble *C. nuda*, differ chemically in producing imbricaric acid and morphologically in having tiny pseudocyphellae rather than large, aggregate ones. Some specimens of *C. braunsiana* with poorly developed isidia may resemble *C. nuda*, but they have very small pseudocyphellae.

This taxon has been recognized in Japan as *Cetraria collata* f. *nuda* (Hue) Zahlbr., and its taxonomy has been confused with that of *Cetrelia chicitae* (the "*Cetraria collata* f. *isidiata*" of the Japanese literature). The reasons for recognizing these three variations as species are discussed in the treatment of *Cetrelia braunsiana* (see p. 495).

*Cetrelia nuda* is the only species in the genus for which any information on the physiological ecology is available. Hosokawa and his coworkers (1964) reported that in this lichen, called *Cetraria collata* f. *nuda* in their paper, apparent photosynthesis increases both with increasing light and increasing relative humidity, the maximum photosynthesis as measured by carbon dioxide uptake being at 50,000 Lux and 90 percent relative humidity. They believe that these results correlate well with their observation that in closed forests *Cetrelia nuda* occurs primarily in the crowns as opposed to the trunks or the bases of the trees. Cryptogams habitually more abundant at lower levels in the same study sites, they showed, have maximum rates of photosynthesis at much lower light intensities—for example, at about 10,000 Lux for the moss *Thuidium cymbifolium* Doz. & Molk., an inhabitant of the tree base. Furthermore, at high light intensities, *C. nuda* carries on appreciable photosynthesis even when the relative humidity is reduced to 70 to 80 percent. These data would seem to indicate that *C. nuda* has very high light requirements and yet is also at least somewhat adapted to effective photosynthesis at the lower relative humidities that are encountered in places of high illumination.

CHEMICAL ANALYSIS.—All 22 samples of this species tested contained atranorin and alectoronic acid. Twenty of the samples tested also contained α-collatolic acid. Crystals of atranorin were observed in the GA*o*-T solution and sometimes in the GE solution. The substance was also demonstrated chromatographically. Alectoronic acid and α-collatolic acid in mixture were detected by chromatography after observing the crystals in the GE and GAW solutions. Many samples were also checked with 10 percent NaOH to verify the absence of microphyllinic acid.

NOMENCLATURE.—Hue considered this to be a forma of *Platysma collatum*, which he believed to be a sorediate species.

REPRESENTATIVE SPECIMENS EXAMINED:

JAPAN: HONSHU: Onikobe, *Faurie* 283 (PC). Togakushi, *Faurie* 777 (*pro parte*) (PC, 2 specimens). Prov. Aki: Yamagata-gun, Furuyashiki-Mt. Osoreranka, *Kotake*, 1956 (TNS). Prov. Izu: Mt. Amagi, *Asahina*, 1927 (TNS). Prov. Kai: Pass Syosen, *Kurokawa* 521285 (TNS). Prov. Kii: Mt. Koya, *Numajiri* 699 (TNS). Prov. Kozuke: Mt. Akagi, *Asahina*, 1935 (TNS). Prov. Musashi: Chichibu, Mt. Ryogami, *Kurokawa* 550572 (LD, TNS); Nippara, Pass Sengen, *Asahina* 71a (TNS); Mt. Shiroiwa, *Kurokawa* 50380B, 50431B, 510274 (TNS). Prov. Mutsu: Kise, *Murai*, 1933 (TNS). Prov. Sagami: Hakone, Owaku-dani, *Watanabe*, 1955 (TNS). Prov. Shimotsuke: Nikko, *Faurie* 577 (PC); Nikko, Yumoto, *Asahina*, 1952 (TNS). Prov. Shinano: Shibunoyu, Mt. Yatugatake, *Kurokawa* 58197 (MSC). Prov. Suruga: Fujiyama, *Faurie* 508 (*pro parte*), 569 (PC); Mt. Fuji, Omiya-guchi, 2-gome, *Asahina*, 1925, 1926, 1932, 1934 (TNS, 7 collections); Mt. Fuji, Umagayeshi, *Almquist*, 1879 (S). Prov. Yamato: Mt. Omine, Yosigayado, 1,600 m., *Tagawa* 269 (TNS).

SHIKOKU: Prov. Awa: Mt. Ken-zan, *Togashi*, 1956 (TNS). Prov. Iyo: Kitauwa-gun, Mt. Nametoko, *Ogata*, 1928, 1930 (TNS, 2 collections). Prov. Tosa: Mt. Tsutsujo-Mt. Tebako, *Iwatsuki* 1787, 1806, 1811 (TNS).

KYUSHU: Prov. Bungo: Mt. Kuro-dake, *Omura*, 1950 (TNS). Prov. Buzen: Shimoge-gun, Mt. Ura-hiko, *Omura*, 1951 (TNS). Prov. Higo: Mt. Ichibusa, *Fujikawa*, 1933 (TNS).

FORMOSA: Mt. Ali, 2,200 m., *Kurokawa* 13, 37 (TNS); Mt.Tsu-Tson-San, Mt. Ali, 2,300–2,900 m., *Kurokawa* 122 (TNS).

CHINA: YUNNAN: Kou-toui, above Mo-so-yn, 3,000 m., *Delavay*, 1887 (PC); Schweli-Salween-Scheidegebirge, 25°45′N, 2,000–2,800 m., *Gebauer*, 1914 (WU); Mekong-Salween-Scheidegebirge, 26°10′N, *Gebauer*, 1914 (W; WU, 2 collections).

**11. Cetrelia olivetorum** (Nyl.) Culb. & Culb., comb. nov. PLATE 18

*Parmelia olivetorum* Nyl., Not. Sällsk Fauna Fl. Fenn. Förhandl., n. ser. 5:180. 1866. Type: Switzerland, collector unknown, s.d. (H-Herb. Acharius, lectotype).

*P. perlata* f. (?) *rubescens* Th. Fr., Lich. Scand. 112. 1871. Type: Switzerland, collector unknown, s.d. (H-Herb. Acharius, lectotype).

*P. rubescens* (Th. Fr.) Vain., Bot. Mag. [Tokyo] 35:47. 1921.

*P. cetrarioides* var. *rubescens* (Th. Fr.) Du Rietz, Nyt Mag. Naturv. 62:75. 1924.

*Pseudoparmelia aradensis* Gyeln., Acta Fauna Fl. Univ., ser. 2 Bot. [Bucareşti] 1(5–6):6. 1933. Type: Rumania, Arad, *Kümmerle & Jávorka* (BP, holotype).

*Parmelia olivaria* f. *subvenosa* Gyeln., Repert. Spec. Nov. Fedde 36:302. 1934. Type: Hungary, prope Budapest, *Timkó* (BP, holotype).

[Not *P. perlata* β *olivaria* Ach., Meth. Lich. 217. 1803.]

[Not *P. perlata* β *olivetorum* Ach., Lichenogr. Univ. 458. 1810.]

Thallus small to medium, 6–14 cm. broad; lobes 0.5–1.8 cm. broad. Upper surface light tan or brownish, smooth, sometimes slightly convex, pseudocyphellate, the pores abundant and very small, rarely exceeding 0.5 mm.; the margins of most lobes with dense, fine soredia. Lower surface black, the margins chestnut brown or colored like the upper surface, rarely punctate; rhizines few, black. Upper cortex 19–31$\mu$ thick; medulla 96–239$\mu$ thick; lower cortex 16–25$\mu$ thick. Apothecia rare (unknown in Asian specimens), 0.1–0.7 cm. broad, not perforate;

hymenium 62–109$\mu$ thick; subhymenial layers 62–84$\mu$ thick, the proper exciple underlain by a thick layer of algae. Spores ellipsoid, 12–15 × 7–10$\mu$. Pycnidia unknown.

MEDULLARY REACTIONS.—K−, C+ pink or red, PD−.

CONSTITUENTS.—Olivetoric acid and atranorin.

DISTRIBUTION (Map, Figure 7).—Appalachian Mountains and northeastern United States and adjacent Canada; southern Scandinavia to the high mountains of southern Europe; high mountains of southwestern China, Formosa, and Japan; over boulders and on tree trunks.

Although *Cetrelia olivetorum* is very closely related to *C. cetrarioides* and *C. chicitae*, it can almost invariably be distinguished from them by the experienced eye. The sum total of its small, difficult-to-describe yet distinctive traits—the slightly convex lobes, the abundant but extremely minute pseudocyphellae, the extremely fine but abundant marginal soredia, and the total lack of laminal soredia—makes it possible to name most specimens at sight. In the southern Appalachians, where this species can be found growing on the same boulders with *C. chicitae*, it almost invariably shows tinier pseudocyphellae and a slightly different habit than the latter species. Nevertheless, some individuals of *C. chicitae* and *C. olivetorum* are so similar that chemical tests are required for positive identifications. *Cetrelia olivetorum* can be distinguished by its distinctive, pinkish-rose medullary reaction with C due to the presence of olivetoric acid. *Cetrelia cetrarioides* produces perlatolic acid or imbricaric acid and *C. chicitae* produces alectoronic and $\alpha$-collatolic acids, explaining why neither of the species gives a positive reaction with C.

The lack of information about the precise range of this species is in part due to the fact that it is relatively rare and in part because it has been mistaken for the commoner *Cetrelia cetrarioides*. The species seems to be restricted to regions of relatively cool summers and ample rainfall. In all but the northern part of its range, these conditions are met with only at higher elevations and all the southern stations of the species are in mountains. The species usually grows with bryophytes over shaded boulders or on the trunks of trees in moist forests.

The American range is the most accurate part of the map of the total world distribution (Figure 7). Ahti (1964) made a detailed study of the region between the north shore of Lake Superior and Hudson Bay. He records the species from a single locality a little over 100 miles north of the northernmost locality mapped and notes that the lichen there is "rare." Lynge (1921) records a few localities in southern Norway and Du Rietz (1924) and Hakulinen (1963) attribute it to Finland but without citing precise localities. Records for the southern part of the range in Europe are doubtless nearly accurate, the localities corresponding to the higher mountains there.

Generalizations about the distribution in Asia are impossible, yet it seems significant that very few specimens from Japan are present in herbaria in spite of intensive lichenological collecting in that country. On the other hand, a fairly large number of well developed specimens are known from the high mountains of Yunnan Province, and the species may achieve its maximum abundance in Asia in southwestern China.

The frequency with which *Cetrelia olivetorum* has been found mixed with *C. cetrarioides* in packets in herbaria indicates that these species often grow together in nature and doubtless have a very similar physiological ecology.

CHEMICAL ANALYSIS.—All 19 samples tested contained atranorin and olivetoric acid. Olivetoric acid was readily identified in most samples by its crystals in the GE, GAW, and GA*o*-T solutions. To avoid confusion with anziaic acid, all extracts were also checked chromatographically. Physodic acid, known to occur with olivetoric acid in *Cetraria ciliaris* (C. F. Culberson, 1964), was not found in any of the samples of *Cetrelia olivetorum* tested.

NOMENCLATURE.—The specific epithet *olivetorum* is a variation of the earlier Acharian epithet *olivaria* which alluded to the olive trees in southern Europe from which the (different) plants originally called *olivaria* reputedly came. The present species does not grow in the olive region of Europe and the name is wholly inappropriate. It might be noted, however, that olivetoric acid, the characteristic constituent of the medulla of this species, was extracted for the first time from *Cetrelia olivetorum* and was named for it.

The name *olivetorum* has been a source of considerable confusion inasmuch as Acharius and Nylander both used it at different ranks for different taxa. Acharius (1803) named a broad-lobed *Parmelia* from olive trees *P. perlata β olivaria* Ach. and later, for some reason, referred to the same taxon as *P. perlata β olivetorum* Ach., placing the earlier epithet *olivaria* as a synonym (Acharius, 1810). In 1866 Nylander used the epithet *olivetorum* at the species rank and indicated Acharius as the originator of the name although he used it for a taxon different from the one for which Acharius had coined it.

The appropriate sheet in the Acharian herbarium contains three specimens, the illegitimate varietal name *olivetorum* of Acharius being written closest to one which appears to be *Parmelia reticulata* Tayl., a species which could have been collected on olive trees in Europe although its geographic origin is not given. The medulla of this specimen is C−. Both of the other specimens belong to the species under consideration here; their medullary reaction is C+ red, and the larger specimen is labeled "Helvetia." Since *Cetrelia olivetorum* does not grow in the olive zone of Europe, neither of the two Swiss specimens can be associated with the Acharian epithets *olivaria* or *olivetorum*. These two specimens, with their distinctive medullary reactions with C, are surely the ones Nylander referred to in his diagnosis of *Parmelia olivetorum*: "Ach. ex hb. ipsius, cui speciei medulla thalli ope hypochloritis calici erythrinice tingitur." The binomial *Parmelia olivetorum* must be attributed to Nylander alone (Art. 72) and typified upon one of the C+ specimens. The larger specimen labeled "Helvetia" is the lectotype. This specimen is also designated as the lectotype of *P. perlata* f. (?) *rubescens*, a taxon described apparently as a forma by Th. Fries who seems to have understood the nomenclatural history of the *olivetorum* names in spite of the solution that he offered by proposing another name altogether.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.A.: MAINE: Knox Co.: Rockland, *Merrill, Lich. Exs.* 99 (DUKE). York Co.: Kennebunkport, *Pier*, 1917 (UC, DUKE).

NEW HAMPSHIRE: Cheshire Co.: Alstead, *Seymour*, 1921 (UC, DUKE). Grafton Co.: North Woodstock, collector unknown (DUKE).

VERMONT: Caledonia Co.: McIndoe's Falls, *Bliss*, 1918 (DUKE).

NEW YORK: Essex Co.: Wilmington, *Brodo* 499 (DUKE).

PENNSYLVANIA: Monroe Co.: Mt. Pocono, *Kaiser* 1910 (DUKE).

WEST VIRGINIA: Pocahontas Co.: Gaudiner Knob, *Hale, Lich. Amer. Exs.* 56 (UC).

VIRGINIA: Giles Co.: Mountain Lake, *Culberson* 11180, 11238 (DUKE). Madison Co.: Shenandoah National Park, *Hale* 19213 (*pro parte*) (US). Page Co.: Little Stony Man Cliffs, Shenandoah National Park, *Hale* 19219 (US); Skyline Drive, Crescent Rocks, *Hale* 18167 (US).

NORTH CAROLINA: Avery Co.: Near the Avery-Caldwell County line, *Culberson* 11770 (DUKE). Rockbridge Co.: Mile 35, Blue Ridge Parkway, *Hale* 17813 (US).

OHIO: Locality unknown, *Sullivant* (CB).

MICHIGAN: Isle Royale: Rock Harbor, *Harper* 160 (UC, DUKE).

WISCONSIN: Langlade Co.: Langlade, *Culberson* 2007 (DUKE). Price Co.: Park Falls, *Culberson* 1814 (DUKE).

JAPAN: Prov. Echigo: Sasa-ga-mine, *Togashi*, 1950 (DUKE).

FORMOSA: Mt. Ali, Mt. Tsu-Tson-san, 2,300–2,900 m., *Kurokawa* 133 (TNS). Prov. Nantoh, Lisan, *Kurokawa* 880 (TNS).

CHINA: SZECHWAN: Mt. Lose-schan, south of Nengyüen, 3,950 m., *Handel-Mazzetti* 1441 (W).

YUNNAN: Lenago Pass between Mekong and Yangtze, 27°43′ N, *Gebauer*, 1914 (W, WU); Fang-Yang-Tchang, above Mo-To, *Delavay*, 1887 (PC); Long, above Ta-pin-tze, *Delavay*, 1887 (PC); Koua-la-po, *Delavay* 1595 (*pro parte*) (PC); Hee-chan-men, *Delavay*, 1887 (PC); Yen-tze-hay, *Delavay*, 1887 (PC, 2 collections).

NEPAL: Above Sauwala Khola, 10,500 ft., *Stainton et al.* 43796 (*pro parte*) (BM).

RUMANIA: TRANSYLVANIA: Hunyad, *Lojka* (PC); Arad, *Kümmerle & Jávorka*, s.d. (BP).

POLAND: Bieszczady Zachnodnie Mountains, Puszcza Bukowa, Mt. Paportna, 810 m., *Glanc*, as *Tobol., Lichenoth. Polonica* 174 (DUKE).

HUNGARY: Near Budapest, m. Nagyhárshegy, *Timkó* (BP).

SWITZERLAND: Léman, collector unknown (PC).

GERMANY: BAVARIA: München, *Arnold, Lich. Monacensis Exs.* 324a,b, *Arnold, Lich. Monacensis Exs.* 6 (PC).

FRANCE: CÔTES-DU-NORD: Forêt de Lorges, *des Abbayes*, 1929 (Herb. des Abbayes).

FINISTÈRE: Forêt de Cranou, *des Abbayes*, 1933 (Herb. des Abbayes).

HAUTES-PYRÉNÉES: Cauterets, *Lamy de la Chapelle* (PC).

12. **Cetrelia pseudolivetorum** (Asah.) Culb. & Culb., comb. nov. PLATE 19

*Parmelia* (*Amphigymnia*) *pseudolivetorum* Asah., Journ. Jap. Bot. 27:16. 1952. Type: Japan, Mt. Fuji, *Asahina* (TNS, holotype).

Thallus small to large, 0.7–18.0 cm. broad; lobes 0.5–1.5 cm. broad. Upper surface grayish or grayish-white or uniformly light brownish or tan in old herbarium specimens, smooth or becoming cracked, pseudocyphellate, the pores small, to 0.5 mm. broad, punctiform or slightly elongate, the margin and occasionally the surface with granular, simple or coralloid isidia, often grading into dorsiventral, dissected lobulae. Lower surface black, the margins brown or colored like the upper surface, not punctate; rhizines few, black. Upper cortex 16–30μ thick; medulla 150–200μ thick; lower cortex 11–17μ thick. Apothecia very rare, 0.4–1.7 cm. broad, mostly perforate; hymenium 53–78μ, hyaline; subhymenial layers 40–53μ thick. Spores 8, ellipsoid, (11–)16–22× 9–12μ. Pycnidia unknown.

