GRAY HERBARIUM OF HARVARD UNIVERSITY

CONTRIBUTIONS

Nos. 185-191

1959-62

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXV

THE WILLOWS OF BOREAL WESTERN AMERICA

By

Hugh M. Raup

SPORANGIA OF THE FERN GENERA ALLIED WITH POLYPODIUM AND VITTARIA

By

Kenneth A. Wilson

THE SOMATIC CHROMOSOMES OF RUDBECKIA AND RELATED GENERA OF THE COMPOSITAE

By

Robert E. Perdue, Jr.

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

1959

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXV

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

1959

Issued March 27th

THE LEXINGTON PRESS, INC., LEXINGTON, MASSACHUSETTS

THE WILLOWS OF BOREAL WESTERN AMERICA

By

HUGH M. RAUP

CONTENTS

INTRODUCTION

The present paper is designed primarily for the description and identification of the willows known to occur in the northern part of North America west of Hudson and James Bays. The southern limits of the area treated form an irregular line connecting the southern end of the Alaska Panhandle, the upper Peace River, Lesser Slave Lake, Athabaska and McMurray on the Athabaska River, thence running eastward across northern Saskatchewan and Manitoba to about long. 96°W., and southeastward from there to include the southwestern shores of James Bay. It will also cover present knowledge of the willows of the western arctic islands.

In a paper published in 1943, I covered to the best of my knowledge the willow flora of boreal America westward to include the western shores of Hudson and James Bays, and to include that part of the District of Keewatin that lies in the basins of the Kazan River and Baker Lake, and in the basin of the Dubawnt River up as far as Dubawnt Lake. In northern Manitoba and Ontario that treatment covered the country westward approximately to long. 96°W. and southward to about lat. 51°. The areas just noted, therefore, bordering Hudson and James Bays on the west, constitute a region of overlap between my earlier paper and the present one.

I have drawn freely from the works of several recent students of northwestern American flora, notably those of Dr. A. E. Porsild and Dr. Eric Hultén. Porsild has traveled and collected widely in the Northwest Territories, Yukon and Alaska. His published papers contain a wealth of material pertinent to the present study (1943, 1945, 1951, 1955, 1957). The most comprehensive treatment of any large proportion of the northwestern American willows is in Hultén's *Flora of Alaska and Yukon* (1942, 1949). These papers, particularly that of Hultén, are so comprehensive, and cover so well the knowledge of the genus in the regions treated up to the times at which they were written, that I have used them as a sort of "datum plane" for the present study. There are, however, many instances in which I have differed from them in their interpretations of species and relationships, and on these occasions it has been necessary to go back into some of the earlier literature.

Further materials are in my own studies of the vascular plants of the southern and central parts of the Mackenzie drainage basin (1934, 1935, 1936, 1942, 1947), and additional specimens and notes gathered in the years 1943, 1944 and 1948 by my field associates and myself along the Alaska Highway between Dawson Creek in east central British Columbia, and Fairbanks in central Alaska. For data on the eastern part of the area, I have used for the most part my own study of *The Willows of the Hudson Bay Region and the Labrador Peninsula,* and a paper by Dr. H. J. Scoggan of the National Herbarium of Canada on *The Flora of Manitoba* (1957). Many suggestions for range extensions have come from the excellent series of manuscript maps accumulated by Dr. A. E. Porsild of the National Museum of Canada.

Several small or more or less localized collections made in recent years have been available to me, and have been of great value for the filling in of ranges and general knowledge of the species. Of particular note are those of the late

J. P. Anderson between Tanacross and Whitehorse in 1944, of Dr. C. H. D. Clarke in the vicinity of Kluane Lake and along the Haines Road in 1943 and 1944, of M. P. and R. T. Porsild at Johnson Crossing, Whitehorse, and on the Haines Road in 1944, of Dr. J. E. Cantlon and his associates along the Lower Colville River in 1953, and of Dr. T. M. C. Taylor and his associates along the Alaska Highway between Dawson Creek and Haines Junction, and along the Haines Road, in 1956. Likewise I have had access to the recent collections of Dr. H. J. Scoggan in northern Manitoba, and to those of Dr. W. K. W. Baldwin in northern Ontario and Manitoba.

Most of the herbarium material studied has been found at Harvard (GH, A), the New York Botanical Garden (NY), and especially in the rich collections of the National Museum of Canada at Ottawa (CAN). Other herbaria consulted are at the Bailey Hortorium at Cornell (BH), the Philadelphia Academy of Science (PH), the Universities of British Columbia (V) and Alberta (ALTA), the U. S. National Museum in Washington (US), the Department of Agriculture (Science Service) of Canada at Ottawa (DAO), the Naturhistoriska Riksmuseet at Stockholm (S), the British Museum (BM), Kew (K), and the University of Copenhagen (C).

The keys and dispositions of species have been strongly influenced by the work of Schneider, Ball, and Fernald on American willows during the past forty years. The only recent attempt at a complete monograph of the American species is that of Dr. Camillo Schneider, published between 1918 and 1921. The basic organization of my treatment of our willows, and much of the structure of the keys, are derived from Schneider's monograph. Material from Dr. M. L. Fernald's studies comes mainly from his treatment of the genus in the 8th edition of *Gray's Manual* (1950), though frequent reference has been made to several of his earlier papers published in *Rhodora*. Several papers by Dr. C. R. Ball and Dr. P. A. Rydberg have been used freely, and will be referred to in appropriate places in the text.

The inherent variability within species of willows makes definitive keys difficult to construct. Many species must be segregated, not on single unit characters, but often upon elaborate combinations of characters. Thus the keys must be in large measure descriptive. Further, the grouping of species into natural sections is at present inadequate, so that synoptic keys are less workable than purely artificial ones. I have made no attempt at a key to male specimens. This is due to the fact that our knowledge of variability in the male flowers is poorly developed, and to the fact that for several species no male flowers have ever been collected.

The key to sterile specimens, especially, is far from satisfactory. Its use must be restricted to well-developed, normal leafy material, for it does not take into account the often abnormally large and unusually-shaped leaves of rank-growing sprouts. The fickleness of vegetative characters in the willows is well illustrated by this key. Any major subdivision that might be chosen would leave a number of species in which the characters used would be combined: leaves serrate vs. entire, green beneath vs. glaucous beneath, pubescent vs. glabrous, obovate or oblanceolate vs. ovate or lanceolate, etc. Many species must therefore appear at several points in the key, probably at more places than I have given them. Such difficulties pyramid as the willow flora becomes larger. For small floras, containing twenty-five species or less, keys to sterile material are relatively simple. Fully as troublesome as the one I have attempted here is that of Schneider for all the American willows known to him at the time of his studies (1921: 107-16).

The terminal points in the main keys are in some cases individual species, and in others groups of species. Keys to the species within these groups will be found in the ensuing text immediately preceding the description of the first species named in each group.

No attempt has been made to give complete citations of synonyms, or of the many papers in which lists of willows or discussions of species have been published. Likewise I have omitted the citation of a great many of the specimens that I have seen in the preparation of the paper. However, references to the original descriptions of all the taxa maintained are given, and enough synonymy to make the list comparable with the more recent papers on the willows of the region. Literature necessary to discussions of the willow flora as a whole or of individual species is cited by author, year and page, and will be found listed alphabetically at the end of the paper. Specimens are cited only in cases of little-known species, or for species with limited or notably discontinuous ranges. Collection numbers cited without the names of collectors are from material gathered by my own field parties in the vicinity of the Alaska Highway in 1943, 1944, and 1948.

PROBLEMS IN THE DEFINITION AND ARRANGEMENT OF SPECIES

Salix is abundant throughout the whole region, not only in number of individuals, but also in number of species. Its species make up a major part of the shrubby flora of muskegs, prairie and swamp margins, open woods, and tundra. The genus is notorious for the variation that occurs within species, and for poor definition of morphological boundaries between many of the commonly recognized species. In the present treatment I have recognized 98 species and lesser categories. Of the 98 taxa, 61 have been given specific names.

A century and a half of study in so variable a group of plants as the American willows, together with a strong tendency to use a binomial system of nomenclature, have led inevitably to the description of many species of unequal taxonomic soundness. Much of the reputation of the willows as a difficult and frustrating genus to work with — *terra incognita* to most botanists and collectors — is due to lack of understanding of relationships among the many microspecies that have been described and given binomials. If it were possible to make a logical and widely accepted synoptic arrangement of the species in well-defined sections or subgenera, some of the confusion could be resolved. But the subgenera of *Salix* are not clearly defined, nor is there general agreement on how they should be constituted.

Certain of the species included in the present treatment are clearly defined. Occasional hybrids among them or between them and other species are found, but usually these are rather easily recognized as such and probably do not go beyond the F_1 generation. The ranges of such species do not overlap those of any other closely related species in our region, though a few of them may do so elsewhere. There are 20 of them, and they are as follows: *S. fragilis*, *S. interior*, *S. Setchelliana*, *S. polaris* subsp. *pseudopolaris*, *S. herbacea*, *S. glacialis*, *S. Turnorii*, *S. Farrae*, *S. cordata*, *S. commutata*, *S. Chamissonis*, *S. pyrifolia*, *S. Barrattiana*, *S. amplifolia*, *S. candida*, *S. Bebbiana*, *S. fallax*, *S. gracilis*, *S. arbusculoides*, *S. sitchensis*. Some of them, such as *S. Setchelliana*, *S. Turnorii*, *S. amplifolia*, and possibly *S. fallax*, are highly localized or more widespread endemics so far as present knowledge goes. Others, such as *S. Bebbiana*, are among the commonest and most widely distributed willows in the region. Most of the variants that have been described within these well-defined species have proved to have poorly-defined geographic segregation or none at all.

None of the remaining 41 species can be isolated in the above manner. They can, however, be arranged in groups, each containing two or more closely related species whose ranges commonly overlap, and among which intermediates are common. It is unknown whether these intermediate forms are the result of introgressive hybridization, or are brought about by genetic segregation within large species populations rich in biotypes. Usually the species included in the groups show fairly well-defined geographic distributional patterns, while minor variants within the species have none or very poorly-defined ones. A few of the groups, such as those related to *S. glauca* and *S. rigida,* would be enlarged by additional species if a larger geographic area were involved, but I have included only the forms known to occur in the region upon which this paper is based.

The following arrangement of the 41 species into 16 groups is tentative, intended to be merely suggestive of what I believe to be the probable relationships. If put into practice it would involve a trinomial nomenclature, or quadrinomial if minor varietal trends were recognized. The species themselves (as treated in the present paper) would become subspecies within the groups. Although in a few cases the relationships seem sufficiently clear at present to justify setting up such a nomenclature, in most of the groups more detailed study is needed before this can be done properly. Therefore I prefer to leave the arrangement tentative for the time being.

Salix lucida group: *S. lucida, S. lasiandra, S. serissima.*
Salix reticulata group: *S. reticulata, S. vestita.*
Salix rotundifolia group: *S. rotundifolia, S. Dodgeana, S. phlebophylla.*
Salix arctica group: *S. arctica, S. arctophila.*
Salix ovalifolia group: *S. ovalifolia, S. stolonifera, S. flagellaris.*
Salix glauca group: *S. glauca, S. niphoclada, S. brachycarpa, S. cordifolia.*
Salix MacCalliana group: *S. MacCalliana, S. Tyrrellii.*
Salix rigida group: *S. rigida, S. lutea, S. mackenzieana.*
Salix Barclayi group: *S. Barclayi, S. myrtillifolia.*
Salix glaucophylloides group: *S. glaucophylloides, S. padophylla.*
Salix Richardsonii group: *S. Richardsonii, S. calcicola.*
Salix alaxensis group: *S. alaxensis, S. silicicola.*
Salix arbutifolia group: *S. arbutifolia, S. pedicellaris, S. athabascensis, S. hebecarpa.*
Salix discolor group; *S. discolor, S. Scouleriana.*
Salix phylicifolia group: *S. phylicifolia, S. pulchra, S. planifolia.*
Salix pellita group: *S. pellita, S. subcoerulea.*

The 16 species-groups may be arranged in five main categories. First are those whose segregates are eastern and western in the northern part of the continent, with well-defined areas of overlap among them. An arctic-alpine subcategory of these is represented by three groups. The *S. reticulata* group (Map 3),[1] in which *S. reticulata* itself has a wide transcontinental range, contains also *S. vestita* which is primarily eastern arctic and subarctic. The latter has also an isolated area in the Rocky Mountains outside the range of the former. The two overlap on the outer Labrador coast and in the southern Hudson Bay region. The *S. arctica* group (Map 7) likewise has a wide-ranging element (*S. arctica, sens. lat.*) and an eastern element (*S. arctophila*) which has its largest development in the eastern Arctic but has a western extension to northeastern Alaska. These two have a large area of overlap in the eastern Arctic. The *S. Richardsonii* group (Map 18) has a pattern of ranges somewhat similar to that of the *S. reticulata* group, but *S. Richardsonii* does not have so extensive a range in the eastern Arctic, and the area of overlap between it and *S. calcicola* is limited to the northwestern shores of Hudson Bay and southern Baffin Island. However, like *S. vestita*, *S. calcicola* has an isolated area in the Rocky Mountains where apparently it has no contact with *S. Richardsonii.*

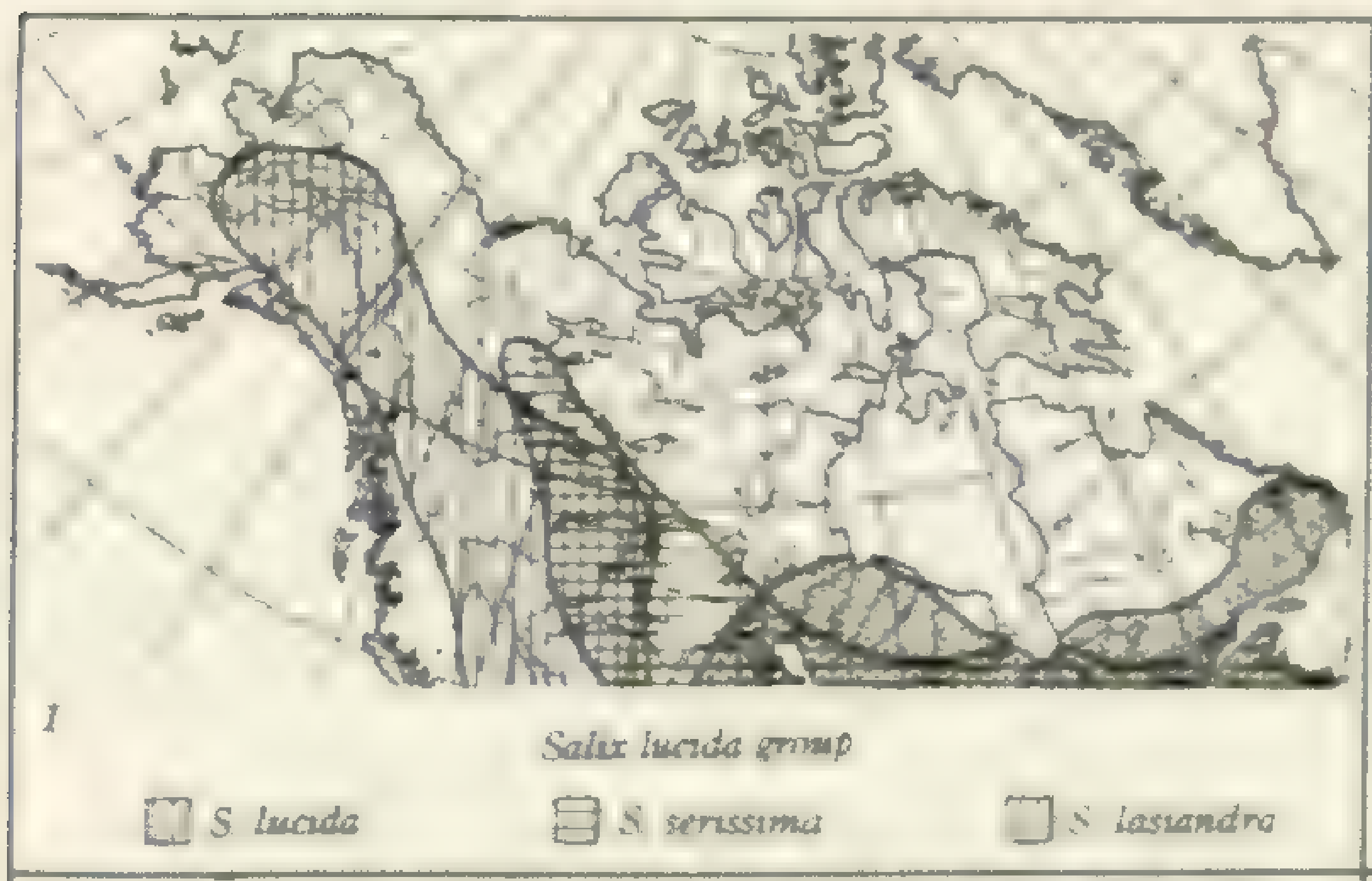
The second subcategory is composed of four groups which are more or less confined to the forested regions. First among these is the *S. lucida* group (Map 1) in which *S. lucida* (*sens. lat.*) is primarily eastern, extending from Newfoundland and the southern Labrador coast to north central Manitoba and eastern Saskatchewan. *Salix serissima* is somewhat more southern in the East, but reaches northwestward to the central Mackenzie basin. *Salix lasiandra* (*sens. lat.*) is primarily a western interior mountain species that extends from the central and southern Mackenzie drainage basin to western interior Alaska. Thus the eastern and western extremes in this group do not overlap, but they are connected through the closely related *S. serissima.* The *S. Barclayi* group (Map 14) as a whole is transcontinental, with *S. myrtillifolia* the more wide-ranging of the two species. There is a large area of overlap in the

---

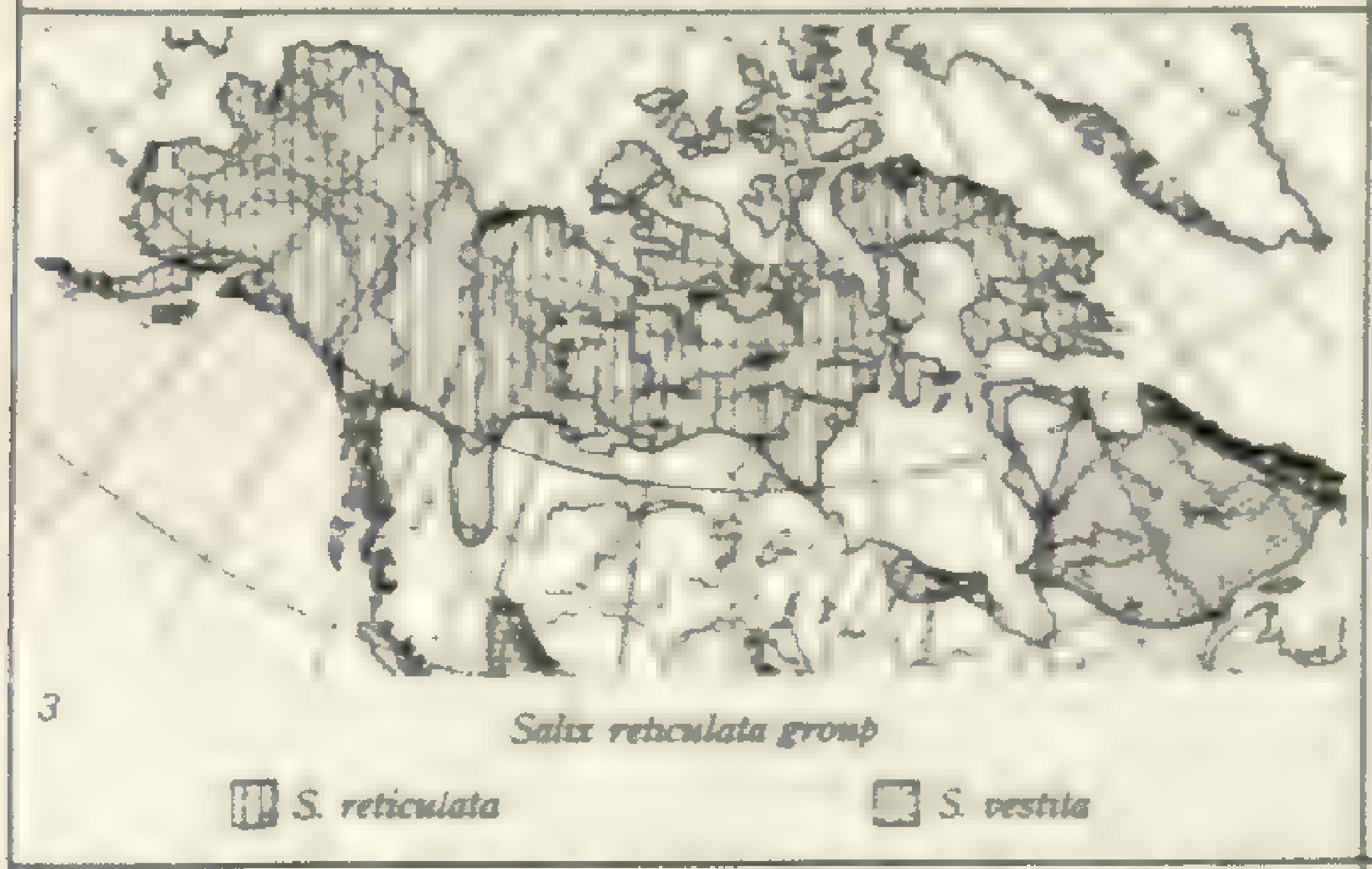
[1] It should be emphasized that the maps presented here are generalized. Most of them are based upon maps showing collection localities by dots, and are made by connecting the dots that mark the outside limits of the ranges. With the exception of maps 8 and 9, the base map used is by J. Paul Goode, copyrighted and published by the University of Chicago Press.

northern Rocky Mountains, Yukon, and eastern Alaska. *Salix glaucophylloides* and *S. padophylla* (Map 15) appear to be, respectively, eastern and western variants in a single population of closely related willows. They have an area of overlap in northwestern Ontario and eastern Manitoba. *Salix rigida* is a strictly eastern representative of its group (Map 12), extending westward approximately to central Ontario. There it overlaps with *S. lutea*, showing so many intermediate forms that the two species can scarcely be separated. The westernmost element, *S. mackenzieana*, is primarily an interior species in our region, overlapping *S. lutea* in the eastern foothills of the northern Rockies and the southern Mackenzie basin. *Salix discolor* and *S. Scouleriana* are well-defined eastern and western segregates in the *S. discolor* group (Map 25), with a region of overlap in Alberta, central Saskatchewan, and western Manitoba.

The third subcategory is a more complex one, involving ranges that are in both forested and arctic-alpine areas. The most elaborate of these is in the *S. glauca* group (Map 10). *Salix glauca* (*sens. lat.*) has the widest range in this group, occupying both forest and tundra. It has its greatest range expansion in the west, but has a long extension eastward to southern Baffin Island. In the Hudson Bay country it overlaps the eastern *S. cordifolia* (*sens. lat.*), and there is a welter of intermediate forms (particularly in what has been called *S. cordifolia* var. *callicarpaea*). *Salix niphoclada* seems to be a northern arctic and subarctic segregate, overlapping *S. glauca* in much of interior Alaska, Yukon, northern British Columbia, and the District of Mackenzie. However, it extends farther into arctic Canada and the southern arctic islands than any other member of the *S. glauca* group. *Salix brachycarpa* (*sens. lat.*) appears to be a more southern segregate in the group, reaching northward not far beyond the timberline, and extending into the central Rockies of the United States. It is of interest to note that there is a region in the District of Keewatin where all four of the segregates in the *S. glauca* group come close together and probably overlap their ranges. Another complex group is that related to *S. arbutifolia* (Map 23). The largest element here is *S. pedicellaris* var. *hypoglauca* which ranges westward in the forested country from eastern Quebec to the Rocky Mountains and the central Mackenzie River valley. *Salix arbutifolia*, on the other hand, is a more arctic species with its largest development in Alaska but with a long arctic extension eastward to the


1

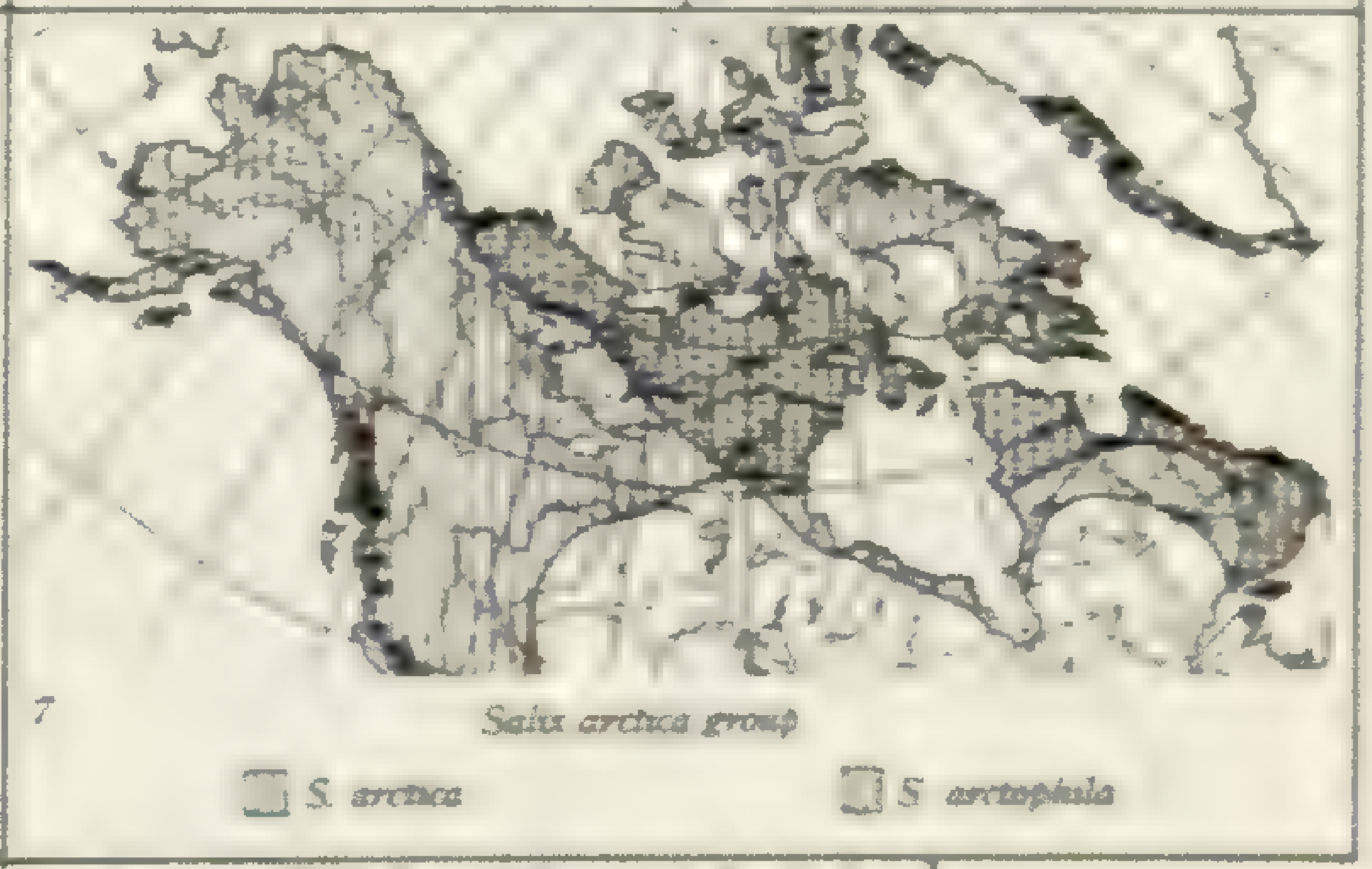

2


3


4


5

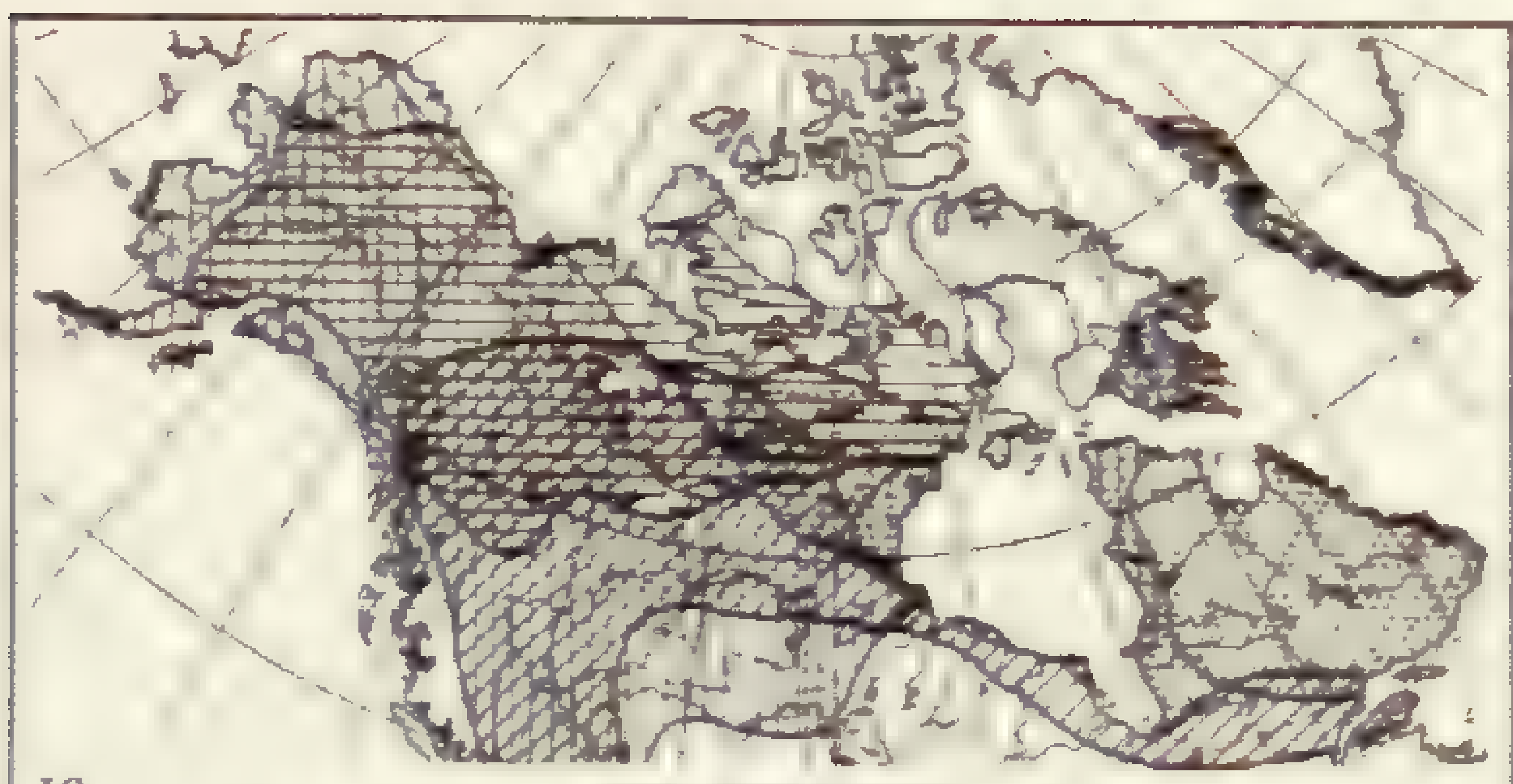

6


7


8


9

District of Keewatin. Present knowledge of the ranges provides no overlap of these two species, though they are close together in the District of Mackenzie. However, they appear to be connected through *S. athabascensis* in Yukon and eastern Alaska. The fourth species in the group, *S. hebecarpa*, is known only in two isolated localities: one on the Gaspé Peninsula, where it is surrounded by the *S. pedicellaris* population, and the other on the Seward Peninsula



10 Salix glauca group

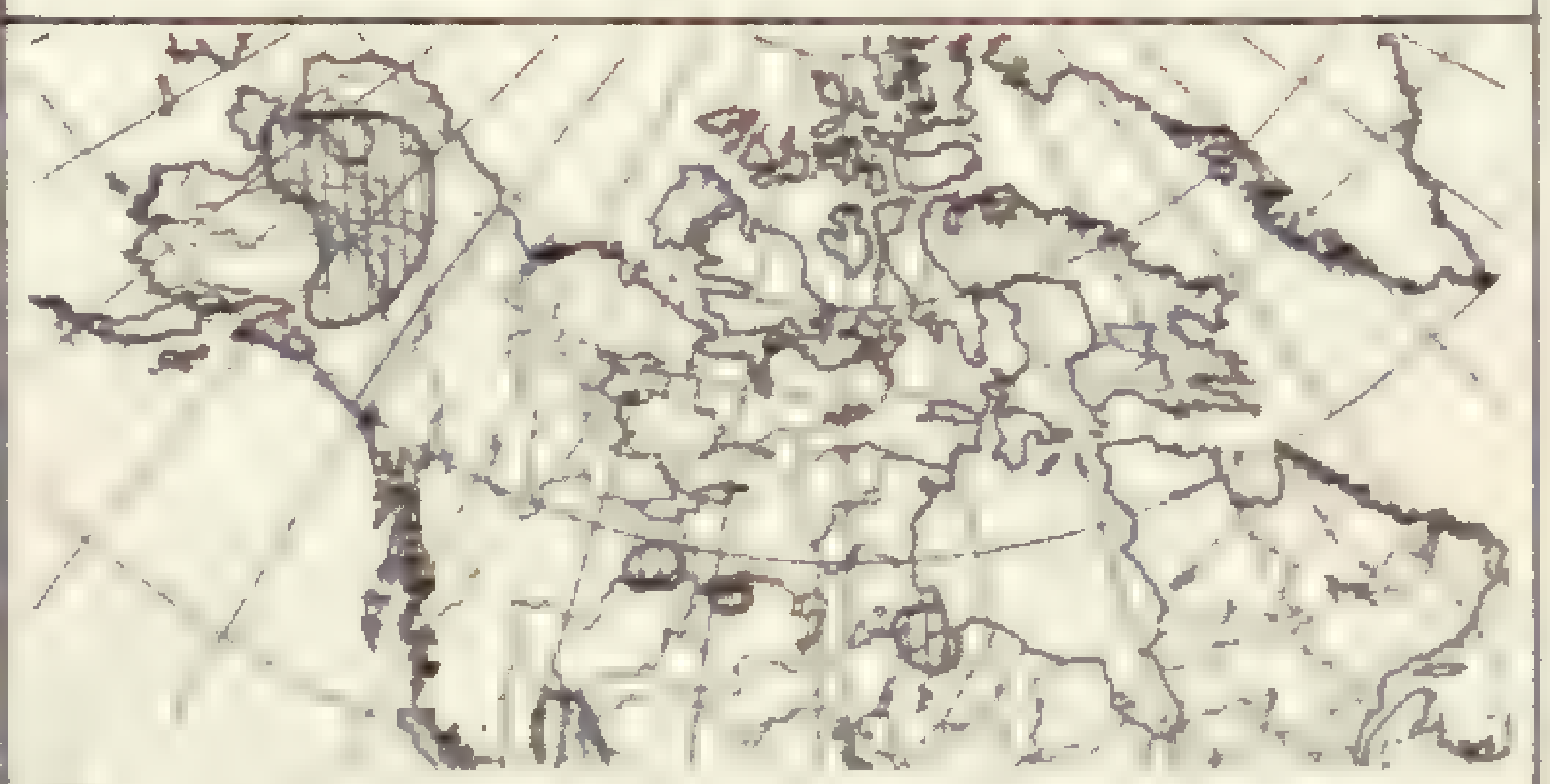
▥ S. glauca
▤ S. niphoclada
▨ S. brachycarpa
▩ S. cordifolia