MEDULLARY REACTIONS.—K–, C+ pink, P–, UV–.

CONSTITUENTS.—Olivetoric acid and atranorin.

DISTRIBUTION (Map, Figure 9).—The mountains of central Japan, Formosa, and Yunnan, China, and the Himalayas; usually on rock or over boulders with bryophytes.

*Cetrelia pseudolivetorum* has a pink medullary reaction with C due to the presence of olivetoric acid thereby distinguishing it from the two morphologically similar species for which it would most probably be mistaken, *C. japonica* (with microphyllinic acid) and *C. sinensis* (with imbricaric acid). In reality, though, the bulk of the specimens of *C. pseudolivetorum* differ morphologically from these species (see the discussion of *C. japonica*, pp. 511–512).

Some forms of *Cetrelia pseudolivetorum* with isidia or isidioid lobulae instead of the expanded dorsiventral lobulae more typical of the species might be mistaken for the common Japanese species *C. braunsiana*. The latter species has very delicate coralloid isidia and is C– but KC+ because of its production of alectoronic acid. The two species can usually be distinguished without the need of chemical thallus spot tests, however.

*Cetrelia pseudolivetorum* might also be mistaken for some rare forms of *C. sanguinea* with well-developed lobulae. If it has small marginal isidia, it might be mistaken for *C. isidiata*. Both these species give a red (rather than a pinkish) medullary reaction with C and both produce anziaic acid rather than the olivetoric acid.

Although chemically identical, *Cetrelia olivetorum* and *C. pseudolivetorum* are morphologically distinct. The margins of *C. olivetorum* have extremely fine, powdery, white soredia while those of *C. pseudolivetorum* have isidioid lobulae or similar outgrowths. There are no integradations between the two species although badly damaged specimens of *C. pseudolivetorum*, in which the delicate marginal appendages have been broken off exposing the white medulla, might be mistaken for *C. olivetorum*.

*Cetrelia pseudolivetorum* shows considerable variability, but the variation is so continuous that there is no reason to suspect that the population is not sufficiently uniform to be considered a single species. Forms with coralloid marginal isidia recalling those of *C. braunsiana* may be found, while in other extreme variants the marginal outgrowths take the form of the exaggerated, expanded, dorsiventral lobulae of certain forms of *C. japonica* and *C. sinensis*. But all the intergradations are present as well, and these minor variations need not be reflected in the taxonomy.

This species is restricted to the mountains of southern and southeastern Asia and Japan. The elevation data for the known localities indicate a vertical range of about 1,500–3,600 m. with most of the specimens coming from about 2,000–3,000 m. Unfortunately the labels of the specimens give few habitat data, but when a substrate has been noted, it is usually rock. In reality, however, the habitat ecology of this species is probably very similar to that of others in the genus. For example, a particularly rich collection made on shrubs at about 10,500 feet in Nepal by Stainton, Sykes, and Williams consisted of a mixture of *Cetrelia pseudolivetorum*, *C. olivetorum*, *C. braunsiana*, and *C. collata*. Or it might be that distinct ecological races with regard to substrate preference exist in some correlation with the morphological plasticity noted above. Systematic field studies might be expected to elucidate this point.

CHEMICAL ANALYSIS.—Thirty-one samples of this species were tested in the same manner as described for *Cetrelia olivetorum*. All contained atranorin and olivetoric acid.

REPRESENTATIVE SPECIMENS EXAMINED:

JAPAN: Prov. Shinano: Lake Shirakaba, *Asahina* 58505 & *Togashi* (DUKE); Mt. Norikuratake, *Asahina* 52805 (TNS). Prov. Shimotsuke: Nikko, Chuzenji, *Nakaji* 2510 (TNS). Prov. Suruga: O-miya-guchi, 1-go-han, Mt. Fuji, *Asahina* 34125 (TNS); Lake Saiko (Nishi-no-umi), near Mt. Fuji, *Culberson* 10078, 10643 (DUKE).

FORMOSA: Mt. Ali, Mt. Tsu-Tson-San, 2,300-2,900 m., *Kurokawa* 121, 134, 137 (TNS). Between Su-Su-Lu and Mt. Ali, 200-2,200 m., *Kurokawa* 611 (TNS). Mt. Nan-Fu-Ta-San, 1,500-2,400 m., *Kurokawa* 928 (TNS). Mt. Shin-Kao-San, Mt. Shi-San, 3,300-3,600 m., *Kurokawa* 332 (TNS); the same, 3,100-3,300 m., *Kurokawa* 253 (TNS); Pianan to Sunlien, *S. Asahina* 3608 (TNS).

CHINA: Moupin (eastern Tibet). Without precise locality, *David* 1869 (PC, 2 collections).

YUNNAN: Tsang-chan, above Ta-li, 4,000 m., *Delavay*, 1885 (PC, 2 collections); the same, *Delavay*, 1888 (PC, 3 collections); Yen-tze-hay, 300 m., *Delavay*, 1887, (PC); Hee-chan-men, *Delavay*, 1887 (PC); Fang-Yang-Tchang, above Mo-so-yn *Delavay*, 1887 (PC); Lopin-chan Pass, 3,200 m., *Delavay*, 1888 (PC); Lopin-chan Pass, above Lan-Kong, *Delavay*, 1888 (PC, 2 collections); Lopin-chan Pass, *Delavay*, 1888 (PC).

SIKKIM: Wallanchoon, *Hooker* 2087 (K).

INDIA: Chakrata, *Awasthi* 501 (H).

NEPAL: Above Sauwala Khola, 10,500 ft., *Stainton et al.* 4379b (*pro parte*) (BM).

**13. Cetrelia sanguinea** (Schaer.) Culb. & Culb., comb. nov. PLATE 19

*Cetraria sanguinea* Schaer. *in* Moritzi, Zoll., Syst. Verz. Java Pflanz. 129. 1845–1846 (1846). Type: Java, Mt. Pangerano, *Zollinger*, 1842–1844 (G, holotype).

*Imbricaria sanguinea* (Schaer.) Schwend. *in* Naegeli, Beitr. Wiss. Bot. 3:159. 1863.

*Platysma sanguineum* (Schaer.) Hue, Ann. Jard. Bot. Buitenzorg 17:177. 1901.

*Parmelia megaleia* Nyl., Synops. Lich. 1:378. 1860. Type: Java, *Junghuhn* (PC, lectotype).

*Platysma megaleium* (Nyl.) Nyl., Flora 52:290. 1869.

*Imbricaria megaleia* (Nyl.) Jatta, Nuov. Giorn. Bot. Ital., n. ser. 9:469. 1902.

*Platysma subperlatum* Nyl., Flora 49:130. 1866. Type: Java, Togoe, *Kurz*, 1861 (H-Herb. Nylander, lectotype).

*Aspidelia wattii* Stirt., Trans. & Proc. New Zealand Inst. 32:82. 1899 (1900). Type: Himalayas, *Watt* 7070 (BM). (Invalidly published; cf. Culberson, 1966a).

Thallus medium to large, 11–24 cm. broad; lobes 0.5–1.5 cm. broad. Upper surface whitish or tan, brownish in old herbarium specimens, sometimes brownish or blackish toward the margins, smooth to minutely wrinkled, pseudocyphellate, the pores small, rarely more than 0.5 mm. broad and often inconspicuous or even lacking altogether on some lobes, the margins of the lobes entire to sometimes minutely lacerate or beset with lobulae. Lower surface jet-black, the margins often dark brown, not punctate; rhizines few, black. Upper cortex 16–25μ thick, impregnated with a noncrystalline brown pigment; medulla 93–170μ thick; lower cortex 16–28μ thick. Apothecia frequent, very large, perforate, cup-shaped when young, irregularly expanded and radially lacerate with maturity, 1.5–4.2 cm. broad, the thalloid exciple densely pseudocyphellate; hymenium 60–93μ thick; subhymenial layers 43–61μ thick, impregnated with a yellow pigment turning reddish brown with $FeCl_3$. Spores 8, 17–22×9–14μ, the spore wall about 2μ thick. Pycnidia large, marginal; conidia 1×4μ, rod-shaped.

MEDULLARY REACTIONS.—K−, C+ bright red, PD−.

CONSTITUENTS.—Anziaic acid and atranorin.

Distribution (Map, Figure 15).—In the high mountains of Japan, southwestern China, Java, and Sumatra; on the bark of trees and shrubs.

While *Cetrelia sanguinea* resembles a number of other species in habit, the one for which it might most easily be mistaken is *C. davidiana*, the only closely related C+ species. In *C. davidiana*, however, the reaction produces a pink coloration instead of the red one characteristic of *C. sanguinea* and reflects the presence of olivetoric acid rather than anziaic acid. Of course, microchemical or chromatographic analyses are required for a precise determination of the substance responsible for positive reactions with C and critical taxonomic identifications here should not be made without them.

A single Japanese collection containing anziaic acid closely resembles many of the plants of *Cetrelia sanguinea* from Java where the species has been the most extensively collected. It lacks apothecia and has marginal lobulae somewhat resembling those of *C. japonica*. A chemical study of the many specimens referred to *C. japonica* in herbaria upon the basis of gross morphology alone might well extend the known Japanese range of *C. sanguinea*.

In restricted areas within its range the species may be very common. For example, there are many specimens in herbaria from Mt. Pangerango, the type locality, where collections of the species have repeatedly been made incidental to other explorations, an apparent testimony to the abundance and conspicuousness of the lichen there. From labels giving elevation data, the species in the East Indies seems to be found between 1,400 and 3,800 m., most of the specimens coming from about 3,000 m. The Japanese specimen is also from a mountain locality.

Chemical analysis.—The species is very uniform in the lichen substances produced. Of the 67 specimens tested microchemically, all produced atranorin and anziaic acid. Atranorin was usually observed in the GAo-T solution, and the absence of the colorless needles formed by olivetoric acid in this solution was noted. Some samples also showed atranorin in the GE solution. Anziaic acid usually crystallized from the GAW solution, but less often also from the GE solution. All extracts were chromatographed to verify the presence of atranorin and anziaic acid. The crystals of anziaic acid in the GAW solution were quite variable, but no additional compounds were suspected on the basis of the chromatographic results.

The apothecia of this species may contain a yellow pigment (not usnic acid) which was not identified.

The generic name *Aspidelia* Stirt., under which Stirton included the description of a species based upon a specimen referable to *C. sanguinea* (see synonymy above), was published without a generic description and is thus invalid and cannot be taken up for *Cetrelia* or for any other genus (Culberson, 1966a).

ADDITIONAL SPECIMENS EXAMINED:

JAPAN: HONSHU: Mt. Osore-san, *Sato,* 1935 (H).

JAVA: Mt. Pangerango, 3,000 m., *Möller,* 1897 (LD, S); the same, *Poch,* 1906 (WU); the same, 2,500 m., *Schiffner* 3007 (M); the same, 3,050 m., *Hochreutiner* 936 (G); Mt. Gede, *Karsten,* s.d. (TUR); the same, 2,400 m., *Hochreutiner* 876 (G); Tjibodas, Mt. Gede, 1,400 m., *Palmer & Bryant* 822 (US); Mt. Ardjoeno, 3,800 m., *Groenhart* 160 (H); Res. Pasoeroean, Goenoeng Ardjoena, track from Lalidzina to Ardjoeno-top, *Du Rietz* 18a:1, 18a:2, 24:4, 51:3 (UPSV); the same, Lalidjina-Welirang-track, *Du Rietz* 54:3, 60:3, 60:4, 60:5, (UPSV); the same, Tretes-Lalidjina-track, *Du Rietz* 95:7, 95:17a, 95:17b, 99:1 (UPSV); and the same, *Skottsberg* 1929 (UPSV, 14 collections).

SUMATRA: Mt. Singalang, 2,500 m., *Schiffner* 3441 (W, WU).

CHINA: YUNNAN: Mekong-Salween-Scheidegebirge, *Gebauer,* 1914 (W).

PAKISTAN(?): Himalayas, Lingalelah Range, 12,000 ft., *Watt* 7070 (BM).

**14. Cetrelia sinensis** Culb. & Culb., sp. nov. PLATE 20

Thallus maximus, 17–26 cm. latus; laciniae 1–2 cm. latae, marginibus dense instructae vel planta tota saepe cristata lobulis palmatis vel subpalmatis, vel angustis et isidioideis, vel expansis et foliosis. Superficies superior aequaliter pallide cinerea (albida apud plantas vivas?), levis, pseudocyphellata, pseudocyphello punctato vel nonnihil elongato parvae (ca. 0.5 mm. latae). Superficies inferior picea, marginibus ad extremos lacinianum pallida, non punctata; rhizinae nigrae. Cortex superior 19–28$\mu$ crassus, subprosoplectenchymatosus, strato corticali summo ferrungineo-colorato, medulla 140-183$\mu$ crassa; cortex inferior 16–22$\mu$ crassus. Apothecia ignota. Pycnidia magna, nigra, in marginibus laciniarum; conidia 1.5×6$\mu$, recta.

Thallus large to very large, 17–26 cm. broad; lobes 1–2 cm. broad, the margins densely fringed with palmately or subpalmately divided lobulae, narrow and isidioid or more broadly expanded and lobelike, so dense that the specimens may appear cristate. Upper surface uniformly light brown (perhaps grayish-white when fresh), smooth, pseudocyphellate, the pores punctiform or somewhat elongate, very small (ca. 0.5 mm. broad). Lower surface jet-black, a marginal zone near the tips of the lobes colored like the upper surface, apparently not punctate; rhizines black. Upper cortex 19–28$\mu$ thick, subprosoplectenchymatous and essentially pseudoparenchymatous, the upper part of the cortex suffused with a brownish, noncrystalline pigment; medulla 140–183$\mu$ thick; lower cortex 16–22$\mu$ thick, prosplectenchymatous. Apothecia unknown. Pycnidia large, black, restricted to the marginal lobulae; conidia 1.5 × 6$\mu$, rod-shaped.

TYPE.—"Sur les pierres dans les bois aux sources du Lan-Kien-ho, près du col Hee-chan-men," Yunnan, China, *Delavay* 30 (PC, holotype).

MEDULLARY REACTIONS.—K−, C−, KC−, PD−.

CONSTITUENTS.—Imbricaric acid and atranorin.

DISTRIBUTION (Map, Figure 18).—High mountains of Yunnan, China, and Formosa; over boulders (and on trees?), apparently very rare.

Since this species is known from only two collections, it is not possible to assess its morphological variability. It appears, however, that it may not be different morphologically from *Cetrelia japonica,* which contains microphyllinic acid. *Cetrelia sinensis* must be identified by the presence of imbricaric acid. See the discussion for *Cetrelia japonica* (p. 511) for a further discussion of morphologically similar species and their distinguishing characteristics.

CHEMICAL ANALYSIS.—The six known specimens (from two collections) of the species were tested and all contained imbricaric acid and atranorin. Hydrolysis of the residues from two samples and chromatography of the products show a faint spot at a position corresponding to olivetol-2-carboxylic acid. It may or may not be due to the presence of perlatolic acid.

ADDITIONAL SPECIMENS EXAMINED:

FORMOSA: Mt. Shin-Kao-San, Mt. Shi-San, 3,300–3,600 m., *Kurokawa* 449 (TNS).

CHINA: YUNNAN: Lan-Kien-ho near Hee-Chan-men, *Delavay* 30 (PC).

## ***Platismatia*** **Culb. et Culb., gen. nov.**

Thallus 5–18(–23) cm. latus; laciniae (0.1–)0.3–2.2(–2.5) cm. latae. Superficies superior pallide cinerea vel citrella, viridiolivacea, vel apud exemplaria vetera herbarii aequaliter obscure citrella, saepe rugosa, pseudocyphellata vel isidiata sed raro sorediata. Superficies inferior nigra, rhizinata, saepe punctata. Cortex superior (15–)18–28(32)μ crassus, prosoplectenchymatosus; medulla (30–)65–210(–280)μ crassa, alba; cortex inferior (10–)13–28(–30)μ crassus. Apothecia (0.1–)0.4–1.5(–4.0) cm. lata, marginalia vel submarginalia, vulgo perforata; hymenium (34–)39–70(–125)μ crassum; asci IKI+ caerulescentes; strata subhymenialia (13–)18–50(–78)μ crassa, IKI+ caerulescentia, viridicaerulescentia, lavendulina, vel purpurea, subtus fere sine algis. Sporae 8-nae, parvae, ellipsoideae vel subglobosae, (3.5–)5–8(–10) ×3 5μ. Pycnidia marginalia, immersa, saepe deficientia; conidia rara, 1×5(–7)μ, recta, extremis non inflatis. Typus generis *P. glauca* est.

Thallus 5–18(–23) cm. broad; lobes (0.1–)0.3–2.2(–2.5) cm. broad. Upper surface ashy-white, tan, or greenish-brown (uniformly dull tan in old herbarium specimens), often rugose, pseudocyphellate in some species, isidiate in some species, rarely sorediate. Lower surface black, with few rhizines, punctate in some species. Upper cortex (15–)18–28 (–32)μ thick; medulla (30–)65–210(–280)μ thick; lower cortex (10–) 13–28(–30)μ thick. Apothecia (0.1–)0.4–1.5(–4.0) cm. broad, marginal or submarginal, commonly perforate; hymenium (34–)39–70(–125)μ, the asci IKI+ blue; subhymenial layers (13–)18–50(–78)μ thick, IKI+ blue, blue-green, lavender, or purple, usually without underlying algae. Spores 8, small ellipsoid or subglobose, (3.5)5–8(–10) × 3–5μ. Pycnidia marginal, immersed, often absent; conidia rare, 5–(7) × 1μ, rod-shaped, the ends not inflated.

CONSTITUENTS.—Atranorin and caperatic acid; fumarprotocetraric acid in one species.