11 Salix MacCalliana group

▥ S. MacCalliana
▣ S. Tyrrellii

12 Salix rigida group

▩ S. rigida
▤ S. lutea
▥ S. mackenzieana

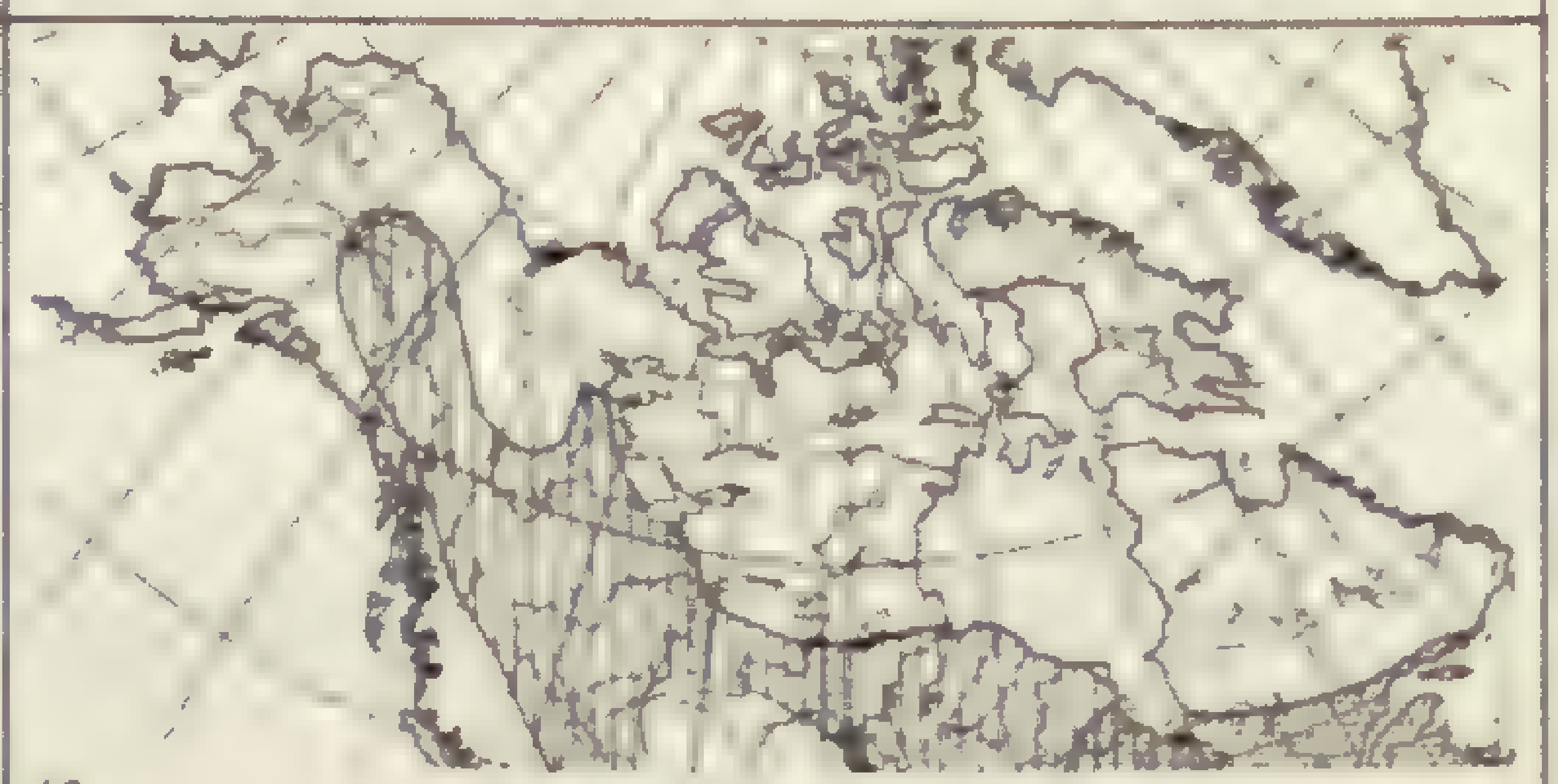


13

▥ Salix Farrae
▩ Salix Turnorii

14 Salix Barclayi group

▩ S. Barclayi
▩ S. myrtillifolia

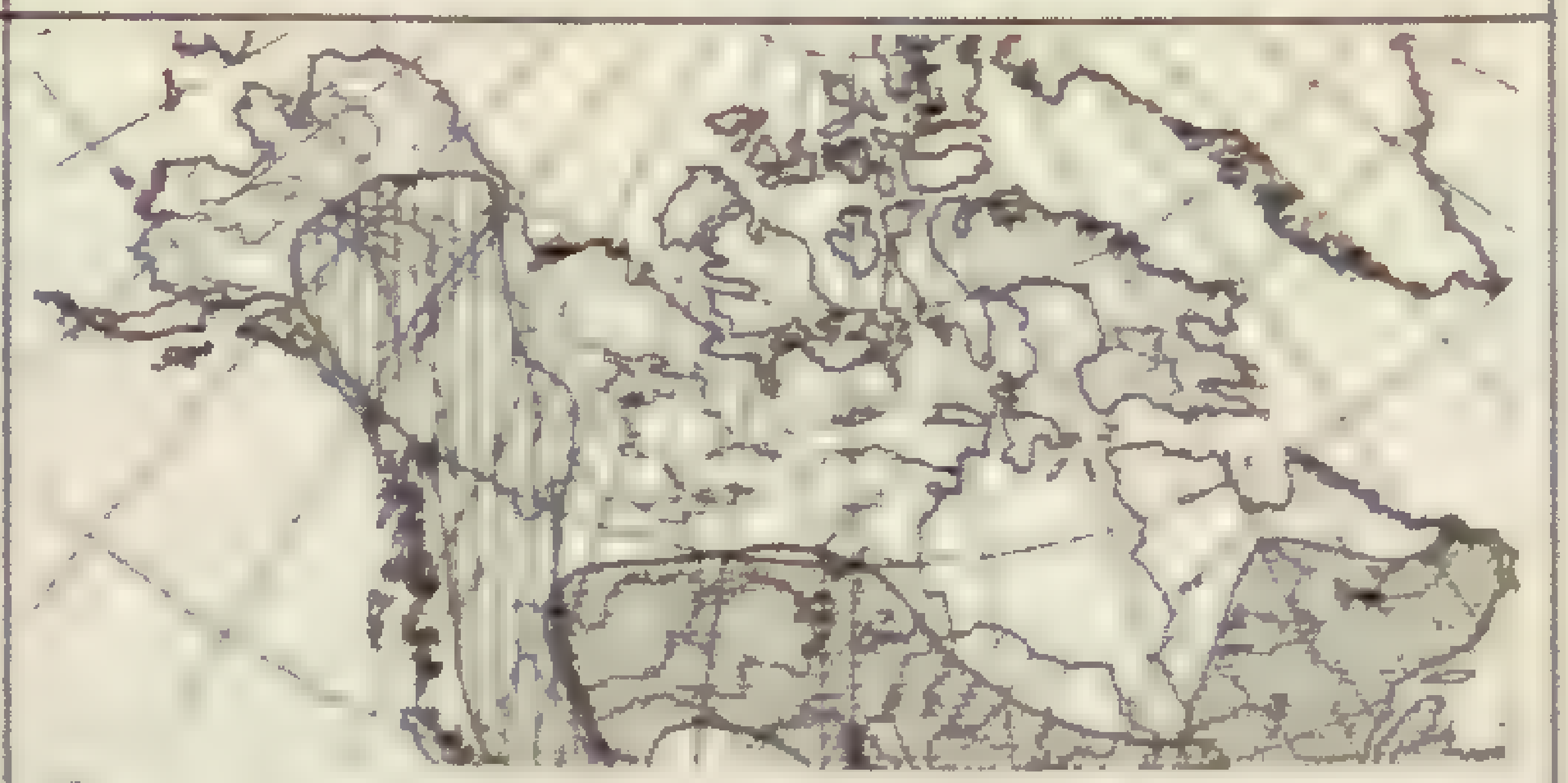


15 Salix glaucophylloides group

▩ S. glaucophylloides
▩ S. padophylla

16

▤ Salix Chamissonis
▩ Salix commutata
▩ Salix cordata

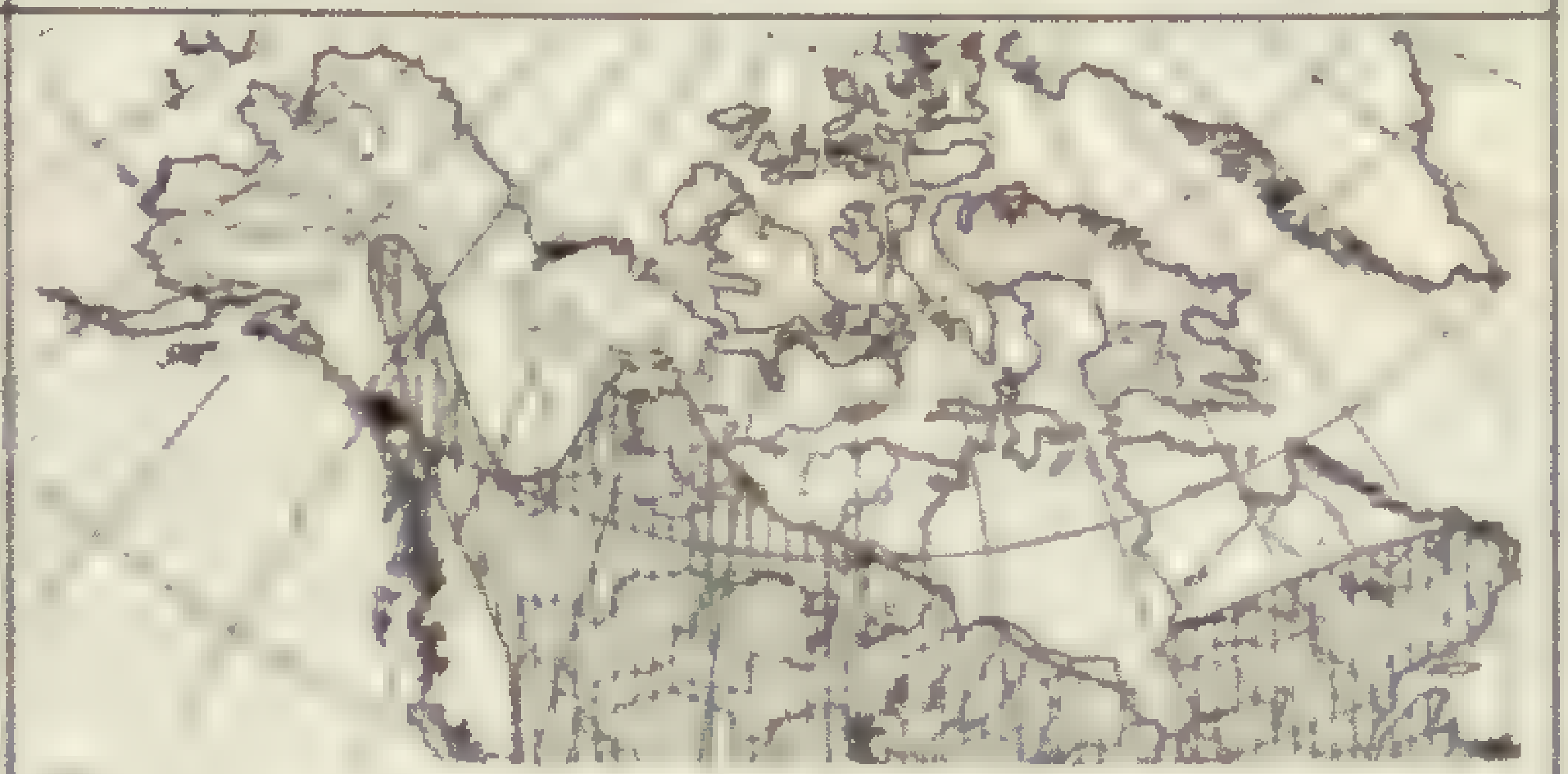


17

▥ Salix Barrattiana
▩ Salix pyrifolia

18 Salix Richardsonii group

▩ S. Richardsonii
▩ S. calcicola



19

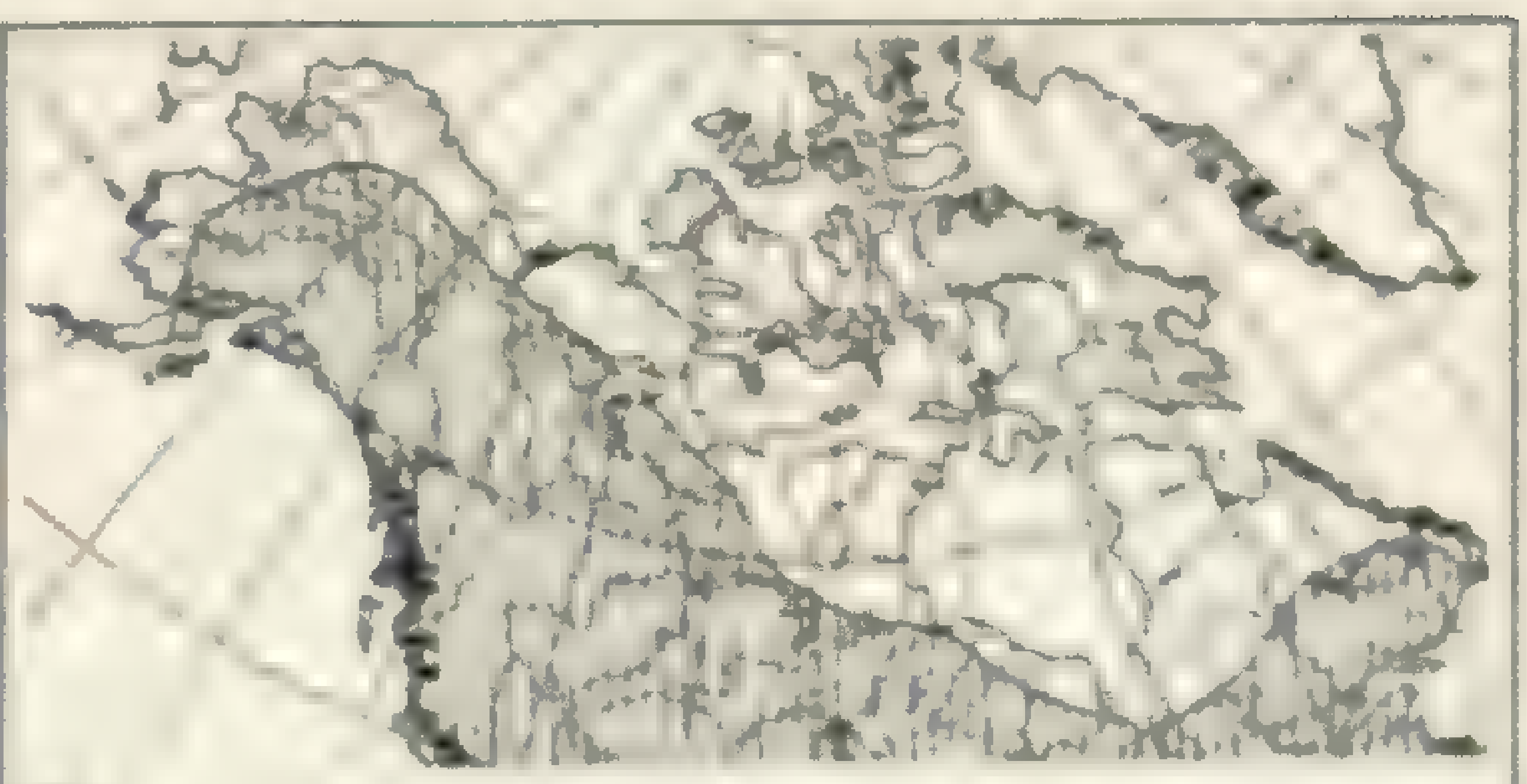
▣ Salix amplifolia
▩ Salix candida

of Alaska, within the range of *S. arbutifolia*. *Salix planifolia* is a wide-ranging eastern element in the *S. phylicifolia* group (Map 26), extending westward in the forested country and adjacent tundra to southern Yukon and northwestern Mackenzie. In the latter regions it overlaps the

20

Salix alaxensis group

▦ *S. alaxensis* ● *S. silicicola*

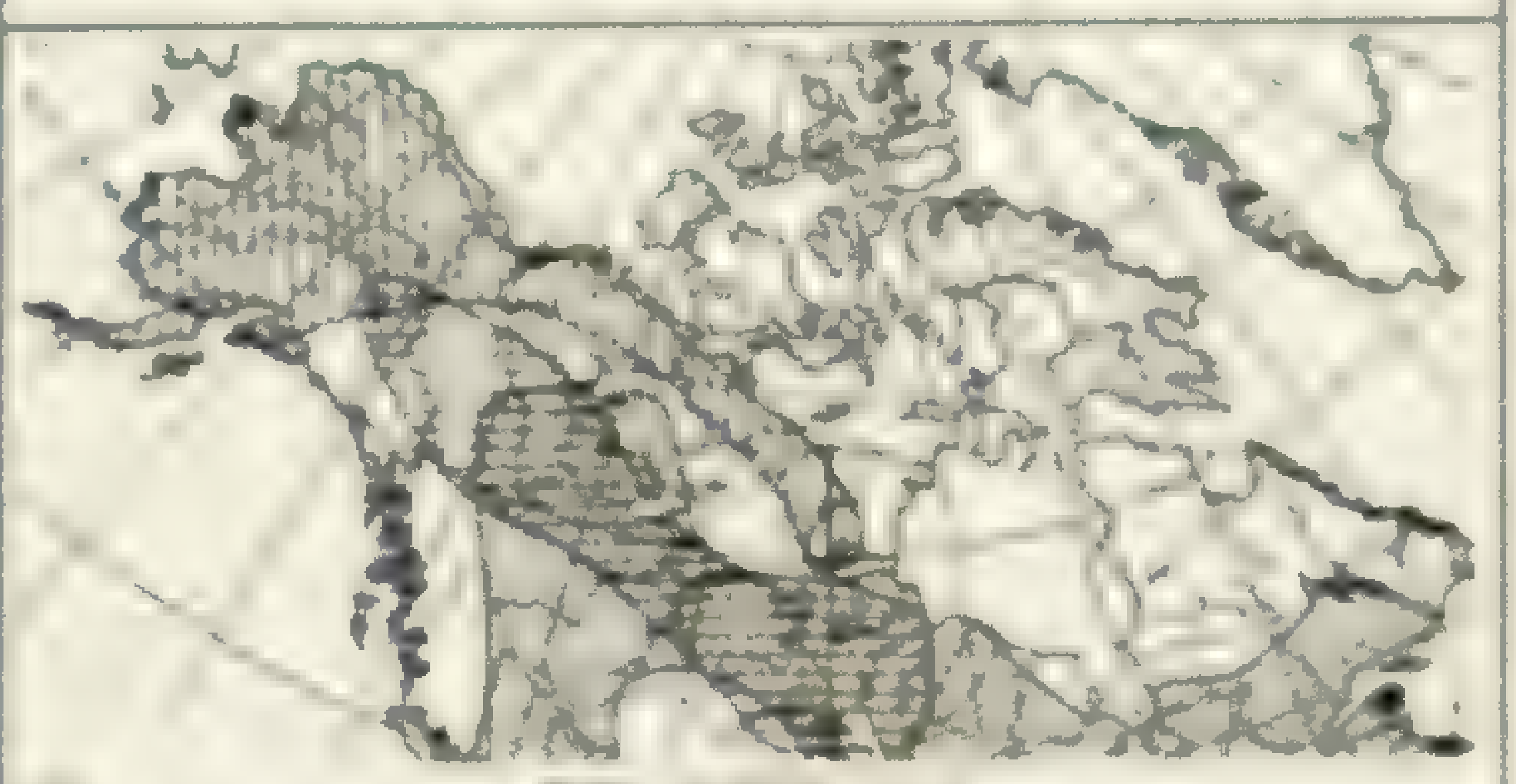


21

▨ *Salix Bebbiana*

22

▨ *Salix fallax*



23

Salix arbutifolia group

▨ *S. arbutifolia*

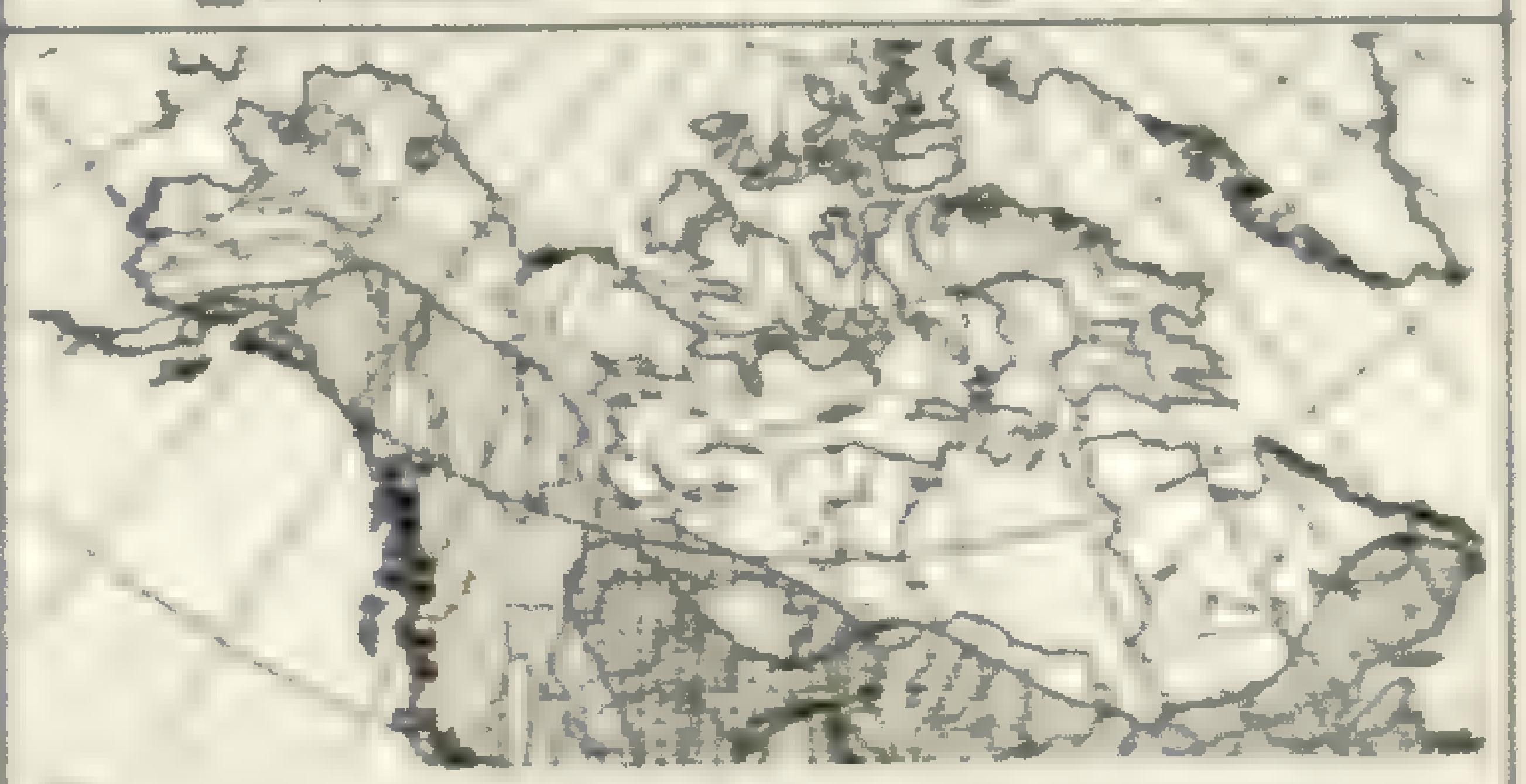
▨ *S. pedicellaris*

▨ *S. athabascensis*

● *S. hebecarpa*

24

▤ *Salix sitchensis* ▥ *Salix gracilis*



25

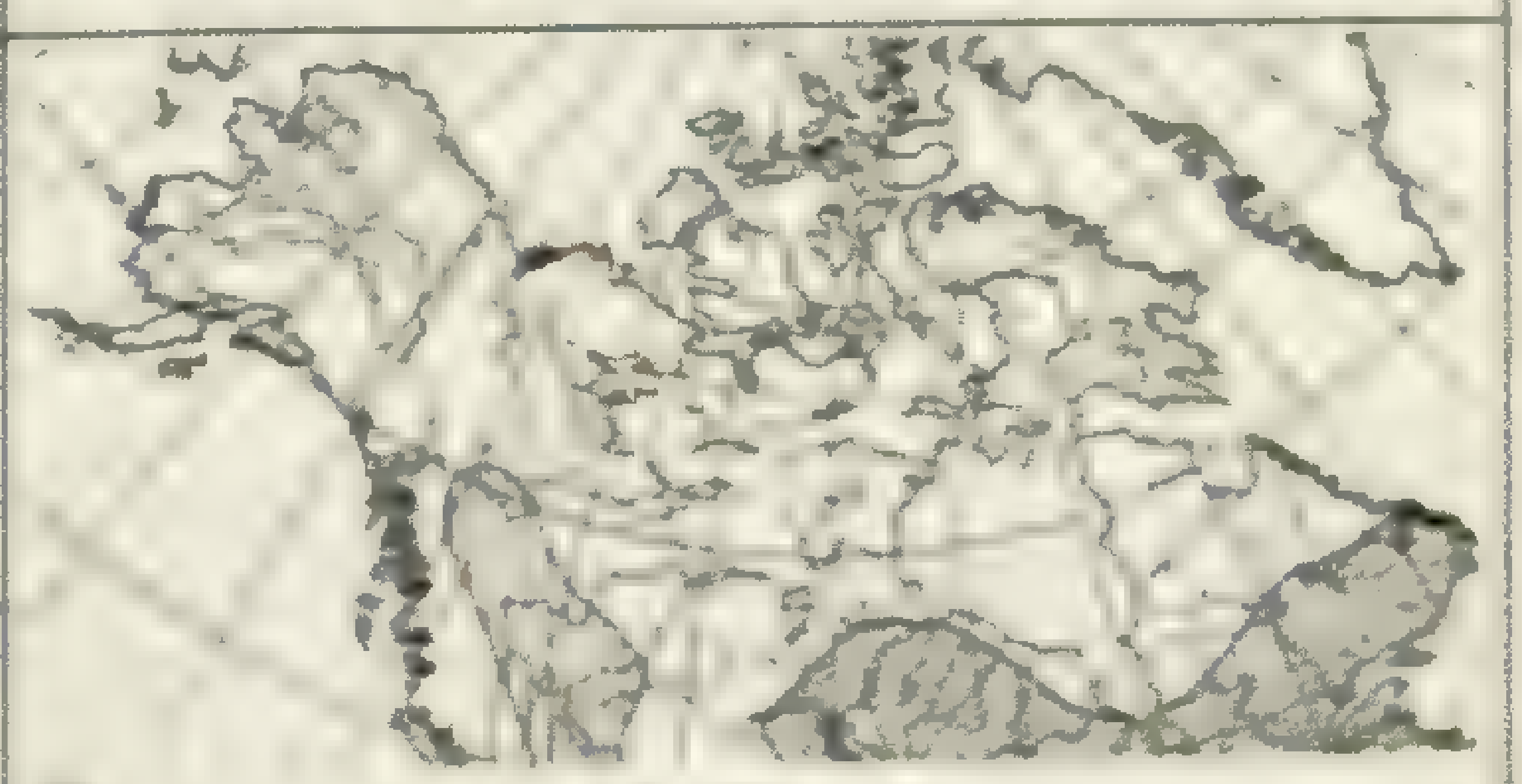
Salix discolor group

▨ *S. discolor* ▨ *S. Scouleriana*

26

Salix phylicifolia group

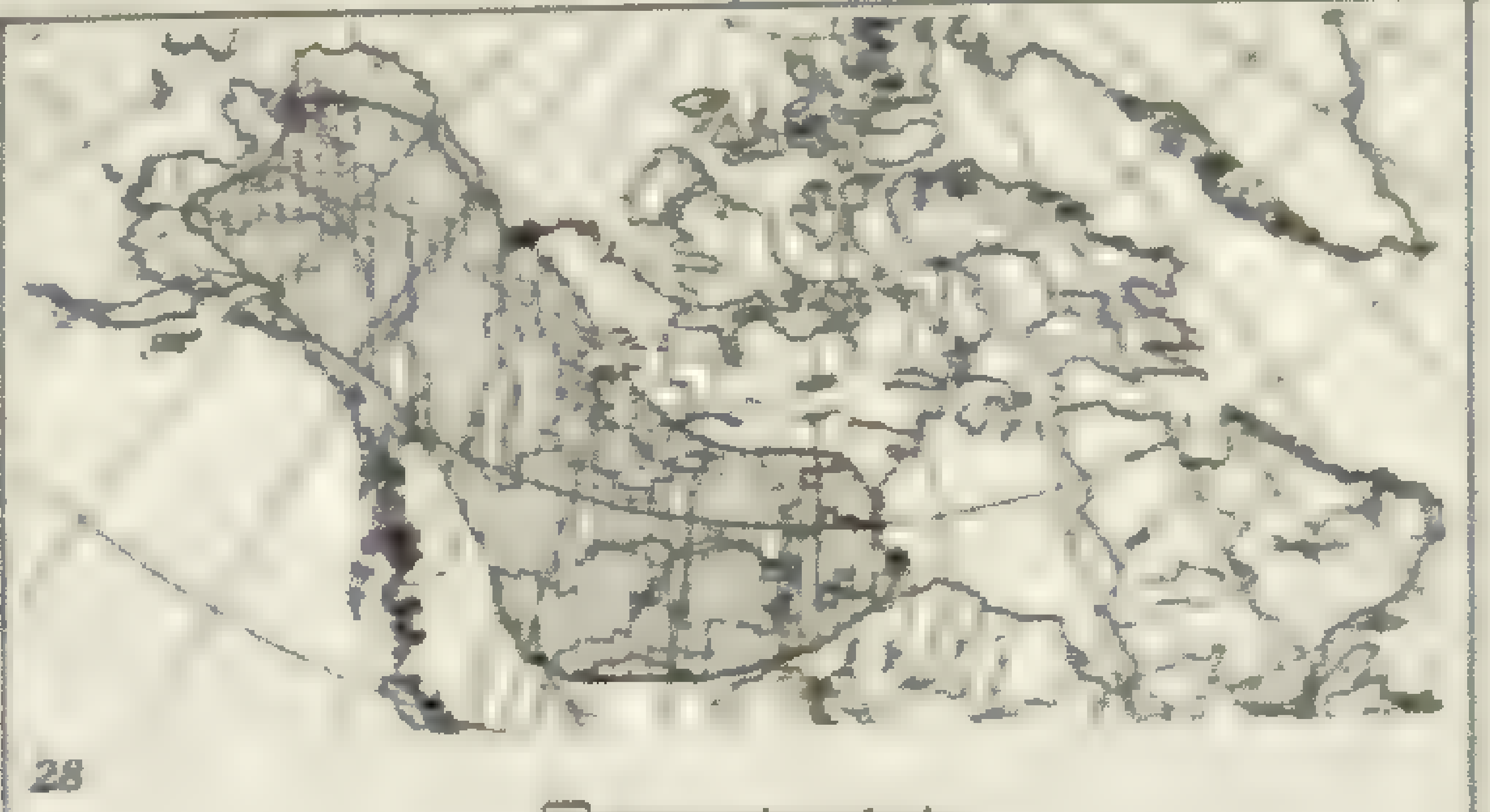
● *S. phylicifolia* ▨ *S. pulchra* ▨ *S. planifolia*



27

Salix pellita group

▨ *S. pellita* ▨ *S. subcoerulea*



28

▨ *Salix arbusculoides*

range of its far northwestern counterpart, *S. pulchra*. *Salix phylicifolia*, a Eurasian species included in our flora with some hesitation, is known only in southwestern Yukon and along the lower Kuskokwim River in Alaska.

The second category of ranges is represented only by the two species in the *S. pellita* group (Map 27). *Salix pellita* is a species of the forested country, ranging from Newfoundland to central Saskatchewan. *Salix subcoerulea* is characteristic of the northern Rocky Mountain region and reaches northwestward into the upper Liard River valley. These two species are so closely related as almost to defy taxonomic separation, but apparently their ranges do not overlap in Alberta or Saskatchewan. Further collection in the region between them may fill in the gap.

A third category is made up of the *S. ovalifolia* group (Map 8), with relatively narrow, overlapping ranges confined to the northwestern coastal strip. The most extensive of these ranges is that of *S. flagellaris* (incl. *S. arctolitoralis*), along the Arctic and Bering Sea coasts from the Mackenzie delta to the Aleutians, and southeastward along the Alaska panhandle. *Salix ovalifolia* extends along the coast from Cape Lisburne to the Aleutians, and has an isolated locality at White Pass. *Salix stolonifera* is primarily southern in Alaska, reaching from the Aleutians to the southern end of the Alaska panhandle. However, it has been found recently at Jago Lake in extreme northeastern Alaska, and about 40 miles east of Cape Lisburne.

The fourth category is formed by the *S. rotundifolia* group (Map 5), two of whose species, *S. rotundifolia* and *S. phlebophylla,* have nearly coincident ranges in Alaska and Yukon. *Salix phlebophylla* appears to extend farther eastward, reaching the Mackenzie delta in the north, and the White Pass region at the southeast. The closely related *S. Dodgeana* is known only from two widely separated localities, in the Rocky Mountains of Wyoming and southwestern Montana, and in the Mackenzie Mountains.

The fifth category is characterized by two groups, in each of which there is a well-defined wide-ranging species, and an equally well-defined localized segregate in or near the range of the main species. In the *S. alaxensis* group (Map 20) the main species is a western arctic and subarctic form, ranging from Hudson Bay to western Alaska and far south in the northern Rocky Mountains. *Salix silicicola* is, with present knowledge, a closely related localized endemic near the south shore of Lake Athabaska. *Salix Tyrrellii* (Map 11), also apparently a localized endemic in the same place, is within the range of the more southern *S. MacCalliana.* The latter extends from central British Columbia eastward to Hudson and James Bays. *Salix MacCalliana* and *S. Tyr-*

rellii are related to the *S. glauca* group, but their vegetative habit is so distinctive that I have maintained them in a small group by themselves.

HYBRID WILLOWS

There has been a tendency among some modern students of willows to recognize a multitude of natural hybrids. Of necessity such interpretations must be based upon the inspection and comparison of specimens; and in most cases the comparisons are based upon a small number of specimens, so that modern methods for the statistical study of variation in form, and of introgressive hybridization, are not possible. Under these circumstances it seems to me less confusing and more useful for further study to attach intermediate specimens to the species they most nearly resemble, than to set them aside as "inspection hybrids" — essentially nameless waifs that are apt to be missed by monographic or floristic students, and that may or may not actually be hybrids. The recognition of hybrids among the willows by simple comparison of a few specimens, if carried to its logical conclusion, can lead to utter taxonomic confusion where this is not warranted. From seeing two species as parents of a given specimen, it is a short step to seeing three, or even four or five; and if this is done consistently, many of the species boundaries in *Salix* can be broken down, so that a large proportion of the plants become hybrids. But this submerges the realities, for most of the great species complexes in *Salix* are real. For the present it seems best to preserve as much of this order as possible.

NOTES ON THE GEOGRAPHIC DISTRIBUTION OF THE SPECIES

Within the area covered by the present treatment, and with present knowledge of species ranges, the Territory of Yukon has the largest number of species (39). Northern British Columbia has 37, Alaska 37 and the District of Mackenzie 35. Eastward and northeastward in the Northwest Territories the numbers decline: Keewatin 18, and the western arctic islands (in the District of Franklin) 12. The decline in numbers eastward in the provinces of Canada is not so striking: northern Alberta 30, northern Saskatchewan 27, northern Manitoba 28, and northern Ontario 24. Lists of species for each of these geographic divisions are given below.

It should be emphasized that these lists, as well as those on species ranges that follow them, represent only present knowledge of the ranges so far as I have been able to gather it together. They are by no means definitive, and will without doubt be added to as more collections accumulate, or subtracted from as our concepts of the species change. There are still huge areas in the Northwest from which we have no plant collections at all; and even in those from which we have a great many the willow flora has been gathered critically in only a few widely separated localities. Some examples will illustrate. It is probable that as the Mackenzie Mountain system is further explored, more species of the Rocky Mountains will be found there, as well as more of the species that we now think of as peculiar to Alaska or neighboring Yukon. A few records suggest that more eastern arctic plants will be found there also. At the same time, further study of such difficult species complexes as the *S. rotundifolia, S. ovalifolia, S. glauca,* and *S. arbutifolia* groups may well alter our definitions of the species used in the present geographic arrangement. Any of these things can alter the definitions of ranges, and change the apportionment of species among the territories and provinces. What has been said about the Mackenzie Mountains applies also to the great area of overlap between the eastern and western species of the forested country, in the north central plain of the continent. It applies as well to many smaller areas from which critically made collections are scanty.

ALASKA: *S. lasiandra, interior, reticulata, Setchelliana, polaris* subsp. *pseudopolaris, rotundifolia, phlebophylla, arctica, arctophila, ovalifolia, stolonifera, flagellaris, glacialis, glauca, niphoclada, Farrae, Barclayi, myrtillifolia, padophylla, commutata, Chamissonis, Richardsonii, Barrattiana, amplifolia, alaxensis, candida, Bebbiana, fallax, arbutifolia, pedicellaris, athabascensis, hebecarpa, Scouleriana, phylicifolia, pulchra, arbusculoides, sitchensis.*

YUKON: *S. lasiandra, interior, reticulata, Setchelliana, polaris,* subsp. *pseudopolaris, rotundifolia, phlebophylla, arctica, arctophila, ovalifolia, stolonifera, flagellaris, glauca, niphoclada, brachycarpa, cordifolia, mackenzieana, Farrae, Barclayi, myrtillifolia, padophylla, commutata, Chamissonis, Richardsonii, Barrattiana, alaxensis, candida, Bebbiana, fallax, arbutifolia, pedicellaris, athabascensis, Scouleriana, phylicifolia, planifolia, pulchra, subcoerulea, arbusculoides, sitchensis.*

MACKENZIE: *S. lasiandra, serissima, interior, reticulata, polaris* subsp. *pseudopolaris, herbacea, Dodgeana, arctica, arctophila, flagellaris, glauca, niphoclada, brachycarpa, lutea, mackenzieana, Farrae, Barclayi, myrtillifolia, padophylla, commutata, Chamissonis, pyrifolia, Richardsonii, Barrattiana, alaxensis, candida, Bebbiana, arbutifolia,* *pedicellaris, athabascensis, gracilis, Scouleriana, planifolia, pulchra, arbusculoides.*

KEEWATIN: *S. reticulata, herbacea, arctica, arctophila, niphoclada, brachycarpa, cordifolia, Farrae, myrtillifolia, pyrifolia, Richardsonii, calcicola, alaxensis, candida, arbutifolia, planifolia, arbusculoides.*

WESTERN FRANKLIN: *S. reticulata, polaris* subsp. *pseudopolaris, herbacea, arctica, arctophila, glauca, niphoclada, cordifolia, Richardsonii, calcicola, alaxensis, planifolia.*

NORTHERN BRITISH COLUMBIA: *S. lasiandra, interior, reticulata, polaris,* subsp. *pseudopolaris, phlebophylla, arctica, ovalifolia, stolonifera, flagellaris, glauca, niphoclada, brachycarpa, MacCalliana, lutea, mackenzieana, Farrae, Barclayi, myrtillifolia, padophylla, commutata, pyrifolia, Richardsonii, Barrattiana, alaxensis, candida, Bebbiana, fallax, pedicellaris, athabascensis, gracilis, discolor, Scouleriana, planifolia, pulchra, subcoerulea, arbusculoides, sitchensis.*

NORTHERN ALBERTA: *S. lasiandra, serissima, fragilis, interior, vestita, arctica, glauca, brachycarpa, MacCalliana, lutea, mackenzieana, Farrae, Barclayi, myrtillifolia padophylla, commutata, pyrifolia, calcicola, Barrattiana, alaxensis, candida, Bebbiana, pedicellaris, athabascensis, gracilis, discolor, Scouleriana, planifolia, subcoerulea, arbusculoides.*

NORTHERN SASKATCHEWAN: *S. lucida, lasiandra, serissima, interior, herbacea, arctica, glauca, brachycarpa, MacCalliana, Tyrrellii, lutea, Turnorii, Farrae, myrtillifolia, padophylla, pyrifolia, silicicola, candida, Bebbiana, pedicellaris, athabascensis, gracilis, discolor, Scouleriana, planifolia, pellita, arbusculoides.*

NORTHERN MANITOBA: *S. lucida, serissima, interior, reticulata, vestita, herbacea, arctophila, glauca, brachycarpa, cordifolia, MacCalliana, lutea, Farrae, myrtillifolia, padophylla, cordata, pyrifolia, calcicola, candida, Bebbiana, pedicellaris, athabascensis, gracilis, discolor, Scouleriana, planifolia, pellita, arbusculoides.*

NORTHERN ONTARIO: *S. lucida, serissima, interior, reticulata, vestita, arctophila, brachycarpa, cordifolia, MacCalliana, rigida, lutea, myrtillifolia, glaucophylloides, padophylla, cordata, pyrifolia, calcicola, candida, Bebbiana, pedicellaris, gracilis, discolor, planifolia, pellita.*

Another way of organizing what knowledge we have of geographic distribution among the willows is in terms of actual species ranges. This could be carried to somewhat greater detail than will be found in the following pages, but for present purposes some general categories should prove useful.

RARE OR HIGHLY LOCALIZED SPECIES

S. fragilis: an introduced species collected in our region thus far only at Athabasca in Alberta. *S. vestita*: common at Hudson Bay, but with an isolated population in the Rocky Mountains. *S. Dodgeana*: found in our area only on the eastern alpine slopes of the Mackenzie Mts., along the Canol Rd. *S. cordifolia*: common in places at Hudson Bay, but known in the West only from the vicinity of Kluane Lake. *S. Tyrrellii, S. Turnorii*, and *S. silicicola*: known thus far only from their type locality near the south shore of L. Athabaska, in northwestern Saskatchewan. *S. calcicola*: common in places at Hudson Bay, but with a single western locality in the vicinity of Banff. *S. amplifolia*: known only from Yakutat Bay in southern Alaska. *S. hebecarpa*: known in our region only at Teller, Alaska. *S. phylicifolia*: collected thus far only in two localities, in southwestern Yukon, and in the lower Kuskokwim valley of Alaska.

SPECIES WITH DISTINCT THOUGH LIMITED RANGES IN OUR REGION

In alpine or arctic tundra: *S. Setchelliana*: central and eastern Alaska, and southwestern Yukon. *S. rotundifolia* and *S. phlebophylla*: widespread in Alaska, Yukon, and northwestern Mackenzie. *S. ovalifolia, S. stolonifera, S. flagellaris* and *S. glacialis*: apparently restricted to the coastal fringes of Alaska and northern Yukon, or to parts of these coasts. *S. Chamissonis*: western and central Alaska, northern Yukon, and the western border of Mackenzie.

In the forested country: *S. rigida*: northern Ontario. *S. glaucophylloides*: northern Ontario. *S. cordata*: southwestern shores of Hudson Bay. *S. fallax*: apparently with a narrow range from the Rocky Mts. of northern British Columbia to central Alaska. *S. subcoerulea*: Rocky Mts. and foothills of Alberta, northern British Columbia and the southeastern corner of Yukon. S. *sitchensis:* coastal strip and neighboring mountains in northern and central British Columbia and in southern Alaska.

WIDESPREAD SPECIES OF THE WESTERN MOUNTAINS, SOME WITH EXTENSIONS INTO ALASKA AND THE MACKENZIE BASIN

S. lasiandra; S. mackenzieana; S. Barclayi; S. commutata; S. Barrattiana.

SPECIES WITH THEIR PRINCIPAL RANGES IN THE WEST BUT WITH EXTENSIONS EASTWARD

S. polaris subsp. *pseudopolaris*: to the western arctic islands. *S. glauca*: to southern Baffin Island and Greenland. *S. niphoclada*: to northwestern Hudson Bay. *S. brachycarpa*: to Hudson Bay and beyond. *S. MacCalliana*: to the southwestern shores of Hudson and James Bays. *S. Farrae*: to Churchill and York Factory. *S. Richardsonii*: to western Baffin Island. *S. alaxensis*: to northwestern Hudson Bay. *S. padophylla*: to the southwestern shores of Hudson and James Bays. *S. arbutifolia*: to western Keewatin. *S. athabascensis*: to Hudson Bay and L. Winnipeg. *S. Scouleriana*: to western Manitoba. *S. pulchra*: to Great Bear L. and Coppermine. *S. arbusculoides*: to Churchill.

SPECIES WITH THEIR PRINCIPAL RANGES IN THE EAST BUT WITH EXTENSIONS WESTWARD

In the arctic or alpine tundra: *S. herbacea*: to Great Bear L. *S. vestita*: with a small isolated population in the Rocky Mts. *S. arctophila*: to northeastern Alaska. *S. cordifolia*: to Baker L. in Keewatin, and with an isolated population in southwestern Yukon. *S. calcicola*: with a small isolated population in the Rocky Mts.

In the forested country: *S. lucida*: to east-central Saskatchewan. *S. serissima*: to the upper Mackenzie basin. *S. pyrifolia*: to eastern British Columbia and southwestern Mackenzie. S. *gracilis*: to eastern British Columbia and the southern border of Mackenzie. *S. pedicellaris*: to Great Bear L., southeastern Yukon, and the

Rocky Mts. *S. discolor*: to northeastern British Columbia. *S. planifolia*: to northwestern Mackenzie and southwestern Yukon. *S. pellita*: to eastern Saskatchewan.

WIDESPREAD IN THE NORTHERN CENTRAL PLAIN

S. lutea.

WIDESPREAD THROUGHOUT MOST OF THE TUNDRA OR FOREST

Species primarily of the tundra: *S. reticulata; S. arctica.*

Species of the forested country: *S. interior; S. myrtillifolia; S. candida; S. Bebbiana.*

NOTES FOR AN ARRANGEMENT OF SPECIES IN TERMS OF FORM, SIZE, AND HABITAT PREFERENCE

A combination of form, size, and habitat groupings among the species may be of some assistance to collectors or to students of vegetational geography. As in the case of species ranges, the arrangement given below is tentative and incomplete. It can be used only as a point of departure, because observations of the behavior of the species of *Salix* with relation to habitat preference and the flexibility in their growth habits are too scanty to justify good generalization. I have made no attempt to classify the tundra species as to habitat. This is due in part to my lack of field experience with some of them, in part to the extraordinary plasticity of many of them in their capacity to occupy more than one kind of site, and in part to the extreme local variability and instability of the tundra habitat itself.

The willows of this region are most abundant in species and individuals on the most "open" lands, i.e., on lands with few or no trees, and least abundant in forests. Further, they are more frequent on the wetter soils than on the drier ones. In these circumstances, willows are most abundant in the arctic and alpine tundra, where there are no trees and the soils are nearly always damp; and they are least common in dry upland woods. Within the forested regions, in terms of moisture and the absence of trees, conditions analogous to those of tundra are most nearly met with at the margins of muskegs and wet meadows, and at the margins of floodplain forests. There are nearly as many species of willows in this marginal vegetation as there are in the tundra. Next in a descending order of abundance are the species found on the gravelly and sandy shores of lakes, and on gravel and sand bars along the larger streams in mountains and foothills. Then come the willows of shrubby or partially forested muskegs; of moist, rich upland forests; of sand dunes; of the dense forests of river floodplains; and finally of the drier forests of upland plateaus and hills.

The forms and sizes of willows may be arranged in two main divisions: species that are consistently prostrate, sometimes with creeping branches that root at the nodes, or with decumbent branches that ascend above the ground only 10-20 cm.; and those with upright or strongly ascending growth habit. The latter group can be divided roughly into those that are of "medium" height (usually 1.5 meters or less) and those that are taller. These form categories are not sharply defined, for there are some species that are ordinarily upright and often as much as several meters tall which are capable of living as depressed shrubs on exposed sites. However, there are not many of these, and their characteristics are fairly well known. By far the greater proportion of the prostrate willows grow in the arctic or alpine tundra. Only two or three of them are to be found within the forest, and these only a short distance below or south of the timberline. Most of the medium-sized species are to be found in swales or along streams in the tundra, or on relatively open land in the forested country. Most of the species in the forests or immediately marginal to them are the taller ones.

SPECIES OF ARCTIC OR ALPINE TUNDRA

Stems prostrate or trailing, or the branchlets ascending only 1-2 dm.: *S. reticulata; S. vestita; S. Setchelliana; S. polaris* subsp. *pseudopolaris; S. herbacea; S. rotundifolia; S. Dodgeana; S. phlebophylla; S. arctica; S. arctophila; S. ovalifolia; S. stolonifera; S. flagellaris; S. glacialis; S. niphoclada; S. cordifolia; S. Chamissonis; S. calcicola; S. arbutifolia; S. hebecarpa.*

Stems upright or ascending, of medium height, usually 2 m. tall or less: *S. interior; S. glauca; S. niphoclada; S. brachycarpa; S. Farrae; S. Barclayi; S. myrtillifolia; S. commutata; S. Richardsonii; S. calcicola; S. Barrattiana; S. alaxensis; S. Bebbiana; S. planifolia; S. pulchra; S. arbusculoides.*

SPECIES COMMONLY FOUND AT THE FORESTED MARGINS OF MUSKEGS, WET MEADOWS, PRAIRIES, AND OF ACTIVE RIVER FLOODPLAINS

Upright or ascending shrubs, or small trees, 1-10 m. tall: *S. lucida; S. lasiandra; S. serissima; S. fragilis; S. interior; S. MacCalliana; S. rigida; S. lutea; S. mackenzieana; S. Barclayi; S. glaucophylloides; S. padophylla; S. cordata; S. pyrifolia; S. Richardsonii; S. Barrattiana; S. alaxensis; S. Bebbiana; S. gracilis; S. discolor; S. Scouleriana; S. phylicifolia; S. planifolia; S. pellita; S. subcoerulea; S. arbusculoides; S. sitchensis.*

SPECIES FOUND ON GRAVELLY OR SANDY LAKE SHORES, OR ON GRAVEL AND SAND BARS ALONG THE LARGER STREAMS IN MOUNTAINS AND FOOTHILLS

Stems prostrate, with branchlets ascending to 1-2 dm.: *S. Setchelliana.*

Upright or ascending shrubs, 0.5-5 m. tall: *S. lasiandra; S. interior; S. glauca; S. niphoclada; S. brachycarpa; S. lutea; S. mackenzieana; S. Barclayi; S. myrtillifolia; S. padophylla; S. commutata; S. Richardsonii; S. Barrattiana; S. alaxensis; S. candida; S. Bebbiana; S. Scouleriana; S. planifolia; S. pulchra; S. subcoerulea; S. arbusculoides.*

SPECIES OF SHRUBBY OR PARTIALLY FORESTED MUSKEGS

Stems prostrate or trailing, or the branchlets ascending only 1-2 dm.: *S. reticulata; S. myrtillifolia.*

Upright or ascending shrubs, usually 2 m. tall or less: *S. serissima; S. glauca; S. niphoclada; S. brachycarpa; S. Farrae; S. Barclayi; S. myrtillifolia; S. commutata; S. pyrifolia; S. Richardsonii; S. candida; S. fallax; S. pedicellaris; S. athabascensis.*

SPECIES FOUND IN MOIST, RICH, UPLAND FORESTS

Stems prostrate or trailing, or the branchlets ascending 1-2 dm.: *S. reticulata; S. myrtillifolia.*

Upright or ascending shrubs, or small trees, 1-10 m. tall: *S. glauca; S. myrtillifolia; S. padophylla; S. Richardsonii; S. alaxensis; S. Bebbiana; S. Scouleriana; S. arbusculoides.*

SPECIES FOUND AMONG ACTIVE SAND DUNES

Upright or ascending shrubs, usually 0.5-3 (-8) m. tall: *S. glauca; S. brachycarpa; S. Tyrrellii; S. Turnorii; S. amplifolia; S. silicicola; S. Bebbiana; S. Scouleriana.*

SPECIES FOUND IN RIVER FLOODPLAIN FORESTS

Upright or ascending shrubs, or small trees, 1.5-10 m. tall: *S. glauca; S. padophylla; S. Bebbiana; S. Scouleriana; S. arbusculoides.*

SPECIES OF DRY UPLAND FORESTS

Upright or ascending shrubs, or small trees, 1.5-10 m. tall: *S. Bebbiana; S. arbusculoides; S. Scouleriana.*

THE COLLECTIONS OF SPECIMENS

The willows of all this region are badly in need of further collection and study. Many of the species are known only from fragmentary and infrequent collections, so that their true taxonomic significance cannot be assessed properly. As a general rule, willow specimens should not be collected unless they have flowers or fruit; but like most such rules, this one has to be broken on occasion, for reference materials often must be collected in the description of vegetation, whether they make acceptable herbarium specimens or not.

Sterile material should be avoided, however, whenever possible; but if it must be resorted to, care should be taken that it is typical of the plants from which it comes. Young, rank-growing root suckers and sprouts, particularly, should not be used because they commonly have large, atypical leaves. Whenever possible, both male and female material should be gathered, but particular attention should be given to the latter, for our most definitive keys to the willows are based upon specimens with female catkins. In any case, specimens should always be accompanied by notes on the date of collection, and on the form, coloring, and size of the bush or tree from which they come. Good specimens will consist of typical leafy twigs and branchlets with their catkins attached.

Many species of *Salix* show a great deal of seasonal variation in the size, shape, color, texture and pubescence of their leaves, in the pubescence and color of their twigs, and in the form and size of their flowers and fruit. The only way to record this variation is to tag individual plants, and return to them for additional specimens at intervals during the growing season. This is of course impossible unless the collector is settled in a single locality for a period of several weeks, or knows that he will return at intervals during the season. Such periodic collections from the same plant are highly desirable whenever they can be made.

Most of our species are "coetaneous" or "serotinous" in their flowering habits; that is, the flowers appear at about the same time as the leaves in spring or early summer, or, respectively, after the leaves are fairly well grown. Ordinarily, therefore, specimens of these species can be found with flowers or maturing capsules during the summer field season. In "precocious" species, on the other hand, the flower buds are the first to break in the spring, and the catkins are apt to mature and fall off before the leaves are full grown. The precocious species in our flora are as follows: *S. Richardsonii, Barrattiana, candida, discolor, phylicifolia, pulchra, planifolia, subcoerulea, pellita.* In addition there are five other species that commonly flower early and are intermediate between precocious and coetaneous: *S. mackenzieana, gracilis, calcicola, rigida, arbusculoides.*

Some care should be taken in the drying and preservation of specimens. One of the most used characters for the determination of species is the presence or absence of a bluish bloom that sometimes appears on young twigs, and more often on leaves, especially on the lower surface of leaves. This bloom (twigs that have it are said to be "pruinose," while on leaves it is most commonly called "glaucescence" and the leaves are said to be "glaucous") is caused by a waxy substance that is easily driven off by heat. Consequently, if artificial heat is used for drying specimens, notes on the amount and distribution of "glaucescence" on them should be made while the material is fresh. Willow catkins are particularly acceptable to certain small insects which commonly are collected with the specimens and go on eating the catkins while the latter are drying. A light sprinkling of ordinary naptha flake will drive off the pests and at the same time prevent mould.

THE USE OF THIS PAPER

The student who already has some knowledge of willows, and is able to "place" a specimen near its probable relatives, will turn at once to that part of the description of species that includes these relatives. He will narrow his decisions as to the identity of the specimen by comparing descriptions and by using the group keys if they occur; or he may turn back to the general keys to find definitive characters. He will use the notes on geographic distribution and habitat preference as a partial check on his decisions.

The student who has no general knowledge of species or relationships among the willows must gain this knowledge or substitute something for it in order to reach the level of decision with which the above student began. There is no real substitute for the experience upon which such knowledge rests — experience in the observation of finely detailed differences among the plants, or in the learning of species "by acquaintance" in much the same way we learn to know people and are able to call them by name. Nonetheless, it is possible to narrow, more or less mechanically, the fields within which decisions toward identification have to be made. The keys, and the arrangements of species based upon geographic distribution, form, and site preference, may be used as contrivances for narrowing the fields of decision.

The use of the keys will be greatly facilitated if the student learns to make a few simple observations on a given plant at the outset. The more effective of the main keys is that involving female flowering or fruiting material. Here each of the species or species groups is placed in one or another of three series. Some appear in more than one series to take care of variation within species or groups. Series I (5 species) is composed of trees or large shrubs, with catkins whose bracts drop off soon after the flowers expand. In all the willows of Series II and III the bracts remain on to the maturity of the fruit. Most of the species in Series I are also rather easily distinguished by vegetative characters. Series II (19 species) is composed of low, mostly prostrate shrubs, the branches in some species trailing on the ground and sometimes rooting at the nodes. All of these species occur in the arctic or alpine tundra, where most of them have their main ranges. Series III (40 species) includes only upright or ascending shrubs, though some are of low stature. Major subdivisions in both Series II and III are based upon whether the ovaries and their pedicels are glabrous or pubescent, whether the leaves are regularly serrate or entire, whether the leaves are green on both sides or glaucous beneath, whether the ovaries and capsules are essentially sessile or pedicelled, and if the latter, whether the pedicels are long or short.

With a little practice the collector will make these simple observations quickly, and as quickly place his plant in its proper series and get it into a small number of species or species groups. Within this small number he must then make a few more detailed observations for further identification.

The use of information given in the preceding pages on geographic distribution, form, and habitat preference probably can be explained to best advantage by some examples. Let us suppose that a student is working above timberline in the Brooks Range of northern Alaska. He may be making as complete a collection of the flora as possible, or he may be making detailed descriptions of vegetative cover in connection with studies of wildlife or of geomorphic processes. In any case, we will assume that he has no prior knowledge of willows except perhaps that they are "shrubby" plants with woody stems, that they have their flowers and fruits in catkins, and that they have "willow-like" leaves.

The chances are excellent that any willow he picks up will be one of the 37 species listed under "Alaska" on p. 16. Because he is operating in the tundra above timberline he will find by comparison of the Alaska list with that for the tundra on p. 20, that only 27 of the species are common to both lists, and he has narrowed the field by 10. If he now compares his list of 27 Alaska tundra species with the lists of those whose ranges are highly localized or of limited extent (pp. 17-18), he will find that one (*S. hebecarpa*) is extremely rare and known only from Teller, on the Seward Peninsula. Four others (*S. ovalifolia, stolonifera, flagellaris, glacialis*) apparently are restricted to coastal Alaska. Although he should not eliminate these five species entirely, the chances of his finding them in the Brooks Range are remote. He has reduced his field to 22 species and has not yet had to look at the willow he collected.

At this point he must make an initial decision based upon the structural characteristics of the plant in question. One of the least equivocal is whether or not the stems are trailing or prostrate on the ground. Alternatively they could be upright or strongly ascending from their roots. We will assume that they are of the prostrate or trailing kind. Turning again to the list of tundra species on p. 20, he finds that this decision has narrowed the field from 22 to 11 species. Eight of these are strictly prostrate in habit, while the other three (*S. niphoclada, arbutifolia*, and *myrtillifolia*) may be upright or spreading shrubs and have the appearance of prostrate ones. The 11 species are as follows: *reticulata, Setchelliana, polaris* subsp. *pseudopolaris, rotundifolia, phlebophylla, arctica, arctophila, niphoclada, myrtillifolia, Chamissonis*, and *arbutifolia*. All of these species are in Series II of the key to pistillate flowering or fruiting material (pp. 28-30), or they may be separated rather easily with only sterile specimens.

The second example will be drawn from the forested country. We will assume that a student is working along the banks of the Peace River in the great bend between Carcajou and Vermilion, where the river valley lies between the Buffalo Head Hills and the Caribou Mountain Plateau. This area is all in northwestern Alberta, and the list on p. 17 indicates that there are existing records of 30 species of willows in the northern part of that province. Reference to the lists of species that are rare and highly localized or of limited range (pp. 17-18) will give the names of 7 species which it is reasonably safe to eliminate on this basis alone. Six of these are montane or foothills species in western Alberta, and thus far have never been collected so far east as the lower Peace River valley: *Barclayi, calcicola, commutata, Barrattiana, alaxensis, subcoerulea*. The seventh, *S. fragilis*, is an introduced species for which I can find no record in our region except along the Athabaska River east of Lesser Slave Lake. Two more species, *vestita* and *arctica*, can be eliminated on this basis, and also because they are known only in the alpine or arctic tundra, and no tundra exists on the banks of the lower Peace River. Most of the habitats on the banks of the lower Peace are floodplains and semi-open grasslands, both with forested margins. Most of the willows along the river will be found among those listed for such marginal habitats on p. 20. However, small areas of shrubby muskeg are to be expected, and three species more or less restricted to this kind of site (see p. 17) are listed for northern Alberta: *Farrae, pedicellaris,* and *athabascensis.* It is possible that these will turn up on the floodplains, but as yet none of them has been found in the region of the lower Peace except on the neighboring uplands.

Thus we have reduced the number of species probably to be found on the banks of the river between Carcajou and Vermilion to 18; or if we include the muskeg species, to 21. Three of these (*lasiandra, serissima,* and *interior*) are in Series I of the key (p. 28). Seven of the remaining 18 are in that group of Series III species that have glabrous ovaries and capsules (pp. 30-31) (*Farrae, lutea, mackenzieana, myrtillifolia, padophylla, pyrifolia, pedicellaris*). The other eleven, also in Series III, have pubescent ovaries (pp. 31-32) (*glauca, brachycarpa, MacCalliana, candida, Bebbiana, athabascensis, gracilis, discolor, Scouleriana, planifolia, arbusculoides*).

Further examples could be postulated for other regions and other kinds of sites, but the above will be sufficient to suggest the method. The site-wise subdivisions that I have made for the willows of the forested country should be used guardedly, and with allowance for a somewhat greater spread in habitat tolerance than I may have given to some of the species. This is particularly true for species that are situated at or near the margins of their geographic ranges, where they sometimes occupy unusual sites. Further, the concept of the "forest margin" will be conditioned by the definition the student is using for "forest." The term "forest" is used here to mean a vegetation of trees whose crowns form a closed or nearly closed canopy. Open, park-like forest, such as occurs at timberline or in partially timbered muskegs, will show a great variety in the density of willow populations depending upon the extent of closure by trees.

The problem of "intermediate" specimens is sure to arise in the identification of willows. I can only urge the student to be patient with these refractory plants, bringing them as close as he can to recognized species, and then holding them until he has gained a wider acquaintance with the general nature of species in *Salix*. When he has this experience he will find that many of the supposed intermediates will come within the range of variation that seems to be allowable in one or another of the major species. There will, of course, be a residue that cannot be taken care of in this way. Some of the residue might be natural F_1 hybrids, for which there may be evidence in imperfectly or incompletely developed catkins and leaves, or they may be the result of free interbreeding among closely related species or varieties, with recombinations of the characters by which these entities usually are distinguished. Again, it is entirely possible that they are undescribed species in their own right; for in a region as vast as this, in which so little willow collecting has been done, new species are almost certain to be found.

ACKNOWLEDGMENTS

The gathering of material for a study of this kind, extending over a period of several years, is never accomplished without trying the patience of many people upon whom the author must call for assistance. I am deeply indebted to all those who have given me access to their collections and notes, referred me to pertinent literature, helped me with my own collections, or listened stoically while I "thought out loud" about a variety of problems. Most of these persons will, for lack of space, have to remain unnamed, but a few have made outstanding contributions and will be mentioned. Dr. A. E. Porsild has been particularly helpful with the loan of specimens, and by making available to me his manuscript range maps and his huge personal store of knowledge of the northern willows. Dr. Eric Hultén gave me free access to the great collection of northwest American plants upon which much of his *Flora of Alaska and Yukon* was based. Dr. H. J. Scoggan and Dr. W. K. W. Baldwin of the National Herbarium at Ottawa kindly let me have the use of their manuscripts on the willow floras of Manitoba and northern Ontario. Dr. E. H. Moss of the University of Alberta has corresponded with me frequently on the flora of the upper Peace River country in which he has done so much careful work. I am indebted to Mr. George W. Argus for a critical reading of the manuscript and for many helpful suggestions drawn from his first-hand knowledge of Rocky Mountain and Alaska willows.

I am especially indebted to several institutions that have supported my own field work in the North Country. Generous research grants have come from the American Philosophical Society, the American Academy of Arts and Sciences, the National Academy of Science, the Society of the Sigma Xi, and the Milton Fund at Harvard. Two of the journeys on the Highway were made during the war, and would not have been possible without the aid of the Northwest Service

Command of the U. S. Army. Later studies, in 1948, in southwestern Yukon were supported in part by the Wenner-Gren Foundation for Anthropological Research, the Peabody Foundation for American Archaeology, and the Arctic Institute of North America. Throughout all of this field work the National Museum of Canada has been most helpful with the loan of field equipment. My studies in European herbaria were financed by a further grant from the Milton Fund at Harvard.

KEY TO THE SPECIES AND GROUPS, BASED UPON WELL-DEVELOPED FEMALE FLOWERING OR FRUITING SPECIMENS

A. Bracts of the flowers not persistent in fruit, straw-colored; catkins coetaneous or serotinous, borne on leafy peduncles; usually tall shrubs of alluvial soils, or occasionally of muskegs .... *Series I.*
A. Bracts of the flowers persistent in fruit, brownish, yellowish, or black, rarely straw-colored; catkins appearing before, with, or after the leaves, sessile or on leafy peduncles.
 B. Low, prostrate shrubs, some species with rooting branches; catkins appearing with the leaves (coetaneous) or after the leaves (serotinous) .... *Series II.*
 B. Erect shrubs or small trees, with branches never prostrate or rooting (though many are of low and spreading form); catkins usually appearing before or with the leaves .... *Series III.*

SERIES I

1. Petioles provided, toward the upper end or at the base of the blade, with distinct, often irregularly lobed, glands; leaves lanceolate, distinctly and rather closely glandular-serrate; catkins borne singly on leafy peduncles .... *S. lucida* group.
1. Petioles and bases of the blades without prominent glands, or the petioles, at most, viscid toward the upper end; leaves lanceolate to linear, entire or variously toothed, but not finely and closely glandular-serrate; catkins borne singly or 2-3 together.
 2. Leaves with well-developed petioles, coarsely undulate-serrate; petioles somewhat viscid toward the base of the blades .... *S. fragilis.*
 2. Leaves nearly sessile or with very short, non-viscid petioles, sometimes nearly entire but usually with rather distant, often spiny teeth .... *S. interior.*

SERIES II

1. Pistillate flowers with 2 glands, on the inner and outer sides of the base of the pedicels; catkins appearing to be terminal on the branchlets; leaves strongly reticulate-veined .... *S. reticulata* group.
1. Pistillate flowers with only 1 gland, on the inner side of the base of the pedicel; catkins usually on leafy lateral branchlets.
 2. Ovaries and pedicels glabrous, even when young.
  3. Leaves more or less distinctly serrate on the margins.
   4. Leaves regularly serrate around the whole of the margin, green on both sides, not glaucous beneath.
    5. Tiny arctic plants with slender, subterranean branches, the aerial twigs usually with only 2-4 rounded, thin, shiny leaves commonly not much over 1 cm. long .... *S. herbacea.*

5. Larger plants with copiously leafy twigs, the leaves oblong to ovate or oblong-lanceolate; the more prostrate forms of the usually erect .... *S. myrtillifolia* (See *S. Barclayi* group).

4. Leaves irregularly serrate or entire, or with minute, more or less regular teeth around the lower half of the blades; green or glaucous beneath.

6. Leaves somewhat fleshy or leathery in texture, obovate or oblanceolate and tapering gradually to a petiole-like base, rounded, acute, or even retuse at the apex, entire or irregularly serrate; twigs commonly pruinose; pedicels shorter than the glands .... *S. Setchelliana.*

6. Leaves not fleshy; obovate or elliptic, rounded or obtuse at the apex, more or less regularly and finely serrate around the lower half; twigs not pruinose; pedicels usually longer than the glands .... *S. arbutifolia* (See *S. arbutifolia* group).

3. Margins of the leaves entire, or at most with only occasional small teeth.

7. Leaves somewhat fleshy or leathery in texture, obovate or oblanceolate and tapering gradually to a petiole-like base, acute, rounded or retuse at the apex; twigs commonly pruinose .... *S. Setchelliana.*

7. Leaves not fleshy or leathery; twigs not pruinose.

8. Densely matted plants of arctic and alpine tundra, formed by frequent branching of the stems; leaves 2 cm. long or less .... *S. rotundifolia* group.

8. Arctic-alpine plants with elongated prostrate branches; leaves 1-4 cm. long .... *S. ovalifolia* group.

2. Ovaries and pedicels more or less densely pubescent (sometimes only the lower parts of the ovaries).

9. Leaves finely though distinctly serrate all around the margin, obovate, up to 4-5 cm. long and half as wide or more .... *S. Chamissonis.*

9. Leaves entire or nearly so, or serrate only around the lower half.

10. Bracts of the flowers 2-3 times longer than wide, uniformly straw-colored, yellowish, or pale brown, or sometimes darkened a little toward the apex, rather short-hairy, with the hairs much shorter than the bracts .... *S. cordifolia* or forms of *S. niphoclada* (See *S. glauca* group).

10. Bracts of the flowers broader in proportion to their length, the width commonly more than half the length, variously colored but usually with long hairs or merely ciliate at the apex.

11. Prostrate or matted shrubs with leaves 1-2 cm. long; catkins usually 3 cm. long or less; commonly spreading.

12. Small, matted shrubs with leaves 1-2 cm. long (mostly less than 1.5 cm.), with an abundance of marcescent, skeletonized leaves from preceding seasons clothing the stems and forming a conspicuous part of the mats .... *S. phlebophylla* (See *S. rotundifolia* group).

12. Marcescent leaves not abundant, and not forming a conspicuous part of the mats.

13. Styles none or very short, at most 0.1-0.3 mm. long; small prostrate plants with slender branches; leaves ovate or obovate, glabrous, entire, glaucous beneath, 1 cm. long or less .... *S. glacialis.*

13\. Styles 0.5-1 mm. long or a little more; branches matted, much divided; leaves 1-2 cm. long, ovate or obovate .... *S. polaris* subsp. *pseudopolaris.*

11\. Prostrate shrubs with larger leaves and longer catkins.

14\. Leaves 1-3 cm. long, usually more than half that in width, finely serrate around approximately the lower half; capsules glabrous in age; catkins about 2 cm. long .... *S. arbutifolia.*

14\. Leaves up to 8 cm. long (commonly 2-6 cm.), entire or obscurely and irregularly toothed; catkins upright, sometimes as much as 10 cm. long .... *S. arctica* group.

SERIES III

1\. Ovaries and pedicels glabrous, even when young.

2\. Pedicels distinct, 2-6 times as long as the glands.

3\. Leaves with entire margins or serrate only around the lower half, smooth, green above and glaucous beneath .... *S. arbutifolia* group.

3\. Margins of the leaves distinctly serrate.

4\. Leaves green on both surfaces, the lower surface sometimes of a slightly lighter shade.

5\. Leaves acute to acuminate at the apex; slender, erect shrubs up to 3 m. high, with pale grayish-green bark .... *S. Turnorii.*

5\. Leaves rounded or obtuse at the apex; lower shrubs, 2 dm. to 2 m. high, with dark-colored branches .... *S. Barclayi* group.

4\. Leaves green above and glaucous beneath.

6\. Leaves giving off a balsamic fragrance (even long after they are dried), broadly ovate, elliptic, or elliptic-oblong; pedicels of the capsules 2-4 mm. long .... *S. pyrifolia.*

6\. Leaves not giving off a balsamic fragrance.

7\. Leaves usually broadly lanceolate, ovate or obovate, the width commonly 1/3 to 3/5 the length .... *S. glaucophylloides* group.

7\. Leaves usually lanceolate, oblanceolate, oblong-lanceolate, or narrowly obovate, the width commonly 1/6 to 1/3 the length or occasionally a little broader .... *S. rigida* group.

2\. Pedicels none or very short, at most and even in fruit not more than twice the length of the glands.

8\. Stipules of preceding years persistent on the twigs, conspicuous, linear-to half-cordate-lanceolate or reniform, glandular-serrate on the margins or entire; catkins sessile on the twigs of the preceding year, not on leafy peduncles .... *S. Richardsonii* group.

8\. Stipules not persistent after the growing season; catkins borne on leafy peduncles.

9\. Margins of the leaves distinctly and regularly serrate, at least on the lower part and sometimes all around.

10\. Pedicels usually less than 1 mm. long; styles 1-2 mm. long.

11\. Leaves glabrous beneath and becoming glabrous above as they mature .... *S. Barclayi* (See *S. Barclayi* group).

11\. Leaves densely grayish-hairy and somewhat silky on both sides .... *S. cordata.*

10\. Pedicels 1-1.8 mm. long; styles 0.5-1 mm. long *S. commutata.*

9\. Margins of the leaves entire, or with occasional teeth at irregular intervals or toward the base.

12\. Styles 3-4 mm. long; a tree-like species of the Pacific slopes .... *S. amplifolia.*

12. Styles 2 mm. long or less.

13. Pedicels about 0.5 mm. long; leaves usually serrate, but sometimes entire .... *S. Barclayi* (See *S. Barclayi* group).

13. Pedicels 1-1.8 mm. long.

14. Leaves glaucous beneath, all entire or occasionally with minute teeth, the blades completely glabrous .... *S. Farrae.*

14. Leaves green beneath, serrate or entire, pubescent on both sides at least on the veins .... ***S. commutata.***

1. Ovaries pubescent (rarely only on the base).

15. Leaves green on both sides, though sometimes of a lighter shade beneath, not glaucous, glabrous except when very young, 3-7 cm. long and 1/4 to 2/5 as wide, glandular-serrate on the margins .... ***S. MacCalliana*** **group.**

15. Leaves glaucous with a bluish bloom on the lower surfaces.

16. Pedicels distinct, 2-6 times as long as the glands.

17. Pedicels short, 0.5-2.4 mm. long; catkins sessile and precocious, or on very short leafy peduncles and appearing with the early leaves .... *S. discolor* group.

17. Pedicels conspicuously longer, 2.5-5 mm. long; catkins borne on well-developed leafy peduncles, and appearing with the leaves.

18. Leaves lanceolate, acuminate, 4-5 times as long as wide, entire or finely toothed, pubescence if present giving a somewhat silvery appearance to the under surfaces; bracts 1-2 mm. long .... ***S. gracilis.***

18. Leaves ovate, oblong, obovate, or ovate-lanceolate, the width 1/3 to ½ the length, entire or dentate, pubescence if present not silky in appearance; bracts commonly 2.5-3.5 mm. long .... *S. Bebbiana.*

16. Pedicels none or very short, even in fruit scarcely more than twice the length of the glands.

19. Flowering twigs more or less distinctly pruinose with a bluish bloom.

20. Lower surfaces of the leaves with a permanent covering of whitish, felt-like, opaque pubescence; styles 2 mm. long or more; catkins coetaneous .... *S. alaxensis* var. *longistylis* (See *S. alaxensis* group).

20. Pubescence on the lower surfaces of the leaves, if present, shining and not felt-like or opaque; styles usually less than 2 mm. long; catkins precocious.

21. Lower surfaces of the leaves with a silvery, shining pubescence .... ***S. pellita*** **group.**

21. Leaves glabrous beneath except on the midribs and main veins .... ***S. phylicifolia*** **group.**

19. Flowering twigs not pruinose.

22. Bracts of the flowers more or less uniformly colored, yellowish-straw-colored or yellowish-brown, pubescent with short hairs that are much shorter than the bracts themselves .... ***S. glauca*** **group.**

22. Bracts of the flowers of two colors, grayish-brown to black toward the apex, or if nearly all of one color, grayish-brown to black, with hairs often as long as or longer than the bracts themselves.

23. Lower surfaces of the leaves, even in age, densely white- or light gray-tomentose or silky.

24. Leaves linear-lanceolate or narrowly oblong, commonly 5-7 times longer than wide, with entire or undulate margins; young twigs, lower leaf-surfaces, and capsules covered with a dense, whitish wool; upper leaf-surfaces commonly grayish-pubescent, giving the whole shrub a hoary appearance .... *S. candida.*

24. Leaves broader in proportion to their length, usually only 3-4 times as long as wide.

25. Pubescence of the lower leaf-surfaces giving them a silvery, shining, or satin-like appearance.

26. Catkins precocious; bracts of the flowers about 1-1.5 mm. long; twigs usually pruinose but sometimes with the bluish bloom lost .... *S. pellita* group.

26. Catkins coetaneous; bracts of the flowers 1.5-2 mm. long; twigs never pruinose .... *S. sitchensis.*

25. Pubescence of the lower surfaces of the leaves dull white or dull grayish, not shining.

27. Leaves thickly felted beneath or on both sides with a white tomentum, the mid-veins on the lower surfaces, where visible through the tomentum, yellowish; stipules rather distantly glandular on the margins .... *S. alaxensis* group.

27. Leaves whitish or light grayish hairy-pubescent on both sides, somewhat silky in appearance; midribs on the surfaces of the leaves not yellowish; stipules densely glandular on the margins .... *S. Barrattiana.*

23. Lower surfaces of the leaves glabrous or somewhat pubescent, but not with a dense whitish or grayish pubescence or tomentum.

28. Leaves distinctly, regularly, and often conspicuously glandular-serrate on the margins.

29. Styles 0.2-0.8 mm. long; bracts about 0.5-1 mm. long .... *S. arbusculoides.*

29. Styles 0.5-2 mm. long; bracts about 2 mm. long.. *S. phylicifolia* (See *S. phylicifolia* group).

28. Leaves entire, or the margins with occasional small glandular teeth at irregular intervals, or with serrations only around the lower half.

30. Catkins coetaneous, borne on leafy peduncles; bracts short, 1.3 mm. long or less; styles 0.3-0.8 mm. long.

31. Leaves obovate to elliptic, up to 7 cm. long, usually more than twice as long as wide (sometimes 4 X); petioles 5-13 mm. long (mostly 8-10 mm.) .... *S. fallax.*

31. Leaves obovate to elliptic, 4.5 cm. long or less, usually broader in proportion to length, commonly less than twice as long as wide; petioles 2-6 mm. long (mostly 3-4 mm.) .... *S. arbutifolia* group.

30. Catkins precocious, appearing before the leaf-buds break, sessile on the branchlets; or if coetaneous and borne on leafy peduncles, the bracts of the flowers 1.5-2 mm. long, and the styles 0.8-2 mm. long .... *S. phylicifolia* group.

KEY TO SPECIES AND GROUPS, BASED UPON STERILE LEAFY PLANTS EXCLUSIVE OF RANK-GROWING SPROUTS

1. Leaves regularly crenate-serrate or dentate all around the margins.

2. Petioles provided, at the distal end or at the base of the leaf blade, with distinct, often irregularly lobate glands; leaves distinctly and rather closely glandular-serrate .... *S. lucida* group.