Certain authors have referred some members of the *Cetraria glauca* group, which constitutes the genus *Platismatia*, to the genus *Platisma* (sometimes written as the orthographic variant "*Platysma*"). *Platisma* as a generic name has probably been associated primarily with the species *Cetraria glauca* more than with any other species, at least in the minds of most lichenologists, and we hoped that it could be used for the *Cetraria glauca* group essentially in the sense that Dahl (1952) had proposed earlier. The genus had not been typified, however, and when an exhaustive nomenclatural study of the *Platisma* names was made (Santesson and Culberson, 1966), it was impossible to typify any of them in such a way that they could be used for this or any other group of plants. The new generic name *Platismatia* is a madeup derivative from the old name *Platisma*.

### Artificial Key to the Species of *Platismatia*

1. Thallus isidiate or sorediate.
  2. Upper surface or margins of lobes isidiate or sorediose-isidiate.
    3. Some lobes becoming narrow, coralloid, fruticose appendages of the normally foliose thallus; upper surface not pseudocyphellate; lower surface not punctate.
      4. Lobes of the foliose part of the thallus expanded, commonly more than 5 mm. wide; broadly distributed . . . . . **3. P. glauca** (some forms)
      4. Lobes of the foliose part of the thallus narrow, strap-shaped, less than 5 mm. wide; northwestern North America . . **4. P. herrei** (rare forms)
    3. All the lobes broadly foliose, none becoming coralloid or fruticose; upper surface pseudocyphellate; lower surface punctate or not.
      5. Upper surface with prominent, vertical, reticulate ridges, the isidia confined primarily to the crests of the ridges; thallus IKI– ; lower surface not punctate; North America and Europe . . . . **7. P. norvegica**
      5. Upper surface without prominent reticulate ridges but often with poorly defined, interrupted ones; thallus IKI– or IKI+; lower surface punctate or not.
        6. Upper surface pseudocyphellate, IKI– or IKI+ ; lower surface punctate or not; isidia rarely on the margins of the lobes; Asia.

7. Pseudocyphellae minute, inconspicuous, usually confined to the crests of the thallus ridges; thallus surface IKI−; lower surface usually punctate; mountains of southern Asia and Japan. **1. P. erosa**
7. Pseudocyphellae large and conspicuous, round to elliptical, scattered; thallus surface IKI+; lower surface not punctate; Japan. **5. P. interrupta**
6. Upper surface not pseudocyphellate, IKI+; lower surface not punctate; isidia commonly on the margins of the lobes; America or Europe.
8. Lobes broadly foliose, not strap-shaped, commonly more than 5 mm. wide; widely distributed . . . . . . **3. P. glauca** (some forms)
8. Lobes narrow and strap-shaped, less than 5 mm. wide; northwestern North America . . . . . . . . . . . . . . . . **4. P. herrei**
2. Upper surface sorediate, not isidiate.
9. Upper surface conspicuously pseudocyphellate; Japan. **5. P. interrupta** (some forms)
9. Upper surface not pseudocyphellate; widely distributed but absent from Japan . . . . . . . . . . . . . . . . **3. P. glauca** (some forms)
1. Thallus neither isidiate nor sorediate.
10. Upper surface with sharply defined, continuous, reticulate ridges, not pseudocyphellate; medulla of American plants PD+ orange-red.
11. Medulla PD−; lower surface punctate; Formosa . . **2. P. formosana**
11. Medulla PD+ orange-red; lower surface not punctate; northwestern North America . . . . . . . . . . . . . . . . **6. P. lacunosa**
10. Thallus without sharply defined reticulate ridges but often with inconspicuous, interrupted ridges and folds or thallus pitting, pseudocyphellate or not; medulla PD−.
12. Upper surface pseudocyphellate; apothecia unknown; Asia.
13. Pseudocyphellae large and conspicuous; upper surface not commonly blackened; lower surface not punctate; Japan . . **5. P. interrupta**
13. Pseudocyphellae small; upper surface or margins commonly darkened or mottled with black; lower surface punctate; Asia.
14. Thallus surface reticulately lined, the pseudocyphellae associated with the lines; mountains of southern Asia and Japan. **1. P. erosa** (nonisidiate forms)
14. Thallus surface without conspicuous lines; the margins of some lobes blackening conspicuously; Sabah (Borneo) . . . **8. P. regenerans**
12. Upper surface not pseudocyphellate; apothecia common; North America.
15. Lobes narrow and strap-shaped, rarely reaching 5 mm. broad; western North America . . . . . . . . . . . . . . . . **9. P. stenophylla**
15. Lobes broadly expanded, usually exceeding 5 mm. broad; eastern North America . . . . . . . . . . . . . . . . **10. P. tuckermanii**

**1. Platismatia erosa** Culb. & Culb. sp. nov. PLATE 20

*Cetraria formosana* var. *isidiata* Zahlbr., Repert. Spec. Nov. Fedde 33:60. 1934. Type: Mt. Niitaka (=Mt. Morrison), Formosa, *Sasaki* (W, holotype).

Thallus mediocris, ad 11–12 cm. latus; laciniae 0.5–2 cm. latae. Superficies superior sordide citrella vel pallide grisea, marginibus laciniarum olivacea, reticulata, reticulo, saepe nigrescente; isidiata, isidiis fere raris, brevibus, pinquibus, simplicibus et in reticulo positis sed coralloideis, in marginibus laciniarum. Superficies inferior punctata, picea, marginibus fusca vel pallida; rhizinae paucae, simplices vel fasciculatae, nigrae, solum in partibus vetustioribus thalli. Cortex superior 22–26 (–28)μ crassus; medulla 50–90(–114)μ crassa, IKI—; cortex inferior 16–21(–26)μ crassus. Apothecia rarissima, ad 7 mm. lata, submarginalia, perforata; hymenium 39–47μ crassum; asci IKI+ intense caerulescentes; strata subhymenialia 21–29μ crassa, IKI+ lavendula; sporae 8-nae, ellipsoideae, 3–4×5–8μ. Pycnidia ignota.

Thallus medium, to 11–12 cm. broad, loosely attached; lobes 0.5–2 cm. broad, broadly rounded. Upper surface light tan or ashy-gray, tinged with brown at the margins of the lobes, broadly reticulately ridged and veined, the crests of the ridges often darkening, and pseudocyphellate with minute pores and often bearing isidial scars resembling pseudocyphellae; isidiate, the isidia usually infrequent, short, stout, or simple and usually confined to the ridges or thallus cracks but becoming coralloid and well developed at the margins of the lobes in some specimens. Lower surface punctate, jet-black, the marginal zone light brown or tan; rhizines few, simple or fasciculate, black, confined to the older parts of the thallus. Upper cortex 22–26(–28)μ thick; medulla 50–90(–114)μ thick, IKI—; lower cortex 16–21(–26)μ thick. Apothecia very infrequent, to 7 mm. broad, submarginal, perforate; hymenium 39–47μ thick, the asci IKI+ dark blue; subhymenium 21–29μ thick, IKI+ lavender, without underlying algae; spores 8, ellipsoid, 3–4× 5–8μ. Pycnidia unknown.

TYPE.—Yatsu-ga-take, Mount Kitayoko-dake, Province of Shinano, Japan, *Kurokawa* 58349 (TNS, holotype).

MEDULLARY REACTIONS.—K—, C—, KC—, PD—.

CONSTITUENTS.—Caperatic acid, atranorin, and an unidentified yellow pigment.

DISTRIBUTION (Map, Figure 30).—Mountains of Honshu, Japan, Formosa, Philippines, Java, Vietnam, Sikkim, and Nepal; on tree trunks.

*Platismatia erosa* is distinguished by the broadly "eroded" reticulation of its upper surface, the pseudocyphellae and isidial scars associated with the thallus ridges, and the puncta on the lower surface.

In Japan some specimens of *Platismatia erosa* have previously been referred to *Cetraria formosana* as var. *isidiata*, but the plants differ from *P. formosana* in a number of ways. The thallus folds and ridges, sharp and conspicuous in *P. formosana*, are less distinct in *P. erosa*. *Platismatia formosana* never has isidia, and *P. erosa* is typically isidiate, although rarely richly so, and some fragmentary or poorly developed specimens may lack isidia altogether. The crests of the thallus ridges in *P. erosa* always bear at least a few pores. While most of these pores are doubtless pseudocyphellae, some of them seem to be scars where isidia have broken off. Holes in the upper cortex such as these, regardless of their origin, are unknown in *P. formosana*.

*Platismatia erosa* also superficially resembles *P. norvegica* although their ranges do not overlap anywhere. It differs from *P. norvegica* in having pseudocyphellae on the upper thallus surface and puncta on the lower surface while the latter species never produces these pores. Although reticulate on the upper surface, *P. erosa* lacks the delicate yet sharp and continuous network that ornaments the surface of *P. norvegica*. The species also differ in many minor characteristics such as the morphology of the isidia. The isidia of *P. erosa* are short and very coarse and usually simple while those of *P. norvegica* are slender, delicate, and often coralloid.

*Platismatia erosa* as it is represented in Japan and in the high mountains of the mainland of southern Asia is a very clearly defined species of conservative variation. Since most of the specimens seen in this study were from these regions, a few somewhat different-looking plants from the Philippines and Java are assigned to this species with reluctance and qualification. The anomalous southern plants differ in their habit by a number of subtle, hard-to-describe ways from those of the main part of the distribution to the north. They have larger and more abundant pseudocyphellae on the upper surface, fewer puncta on the lower surface, more richly developed isidia, and less well defined thallus ridges and reticulations. These southern plants (especially the Javanese ones) when considered together, however, seem to be quite uniform. Perhaps they belong to a distinct taxon.

Some individuals of *Platismatia erosa*, and especially the atypical southern specimens provisionally referred to this species, may also superficially resemble *P. regenerans* from Sabah. The latter species, however, has no isidia, and it has pseudocyphellae which are larger and more conspicuous than those of typical *P. erosa*. It also lacks the ridging seen in *P. erosa*, and its upper surface is entirely smooth.

CHEMICAL ANALYSIS.—Of the 17 samples tested, nine were extracted directly with acetone. The residues from these extracts all showed caperatic acid in both the GE solution (two crystal forms) and the GAW solution, and atranorin in the GE and GA*o*-T solutions. Residues from eight samples extracted with cold benzene showed atranorin in the GE and GA*o*-T solutions (Plate 2, Figure 7) but no protolichesterinic acid in the GE solution. The residue from a subsequent acetone extract gave the characteristic crystal forms of caperatic acid in the GE solution (Plate 3, Figure 18) and in the GAW solution (Plate 2, Figure 11). In addition to atranorin and caperatic acid, nine samples showed yellow crystals in the GE solution (Plate 6, Figure 35) which may be due to an unidentified yellow pigment. Some residues containing the yellow pigment also showed clusters of fine yellowish-tan needles (Plate 6, Figure 36) in the GAo-T solution. The same combination of yellow crystals in the GE solution and fine needles in the GAo-T solution was observed in preparations from some samples of *Platismatia interrupta*, *P. formosana*, and *P. regenerans*, suggesting that the same substance or combination of two substances occurs in these species as well.

ADDITIONAL SPECIMENS EXAMINED:

JAPAN: HONSHU: Prov. Kai: Mt. Kobushi, 2,000 m., *Asahina*, 1933 (TNS, 3 collections). Prov. Shinano: Mt. Tadeshina, *Kurokawa* 510038 (TNS); Yatsu-ga-take, Mt. Tengu, *Kurokawa* 58240 (TNS, US); Yatsu-ga-take, Takami-ishi, *Kurokawa* 58301 (TNS); Yatsu-ga-take, Mt. Kitayoko-dake, *Kurokawa* 58349 (TNS); Yatsu-ga-dake, Mt. Naka-no-dake, *Togashi & Kurokawa* (TNS). Prov. Musashi: Mt. Kobushi, Pass Karisaka, *Kurokawa* 521018 (TNS).

FORMOSA: Mt. Niitaka, *Sasaki*, 1927 (W).

PHILIPPINES: MOUNTAIN PROV.: Mt. Data, Barrio, *Hale* 26301, 26751 (US); the same, Heald Logging Area 9, *Hale* 26082, 26105 (US).

JAVA: Res. Pasoeroean, Goenoeng Ardjoena, Lalidjina-Welirang-track, *Du Rietz* 61:2, 61b:2, 62:1, 65:3, 68:1 (UPSV); the same, track from Lalidjina to Ardjoeno top, *Du Rietz* 36:1 (UPSV).

VIETNAM: Langbian Mountains near Dalat, 1,800 m., *Tixier*, 1962 (DUKE).

CHINA: YÜLINGKONG: Gomba La, 3,700 m., *Smith* 14062 (UPS).

SIKKIM: No locality, *Thomson* (H-Herb. Nyl., K, M); no locality, *Thomson*, 289 (G,M). East Himalayas, 8,500 ft., *Awasthi* 354 (H).

NEPAL: East Nepal, Mewakhola Valley, 11,000–11,500 ft., *Awasthi* 2292 (UPS); Khumbu, 3,900–4,000 m., *Poelt* L36, L37 (M).

2. **Platismatia formosana** (Zahlbr.) Culb. & Culb., comb. nov. PLATE 25

*Cetraria formosana* Zahlbr., Repert. Spec. Nov. Fedde 33:59. 1933–1934 (1934). Type: Formosa, Mt. Arisan, *Asahina* F.89 [not "84" as in the original citation]. (W, holotype).

Thallus small to medium, 5–19 cm. broad; lobes 0.3–2.5 cm. broad. Upper surface ashy-white or gray (uniformly brown in old herbarium specimens), abruptly interrupted with broad reticulate ridges up to 1 mm. high at right angles to the surface, not pseudocyphellate. Lower surface black toward the center, but large zones, especially toward the margin, chestnut-brown, punctate, the entire lower surface covered with abundant, tiny pores; rhizines few, black, simple or compound-fasciculate. Upper cortex 19–31$\mu$ thick; medulla 29–102$\mu$ thick between the ridges, IKI—; lower cortex 10–25$\mu$ thick. Apothecia infrequent, submarginal, perforate, 1.5–4.0 mm. in diameter; hymenium 39–47$\mu$ thick; subhymenial layers 18–26$\mu$., without underlying algae. Spores 8, small, ellipsoid, 5–7×3–4$\mu$. Pycnidia marginal, immersed, only the ostiole visible; conidia 1×5–7$\mu$, rod-shaped, the ends not inflated.

MEDULLARY REACTIONS.—K—, C—, KC—, P—.

CONSTITUENTS.—Caperatic acid, atranorin, and an unidentified yellow pigment.

DISTRIBUTION (Map, Figure 28).—Mountains of Formosa.

The thallus of *Platismatia formosana* has a broad and severe reticulation that is particularly striking. The long, continuous ridges are composed of both cortex and medulla and may be as high as 2 mm. with perfectly vertical sides and without correspondingly deep depressions in the lower surface of the thallus. The sharpness of the ridges is striking in comparison to the worn, more gentle ridges of *P. erosa*, although the overall pattern of ridging of the thallus surface is highly similar and the species are obviously very closely related.

*Platismatia formosana* might be compared with *P. lacunosa*, but their patterns of thallus ridging are quite different. In *P. formosana* the spaces between the broadly separated, vertical ridges are flat while in *P. lacunosa* the sloping ridges are separated by U-shaped valleys. The two species can be separated immediately by their medullary reactions with *p*-phenylenediamine: *P. formosana* is negative while *P. lacunosa* is brick-red due to the presence of fumarprotocetraric acid.

The species is known only from the mountains of Formosa and earlier records for it from Japan (Sato, 1943) are doubtless all referable to *Platismatia erosa.*

CHEMICAL ANALYSIS.—Two samples were tested and both showed atranorin and caperatic acid. Both crystal forms of caperatic acid were observed in the GE recrystallization of the acetone extract. Both samples also showed a yellow pigment (not usnic acid) soluble in warm benzene and recrystallizing from the GE solution. The crystals in this solution resemble those from *P. erosa* (Plate 6, Figure 35), and one sample also gave the clusters of fine needles in the GAo-T solution that seemed to be the same as those associated with the occurrence of the yellow pigment in *P. erosa* and *P. interrupta* (Plate 6, Figure 36). The same yellow pigment may also occur in *P. regenerans.*

ADDITIONAL SPECIMENS EXAMINED:

FORMOSA: Mt. Arisan, Numanodaira, above 7,000 ft., *Asahina* F.89 (W); Mt. Niitaka (=Mt. Morrison), *Sasaki*, 1927 (W), *Suzuki*, 1935 (H); the same, Hattsu-kan, *Suzuki*, 1935 (TNS, 3 collections); Mt. Daibu, *Yasuda* 448 (H).

**3. Platismatia glauca** (L.) Culb. & Culb., comb. nov. PLATE 21

*Lichen glaucus* L., Sp.Pl.1148. 1753. Type: Europe, Linnean Herbarium Sheet 1273–139 (LINN, lectotype).

*Cetraria glauca* (L.) Ach., Method. Lich. 296. 1803.

*C. glauca* var. *chilensis* Räs., Ann. Bot. Zool.-Bot. Fenn. Vanamo 20(3):4. 1955. Type: Chile, Prov. Chiloé, Petrohué, *Hosseus* 167 (M, isotype).

*Lobaria glauca* (L.) Hoffm., Deutschl. Fl. oder Bot. Taschenb., Theil für das Jahr 1795, Cryptogamie. 149. 1795 (1796).

*Parmelia glauca* (L.) Hepp, Lichenen-Fl. Würzburg. 23. 1824.

*Physcia glauca* (L.) DC. *in* Lam. & DC., Fl. Franç., ed. 3, 2:401. 1805.

*Platysma glaucum* (L.) Frege, Deutschl. Bot. Taschenb., 2. Theil für das Jahr 1812. 167. 1812. [Not seen.]

Thallus medium, 8–15 cm. broad; lobes 0.3–2.0 cm. broad, the margins with soredia, simple or coralloid isidia, or both, or branched and divided into fruticose lobes, which in turn may be sorediate or isidiate or both. Upper surface whitish or whitish-green or tinged with yellow or, especially in South American specimens, very distinctly yellow, often with darkened areas, smooth to strongly reticulately wrinkled, not pseudocyphellate, smooth or with coralloid or sorediose isidia in discrete patches or diffusely scattered. Lower surface jet-black, the margins brown, colored like the upper surface or white, smooth or reticulately wrinkled and pitted, not punctate; rhizines few to many, simple or compound, brown or black. Upper cortex 16–26$\mu$ thick, prosoplectenchymatous; medulla white, 62–155(–200)$\mu$ thick, IKI+ lavender; lower cortex 16–25$\mu$ thick, prosoplectenchymatous. Apothecia very rare, 0.5–1.0 cm. broad, marginal, perforate or not; hymenium 34–56$\mu$ thick, the asci IKI+ blue or blue-green; subhymenial layer 16–52$\mu$ thick, IKI+ lavender or bright purple, not underlain by algae; spores 8, small, ellipsoid to ovoid, 3.5–8.5×3–5$\mu$. Pycnidia not seen. (See the taxonomic discussion below.)

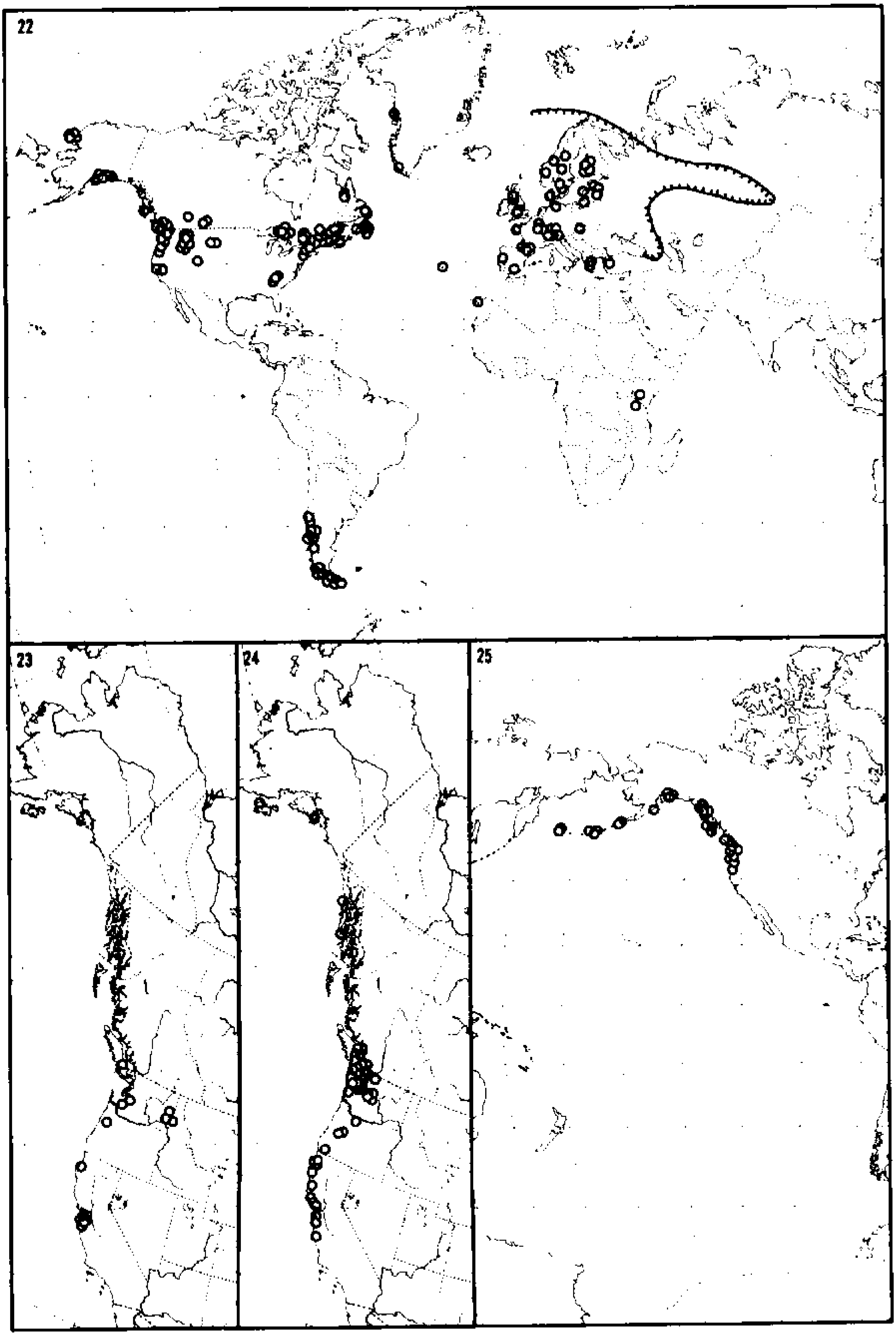
MEDULLARY REACTIONS.—K−, C−, KC−, PD−.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 22).—Southern Greenland, northeastern and northwestern North America and coastal Alaska, Patagonia, central Asia (U.S.S.R.) west through all of Europe, the Canary Islands and the Azores, and in the high mountains of Kenya and Tanzania; on tree trunks and on rocks and boulders.

No other species treated in this monograph has a broader range of morphological variation than *Platismatia glauca*. There is a bewildering range of forms from plants with lobes bearing soredia to sorediose isidia to coralloid isidia to isidioid fruticose branches. All these traits, however, intergrade, and all possible combinations of characters can be found in the herbarium, although certainly not at every locality in the field where the species occurs. If only the extremes of the variations were seen, it would be unbelievable that all the forms constituted a single species. In spite of the plastic morphology of this species, far fewer infraspecific taxa of it have been described than one might expect, considering the taxonomic tradition in Europe. All this reflects, we believe, a general recognition by lichenologists of the innate continuity of the variation in this doubtless very ancient species.

When a large series of specimens is examined or when the species is studied in the field, one is tempted to see distinct local races. For example, the eastern North American populations seem to have a somewhat shiny thallus surface as compared to that of the western North American populations which seem to be much duller. These apparent differences, however, could not be associated with any con-



FIGURES 22–25. Distributions. 22. *Platismatia glauca* (L.) Culb. & Culb. 23. *P. stenophylla* (Tuck.) Culb. & Culb. 24. *P. herrei* (Imsh.) Culb. & Culb. 25. *P. lacunosa* (Ach.) Culb. & Culb.

stant or demonstrable structural or chemical differences. Similarly, the South American plants in general look more distinctly yellow than those from the Northern Hemisphere. No chemical explanation for this color difference could be found.

In the present study no pycnidia of this species were seen. Hillmann and Grummann (1957), however, note in the description of this species in their flora of Brandenburg: "Pykniden selten, randständig, braun oder schwärzlich. Pyknokonidien gerade, an einem Ende verdickt, 6–7×0.8–1.0μ."

It is not surprising that the species showing the greatest morphological variation of all those treated here should also have the broadest geographic range. *Platismatia glauca* is a boreal to temperate species, but it is conspicuously absent from eastern Asia where it is replaced by other members of the genus, notably *P. interrupta* and *P. erosa*. In Africa it is known with certainty only from Mt. Aberdare in Kenya and Mt. Kilimanjaro in Tanzania, although Flagey (1896) cites it from the Atlas Mountains of North Africa. These localities, moreover, are the only certain African stations for any species of "*Cetraria*" in the broad sense.

The map of the total range of *Platismatia glauca* (Figure 22) is only approximate. Too few Soviet specimens with adequate geographic information were seen to allow the construction of a meaningful map for eastern Europe and central Asia. The outlined eastern part of the range of the species in the Old World is based on a map published by Rassadina (1950) in her careful study of *Cetraria* in the U.S.S.R. Since there are no differences in the taxonomy of *P. glauca* at the species level between her treatment and ours, we have used directly the information that she gives. Also, in the range as indicated for western North America, the real distribution may actually extend a bit farther north than we have mapped it.

Although *Platismatia glauca* is widely distributed, it is rare in large parts of its range, for example in the southern parts of its distribution in North America. In Europe the species is doubtless by far most common in the milder western parts and in the British Isles.

CHEMICAL ANALYSIS.—Eleven samples from throughout the range of the species were tested and all contained caperatic acid but no protolichesterinic acid. The cold benzene extract showed atranorin in the GE and GA*o*-T solutions but no recognizable fatty acid in the GE or GAW solutions. The subsequent acetone extract contained caperatic acid (GE, GAW, and GA*o*-T). Tests in the GE solution gave mixed crystal forms of caperatic acid (Plate 3, Figures 14 and 16). The acetone extracts were also chromatographed in pyridine-ethyl acetate-water (1:2:1) and sprayed with a stable PD solution, but no PD+ compounds other than atranorin were detected.

NOMENCLATURE.—The oldest specific epithet for this polymorphic, widely distributed lichen is *Lichen glaucus*, from Linnaeus' *Species Plantarum* (1753). There are, however, several other old specific epithets that also refer to *Cetraria glauca* (L.) Ach. sens. lat.: *Lichen fallax* Web. (Spicilegium Florae Goettingensis. 244. 1778), *Lichen fraudulentus* Gmel. (in L., Syst. Nat., ed. 13, 2 [2]:1371. 1791), and *Lichen membranaceus* Lam. (Encycl. Méthod., Bot. 3: 492. 1789 [1791–1792]). Zahlbruckner (1930) lists nomenclatural synonyms of all these basionyms. None of these old names has been typified in the present study because none is required for the present taxonomic treatment. In the event that a future interpretation recognizes more than one species, it will be necessary to determine the precise reference through typification of these names before assigning specific epithets to segregates of *Platismatia glauca* sens. lat.

In addition to the above names, the epithet *Lichen ampullaceus* L. (Sp. Pl. 1146. 1753) has traditionally been assumed to refer to *Platismatia glauca*. There is no specimen bearing the epithet *ampullaceus* in the Linnean Herbarium. From the original description ("Lichen foliaceus planiusculus lobatus crenatus, peltis globosis inflatis"), however, the name has often been interpreted to refer to monstrous forms of *P. glauca* infected by parasitic fungi (cf. Santesson and Culberson, 1966). If so, the name can be rejected as based upon a monstrosity.

REPRESENTATIVE SPECIMENS EXAMINED:

GREENLAND: JULIANEHAAB DISTRICT: Upernivíarssuk, *Dahl*, 1937 (US); Qagssiarssuk, *Dahl*, 1937 (US).

MIQUELON ISLAND: Locality unknown, *Delamare*, s.d. (COLO).

CANADA: LABRADOR: Bottle Harbor, *Waghorne*, 1882 (US).

NEWFOUNDLAND: St. John, *Fries*, 1871 (S); Codroy Valley, Oregans, *Hall* 34, 35, 36, 41 (WIS).

QUEBEC: Gaspé-Est: Bonaventure Island, off Percé, *Imshaug* 26501 (MSC), *Shushan* S23026 (COLO). Montmorency: Laurentides National Park, Lac Jacques Cartier, *Imshaug* 26336 (MSC). Matane Co.: Mont Blanc, *Frère Fabius*, 1953 (DUKE, 4 collections). Frontenac Co.: Mont Megantic, Masson 6068 (WIS).

NOVA SCOTIA: Chester, *Greenwood* 1558 (COLO-ABS).

NEW BRUNSWICK: Albert Co.: Fundy National Park, Herring Cove, *Imshaug* 26532, 26585 (MSC).

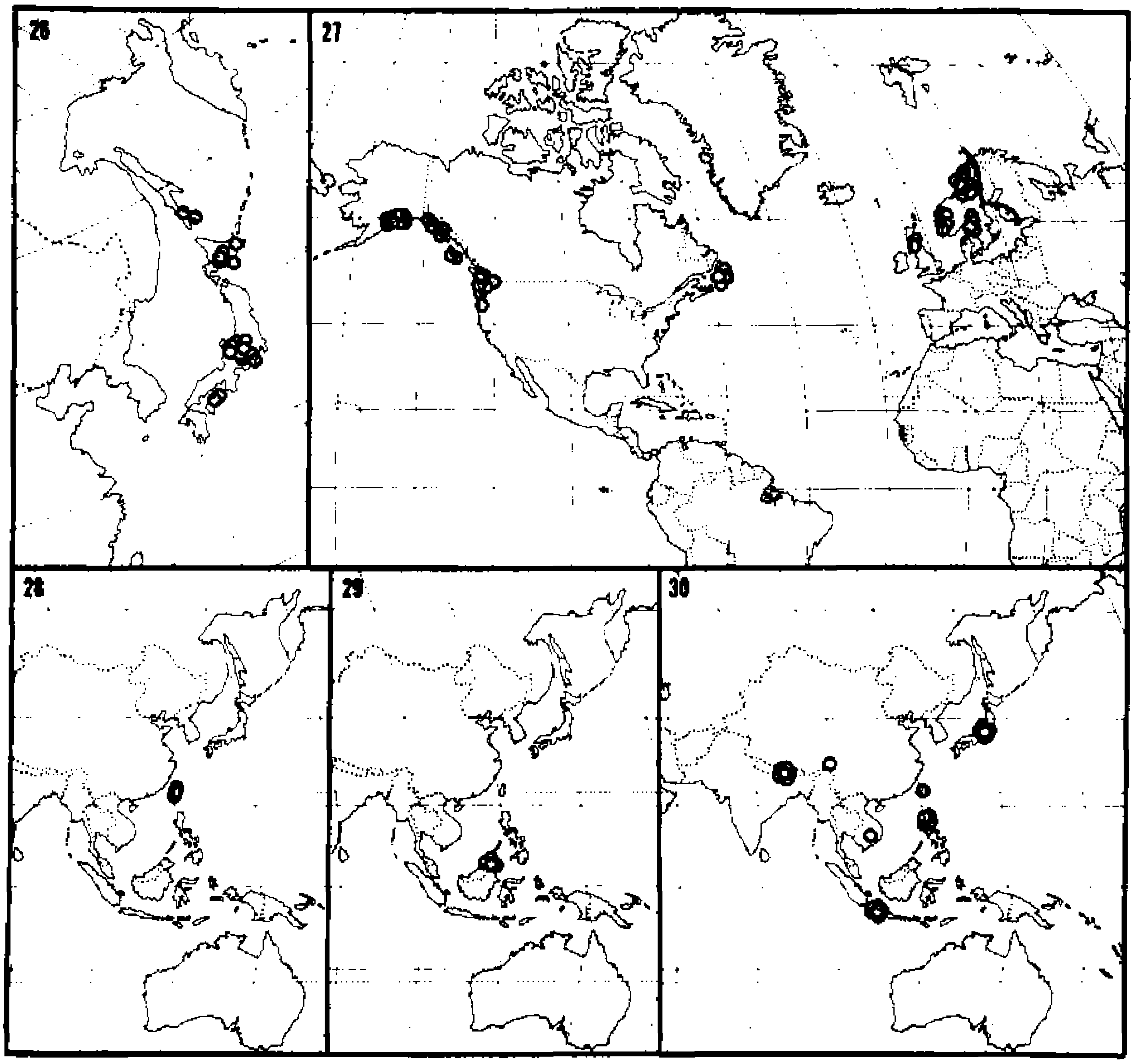
ONTARIO: Groundhog River, west of Timmins, *Wetmore* 6247 (COLO, MSC, US).

SASKATCHEWAN: Cypress Hills, *Lamb* 6133 (DUKE, WIS).

ALBERTA: Banff National Park, Johnson Creek, *Weber* S23560 (COLO).

BRITISH COLUMBIA: Queen Charlotte Islands: Graham Island, *Persson* (COLO). Vancouver Island: Locality unknown, *Lyall*, 1858–1859 (US, 2 collections); Comox, *Macoun* 88 (CAL, MSC, US, WIS).

U.S.A.: MAINE: Hancock Co.: Mt. Desert Island, *Davis* 21, 46 (US). Knox Co.: Camden, *Merrill, Lich. Exs.* 139 (US). Piscataquis Co.: Mt. Katahdin, *Degelius*, 1939 (US). Washington Co.: Cutler, *Davis* 14g (US); North Lubec, *Cummings, Decades North Amer. Lich.* 279 (MSC, US).



FIGURES 26–30. Distributions. 26. *Platismatia interrupta* Culb. & Culb. 27. *P. norvegica* (Lynge) Culb. & Culb. 28. *P. formosana* (Zahlbr.) Culb. & Culb. 29. *P. regenerans* Culb. & Culb. 30. *P. erosa* Culb. & Culb.

NEW HAMPSHIRE: Coos Co.: Mt. Washington, *Llano*, 1941 (WIS). Grafton Co.: Mt. Lafayette, *Kaiser* 64 (COLO–ABS).

VERMONT: Lamoille Co.: Mt. Mansfield, *Cain* 25549 (COLO), *Merrill* 1922 (DUKE).

MASSACHUSETTS: Berkshire Co.: Mt. Greylock, *Imshaug* 24095 (MSC).

NEW YORK: Ulster Co.: Cornell Mountain, *Imshaug* 24062 (COLO, MSC).

TENNESSEE: Sevier Co.: Mt. Le Conte, *Degelius*, 1939 (US, 2 collections).

NORTH CAROLINA: Avery Co.: Roan Mountain, *Hale* 18086 (US).

MICHIGAN: Keeweenaw Co.: Isle Royale National Park, *Wetmore* 2509 (COLO, DUKE, MSC).

MINNESOTA: Cook Co.: Susie Islands *Thomson* 4023 (WIS).

SOUTH DAKOTA: Lawrence Co.: Benchmark, *Wetmore* 8503 (MSC).

MONTANA: Flathead Co.: Glacier National Park, Fish Lake, *Imshaug* 7287 (WIS). Missoula Co.: South of Missoula, *Stickney* PFS–573 (WIS). Sanders Co.: South of Thompson Falls, Dry Creek, *Stickney* 1005, 1005a, 1005b (WIS).

WYOMING: Crook Co.: Taylor Divide Road, *Wetmore* 9824 (MSC).

COLORADO: Boulder Co.: Bull Gulch, *Erdman*, as *Weber*, *Lich. Exs.* 4 (COLO, DUKE, MSC, WIS).

Alaska: Prince William Sound, Thum Bay, Knight Island, *Eyerdam* 254, 282, 284 (CAL). Washington Bay, Kuiu Island, *Eyerdam* 1080, 1086, 1142 (COLO). Kenai Peninsula, Seward, *Hultén*, 1932 (UPS); Admiralty Island, Windfall Harbor, *Stephens* 243 (CAL).