2. Petioles and bases of the blades without glands.

3. Low, prostrate shrubs with branches trailing; or depressed shrubs with twigs ascending 1-2 dm.

4. Leaves rather thick and fleshy or leathery, bluish-green on both sides, or green, or glaucous only beneath; twigs commonly pruinose .... *S. Setchelliana.*

4. Leaves relatively thin, not fleshy or leathery, not bluish-green above; twigs never pruinose.

5. Leaves usually clothed beneath with long, white, silky appressed hairs, though sometimes glabrate in age except on the veins; low forms of .... *S. vestita.*

5. Leaves glabrous.

6. Leaves rounded or broadly obovate, at most not more than twice as long as wide and usually much less.

7. Leaves rounded at the base, scarcely if at all longer than wide .... *S. herbacea.*

7. Leaves wedge-shaped at the base, commonly somewhat longer than wide .... *S. Chamissonis.*

6. Leaves oblong, oblong-ovate, or oblong-oblanceolate, usually 2-3 times as long as wide; low forms of .... *S. myrtillifolia.*

3. Upright shrubs, a few dm. to a few m. high.

8. Leaves linear or narrowly lanceolate, 8-10 times longer than wide, nearly sessile or with very short petioles, sometimes nearly entire on the margins, but usually with rather distant spiny teeth .... *S. interior.*

8. Leaves usually broader in proportion to their length, rarely linear, and mostly serrate or crenate-serrate.

9. Leaves permanently silky or hairy on both sides.

10. Leaves entire or finely and rather inconspicuously serrate, densely whitish or light grayish silky on both sides, upright in habit of growth; alpine shrubs (occasionally on river gravels at lower altitudes) of the northwestern mountains .... *S. Barrattiana.*

10. Leaves conspicuously glandular dentate-serrate, green and densely grayish-hairy and somewhat silky on both sides, more spreading in habit; eastern subarctic and north temperate shrubs .... *S. cordata.*

9. Leaves not permanently silky or hairy on both sides.

11. Leaves conspicuously acuminate at the apex, usually with long lanceolate or caudate tips.

12. Branchlets brittle, easily broken off at the base; introduced trees, with leaves rather coarsely undulate-serrate .... *S. fragilis.*

12. Branchlets not brittle; native, often tall, spreading shrubs with closely glandular-serrate leaves .... *S. rigida* group.

11. Leaves obtuse, acute or short-acuminate, but not conspicuously long-acuminate at the apex.

13. Dried stipules persistent on the twigs for 1-5 years .... *S. Richardsonii* group.
13. Stipules not persistent.
  14. Leaves elliptic to lanceolate or oblanceolate, usually 3-6 times longer than wide.
    15. Leaves green on both sides, rather firm and leathery in texture.
      16. Tall, upright and somewhat pyramidal shrubs with pale grayish-green bark except on the young twigs which are red; leaves pale green .... *S. Turnorii.*
      16. More spreading shrubs with dark reddish or brown bark; leaves bright green .... *S. MacCalliana* group.
    15. Leaves glaucous beneath.
      17. Pubescence on the under surfaces of the leaves long, appressed, and slightly tangled .... *S. phylicifolia.*
      17. Pubescence on the under surfaces of the leaves minute, straight and appressed, giving a slightly satiny appearance.
        18. Pubescence of mixed white and tawny or rust-colored hairs; petioles 6-10 mm. long or more .... *S. gracilis.*
        18. Pubescence almost entirely of white hairs; petioles averaging somewhat shorter, 4-8 mm. *S. arbusculoides.*
  14. Leaves usually oblong, ovate, or obovate, averaging broader in proportion to their length than in the above five species; or if narrower, not glaucous beneath.
    19. Shrubs usually of mossy muskegs or mossy tundra.
      20. Leaves green on both sides .... *S. Barclayi* group.
      20. Leaves glaucous beneath.
        21. Leaves giving off a balsamic fragrance, even long after drying, broadly ovate, elliptic, or elliptic-oblong .... *S. pyrifolia.*
        21. Leaves without a balsamic fragrance.
          22. Leaf margins conspicuously serrate .... cf. *S. Barclayi* group.
          22. Leaf margins finely and inconspicuously serrate .... *S. athabascensis.*
    19. Shrubs usually found on alluvial soils or in upland woods.
      23. Leaves glabrous, even when young .... *S. glaucophylloides* group.
      23. Young leaves pubescent, glabrescent in age or the pubescence often persisting on old leaves .... *S. Bebbiana.*

1. Leaves entire or nearly so, or with a few scattered inconspicuous teeth, or serrate only around the lower part of the blade.
  24. Low prostrate shrubs with branches trailing on the ground or in moss, often rooting at the nodes, or depressed shrubs with branches ascending to one or two decimeters.
    25. Leaves green on both sides, not glaucous beneath.
      26. Dead, dry leaves persistent through one or many years, sometimes only as skeletonized remains .... *S. rotundifolia* or *S. phlebophylla*, in the *S. rotundifolia* group.
      26. Dead leaves never persistent on the stems.
        27. Leaves minute, mostly 4-5 (occasionally 7) mm. long, the veins slightly incised above, prominent beneath, the blades somewhat fleshy or leathery .... *S. Dodgeana.*

27. Leaves larger, up to 5 cm. long, the veins not prominently incised above or raised beneath.

28. Leaves usually not over 2.5 cm. long and commonly smaller, the blades thin .... *S. polaris* subsp. *pseudopolaris*.

28. Leaves rather thick and fleshy, commonly more than 2.5 cm. long .... *S. Setchelliana*.

25. Leaves glaucous beneath.

29. Leaves strongly reticulate-veined, which shows conspicuously beneath, rounded, obovate, or oval in outline; stems trailing.

30. Leaves prominently incised-reticulate on the upper surface, 1.5 to 4 cm. long, borne on long reddish petioles. *S. reticulata*.

30. Leaves not prominently incised above, usually 1 cm. long or less, borne on relatively short petioles .... *S. glacialis*.

29. Leaves not conspicuously reticulate-veined beneath; of various shapes.

31. Twigs pruinose, and the leaves glaucous on both surfaces; leaves rather thick and fleshy or leathery, entire or coarsely and irregularly serrate; a depressed shrub with ascending branches .... *S. Setchelliana*.

31. Twigs not pruinose.

32. Leaves finely glandular-serrate only around the lower part of the blade; trailing shrubs with elliptic to obovate leaves, 3 cm. long or less, the width usually more than half the length .... *S. arbutifolia*.

32. Leaves entire around the whole margin or, at most, obscurely and usually irregularly serrate.

33. Adult leaves averaging less than twice as long as broad.

34. Prostrate shrubs with trailing stems .... *S. ovalifolia* group.

34. Prostrate shrubs with ascending branches which are spreading and often gnarled.

35. Leaves rounded to heart-shaped at the base, soon glabrous; decumbent forms of .... *S. calcicola*.

35. Leaves acute or obtuse at the base, hairy-pubescent beneath at least on the veins; low forms of .... *S. cordifolia*.

33. Adult leaves averaging more than twice as long as broad.

36. Shrubs with trailing branches, often forming dense mats .... *S. arctica* group.

36. Prostrate or ascending shrubs, with gnarled, spreading branches.

37. Petioles 2 mm. long or less; prostrate forms of .... *S. niphoclada*.

37. Petioles longer, more than 2 mm.; prostrate forms of .... *S. glauca* or *S. cordifolia* (See *S. glauca* group).

24. Upright shrubs, with branches not trailing or ascending from prostrate stems.

38. Leaves green on both sides, sometimes paler beneath, but not glaucous.

39. Leaves linear or narrowly lanceolate, 8-10 times longer than wide, nearly sessile or with very short petioles .... *S. interior*.

39. Leaves usually broader in proportion to their length, not linear, borne on well-developed petioles.

40. Leaves commonly rounded or somewhat heart-shaped at the base; mostly shrubs of muskegs or swampy tundra.

41. Leaves thinly tomentose above when young, glabrous beneath, commonly becoming blackened in drying .... *S. Barclayi.*

41. Leaves densely grayish-tomentose on both sides when young, not blackening in drying .... *S. commutata.*

40. Leaves more frequently obtuse or wedge-shaped at the base; shrubs of dry woods, prairie margins, or floodplain forests .... *S. Bebbiana.*

38. Leaves glaucous beneath, or the lower surfaces obscured by thick tomentum.

42. Lower surfaces of the leaves covered thickly with permanent pubescence or tomentum.

43. Pubescence on the under surfaces of the leaves shining, silvery, satin-like.

44. Twigs pruinose; species of the Rocky Mts. and of north temperate eastern America .... *S. pellita* group.

44. Twigs not pruinose; a Pacific slope species .... *S. sitchensis.*

43. Pubescence on the under surfaces of the leaves opaque, not shining.

45. Leaves linear-lanceolate or narrowly oblong, commonly 5-7 times as long as wide, the upper surfaces impressed-reticulate and grayish pubescent at least when young; the whole plant having a hoary appearance .... *S. candida.*

45. Leaves broader in proportion to length, usually not more than 4 times longer than wide, not conspicuously impressed-reticulate above.

46. Stipules glabrous or with a few long hairs .... *S. Barrattiana.*

46. Stipules densely tomentose or hairy-tomentose .... *S. alaxensis* group.

42. Lower surfaces of the leaves glabrous, hairy, or pubescent, but not densely covered with a thick, permanent tomentum or pubescence.

47. Leaves sessile or on petioles usually less than 2 mm. long; shrubs usually less than 1 m. tall, upright or depressed, with grayish-green leaves.

48. Leaves oblong-ovate to rounded, usually much less than twice as long as wide .... *S. calcicola.*

48. Leaves longer in proportion to their breadth, usually twice as long as wide or more.

49. Leaves elliptic to narrowly obovate, 2-4.5 cm. long .... *S. niphoclada.*

49. Leaves ovate or obovate to oblanceolate, averaging smaller than in the last (1.5-3 cm. long) .... *S. brachycarpa.*

47. Leaves borne on well-developed petioles more than 2 mm. long.

50. Stipules evident, and persistent through 2 or more years on old wood.

51. Leaves usually pubescent, though sometimes glabrate in age .... *S. glauca* var. *stenolepis.*

51. Leaves glabrous.

52. Twigs, even when older than one year, heavily pubescent, never pruinose; stipules broad at the base and prominently glandular-serrate on the margins .... *S. Richardsonii* group.

52. Twigs older than one year glabrous or thinly pubescent, commonly pruinose; stipules linear, narrow to the base, without prominent glands on the teeth .... *S. pulchra.*

50. Stipules not persistent beyond the growing season.

53. Leaves linear-lanceolate or narrowly oblong, commonly 5-7 times longer than wide, the upper surfaces impressed-reticulate and grayish-pubescent at least when young; the whole plant having a hoary appearance .... *S. candida.*

53. Leaves not as above, shorter in proportion to breadth.

54. Twigs yellowish, or yellowish with reddish streaks or blotches; tall shrubs with pale, yellowish-green, acuminate leaves that are usually serrate but sometimes entire .... *S. lutea.*

54. Twigs gray, brown, or reddish, not yellow.

55. Leaves oblong-ovate to rounded, usually much less than twice as long as wide, up to 5 cm. long .... *S. calcicola.*

55. Leaves not broadly oblong-ovate to rounded, consistently longer in proportion to breadth than the above, or if relatively broader, obovate to broadly elliptic and averaging shorter (1-3 cm.).

56. Pubescence on the under surfaces of the leaves of minute, straight, appressed hairs, giving a slightly satiny appearance.

57. Pubescence of mixed white and tawny or rust-colored hairs; petioles 6-10 mm. long or more .... *S. gracilis.*

57. Pubescence almost entirely of white hairs; petioles averaging somewhat shorter, 4-8 mm. .... *S. arbusculoides.*

56. Pubescence on the under surfaces of the leaves various or none, not satiny.

58. Low, erect or spreading shrubs, usually less than 1 m. tall; leaves 1-5 cm. long.

59. Erect or spreading shrubs sometimes nearly 1 m. tall; leaves 1-5 cm. long.

60. Leaves rather stiff, leathery, entire, dark bluish-green above, obovate, glabrous, 2-4.5 cm. long usually 2.5-4 times longer than broad .... *S. pedicellaris.*

60. Leaves thin and more delicate in texture, shiny green above, obovate to elliptic, usually less than twice as long as broad, the margins commonly minutely serrate around the lower half .... *S. arbutifolia.*

59. Low, spreading shrubs, commonly not over 3 or 4 dm. tall; leaves usually 3 cm. long or less.

61. Resembling *S. pedicellaris* var. *hypoglauca*, except for its spreading habit and smaller leaves (3 cm. long at most); known in our region only in the Bering Straits area .... *S. hebecarpa.*

61. Leaves broadly ovate, oblong, or elliptic 1.5-3 cm. long, commonly obtuse at the base, grayish-green, pubescent or glabrate .... *S. cordifolia.*

58. Taller shrubs or small trees, usually more than 1 m. tall, or if smaller the leaves differing from those of the preceding 3 species.

62. Tall shrubs or small trees, commonly 3-8 m. high.
  63. Leaves usually 4-6 cm. long and ¼ to ½ as wide, elliptic, oblong, ovate, or oblanceolate, dull grayish-green above, and usually with rather prominent raised veins beneath; common in lowland and mountain slope woods and thickets throughout the region .... *S. Bebbiana.*
  63. Leaves larger at maturity, commonly up to 8 cm. long, distinctly obovate.
    64. Leaves commonly about twice as long as wide; a species known only from the Yakutat Bay region of Alaska .... *S. amplifolia.*
    64. Leaves usually about 3-4 times as long as wide .... *S. discolor* group.
62. Medium shrubs, usually 1-3 m. tall.
  65. Predominant leaf-shape elliptic, elliptic-oblong, or ovate-elliptic, i. e., broadest near or below the middle (some lanceolate leaves will be found in these plants, but usually they are least numerous).
    66. Twigs reddish or reddish-brown, usually glabrous and shining.
      67. Leaves dark green and shining above.
        68. Leaves entirely glabrous, the margins entire or with occasional, irregularly-spaced, small teeth; common in damp thickets at the margins of wet meadows and muskegs, and extending northwestward to the upper Yukon valley where it merges with the closely related *S. pulchra* .... *S. planifolia.*
        68. Leaves finely pubescent when young, but becoming glabrous in age, usually finely crenate-dentate, but sometimes entire or nearly so; a rare species in North America, known thus far only from two collections: in southwestern Yukon and along the lower Kuskokwim R. .... *S. phylicifolia.*
      67. Leaves yellowish-green and rather dull above; a species of the northern Rocky Mts. and Alaska .... *S. Farrae.*
    66. Twigs gray, glabrous or pubescent; leaves dull grayish-green above, usually with rather prominent raised veins beneath, glabrous or pubescent; common in lowland and mountain slope woods and throughout the region .... *S. Bebbiana.*
  65. Predominant leaf-shapes obovate or oblanceolate, i. e., broadest above the middle (ovate lanceolate, or elliptic forms will be found on these plants, but they will be in the minority).
    69. Leaves rather dull grayish-or bluish-green 3-8 cm. long, about 2.5-4 times longer than wide, commonly pubescent below or on both sides; twigs usually grayish-pubescent; an abundant and highly variable species in muskegs, damp meadows and open woods below timberline, and in alpine scrub; pistillate plants seldom seen without aments, for it

flowers late, and the dead aments often persist on the branchlets into the following season .... *S. glauca.*

69\. Leaves bright green and glabrous above when mature.

70\. Leaves 2.5-5 cm. long (av. about 3 cm.), usually about half as wide as long, thinly appressed-hairy beneath, though finally becoming glabrous when old, shrubs usually less than 1.5 m. tall; rare or occasional in muskegs and wet meadows .... *S. athabascensis.*

70\. Leaves 2-7 cm. long (av. about 4 cm.), usually 1/3-1/2 as wide as long, slightly silky when young but soon becoming glabrous; somewhat taller than the last, up to 2 m. (cf. also *S. Barclayi* which sometimes has nearly entire leaves) .... *S. fallax.*

DESCRIPTION OF THE SPECIES

SALIX L. WILLOW

Shrubs or small trees, ranging in size from tiny alpine plants only 2 or 3 cm. high to trees up to 10 m., and occupying almost the entire spread of available habitats. Buds with a single scale; flowers borne in catkins or aments, each of which is a simple spike of flowers on a central axis; catkins sessile on branchlets of the preceding year, or on short leafy peduncles on these branchlets; male and female flowers nearly always on separate plants; the individual female flower consists of a single, 1-celled ovary, with a distinct style or none, and 2 stigmas each of which may be divided; ovary sessile or borne on a short pedicel, subtended by a single small bract; in the axil of the pedicel (ventral to it) is a small nectary, or gland (called the "ventral gland"), and in some species there is a second gland in the axil between the bract and the pedicel (dorsal to the latter, and called a "dorsal gland"); in fruit the ripened ovary forms a capsule which splits down two sides from the apex, freeing large numbers of small seeds each of which is supplied with a mass of silky down that is easily blown by the wind; staminate flowers of similar structure except that the ovary is replaced by stamens, numbering from 1 to 12 depending upon the species.

KEY TO THE SALIX LUCIDA GROUP

A. Leaves green on both surfaces, not glaucous beneath though sometimes paler green

  B. Young branchlets glabrous or soon glabrate

    C. Leaf blades more or less abruptly caudate-acuminate, usually not more than three times longer than wide (except in var. *angustifolia*); a temperate eastern American species, closely related to the following .... *S. lucida.*

    C. Leaf blades more gradually caudate-acuminate, usually 4-5 times longer than wide; a species of western America .... *S. lasiandra* var. *caudata.*

  B. Young branchlets pubescent .... *S. lasiandra* var. *recomponens.*

A. Leaves glaucous beneath

D. Leaves mostly acute at the apex, scarcely acuminate, the width not much less than 1/3 of the length .... *S. serissima.*

D. Leaves usually acuminate at the apex, width more commonly 1/4 the length or less

  E. Young branchlets glabrous or soon glabrate .... *S. lasiandra* (typ.).

  E. Young branchlets usually densely pubescent .... *S. lasiandra* var. *lancifolia.*

Salix lucida Muhl. in Neue Schr. Ges. Naturf. Fr. Berlin 4:239 (1803)

Large shrubs or small trees, in our region up to 3 m. high with slender trunks and brown, shiny, glabrous twigs; leaves lanceolate to ovate-lanceolate, up to 1.5 dm. long and 5 cm. wide, usually long-caudate, serrate at the apex, wedge-shaped to rounded or even cordate at the base, finely glandular-toothed, glabrous, green on both sides but somewhat paler green beneath, shiny above, on petioles up to 15 mm. long; summit of the petiole at base of blade with large glands; catkins appearing with the leaves, on leafy peduncles, the pistillate up to 5 cm. long; capsules 5-6.5 mm. long, glabrous, on pedicels up to 1 mm. long; bracts yellowish, thinly hairy, falling off soon after the expanding of the catkins; styles 0.5 mm. long; staminate catkins up to 5 cm. long; stamens 3-5 or more; filaments pubescent below.

An eastern species of temperate America (Map 1) which has been collected at Moose Factory, York Factory, and in the valleys of the Hayes and Nelson Rivers west of Hudson Bay (Raup, 1943: 93; Scoggan, 1957:231). The extent of its range westward in northern Manitoba and Saskatchewan is unknown, though Breitung (1947:83) reports it common along streams in east central Saskatchewan. A leaf variant, var. *angustifolia* Anders. in Proc. Amer. Acad. Sci. 4: 54 (1858), has also been collected near Moose Factory. Its leaves are narrowly lanceolate and taper gradually to acuminate tips, while in the typical species they are more abruptly narrowed to the long, caudate-acuminate tips.

Salix lucida appears to be the principal eastern element in a series of overlapping species that make up what I have called the "*S. lucida* group," in which the more western elements are *S. serissima* and *S. lasiandra.*

Salix lasiandra Benth. Pl. Hartweg. 335 (1857)

Tall shrubs, or small trees up to 6 or 8 m. high, with reddish, shiny twigs; leaves 6-12 cm. long, 1.5-3 cm. wide, mostly lanceolate though sometimes oblanceolate, acuminate at the apex, acute to rounded at the base, finely and regularly crenate-serrate on the margins, rather leathery in texture, dark green and shiny above, paler green or glaucous beneath, glabrous or glabrate, on petioles that have small glands on each side near the base of the blade; pistillate catkins up to 10 cm. long, on leafy peduncles, appearing with the leaves; capsules glabrous, up to 7 mm. long, on pedicels 1.5-2 mm. long; scales 2-3 mm. long, pale, hairy toward the base; styles very short; staminate catkins 2-6 cm. long; stamens about 5; filaments hairy at the base.

Occasional to common on sand and mud bars along the major streams in the central and southern parts of the Mackenzie basin, and common locally in the Alaska Highway region from Lesser Slave L. to the Tanana valley. It occurs sporadically in the lower Yukon valley and in the Endicott Mountains of Alaska, and down the Mackenzie R. at least to Simpson and possibly as far down as Norman (Raup, 1947: 149). Porsild (1951: 138) found it along the Canol Rd. as far up as mi. 127, along the Lower Lapie R. The easternmost collections I have seen are from Sand Pt., on the north shore of L. Athabaska (Raup, 1936: 228-9). Map 1.

Salix lasiandra is a highly variable species, particularly in the shape and coloring of the leaves, and in the pubescence of the branchlets. Some students have regarded these variations as separate species, but I prefer to consider them merely as phases, with recombinations of characters. Four such phases have been identified in our region. The following key, modified from a treatment by Ball (1926: 146), will distinguish them. Still other forms are likely to appear as more collections accumulate.

A. Leaves pale or somewhat glaucous beneath
  B. Young branchlets glabrous or soon glabrate .... *S. lasiandra* (typ.).
  B. Young branchlets usually densely pubescent ...... var. *lancifolia.*
A. Leaves green beneath
  C. Young branchlets glabrous or soon glabrate .... var. *caudata.*
  C. Young branchlets pubescent .... var. *recomponens.*

Specimens determined as typical *S. lasiandra* were collected by *Brinkman 4035, 4303* (BH), in the vicinity of Lesser Slave L., and the species should be looked for in the upper Peace R. region. Both the typical form and var. *lancifolia* (Anders.) Bebb in Watson, Bot. Calif. 2: 84 (1879) have been found in the central Mackenzie basin (Raup, l.c.), and the latter was collected in the vicinity of Summit L. by *Taylor et al, 4* (V); by our field parties along the Liard R. south of Watson L., *10967, 10968, 10969;* and by Setchell at Fairbanks, *433* (GH). This variety has also been found along the Yukon at Dawson by *Eastwood 112, 113, 128, 304, 466* (K). Variety *caudata* (Nutt.) Sudw. in Bull. Torr. Bot. Cl. 20: 43 (1893) (*S. caudata* (Nutt.) Heller) was collected by our party along the Alaska Highway at the Sikanni R., *10402.* Variety *recomponens* Raup in Sargentia 6: 149 (1947) is known thus far only from its type collection on a sand bar along the Mackenzie R. near Simpson, *Raup 9073, 9076* (A).

Salix lasiandra is closely related to *S. serissima* and *S. lucida.* It is the westernmost phase in a continuous population of *lucida*-like willows that extends across most of the northern forested part of the continent.

Salix serissima (Bailey) Fern. in Rhod. 6: 6 (1904)

S. lucida Muhl. var. *serissima* L. H. Bailey ex Arthur in Bull. Geol. Nat. Hist. Surv. Minn. 3: 19 (1887).

Shrubs up to 4 m. high, with glabrous, shiny, yellowish-brown twigs; leaves 5-10 cm. long, 1-3.5 cm. wide, elliptic to oblong-lanceolate, short-acuminate at the apex, acute to rounded at the base, finely and regularly glandular-serrate on the margins, glabrous, dark green and shiny above, pale or somewhat glaucous beneath, on petioles that have glands on each side near the base of the blade; pistillate catkins appearing with the leaves or later, 2-3.5 cm. long, up to 2 cm. thick, on leafy peduncles; capsules glabrous, up to 10 mm. long, on pedicels 1-2 mm. long; bracts up to 2.5 mm. long, yellowish, short-hairy; styles less than 0.5 mm. long; staminate catkins 1-2 cm. long; stamens usually 5, the filaments thinly hairy.

Salix serissima has been collected in the vicinity of Lesser Slave L., *Brinkman 4648* (BH) and northward to the upper Mackenzie valley where it appears to reach its northwestern limit (Hay River, *Lindsey 115*, CAN; Mackenzie R. above Providence, *Porsild 16554*, CAN; lower Keele R., *Lindsey 341, 343*, CAN). It is closely related to the western *S. lasiandra*, and the two species appear to integrade in the southern and central Mackenzie basin (Raup, 1934: 142-3; 1936: 228-9). Map 1. *Salix serissima* is usually distinguished from *S. lasiandra* by its shorter catkins, longer pedicels, less acuminate leaves, and by its later flowering time (mid-to late summer). I have seen specimens from the north shore of L. Athabaska, *Raup 6353* (A), and from the Cypress Hills, *Breitung 5104* (K). Its northern limit in the Hudson Bay region seems to be west of James Bay, and I have seen specimens from the west coast of that Bay, and from the upper Severn R. (1943: 92-3). See note under *S. lucida.*

Salix fragilis L. Sp. Pl. 1017 (1753)

Tall trees or large shrubs, with thick, rough bark, and greenish to reddish glabrous twigs that are brittle and easily broken off at the base; leaves lanceolate, up to 15 cm. long and 4 cm. wide, glabrous or soon glabrate, green on both sides or somewhat glaucous beneath, glandular-serrate on the margins, acuminate at the apex, usually wedge-shaped at the base, on petioles up to 1.5 cm. long; catkins appearing with the leaves, borne on leafy peduncles, the pistillate up to 7 cm. long; capsules about 5 mm. long, glabrous, on pedicels 1 mm. long or less; bracts oblong, ciliate on the margins, falling off soon after the catkins expand; styles 0.3-0.7 mm. long; staminate catkins 3-5 cm. long; stamens usually 2; filaments hairy at the base.

Salix fragilis is an introduced species, brought from Europe and widely spread from cultivation in temperate eastern America. I have seen a single collection of it from our region, in the Mackenzie drainage basin (*Ball 116493*, (CAN), on the bank of the Athabaska R., east of Lesser Slave L., at Athabaska Landing).

Salix interior Rowlee in Bull. Torr. Bot. Cl. 27: 253 (1900)

Salix longifolia Muhl., non Lam.

Upright shrubs, sometimes as much as 3-4 m. high, with smooth, brownish twigs, leaves 5-14 cm. long, 5-10 mm. wide, narrowly lanceolate to linear, glabrous or glabrate, sometimes nearly entire but usually with sharp, rather widely-spaced teeth, sessile or on very short petioles, some of them nearly opposite on the twigs; catkins appearing with the leaves, on leafy peduncles, the pistillate up to 8 cm. long; capsules as much as 9 mm. long though usually shorter, silky, or glabrous in age, on pedicels up to 1.5 mm. long; bracts up to 3 mm. long, pale yellow, deciduous soon after the catkins expand, thinly pubescent; styles obsolete; staminate catkins 2-4 cm. long; stamens 2; filaments hairy.

Common on sandbars along the larger rivers (and occasional on sandy lake shores) northward to York Factory, to the vicinity of Good Hope on the Mackenzie, to the upper Liard R. and reappearing in the Yukon, Tanana and Porcupine River valleys. It has also been collected along the Colville R. in northern Alaska (Umiat, *Spetzman, 2141*, US). It was not seen in the upper Yukon drainage in the region of Whitehorse, though it is known from the Dawson district (Hultén, 1942: 504-5). Map 2. All but two of the specimens I have seen from our region represent var. *pedicellata* (Anders.) Ball in Can. Field-Nat. 40: 175 (1926), which has very narrow leaves (usually not over 6 mm. wide). The exceptions came from along the Liard R. south of Watson L., *10965*, and from the delta of the Slave R., *Raup, 561* (GH). Both of these have the broader leaves of the typical species (1 cm. or more). Another phase of the species, forma *Wheeleri* (Rowlee) Rouleau in Nat. Canad. 71: 268 (1944), has been reported by Scoggan (1957: 231) along the Nelson R. about 30 mi. from York Factory. It is distinguished by the more or less permanent silvery-silky pubescence on its leaves.

KEY TO THE SALIX RETICULATA GROUP

A. Prostrate shrubs, with leaves glabrous or nearly so, borne on elongate petioles (up to 3 cm.); lateral veins of the leaves few, the lower ones rising from near the base .... *S. reticulata.*

A. Shrubs with prostrate or erect branchlets; leaves usually conspicuously silky-hairy on both sides (or occasionally glabrate), the lateral veins well scattered along the midrib; petioles not much longer than the buds .... *S. vestita.*

Salix reticulata L. Sp. Pl. 1018 (1753)

Prostrate shrubs, trailing along the ground and ascending only a few centimeters above the surface; twigs smooth, purplish-tinged when young; leaves rounded, obovate, or oval in outline, as much as 4 cm. long but usually shorter, dark green above, the veins deeply impressed to form a reticulate pattern, conspicuously glaucous beneath, sometimes silky when young but soon glabrous, borne on long, reddish petioles, entire on the margins or nearly so; catkins slender, reddish, up to 3 cm. long, appearing terminal on the branchlets; capsules 3-4 mm. long, sessile, densely pubescent; bracts about 2 mm. long, rounded, greenish with dark tips, hairy; styles nearly obsolete; stamens 2; filaments hairy at the base.

Common to abundant, sometimes forming loose mats on the ground in damp alpine tundra, and in mossy muskegs below timberline, throughout our region southward in Alaska to the region of Glacier Bay and White Pass, in the Rocky Mts. to Banff, and in the central plain to Great Slave L. It is also found on the western coasts of Hudson and James Bays (Porsild, 1957: 175, map 118). Easily distinguished from other prostrate alpine willows by its broad, glabrate, conspicuously reticulate-veined leaves on long, slender, reddish petioles. The leaves of *S. glacialis*, though rather strongly reticulate beneath, are smaller and have shorter petioles. Map 3.

Salix reticulata is closely related to *S. vestita*, and overlaps the northern part of the latter's range. Together they form what I have called the "*S. reticulata* group."

Salix vestita Pursh, Fl. Amer. Sept. 2: 610 (1814)

Depressed or ascending shrubs, usually less than 6 dm. high but sometimes as much as 1 m., with stout, spreading branches and pubescent or glabrous twigs; leaves rather thick, rounded to obovate, elliptic or oblong, 1-8 cm. long (usually 2-4), closely crenate on the margins, obtuse, rounded, or heart-shaped at both ends, dark green above and glaucous beneath, the upper surfaces with deeply impressed veins, the lower surfaces clothed with long, white, silky, appressed hairs, or in age glabrate except on the veins; petioles 2-8 mm. long; catkins appearing with or after the leaves, on leafy peduncles; capsules 3-5 mm. long, nearly sessile, brownish, glabrous; bracts up to 1.5 mm. long, blackish toward the tips; styles short or obsolete; stamens 1 or rarely 2; filaments glabrous.

A predominantly eastern arctic species (Map 3), of somewhat more southern range than *S. reticulata*, that has been collected as far south as northern Manitoba and has an apparently isolated population in the Rocky Mts. I have seen specimens from Churchill and Fort Severn, and Scoggan (1957: 232) reports collections from York Factory and from the Hayes R. at various points up to 100 mi. S. W. of Hudson Bay. The material from Churchill and from the Rocky Mts. represents var. *erecta* Anders. ex DC. Prod. 16^2: 300 (1868), which may be distinguished from the species by the following characters.

A. Capsules narrowly ovoid, definitely tapering to the blunt tip; pistillate catkins 0.5-3 cm. long; staminate catkins 0.6-2 cm. long; leaves obovate or orbicular, usually somewhat retuse and reticulately veined .... *S. vestita* (typ.).

A. Capsules only slightly tapering to the broad rounded summit; pistillate catkins 2-5 cm. long; staminate catkins 1-3 cm. long; leaves elliptic or oblong, often subacute, usually plane above .... **var. *erecta*.**

Salix vestita is closely related to *S. reticulata*, and the two may be considered as segregates within an *S. reticulata* group.

Salix Setchelliana Ball, Univ. Calif. Publ. Bot. 17: 410-12 (1934)

Prostrate shrubs; branchlets sometimes ascending to 15 or 20 cm. above the ground, pruinose, pubescent when very young, but soon glabrate; leaves somewhat fleshy or leathery, obovate or oblanceolate, tapering to the base and almost without petioles, rounded or retuse at the apex, the margins entire or irregularly glandular-serrate, green or bluish-green and shiny above, green or glaucous beneath, nearly glabrous when full-grown; catkins appearing with the leaves on short leafy peduncles, up to 2 cm. long; capsules glabrous, up to 7 mm. long, borne on very short pedicels; bracts up to 4 mm. long, pale yellow, ciliate on the margins, sometimes notched at the apex; styles 0.2-0.3 mm. long; stamens 2; filaments hairy.

A distinctive species originally described from material collected in Mount McKinley Park in 1932. Later collections have shown that it has a rather wide range in Alaska and southwestern Yukon. I have seen the following specimens: south end of Kluane L., *Anderson 9493* (GH, CAN); gravelly lake beaches near Burwash, Kluane L., *12271*, *13306*, *13321*. Hultén (1942: 507-8; 1949: 1732) cites material collected by Anderson just west of the Donjek R. bridge, and by Müller between Kluane L. and the Donjek R. Argus (personal communication) reports a specimen in the University of Alaska Herbarium collected at Palmer by Anderson; and Spetzman cites a specimen collected by Gudin at the Itkillik Lakes in the Brooks Range. The species is locally abundant in the Kluane L. area, and is conspicuous on gently sloping, wave-washed shores near Burwash. Map 4.

Salix polaris Wahl. Fl. Lapp, 261 (1812)

Represented in our flora entirely by subsp. *pseudopolaris* (Flod.) Hultén in Fl. Alaska & Yuk. 510 (1942) (*S. pseudopolaris* Flod. in Vet. Akad. Ark. Bot. 20A, No. 6, p. 8, 1926; *S. polaris* var. *selwynensis* Raup in Contr. Arn. Arb. 6: 144, 1934), to which the following description applies. Prostrate, small, trailing shrubs, often forming dense mats by the frequent branching of the stems; leaves broadly rounded or obovate, entire at the margins, glabrous or with white hairs on the margins, sometimes as much as 2.5 cm. long but usually much less, green on both sides; catkins appearing with the leaves, on leafy peduncles, short (usually less than 3 cm.) and thick, few-flowered; capsules pubescent, 5-7 mm. long, nearly sessile; bracts up to 2 mm. long, obovate, mostly dark brown to black, glabrous or thinly hairy; styles 0.5-1 mm. long; stamens 2; filaments glabrous.

Common to abundant in the alpine and arctic tundra of western and interior Alaska, Yukon, and to the eastern slopes of the Mackenzie Mts. and the Arctic Coast east of the Mackenzie delta (Hultén, l.c.; Porsild, 1951: 139-40; 1945: 18). It is found southward in the Rocky Mts. to the Peace R. (Raup, l.c.) and is noted by Porsild as common on Banks and Victoria Islands (1955: 100-1). It is a common alpine species in the vicinity of the Alaska Highway. Thus far it has not been collected within the continental borders east of the Mackenzie Mts. except on the coast just east of the Mackenzie delta (Porsild, 1957: 175, map 119). Map 6.

Salix herbacea L. Sp. Pl. 2: 1918 (1753)

Tiny shrubs with their main branches slender, subterranean, and rooting at the nodes; leaves 1-3 cm. long, rounded or retuse, thin, glabrous and shiny, green on both sides, crenate-serrate, on slender petioles, usually only 2-4 leaves on each twig projecting above moss in which it grows; catkins appearing with the leaves or later, 5-8 mm. long, each usually with only 2-8 flowers, ovoid in shape; capsules glabrous, 5-6 mm. long, nearly sessile; bracts very short, obovate, nearly glabrous on the outer surface, but with long white hairs on the inner side; styles 0.5 mm. long or less; stamens 2; filaments glabrous.

An arctic alpine species that is predominantly eastern in America (Porsild, 1957: 175, map 114). It appears on the northwest coast of Hudson Bay (Raup, 1943: 97-8) and north to the Arctic Coast. Porsild (1943: 27-8) has collected it in the interior of Keewatin and at Great Bear L.; and there are collections from Artillery L., and Bathurst Inlet. Scoggan (1957: 232) reports collections of it at Nejanilini, Baralzon, and Nueltin Lakes in northern Manitoba. Map 6.

KEY TO THE SALIX ROTUNDIFOLIA GROUP

A. Small, matted shrubs with glabrous, ovate or elliptic leaves 1-2 cm. long, and with an abundance of marcescent, skeletonized dead leaves from several preceding seasons clothing the stems and forming a large part of the mats .... *S. phlebophylla.*

A. Marcescent leaves not abundant though a few may persist through one year, not forming conspicuous parts of mats; leaves very small, rounded or ovate, 4-10 mm. long (mostly 4-7 mm.); tiny matted plants of alpine tundra

  B. Lateral veins of the leaves more or less raised on both sides, even the veinlets prominent .... *S. rotundifolia.*

  B. Lateral veins of the leaves slightly incised above, prominent beneath, the veinlets not visible .... *S. Dodgeana.*

Salix rotundifolia Trautv. in Nouv. Mém. Acad. Mosc. 2: 304 (1832)

A tiny species that forms mats of thin branchlets in rather dry alpine tundra, the whole plant often not more than 2-3 cm. high. Leaves rounded or ovate, smooth, shiny, green on both sides, delicate in texture, entire, usually less than 1 cm. long, and commonly half that, dead dry ones persisting for about one year; catkins very short, often no more than 1 cm. long, with half a dozen flowers or so; capsules glabrous; bracts about 2 mm. long, dark brown to black, thinly hairy; styles distinct but short; stamens 2; filaments glabrous.

Apparently restricted, in its American range, to Alaska (Hultén, 1942: 508-9) and neighboring Yukon, where it is an arctic and alpine species. It has been collected in only one place in the vicinity of the Alaska Highway, on rock ledges and scree slopes above timberline on a mountain near the southeastern end of Kluane L. at mi. 1064: ***12167, 12168, 12294.*** Map 5.

Salix rotundifolia is one of three closely related species that I have placed together in an "*S. rotundifolia* group." The others are *S. phlebophylla* and *S. Dodgeana.* All are diminutive arctic-alpine plants whose ranges overlap, and among which intermediates are commonly found.