Washington: Clark Co.: 5 mi. east of Vancouver, *Pechanec* S4717 (COLO). Island Co.: Langley, *Grant*, 1923 (WIS, 2 collections). Jefferson Co.: Olympic Rain Forest, *Howard* 4317 (WTU). King Co.: Red Mountain, *Eyerdam* 1557 (COLO, WTU). Lewis Co.: Tenina, *Frye* (COLO–ABS). Pierce Co.: Mt. Rainier National Park, White River, *Imshaug* 391 (US, WIS). Snohomish Co.: Marysville, *Grant*, 1929 (CAL, US). Spokane Co.: North of Spangle, *Cooke* 23203 (COLO-ABS, WIS). Stevens Co.: Springdale, *Cooke* 23237 (WIS). Thurston Co.: Olympia, *Becking* 5203462d (WTU). Whatcom Co.: Maple Mead Farm, *Herre*, 1949 (WIS). Whiteman Co.: Kamiak Butte, *Imshaug* 16446 (MSC).

Oregon: Benton Co.: Corvallis, *E. J. K.*, 1921 (WIS). Hood River Co.: Cloud Gap, *Hale* 21558 (DUKE). Jackson Co.: Medford, *Darrow* 233 (WIS). Lane Co.: Oakridge, *Howard* 4713 (WTU). Union Co.: Mill Creek, *Sheldon* 9010 (US).

Idaho: Bonner Co.: Sandpoint, *Knox* S15842, S15844 (COLO). Idaho Co.: Nez Perce National Forest, *Cooke* 20694, 20708 (WIS). Nez Perce Co.: Clearwater Canyon, *Cooke* 22910, 22918 (WIS). Lattah Co.: St. Joe, *Herre* 7457 (COLO, WIS). Lewis Co.: Winchester, *Cooke* 25107 (WIS).

California: Siskiyou Co.: Locality unknown, *Herre*, 1942 (WIS). Sonoma Co.: Santa Rosa, *Baker*, 1897 (UC).

CHILE: Malleco: Pidir-Nalmel, *Sparre* 5092 (S); Angol, *Dusén*, 1896 (UPS).

Cautín: Volcán Llaima, *Sparre* 4826 (S).

Valdivia: Lago Panguipulli, *Santesson* 3943 (UPS); Lago Riñihue, Enco, *Santesson* 7249, 7273, 3607 (UPS).

Aysén: Coyhaique, *Santesson* 4397, 4453, 4484 (UPS); Puerto Aysén, *Santesson* 4323.

Chiloé: Petrohué, *Hosseus* 167 (M).

Magallanes: Isla Riesco, *Santesson* 2084, 9011a, 8198 (UPS); Lago del Toro (Maravilla), *Santesson* 6330, 6505 (UPS); Tierra del Fuego, Canal Whiteside, Puerto Yartou, *Santesson*, *Lich. Austroamer.* 469b (LD, MSC, UPS); Canal Beagle, *Santesson* 7445 (UPS); Isla Hoste, *Santesson* 1333 (UPS); Punta Arenas, *Santesson* 5116 (UPS).

ARGENTINA: Río Negro: Lake Nahuel Huapí, *Lamb* 5834 (UPS); Lago Frias, *Lamb* 5984 (UPS).

Tierra del Fuego: Lago Fagnano, *Santesson* 1583 (UPS); Ushuaia, *Dusén* 247 (UPS), *Dusén*, 1896 (GB, S, UPS), *Santesson* 433, 1215 (UPS), *Skottsberg*, 1902 (S, 3 collections), *Santesson*, *Lich. Austroamer.* 469a (LD, MSC, UPS); Sierra Alvear, *Santesson* 706 (UPS).

NORWAY: Hordaland: Granvin, *Havaas*, 1910 (DUKE).

Sörtröndelag: Leinstrand, *Hoëg*, as *Magn.*, *Lich. Sel. Scand. Exs.* 260 (GB, S).

SWEDEN: Dalarne: Lima, *Hasselrot* (S).

Jämtland: Åre, *Hasselrot* (S).

Småland: Bunn, *Santesson*, 1932 (S).

Västergötland: Koläby, Trädet, *Vrang*, *Krypt. Exs. Vindobon.* 2763 (MSC, UC).

Värmland: N. Ny, *Hasselrot*, 1938 (S).

FINLAND: Etelä-Häme: Lammi, *Ulvinen*, 1960 (UC).

Pohjois-Karjala: Keitele, Vuonamo, *Huuskonen*, 1960 (UC).

U.S.S.R.: Estonia: Eesti, Kedder, *Wasmuth*, 1910 (H); Distr. Keila, Vääna, *Pärn*, 1960 (DUKE); Tallin-Pääskula, *Pärn*, 1960 (DUKE); Insula Saaremaa, *Sünnaa*, s.d. (DUKE).

LITHUANIA: Peninsula Kura, *Trass*, 1959 (DUKE).

SIBERIA: Sajangebirge, *Plotnikov*, 1927 (DUKE).

TURKEY: Mt. Ida, *Cyrén*, 1933 (S).

SCOTLAND: INVERNESS-SHIRE: Moidart Peninsula, Shiel Bridge, *Culberson & Culberson* 11827 (DUKE).

ARGYLLSHIRE: Ardnamurchan Peninsula, Kilchoan, *Culberson & Culberson* 11586 (DUKE).

WALES: BRECONSHIRE: Hay-on-Wye, *Culberson & Culberson* 11859 (DUKE).

CAENARVONSHIRE: Gwynant Lake, *Culberson & Culberson* 11926 (DUKE).

RADNORSHIRE: Penybont, *Culberson & Culberson* 11851 (DUKE).

DENMARK: JYLLAND: River Gudenna, Borre Forest, *Leth*, 1870 (UC).

GERMANY: SCHLESWIG-HOLSTEIN: Schleswig, *Saxen*, 1957 (DUKE).

BREISGAU: Freiburg, *Lösch*, as *Arn*., *Lich. Exs.* 1723 (PC).

HOLLAND: GELDERLAND: Bermekon, *Maas Geesteranus* 2480 (S).

CZECHOSLOVAKIA: Banska Stiavnica, Finkova, *Suza*, *Lich. Bohemoslov* 56 (DUKE).

GREECE: THESSALIA: Mt. Olympos, *Szatala*, as *Kofaragó-Gyeln.*, *Lichenoth.* 193 (BM).

PELOPONNESOS: Messina, *Degelius*, 1955 (GB).

FRANCE: ARDENNES: Montherme, *Culberson & Culberson* 10530 (DUKE).

FINISTÈRE: Roc Trévezel, *Culberson & Culberson* 10503 (DUKE).

HAUTE-GARONNE: Lac d'Oô, *Culberson & Culberson* 11895 (DUKE).

HAUTES-PYRÉNÉES: Cauterets, *Jeanjean* 7771 (DUKE); Pont d'Espagne, *Culberson & Culberson* 11713 (DUKE).

VOSGES: Schiessrothried, *Werner*, 1959 (MSC, 2 collections).

SPAIN: JAÉN: Sierra de Cazola, *Degelius*, 1952 (S).

PORTUGAL: BEIRA ALTA: Serra da Estrela, *Tavares*, 1946 (S).

CANARY ISLANDS: Palma, *Pitard*, 1883, 1886, 1906 (DUKE, 3 collections); the same, *Bornmuller* (W).

AZORES: Pico, *Persson*, 1937 (UPS, 2 collections).

KENYA: Mt. Aberdare, *Fries & Fries*, 1922 (UPS).

TANZANIA: Kilimanjaro, above Marangu, 3,225 m., *Hedberg* 1374e (UPS).

**4. Platismatia herrei** (Imsh.) Culb. & Culb., comb. nov. PLATE 22

*Cetraria herrei* Imsh., Bryologist 57:6. 1954. Based on *C. glauca* b. *stenophylla*.

*Cetraria glauca* b. *stenophylla* Tuck., Synops. No. Amer. Lich. 1:36. 1882. Type: U.S.A., Oregon, *Hall*, 1871 (FH, lectotype).

*Cetraria tuckermanii* Herre, Proc. Washington Acad. Sci. 7:340. 1906. (Not Oakes *in* Tuck., 1843). Based on *C. glauca* b. *stenophylla*.

Thallus medium, 9–12 cm. broad; lobes linear, narrow, 0.5–4 mm. broad, sometimes much broader (up to 8 mm.) near the base. Upper surface whitish or pale, smooth to very minutely pitted or wrinkled, not pseudocyphellate or sorediate, isidiate, the isidia simple to branched and coralloid, densely fringing the margins, rarely on the upper surface. Lower surface white or pale with conspicuous, discrete, well delimited, jet-black or dark brown zones, especially in the older parts; rhizines black, rare, a few at the places of attachment only. Upper cortex 21–26$\mu$ thick, medulla 91–177$\mu$ thick, the hyphae oriented parallel to the axis of the lobe, IKI+ lavender; lower cortex 15–26(–31)$\mu$ thick, prosoplectenchymatous. Apothecia not common, 3–8 mm. broad, terminal, imperforate; hymenium 47–65$\mu$ thick; subhymenium 13–18$\mu$ thick. Spores 8, ellipsoid or spheroid, 4–5 × 5–8$\mu$. Pycnidia few, black, minute, marginal; conidia $1 \times 5\mu$, rod-shaped.

Medullary reactions.—K−, C−, KC−, P−, UV−.

Constituents.—Caperatic acid and atranorin.

Distribution (Map, Figure 24).—Extreme western North America from southern Alaska south to central California; on the bark of trees.

*Platismatia herrei* is one of the most beautiful and intricately formed species in the genus. It can be distinguished from all other members of the genus by the delicate but conspicuous isidia fringing the edges of the linear lobes. In some specimens there are fruticose coralloid structures on the margin identical to (but invariably smaller than) those seen in some forms of *P. glauca*. Occasional specimens of *P. herrei*, indeed, show the typically narrow, linear lobes arising from much broader basal ones making one wonder if the plants called *P. herrei* might represent only a localized western race of *P. glauca*. But although some specimens may superficially give this impression, the distinctively narrow lobes, the characteristically delicate marginal corolloid isidia, and the black mottling in conspicuous discrete patches of the undersurface are so different from the traits of the typical race of *Platismatia glauca* inhabiting the Pacific Northwest that the distinctness of the species is beyond doubt.

*Platismatia herrei* is an excellent example of a North American endemic species with an extreme Pacific coastal distribution. Its range is almost identical in extent to the coastal portion of the distribution of western hemlock, *Tsuga heterophylla* (Raf.) Sarg.

Chemical analysis.—Five samples of this species were tested. The benzene extracts showed atranorin in the GE and GA*o*-T solutions and by chromatography. No fatty acids were observed in these extracts, but the subsequent acetone extracts showed caperatic acid in the GE, GAW, and GA*o*-T solutions. Tests for atranorin in the GA*o*-T solution showed two types of yellow crystals—one typical of atranorin and the other smaller and more sharply curved.

Additional specimens examined:

U.S.A.: Alaska: Hecla Island, *Foster*, 1913 (COLO). Prince William Sound, Knight Island, Thum Bay, *Eyerdam* 305 (WIS). Washington Bay, Kuiu Island, *Eyerdam* 428 (COLO). Kodiak Group, Raspberry Island, Port Vita, *Eyerdam* 390 (WIS).

Washington: Clallam Co.: Swan Bay, Ozette Lake, *Brown & Muenscher* 143 (UC, US); West Fork, Twin Rivers, *Eyerdam* 3162 (COLO); Sequin, *Grant* 41 (COLO-ABS); Olympic Mountains, *Grant* 3001 (COLO-ABS). Jefferson Co.: Port Discovery, *Brown & Muenscher* 142 (UC, US). Pierce Co.: Mt. Rainier National Park, Van Trump Trail, *Howard* 4202 (COLO, WTU); the same, White River, *Imshaug* 414, 434 (US); the same, Tahoma Creek, *Imshaug* 1741 (US); the same, Eagle Peak Trail, *Imshaug* 1563 (US). Snohomish Co.: Mt. Pilchuck, *Larrison*, 1947 (WIS); Marysville, *Grant*, s.d. (COLO). Whatcom Co.: Mt. Baker, 2,000 ft., *Herre* 3234 (COLO-ABS).

OREGON: Locality unknown, *Hall*, 1871 (FH). Josephine Co.: Between Cave Junction and O'Brien, *Weber* 8044 (COLO). Lane Co.: Florence, *Marr*, 1941 (COLO); Eugene, collector unknown, 1936 (COLO).

CALIFORNIA: Locality unknown, *Bolander* 28 (FH). Humboldt Co.: Eureka, *Howe, Lich. Boreali-Amer.* 143 (WIS), the same, *Howe*, as *Cummings et al., Decades of North Amer. Lich.* 213 (DUKE, MSC, US, WIS); Pepperwood, *Tavares* 361 *& Seear* (UC). Jackson Co.: Highway 227, *Tavares* 111d *& Chisaki* (UC). Marin Co.: Mt. Tamalpais, *Schneider*, 1903 (UC); Tomales Bay, *Mann & Bolander* 31 (UC); Inverness, *Tavares* 564 (UC). Mendocino Co.: South fork of Eel River below Elder Creek, 1,000 ft., *Tavares & Sharsmith*, 1961 (UC). Monterey Co.: Locality unknown, *Booth*, 1878 (FH). Santa Cruz Co.: Boulder Creek, 700 ft., *Hasse* 3051 (UC). Sonoma Co.: Gualala, *McMillan* 110 (UC); 24 mi. south of Gualala, *Seear & Tavares* 318c (UC).

CANADA: BRITISH COLUMBIA: Islands, Gulf of Georgia, *Hill* (COLO-ABS); Mayan Island, *Hill*, 1904 (COLO-ABS); Queen Charlotte Islands, Moresby Island, head of Bigsley Inlet, *Persson* 14 (COLO); Thurlow Island, *Dawson*, 1885 (H); Victoria, Mt. Douglas, *Kverno* S1987 (COLO, US); Vancouver Island, *Lyall*, 1858-1859 (US, WIS), *Macoun* 16 (US); the same, Port Renfrew, *Herre*, s.d. (UC); the same, Nanaimo, *Macoun* 97 (UC, MSC, US, WIS), *Krajina et al.* 3729 (DUKE).

**5. Platismatia interrupta** Culb. & Culb., sp. nov. PLATE 22

Thallus parvus vel mediocris, 6–12 cm. latus; laciniae 0.3–2.0 cm. latae. Superficies superior grisea (sordide citrella apud exemplaria vetera herbarii) vel marginibus pallide fusca, levis vel reticulis interruptis indistincte rugosa, pseudocyphellata, pseudocyphellis conspicuis, rotundis, elongatis vel confluentibus, granulose-sorediatis vel subisidiatis. Superficies inferior picea, marginibus castanea vel albida, non punctata; rhizinae paucae, nigrae. Cortex superior 18–26$\mu$ crassus, prosoplectenchymatosus; medulla 65–104$\mu$ crassa, IKI— vel IKI+ dilute violacea; cortex inferior 13–21$\mu$ crassus. Apothecia et pycnidia ignota.

Thallus small to medium, 6–12 cm. broad; lobes 0.3–2.0 cm. broad. Upper surface gray (uniformly light in old herbarium specimens) or tinged with light brown on the margins, smooth to very obscurely wrinkled with a discontinuous reticulation, pseudocyphellate, the pores conspicuous, round to irregular, elongate or confluent, becoming coarsely sorediate or isidioid in some specimens. Lower surface jet-black at the center, a marginal zone up to 2 cm. broad chestnut brown or conspicuously white (or light brown in old specimens), not punctate; rhizines very few, black. Upper cortex 18–26$\mu$ thick, prosoplectenchymatous, with minute brownish crystals, IKI— or IKI+ very pale lavender; medulla white, 65–104$\mu$ thick; lower cortex prosoplectenchymatous, 13–21$\mu$ thick, crystals absent or, if present, only a few in the light-colored zone. Apothecia and pycnidia unknown.

TYPE.—Mount Norikura, Shinano Province, Japan, *Asahina*, 1952 (TNS, holotype).

Medullary reactions.—K—, C—, KC—, PD—.

Constituents.—Caperatic acid, atranorin, and an unidentified yellow pigment.

Distribution (Map, Figure 26).—Sakhalin Island and Japan, especially in the mountains; very common on tree trunks and over boulders.

*Platismatia interrupta* is very common in Japan and is, in fact, one of the most abundant of all the macrolichens there. It is obviously the Far Eastern equivalent of *P. glauca*, a species that is exceedingly common in large areas of the Northern Hemisphere but which is apparently absent from the extreme Orient altogether.

*Platismatia interrupta* differs from P. *glauca* in having pseudocyphellae on the upper surface of the lobes and an indistinct and discontinuous reticulation of the upper surface that reminds one of a further, almost complete breakdown of the reticulate ornamentation of the upper surface of *P. erosa*. In addition, the upper surface of *P. interrupta* is IKI—, or nearly so, while it is blue in *P. glauca*.

The only Japanese species for which the common *Platismatia interrupta* might be mistaken is the rare *P. erosa*. The upper surface of *P. interrupta* is not pseudocyphellate in the same manner as *P. erosa*, and the habit of the reticulation is different. The pseudocyphellae in *P. interrupta* are large, conspicuous, and generally distributed, but they are small, inconspicuous, and confined to the crests of the ridges in *P. erosa*.

Some especially isidiate individuals of *P. interrupta* may resemble *P. norvegica*. *Platismatia norvegica* has much more prominent reticulate ridging and lacks the conspicuous pseudocyphellae characteristic of *P. interrupta*.

One specimen with pseudocyphellae typical of *P. interrupta* but with essentially strap-shaped lobes with marginal isidia was seen from Sakhalin Island (Aikawa, *Asahina*, 1932, TNS). With the exception of the pseudocyphellae, its habit much resembled that of the Pacific North American *P. herrei*. More material from the North Asiatic Pacific will be required to determine whether this combination of characters is typical of another distinct, major population there, but for the present the specimen is referred to *P. interrupta*. It should be pointed out, however, that entirely typical specimens of *P. interrupta* are known from Sakhalin Island as well.

Chemical analysis.—Most tests made on this species were performed by extraction of the sample in acetone without prior extraction in benzene. All samples contained atranorin and caperatic acid, which was observed in both crystal forms in the GE and GAW solutions. Fourteen of the 20 samples tested also showed a yellow pigment recrystallizing in the GE solution. This substance seems to occur in *P. erosa, P. formosana*, and *P. regenerans* as well. It may be a constant component, but samples which did not give a positive test for the pigment were not retested.

The GA*o*-T solution gave yellow crystals typical of the atranorin condensation product as well as smaller finer yellow crystals (Plate 2, Figure 9). In addition, the GA*o*-T solution sometimes showed clusters of very fine colorless needles (Plate 6, Figure 36) which were not identified but which may be due to the substances producing the unidentified yellow crystals observed in the GE solution.

NOMENCLATURE.—The many references to "*Cetraria braunsiana* (Müll. Arg.) Zahlbr." in the Japanese botanical literature all relate to the present species, the result of a consistent misapplication of the name of a different plant altogether.

ADDITIONAL SPECIMENS EXAMINED:

U.S.S.R.: SAKHALIN: Ho-e, *Fujikawa*, 1932 (TNS); Kashiho, *Ishiyama*, 1932 (TNS).

JAPAN: HOKKAIDO: Prov. Hidaka: Mt. Apai, *Ikuse*, 1956 (TNS). Prov. Ishikari: Horonaizawa, *Asahina*, 1935 (TNS); Hot Spring Matsuyama, *Asahina*, 1935 (TNS); Mt. Tomuraushi, *Fujikawa*, 1935 (TNS). Prov. Kushiro: Lake Masyu, *Togashi*, 1953 (TNS).

HONSHU: Prov. Ettyu: Mt. Tate-yama, Waterfall Syo-myo, *Nishijima*, 1935 (TNS); Makawa, *Asahina*, s.d. (TNS). Prov. Izu: Mt. Amagi, *Asahina*, 1927 (TNS). Prov. Kai: Mt. Fuji, Yoshida-guichi, 1-gome, *Togashi* (TNS); the same, *Hisauchi*, 1928 (TNS); Mt. Kinpu-san, *Kurokawa* 521207 (TNS); Mt. Mizugaki, *Kurokawa* 521133 (TNS); Mt.Ko-fuji, *Asahina*, 1935 (TNS). Prov. Musashi: Pass Mikuni, *Kurokawa* 520764 (TNS). Prov. Mutsu: Mt. Osoresan, *Kurokawa* 550447 (TNS); Montagne d'Aomori, *Faurie*, 1897 (PC). Prov. Shinano: Mt. Yatsu-gatake, *Kurokawa* 520674 (TNS), *Kurokawa* 58240 (MSC); the same, Takami-ishi, *Kurokawa* 58300 (TNS); the same, Mt. Iwo-dake, *Kurokawa* 58436 (TNS); Yumatazawa, *Kurokawa* 51672 (TNS); Ikenotaira, Daimon Pass, *Asahina et al.*, 1959 (TNS); Heights Tadeshina, *Kurokawa* 58323 (TNS); Mt. Norikura, *Asahina*, 1952 (TNS, 2 collections); Mt. Daitenjo, *Kurokawa* 520518 (TNS); Mt. Gaki-dake, *Kurokawa* 520598, 520599, 520642 (TNS); Mt. Tsupakura, *Kurokawa* 520550 (TNS); Mt. Kimpu, *Asahina et al.*, 1960 (TNS); Suwa-gun, Koto-mura, Suguridaira, *Kurokawa* 58271 (TNS). Prov. Shimotsuke: Nikko, Karikomi-ko, *Culberson & Culberson* 11052, 10629 (DUKE), *Nuno*, 1961 (TNS); Nikko, Yumoto, *Nuno*, 1961 (TNS); Nikko, Yunc-ko, collector unknown (TNS, 2 collections). Prov. Suruga: Mt. Fuji, *Asahina* 72 (UPS); Mt. Fuji, between 5- and 3-gome, *Culberson & Culberson* 10655, 10662, 10669, 10757, 10806 (DUKE); Mt. Fuji, Subashiriguchi, *Asahina*, 1924 (TNS, 2 collections).

SHIKOKU: Prov. Awa: Mt. Kenzan, *Fujikawa*, 1934 (TNS), *Togashi*, 1956 (TNS). Prov. Iyo: Mt. Ishizuchi, *Fujikawa*, 1933 (TNS).

**6. Platismatia lacunosa** (Ach.) Culb. & Culb., comb. nov. PLATE 23

*Cetraria lacunosa* Ach., Method. Lich. 295. 1803. Type: North America, *Herb. Swartzii* (S, neotype).

*C. lacunosa* f. *cavernosa* (Menz.) Merr., Bryologist 13:26. 1910.

*Lichen cavernosus* Menz. *in* Ach., Lichenogr. Univ. 508. 1810 (synonym).

*Platysma lacunosum* (Ach.) Nyl., Bot. Not. 1855:137. 1855 (1856).

Thallus small to large, 5–16 cm. broad; lobes 0.6–1.5 cm. broad. Upper surface gray (uniformly brown or tan in old herbarium specimens), the margins conspicuously blackening, prominently ridged by strong reticulations rising at right angles to the surface, not pseudocyphellate. Lower surface black at the center, chestnut brown at the margins, somewhat reticulately wrinkled, not punctate; rhizines few, black. Upper cortex 19–25(–29)μ thick; medulla 90–280μ thick (measurements taken between the major wrinkles), IKI –; lower cortex 13–16μ thick. Apothecia uncommon, submarginal, 0.4–2.0 cm. in diameter, expanded and irregular at maturity, apparently not perforate; hymenium 62–124μ; hypothecium and proper exciple 22–50μ thick, the limit between the two zones visible in some preparations by a somewhat differential coloration with IKI; algae in groups but usually not in a continuous layer under the proper exciple. Spores 8, ellipsoid to ovoid, 7–10×3–4.5μ. Pycnidia marginal to submarginal or even superficial (on the crests of the reticulations), the ostiole round to irregular at maturity; conidia 1×5–7μ, rod-shaped.

Medullary reactions.—K –, C –, KC –, PD + orange-red.

Constituents.—Fumarprotocetraric acid, caperatic acid (at least in some specimens), and atranorin.

Distribution (Map, Figure 25).—The extreme west coast of North America and the coastal islands from the Aleutians and southern Alaska south to northern California; on the bark of trees (alder, hemlock, spruce) and on rock.

Although *Platismatia lacunosa* superficially somewhat resembles *P. formosana* and *P. erosa*, it can be distinguished from these and from all other species in the genus by its positive, brick-red medullary reaction with *p*-phenylenediamine due to the presence of fumarprotocetraric acid. It should not be assumed, however, that *P. lacunosa* is a mere chemical "strain" of another species; its morphological traits are quite distinct. The reticulate ridging of the upper surface that is so distinctive results from U-shaped depressions between ridges rather than the flat-bottomed spaces between thallus ridges as in the other species.

Chemical analysis.—The samples were extracted with benzene at room temperature to remove atranorin, which was demonstrated in the GE and GAo-T solutions. The warm acetone extract of all but one of the eight samples tested contained caperatic acid (GE, GAW, and GAo-T). When chromatographed in pyridine-ethyl acetate-water, the acetone extracts showed fumarprotocetraric acid. Traces of other substances detected on these chromatograms could not be identified. One very faint spot with an $R_f$ resembling that of protocetraric acid was found not to be this substance on the basis of a faint yellow fluorescence in UV light as compared to the characteristic quenching produced by protocetraric acid under the same conditions.

NOMENCLATURE.—There is a problem in the typification of this species. The Acharian Herbarium in Helsinki contains no specimens labeled *Cetraria lacunosa*. All the specimens which Acharius may have had of it, including the holotype, have apparently been lost. In Stockholm, however, there is a specimen labeled "*Cetraria lacunosa* Ach." and, written just below this but in a different hand: "Acharius scripsit" and "Herb. Swartzii." The exact history of this specimen is unknown, but there is no reason to doubt the indication that Acharius annotated it and that it was part of the herbarium of his colleague Swartz. The specimen is undated, and we do not know whether Acharius saw it before the publication of *Cetraria lacunosa* in 1803, although it is most probable that he did and that his specimen should, therefore, be considered the lectotype. In the absence of the critical historical information, however, it cannot be so designated and must be considered a neotype instead. The proper designation for type specimens selected under the conditions met with here—a common predicament in typifying many of the old names of lichens—has been discussed in detail (W. L. Culberson, 1963).

ADDITIONAL SPECIMENS EXAMINED:

U.S.A.: ALASKA: Unalaska, *Setchell et al.*, 1899 (UC), *Eyerdam*, 1932 (UC), *Hultén* 5277, 5278, 5279 (UPS); Prince William Sound, Thum Bay, Knight Island, *Eyerdam* 238, 252, 264 (UC); the same, Hinchinbrook Island, *Norberg* 328 (WIS); Port Vita, Raspberry Island, Kodiak Group, *Eyerdam* 365 (WIS); Revillagigedo Island, Ketchikan, *Eyerdam* 262 (UC); Annette Island, *Eyerdam* 497 (WIS); Admiralty Island, Windfall Harbor, *Herre* 251; Orca, *Setchell*, 1899 (UC); Attu Island, Engineers Canyon, *Hardy* 30 (S, UPS); Adak Island, Chapel Cove, *Hultén* 5875 (UPS); Atka Island, *Eyerdam*, 1932 (S), *Hultén* 5790 (UPS), *Kobayashi*, 1931 (TNS, 6 collections); Ketchikan, Deer Mountain, 1,500 ft., *Baker*, 1956 (COLO), Washington Bay, Kuiu Island, *Eyerdam* 428 (COLO), *Eyerdam* 414, 427, 509, 825 (WIS).

WASHINGTON: Grays Harbor Co.: Montesano, *Heller* 4310 (US). Jefferson Co.: Hoh River Ranger Station, *Becking* 530656 (COLO); mouth of Hoh River, *Brown & Muenscher* 154 (UC, US).

OREGON: Locality unknown, *Hall*, 1876 (US, 2 collections). Lincoln Co.: Yaguina Bay, *Hall*, 1871 (FH); Waldport, *Howard* 4628 (WIS, WTU). Marion Co.: Silverton, Powers Creek, *Foster* 1200 (US).

CALIFORNIA: Humboldt Co.: Lawrence Creek, *Park* 3512 (UC).

CANADA: BRITISH COLUMBIA: Queen Charlotte Islands, Moresby Island, 650 m., *Persson* 1957 (COLO); Vancouver Island, Comox, *Macoun* 28 (US).

7. **Platismatia norvegica** (Lynge) Culb. & Culb., comb. nov. PLATE 23

*Cetraria lacunosa* f. *norvegica* Lynge, Videnskaps; Skrift., Mat.-Naturv.-Kl. [Kristiania] 1921(7):196. 1921. Type: Norway, Hordaland, Store Kalsø, *Lynge*, 1920 (O, lectotype).

*C. norvegica* (Lynge) Du Rietz, Bot. Not. 1924:59. 1924.

*C. norvegica* f. *sorediata* Degel., Acta Phytogeogr. Suec. 7:52. 1935. Type: Norway, Monte Seljuåsen prope Raegefjord, *Degelius*, 1932 (not seen).

*C. tuckermanii* var. *sorediata* (Degel.) Räs., Kuopion Luonnon Ystäväin Yhdistyksen Julkaisuja, Sarja B. 2(6):46. 1952.

Thallus medium to large, 7–23 cm. broad; lobes 0.5–2.5 cm. broad. Upper surface gray, yellowish-gray or (especially in American specimens) distinctly yellowish, ridged, the sharp, low ridges at right angles to the surface of the thallus, pseudocyphellate, the pores generally confined to the crests of the ridges, minute, often isidiate and indistinct; isidia usually abundant along the margins of the ridges, generally associated with the pseudocyphellae. Lower surface jet-black, a marginal zone up to 1 cm. wide brown or colored like the upper surface, not punctate; rhizines black, few, usually simple. Upper cortex 19–31μ thick; medulla white, 31–217μ thick, much thicker in the ridges, IKI+ pale lavender or (apparently) IKI−; lower cortex 16–31μ thick. Apothecia rare (unknown in America), irregular, perforate, 0.7–1.5 cm. broad; hymenium 51–93μ; thick subhymenial layers measuring together 43–78μ thick, immediately underlain by a dense zone of algae. Spores 8, ellipsoid, 6–8.5×3–4μ. Pycnidia immersed, marginal; conidia not seen.

Medullary reactions.—K−, C−, KC−, PD−.

Constituents.—Caperatic acid and atranorin.

Distribution (Map, Figure 27).—Newfoundland and Miquelon Island, Canada, the western coast of North America from southern Alaska to Oregon; Norway, Sweden and southern Finland, Scotland; on rocks and the trunks of trees.

The reticulate and usually isidiate thallus of *Platismatia norvegica* is so distinctive that the species is easy to recognize. In Europe it always seems to have an adequate development of isidia, immediately distinguishing it from *P. glauca*. In western North America, however, the extent of isidia production is extremely variable, and many specimens from densely isidiate to essentially nonisidiate can be seen in herbaria, but these are marked by the same sharp, low, reticulate ridges that the isidiate plants have. This reticulation and the distinct pseudocyphellae usually associated with the ridges make these nonisidiate specimens appear quite different from *P. glauca*. *Platismatia norvegica* and *P. glauca* apparently often grow together in the Pacific Northwest as witnessed by mixtures of the species in herbarium packets. Although nonisidiate plants seem to be found only among the American populations of *P. norvegica*, the isidiate plants in the same population are indistinguishable from the European ones.

In his original description, Lynge considered this lichen species as a form of *Cetraria* (=*Platismatia*) *lacunosa*, but it differs sharply from that species both in morphology and chemistry. *Platismatia norvegica* has a pseudocyphellate, usually isidiate, minutely but sharply ridged thallus, while *P. lacunosa* has a nonpseudocyphellate, nonisidiate, deeply reticulately ridged and pitted thallus. The medulla of *P. norvegica* is negative with *p*-phenylenediamine while that of *P. lacunosa* is brick-red.

In an occasional rare specimen of *P. norvegica* there is the development of large capitate soralia on the surface of the lobes. This modification was named *Cetraria norvegica* f. *sorediata* by Degelius. Though conspicuous, these soralia are so foreign to the scattered, granular type produced normally in the genus (as in *P. glauca* and *P. interrupta*) that they give every impression of being eruptions of the medulla through the upper cortex as the result of some external or pathological influence altogether. The occurrence of these peculiar soralia is so infrequent and their structure so bizarre that they are given no taxonomic recognition here.

*Platismatia norvegica* is an extremely oceanic species. It is not found beyond the area of very wet climates devoid of temperature extremes that characterize the region of the Pacific Northwest and the oceanic province of northwestern Europe. The belated recognition of the specific distinctness of this species in the well-known flora of Scandinavia prompted a number of reports and studies that ended with Ahlner's (1948) comprehensive treatment of the species in Scandinavia with a map of all collections; the reader is referred to this publication for details of the northern European range. In that paper and in Hakulinen's (1963) lichen flora of Finland, the species is also reported from extreme southern Finland. No Finnish species were seen in the present study, but we have no reason to doubt the correctness of those records.

A map of the worldwide distribution of *Cetraria norvegica* was also published by Ahlner (1948). The map in the present treatment (Figure 27) does not differ qualitatively from Ahlner's although we have added more American localities. The present study and the data collected by Ahlner (1948) also show that although the species grows on both trees and on rocks, it is more common on bark in the southern part of its range and on rocks in the northern part even though both substrate types are generally present throughout the range.

CHEMICAL ANALYSIS.—The seven samples tested contained caperatic acid and atranorin. No protolichesterinic acid was detected in the benzene extract after treatment with the GE or GAW solutions. Atranorin was proved in this extract in the GE and GA*o*-T solutions. The subsequent acetone extract contained more atranorin in addition to caperatic acid as found by treating the extract with the GE, GAW, and GA*o*-T solutions. No other fatty acids were detected. No other substances reacting with PD were found in the acetone extract after chromatography in pyridine-ethyl acetate-water (1:2:1). In the GA*o*-T solution, smaller crystals similar to the *o*-toluidine derivative of atranorin occurred in abundance accompanied by those of the typical atranorin derivative.

Nomenclature.—Lynge listed about 30 specimens with the original diagnosis of *Cetraria lacunosa* f. *norvegica*. No type specimen was designated, but when Du Rietz elevated the forma to specific rank, he indicated as the type a Norwegian specimen collected by himself but not among those originally cited by Lynge. Since a taxon must be typified from the original material if possible, we have picked Lynge's collection from Store Kalsø in Hordaland as the lectotype. It is a large, well developed example of the species.

Representative specimens examined:

CANADA: Newfoundland: Locality unknown, *Despreaux*, 1828 (UPS); King Cove, *Dammon* 1 (US); St. John, *Fries*, 1871 (S, 2 collections).

British Columbia: Queen Charlotte Islands, Graham Island, *Persson* 26, 54 (COLO); Vancouver Island, Nanaimo River Valley, *Szczawinski* 558 (US); the same, Port Renfrew, *Schneider*, s.d. (UC); the same, Comox, *Macoun* 122 (WIS).

MIQUELON ISLAND: Locality unknown, *Delamare*, 1886 (DUKE, PC), *Delamare*, as *Arn., Lich. Exs.* 1366 (PC).

U.S.A.: Alaska: Kodiak Island, Kodiak, *Hultén* 5053 (UPS), *Eyerdam* 79 (WIS); Admiralty Island, Windfall Harbor, *Herre* 251 (UC); Glacier Bay, Beardsley Island, *Stephens* 242 (UC); Prince William Sound, Knight Island, *Eyerdam* 252, 254 (UC), *Norberg*, 1940 (S), College Fjord, *Viereck* 2419–B, Bainbridge Glacier, *Viereck* 1992–A (COLO); Kenai Peninsula, Seward, *Hultén* 7887 (UPS); Yukutat, *Schmuck* 19 (WIS); Juneau, *Hultén* 8558 (UPS).