Salix Dodgeana Rydb. in Bull. N. Y. Bot. Gard. 1: 277 (1899)

Tiny mat-forming shrubs, scarcely over 2 cm. high, with short, mostly underground stems, the aerial parts densely leafy, glabrous and yellowish-green when young; leaves glabrous, 4-5 mm. long (sometimes up to 7 mm.), usually 2-3 mm. wide (or 4 mm. in larger ones), oblong or oval, obtuse or acutish at the apex, narrowed at the base to very short petioles, entire on the margins, bluish-green, the veins prominent on the lower surfaces and slightly incised above; pistillate catkins usually with only 2 flowers; capsules glabrous when mature, 2.5-4 mm. long, sessile or nearly so; bracts oblong, about 1 mm. long, glabrous except for the ciliate-hairy margins; styles obsolete; staminate catkins usually 3-4 flowered; stamens 2; filaments glabrous.

Salix Dodgeana was originally described from material collected on Electric Peak in Yellowstone Park, and has since been found in alpine situations in several places in the Rocky Mts. of Wyoming and southwestern Montana. In his original description Rydberg also cited a specimen from Atka Island in the Aleutians (***Turner 1293*** in part). I have not seen this material, but Schneider's description of it (Bot. Gaz. 67: 54, 1919) indicates that it belongs in *S. phlebophylla.* Hultén

(1942: 511) agrees with Schneider's diagnosis. Porsild (1945: 18) reported three collections of *S. phlebophylla* along the Canol Rd. east of the Yukon-Mackenzie divide. Later study of this material convinced him that it represented *S. Dodgeana*, an opinion with which I concur, for I have seen the specimens and they are a good match for the type of *S. Dodgeana*. Otherwise the species is unknown in our region. It is closely related to *S. rotundifolia* and *S. phlebophylla*. Map 5.

Salix phlebophylla Anders. Öfvers. Vet. Akad. Förh. (Stockh.) 15: 131 (1858)

A very small willow of the arctic and alpine tundra, forming dense mats of branching stems; leaves glabrous, ovate or elliptic, 1-2 cm. long, rather prominently few-veined, entire, green on both sides; catkins commonly 1.5-3 cm. long; capsules glabrous or slightly pubescent when young, on very short pedicels; bracts up to 1.5 mm. long, black with white hairs; styles distinct, but short; stamens 2; filaments glabrous; dry, partially skeletonized remains of dead leaves marcescent, remaining on the twigs for several years and clothing them densely.

Widespread in the tundra of the Arctic Coast and interior mountains of Alaska (Hultén, 1942: 511-12). Porsild could find no record of it in Yukon except on the Arctic Coast (1951: 140), and it has not been found in the immediate vicinity of the Alaska Highway though it is to be expected there. Porsild's record for it on the eastern alpine slopes of the Mackenzie Mts. (1945: 18) he now believes should be applied to *S. Dodgeana*. He has collected it along the Arctic Coast eastward to just beyond the Mackenzie River delta (1943: 28). Map 5. *Salix phlebophylla* resembles *S. rotundifolia*, but is easily distinguished from that species by the masses of marcescent leaves that clothe its stems. I regard it as one of a closely related series including *S. rotundifolia* and *S. Dodgeana*.

KEY TO THE SALIX ARCTICA GROUP

A. Leaves usually dark green and lustrous above, the lateral veins numerous and extending out from the midribs at wide angles, sometimes nearly perpendicularly; glands short and broad, scarcely twice as long as thick, broadly truncate at the apex, half the length of the pedicels of the capsules .... *S. arctophila*.

A. Leaves usually pale green above, opaque or slightly lustrous, the lateral veins few and extending out from the midribs at much smaller angles; glands oblong, mostly 2½-4 times as long as thick; pedicels of the capsules shorter than the glands or rarely a little longer .... *S. arctica* (*sens. lat.*).

Salix arctica Pall. Fl. Ross. 1, 2: 86 (1788)

An extremely variable and widespread arctic and northern alpine species with trailing branches often forming dense mats; leaves entire or essentially so, green above and glaucous beneath, obovate, oval, oblong, or elliptic in outline, borne on well-defined petioles, acute, obtuse to rounded or retuse at the apex, sometimes villous when young, but glabrate at maturity, varying from 2 to 8 cm. in length; pistillate catkins up to 9 cm. long or more, much longer than thick; capsules 8-10 mm. long, pubescent, or in some forms becoming glabrate in age, sessile or on very short pedicels; bracts about 2 mm. long, dark brown or black, long-hairy; styles up to 1.5 mm. long; staminate catkins up to 5 cm. long; stamens 2; filaments glabrous.

In this treatment I am making of *S. arctica* a broad and inclusive species. It is so variable, and has been so commonly collected and studied that inevitably its many phases have been given separate names. Even the typification of these names has not all been worked out, much less the real relationships among the plants. For those who wish to look further into the matter, the following are some of the more recent discussions of it: Schneider, Bot. Gaz. 66: 117-135 (1918); Hultén, 1942: 513-20; Porsild, 1951: 140-141; 1957: 70; Raup, 1943: 98-100; 1947: 150-51; Polunin, 1940: 157-9; Ball, 1950: 224-41.

Eastern arctic forms of *S. arctica* have been variously treated, by some students as a separate species and by others as a group of varieties of the main species. Schneider maintained them under *S. anglorum* Cham. in Linnaea 6:541 (1831) and a group of varieties of it, and Ball (1952a: 16) has followed the same course (see also Ball, 1950b: 224-41). Fernald (1950: 508-9) recognized *S. arctica* as a single species in North America, with several eastern varieties. In my treatment of the willows of the Hudson Bay region and the Labrador Peninsula (1943: 98-100), I discussed the pros and cons of the matter at some length and maintained the eastern forms as a group of rather poorly defined varietal segregates in a single widespread *S. arctica* population in the eastern Arctic. The commonest of these eastern forms is the plant I then called *S. arctica* var. *Brownei* Anders. in DC. Prod. 16^2: 286 (1868) (*S. anglorum* Cham.). It is distinguished with great difficulty, as being generally less robust than the typical species, and in having leaves that are, on the average, somewhat smaller. Similar forms are to be found in the western range of the species, however, and I do not now consider them to have any taxonomic validity.

Schneider, in Bot. Gaz. 67: 57-8 (1919), described a *Salix hudsonensis* from the western coast of Hudson and James Bays. In an earlier publication, Bot. Gaz. 66: 342 (1918), he had identified most of this material as a hybrid of *S. fullertonensis* and *S. groenlandica* (*S. arctophila*). The type of his *S. hudsonensis* was collected by *E. A. & A. E. Preble 43* about 50 miles south of Cape Eskimo. Schneider thought that it was most nearly related to *S. arctophila*, but in distinguishing it from the latter he pointed out that it had shorter pedicels and more elongated glands. Examination of the type material shows that the lateral veins of the leaves come off at sharply acute angles, rather than at wide angles as in *S. arctophila*. But these are the principal characters by which *S. arctophila* differs from *S. arctica*, so that *S. hudsonensis* merges with the huge and highly variable population that makes up *S. arctica* in the broad sense. Ball has observed this (1950b: 224-41) and proposes that *S. hudsonensis* is identical with the *S. anglorum* var. *antiplasta* described by Schneider in Bot. Gaz. 66: 134-5 (1918) from specimens collected on Mt. Albert in the Gaspé Peninsula. Comparison of descriptions and type specimens has led me to the same conclusion. This plant will here be called *S. arctica* var. *antiplasta* (Schn.) Fern. in Rhod. 48: 44 (1946).

Some of the specimens cited by Schneider under *S. hudsonensis*, however, are not in agreement with his description or the type material. They have broadly elliptic-ovate to somewhat rounded leaves that are mostly blunt or rounded at the apex and wedge-shaped to subcordate at the base. The following collections have these characters: Hudson Bay, lat. 55°-56°, *J. M. Macoun 18822* (CAN); Fullerton, Hudson Bay, *J. M. Macoun 79148* (CAN); mouth of the Albany R., James Bay, *Spreadborough 62618* (CAN). They agree with *S. arctica* var. *kophophylla* (Schn.) Polunin in Jour. Bot. 77: 271 (1939) (*S. anglorum* var. *kophophylla* Schn. in Bot. Gaz. 66: 130-3, 1918).

Hultén has maintained, tentatively, three "species" in his treatment of the *arctica*-group in Alaska and Yukon: *S. arctica* Pall., *S. crassijulis* Trautv., and *S. torulosa* Trautv. He has given them a rather well-defined geographic segregation: *S. arctica* on the Arctic Coast and in the Bering Straits region; *S. crassijulis* on the southern coastal mountains of Alaska, the Aleutians, and in the Bering Straits region; *S. torulosa* on the interior mountains of Alaska and Yukon, but also appearing at Bering Straits. The key characters by which he distinguishes them are as follows (1942: 502):

A. Scales light brown, oblong or pointed, styles about 1-1.5 mm. long, capsules light brown .... *S. torulosa.*

A. Scales round, in age becoming black from the tip, thus often bicolored or entirely black, rounded or orbicular, styles long

  B. Leaves orbicular to obovate, often on long petioles, catkins large and thick on leafy peduncles, styles long and stout (about 2 mm.), capsules short-pedicelled .... *S. crassijulis.*

  B. Catkins smaller, on shorter peduncles, styles shorter, capsules sessile .... *S. arctica.*

It should be noted that all of these characters involve degrees of difference within narrow ranges of color, shape or size. When they are applied to a large number of specimens the geographic segregation proposed by Hultén immediately breaks down. Porsild evidently had this experience when he was unable to see *S. torulosa* in any of his many collections of *S. arctica* along the Canol Rd., though he cites a number of specimens along the more southern parts of it that approach *S. crassijulis*. I have been unable to segregate from our Alaska Highway collections any widespread *torulosa*-form, and I have seen plants of the *crassijulis*-form in the mountains of the interior mixed freely with the other two. Larger collections and further study may bring out a more realistic definition of segregates, but for the present I prefer to consider the existing ones only as intermingled varietal phases of a single species. As such I propose the following names for them: *S. arctica* Pallas (l.c.); *S. arctica* var. *torulosa* (Trautv.) Raup, stat. nov. (*S. torulosa* Trautv. in Mém. Soc. Nat. Mosc. 2: 309, 1832); *S. arctica* var. *araioclada* (Schn.) Raup in Sargentia 4: 100 (1943) (*S. anglorum* var. *araioclada* Schn. in Bot. Gaz. 66: 133, 1918; Jour. Arn. Arb. 3: 67, 1921; *S. crassijulis* Trautv. in Mém. Soc. Nat. Mosc. 2: 308, 1832, at least as to American plants).

I am unable to separate the forms with relatively large, thin, broad leaves that have been called var. *araioclada* in the East from those called *S. crassijulis* in the West. The affinities of *S. torulosa* (as interpreted by Hultén) among the American forms of *S. arctica* need further study. Hultén says that it differs "from *S. crassijulis* in the long and narrow oblanceolate light green leaves, glabrous on both sides except in the margin and sometimes along the median nerve below" (1942: 520). In leaf-form this suggests var. *antiplasta*, and it is of interest to note that Ball (l.c.) has given the latter a wide range in the Rocky Mts. On the other hand, I saw material at Stockholm cited by Hultén under *S. torulosa* (such as *Jones 9031*, from Nome) which has broadly obovate leaves, obtuse to rounded at the apex and wedge-shaped to nearly round at the base. These suggest var. *kophophylla.*

Within the region covered by the present treatment, therefore, five phases of *S. arctica* Pallas may be recognized: *S. arctica* (typ.); var. *antiplasta;* var. *kophophylla;* var. *araioclada;* and var. *torulosa.* It should be emphasized that these forms are poorly defined, and that the following key will do little more than indicate trends.

A. Leaves obovate, obovate-oblong, ovate, ovate-rounded, or broadly elliptic, rounded to subacute at the apex, tapering to rounded or nearly cordate at the base, the width usually one-half to four-fifths the length; scales of the flowers black or with black tips, usually rounded
  B. Well-developed leaves usually 3-6 cm. long and 2-4 cm. wide, thin-papery, usually obovate in general outline, obtuse to rounded at the apex, and tapering to the base; pistillate catkins up to 9 cm. long at maturity .... *S. arctica* (typ.).
  B. Well-developed leaves more broadly proportioned, commonly broadly obtuse to rounded or subcordate at the base, thin-papery or thick and firm in texture; fruiting catkins usually not over 5.5 cm. long
    C. Young leaves hairy above though glabrous, thick and firm in texture at maturity, 1.5-3.5 cm. long, 1.2-3 cm. wide, somewhat plicate at the apex; twigs purplish; fruiting catkins usually 3.5 cm. long or less .... var. *kophophylla.*
    C. Young leaves glabrous above, thin-papery when mature, up to 5 cm. long and 3 cm. wide; twigs yellowish; fruiting catkins up to 5.5 cm. long .... var. *araioclada.*
A. Leaves narrowly oblong-lanceolate or -obovate, narrowly oval, or elliptic, the width commonly less than half the length; scales of the flowers black or brown
  D. Leaves firm in texture, thick, usually acute at both ends, commonly plicate at the apex; scales black or black-tipped, rounded or sometimes acute at the apex .... var. *antiplasta.*
  D. Leaves thin-papery, more obtuse at base and apex; scales brown, acute at the apex .... var. *torulosa.*

Salix arctica (*sens. lat.*) is common in the arctic and alpine tundra from Hudson Bay to western Alaska and in the arctic islands (see Porsild, 1957: 176, map 125). It extends southward in the coastal mountains to the Puget Sound region, and in the Rocky Mts. to the vicinity of Banff. There seems to be a gap in its range along the Arctic Coast from northern Yukon to Cape Lisburne (Raup, 1947: map, Pl. 21). It occupies a wide variety of habitats, from dry to wet, and from much disturbed soils to the more stable ones. Its imperfectly segregated varieties, once thought to have a certain amount of geographic definition, have with more recent collections been shown to have wide distributions within the range of the species as a whole. In what I have called the "*S. arctica* group" of willows, therefore, I have included only two species: the multiform *S. arctica* Pall., and the closely related, primarily eastern arctic *S. arctophila*. Map 7.

Salix arctophila Cock. ex Heller, Cat. N. Amer. Pl. (ed. 3) 89 (1910)

Low, trailing shrubs with glabrous twigs; leaves elliptic to obovate, 2.5-4 cm. long, 1.5-3 cm. wide, rounded to acutish at the apex, rounded to wedge-shaped at the base, entire on the margins or nearly so, glabrous, dark green and shiny above, glaucous beneath, the lateral veins usually numerous, parallel, rather prominent, and leaving the midrib at a somewhat wider angle than those of *S. arctica*; catkins appearing with the leaves, the pistillate 3-10 cm. long, upright, on leafy peduncles; capsules 7-10 mm. long, pubescent or occasionally glabrous, nearly sessile; bracts obovate, blackish toward the tip, 2-2.5 mm. long, long-hairy; styles 1-1.5 mm. long; stamens 2; filaments hairy toward the base.

Common in eastern American arctic-alpine situations (Raup, 1943: 100-101), and extending westward in the tundra to the Arctic Coast west of the Mackenzie delta (Porsild, 1943: 27; 1957: 176, map 123). Specimens recently collected by Cantlon & Gillis in the Jago L. region of northeastern Alaska (*57-1456, 57-1078, 57-946*) extend the species a little farther westward along the coast. Map 7. Hultén's record of it in Alaska is based entirely upon a sterile specimen collected at Nome by *G. N. Jones 9042*. I have seen this specimen at Stockholm, and cannot identify it as *S. arctophila*. It strongly suggests some form of *S. arctica* or *S. ovalifolia*. *Salix arctophila* is closely related to *S. arctica*. It differs from the latter in leaf venation, and also in having relatively short, broad ventral glands (scarcely twice as long as broad). Many intermediate forms occur. Plants with glabrous capsules may be called forma *lejocarpa* (Anders.) Fern. in Rhod. 28: 178 (1926).

KEY TO THE SALIX OVALIFOLIA GROUP

A. Leaves broadly ovate to rounded, the width commonly 4/5 the length or more
  B. Styles short, usually 0.5 mm. long or less; branches not strongly stoloniferous .... *S. ovalifolia.*
  B. Styles 1-2 mm. long; branches often with slender subterranean stolons .... *S. stolonifera.*
A. Leaves obovate or elliptic, commonly not more than ½ as wide as long .... *S. flagellaris.*

Salix ovalifolia Trautv. in Mém. Soc. Nat. Mosc. 2: 306 (1832)

Stems prostrate, trailing; leaves broadly ovate to rounded, 1-2.5 cm. long, four-fifths as wide as long or more, entire at the margins, rounded at the apex and base or tapering rather abruptly at the base to slender petioles, firm in texture, glaucous beneath, glabrous; catkins borne on leafy peduncles, the pistillate up to 2 or 3 cm. long; capsules glabrous and often glaucous, 5-7 mm. long; styles short (usually 0.5 mm. long or less); bracts about 1.5 mm. long, reddish brown, hairy; styles about 0.5 mm. long; staminate catkins up to 1.5 cm. long; stamens 2; filaments glabrous.

Apparently restricted to Alaska, where it has been collected at White Pass, *Eastwood 927* (CAN), but otherwise, according to Hultén (1942: 521-2), is known only in western coastal Alaska and the Aleutians. Map 8.

I have not seen the specimens cited by Schneider (Bot. Gaz. 66: 138-9, 1918) under *S. ovalifolia* var. *pubescens* and var. *subarctica.* Both of these varieties have slightly pubescent capsules. Hultén (l.c. 520-21) considered some similar plants identical with *S. hebecarpa* Fern., while others he treated as hybrids of *S. ovalifolia* and *S. glacialis* (l.c. 524) or *S. ovalifolia* and *S. arctica* (*S. crassijulis*, l.c. 517).

I regard this species as the principal one in what I am calling an "*S. ovalifolia* group," which is discussed more fully below.

Salix stolonifera Cov. in Proc. Wash. Acad. Sci. 3: 333 (1901)

A prostrate, trailing, alpine species that is very closely related to *S. ovalifolia.* Its leaves are slightly less broad in proportion to their length, but hardly enough to be outside the range of variation in the latter. The principal distinguishing character is in the length of the styles which in *S. stolonifera* are 1-2 mm. long, while in *S. ovalifolia* they are 0.5 mm. long or less. This character appears to be consistent in all the herbarium material I have seen, but whether it justifies the separation of the two as species is questionable. Hultén (1942: 522) suggests that these two species and *S. glacialis* Anders. may be merged eventually as geographic races of a single entity. This probably is true for *S. stolonifera* and *S. ovalifolia,* but *S. glacialis* appears to me worthy of its own specific rank.

Salix stolonifera as here defined seems to be limited to coastal Alaska, and to southwestern Yukon. I have seen the following specimens from our region: White Pass, *Cowles 979* (GH); same, *Malte,* Aug. 24, 1916 (CAN); mountains south of Burwash, *Clarke 217* (CAN); Haines Rd. near Yukon-Pacific divide, *Taylor et al. 820, 1179, 1194* (V); Jago L., *Cantlon & Gillis 57-1305*; about 40 mi. east of Cape Lisburne, *Cantlon & Gillis 57-149, 57-209.* Map 8.

Salix flagellaris Hultén in Sv. Bot. Tidskr. 34: 376 (1940)

Maintained as a specific entity with much hesitation. The type was collected by *Walpole 1672* (US) on the Kruzgamapa R. in the Seward Peninsula, and Hultén cites specimens from Muir Glacier, the Katmai region and Stepovak Bay on the Alaska Peninsula, and from the Colville Delta on the Arctic Coast. I have seen a part of the type at Stockholm. Hultén distinguishes the species from *S. ovalifolia* by its narrower, thin, light green leaves, and by its long subterranean branches; and from *S. stolonifera* by its short styles (0.5 mm. or less) and also by its narrower leaves. Even on the type there are leaves that measure 17 x 12 mm., 10 x 6 mm., and 16 x 10 mm., not far different in size or proportions from many that are found on the two related species. The texture and color of the leaves, and the length and position of the branches, are all characters that are easily modified by site conditions or by advancing maturity. Staminate catkins apparently are unknown.

I venture to place here tentatively another closely related species described by Hultén, *S. arctolitoralis* (see Hultén, 1942: 524-5). He regards it as most nearly related to *S. stolonifera*, differing from that species by its shorter styles, larger capsules, and by its larger and narrower leaves. In his key he separates it from *S. ovalifolia* and *S. flagellaris* (l.c., p. 499) by its supposedly non-glaucous capsules and elliptic leaves. The type was collected at Kotzebue by *Anderson 4705*. The character of glaucescence is a fickle one at best, and if the glaucescence is present it is often driven off by artificial heat. The type which I saw in the Stockholm Herbarium, has some glaucous capsules, and the leaves range from elliptic to obovate or almost oblong. Other specimens cited by Hultén which also have some glaucescence on the capsules are: Deering, *Anderson 4806*; Pt. Lay, *Anderson 4417*; same, *Mason 6425*; Mackenzie Delta, *Porsild 7363*. Other specimens showing some distinctly obovate or oblanceolate leaves are: *Porsild 7363*; *Anderson 4806*; Kivelina, *Anderson 4626*; Nome, *Jones 9038, 9039*. Map 8.

In view of the preceding discussions, I propose that we have in the tundra of Alaska, Yukon and northwestern Mackenzie an *S. ovalifolia* group of trailing, freely branched willows with small (1-4 cm.), essentially entire and glabrous leaves, with short catkins borne on leafy peduncles, and with glabrous capsules which are commonly glaucous. A sub-group with long styles (1-2 mm.) and broad to rounded leaves (width commonly 4/5 the length or more) has been called *S. stolonifera*. A short-styled sub-group (styles 0.5 mm. or less) may be divided into those with broad to rounded leaves, now called *S. ovalifolia*; and those with narrower, elliptic to obovate or oblanceolate leaves, called *S. flagellaris* (incl. *S. arctolitoralis*).

Salix glacialis Anders. in Öfvers. Vet. Akad. Förh. (Stockh.) 15: 131 (1858)

Known thus far only on the arctic and western coasts of Alaska, with one station on Akutan in the Aleutian Islands, and one on St. Lawrence Island (Hultén, 1942: 523-4). Map 9. Hultén characterizes it, from his studies of this material, as a decumbent, dwarf shrub having long, slender, reddish-or yellowish-brown branches, small, obovate, ciliate leaves, distinctly and often densely gray-hairy capsules, and short thick styles. The catkins are borne on leafy peduncles, and are 1.5 cm. long or less. Staminate flowers have 2 stamens with glabrous filaments; staminate catkins up to 1.5 cm. long. I saw much of the material cited by Hultén at Stockholm, and found the species a rather distinctive one. In general form it resembles *S. ovalifolia*, but has pubescent capsules. Its leaves are strongly glaucous and prominently reticulate-veined beneath, suggesting *S. reticulata* in this respect. The leaves are glabrous except for ciliate margins.

Schneider (Bot. Gaz. 66: 139, 1918) described *S. ovalifolia* var. *camdensis*, based upon material collected by F. Johansen at Camden Bay on the eastern arctic coast of Alaska. His description is not a complete one and says nothing about pubescence on the capsules. I have not seen the type collection, but Hultén examined it and stated (l.c. 524-5) that it was identical with *S. glacialis* Anders.

KEY TO THE SALIX GLAUCA GROUP

A. Petioles well developed, more than 2 mm. long
  B. Leaves usually much longer than broad, those of the peduncles about 2.5-4 times longer than wide; mostly upright (though often low) shrubs .... *S. glauca*.

B. Leaves usually short-oblong or short-ovate to rounded, those of the peduncles usually less than 2.5 times longer than wide; very low, spreading or somewhat matted shrubs .... *S. cordifolia.*

A. Petioles of the leaves short, none, or at most 1-2 mm. long

C. Catkins short-oblong to spherical; leaves averaging 1.5-3 cm. long .... *S. brachycarpa.*

C. Catkins cylindrical, usually more than twice as long as thick; leaves averaging 2-5 cm. long .... *S. niphoclada.*

Salix glauca L. Sp. Pl. 1019 (1753)

Erect or spreading shrubs which, due to pubescence or glaucescence or both, have a dull grayish-green appearance when seen in the aggregate. They are commonly a meter or so tall, but may reach 2 m. on suitable sites, or be depressed, almost trailing, shrubs in exposed places; twigs grayish-pubescent when young, glabrate in age; leaves borne on well-developed petioles, occasionally elliptic, but nearly aways broadest above the middle to make them obovate or broadly oblanceolate, entire at the margins or with a few scattered, obscure, glandular teeth toward the base, obtuse or acute at the base, obtuse (or almost rounded) to acute at the apex, dull green above, glaucous beneath, pubescent or hairy on both sides when young but commonly glabrate above when mature (in some forms densely pubescent even in age), commonly varying from 2 to as much as 10 cm. in length; catkins appearing with the leaves or after them, on leafy peduncles, usually more than twice as long as thick, the pistillate commonly 5 cm. long or more; capsules densely grayish pubescent, styles usually less than 1 mm. long, pedicels none or very short, even in fruit scarcely more than twice the length of the glands; bracts oblong to obovate, rounded or occasionally pointed at the tip, short-hairy, yellowish or yellowish-brown; staminate catkins usually no more than 3.5-4 cm. long; stamens 2; filaments hairy at the base or sometimes glabrous.

Salix glauca is the principal species in a huge complex of northern willows which extends throughout the northern part of the boreal forest, far into the arctic tundra, and southward into the central Rocky Mts. This complex, which I shall call the "*S. glauca* group," contains many species and varieties within which there are so many variations, and among which there are so many intergradations, that anything more than an approximation of their true relationships is, with present knowledge, well-nigh impossible. In the present treatment I can claim nothing beyond such an approximation, and it should be clearly understood that my arrangement is only one of many that could be constructed. My only defense for it is that it comes closest, for the time being, to a rational interpretation of my own personal experience with these willows in the field and in herbaria. The nomenclature of the group is voluminous and tangled. I have threaded my way through some parts of it, but even if I were able to include it all, the present work would only be obscured by it. For those who wish to delve more deeply into names and relationships, references will appear at appropriate places in the following pages. The species that are included in the *S. glauca* group for our region are: *S. glauca*, *S. niphoclada*, *S. brachycarpa*, *S. cordifolia*. Two other species, *S. MacCalliana* and *S. Tyrrellii*, could be included in the group on the basis of their catkin characters, but their vegetative characters are so distinctive that I prefer to place them for the time being in a separate group.

Salix glauca, considered in a broad sense, has a wide range in our region, extending from Hudson Bay westward to western Alaska (Map 10). However, it does not extend northward much beyond the arctic treeline. Southward it reaches to the northern edges of the Great Plains, and into the central Rocky Mts. (Raup, 1947: map, Pl. 21). It grows in muskegs, open woods, prairie margins, wet meadows, lake beaches, and in various forms of alpine and arctic tundra, from the damp, mossy types where it is associated with dwarf birch, to dry ledges and scree slopes. It is apt to loom large in any collection of willows from this region, for its abundance and extreme variability in form, size and habitat selection continually tempt the collector. They also tempt the student who is looking for describable novelties, particularly if he has only limited collections from a relatively small area.

Four phases are here recognized within the mass of willows that answer to the above description of *S. glauca*. I am at present inclined to assign them a somewhat greater validity than the various western forms of *S. arctica*, because they show a little better geographic segregation, and in some cases a better segregation in terms of site. However, none of them is sharply defined, and intermediates among them are frequent.

The typical species is widely distributed throughout the forested parts of the region, though it is found occasionally beyond or above the timberline. Much more abundant, and occupying the greatest variety of habitats, is var. *acutifolia* (Hook.) Schn. in Bot. Gaz. 66: 327 (1918). Most of the extensions of the species into the alpine and arctic tundra appear to be of this variety. Variety *Aliceae* Ball in Univ. Calif. Publ. Bot. 17: 416 (1934) (var. *poliophylla* (Schn.) Raup in Jour. Arn. Arb. 17: 233, (1936) has been found at Great Slave and Great Bear Lakes and at Good Hope and Aklavik on the Mackenzie R. (Ball, l.c.), but otherwise seems to be restricted to southwestern Yukon and central Alaska westward to the coast.

The fourth phase is var. *stenolepis* (Floderus) Polunin in Nat. Mus. Can. Bull. 92: 163-4 (1940). In 1947 I described an *S. glauca* var. *perstipula* (1947: 154-5, Fig. 13) which was distinguished by having linear-lanceolate, accuminate stipules that were persistent for as much as 5 years. The type material for var. *perstipula* came from the vicinity of Brintnell L. in the Mackenzie Mts. Since then it has been collected several times by Porsild along the Canol Rd. (1951: 142) and by Wynne-Edwards on the eastern slopes of the Mackenzie Mts. In the vicinity of the Alaska Highway I have collected it only in southwestern Yukon, from Mt. White to the region of Kluane L. However, I have seen a specimen of it from the Glenn Highway (near Eureka Roadhouse in the mountains of southern Alaska) collected by *Anderson 8467* (GH) and it is to be expected elsewhere in the interior of Alaska. Polunin's var. *stenolepis* (*S. stenolepis* Floderus in Herb.) was based on material collected by Malte at Lake Harbor in southern Baffin Island (Type: *Malte 118812*, CAN). When I described var. *perstipula* I had not seen this type material, but because Polunin's description said nothing about the persistance of the stipules, I presumed that they were not persistent. Since then I have seen the Malte collection, as well as other specimens cited by Polunin, and find them a good match for var. *perstipula*, with stipules persistent for several years. Further, I have seen several specimens from the tundra west of Hudson Bay that have the same character. Except for the persistent stipules, all or most of var. *stenolepis* would be placed in *S. glauca* var. *acutifolia*, and seems to parallel this variety in having a wide range of habitats which extends far into the arctic tundra. Whether it should be maintained as a separate variety or only as a form of var. *acutifolia* is open to question, but for the present I shall leave it with a varietal status.

Present knowledge suggests, therefore, that of the two most abundant and widely distributed forms, var. *acutifolia* has the greater range and the greater flexibility or plasticity in its selection of habitats. Both of the other variants, though they occur within the ranges of the first two, are more limited geographically.

The following key will serve to indicate the four phases noted above.

A. Stipules persistent on the twigs, sometimes for as long as 5 years, appearing as narrowly lanceolate, dried appendages, often 1cm. long or more, their margins glandular .... var. *stenolepis.*

A. Stipules not persistent on old wood, falling off within the first year.

  B. Leaves densely grayish-hairy or tomentose on both sides, even in age, averaging shorter and broader than in the other varieties .... var. *Aliceae.*

  B. Leaves grayish-pubescent on both sides when young, but lacking the long-hairy appearance of var. *Aliceae*, and usually glabrate in age, at least on the upper sides

    C. Most of the leaves with an obtuse angle at the apex, or almost rounded .... *S. glauca* (typ.).

    C. Most of the leaves with an acute angle at the apex .... var. *acutifolia.*

Hultén's treatment of the various forms of *S. glauca* differs considerably from the above, and deserves some discussion here. I have already published some notes on the "*S. glauca* problem" (1943: 102-4; 1947: 152-3), and will now only summarize them.

Most of the confusion surrounding the study of the forms of *S. glauca* in America seems to stem from varying interpretations of three questions and the observations concerning them. All of these interpretations have been conditioned historically by the gradually enlarging collections of the group, by the geographic spread of the collections, and by the increasingly critical faculties of the collectors. First is the question as to whether true *S. glauca* occurs in America at all. It was originally described by Linnaeus (1753) from specimens collected in Lapland. The earliest description of anything in the *glauca*-group in America was by Pursh (1814: 611), and was based upon specimens from Labrador: *S. cordifolia*. This species differs sufficiently from typical *S. glauca* in leaf shape and size, and in habit of growth, that it is not apt to be confused with the latter. Pursh made no mention of *S. glauca* when he described it. Material more nearly resembling the typical species began to appear in the collections of Richardson and Drummond on the occasion of the Franklin Expeditions to the northern interior of the continent (1819-27), and in a few early Alaskan collections. From study of these collections came a confusion of names that are now difficult and in some cases impossible to typify (see Schneider, Bot. Gaz. 66: 318 et seq. for a discussion of this tangle). The great Swedish salicologist, Andersson, studying this material about the middle of the nineteenth century, concluded that a considerable part of it represented a variety of he true *S. glauca*. He identified it with the *S. villosa* which appears in Hooker's Fl. Bor. Am. 2: 144 (1838). At about the same time Hooker recognized a var. *acutifolia* of his *S. villosa*, which seems to be identical with the common plant that we now call *S. glauca acutifolia*. Rydberg (1899: 271) thought that if true *S. glauca* were present in America it was very rare, and that all or nearly all American material of it represented one or another segregate. Coville, reporting on the willows of the Harriman Alaska Expedition (1901: 321), was unable to distinguish much of the Alaskan material from the typical species, and therefore maintained *S. glauca* as a valid species in the Alaskan flora. Schneider (l.c.) remained unconvinced, however, and would have placed most of the specimens that I have called *S. glauca* in var. *glabrescens* (Anders.) Schn. My own studies of northwestern willows have led me to agree with Coville, and both Hultén and Porsild are also following this trend.

The second question centers in the concept of *Salix desertorum* Richardson. Of all the American willows that are closely allied to typical *S. glauca* it was the first one described (Bot. App. Frankl. Journey, 753, 1832); therefore its name might have some claim to priority. In spite of the fact that Richardson made an ample collection of it in the place where he found it (at Fort Franklin on Great Bear Lake), and published a rather good description of it, the species has long remained an enigma to most students. I have seen parts of the type collection in the herbaria at Harvard and the New York Botanical Garden, at the National Herbarium of Canada, in the Barratt Herbarium at Wesleyan University, Middletown, Conn., and at Kew. The specimens all appear to have come from very low plants, many of them with a somewhat fastigiate habit of growth so that the catkins (immature though well formed) are numerous in rather close bunches. Its name has been applied, over the years, to various segregates in the *S. glauca* group, such as *S. brachycarpa*, and one or another of the varieties of *S. cordifolia*, or to some forms of *S. glauca* itself.

I have seen only two other collections that I could match with Richardson's type material. One of these is my no. *534*, from Taltheilei Narrows in the eastern arm of Great Slave L. Here the plants grew on an exposed rocky headland in thin, droughty soil, and hardly more than 2 dm. high (Raup, 1931: 241-4, Pl. 218). They show several stages of transition in leaf, catkin and growth form from those that match the Richardson material to others that are readily identified with *S. glauca* or its var. *acutifolia*. Striking differences are found even on a single plant. The second collection was made by Lindsey (*71*, CAN) on Et-then Island in Great Slave L., and closely resembles Richardson's type. From study of these specimens I have concluded that *S. desertorum* is best interpreted as an aberrant form of *S. glauca* caused by local site factors, and as having no viable taxonomic status.

However, Hultén has chosen to maintain a concept of *S. desertorum;* and in doing so he revives for it the combination *S. glauca* subsp. *desertorum* (Richardson) Andersson in Öfvers. Vet. Akad. Förh. Stockh., 15: 129 (1858). It is difficult to know what forms he proposes to cover with ssp. *desertorum.* He says they are "apparently very closely related to *S. glauca* but differ in having the leaves almost completely glabrous on the upper side or with hairs only on the mid-vein of, especially, the younger leaves. Such specimens have practically sessile, very strongly tomentose capsules with large stigmas and comparatively large oblong light brown catkin scales rounded at the apex. The catkins are small and narrow. The plant is evidently a low shrub" (l.c., p. 526). This brief description would cover a great deal of the material here called *S. glauca* and var. *acutifolia,* particularly specimens from low-grown shrubs in exposed places. Much of the material that has been called var. *acutifolia,* on the other hand, Hultén deals with in an entirely different way (see below). His meaning is further confused by the following statements: "There seems to be no doubt that this Alaskan plant is identical with the eastern American called *S. cordifolia* var. *callicarpaea* . . . *S. desertorum* seems to me to be the arctic American *S. glauca* representative distributed from Alaska to Newfoundland . . ." Even if the dubious *S. desertorum* were allowed some taxonomic significance, it would be sufficiently difficult to crowd into it all the varied western forms that Hultén proposes; to add to it the commonest variety of the eastern *S. cordifolia* takes the concept of Richardson's *S. desertorum* so far away from its original meaning that it becomes unrecognizable. Should it ever be deemed advisable to merge *cordifolia* with the western *glauca* complex, this can be done much more readily by relating *S. cordifolia* var. *callicarpaea* to *S. glauca* in the Hudson Bay region where they overlap, than by way of the doubtful *S. desertorum* (see Raup, 1943: 102-8).

As with several other species of *Salix,* Hultén found himself with a residuum of specimens which he accounts for by hybridization. One small group from the Bering Straits region he designates "*Salix glauca* x *Farrae Walpolei.*" I have seen none of these specimens and can have no opinion on them. Hultén (l.c., p. 528) says that they "agree with *S. Farrae Walpolei,* except that they have pubescent capsules and leaves hairy especially on the lower side." He cites a much larger amount of material under "*Salix glauca* x *pseudomonticola.*" This he divides into three categories depending upon which of their supposed parents the specimens most nearly resemble. Those closest to *S. glauca* he says form "the bulk of specimens named by Schneider *S. glauca acutifolia.*" He cites approximately 80 specimens under this hybrid, of which I have examined 54. Two of them (*Mexia 2245,* and *Eastwood 705*) have imperfect catkins and may be recent crosses. Two others (*Eastwood 237, 479*) are hermaphroditic, with both sexes in the same catkins; I have one other record of this phenomenon in our region, in our no. *12217* from the shore of Kluane L. Another of the citations, *Eastwood 620,* is a sterile specimen of *S. Scouleriana.* I had no difficulty in putting all except the last, and the two with imperfect catkins, in *S. glauca* or its var. *acutifolia,* about equal numbers in each. I am unable to see the entirely different *S. padophylla* (= *S. pseudomonticola*) as an influence in any of this group.

The third confusing element in the interpretation of *S. glauca* is what I shall call its "apparently inherent variability." The extent of this could become known only with the gradual accumulation, over many years, of enough specimens and field studies to bring it out. For many parts of the *S. glauca* group there still is not nearly enough material with which to work. Not only is there wide variation in form, but also in the capacity to occupy differing sites. I do not think that the taxonomic realities in *S. glauca* or in the group of entities related to it will be understood until the full range of their variability is better known, and until we have some light on its causes.