Washington: Grays Harbor Co.: Pacific Beach, *Foster* 1359 (COLO–ABS). Jefferson Co.: Mouth of the Hoh River, *Brown & Muenscher* 154 (UC, WTU). Pacific Co.: Willapa Bay, Toka Point, *Foster* (COLO–ABS). Pierce Co.: Mt. Rainier National Park, *Pechanec* (COLO). Whatcom Co.: Mt. Baker, *Howard* 1180a (LD).

Oregon: Marion Co.: Silverton, Powers Creek, *Foster* 1200 (US).

SWEDEN: Jämtland: Åre, *Ahlner*, 1951 (DUKE), *Hasselrot*, 1937 (LD), *Håkansson*, 1949 (LD), *Santesson* 48443, 48443b (UPS); Frostviken, *Stenholm*, 1918 (GB).

Dalarne: Malung, *Hasselrot*, 1934 (LD, 4 collections), *Hasselrot*, 1937 (S), *Hasselrot*, as *Magn., Lich. Sel. Scand. Exs.* 184 (GB, LD, S); Lima, *Hasselrot*, 1934 (LD).

Värmland: Munkfors, *Sundell*, 1952 (LD); Dalby, *Persson*, 1948 (S).

Västergötland: Bredareds, *Hasselrot*, 1961 (S).

NORWAY: Nördland: Elsfjord, *Ahlner*, 1939 (S); Nord-Rana, *Ahlner*, 1937 (S).

Nord-Tröndelag: Egge, *Ahlner*, 1934 (S); Grong, *Österlind*, 1938 (LD); Vaerdal, *Österlind*, 1932 (LD); Sörli, *Ahlner*, 1938 (S); Malm, *Ahlner*, 1938 (S, 2 collections).

Hordaland: Herdla, *Santesson*, 1937 (US); Voss, *Ahlner*, 1937 (S).

Rogaland: Hjelmeland, *Degelius*, 1947 (LD); Solendal, *Hasselrot*, 1939 (S); Rege Fjord, *Hasselrot*, 1939 (US).

Sogn og Fjordane: Eid, *Ahlner*, 1937 (S).

SCOTLAND: Loch Rannoch, *ex herb. Stirton* (BM, 2 collections); Killin, Craig Chaillech, *M'Andrew*, 1885 (BM).

**8. Platismatia regenerans** Culb. & Culb., sp. nov. PLATE 24

Thallus parvus vel mediocris, 4–8 cm. latus; laciniae 0.3–1.2 cm. latae, marginibus ascendentes. Superficies superior albida vel pallide cinerea centro et marginibus nigra vel sepiacea, levis, pseudocyphellata, pseudocyphellis parvissimis et inaequalibus, corporibus parvis, regenerantibus(?), isidioideis vel complanatis in partibus vetustioribus praedita. Superficies inferior picea, marginibus castanea, vulgo reticulato-rugosa, rhizinata, fere punctata. Cortex superior prosoplectenchymatosus, 21–31μ crassus; medulla (104–)120–180(–208)μ crassa, IKI—; cortex inferior 18–26μ crassus. Pycnidia et apothecia ignota.

Thallus small to medium, 4–8 cm. broad; lobes 0.3–1.2 cm. broad, the margins ascending. Upper surface whitish or pale gray, the center and margins black or dark brown, smooth, pseudocyphellate, the pores very small and irregular, the older parts of the surface with scattered regenerative(?) bodies, isidioid or flattened and lobule-like, mostly less than 0.5 mm. broad. Lower surface black, the margins dark brown, commonly reticulately rugose, rhizinate, usually punctate. Upper cortex prosoplectenchymatous, 21–31μ thick; medulla white (104) 120–180(–208)μ thick, IKI—; lower cortex 18–26μ thick. Pycnidia and apothecia unknown.

TYPE.—Tourist Trail, just above Kambarabga radio tower, Kinabalu National Park, Sabah (Borneo), 2,000 m. alt., *Hale* 28207 (US, holotype).

MEDULLARY REACTIONS.—K—, C—, KC—, PD—.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 29).—The high mountains of Sabah (Borneo).

The only species with which *Platismatia regenerans* might be confused is *P. erosa*. It differs from *P. erosa* in that it lacks true isidia although it may have a few flattened, apparently regenerative lobulae on the older parts of the thallus that might be mistaken for isidia.

CHEMICAL ANALYSIS.—The residue from the benzene extract of four samples tested showed atranorin in the GE and GA*o*-T solutions. These residues did not give positive tests for protolichesterinic acid in the GE or GAW solutions. The residues from subsequent acetone extractions contained more atranorin and caperatic acid. Both crystal forms of caperatic acid were observed in the GE solution, and caperatic acid was also detected in the GAW and GA*o*-T solutions. This species may also contain the unidentified substance (or substances) observed in *P. erosa*, *P. formosana*, and *P. interrupta*. One specimen showed yellow crystals in the GE solution, and another gave clusters of long fine needles in the GA*o*-T solution.

SPECIMENS EXAMINED:

SABAH (BORNEO): Kinabalu National Park, Tourist Trail, just above Kambarabga radio tower, 2,000 m., *Hale* 28207, 28932 (US); the same, woods below second radio tower (above Kambarabga), 2,200 m., *Hale* 28642 (US); the same, open ridge between East and West Mesilau Rivers, 1,800 m., *Hale* 29084 (US).

9. **Platismatia stenophylla** (Tuck.) Culb. & Culb., comb. nov. PLATE 24

*Cetraria lacunosa* b. *stenophylla* Tuck., Synops. No. Amer. Lich. 1:35. 1882.
Type: U.S.A., California, *Bolander* (FH, holotype).
*Cetraria stenophylla* (Tuck.) Merr., Bryologist 13:27. 1910.

Thallus medium, 5–10 cm. broad; lobes linear, narrow, (0.5)1–4 mm. broad, often becoming trough-shaped as the margins roll inwards, the margins occasionally with small lobulae oriented at right angles to the axis of the lobes, often attached to the substrate only at the base. Upper surface whitish, tan, pale brown or occasionally somewhat darkening, smooth, not pseudocyphellate, sorediate, or isidiate. Lower surface whitish, tan, or brown, not punctate, minutely reticulate-rugose, sometimes appearing veined with the crests of the ridges darkening; rhizines rare, a few at the place of attachment only. Upper cortex 16–23μ thick; medulla 86–150(–208)μ thick, IKI+ lavender; lower cortex (13–)16–21μ thick. Apothecia common, especially in the southern part of the range, terminal, 0.4–1 cm. broad, perforate or not; hymenium 39–52μ thick, subhymenium 18–34μ, thick, often underlain with algae; spores 8, small, ellipsoid or spheroid 4–5×5–8μ. Pycnidia few, black, marginal; conidia 1×5–8μ, rod-shaped.

MEDULLARY REACTIONS.—K−, C−, KC−, PD−.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 23).—Western North America from Vancouver Island south to west-central California; on trees, usually near the shore.

*Platismatia stenophylla* is a well defined species with narrow, linear lobes, a trait shared in this genus by only *P. herrei* which is easily distinguished from the present species by its abundant marginal isidia. In the northern part of the range, *P. stenophylla* has more darkly colored thalli with strongly incurved margins and a paucity of apothecia. The southern plants are more robust, stouter, and fruit more freely. In spite of these tendencies, specimens cannot be assigned to their geographical origin with high accuracy upon habit alone, and intermediate forms are common.

*Platismatia stenophylla* has the most narrowly restricted geographic range of any of the American species of the genus.

CHEMICAL ANALYSIS.—The five samples tested of this species showed atranorin in the GE and GA*o*-T solutions and by chromatography. The benzene extract seemed to contain only atranorin while the subsequent acetone extract consisted of this depside mixed with caperatic acid, which was identified by the crystals in the GE and GAW solutions. No other fatty acids were noted.

ADDITIONAL SPECIMENS EXAMINED:

CANADA: BRITISH COLUMBIA: Vancouver Island, Nanaimo Lakes, *Krajina et al.* S-15 (DUKE).

U.S.A.: WASHINGTON: Lewis Co.: Deschutes Park, Snoqualmie National Forest, *Buchta & Hedglin*, 1958 (WTU). Pierce Co.: Mt. Rainier, *Flett*, 1919 (US). Spokane Co.: Spangle, *Cooke* 23198 (WIS). Whitman Co.: Kamiak Butte, *Imshaug* 16462 (MSC).

OREGON: Benton Co.: Corvallis, *Becking* 5304666 (COLO).

IDAHO: Latah Co.: Palouse Range Ridge, *Imshaug* 16413 (MSC).

CALIFORNIA: Humboldt Co.: Locality unknown, *Bolander* (FH, US). Santa Cruz Co.: Castle Rock, *Herre* 1025, 1942, 4715 (WIS), *Herre* 3235 (COLO), *Shushan* 14737 (DUKE, US); Devils Canyon and Castle Rock, *Herre*, as *Krypt. Exs. Vidobon.* 1553 (US); Skyline Boulevard, south of Page Mill Road, *Wiggins* C-68 (DUKE); Ben Lomond, *Thiers* 9158 (WIS). San Mateo Co.: Hubbard Park, *Thiers* 9232 (WIS).

**10. Platismatia tuckermanii** (Oakes) Culb. & Culb., comb. nov. PLATE 25

*Cetraria tuckermanii* Oakes *in* Tuck., Amer. Journ. Sci. & Arts 45:48. 1843. Type: U.S.A., Massachusetts, Cambridge, *Tuckerman*, 1838 (FH, neotype).

*C. lacunosa β atlantica* Tuck., Proc. Amer. Acad. 1:208. 1847. Type: Lake Superior, *Agassiz* (FH, lectotype).

*C. atlantica* (Tuck.) Du Rietz, Bot. Not. 1925:10. 1925.

Thallus medium, to 7–12 cm. broad, loosely attached; lobes rounded, 0.4–2.2 cm. broad. Upper surface ashy-white or gray, irregularly or reticulately pitted, often conspicuously so, without pseudocyphellae, soredia, or isidia. Lower surface white or slightly tan with well defined patches becoming black or dark brown, especially toward the center of the thallus, minutely and reticulately pitted, not punctate; rhizines few, black at the center, pale or tipped with white nearer the margin. Upper cortex 18–26(–29)μ thick; medulla 109–182(–234)μ thick, the hyphae loosely interwoven, IKI –; lower cortex 16–23(–29)μ thick. Apothecia common, marginal or submarginal, 2–10 mm. broad, usually perforate; hymenium (39–)50–65(–73)μ; subhymenium 18–26 (–34)μ, IKI+ lavender, underlain by at least a few algae; spores 8, ovoid to subglobose, 4–5×6–8μ. Pycnidia common, blackening, marginal or submarginal, immersed, the ostiole minute; conidia rod-shaped, ca. 1×5–8μ.

MEDULLARY REACTIONS.—K –, C –, KC –, PD –.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 31).—Southern Ontario and Quebec, Newfoundland to the Lake States and south in the Appalachians to Alabama and Georgia; on the bark of trees, primarily of conifers, and occasionally on old wooden fences.

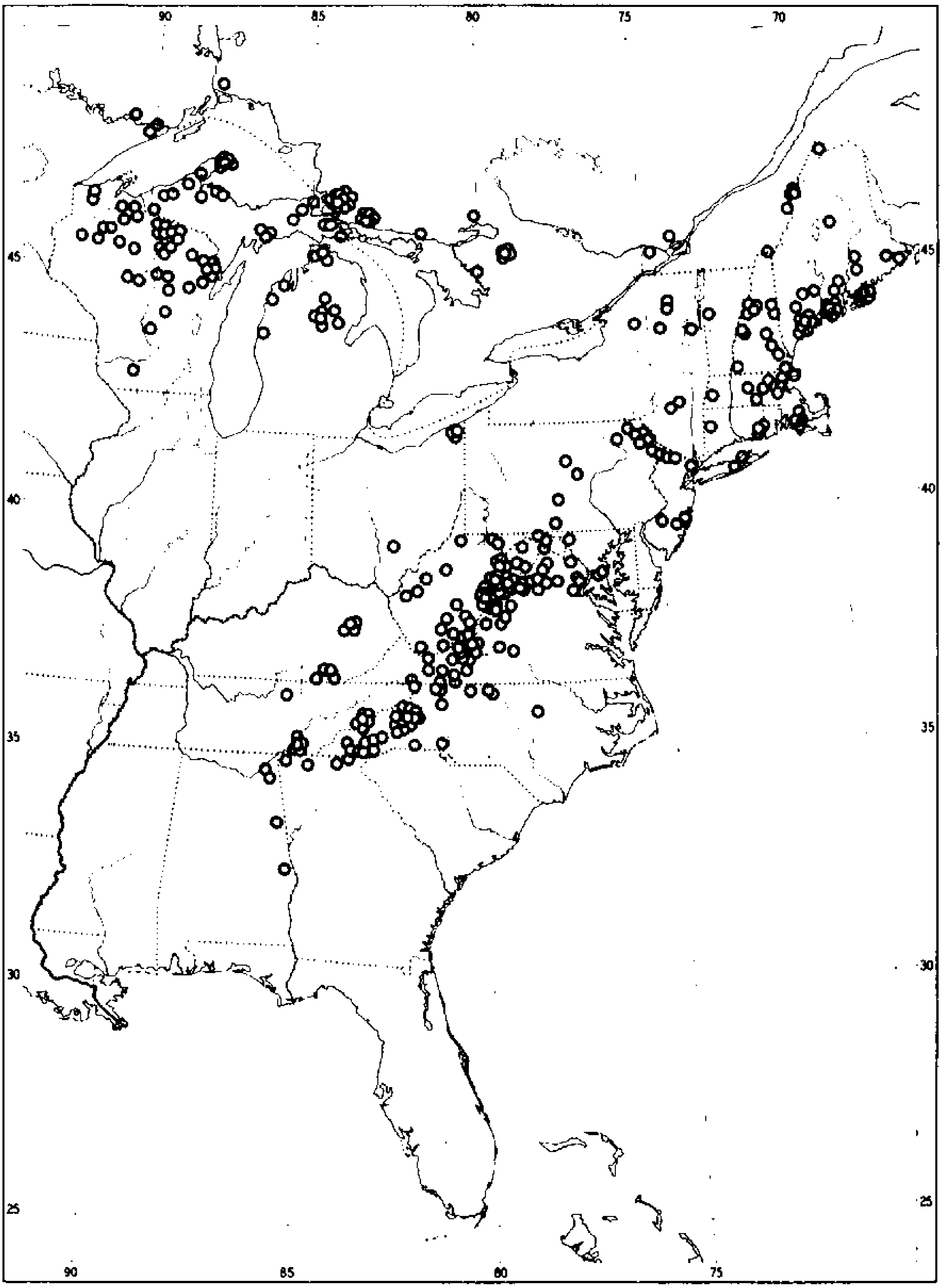


FIGURE 31. Distribution of *Platismatia tuckermanii* (Oakes) Culb. & Culb.

*Platismatia tuckermanii* is quite distinct from all other species. In the past it has been mistaken for *P. lacunosa* although the ranges of the species do not overlap. The thallus of *P. tuckermanii* is broadly reticulate, but it lacks the deep, sharp, thallus folds and ridges that characterize *P. lacunosa* and differs chemically in lacking fumarprotocetraric acid and therefore reacts negatively with *p*-phenylenediamine.

In herbarium collections, members of the *Cetraria ciliaris* Ach. and related species have often been mistakenly identified as *Platismatia tuckermanii,* doubtless because these plants regularly grow together throughout their range. The members of the *Cetraria ciliaris* group all have marginal stalked pycnidia, usually have marginal cilia, and the most common species have aromatic constituents (alectoronic, α-collatolic, olivetoric, and physodic acids) which give positive reactions with C or KC. *Platismatia tuckermanii* lacks all of these traits. There are also fundamental differences in the anatomy of the upper cortex between the species.

*Platismatia tuckermanii* is also sometimes mistaken for *P. glauca* although almost invariably it is the more abundant of the two species in places where they grow together. It can be differentiated at once from esorediate and nonisidiate specimens of *P. glauca* by its negative thallus reaction with IKI which in *P. glauca* is strongly positive, producing a deep blue-black coloration. Although many morphologic characters separate the two species, the IKI test is quickly used and definitive.

*Platismatia tuckermanii* is broadly distributed in northeastern temperate North America. The species belongs to the northern conifer-dominated forests and becomes rare abruptly outside of this vegetational region.

*Platismatia tuckermanii* shows a strong preference for the bark of coniferous trees. In northern Wisconsin where the species is common, its presence at breast height in quadrats on 2,000 randomly selected trees was analyzed (Culberson, 1955). It was found on 19 percent of the white pines (*Pinus strobus*), 7 percent of the jack pines (*Pinus banksiana*), 2 percent of the lindens (*Tilia americana*), and about 1 percent of the red pines (*Pinus resinosa*), hemlocks (*Tsuga canadensis*), red oaks (*Quercus rubra*), yellow birches (*Betula lutea*), and sugar maples (*Acer saccharum*). It was absent from the white birches (*Betula papyrifera*), red maples (*Acer rubrum*), beeches (*Fagus grandifolia*), and poplars (*Populus* spp.). Elsewhere in its range its preference for coniferous trees is also obvious. It is also sometimes found on old wooden fences but almost never on rocks.

CHEMICAL ANALYSIS.—Seven samples were tested and all contained atranorin as demonstrated in the GE and in GA*o*-T (Plate 2, Figures 8 and 10) solutions. The benzene extract gave no crystals of protolichesterinic acid in the GE or GAW solutions, but the subsequent acetone extract showed caperatic acid. Crystals of caperatic acid were observed in the GE (in both crystal forms), GAW, and GA*o*-T solutions. The acetone extract chromatographed in pyridine-ethyl acetate-water showed no components reacting with PD other than atranorin.