Salix niphoclada Rydb. in Bull. N. Y. Bot. Gard. 1: 272 (1899)

Upright or spreading shrubs, sometimes decumbent and less than 2 dm. high, or sometimes upright and 1-1.5 m. tall, with grayish-pubescent branchlets; leaves 2-4.5 cm. long, sessile or with petioles only 1-2 mm. long, elliptic to narrowly obovate, entire, grayish-pubescent even in age, or sometimes glabrate above; catkins appearing with the leaves, the pistillate up to 4 cm. long, much longer than thick, borne on leafy peduncles; capsules as much as 6 or 7 mm. long, though commonly shorter, nearly sessile or on very short pedicels; styles short or nearly obsolete; bracts of one color, yellowish-strawcolored or yellowish-brown, pubescent with short hairs that are much shorter than the bracts themselves; staminate catkins up to 2.2 cm. long; stamens 2; filaments glabrous, or sometimes hairy toward the base.

Occasional in damp meadows, crevices, and on sandy lake shores, from the northwest coast of Hudson Bay westward to Alaska (Porsild, 1957: 176, map 121). Northward it extends to the arctic coast (Porsild, 1943: 27, under *S. fullertonensis*), and to Banks and Victoria Islands (Porsild, 1955: 100). From the northern Rocky Mts. to Alaska it occurs mostly below timberline, though it is occasionally found in alpine tundra. Porsild (1951: 142) collected it in three places along the Canol Rd., and Hultén (1942: 530-1) gives it a wide though somewhat scattered range in northern, western, and interior Alaska. It was originally described from material collected along the Mackenzie R. about 30 miles north of the Arctic Circle, and has been collected southward in the Mackenzie basin as far as Great Slave L. **Map 10.**

It will be noted from the keys and from the above description that *S. niphoclada* differs from *S. brachycarpa* (see below) chiefly by its longer catkins and leaves, taller growth, and by a stronger tendency to glabrescence in the leaves. It is like the latter species in having sessile or nearly sessile leaves; in this character the two species differ from others of the *S. glauca* group found in our region.

Hultén (l.c., pp. 529-32) recognizes three other willows in Alaska and Yukon that should be discussed here, for I believe them to be scarcely if at all separable from *S. niphoclada*. The first has been called *S. brachycarpa* var. *Mexiae* Ball in Univ. Calif. Publ. Bot. 17: 412-14 (1934), which differs from *S. brachycarpa* chiefly by its longer catkins and peduncles, taller growth, and larger leaves which tend to glabrescence in age. But these are precisely the characters by which *S. niphoclada* is separated from *S. brachycarpa*. In fact Ball's rather full description of var. *Mexiae* could as well be used for *S. niphoclada*. I have seen a cotype (pistillate) of var. *Mexiae*

(*Mexia, 2131*, US), and did not hesitate to place it in *S. niphoclada*. The second is *Salix Muriei*, described by Hultén from specimens collected by Murie at Salcha Slough near Fairbanks. I saw parts of this type material at Stockholm and in Herb. US., and could not separate it from *S. niphoclada* except by its glabrous leaves, the character emphasized by Hultén. In view of the tendency of *S. niphoclada* toward glabrescence in the leaves, *S. Muriei* can be looked upon merely as a glabrous-leaved phase analogous to the var. *antimima* of *S. brachycarpa*, and I therefore propose that it be called *S. niphoclada* Rydb. var. *Muriei* (Hultén) Raup, stat. nov. (*S. Muriei* Hultén, Fl. of Alaska and Yukon, pp. 531-2, 1943). It has been collected in the eastern interior of Alaska and in the Dawson district of Yukon.

The third "species" is *S. fullertonensis*, described by Schneider (Bot. Gaz. 66: 340-3, 1918) from specimens collected by *J. M. Macoun 79164* at Fullerton, on the northwest coast of Hudson Bay. It had been regarded as endemic to northwestern Hudson Bay, the Great Bear L. region, and the central arctic coast until Hultén included it in his Flora of Alaska and Yukon (see Porsild, 1943: 27; Raup, 1943: 109-10). In leaves, petioles and catkins it closely resembles *S. niphoclada*, but apparently has a prostrate habit, with slender creeping branches. The sole basis for Hultén's inclusion of it is a specimen collected by *Jones 9045* at Nome, on the Seward Peninsula. In Stockholm I saw a fragment of the type of the species, and the Jones specimen from Nome. The label of the latter states that the plant grew "prostrate on tundra." Both of these specimens (photographs of the type were also at hand) show whip-like branches that must have been at least decumbent. Otherwise I could not have distinguished them from *S. niphoclada*.

Most of the willows in the *S. glauca* group are extremely "flexible" or "plastic" in their habit of growth. In exposed, relatively dry situations both above and below timberline they are low-grown, sometimes no more than 10-15 cm. high, while in less exposed places in the immediate vicinity they may be 1 m. tall or more, with many transition phases between these two extremes. In my field notes on collections of *S. niphoclada* along the Alaska Highway are the following comments which indicate this: no. 10591, from alpine crevices in Summit Pass, "depressed shrubs"; no. 11899, from margin of prairie near mi. 1021, "low shrubs, 15-30 cm. high, semi-trailing"; no. 12358, from gravelly-sandy shore of Kluane L., "shrub 60 cm. high"; no. 12403, dry bluff near shore of Kluane L., "shrubs 60-120 cm. high." Likewise I have well-developed flowering or fruiting specimens of *S. glauca* from shrubs ranging from 15 to 90 cm. tall in the immediate vicinity of one another. On open mud flats at the mouth of Slim's R., Kluane L. (no. *12625*) I have the following note on this species: "shrubs 30-60 cm. high, sometimes decumbent." In a group with such flexibility as this, and in the absence of any experimental evidence that genetic segregation has occurred, it seems unjustifiable to give specific rank to decumbent or trailing forms. However, for those who wish to give a name to these forms I propose *Salix niphoclada* Rydb. var. *fullertonensis* (Schn.) Raup, stat. nov. (*S. fullertonensis* Schn., Bot. Gaz. 66: 340, 1918).

Another Alaskan species in the *niphoclada* complex mentioned by Hultén, but only in his list of unidentified names (l.c., pp. 553-4), is

S. lingulata Anders. I have seen no authentic material of this poorly known plant, but judging by what descriptions and discussions I have at hand (see also Schneider, Bot. Gaz. 66: 353), I agree with Hultén that it is probably identical with *S. niphoclada*.

Finally, it should be emphasized that *S. niphoclada* is closely related to *S. glauca*. It is distinguished from the latter by its very short or obsolete petioles (a character that appears to be consistent through large series of specimens), by a somewhat lower habit of growth, and by catkins which average shorter than those of *S. glauca*. In these respects it shows a variation, within the *S. glauca* group as a whole, in the direction of *S. brachycarpa*. Geographically it is an arctic and subarctic variant, whereas *S. brachycarpa* is primarily a northern and central Rocky Mt. one. Both of these variants exist within the range of *S. glauca* s.l. (Raup, 1947: Pl.21) overlapping each other in northern British Columbia and southern Yukon. It may well be that *S. niphoclada* is not worthy of specific rank, and should be considered only as a subspecies of *S. glauca*.

Salix brachycarpa Nutt. N. Am. Sylva 1: 69 (1842)

Low upright shrubs, usually less than 1m. high, with grayish-villous spreading branches; leaves mostly 1.5-3 cm. long, ovate or obovate to oblanceolate, entire or essentially so, densely gray-hairy or in some forms glabrescent, essentially without petioles or with very short ones (at most 1-2 mm. long); catkins appearing with the leaves, on leafy peduncles, short-oblong to nearly spherical in shape, usually not more than 2 cm. long; capsules grayish-wooly, up to 5 or 6 mm. long, sessile or nearly so, with short or almost no styles; bracts of the flowers of one color, yellowish-strawcolored or yellowish-brown, pubescent with hairs that are much shorter than the bracts themselves; stamens 2; filaments hairy toward the base.

Salix brachycarpa is distinctive in the *S. glauca* group because of its short catkins. I have seen the following specimens of the typical form: Pt. Comfort, James Bay, *Potter 905* (GH); Mackenzie R. between Blackwater R. and Norman, *Crickmay 162* (CAN); Lone Mt., *Wynne-Edwards 8459* (CAN); bank of Henry Cr., *Henry 146* (PH); near Norman R., *Henry 105* (PH); near Akie Pass, *Henry 555* (PH); Sand Cr. Pass, *Henry 943* (PH); damp meadow in Summit Pass, *10665*; gravel fan on east shore of Muncho L., *10854, 10855*; Alaska Highway, mi. 472, near Muncho L., *Taylor et al. 1595* (V); Highway at Liard R., mi. 497, *Taylor et al. 337* (V); wet meadows and muskegs along Liard R. south of Watson L., *11010, 11011, 11012*; Highway near Cracker Cr., mi 988, *Anderson & Brown 10332* (S). Scoggan (1957: 233) reports the typical species also from Churchill and York Factory in northern Manitoba. Map 10.

A form with glabrescent leaves, called var. *antimima* (Schn.) Raup in Rhod. 33: 241 (1931) appears to be southern in the western and central parts of our area, but farther eastward it extends into the arctic tundra. It has been collected several times in the neighborhood of Churchill and at the southern end of James Bay (Raup, 1943: 108-9; and Scoggan, 1957: 233). I have seen a specimen of it collected by *Tener 386* (CAN), at the junction of the Bailey and Back Rivers in the northeastern part of the District of Mackenzie, and I have noted it in the Wood Buffalo Park of northern Alberta

(1935: 122-3). It also occurs in the northern Rocky Mts.: Aylard Summit, *Henry 439* (PH); Graham R., *Henry 506, 507B, 509* (PH); Nelson R., *Henry 549A, 550* (PH). Still another variant is var. *psammophila* Raup in Jour. Arn. Arb. 17: 230-1 (1936), known thus far only from its type locality among inland shifting sand dunes south of William Pt., L. Athabaska. It is a shrub 9-12 dm. high with erect branches, broadly ovate (rarely obovate) leaves that are rounded to heart-shaped at the base and densely white silky-pubescent on both sides.

Hultén (1942:529-30) probably is correct in his opinion that typical *S. brachycarpa* has little to do with Alaskan willows that have been attached to it. Forms described by Ball as var. *Mexiae* of this species (1934: 412-14) seem more closely related to, if not identical with, *S. niphoclada* Rydb. (see above).

Salix cordifolia Pursh Fl. Am. Sept. 2: 611 (1814)

Probably represented in our flora by its var. *callicarpaea* (Trautv.) Fern. in Rhod. 28: 184 (1926), which is here a depressed or decumbent shrub, with broadly ovate or obovate, entire or nearly so, petioled leaves that are 1.2-5 cm. long, rounded or broadly obtuse at the apex and acute or obtuse at the base, hairy-pubescent on both sides though less so and glabrescent above, pale green above and glaucous beneath; catkins on leafy peduncles, the pistillate 2 cm. long or more, much longer than thick; capsules 6-10 mm. long, light grayish-pubescent, on very short pedicels; bracts yellowish-brown, short-hairy; staminate catkins up to 2.5 cm. long; stamens 2; filaments glabrous or hairy toward the base.

Salix cordifolia is the principal eastern American segregate in the *S. glauca* group. It has been collected at the southern end of James Bay and along the Kazan R. in the vicinity of Yathkyed L., *Porsild 5788, 6024* (CAN). Porsild (1957: map 122) places its western limits at Bathurst Inlet and northeast of Great Slave L. Scoggan (1957: 233) reports collections from Churchill, Knife L., York Factory, and along the lower Nelson R. Forms that I have identified as typical *S. glauca* or its var. *acutifolia* have come from the eastern shores of Hudson Bay and the more southern arctic islands (Raup, 1943: maps, Pl. 2). A variant of *S. glauca* var. *acutifolia*, var. *stenolepis* (Flod.) Polunin, was described from southern Baffin Island. Consequently there is an area of overlap between *S. glauca* and *S. cordifolia* in the Hudson Bay region. In the region treated in this paper I have seen also a collection that is identified as *S. cordifolia* var. *callicarpaea*, from an alpine scree slope on a mountain south of mi. 1064, Alaska Highway near the southeastern end of Kluane L., *12281*. The leaves and catkins are young, and perhaps not fully expanded (collected July 7). *Salix cordifolia* is not recorded by either Hultén or Porsild for Alaska, Yukon, or northern British Columbia. For discussions of *S. cordifolia* and its eastern variants see Fernald (1926: 181-8), and Raup (1943: 105-8). Map 10.

KEY TO THE SALIX MACCALLIANA GROUP

A. Leaves small, at most about 3.5 cm. long; capsules sessile or on pedicels less than 2 mm. long; styles 2-2.5 mm. long .... *S. Tyrrellii.*

A. Leaves commonly 7-8 cm. long; capsules on pedicels up to 2 mm. long; styles 1.3 mm. long or less .... *S. MacCalliana.*

Salix MacCalliana Rowlee in Bull. Torr. Bot. Cl. 34: 158 (1907)

Tall, upright shrubs, up to 2 m. or more in height, with purplish-brown branchlets that are pubescent when young but soon glabrous; mature leaves rather firm and leathery in texture, elliptic-lanceolate or narrowly elliptic-oblong, as much as 7 or 8 cm. long by 2.5 cm. wide though more commonly smaller, obtuse or acute at the base, acute or acuminate at the apex, pubescent when young but glabrate in age, the margins finely and regularly glandular-serrate, bright green above and only a little paler green beneath, not glaucous, borne on well-formed petioles; catkins appearing with the leaves, on leafy peduncles, the pistillate up to 5 cm. long or more and about 2 cm. thick; capsules grayish silky-tomentose, on pedicels which in fruit are up to 2 mm. long, and with styles up to 1.3 mm. long or less; bracts obovate-oblong, yellowish, short-hairy or glabrescent toward the tips; staminate catkins 2-2.5 cm. long; stamens 2; filaments hairy at the base.

Common in the Wood Buffalo Park in northern Alberta (Raup, 1935: 123) and occasional in the Peace R. region; Dixonville, north of Grimshaw, *Moss 6143* (ALTA, GH); Deep Cr., B.C., *Henry 675* (A, PH); near stream east of Rabbit R., *Henry 919* (A, PH). Numerous specimens have also been collected in the region between the western shores of Hudson and James Bays and L. Winnipeg: Moose R. estuary, *Baldwin 1463* (CAN); Attawapiskat, James Bay, *Dutilly & Lepage 15473* (CAN); York Factory, *Scoggan 6028* (CAN); Nelson R. 20 mi. northeast of Norway House, *Scoggan 3003* (CAN); Hayes R., 130 mi. northeast of L. Winnipeg, *Scoggan 5318* (CAN); Riverton, 75 mi. north of Winnipeg, *Scoggan 9023* (CAN). Map 11.

Salix MacCalliana is a distinctive species which, superficially, has little resemblance to the *S. glauca* group, particularly because of its serrate, non-glaucous, bright green leaves. It is related to this group, however, because of its clearly *glauca*-like catkins. I prefer to maintain it, for the time being, as the principal species in an "*S. MacCalliana* group" which will include the closely related but poorly known *S. Tyrrellii.* It should be looked for throughout the southern part of our region, where it probably is more common than existing collections indicate. It grows in damp meadows at the margins of prairies, lakes, or sluggish streams.

Salix Tyrrellii Raup in Jour. Arn. Arb. 17: 231-2 (1936)

Spreading shrubs, up to 2 m. high, with reddish bark and reddish twigs that are glabrous even when young; leaves 2-3.5 cm. long, 4-8 mm. wide, lanceolate to elliptic, rarely oblanceolate, acute to acuminate at the apex, acute at the base, green and shiny on both sides, somewhat leathery in texture, irregularly and minutely though conspicuously glandular-serrate on the margins, the teeth usually 2-3 per 5 mm., borne on petioles 2-6 mm. long; pistillate catkins (immature) appearing with the leaves, 1-2.5 cm. long, about 0.8 cm. thick, on short leafy peduncles; capsules 3-4 mm. long, densely white-hairy, sessile or on pedicels less than 1 mm. long; bracts about 3 mm. long, narrowly lanceolate, acute, yellowish in the upper part, glabrate toward the apex; styles 2-2.5 mm. long; staminate catkins unknown.

Salix Tyrrellii is known thus far only from its type locality among inland shifting sand dunes south of William Pt., L. Athabaska. (Map 11) The specimens, collected Aug. 16 and 20, 1935, have well-formed but immature catkins. The long, narrow, yellowish bracts, the coetaneous catkins borne on leafy peduncles, and the short-pedicelled, pubescent ovaries relate it to *S. glauca* but it is closest to the unique *S. MacCalliana*. From the latter it differs in having leaves that are much smaller and have fewer, more salient teeth. Its leaves are acute to acuminate, and mostly elliptic or lanceolate, while in *S. MacCalliana* they are only subacute and commonly oblanceolate. Its styles are 2-2.5 mm. long while in the latter species they are 0.8-1.3 mm. long.

KEY TO THE SALIX RIGIDA GROUP

A. Twigs yellowish, though sometimes with reddish blotches or streaks; pedicels 1-3 mm. long .... *S. lutea.*
A. Twigs reddish to brown, or yellowish only when very young
  B. Pedicels of the fruiting capsules 3-4 mm. long; leaves glabrous from the first, or nearly so .... *S. mackenzieana.*
  B. Pedicels of the fruiting capsules 1-1.5 mm. long; leaves pubescent, at least when young .... *S. rigida.*

Salix rigida Muhl. in Neue Schrift. Ges. Nat. Fr. Berlin 4: 236, t. 6, f. 4 (1803)

Salix cordata Muhl., not Michx. See Fernald, 1946: 27-38.

Shrubs up to about 3 m. high, the twigs reddish and pubescent when young but soon glabrate; leaves oblong-lanceolate, rounded to somewhat heart-shaped at the base, short-acuminate at the apex, glabrous or soon becoming so, closely glandular-serrate, up to 4.5 cm. broad and 3-6 times as long, dark green above and glaucous beneath, on petioles up to 14 mm. long; catkins appearing before or with the leaves, 2-5 cm. long, nearly sessile or on very short leafy peduncles; capsules up to 6 mm. long, glabrous, on pedicels 1-1.5 mm. long; bracts up to 1.5 mm long, dark brown, pubescent; styles about 0.5 mm. long; stamens 2; filaments glabrous.

A species of temperate eastern America, included here because it has been collected at Moose Factory and on the western shore of James Bay. Though this seems to be its northwestern limit, it should be looked for farther westward, in northern Manitoba and Saskatchewan. Scoggan, however, (1957: 234) is inclined to exclude *S. rigida* from the Manitoba flora, assigning many specimens previously referred to it to *S. lutea*. A pistillate specimen from Moosonee, *Dutilly & Lepage 12063* (GH) looks to me like good *S. rigida*, and is matched by sterile specimens from Albany and Attawapiskat, *Dutilly & Lepage 16206, 15529,* (GH). Map 12.

Salix rigida is the easternmost element in a series of overlapping species that I have called the "*S. rigida* group." Farther west are the closely related species *S. lutea* and *S. mackenzieana.*

Salix lutea Nutt. N. Am. Sylva 1: 63 (1842)

Upright shrubs, up to 4 or 5 m. tall, with yellowish twigs that are finely pubescent when young, but soon glabrous; leaves lanceolate, up to 7 cm. long, one-fifth to one-fourth as wide as long, glabrous when mature, acuminate at the apex, rounded to somewhat cordate at the base, petioled, closely glandular-serrate or sometimes nearly entire on the margins, yellowish-green above and glaucous beneath; catkins borne on very short peduncles that have 2 or 3 small leaves, the pistillate 2-4 cm. long; capsules glabrous, 4-5 mm. long, on pedicels up to 3 mm. long; bracts of 2 colors, 1-1.3 mm. long, thinly hairy; styles 0.2-0.5 mm. long; staminate catkins 2-3 cm. long; stamens 2; filaments glabrous.

Common on the higher parts of sand and mud bars in the Athabaska-Peace delta, and northward to the lower Slave R. Reported by Cody (1956: 110) from the delta of Hay R., at Great Slave L. Farther east it is found around the southern end of James Bay and along streams draining into it from the forested country (Raup, 1943: 110; 1936: 234). Scoggan (1957: 234) states that it occurs throughout the southern three-fouths of the Province of Manitoba, and reports a collection from as far north at York Factory. Breitung (1947: 83) notes it as common on alluvial soil in east central Saskatchewan. It is occasional on river sand bars in the upper Peace R. region, and I have collected it northward along the Alaska Highway to the Sikanni R. Map 12.

Salix lutea is closely related to *S. mackenzieana* and *S. rigida*, from which it differs mainly in its yellowish twigs and yellowish-green leaves. Intermediates are common.

Salix mackenzieana Barr. apud Anders. in Öfvers. Sv. Akad. Förh. 15: 125 (1858)

Tall spreading shrubs, usually 2-3 m. high in our region; twigs brown, pubescent when young but glabrate in age; leaves lanceolate or oblanceolate, up to 1 dm. long, commonly one-third as wide as long, acuminate at the apex, more or less cordate at the base, glabrous, rather finely glandular-serrate, bright green above, glaucous beneath, borne on prominent petioles; catkins appearing with the leaves, the pistillate 4-6 cm. long, on leafy peduncles; capsules glabrous, 5-7 mm. long, on pedicels 3-4 mm. long; bracts of two colors, about 1 mm. long; styles about 0.5 mm. long; staminate catkins about 4.5 cm. long; stamens 2; filaments glabrous.

Occasional to common along the Mackenzie R., northward probably to Norman. I have collected it on sand bars near Fort Simpson, and it is likely that the Mackenzie material noted by Hooker in Fl. Bor.-Amer. 2: 149, "Between Fort Franklin and Cumberland House" belongs here. The species is common in the upper Peace R. region, and apparently occasional along the Alaska Highway northwestward to Whitehorse, growing in damp thickets on sandbars along the larger streams. Porsild (1951:43) made a single collection of it on the Canol Rd. west of the Mackenzie Mts., along the Pelly R. near mi. 136. Apparently unknown in Alaska. Map 12.

It should be noted that *S. mackenzieana* is a northwestern phase in a complex of closely related willows involving, from east to west, *S. rigida*, *S. lutea*, and *S. mackenzieana*. A more southerly phase in the Rocky Mts. is *S. monochroma* Ball (1921a: 431-5).

Salix Turnorii Raup in Jour. Arn. Arb. 17: 234-5 (1936)

Erect shrubs narrowly pyramidal in form up to 3 m. high, with pale grayish-green bark except the young twigs which are red, the young twigs thinly pubescent and soon glabrate; leaves 2-3.5 cm. long, 0.6-1 cm. wide, lanceolate, elliptic, or oblanceolate, acute to acuminate at the apex, acute to somewhat rounded at the base, on petioles 2-5 mm. long, pale green on both sides, but a little paler beneath, somewhat leathery in texture, finely and regularly glandular-serrate on the margins, silky beneath when young but soon glabrous; pistillate catkins 1-3 cm. long, 1-1.5 cm. thick, borne on short leafy peduncles, appearing with the leaves; capsules about 5 mm. long, glabrous, reddish-brown, on pedicels 2-3 mm. long; bracts narrowly linear or linear-lanceolate, about a third the length of the pedicels, glabrous or thinly pubescent, reddish-brown; styles about 0.5 mm. long; staminate catkins unknown.

Known thus far only from its type locality among inland shifting sand dunes south of William Pt., L. Athabaska, where it is common (Map 13). *Salix Turnorii* is unique among northern willows, and as yet I can only suggest a place for it among the usually recognized sections of the genus. Other novelties in *Salix* that were described from the same locality — *S. Tyrrellii*, *S. silicicola*, and *S. brachycarpa* var. *psammophila* — can be related to other species or species groups, but *S. Turnorii* seems to be as unique in its way as *S. Setchelliana*, *S. pyrifolia*, *S. arbusculoides*, *S. argyrocarpa*, and others that stand alone. About the most that can be said is that with its glabrous, long-pedicelled capsules, and with its regularly glandular-toothed leaves that are sometimes rounded at the base, it suggests the Section Cordatae. But beyond this the likeness does not go, for the shrubs have a narrowly pyramidal form, the bark except for the red young twigs is conspicuously pale grayish-green, and the leaves are much smaller than those of anything in the Cordatae except *S. myrtillifolia*, to which *S. Turnorii* bears no resemblance otherwise.

Salix Farrae Ball, in Contr. U. S. Nat. Herb. 22: 321 (1921)

Spreading shrubs up to 1.5 m. high, with reddish-brown, shiny branches, the seasonal shoots yellowish, finely hairy but soon glabrate; leaves elliptic, lanceolate, or oblanceolate, up to 6-7 cm. long and a third to a half as wide, acute at the apex, acute or somewhat rounded at the base, entire on the margins or essentially so, glabrous, slender-petioled, yellowish-green above and glaucous beneath; catkins appearing with the leaves, the pistillate up to 3.5 cm. long and 1 cm. thick, borne on leafy peduncles; capsules 4-6 mm. long, glabrous, on short pedicels (1-1.5 mm. long); bracts 1 mm. long or less, yellowish at the base and brown at the apex, glabrous or thinly hairy; styles 0.8 mm. long or less; staminate catkins about 1.5 cm. long; stamens 2; filaments glabrous.

Typical *S. Farrae* is occasional to common in swampy ground in the Rocky Mts. northward at least to the Banff region, and has been found on the Caribou Mt. Plateau in the western part of the Wood Buffalo Park (Raup, 1935: 123). Also I have seen two specimens collected by *Scoggan 5939*, *6126* (CAN) at York Factory, on the western coast of Hudson Bay which I have referred to this species. *Salix*

Farrae is represented in central and western Alaska and in collections from the arctic slope in northern Alaska by var. *Walpolei* Cov. & Ball in Bot. Gaz. 71: 435 (1921). It differs from the above description in having more pubescent branchlets, brown seasonal shoots, somewhat larger and broader leaves with more conspicuous serration, and longer catkins. Both the species and the variety are to be expected in northern B. C. and Yukon, and should be looked for in the boreal forests east of the northern Rocky Mts. There are such large gaps in the known distribution of *S. Farrae* s.l. that I have preferred to map it as a group of isolated populations (Map 13). Apparently it has not been collected in the Rocky Mts. of northern British Columbia, or anywhere along the Alaska Highway in British Columbia and Yukon, or along the Canol Road. It has been found in the Mackenzie basin only in the Caribou Mts., and eastward only in the neighborhood of York Factory.

Ball, in a later publication (1942: 230-32), raised var. *Walpolei* to specific rank, took it out of the Section Cordatae, and related it to *S. pyrifolia* in the Section Balsamiferae of Schneider. *Salix pyrifolia* is a distinctive species, so much so that Schneider described a new section of the genus for it. The close relationship of var. *Walpolei* to *S. Farrae* is to me so obvious, and its lack of resemblance to *S. pyrifolia* so clear, that I prefer to retain it for the time being in its original position (see also Hultén, 1942: 532-3, under *S. Farrae* subsp. *Walpolei*).

KEY TO THE SALIX BARCLAYI GROUP

A. Pedicels 2-3 mm. long; shrubs usually less than 1 m. high, commonly 2-3 dm., with branches spreading in the moss of muskegs; the leaves about 2-2.5 times as long as wide, oblong, oblong-ovate, or oblong-oblanceolate; or if taller and more upright shrubs, the leaves much longer than broad, the margins making an acute angle toward the apex but with the apex itself blunt .... *S. myrtillifolia.*

A. Pedicels about 0.5 mm. long; shrubs commonly 1-2 m. tall; leaves 2-4 times as long as wide, ovate or obovate, acute at the apex .... *S. Barclayi.*

Salix Barclayi Anders. in Öfvers. Sv. Vet. Akad. Förh. 15: 125 (1858)

Shrubs commonly 1-2 m. tall, occasionally up to 4 m. in lowland sites, and in alpine sites less than 1 m.; branchlets blackish, tomentose to glabrate; leaves up to 8 cm. long, one-fourth to one-half as wide, ovate or obovate, acute at the apex, wedge-shaped to rounded at the base, petioled, crenate-serrate or almost entire on the margins, thinly tomentose above when young, but glabrate in age, glabrous beneath, usually glaucous beneath but sometimes green or nearly so; catkins appearing with the leaves, the pistillate up to 6 cm. long and about 1.5 cm. thick, borne on leafy peduncles; capsules 6-8 mm. long, glabrous or occasionally thinly silky, on pedicels about 0.5 mm. long; bracts long-hairy, about 1 mm. long; styles 1-1.5 mm. long; staminate catkins 1-3 cm. long; stamens 2; filaments glabrous.

It will be seen from the above description that *S. Barclayi* is an extremely variable species in growth habit, leaf structure and color, and in its wide selection of habitats. Like *S. myrtillifolia*, its leaves have a tendency to blacken in drying, making their natural color often difficult to define. It is common in the northern Rocky Mts., occasional in the upper Liard valley and in southwestern Yukon, and common in the regions of White Pass and the Haines Rd. Porsild (1951: 143-4) says that "it is the most common thicket-forming species in south-east Yukon where it is ubiquitous on well-drained soil on river-flats and by alpine streams on mountain slopes to or slightly above timber-line." In Alaska, according to Hultén, (1942: 533-5; 1949: 1732), it is confined to the southern coastal areas and the Alaska Range (see also Raup, 1947: map, Pl. 21). However, Ball in both Jordal (1951) and Spetzman (1951) cites specimens of it from the Brooks Range and the arctic slope of Alaska. I have not seen this material, and can have no opinion on it. However, Cantlon & Gillis have sent me specimens from the region of Jago L. in northeastern Alaska which I have determined as *S. Barclayi: 57-558, 57-2013, 57-2435.*

Various hybrids between *S. Barclayi* and other species have been reported. Hultén (l.c.) has noted them with *S. crassijulis* (*arctica*), *S. glauca*, and *S. pseudomonticola* (*padophylla*). Porsild (l.c.) suggests one with *S. planifolia.* On an alpine slope just above timber-line in Summit Pass our field party in 1943 found plants that suggested a hybrid of *S. Barclayi* and *S. reticulata* (no. *10470*). None of these suspected hybrids can be evaluated with any degree of confidence.

Salix Barclayi is closely related to *S. myrtillifolia*, and together these species make up an "*S. Barclayi* group" with a wide range in the boreal forest region of the continent. The ranges of the two overlap in the northern Cordillera and in eastern Alaska, and the species might properly be interpreted as rather well-defined geographic segregates in a continuous population of *Barclayi*- or *myrtillifolia*-like willows that extends from the Aleutians to Newfoundland.

Salix myrtillifolia Anders. in Öfvers. Sv. Vet. Akad. Förh. 15: 132 (1858)

Low shrubs, usually less than 1 m. high and commonly only 2-3 dm., with upright or spreading branches that are brown or grayish-brown and smooth; leaves 2-8 cm. long, 1-3 cm. wide, oblong, oblong-ovate, or oblong-oblanceolate, glabrous, obtuse or acutish at the apex, usually rounded at the base, dark green and shiny above and only a little paler (not glaucous except in var. *brachypoda*) beneath, regularly and closely dentate-serrate on the margins; catkins appearing with or later than the leaves, the pistillate 2-3 cm. long, borne on leafy peduncles; capsules 6-7 mm. long, glabrous, on pedicels 2-3 mm. long; bracts 0.7-0.8 mm. long, gray-hairy, brown or grayish-brown; styles up to 0.8 mm. long; staminate catkins 1.5-2.5 cm. long; stamens 2; filaments glabrous.

Common to abundant in damp woods and thickets, particularly in mossy muskeg thickets, throughout most of the forested parts of our region, up to timberline in the mountains, and northward to the arctic tree-line (Raup, 1947: map, Pl. 21). Map 14. It is extremely variable in habit of growth and in the size and form of its leaves. In mossy muskegs it is a low shrub, 1-3 dm. high, with small leaves, while on stream banks, lake shores, and prairie margins it grows to 3 m. high and has leaves as much as 5 cm. long. In these larger plants there is a series of forms transitional to var. *pseudo-myrsinites* (Anders.) Ball ex Hultén, Fl. Alaska & Yuk. 538 (1943), distinguished by having leaves much longer than broad, the margins making an acute angle toward the apex but with the apex itself often blunt, somewhat paler green beneath than in the typical species, and by having slightly longer styles. I have found these forms especially common in the region along the Alaska Highway between Dawson Creek and Nelson, and in southern and southwestern Yukon. Hultén (1942: 537-8) cites them from central Alaska, the Alaska Range district, the central Pacific Coast district of Alaska, and from the upper Yukon region. Variety *pseudo-myrsinites* appears to be identical with many northern Rocky Mt. plants that have been called *S. pseudocordata* (Anders.) Rydb. An eastern variant of the species is var. *brachypoda* Fern. in Rhod. 16: 172 (1914), distinguished mainly by having the under surfaces of its leaves glaucous. I have seen no specimens of this variety from our region, but Dutilly, Lepage, and Duman (1953: map, fig. 13) indicate a record for it at the mouth of the Moose R., James Bay.

Salix myrtillifolia as a whole seems to be unknown in western Alaska. The westernmost specimens I have seen are from Farewell L. on the south fork of the Kuskokwim R. in the edge of the Alaska Range, *Drury 2387* (GH); and from McGrath, on the upper Kuskokwim R., *Drury 3793* (GH). Porsild collected it in many places along the Canol Rd. in the Mackenzie Mts. (1951: 144-5), where he considered it restricted to calcareous soils in the river valleys. Spetzman (1951) reports it on the arctic slope of Alaska, and I have seen specimens collected by *Borman, Rebuck* and *Cantlon 68, 361* from the vicinity of Umiat on the lower Colville R. It is closely related to *S. Barclayi*, and the ranges of the two species overlap in the northern Cordillera and in southern Alaska. Intermediates between them are not uncommon.

KEY TO THE SALIX GLAUCOPHYLLOIDES GROUP

A. Leaves somewhat leathery and thickened when full-grown, lanceolate, ovate, or obovate, the width commonly 1/3 to 1/2 the length .... *S. glaucophylloides*.

A. Leaves not leathery and thickened, broadly ovate, elliptic, or obovate, the width commonly ½ to 3/5 the length .... *S. padophylla*.

Salix glaucophylloides Fern. in Rhod. 16: 173 (1914)

Shrubs or small trees up to 5 m. high, the twigs usually brown, shiny, glabrous or soon glabrate; leaves oblong, lanceolate, or narrowly ovate, green and shiny above, strongly glaucous beneath, somewhat leathery in texture, 3-12 cm. long, 1.5-6 cm. wide, acute to short-acuminate at the apex, wedge-shaped, rounded, or heart-shaped at the base, closely glandular-crenate-serrate on the margins, on petioles up to 12 mm. long; stipules half-cordate, coarsely toothed, persistent for a while; catkins appearing with the leaves, on leafy peduncles, the pistillate up to 6 cm. long; capsules 7-10 mm. long, glabrous, on pedicels up to 1.5 mm. long; bracts 1.5-2 mm. long, blackish, long-hairy; styles up to 1.5 mm. long; staminate catkins 2-4 cm. long; stamens 2; filaments glabrous.

A species of north temperate eastern America, included here because it has been collected in the Moose R. estuary on the southwestern shore of James Bay (see Raup, 1943: 111), and at Attawapiskat on the western shore of that bay, *Dutilly & Lepage 15479* (GH). It should be looked for farther westward in Ontario, and in northern Manitoba and Saskatchewan. Map 15.

Salix glaucophylloides appears to be closely related to *S. padophylla*, and I have therefore placed them together in a group. Their ranges overlap in northern Ontario. These things suggest that they are eastern and western segregates in a continuous population, further understanding of which will require more detailed study. See note under *S. padophylla.*

Salix padophylla Rydb. in Bull. Torr. Bot. Cl. 28: 499 (1901)

Salix padifolia Rydb., ibid. 28: 272-3 (1901). *Salix pseudomonticola* Ball in Contr. U. S. Nat. Herb. 22: 321 (1921). *Salix pseudomonticola* Ball var. *padophylla* (Rydb.) Ball in Jour. Wash. Acad. Sci. 28: 450-52 (1938).

Shrubs usually 1-3 m. tall, but sometimes up to 4 or 5 m., with reddish-brown, shiny twigs that are glabrous except when young; leaves up to 6 cm. long and commonly one-half to three-fifths as wide as long, ovate, elliptic, or obovate, acute at the apex, usually cordate at the base but sometimes rounded, glandular-crenate serrate on the margins, petioled, glabrous, green above, glaucous beneath, rather prominently veined; catkins appearing with the leaves, sessile on the twigs or nearly so, 3-7 cm. long; capsules glabrous, 6-8 mm. long, on pedicels 1-1.5 mm. long; bracts of two colors, commonly 1.5-2 mm. long, long-hairy; styles 1 mm. long or less; stamens 2; filaments glabrous.

Occasional in lowland thickets, at stream borders, and in aspen-willow woods in the Wood Buffalo Park (Raup, 1935: 124), in the Peace R. region, and on the lower slopes of the mountains northwestward from the eastern foothills of the Rockies to southwestern Yukon. Hultén (1942: 535-6; 1949: 1732) notes it as common in the upper Yukon valley and at least occasional in east-central Alaska, and Argus informs me (personal communication) that it is locally common in the Fairbanks district. Porsild (1951: 144) collected it at Whitehorse and along the southern part of the Canol Rd. He also reports it (personal communication) northward along the Mackenzie R. to a short distance below Norman. In recent years *S. padophylla* has been reported at many places in the forested country west of Hudson and James Bays, in northern Ontario and Manitoba (Scoggan, 1957: 235). I have seen most of the material upon which these records are based, and can find no real difference between them and the western specimens of the species. They constitute still another long eastward extension of range for what has been thought to be a Cordilleran species complex (see also *S. MacCalliana*, *S. Farrae*, *S. Scouleriana*, *S. brachycarpa*). Although the catkins of this species are coetaneous, the leaves and capsules mature so early in the summer that in the usual collecting season it is difficult to find good flowering or fruiting specimens. Map 15.

Salix padophylla appears to be a close western relative of *S. glaucophylloides*, the ranges of the two species overlapping in the region of James Bay. The leaves of *S. glaucophylloides* are a little narrower in proportion to length than those of *S. padophylla*, and tend to become somewhat thickened and leathery as they mature. Leaf venation is similar in the two species. An apparent difference is that in *S. glaucophylloides* the catkins are borne on short, leafy peduncles, while in *S. padophylla* they are sessile or nearly so. However, this is a variable character in both species. In his original description of *S. pseudomonticola* Ball (l.c.) stated that the catkins were "nearly sessile." Later he reduced *S. padophylla* Rydb. to varietal status and attached it to his *S. pseudomonticola*, and in doing so he said that var. *padophylla* differed "from the species, *S. pseudomonticola* Ball, chiefly in having the aments borne on short leafy peduncles, whereas those of the species are sessile and scarcely even bracted at base." In my own experience with this species in the Northwest I have found the catkins sessile, or on short peduncles with or without 1-3 small leafy bracts. I have seen specimens of *S. glaucophylloides*, on the other hand, with very short peduncles (1 cm. or less) bearing only a few small bracts and resembling such forms of *S. padophylla*. Forms of the latter species collected in the vicinity of James Bay commonly have leafy peduncles, and I have seen a specimen from the Wiachuan R. on the east coast of the Bay, *Dutilly & Lepage 14302* determined by Ball as *S. pseudomonticola* var. *padophylla*. Considering these intergradations, therefore, I regard the character of the peduncles as scarcely definitive. The same may be said of the pubescence on the twigs. Some forms of *S. glaucophylloides* have a heavy pubescence on the young twigs, some of which persists for two or more years. In some of the more southern forms the leaves are also densely pubescent (var. *albovestita* (Ball) Fern.). There is considerable variation in the twig pubescence of *S. padophylla*, but in most cases it closely resembles that of the northern forms of *S. glaucophylloides*, in which the pubescence persists for only one year. Pubescence on the twigs shows a similar "unilateral" variation in other species groups such as that containing *S. planifolia* and *S. pulchra*. In this pair of species it is the northwestern one, *S. pulchra*, that has a variant with dense, persistent pubescence (var. ***yukonensis***).

Salix cordata Michx. Fl. Bor.-Amer. 2: 225 (1803)

Salix adenophylla Hook., Fl. Bor.-Amer. 2: 146 (1839); not ***S. cordata*** **Muhl.**

Shrubs up to 1.5 m. high, with twigs densely grayish hairy; leaves broadly lanceolate-oblong to oblong-ovate, long-acuminate at the apex, rounded or heart-shaped at the base, up to 13 cm. long and 6 cm. wide, glandular-dentate-serrate on the margins, green and densely grayish-hairy and somewhat silky on both sides, especially beneath, on petioles usually 12-15 mm. long but sometimes much longer; catkins appearing with the leaves, on leafy peduncles, the pistillate up to 6 cm. long; capsules 5-8 mm. long, glabrous, on pedicels up to 1 mm. long; bracts brown, with long white hairs; styles up to 1.5 mm. long; staminate catkins 2 cm. long or less; stamens 2; filaments glabrous.

An eastern subarctic and north temperate species which has been collected on the western and southwestern shores of James Bay, along the lower Severn R., and at Weenusk on the shore of Hudson Bay at lat. 55° 15', *Dutilly & Lepage 16894* (GH; cf. Raup, 1943: 111-12). There is also a Churchill record based on a sterile specimen reported by Grøntved (1936: 32). The species should be looked for farther westward in northern Manitoba and Saskatchewan. Map 16.

Salix commutata Bebb in Bot. Gaz. 13: 110 (1888)

Shrubs 1-3 m. high, in our region mostly 1-2 m., the twigs gray-hairy when young but glabrate in age; leaves up to 8 cm. long and commonly half that in width or nearly so, elliptic to broadly oblanceoate or obovate, acute or obtuse and abruptly pointed at the apex, rounded at the base, entire or with a few inconspicuous glandular serrations on the margins, densely grayish-tomentose on both sides when young, becoming glabrate in age, green on both sides, petioled; catkins on leafy peduncles, the pistillate up to 5 cm. long; capsules 5-7 mm. long, glabrous, reddish and giving the catkins a reddish tinge, on pedicels about 1 mm. long; bracts densely woolly, about 1 mm. long; styles 1-1.5 mm. long; staminate catkins 2-5 cm. long; stamens 2; filaments glabrous.

I have seen the following specimens of *S. commutata* from our region: open spruce woods by small lake, Summit Pass, 10668; L. Atlin, *Eastwood 665* (S); L. Bennett, *Macoun*, July 8, 1902 (S); White Pass, *Eastwood 920, 834* (CAN); same, *Eastwood 879* (K); same, *Eastwood 912* (S); Whitehorse, *Eastwood 616* (K); Haines Rd., B.C.-Yuk. boundary, *Taylor et al. 1079* (V); Haines Rd., mi. 75-83, *Taylor et al. 817, 928, 1381* (V); Alaska Range (southern slope), *Viereck, 1053* (Hb. Argus). Porsild (1951: 144) notes it as common in alpine meadows along the Canol Rd., and I have collected it at Brintnell L. in the Mackenzie Mts. (1947: 156). In Alaska it appears to be restricted to the southern coastal districts (Hultén, 1942: 536-7; 1949: 1732; see also Raup, 1947: map, Pl. 21). It is also found in the Rocky Mts. of southern B. C. and Alberta. Map 16.

Forms with less conspicuous pubescence on the leaves, and more serration on their margins, have been referred by Ball (1923: 498; 1930: 333) to var. *denudata* Bebb in Bot. Gaz. 13: 111 (1888). Hultén (l.c.) is inclined to disregard this variety, however, and apparently assigns forms with more leaf serration to a hybrid with *S. myrtillifolia*. Specimens from L. Atlin and Skagway, narrow-leaved and with the leaves somewhat glaucous beneath, he calls hybrids of *S. commutata* and *S. Barclayi*. One of these, L. Atlin, *Eastwood, 665*, I have not hesitated to call *S. commutata*. Porsild (l.c.) notes specimens from the Canol Rd. that resemble the *S. myrtillifolia* hybrid, and an extreme form which he suspects is a hybrid of *S. commutata* and *S. Chamissonis*. None of the supposed hybrids can with present knowledge be anything more than suggested. For the time being I prefer to cover them with Bebb's var. *denudata*, allowing for ample variation in the characters that define it.

Salix Chamissonis Anders. in DC. Prod. 16^2: 290 (1868)

Prostrate shrubs with grayish or brownish twigs that are glabrous or glabrate; leaves up to 4.5 cm. long and 2.5 cm. wide, but usually smaller than this, broadly obovate or sometimes nearly round, obtuse to rounded at the apex, wedge-shaped at the base, petioled, closely glandular-serrate on the margins, green on both sides but paler beneath; catkins appearing with the leaves, the pistillate about 4 cm. long, on leafy peduncles; capsules 4 mm. long or more, pubescent, on very short pedicels or nearly sessile; bracts up to 2 mm. long, blackish, hairy; styles about 1 mm. long; staminate catkins 3-3.5 cm. long; stamens 2; filaments glabrous.

Salix Chamissonis appears to be rare in our region, and confined to the western Arctic (Map 16). Porsild (1943: 27) reports a collection of it from the Richardson Mts. west of the Mackenzie delta, and there are also records from the Rat and Porcupine Rivers. Hultén 1942: 509-10) cites specimens only from St. Lawrence Isl. in Bering Sea, from the Seward Peninsula, from the L. Iliamna region, and from the upland tundra between Fairbanks and Circle. Porsild did not find it along the Canol Rd., but cites material collected in Macmillan Pass on the Yukon-Mackenzie divide (1951: 139) which he thinks may be a hybrid of *S. Chamissonis* and *S. arctica*. I have seen a part of this collection, and am inclined to relate it most closely to *S. arctica*, though it has low, crenate teeth on the leaves.

Salix pyrifolia Anders. in Svensk Vetensk. Handl. 6: 162 (1867)

Upright shrubs, in our region 1-3 m. high, with shiny, reddish-brown or greenish branches; leaves commonly 3-5 cm. long and more than half that in width, ovate to oblong-lanceolate, acute at the apex, usually rounded to cordate at the base, thin, delicate and nearly transparent when young, showing a purplish tinge at one stage of development, thin but rather firm when mature, green above, glaucous beneath, prominently reticulate veined beneath, glabrous, finely glandular-serrate on the margins, borne on long slender petioles; catkins appearing with the leaves, the pistillate up to 9 cm. long and 2 cm. thick, borne on leafy peduncles; capsules widely spreading or reflexed, glabrous, 6-9 mm. long, on pedicels 2-4 mm. long; bracts narrow, hairy, 1.5 mm. long or more; styles 0.5-1 mm. long; staminate catkins 2-4 cm. long; stamens 2; filaments glabrous; whole plant giving off a strong balsam-like fragrance, which in specimens persists long after drying.

Apparently rare or occasional in the more southerly parts of the forested country. I have found it growing at the margins of muskegs and sloughs northward in the Mackenzie basin to L. Athabaska and the Wood Buffalo Park (1936: 235). Scoggan (1957: 235) reports a collection on the Cochrane R., lat. 58° 15', in northern Manitoba, and Porsild (personal communication) has a record for it in the southeastern corner of the District of Mackenzie. In west central Alberta and neighboring British Columbia I have seen the following specimens: Lesser Slave L. district, *Brinkman* **3934** (**BH**); wet mossy thickets about 10 mi. south of the Beatton R., *10121*, *10122*, *10270*, *10271*; thicket on bluff near Beatton R., *10271*. The species should be looked for in muskeg thickets throughout the upper Peace R. country, and northward at least to Nelson. Map 17.

KEY TO THE SALIX RICHARDSONII GROUP

A. Stipules linear- to half cordate-lanceolate, acuminate, glandular-serrate; petioles 5-15 mm. long .... *S. Richardsonii*.

A. Stipules half-cordate to reniform, entire or glandular-dentate; petioles usually not more than 2 mm. long and rarely over 4 mm. long .... *S. calcicola.*

Salix Richardsonii Hook. Fl. Bor.-Am. 2: 147 (1839)

Upright shrubs commonly 1-2 m. high, with stout, densely hairy young twigs; leaves up to 8 cm. long, varying from comparatively narrow (the width one third to one fourth the length) to nearly as broad as long, glabrous, the margins usually glandular-serrate in the lower part and occasionally to the apex, acute at the apex, acute or obtusish at the base, green above and glaucous beneath, petioled; stipules prominent and persistent for several years, long and narrow, with prominent glandular teeth around their margins; catkins appearing before the leaves, sessile on the twigs; capsules glabrous, sessile or on very short pedicels; bracts hairy, about 2mm. long; styles 1.5-2.5 mm. long; staminate catkins up to 3.5 cm. long; stamens 2; filaments glabrous.

Essentially an arctic-alpine species, though it is occasionally found in the edge of the timber or on stream banks and lake shores at low altitudes. It seems to be most abundant in the tundra of northwestern Mackenzie, Yukon, and Alaska, but has been found as far east as Hudson Bay and Baffin Isl. (Raup, 1947: map, Pl. 21). Hultén (1942: 538-9; 1949: 1732) gives it a wide range in northern and interior Alaska, but apparently it avoids the southern coastal districts. Porsild (1951: 145) found it common along the Canol Rd. I collected it at several places in the mountains between Summit Pass and central Alaska (see Porsild, 1957: 175, map 117). Map 18.

As noted above, *S. Richardsonii* is extremely variable in leaf shape and serration, but it is easily distinguished by its combination of densely hairy twigs, smooth leaves and capsules, and persistent glandular stipules. It is one of a small group of willows in our region that have persistent stipules — *S. pulchra*, *S. glauca* var. *stenolepis*, *S. Barrattiana* var. *marcescens*, *S. calcicola*, *S. Richardsonii* — all of which are easily told apart on other characters.

Salix Richardsonii bears a close relationship to *S. calcicola*, and I venture to put them together in what I have called an "*S. Richardsonii* group." The ranges of the two species overlap in the northern Hudson Bay region and the adjacent arctic islands; but otherwise they are geographically segregated. I have not seen enough specimens from the area of overlap to determine whether intermediates occur there.

Salix calcicola Fern. & Wieg. in Rhod. 13: 251 (1911)

Ascending or prostrate shrubs, up to 5 dm. high, with spreading, gnarled branches, young twigs densely hairy, the older ones glabrous; leaves oblong-ovate to rounded, up to 5.5 cm. long and 4.5 cm. wide, glabrous or soon becoming so, mostly entire at the margins, green above and glaucous beneath, acute or abruptly short-acuminate at the apex, rounded to heart-shaped at the base, borne on short, stout petioles; stipules half-cordate to rounded or reniform, finely glandular-dentate on the margins, sometimes persistent; catkins appearing before or with the leaves, sessile on the twigs, the pistillate 3-8 cm. long; capsules glabrous, 7-9 mm. long, on very short pedicels; bracts blackish, long-hairy; styles 2-3 mm. long; staminate catkins up to 3.5 cm. long and sometimes almost as thick; stamens 2; filaments glabrous.

A predominently eastern American species that has been collected on the western coast of Hudson Bay at Cape Eskimo, Churchill (Raup, 1943: 113 14), and at the mouth of the Nelson R. (Porsild, 1957: 175, map 116). In more recent years it has been found on river gravels along the upper Saskatchewan R. in the vicinity of Banff (Porsild, personal communication), and should be looked for elsewhere in the northern Rocky Mts. It appears to be an eastern segregate in a small group of willows in which *S. Richardsonii* is its western counterpart. Map 18.

Salix Barrattiana Hook. Fl. Bor.-Am. 2: 146 (1839)

Low, upright shrubs, usually 1 m. high or less, with pubescent twigs; leaves commonly 4-7 cm. long and one fourth to one third that in width, acute at the apex, acutish to rounded at the base, elliptic to obovate, serrate on the margins or nearly entire, densely whitish or light grayish silky on both sides, petioled, usually with an upright habit of growth; catkins appearing before the leaves, sessile on the twigs, the pistillate 3-5 cm. long, usually upright in habit; capsules white-silky, about 6mm. long, on pedicels 1-2 mm. long; bracts about 3mm. long, acute, black, silky-hairy; styles 1.2-2.5 mm. long; staminate catkins up to 4 cm. long; stamens 2; filaments glabrous.

Occasional to common in damp alpine meadows from the northern Rocky Mts. to central Alaska and the Mackenzie Mts. It is occasional also on river sand and gravel bars at lower altitudes in the mountains. Hultén's records (1942: 542-3; 1949: 1733) indicate that it is rare and spotty in Alaska, limited to the central and eastern parts of the interior and the north slope. Cantlon & Gillis collected it in 1957 in the vicinity of Jago L., in northeastern Alaska (*911, 1557, 1558*). Porsild (1951: 147-48) found it common along the Canol Rd. It has been reported at Yellowknife, on Great Slave L., by Cody (1956: 110). Map 17.

Salix Barrattiana is conspicuous among northwestern willows, and rather easily distinguished, even at a distance. It usually forms low, dense thickets, light grayish in color, with twigs, leaves and catkins rather stiffly upright. Porsild (l.c.) points out a distinctive character of the species which has been rarely if ever described. The bud scales, stipules and young twigs exude an oily substance, and when specimens are pressed the papers in which they dry are stained a yellowish color.

Varieties based upon differences in leaf shape were described by Andersson (1868: 274): var. *latifolia* and var. *angustifolia*, and Hultén (l.c.) proposes that the few Alaskan and Yukon specimens he cites belong to var. *angustifolia*. Schneider, however, after seeing many specimens (Jour. Arn. Arb. 1: 216-17, 1920), gave these variations little or no taxonomic significance. In 1947 I described a var. *marcescens*, in Sargentia 6: 157-8 (1947), from the Mackenzie Mts., distinguished mainly by having persistent stipules. Porsild (l.c.) suggests that the species is represented in the Northwest Territories, Yukon and Alaska by this variety. However, the specimens collected by our field parties in the vicinity of the Alaska Highway, with one possible exception, do not show persistent stipules, and I am inclined to regard the variety as somewhat more restricted than Porsild proposes. The single exception is no. 11396 from a meadow just below timberline on Mt. White. There is an occasional 1-year-old stipule on this material.

Salix amplifolia Cov. in Proc. Wash. Acad. Sci. 2: 282 (1900)

Tall shrubs or small trees, 3-8 m. high, with densely hairy young twigs that become glabrate after a year or two; leaves commonly 4-5 cm. long but often as much as 8 cm., usually at least half as wide as long, ovate or obovate, obtuse or rounded at the apex, acute or obtuse at the base, pubescent when young but glabrate in age except on the veins beneath, entire on the margins or serrate toward the base, short-petioled; catkins appearing with the leaves, 4-6 cm. long, about 1.5 cm. thick, borne on rather short, leafy peduncles; capsules glabrous, 8-9 mm. long, on pedicels 1-2 mm. long; bracts up to 3 mm. long, hairy, dark-colored at least toward the tips; styles slender, 2-4 mm. long; stamens 2; filaments hairy at the base or glabrous.

Salix amplifolia is a northern Pacific Coast species that has been collected only in the region around Yakutat Bay (Hultén, 1942: 543), where it is conspicuous on coastal dunes and on the lower slopes of the coastal mountains. Map 19.

KEY TO THE SALIX ALAXENSIS GROUP

A. Leaves glabrous or glabrate and bright green on the upper surfaces .... *S. alaxensis*.
A. Leaves thickly covered on both sides with whitish tomentum .... *S. silicicola*.

Salix alaxensis (Anders.) Cov. in Proc. Wash. Acad. Sci. 2: 280 (1900)

Shrubs varying from straggling alpine plants less than 1 m. high, to lowland tree-like forms up to 6 or 8 m. tall, with twigs densely white woolly, or glabrous, yellowish or reddish, and pruinose except when very young; leaves 5-10 cm. long, 2-4 cm. wide, obovate or oblanceolate, acute or rounded at the apex, acute at the base, entire at the margins, glabrous or glabrate and deep green above, covered beneath with a dense, white, felt-like matted pubescence, petioled; stipules linear to linear-lanceolate, 1-2 cm. long or more, distantly glandular on the margins, covered beneath like the leaves with a dense white tomentum; catkins appearing with leaves, sessile on the twigs, the pistillate 3-6 cm. long; capsules densely white-hairy, 6-8 mm. long, sessile or on very short pedicels; bracts blackish toward the tips, 5 mm. long or more, with long white hairs; styles about 2 mm. long; staminate catkins 5 cm. long or less; stamens 2; filaments glabrous.

Salix alaxensis (*sens. lat.*) is one of the commonest and most conspicuous willows in Alaska, Yukon, Mackenzie, the northern Rocky Mts., and the western arctic islands (Map 20). It has been collected in the arctic tundra and the northern edge of the timber as far eastward as Hudson Bay, and south in the alpine tundra of the Rocky

Mts. to the Athabaska Pass. On the coastal mountains it reaches nearly to the southern end of the Alaska panhandle (Raup, 1947, map Pl. 21). The matted white pubescence on the under sides of its leaves makes it stand out sharply among most of the shrubs with which it grows. Three variants have been described for our area, to which the following key applies.

A. Petioles expanded in the lower part, to form sheathes around the buds .... **var. *obovalifolia.***

A. Petioles not expanded to form sheathes around the buds .. . . .
  B. Twigs, even when several years old, densely white **woolly** .... ***S. alaxensis* (typ.).**
  B. Twigs soon glabrate, usually covered with a bluish waxy **bloom (pruinose)** .... **var. *longistylis.***

The typical form of *S. alaxensis* is the commonest one above timberline in the western mountains, where it grows in gullies, along watercourses, or in swales. Here it is usually a low shrub 0.5-2 m. tall. It is found also on river gravels and in floodplain woods at low altitudes, where it is sometimes almost tree-like. The commonest form below timberline is var. *longistylis* (Rydb.) Schn. in Jour. Arn. Arb. 1: 225 (1920) (*S. longistylis* Rydb. in Bull. N. Y. Bot. Gard. 2: 163, 1901) which also grows to large size on lake beaches and river bars. It also is found occasionally as a small shrub above timberline. Our field parties found it in such a habitat at Fraser Loop, on the White Pass & Yukon Ry., *11707*; and I have seen a specimen of it from above timber on the Haines Rd., mi. 85, *Clarke 536* (CAN). Intermediates between this variety and the typical species are commonly seen as one goes up and down mountains. Variety *obovalifolia* Ball in Jour. Wash. Acad. Sci. 28: 443 (1938) was described from material collected in Keewatin, and Ball gives its range as extending from Jasper Park in western Alberta to the western shore of Hudson Bay at Cape Eskimo, thence northward to the Mackenzie valley (see also Raup, 1943: map, pl. 3). Scoggan (1957: 235) also cites a specimen from Churchill. Our field party in 1943 made a single collection which might be placed here: on sliderock at the base of a cliff on the north side of Mt. White, between Teslin and Marsh Lakes, *11311*. However, I have seen many Yukon and Alaska specimens that show expanded, sheathing petioles, suggesting that the variety does not have as good a geographic segregation as Ball indicated, and that it may be only a minor variant.

Porsild's observations of this species complex in the vicinity of the Canol Rd. (1951: 145-7) have led him to regard var. *longistylis* as worthy of specific rank. In that region the altitudinal segregation of the species and the variety seems more sharply defined, with the break at or near timberline. In addition to differences given in the above key, the following, noted by him, should be mentioned. He regards *S. alaxensis* as "tree-like, with gnarled trunk and branches," and *longistylis* as "bushlike, with straight branches"; young leaves of the species as "very fragrant," and those of *longistylis* "not fragrant"; pistillate bracts of the species as "lanceolate-oblanceolate acute, light brown," and those of *longistylis* as "obovate obtuse, almost black." Considering the amount and kind of variation I have seen in all of these characters among northwestern willows, and noting the strong resemblance between *alaxensis* and *longistylis*, I prefer to maintain them, for the present at least, as a single species complex.

Salix alaxensis is a unique species except for a single, distinctive though closely related form that I described in 1936 as *S. silicicola*. Therefore I suggest that until more is known of the latter species, *S. alaxensis* be considered the principal entity in a small group which will include both species.

Salix silicicola Raup in Jour. Arn. Arb. 17: 246-7 (1936)

Erect shrubs with spreading branches and reddish-brown bark, up to 3 m. high, the twigs densely white hairy or white tomentose; leaves 3-6 cm. long, 2-3.5 cm. wide, broadly elliptic to obovate, obtuse to rounded and slightly mucronate at the apex, rounded or slightly wedge-shaped at the base, prominently veined, entire at the margins, thickly covered on both sides with tomentum, grayish to pale green above, white beneath, on white hairy-tomentose petioles 2-10 mm. long; stipules broadly ovate to lanceolate, 3-7 mm. long, somewhat glandular-toothed, hairy-tomentose; pistillate catkins 2-7 cm. long, about 1 cm. thick, densely flowered, sessile on the twigs; capsules about 6 mm. long, hairy, sessile or on pedicels less than 1 mm. long; bracts broadly ovate, 2-2.3 mm. long, blackish toward the tips, obtuse or acute, covered with long white hairs; styles 2-2.5 mm. long; staminate plants unknown.

Occasional on sand dunes and beach ridges on or near the south shore of L. Athabaska, but thus far unknown elsewhere (Map 20). It is a conspicuous willow, clearly related to *S. alaxensis*, from which it differs by its short stipules (up to 7 mm. long as against 22 mm.) that are broadly ovate to lanceolate rather than linear-lanceolate to filiform, and by having persistent, heavy, hairy-tomentose covering on both sides of the leaves instead of being glabrous or glabrate and bright green on the upper surfaces. Also its leaves are consistently broader in proportion to their length than those of *S. alaxensis*, as well as more strongly obovate and obtuse.

Salix candida Flügge apud Willd. Sp. Pl. 4: 708 (1806)

Upright shrubs, in our region usually 1 m. high or less, the twigs smooth and reddish in age, but covered with a white woolly pubescence when young; leaves 5-10 cm. long, 0.5 to 1.5 cm. wide, oblong or oblong-lanceolate, acute at both ends, entire or undulate on the margins, the margins commonly inrolled toward the lower surface, dull white-tomentose on both sides when young, often retaining this tomentum in age or becoming glabrate and showing dark green above; catkins appearing before the leaves, the pistillate 2-5 cm. long, rather narrowly cylindric in form, usually sessile on the twigs; capsules 6-7 mm. long, densely white-woolly, on pedicels 1 mm. long or less; bracts pale brown toward the apex, a little over 1 mm. long; styles about 1 mm. long; staminate catkins 1-5 cm. long; stamens 2; filaments glabrous.

Occasional to common in muskeg thickets and wet meadows in the more southerly parts of our region, and apparently sporadic northward in the Mackenzie basin. I have seen specimens from as far north as Churchill on the western coast of Hudson Bay (Raup, 1943:

115), and Porsild cites material from Great Bear L. (1943: 27). My own observations in the Mackenzie basin north to Simpson indicate that the species is confined to regions underlain by Paleozoic or younger rocks in that area. Moss (1953: 212-52) reports *S. candida* at several points in the Peace R. country and just east of Lesser Slave L. Hultén has no record of it in Alaska, but Argus has found it at Big Delta (no. *797*), about 120 mi. southeast of Fairbanks, and there is a specimen in Herb. US collected in 1922 by Murie at Salcha Slough near Fairbanks. Porsild notes it in Yukon only in the vicinity of Whitehorse (1951: 148). I have seen the following specimens from the vicinity of the Alaska Highway: Liard Hot Springs, *10908*, same, *A. E. Porsild 9065* (CAN); same, *Clarke 65* (CAN); wet meadow along Liard R. south of Watson L., *11000*; Whitehorse, *A. E. Porsild 9147, 10663* (CAN); Map 19. Strongly glabrescent forms may be called forma *denudata* (Anders.) Rouleau in Nat. Canad. 71: 266 (1944).

Salix Bebbiana Sarg. in Garden & Forest 8: 463 (1895)

Shrubs 2-6 m. high, sometimes becoming tree-like, the young twigs grayish with a pubescence that sometimes persists for several years; leaves commonly 4-6 cm. long and one fourth to one half that in width, elliptic, ovate, oblong or oblanceolate, acute at the apex, acute to rounded at the base, entire or sparingly toothed on the margins, short-hairy or tomentose when young, sometimes persistently so in age, and sometimes glabrescent, upper surfaces dull green and sometimes with impressed veins, lower surfaces paler green or somewhat glaucous, the veins sometimes prominently raised; catkins appearing with the leaves, usually on short leafy peduncles, the pistillate 2-5 cm. long, often lax and nodding; capsules finely pubescent, up to 8 or 9 mm. long, slender, on pedicels 2-5 mm. long; bracts yellowish brown, narrow, 3 mm. long or a little more, sparingly hairy; styles none or very short; staminate catkins 1-2 cm. long; stamens 2; filaments hairy at the base.

Common to abundant throughout most of the wooded parts of our region, in dry or moderately well-drained soils (Map 21). It is a characteristic species of floodplain poplar and spruce woods, prairie margins, open aspen and poplar woods on dry bluffs, and in burned-over upland woods. In the West it reaches nearly or quite to the timberline and occasionally into the tundra, but in the Hudson Bay region it appears to stop just short of this line (Raup 1943: map, Pl. 4; 1947: map, Pl. 21). Porsild (1951: 148-9) found it common along the Canol Rd. northward to Sheldon L. (mi. 222). Hultén (1942: 544-5; 1949: 1733) gives it a wide range in the forested parts of Alaska, though it appears to be absent from most of the southeastern panhandle.

Several attempts have been made to segregate from this species a form with thin glabrescent leaves, usually under the name *S. perrostrata* Rydb. in Bull. N. Y. Bot. Gard. 2: 163 (1901), or *S. Bebbiana* var. *perrostrata* (Rydb.) Schn. in Jour. Arn. Arb. 2: 71 (1920). Fernald has recognized it as a variety (1950: 513-14), disregarding pubescence and using the following key character:

A. Mature leaves reticulate-rugose beneath . . *S. Bebbiana* (typ.)
A. Mature leaves plane and scarcely reticulate beneath . . . . var. *perrostrata*.

However, intermediates between these two forms are so abundant and widespread in our region, and so common locally, that I am inclined to agree with Hultén (l.c.) that with present knowledge they have but little taxonomic significance. (See also Raup 1943: 116-17; 1947: 159, for discussion of this problem.)

In 1947 (pp. 159-60) I described *S. Bebbiana* var. *depilis* from specimens collected at Brintnell L. in the Mackenzie Mts. These plants are almost completely glabrous, even to the capsules, pedicels and axes of the catkins, and to the very young leaves and twigs. At most there are a few long ciliate hairs on the margins of the floral bracts. A few specimens collected by Miss Alice Eastwood at Dawson and elsewhere in southern Yukon (nos. *238*, *519*, *566*), found in the herbarium of the Arnold Arboretum, appear to represent this glabrous variety. Two of the numbers cited (*238*, *566*) have slightly hairy young twigs and petioles, but no. *519* is almost entirely glabrous. Variety *depilis* probably is only an extreme form in the tendency toward glabrescence that can be seen throughout the range of *S. Bebbiana* as a whole.

Salix fallax Raup in Contr. Arn. Arb. 6: 149-50 (1934)

Shrubs 1-1.5 m. high, the young twigs finely tomentose and reddish-brown, the older ones gray and glabrous; leaves 2-7 cm. long, 0.7-3.2 cm. wide, obovate, entire on the margins, acute or acuminate at the apex, acute at the base, silky when young but becoming glabrous, bright green above and glaucous beneath, on petioles up to 1.3 cm. long; pistillate catkins appearing with the leaves, 3-4 cm. long, 1-1.2 cm. thick, borne on leafy peduncles; capsules 4-6 mm. long, finely appressed-pubescent, on pedicels 1-2 mm. long; bracts rounded, silky-hairy, brown, about 1 mm. long; styles 0.5-0.8 mm. long; staminate catkins unknown.

This species was first described from material collected in 1932 from open muskeg woods in the upper valley of the Peace R. a few miles east of Mt. Selwyn, *Raup & Abbe 4312*. It was not again recognized until Porsild collected three numbers of it from an open muskeg along the Canol Rd. at the lower Lapie R. crossing, near mi. 132: *9537*, *9827*, *9828* (1951: 149). Since then I have seen specimens collected by *Clarke 67* in 1943 at the Liard Hot Springs (CAN), by *Malte 122167*, *95377* (CAN) at Jasper, and by Argus at Fairbanks (*413*). Map 22.

Salix fallax seems most nearly related, judging by the character of its pistillate catkins, to *S. pedicellaris*, and I have therefore placed it near this species in the present treatment. It should be looked for in the mountains of northern B. C. and southern Yukon.

KEY TO THE SALIX ARBUTIFOLIA GROUP

A. Prostrate or decumbent shrubs, the ascending branches usually not more than 3 dm. high.

B. Ovaries thinly pubescent or glabrous when young, glabrous at maturity; leaves more or less regularly and finely serrate around the lower half; trailing shrubs . . . . *S. arbutifolia.*

B. Ovaries pubescent to maturity or becoming glabrate in age; leaves entire all around the margins; repent or prostrate shrubs usually 1-3 dm. high .... *S. hebecarpa.*

A. Upright or spreading shrubs 3-10 dm. high.

C. Ovaries and mature capsules glabrous; pedicels usually 2-4 mm. long; leaves glabrous, dark bluish-green above; entire .... *S. pedicellaris.*

C. Ovaries short-appressed-hairy, remaining so in age or becoming glabrous at maturity; pedicels 1-3 mm. long; leaves thinly appressed-hairy beneath, entire or with minute teeth all around the margins, or if glabrous the margins more or less regularly and finely serrate only around the lower half.

D. Leaves glabrous, more or less regularly and finely serrate around the lower half; pedicels 1.5-3 mm. long; ovaries glabrous at maturity .... *S. arbutifolia.*

D. Leaves thinly appressed-hairy, entire or minutely toothed around the whole margin; pedicels 1-1.5 mm. long; ovaries thinly hairy, or glabrate in age .... *S. athabascensis.*

Salix arbutifolia Pall. Fl. Ross. 1, 2: 79 (1788)

Trailing shrubs only a few centimeters high, or ascending-spreading and up to 6-7 dm. high, with glabrous twigs; leaves 1-3 cm. long and commonly more than half that in width, elliptic to obovate, glabrous, obtuse or rounded at the apex, obtuse or acute at the base, entire at the margins or serrate toward the base, shiny green above and glaucous beneath, petioled; catkins appearing with the leaves, the pistillate about 2 cm. long on leafy peduncles; capsules glabrous or sometimes pubescent when young, 7-8 mm. long, on pedicels 1.5-3 mm. long; bracts about 1 mm. long, hairy, dark colored toward the apex; styles very short or nearly obsolete; staminate catkins up to 1.5 cm. long; stamens 2; filaments glabrous.

A western arctic species whose range in Alaska is given by Hultén (1942: 545-6) as chiefly in the west and north, with eastward extensions in the Alaska and Brooks Ranges. It has also been found in the tundra region between Fairbanks and Circle, and Argus has collected it in a muskeg at Fairbanks. It reaches the southern coast only from Kodiak Island westward. Porsild (1943: 27) cites material from the Arctic Coast extending from northern Yukon eastward beyond the Mackenzie R., and a single number from the Kazan R. in Keewatin. I have seen a specimen also from Back R., *Tyrrell* [illegible] (CAN). Porsild did not find it along the Canol Rd. Map 23.

I agree with Hultén (l.c.) that this plant is the *S. crassijulis* of Andersson (1868: 230) and of Coville (1901: 329). I believe that he is correct also in reducing to it the forms described by Ball as *S. fuscescens* var. *reducta* (1935: 183-4).

Salix arbutifolia was the first species described in a series of willows that appear closely enough related to be called an *S. arbutifolia* group. This group includes *S. pedicellaris* (var. *hypoglauca* and *tenuescens* in our region), *S. athabascensis*, and *S. fuscescens*. *Salix arbutifolia* itself is confined to western arctic Canada and to Alaska. The varieties of *S. pedicellaris* are primarily eastern subarctic and boreal forest plants, but have extensions northwestward (var. *hypoglauca* to Great Bear L., the northern Rocky Mts. and southern Yukon). *Salix athabascensis* occurs in the central part of the Mackenzie basin and westward to the eastern interior of Alaska, with possible eastward extensions to Hudson Bay and central Saskatchewan.

Salix hebecarpa is a localized segregate known in the east only from its type locality on the Gaspé Peninsula, and reported by Hultén from the Seward Peninsula of Alaska. The large areas of overlap between *S. pedicellaris* and *S. athabascensis* suggest that the latter is only a varietal phase of the former. However, until more is known of its range I prefer to maintain it as a species. It reaches considerably farther westward than *S. pedicellaris*, and has not yet appeared in the easternmost parts of the latter's range.

Salix pedicellaris Pursh, Fl. Am. Sept. 2: 611 (1814)

Represented in our region chiefly by its var. *hypoglauca* Fern. in Rhod. 11: 161 (1909), to which the following description applies:

Shrubs usually 1 m. high or less, with glabrous, blackish twigs; leaves 2-4.5 cm. long, 1-2 cm. broad, obovate-oblong to broadly oblanceolate, usually obtuse or rounded at the apex, acute or obtuse at the base, entire at the margins and with the margins inrolled toward the lower surface, glabrous, green above and glaucous beneath; catkins appearing with the leaves, on leafy peduncles, usually about 2 cm. long; capsules glabrous, 5-8 mm. long, on pedicels 2-4 mm. long; bracts about 1 mm. long, yellowish, glabrous or nearly so; styles nearly obsolete; stamens 2; filaments glabrous.

A southerly species in the boreal forests, usually found in muskeg thickets and having a range in our region somewhat similar to that of *S. candida*. In the Hudson Bay country it is occasional or common northward to Churchill (Raup, 1943: 117-18) and to a lake shore on the Tha-anne R. northwest of Churchill in southern Keewatin (Porsild, 1943: 28). In the Mackenzie basin it is common on the sandy shores of ponds just south of L. Athabaska, and occasional northward to Great Bear L. (Raup, 1936: 238; 1947: 160). Apparently rare in the vicinity of the Alaska Highway, from which I can cite the following specimens: Lesser Slave L. district, *Brinkman 4545* (BH); margin of lake in Summit Pass, *Taylor et al. 6, 7, 9* (V); muskeg near western end of Watson L., *11046*. Porsild (1951: 149) reports a collection of it from the Pelly R. valley along the Canol Rd. near m. 136. Moss (1953: 448-70) records it in several muskegs in the upper Peace R. region of western Alberta. Hultén makes no mention of it in the Alaskan flora. Map 23.

A second variant of the species, though unknown elsewhere in our region, has been found in the Wood Buffalo Park of northern Alberta, and should be included here. It is var. *tenuescens* Fern. in Rhod. 11: 162 (1909), and was found in an upland muskeg (Raup, 1935: 125; 1936: 238). It is distinguished by having oblanceolate to linear-oblong leaves that are acute at both ends and not more than 1 cm. wide, and by having rather lax, loosely-flowered catkins with capsules up to 10 mm. long.

Salix pedicellaris is here regarded as closely related to a group of species including *S. arbutifolia*, *S. athabascensis*, and *S. hebecarpa*. See *S. arbutifolia* for further discussion of the group.

Salix athabascensis Raup in Rhod. 32: 111-12 (1930)

Erect shrubs 3-6 dm. high, with finely gray-hairy young twigs; leaves 1-3 cm. long, 0.5-1.5 cm. wide, elliptic or obovate, entire or minutely glandular-dentate on the margins, acute or acuminate at the apex, obtuse to rounded at the base, green and thinly silky-pubescent above, becoming glabrous in age except on the mid-vein, glaucous and thinly appressed hairy beneath and glabrate in age, on petioles up to 6 mm. long; pistillate catkins 1.5-2 cm. long, borne on leafy peduncles; capsules 5-6 mm. long, covered with short appressed hairs on pedicels 1-1.5 mm. long; bracts 1-1.3 mm. long, obtuse or rounded at the apex, brown, silky-hairy; styles about 0.3 mm. long; staminate catkins unknown.

Apparently common locally, though in widely scattered places. I have seen the following specimens from the western part of our area: wet meadow near Liard Hot Springs, *10907*; same, *Clarke 63* (CAN); margin of small pool in willow spruce woods near Liard R. south of Watson L., *10998*, *11001*, *11002*, *11005*, *11007*; thickets and wet meadows at the eastern end of Watson L., *10921*, *11060*, *11061*, *11062*; wet muskeg along road near mi. 1235, west of Tanacross, *12713*; muskeg near Moose L., Wood Buffalo Park, *Raup 8129* (Type; CAN); near Hay R., *Lindsey 103* (CAN); Lower Keele R., *Lindsey 142* (CAN). A few specimens from the eastern part of the area and to the south of it are also referred to *S. athabascensis*: York Factory, *Scoggan 6026* (CAN); Riverton, 75 mi. north of Winnipeg, *Scoggan 9024* (CAN); north of Prince Albert, Sask., *Macoun 12671* (CAN); Goldburn, Sask., *Breitung 456*, *458* (CAN); McKague, Sask., *Breitung 461* (CAN). Map 23.