Nomenclature.—No specific collections were cited with the description of *Cetraria tuckermanii* Oakes and no original collections of undisputed authenticity exist. The neotype selected here (see above) is a specimen in Tuckerman's herbarium (FH) bearing the name "*Cetraria tuckermanii*" and collected in Massachusetts five years before Oakes' description was published. There is no doubt of the reference intended in the application of Oakes' name, and the neotype fits the description well. It is also highly probable that Oakes even examined this very collection when he described the new species.

In his description of *Cetraria lacunosa β atlantica*, Tuckerman cited two specimens, one from New York and the other from Pennsylvania. Today there are no specimens labeled with this name in his herbarium. In the original description the range is given as "Lake Superior to New England." In Tuckerman's herbarium there is a specimen collected by Agassiz and labeled "Lake Superior." This collection, from Louis Agassiz's famous trip, is undoubtedly the material upon which the statement concerning the geographic range in the original description referred. We designate this specimen as the lectotype of *C. lacunosa β atlantica*.

Du Rietz (1925) cited specimen number 468 in *Reliquiae Farlowianae* as the type of *C. lacunosa β atlantica*, but this undated New Hampshire collection, issued simply as *C. lacunosa*, cannot in any way be associated with the original diagnosis of the variety.

### Representative specimens examined:

CANADA. Ontario: Algoma District, Mississagi River, *Cain* 25867, 25870, 25872 (US), Timagami, Gull Lake, *Cain* 26782 (COLO, US); Emo, *Fink* 739 (K, MSC, UC); Ottawa, *Couet* 1899 (PC).

Quebec: Bellechasse Co.: Ste. Camille, *Masson* 5007, 5008, 6182, (WIS). Terrebonne Co.: Parc du Mont Tremblant, *Hermann* 15759 (US). Woburn Co.: Frontenac, *Masson* 6031 (WIS).

U.S.A.: Maine: Hancock Co.: Mt. Desert Island, *Tuckerman*, 1871 (FH). Lincoln Co.: Hog Island, *Wiley*, 1953 (WIS). Piscataquis Co.: Mt. Katahdin, *Degelius*, 1939 (US). Washington Co.: North Lubec, *Cummings, Dec. North Amer. Lich.* 279 (DUKE, WIS).

Vermont: Addison Co.: Bristol, *Faxon*, 1879 (WIS).

New Hampshire: Belknap Co.: Gilmanton, *Blake* 5 (COLO). Carroll Co.: Chocorua, *Farlow, Rel. Farlowianae* 468 (UC, US, WIS). Grafton Co.: North Woodstock, *Cummings, Dec. North Amer. Lich.* 46 (DUKE, MSC, US, WIS).

Massachusetts: Bristol Co.: New Bedford, *Willey* 109 (US). Essex Co.: Manchester, *Seymour*, 1908 (UC). Worcester Co.: Lunenburg, *Sargent*, 1883 (UC).

Connecticut: New London Co.: Norwich, *Setchell*, 1883 (UC).

New York: Essex Co.: Chilson Lake, *Harris*, 1898 (COLO–ABS, US). Greene Co.: Maplehurst, *Dix*, 1929 (DUKE). Suffolk Co.: Riverhead, *Brodo* 1097 (MSC).

New Jersey: Bergen Co.: Closter, *Grout* 6185 (DUKE). Burlington Co.: Chatsworth, *Darrow* 1905 (WIS). Ocean Co.: Lakehurst, *Thomson,* 1940 (WIS). Sussex Co.: Highview Mountain State Park, *Hale* 17291 (DUKE, US).

PENNSYLVANIA: Clinton Co.: Westport, *Hale* 16082 (US). Huntingdon Co.: Penn State Nature Camp, *Thomson,* 1937 (WIS). Monroe Co.: Pocono Pines, *Kaiser,* 1910 (DUKE). Susquehanna Co.: Starruca Station, *Dix,* 1940 (DUKE). Wayne Co.: Scott Center, *Dix,* 1941, 1943 (DUKE, 2 collections).

OHIO: Ashtabula Co.: Orwell, *Bogue* 269 (DUKE). Hocking Co.: Old Man's Cave, *Hale* 13328 (US).

KENTUCKY: Lee Co.: Beattyville, *Hale* 13758 (US). Menifee Co.: 10 mi. southwest of Mariba, *Hale* 13423 (US). Powell Co.: Natural Bridge State Park, *Braun,* 1916 (DUKE). Whitley Co.: Cumberland Falls, *Hale* 13105 (US).

WEST VIRGINIA: Cabella Co.: Milton, *Hale* 10779 (US). Gilmer Co.: Cedarville, *Hale* 10500 (US). Hardy Co.: Mathias, *Gillespie* 15437 (US). Monroe Co.: Peterstown, *Hale* 13064 (US). Pendleton Co.: Judy Gap, *Hale* 10127 (US). Pocahontas Co.: Michael Mountain, *Gray* 3254, (COLO–ABS). Raleigh Co.: Clear Creek, *Hale* 11840 (US). Tucker Co.: Canaan Mountain, *Allard* 10907A (US).

VIRGINIA: Appomattox Co.: Appomattox Surrender Grounds, *Hale* 15610 (US). Culpeper Co.: Jeffersonton, *Hale* 18472 (US). Giles Co.: Mountain Lake, *Culberson* 11251 (DUKE). Grayson Co.: Comers Rock, *Hale, Lich. Amer. Exs.* 60 (COLO, DUKE, MSC, UC, WIS). Page Co.: Shenandoah National Park, *Ireland* 3776 (US). Smyth Co.: Whitetop Mountain, *Hale* 18629 (US). Wythe Co.: Wytheville, *Hale* 12024 (US).

MARYLAND: Anne Arundel Co.: Locality unknown, *Tuckerman,* 1852 (FH). Prince Georges Co.: Cedarville State Forest, *Hale* 14346 (US).

NORTH CAROLINA: Avery Co.: Grandfather Mountain, *Moore* 1897 (DUKE). Gaston Co.: Gastonia, *Culberson* 5258 (DUKE). Jackson Co.: Glenville, *Culberson* 5748 (DUKE). McDowell Co.: Buckcreek Gap, *Culberson* 4873 (DUKE).Macon Co.: Mt. Staula, *Moore* 1592 (DUKE). Mitchell Co.: Spruce Pine, *Culberson* 4847 (DUKE). Orange Co.: Hillsborough, *Culberson* 12069 (DUKE). Yancey Co.: Mt. Mitchell, *Culberson* 4814 (DUKE).

TENNESSEE: Hamilton Co.: Lookout Mountain, *Calkins* 236 (UC). Johnson Co.: Backbone Rock Recreational Area, *Hale* 18408 (US). Sevier Co.: Mt. Le Conte, *Degelius,* 1939 (US).

SOUTH CAROLINA: Greenville Co.: Greenville, *Hale* 7759 (US).

GEORGIA: Dade Co.: Trenton, *Hale* 7383 (US). Murray Co.: Chatsworth, *Hale* 7423 (US). Towns Co.: Hiwassee, *Culberson* 7274 (COLO, DUKE, US). Union Co.: Vogel State Park, *Hale* 7343 (US).

ALABAMA: Cleburne Co.: Cheaha Park, *Hale* 7113 (US). De Kalb Co.: De Soto Park, *Hale* 7024 (US). Jackson Co.: Section, *Hubricht* B2182 (WIS). Lee Co.: Auburn, *Becking* 5910004 (US).

MICHIGAN: Baraga Co.: Covington, *Imshaug* 20846 (MSC). Chippewa Co.: Hulbert, *Thomson* 1008 (WIS). Houghton Co.: Rice Lake, *Wetmore* 1315 (MSC). Keweenaw Co.: Isle Royale, *Wetmore* 2522 (COLO, WIS). Marquette Co.: Cliff Lake, *Imshaug* 4325 (WIS). Schoolcraft Co.: Big Spring Indian Lake, *Imshaug* 19993 (MSC).

WISCONSIN: Adams Co.: Friendship, *Culberson* 3120 (WIS). Ashland Co.: Mellen, Lake Galilee, *Culberson* 3629 (WIS). Door Co.: Porte des Morts Strait, *Culberson* 4145 (WIS). Douglas Co.: Brule River Valley, *Thomson, Lich. Wiscon. Exs.* 39 (COLO, DUKE, MSC, WIS). Iron Co.: 16 mi. south of Hurley, *Culberson* 3125 (MSC, WIS). Taylor Co.: Rib Lake, *Culberson* 4235 (WIS). Oneida Co.: Woodruff, *Thomson, Lich. Wiscon. Exs.* 18 (COLO, DUKE, MSC, US, WIS). Vilas Co.: Lac Vieux Desert, *Cheney,* 1893 (WIS).

# Literature Cited

ACHARIUS, E.

1798. Lichenographiae Suecicae prodromus. xxiv+264 pp. D. G. Björn, Lincopiae.

1803. Methodus qua omnes detectos lichenes. lv+394 pp. C. F. Marquard, Stockholm.

1810. Lichenographia universalis. viii+696 pp. I. F. Danckwerts, Gottingae.

AHLNER, S.

1948. Utbredningstyper bland nordiska barrträdslavar. Acta Phytogeogr. Suecica 22: i–ix+1–257.

AHTI, T.

1964. Macrolichens and their zonal distribution in boreal and arctic Ontario, Canada. Ann. Bot. Fenn. 1:1–35.

ALMBORN, O.

1965. The species concept in lichen taxonomy. Bot. Not. 118: 453–457.

ASAHINA, Y.

1936–1940. Mikrochemischer Nachweis der Flechtenstoffe I–XI. Journ. Jap. Bot. 12: 513–525, 859–872; 13: 529–536, 855–861; 14: 39–44, 244–250, 318–323, 650–659, 767–773; 15: 465–472; 16: 185–193.

ASAHINA, Y., and FUZIKAWA, F.

1935. Untersuchungen über Flechtenstoffe, L. Mitteil.: Über die Bestandteile von *Parmelia perlata* Ach. Chem. Ber. 68: 634–639.

BRETSCHNEIDER, E.

1898. History of European botanical discoveries in China. II. [The facsimile reprint of 1962.] pp. 625–1167. Zentral-Antiquariat der Deutschen Demokratischen Republik, Leipzig.

CRONQUIST, A.

1964. The old systematics. *In* C. A. Leone's (editor) "Taxonomic biochemistry and serology," pp. 3–11. Ronald Press Company, New York.

CULBERSON, C. F.

1963. Sensitivities of some microchemical tests for usnic acid and atranorin. Microchem. Journ. 7: 153–159.

1964. Joint occurrence of a lichen depsidone and its probable depside precursor. Science 143: 255–256.

1965. A note on the chemical strains of *Parmelia furfuracea*. Bryologist 68: 435–439.

CULBERSON, C. F., and CULBERSON, W. L.

1966. The identification of imbricaric acid and a new imbricaric acid-containing lichen species. Bryologist 69: 192–202.

CULBERSON, W. L.

1955. The corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. Ecol. Monogr. 25: 215–231.

1958. The chemical strains of the lichen *Parmelia cetrarioides* Del. in North America. Phyton 11: 85–92.

1963. The lichen genus *Thamnolia*. Brittonia 15: 140–144.

1965. *Cetraria chicitae*, a new and widely distributed lichen species. Bryologist 68: 95–99.

1966a. The lichen genus *Aspidelia* Stirt. Bryologist 69: 113–114.

1966b. The typification of the genus *Platyphyllum* and a proposal for the conservation of *Cetraria* Ach. against *Platyphyllum* Ventenat. Taxon 15: 315–316.

1967. Analysis of variation in the *Ramalina siliquosa* species complex. Brittonia 19: 333–352.

CULBERSON, W. L., and CULBERSON, C. F.
1965. *Asahinea*, a new genus in the Parmeliaceae. Brittonia 17: 182–190.
1967. Habitat selection by chemically differentiated races of lichens. Science 158: 1195–1197.
DAHL, E.
1952. On the use of lichen chemistry in lichen systematics. Rev. Bryol. et Lichénol. 21: 119–134.
DU RIETZ, G. E.
1924. Kritische Bemerkungen über die *Parmelia perlata*-Gruppe. Nyt. Mag. Naturvidensk. 62: 63–82.
1925. Flechtensystematische Studien. V. Bot. Not. 1925: 1–16.
ERDTMAN, H.
1962. The chemistry of forests, humic acids, lichens, lignans, lignins, and conifers. Tappi 45(4): 14A, 16A, 18A, 20A, 26A, 28A, 30A, 34A, 36A, 38A.
ERDTMAN, H., and WACHTMEISTER, C. A.
1957. Phenoldehydrogenation as a biosynthetic reaction. *In* "Festschrift Arthur Stoll," pp. 144–165. Sandoz AG., Basel.
FLAGEY, C.
1896. Catalogue des lichens de l'Algérie. xi+139 pp. Adolphe Jourdan, Alger.
GYELNIK, V.
1933. Lichenes varii novi critici. Acta Fauna Fl. Univ., Ser. II: Bot. [București] 1(5–6): 3–10.
1934. Additamenta lichenologica, I. Rev. Bryol. et Lichénol. 7: 219–222.
HAKULINEN, R.
1963. Jäkäläkasvio. 255 pp. Werner Söderström Osakeyhtiö, Helsinki.
HALE, M. E., JR.
1960. The typification of *Parmelia cetrarioides*. Svensk Bot. Tidskr. 54: 269–272.
1965. A monograph of *Parmelia* subgenus *Amphigymnia*. Contrib. U.S. Nat. Herb. 36: 193–358.
HILLMANN, J., and GRUMMANN, V.
1957. Kryptogamenflora der Mark Brandenburg und angrenzender Gebiete. Band VIII: Flechten. x+898 pp. Gebrüder Borntraeger, Berlin.
HOSOKAWA, T., ODANI, N., and TAGAWA, H.
1964. Causality of the distribution of corticolous species in forests with special reference to the physio-ecological approach. Bryologist 67: 396–411.
LAVEN, L.
1941. *Parmelia cetrarioides* Del. f. *bisoralifera* Laven nova forma. Repert. Spec. Nov. Fedde. 50: 294–295.
LYNGE, B.
1921. Studies on the lichen flora of Norway. Videnskaps. Skrift. Mat.-naturv. Kl. 1921(7): 1–252.
MOSBACH, K.
1961. Die Rolle der Malonsäure in der Biosynthese der Orsellinsäure. Die Naturwissenschaften 48: 525.
1964. On the biosynthesis of lichen substances. Part 1. The depside gyrophoric acid. Acta Chem. Scand. 18: 329–334.
NYLANDER, W.
1855. Europas lafarter. Bot. Not. 1855: 129–154.
OZENDA, P.
1963. Lichens. Handbuch der Pflanzenanatomie, Band 6, Teil 9, Abteilung: Spezieller Teil. x+199 pp. Gebrüder Borntraeger, Berlin-Nicolassee.

RÄSÄNEN, V.

1952. Studies on the species of the lichen genera *Cornicularia, Cetraria* and *Nephromopsis*. Kuopion Luonnon Ystävain Yhdistyksen Julkaisuja 2B(6): 1–53.

[RASSADINA, K. A.]

1950. [The *Cetrariae* of the U.S.S.R.] [In Russian.] Plantae Cryptogamae, Acta Inst. Bot. Acad. Sci. Unionis Rerum Publ. Sovet. Socialist. 5: 171–304.

RICHARDS, J. H., and HENDRICKSON, J. B.

1964. The biosynthesis of steroids, terpenes, and acetogenins. xii+416 pp. W. A. Benjamin, Inc., New York.

SANTESSON, R.

1942. *Pseudoparmelia* Lynge, a lichen genus to be rejected. Svensk Bot. Tidskr. 36: 471–474.

SANTESSON R., and CULBERSON, W. L.

1966. The typification of the homonymic generic names *Platisma* (*Platysma*) proposed for lichens. Bryologist 69: 100–104.

SATO, M.

1943. Index plantarum nipponicarum IV. Lichenes. 128 pp. Tokyo Kagaku Hakubutukan, Tokyo.

SCOTT, A. I.

1965. Oxidative coupling of phenolic compounds. Quart. Rev. [London] 1965: 1–35.

SHIBATA, S.

1965. Biogenetical and chemotaxonomical aspects of lichen substances. *In* "Beiträge zur Biochemie und Physiologie von Naturstoffen. Festschrift Kurt Mothes zum 65. Geburtstag," pp. 451–465. Gustav Fischer Verlag, Jena.

STAHL, E. (editor.)

1965. Thin-layer chromatography, a laboratory handbook. xvi+553 pp. Springer-Verlag, Berlin.

TAGUCHI, H., SANKAWA, U., and SHIBATA, S.

1966. Biosynthesis of usnic acid in lichens. Tetrahedron Letters 42: 5211–5214.

WACHTMEISTER, C. A.

1956. Identification of lichen acids by paper chromatography. Bot. Not. 109: 313–324.

1959. Flechtensäuren. *In* H. F. Linskens' (editor), "Papierchromatographie in der Botanik," pp. 135–141. Zweite, erweiterte Auflage. Springer-Verlag, Berlin.

WHALLEY, W. B.

1963. The biosynthesis of fungal metabolites. *In* P. Bernfeld's (editor) "Biogenesis of natural compounds," pp. 797–829. Macmillan Co., New York.

YAMAZAKI, M., MATSUO, M., and SHIBATA, S.

1965. Biosynthesis of lichen depsides, lecanoric acid and atranorin. Chem. Pharm. Bull. [Tokyo] 13: 1015–1017.

YAMAZAKI, M., and SHIBATA, S.

1966. Biosynthesis of lichen substances. II. Participation of $C_1$-unit to the formation of β-orcinol type lichen depside. Chem. Pharm. Bull. [Tokyo] 14: 96–97.

ZAHLBRUCKNER, A.

1930. Catalogus lichenum universalis. Band VI. 618 pp. Gebrüder Borntraeger, Leipzig.

# Index

(To species and infraspecific taxa. Synonyms in *italics*; page numbers of principal entries in **boldface.**)

U. S. GOVERNMENT PRINTING OFFICE : 1968 O - 277-920