The type material of *S. athabascensis* was dried over rather intense artificial heat which drove off the glaucescence of the leaves. This character, included in the above description, was not mentioned in the original. Otherwise, most of the specimens cited here are similar to the type.

In the *S. arbutifolia* group of willows, of which this species is a part, it is most nearly related to *S. pedicellaris* var. *hypoglauca*, and may prove to be no more than a varietal segregate of the latter.

Salix hebecarpa Fern. in Rhod. 26: 123 (1924)

Repent or prostrate shrubs 1-3 dm. high, with glabrous or glabrate twigs; leaves up to 3 cm. long and 1-4 cm. wide, elliptic-oblong to oblong-ovate, obtuse or rounded at the apex, mostly obtuse at the base, entire on the margins, glabrous, green above and glaucous beneath; pistillate catkins appearing with the leaves, up to 5 cm. long, on leafy peduncles; capsules 4-6 mm. long, pubescent, or glabrate in age, pedicels 1-2 mm. long; bracts not much longer than the pedicels, dark-colored, short-hairy; styles up to 0.7 mm. long.

Hultén (1942: 520-1) cites a specimen collected at Teller, on the Seward Peninsula by Walpole (*1826*, US). Otherwise the species is known only from its type locality on Mt. Albert, in the Gaspé Peninsula in Quebec. I have not seen the Alaskan specimen, but Hultén says that it is a close match for the type material. Map 24.

Ball (1950: 10-16) considered that *S. hebecarpa* is a hybrid of *S. pedicellaris* var. *hypoglauca* and *S. anglorum* (*S. arctica*) or *S. arctophila*. Although he made a good case for the intermediate character of *S. hebecarpa*, there is no experimental evidence for such a cross, and I prefer to let *hebecarpa* stand as a species until more intensive study proves otherwise.

Salix hebecarpa appears to be closely related to *S. arbutifolia* and *S. pedicellaris*, and I have included it in what I have called the *S. arbutifolia* group.

Salix gracilis Anders. in Öfvers. Sv. Vet. Akad. Förh. 15: 127 (1858)

S. petiolaris of auth., not Sm. var. *rosmarinoides* (Anders.) Schn. in Jour. Arn. Arb. 2: 19 (1920).

Shrubs 1-3 m. high, with slender erect or ascending branches, the twigs glabrous or soon glabrate; leaves up to 6 or 7 cm. long when mature, and up to 11 mm. wide, linear or lanceolate, acuminate at the apex, acute at the base, the margins entire or minutely toothed, silvery- or somewhat tawny-silky when young, and remaining so or becoming glabrate in age, shiny green above, glaucous beneath; catkins appearing with the leaves, the pistillate up to 4 cm. long in fruit but shorter when in flower, borne on leafy peduncles; capsules silvery-silky, 5-7 mm. long, on slender pedicels 2.5-4 mm. long; bracts narrow, 1-2 mm. long, yellowish or brown, thinly pubescent; styles obsolete or nearly so; stamens 2; filaments hairy toward the base.

Salix gracilis is reported in the country west of James and Hudson Bays as far north as MacBride L., 56° 52′ N., 99° 57′ W. (Scoggan, 1957: 237). In the Mackenzie basin it is common at the margins of sloughs and semi-open prairies northward at least to Fort Smith. In this region it appears to be restricted to country underlain by Paleozoic or younger rocks (Raup, 1936: 238; 1935: 125; 1947: 160). Farther west I have seen specimens from the Lesser Slave L. district, *Brinkman 3876* (BH); Dawson Creek, *Raup & Abbe 3503, 3532, 3534, 3539* (A); and Cache Cr., north of the Peace R., *Herriot 67* (PH). It is not included by either Hultén or Porsild in the Alaska-Yukon flora. Map 24. Western specimens from our region all appear to represent typical *S. gracilis*. Scoggan, however, gives the typical form (*S. petiolaris* var. *rosmarinoides* in his treatment, l.c.) a more southern range in Manitoba, with its northernmost collection from Norway House. He regards the form seen in the region west of Hudson Bay as var. *textoris* Fern., in Rhod. 48: 46 (1946) (*S. petiolaris* of auth., not Sm.). This variety is distinguished by having somewhat longer capsules (up to 9 mm.); leaves up to 10 cm. long and 2 cm. wide, glabrate or rarely silky when mature, strongly glandular serrate.

In using the name *S. gracilis* Anders. I am following Fernald (1946: 46-8; 1950: 516-17). The species (*sens. lat.*) has long been called, in American studies of the willows, *S. petiolaris* J. E. Smith, Trans. Linn. Soc. 6: 122 (1802). Forms with more delicate, less serrulate leaves (here called *S. gracilis*) have been named, in part, *S. petiolaris* var. *rosmarinoides* (Anders.) Schn. Fernald (Rhod. l.c.) has maintained that Smith's *S. petiolaris*, which was described from a living plant in an English garden sent from somewhere in Scotland by a Mr. D. Dickson, was not the common American species, but was native to the British Isles. Ball (1948: 178-87) has taken issue with this, insisting that Smith's plant was from America, probably introduced to Britain by persons unknown. In the absence of any firm evidence on the geographic origin of Smith's plant, arguments on both sides are bound to be somewhat tenuous and circumstantial. However, the original description states that *S. petiolaris* is a "small, spreading tree," while its American relatives are slender shrubs. It is true that some of our northwestern willows, such as *S. arbusculoides* and *S. Scouleriana* may be either shrubby or tree-like and single stemmed. Ball reports that G. H. Turner has found a few single-stemmed plants of the *petiolaris* type in aspen woods near

Edmonton, Alberta. But plants of this species in eastern America, from which introductions to Britain would have come, are consistently shrubby. Ball believes that shrubs from this source might readily grow as trees in a cultivated English garden. Such an interpretation involves more assumptions than Fernald's, which does not go beyond Smith's simple statements that his *S. petiolaris* was found in Britain, and that it was a tree.

KEY TO THE SALIX DISCOLOR GROUP

A Catkins precocious, sessile on the twigs; pedicels 1.4-2.4 mm. long; leaves lanceolate, obovate, or elliptic, acute at the apex, more or less regularly alternate toward the ends of the twigs .... *S. discolor*.

A. Catkins precocious or appearing with the early leaves, sessile or on very short leafy peduncles; pedicels 0.5-1.5 mm. long; leaves oblanceolate or obovate, rounded or obtuse at the apex, commonly arranged so that they appear fan-like at the ends of the twigs .... *S. Scouleriana*.

Salix discolor Muhl. in Neue Schr. Ges. Nat. Fr. Berlin 4: 234 (1803)

Shrubs or small trees up to 6 m. high, with glabrous or glabrescent twigs; leaves 3-10 cm. long, 1-3 cm. wide, lanceolate, obovate, or elliptic, petioled, acute at both apex and base, irregularly crenate-serrate or sometimes nearly entire on the margins, covered with tawny hairs when young, usually soon glabrate but in some forms with persistent rusty pubescence beneath, bright green above and glaucous beneath; catkins appearing before the leaves, and nearly mature before the leaves come out, the pistillate up to 12 cm. long and 3 cm. thick at maturity, sessile on the twigs; capsules 7-12 mm. long, finely pubescent, on pedicels 1.4-2.4 mm. long; bracts dark red or brown to black, about 2 mm. long, long hairy; styles distinct, about 0.8 mm. long; staminate catkins 1.5-5 cm. long; stamens 2; filaments hairy toward the base.

An early-flowering precocious species of temperate eastern America, known in our region in Manitoba northward at least to the Hayes R. (Scoggan, 1957: 237), and in the Peace R. country east of the Rocky Mts. It flowers, matures its capsules, and drops its catkins so early that by the time collectors usually get into the North Country only sterile specimens are readily available. Hence many northern records are of somewhat doubtful validity. Specimens from the southern part of James Bay and northern Manitoba are in this category (Raup, 1943: 118-19), as are some of those from the Peace R. region. In the latter I can cite the following specimens and records with some degree of confidence: Lesser Slave L., *Brinkman* [illegible]; Grand Prairie, *Groh* [illegible] (DAO, A). Although I have seen no other specimens than these, Moss (1953: 212-52) reports the species from many localities in the Peace R. country, from Lesser Slave L. to Fort St. John, B.C., up the Peace to Vermilion, and northward on the Mackenzie Highway to Steen R. He notes it as occurring in a variety of forest types, from tamarack bogs to pine woods. **Map 25.**

The eastern *S. discolor* and the western *S. Scouleriana* are closely related species, and I have placed them together in an "*S. discolor* group." Their ranges overlap in the forested country between northern Manitoba and the upper Peace R. region just east of the Rocky Mts.

Salix Scouleriana Barratt in Hook. Fl. Bor.-Am. 2: 145 (1839)

Represented in our region chiefly by its var. *coetanea* Ball in Jour. Wash. Acad. Sci. 24: 73 (1934), to which the following description applies. Shrubs or small trees up to 10 m. high, with grayish bark and densely pubescent to glabrate twigs; leaves up to 12 cm. long and commonly one third that in width, oblanceolate or obovate, obtuse or rounded at the apex and sometimes abruptly acute, wedge-shaped at the base, entire or sometimes shallowly crenate-serrate, rather thick and firm in texture, dark green and glabrate above, glaucous and sometimes silvery or reddish pubescent beneath, petioled, commonly arranged at the ends of the twigs so that they appear fan-like; catkins appearing with the leaves or a little before, sessile on the twigs or on very short leafy peduncles, the pistillate up to 5 cm. long; capsules 7-9 mm. long, tomentose, on pedicels up to 1.5 mm. long; bracts black, obovate, long-hairy; styles about 0.5 mm. long; staminate catkins 1-2 cm. long; stamens 2; filaments glabrous.

Salix Scouleriana is a close western relative of S. *discolor.* In the central Mackenzie basin it is known only around L. Athabaska, where it is common (Raup, 1936: 238-9). In the Alaska Highway region it is occasional to common northwestward at least to about mi. 1381 in the Tanana valley, and Argus (personal communication) notes it as common in muskeg spruce woods in the Fairbanks area. However, the range does not seem to be continuous, for it has not been found in southwestern Yukon west of Whitehorse. Hultén (1942: 550-1; 1949: 1733) gives it a limited range in southern coastal Alaska and in the Yukon valley northward to the vicinity of Dawson. Porsild (1951: 151) found it common along the Canol Rd., mostly in open spruce woods on the lowlands. He has collected it also along a small tributary of the Godlin R. along the Canol Rd. east of the Yukon-Mackenzie divide (1945: 18), and I found it in the Brintnell L. region of the Mackenzie Mts. (1947: 160). I have also placed here some specimens collected along the lower Colville R. in the vicinity of Umiat, *Borman, Rebuck & Cantlon 271.* They are from a tall willow growing in the river floodplain. The catkins are normal and were maturing in the second week of July, and they are typical of *S. Scouleriana*; but the leaves are elliptic to elliptic-ovate and sharply acute at the apex. They can be matched in the herbarium, but they are the exception in leaf shape for this species rather than the rule. I have mapped their locality as an isolated one, but more collecting in northern and northeastern Alaska may establish a range connection with more southern populations. Map 25. Collections from the Alaska Highway are mainly from dry pine or aspen woods. The specimens from near mi. 1381 came from well-formed, single-stemmed trees about 10 m. high with trunk diameters up to 13 cm.

Scoggan (1957: 238) reports several specimens from central Manitoba, and one collected by Baldwin at Reindeer L., lat. 57° 37′ N. I have not seen this material, but in view of similar eastern range extensions of other western species, *S. Scouleriana* is to be expected in this region.

Plants whose leaves have a dense, persistent pubescence beneath have been called forma *poikila* by Schneider in Jour. Arn. Arb. 3: 76 (1921) (see also Jour. Arn. Arb. 2: 12, 1920). Our field parties on the Alaska Highway collected two numbers that seem to represent this form: sand dunes at Carcross, *11458A*; sandy bank in pine woods along Lewes R. at Whitehorse, *11175*. I have also seen specimens of it (GH) from Dawson, and from L. Athabaska.

Salix Scouleriana appears to be the western vicariad in a group of willows in which *S. discolor* is the eastern element. In spite of close relationship the two species are rather easily distinguished on leaf and other characters.

KEY TO THE SALIX PHYLICIFOLIA GROUP

A. Leaves finely and more or less regularly serrate on the margin, though some of them occasionally nearly entire; catkins usually coetaneous (sometimes subprecocious), sessile or on prominently leafy peduncles .... *S. phylicifolia.*

A. Leaves entire or with a few small, irregularly spaced teeth; catkins precocious, sessile or with a few small leaves at the base.

  B. Stipules persistent for 3 or more years as dried, linear or linear-lanceolate appendages on old wood .... *S. pulchra.*

  B. Stipules not persistent after one growing season .... *S. planifolia.*

Salix phylicifolia L. Sp. Pl. 2: 1016 (1753)

Upright shrubs about 2 m. high, with dark reddish to blackish twigs that are finely pubescent when young, but soon glabrate; leaves 3-4 cm. long, one-fourth to one-third as wide, elliptic to oblanceolate, mostly acute though sometimes obtuse at the apex, acute at the base, thinly pubsecent beneath and on the mid-vein above when young, green above and glaucous beneath, finely serrate on the margins or sometimes nearly entire, short-petioled; catkins appearing with the leaves or occasionally before, sessile or on leafy peduncles, lax and somewhat nodding, the pistillate 4-5 cm. long; capsules 6-8 mm. long, pubescent, on pedicels 0.5-1 mm. long; bracts about 2 mm. long, blackish in the upper part, hairy; style about 1 mm. long; staminate catkins up to 3.5 cm. long; stamens 2; filaments glabrous.

This species is included here with considerable misgiving. *Salix phylicifolia* has not been recognized on the North American Continent since Pursh demonstrated that its closest relative in eastern America was a distinct species, which he named *S. planifolia*. However, our field party on the Alaska Highway in 1944 collected a willow (*11785*) at the margin of a prairie near mi. 1019 which is so good a match for a great deal of Eurasian material of *S. phylicifolia* in the Harvard Herbarium that I have no other course at present than to identify it as such. The shrub was about 2 m. high, and when seen in mid-June had well-formed leaves, with catkins approaching maturity. Since then I have seen a second collection, made by Dr. William Drury along the lower Kuskokwim R. and identified by him as *S. phylicifolia*. It came from the hills 2 mi. north of Aniak (*1507*, GH, pistillate shrub about 11 dm. high). Although its leaves are more glabrate than in our no. *11785*, the two collections otherwise match each other closely. Map 26.

Salix phylicifolia belongs to a group of three closely related species in America, of which the other two are *S. planifolia* and *S. pulchra.* I have called this series the "*S. phylicifolia* group," but if *S. phylicifolia* proves untenable in the American flora, the group should be named after *S. planifolia,* the next older name. See note under *S. pulchra* for further discussion of the group.

Salix planifolia Pursh, Fl. Am. Sept. 2: 611 (1814)

Shrubs up to 3 m. high, with purplish twigs that are glabrous and sometimes pruinose; leaves 2.5-7 cm. long and one-fourth to one-third that in width, elliptic or elliptic-lanceolate to oblong or oblanceolate, usually acute at both apex and base, glabrous, firm and somewhat leathery in texture, glabrous, dark green and shiny above, glaucous beneath, entire at the margins or irregularly and finely toothed, petioled; catkins appearing before the leaves, sessile or with a few small leaves at the base, the pistillate up to 4.5 cm. long when mature; capsules silky-pubescent, 5-6 mm. long, nearly sessile or on very short pedicels; bracts 1.5-2 mm. long, blackish in the upper part, hairy; styles 0.8-1.5 mm. long; staminate catkins 1-2 cm. long; stamens 2; filaments glabrous.

Common to abundant on stream banks and at wet slough margins westward in the forested regions to the Rocky and Mackenzie Mts.; occasional in the upper Liard R. valley and westward over the Continental Divide to Whitehorse (Map 26). In its eastern range it extends northward in the tundra to the Chesterfield Inlet-Dubawnt L. region west of Hudson Bay, and to southern Baffin Island (Raup, 1943: 119-20). It is common in the Mackenzie basin northward to the lower Mackenzie R. valley. Hultén does not mention it in his Flora of Alaska and Yukon, but Porsild (1951: 150) reports it common along the Canol Rd. (see also Porsild, 1957: 176, map 124). Intermediates between *S. planifolia* and the closely related *S. pulchra* are found in northern B. C. and southern Yukon where the two species overlap. Further discussion of this relationship will be found under *S. pulchra.*

Forms with narrowly oblanceolate, narrowly lanceolate, or narrowly elliptic leaves have been called var. *Nelsonii* (Ball) Ball in Amer. Mid. Nat. 45: 747-9 (1951). These forms occur throughout the range of the species, and like the varieties of *S. pulchra* based on leaf-shape, var. *Nelsonii* is not clearly defined. It is well within the range of variation to be found in the leaves of most species of willows, and until far more material is available for statistical analysis it seems to be of doubtful taxonomic value.

The species varies greatly in form and size, from large upright shrubs growing at the margins of wet meadows to dwarfed spreading forms only a few centimeters high in exposed rocky places. The form of its branchlets also varies along with these differences, the dwarfed plants often having rather heavy, thick twigs.

Salix pulchra Cham. in Linnaea 6: 543 (1831)

Upright shrubs 1-2 m. high, with dark brown to purplish twigs that are commonly pruinose, pubescent when young but soon glabrate; leaves usually 3-6 cm. long, and from one-third to one-half that in width though sometimes narrower, elliptic or in some forms oblong or obovate, usually acute at both apex and base though sometimes (mostly in obovate forms) rounded or abruptly acute at the apex, glabrous, green above and glaucous beneath, entire at the margins, or with a few faint teeth toward the base, petioled; stipules narrowly linear and persistent for several years; catkins appearing before the leaves, sessile on the twigs, the pistillate commonly 5-6 cm. long; 1.5-2 cm. thick; capsules pubescent, 7-8 mm. long, sessile or on very short pedicels; bracts about 2 mm. long, blackish in the upper part, hairy; styles 1.2-2 mm. long, staminate catkins 2.5-3.5 cm. long; stamens 2; filaments glabrous.

Salix pulchra is common in Alaska and Yukon, with minor extensions southward into northern B. C., and eastward into the District of Mackenzie. Along the Alaska Highway it is common northwestward from Summit Pass in the Rocky Mts. Hultén (1942: 547-9; 1949: 1733) gives it almost universal distribution in Alaska except for the southeastern panhandle. Porsild (1951: 149-50) found it common along the Canol Rd. up to the Yukon-Mackenzie divide, and I collected it near Brintnell L. in the Mackenzie Mts. (1947: 160-1). Eastward along the Arctic Coast it reaches beyond the Mackenzie delta, where it is noted by Porsild as common, to Bernard Harbor and Coppermine (1943: 28). I have seen a single specimen from the Mackenzie valley, labeled "Fort Franklin, Mackenzie River," *Richardson* (NY). This species is a characteristic tundra plant of the far Northwest, and occurs below timberline in wet meadows, muskegs, and open wet woods. **Map 26.**

Three varieties of *S. pulchra* have been described from Alaska and Yukon material. They are based mainly upon differences in the pubescence of the young twigs, and in the shape of the leaves. Considering the amount and kind of variation in these characters that occurs throughout most of the genus, variation that seldom shows much geographic segregation, these varieties have doubtful significance. However, for those who wish to try using them, the following key will indicate the trends.

A. Twigs densely pubescent, and remaining so for at least 2-3 years .... var. *yukonensis*.
A. Twigs glabrous or essentially so, even when very young
  B. Leaves rather broadly rhomboid or elliptic, acute at both ends .... *S. pulchra* (typ.).
  B. Leaves obovate, oblong, or narrowly elliptic-oblanceolate
    C. Leaves narrowly to broadly obovate, or obovate-oval, rounded to abruptly acute at the apex, or the newest ones acute .... var. *Looffiae*.
    C. Leaves narrowly oblong, elliptic-oblong, or narrowly elliptic-oblanceolate .... var. *Palmeri*.

Hultén (l.c.) limits the range of var. *yukonensis* Schn. in Jour. Arn. Arb. 1: 72 (1919) to the interior of Alaska, and to the Lewes-Yukon valley in Yukon. Porsild (l.c.) states that along the Canol Rd. it is limited to country below timberline. He thinks it is a distinctive variety, perhaps worthy of specific rank. Our field parties on the Alaska Highway collected it only in the mountains north of Kluane L., where it was growing in alpine tundra. Variety *Looffiae* Ball in Madroño 6: 228-9 (1942) was described from Kodiak Island material, but Ball cites specimens from several places in southern

Alaska, the islands in Bering Sea, and from the interior between the Kobuk R. and Circle. Variety *Palmeri* Ball in Madroño 6: 229-30 (1942) came originally from the Matanuska Valley, though specimens are cited from many places in central southern coastal Alaska, and from central and west-central interior Alaska.

Considerably more significant, for the moment, than this attempted definition of varietal segregates within *S. pulchra* is recognition of its position in a large and continuous population of closely related willows extending from Newfoundland to western Alaska. Its eastern counterpart is *S. planifolia* Pursh, which reaches westward at least to the vicinity of Whitehorse. Thus the two species overlap in northern B. C. and southern Yukon, and in this region numerous intermediates occur. Allowing for minor variations in the shape of the leaves, and the variable presence of a bluish bloom on branchlets, all of which occur in both species, the principal character by which *S. pulchra* may be distinguished is the persistence of its stipules. An additional character not found in *S. planifolia* is the occasional presence of dense pubescence on young twigs of *S. pulchra*, persisting for 2-3 years or more; but this is limited to that part of the population that has been called var. *yukonensis*. If our record of *S. phylicifolia* in S. W. Yukon proves to be correct, this species should be added to the *S. planifolia-S. pulchra* complex, to form the "*S. phylicifolia* group."

KEY TO THE SALIX PELLITA GROUP

A. Lower surfaces of the leaves silvery-tomentose with short, straight, appressed hairs; a western Cordilleran species .... *S. subcoerulea.*

A. Lower surfaces of the leaves silky-tomentose with longer, scarcely straight hairs that are slightly appressed; an eastern boreal forest species, closely related to *S. subcoerulea* .... *S. pellita.*

Salix pellita Anders. in Sv. Vet.-Akad. Handl. 6: 139 (1867)

Shrubs or small trees up to 5 m. high, with greenish or reddish twigs that are usually pruinose with a bluish bloom; leaves 4-12 cm. long, 8-15 mm. wide, linear-lanceolate to more broadly lanceolate or oblanceolate, acuminate at the apex, acute or obtuse at the base, rather thick and firm in texture, entire on the margins or nearly so, green and glabrous above, glaucous and usually densely silky-pubescent beneath, producing a silvery appearance; catkins appearing before the leaves, nearly sessile or subtended by a few small leaves, the pistillate up to 5 cm. long; capsules 4-5 mm. long, densely whitish pubescent, on very short pedicels; bracts 1-2 mm. long, blackish, long-hairy; styles up to 1.2 mm. long; staminate catkins unknown.

A species of north temperate eastern America, which has been collected at Moose Factory, on the western shore of James Bay, at York Factory, and in the valleys of the Hayes and Nelson Rivers (Raup, 1943: 121; Scoggan, 1957: 238). Map 27. Scoggan recognizes a forma *psila* Schn. in Jour. Arn. Arb. 1: 83 (1919) which has leaves whitened but glabrescent beneath. He reports specimens of it from York Factory and from the Nelson R.

Salix pellita is an eastern counterpart of the western *S. subcoerulea*, to which it is closely related. Both should be considered members of an "*S. pellita* group," to which the central Cordilleran *S. bella* Piper can be added.

Salix subcoerulea Piper in Bull. Torr. Bot. Cl. 27: 400 (1900)

Shrubs 2-3 m. high with brown to blackish, glabrous, pruinose twigs; leaves usually oblanceolate though sometimes oblong-oblanceolate or oblong-lanceolate, 3-6 or 7 cm. long, 0.8-2.5 cm. wide, acute or obtuse at the apex and base, entire on the margins or nearly so, green and thinly pubescent above, silvery beneath with a dense short pubescence, petioled; catkins appearing before the leaves, sessile on the twigs, up to 4 cm. long, and 1 cm. thick or less; capsules about 5 mm. long, silvery-silky, on short pedicels up to 1 mm. long; bracts 1.5-2 mm. long, brown to blackish, thinly hairy; styles up to 1.5 mm. long; stamens 2; filaments glabrous.

A Cordilleran species that comes into our region only in the upper Peace and Athabaska R. regions, the northern Rocky Mts., and in the upper Liard valley. The easternmost collection I have seen came from Athabaska Landing, just east of Lesser Slave L., *Ball 2364* (CAN). The farthest northwest that our field parties collected it along the Alaska Highway was at Albert Cr., west of the upper crossing of the Liard R. and just north of the B. C.-Yukon boundary, *13012*. It is not mentioned by Hultén in his Flora of Alaska and Yukon, nor by Porsild in his Botany of S. E. Yukon. It is a conspicuous species because of its strongly pruinose twigs, and the silvery sheen of the lower surfaces of its leaves. It grows in wet meadows and on stream margins at low altitudes, and is a close relative of the eastern *S. pellita* (see note under *S. pellita*). Map 27.

Ball (1951: 740-47) has changed the taxonomic status of *S. subcoerulea*, making it and *S. bella* Piper varieties of *Salix Drummondiana* Barratt. In doing so he raises no question with regard to the typification and identity of *S. Drummondiana* itself, though this has been a debatable subject in American salicology for a long time. I reviewed it in some detail in 1934 (pp. 147-9), and came to the conclusion that the species was of doubtful validity, and that its relationship was in the Sect. Chrysantheae with *S. alaxensis* rather than in the Phylicifoliae with *S. subcoerulea* and *S. pellita*. At that time I had seen a photograph of what had been thought to be the type in the Kew Herbarium, two sheets of co-type material in the herbarium of the New York Botanical Garden, and a specimen in the Barratt Herbarium at Wesleyan University, Middletown, Connecticut, labeled by Barratt himself as the type of the species. Since then I have seen sheets of the type material at Kew and the British Museum. Although there are various minor differences among these specimens, there is in general a close similarity among them which gives the impression that they constitute a single collection, probably all from the same plant. They were collected by Thomas Drummond in the "Rocky Mountains," probably in the region between the Saskatchewan and Athabaska Rivers, and Barratt's description was published in Hooker's Flora Boreali-Americana 2: 144 (1838).

The type material noted above shows certain characters that are of particular significance to the present discussion. The twigs are distinctly pruinose. Schneider (Jour. Arn. Arb. 1: 87-9, 1919), studying limited material and with only a photograph of what he considered to be the type (K), said that the species showed "almost an entire absence of the glaucous bloom of the branchlets." The under surfaces of the leaves in the type specimens are thickly felted with a whitish, opaque tomentum, and are not silvery in appearance. Both of these characters, as well as many others, strongly suggest *S. alaxensis* var. *longistylis*, as I pointed out in an earlier publication (l.c.). Still another characteristic of the type material is that many of its catkins are imperfectly developed, appearing as though the shrub from which they came were an F_1 hybrid of *S. alaxensis* var. *longistylis* and some other willow.

Ball's recent and rather detailed description of *S. Drummondiana* (l.c.) seems to have been made up from composite sources. In his citations of specimens he mentions none of the type material, but he seems to have been influenced by Schneider's statement that this species was not pruinose on the branchlets. On the other hand, he describes the under surfaces of the leaves as "densely silvery-tomentose," which suggests again that he had not seen any of the type material. Otherwise the description apparently was based largely upon specimens in the *S. subcoerulea* complex that answered to the mistaken requirements just noted.

I am inclined to look upon *S. Drummondiana*, as I did in 1934, as an abnormal form most closely related to the *S. alaxensis* group, but whether the abnormality is due to local site conditions or to hybridization is too uncertain to allow any conclusions at present. If it could be proven that *S. alaxensis* and *S. Drummondiana* were synonymous, then the latter would have precedence, for it is the older name.

Salix arbusculoides Anders. in Vet. Akad. Handl. (Stockh.) 6: 147 (1867)

Low shrubs or tall spindling trees up to 3 or 4 m. high with trunk diameters of 5 or 6 cm., the twigs reddish and shiny, glabrous or glabrate; leaves 2-6 cm. long and commonly one-fourth to one-third as wide, elliptic or elliptic-lanceolate, acute at the base and apex, petioled, finely and regularly serrate or entire on the margins, green and glabrous above, delicately silky beneath with short appressed hairs; catkins appearing with the leaves or a little earlier, sessile or with 2 or 3 small leaves on a short peduncle, the pistillate up to 5 cm. long; capsules 4-7 mm. long, pubescent, on pedicels 0.5-1.2 mm. long; bracts about 1 mm. long, blackish, hairy; styles up to 0.8 mm. long; staminate catkins up to 2.5 cm. long; stamens 2; filaments glabrous.

A common species throughout most of the forested parts of our region, from Hudson Bay to western Alaska (Raup, 1943: 121-2). Porsild has found it in the arctic tundra only a short distance beyond the limit of trees, north of Great Bear L. and at Yathkyed L. along the Kazan R. (1943: 27). Scoggan (1957: 238) reports collections from Churchill, and from the Nelson R. at Limestone Rapids. It is common throughout the Mackenzie basin northward to the Mackenzie delta (Porsild, l.c.; Raup, 1936: 239; 1947: 161), and along the Alaska Highway from western Alberta to central Alaska. Hultén (1942: 549-50; 1949: 1733) gives it a wide range in the interior of Alaska and in the upper Yukon valley above the Alaska border. I have seen several specimens collected along the lower Colville R. in the vicinity of Umiat, *Bliss & Cantlon 5058, 5112, 5131, 5262.* Porsild (1951: 150-1) says that it is common in lowland spruce forest along the Canol Rd. northward to the vicinity of Mt. Sheldon, where it was found at altitudes up to 3500 feet. Although there is a record for it on the Kenai Peninsula and I have a specimen from the Katmai region (*Cahalane 39*, US), it appears to be rare in southern coastal Alaska. Map 28.

Salix arbusculoides is a distinctive willow, growing mostly in lowland woods and thickets, but occasionally in rocky places above timberline. In such exposed places it is a low spreading shrub, but in lowland spruce woods it often forms tall, slender, single-stemmed trees. Though extremely variable in growth habit, its leaf and catkin characters are remarkably uniform except for occasional glabrous-leaved forms that have been called var. *glabra* Anders. in Sv. Vet.-Akad. Handl. 6: 148 (1867).

Salix sitchensis Sanson in **Bong., in Mém. Acad.** Imp. Sc. St. Pétersb. **Ser. 6, Math. 2: 162 (1833)**

Shrubs up to 7 m. high, with dark brown to blackish twigs that are glabrous or occasionally pubescent; leaves commonly 3-7 cm. long, 1.5-2.5 cm. wide, oblong-obovate or strongly obovate, acute at the apex or occasionally obtuse, wedge-shaped at the base, entire or obscurely glandular-toothed on the margins, dark green above, pubescent above when young but soon glabrate, covered beneath with whitish silky pubescence consisting of short appressed hairs; catkins appearing with the leaves, 4-7 cm. long, slender and densely flowered, sessile or sometimes on short leafy peduncles; capsules 4-6 mm. long, silky-pubescent, sessile or nearly so; bracts brownish, about 1 mm. long, thinly hairy; styles 0.5-0.7 mm. long; stamen 1; filament glabrous.

Mostly restricted to the coastal areas of southern and southeastern Alaska and southward (Hultén, 1942: 551-2; 1949: 1733). However, Hultén cites a record of it at Lake Lindemann, and it should be looked for throughout the Teslin, Tagish, and Bennett lake regions. It is known in the central interior of B. C. Map 24.

LITERATURE CITED

ANDERSSON, N. J. 1868. Salicineae. In De Candolle, Prod. Syst. Nat. Regn. Veg. 16²: 191-331.

BALL, CARLETON R. 1921a. Undescribed willows of the Section Cordatae. Bot. Gaz. 71: 426-37.

——. 1921b. Notes on willows of Sections Pentandrae and Nigrae. Bot. Gaz. 72: 220-36.

——. 1923. The willows of the Pacific States. Repr. from Abrams, L. An illustrated flora of the Pacific States, Washington, Oregon, California. 1: 486-507.

——. 1926. Canadian willows of the sections Pentandrae, Nigrae and Albae. Can. Field-Nat. 40: 145-152, 171-175.

——. 1930. In Cooper, W. S. The seed-plants and ferns of the Glacier Bay National Monument, Alaska. Bull. Torr. Bot. Cl. 57: 327-38.

——. 1934. New or little known West American willows. Univ. Calif. Publ. Bot. 17: 399-434.

——. 1935. New varieties of western willows. Proc. Nat. Acad. Sci. 21: 181-86.

——. 1938. New varieties and combinations in Salix. Jour. Wash. Acad. Sci. 28: 443-52.

——. 1942. Far western novelties in Salix. Madroño 6: 227-39.

——. 1948. Salix petiolaris J. E. Smith: American, not British. Bull. Torr. Bot. Cl. 75: 178-87.

——. 1950a. Willow hybrids: Salix hebecarpa Fernald and S. simulans Fernald. Rhod. 52: 8-18.

——. 1950b. A review of Salix anglorum and Salix petrophila. Am. Midl. Nat. 43: 224-241.

——. 1951a. New combinations in Salix (Sections Pellitae and Phylicifoliae). Am. Midl. Nat. 45: 740-49.

——. 1951b. In Spetzman, L. A. Plant geography and ecology of the arctic slope of Alaska. Unpublished M.S. thesis, Univ. of Minnesota.

——. 1951c. In Jordal, L. H. A floristic and phytogeographic summary of the southern slopes of the Brooks Range, Alaska. Unpublished Ph.D. thesis, Univ. of Michigan.

——. 1952a. Salix. In Gleason, H. A. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. 2: 6-23.

——. 1952b. In Davis, R. J. Flora of Idaho, 216-35. Dubuque, Iowa.

BREITUNG, A. J. 1947. Catalogue of the vascular plants of central eastern Saskatchewan. Can. Field-Nat. 61: 71-100.

CODY, W. J. 1956. New plant records for northern Alberta and southern Mackenzie District. Can. Field-Nat. 70: 101-30.

COVILLE, F. V. 1901. The willows of Alaska. Proc. Wash. Acad. Sci. 3: 297-362.

DUTILLY, A , E. Lepage, & M. Duman. 1953. Contribution à la flore du bassin de la Baie d'Ungava. Contr. Arct. Inst. Cathol. Univ. Amer. 4: 1-104.

FERNALD, M. L. 1926. Two summers of botanizing in Newfoundland. Salix cordifolia Pursh. Rhod. 28: 181-88.

——. 1946. Technical studies on North American Plants. Rhod. 48: 27-38, 41-9.

—— 1950. Gray's manual of botany. Eighth ed.: 487-519.

FRANKLIN, JOHN. 1823. Narrative of a journey to the shores of the Polar Sea in the years 1819, 20, 21, and 22, with an Appendix on various subjects relating to science and natural history. London.

—— 1828. Narrative of a second expedition to the shores of the Polar Sea in the years 1825, 1826, and 1827, including an account of the progress of a detachment to the eastward by John Richardson. London.

GRØNTVED, JOHS. 1936. Vascular plants from arctic North America collected by the Fifth Thule Expedition, 1921-24. Rept. 5th Thule Exped. 2: 32-35. Copenhagen.

HOOKER, W. J. 1829-1840. Flora Boreali-Americana. London.

HULTÉN, ERIC. 1942. Flora of Alaska and Yukon. Lunds Universitets Årsskrift Avd. 2, Bd. 39. No. 1, Part 3: 498-554.

—— 1949. Flora of Alaska and Yukon. Lunds Universitets Årsskrift Avd. 2, Bd. 39. No. 1, Part 10: 1732-3.

JORDAL, L. H. 1951. A floristic and phytogeographic summary of the southern slopes of the Brooks Range, Alaska. Unpublished Ph.D. thesis, Univ. of Michigan.

MOSS, E. H. 1953. Forest communities in northwestern Alberta. Can. Jour. Bot. 31: 212-52, 448-70.

POLUNIN, N. 1940. Botany of the Canadian Eastern Arctic. Part 1. Pteridophyta and Spermatophyta. Nat. Mus. Can. Bull. 92: 1-408.

PORSILD, A. E. 1943. Materials for a flora of the continental Northwest Territories of Canada. Sargentia 4: 1-79.

—— 1945. The alpine flora of the east slope of the Mackenzie Mountains, Northwest Territories. Nat. Mus. Can. Bull. 101: 1-35.

—— 1951. Botany of southeastern Yukon adjacent to the Canol Road. Nat. Mus. Can. Bull. 121: 1-400.

—— 1955. The vascular plants of the western Canadian Arctic Archipelago. Nat. Mus. Can. Bull. 135: 1-226.

—— 1957. Illustrated flora of the Canadian Arctic Archipelago. Nat. Mus. Can. Bull. 146: 1-209.

PURSH, F. 1814. Flora Americae Septentrionalis. I: 1-358, II: 359-751. London.

RAUP, HUGH M. 1931. Salix glauca L. and its allies in the Athabasca —Great Slave Lake region. Rhod. 33: 241-44.

—— 1934. Phytogeographic studies in the Peace and upper Liard River regions, Canada, with a catalogue of the vascular plants. Contr. Arn. Arb. 6: 1-230.

—— 1935. Botanical investigations in Wood Buffalo Park. Nat. Mus. Can. Bull. 74: 1-174.

—— 1936. Phytogeographic studies in the Athabaska — Great Slave Lake region, I. Catalogue of the vascular plants. Jour. Arn. Arb. 17: 180-315.

—— 1942. Additions to a catalogue of the vascular plants of the Peace and upper Liard River regions. Jour. Arn. Arb. 23: 1-28.

—— 1943. The willows of the Hudson Bay region and the Labrador Peninsula. Sargentia 4: 81-127.

—— 1947. The botany of southwestern Mackenzie. Sargentia 6: 1-275.

SCHNEIDER, CAMILLO. 1918-21. Notes on American willows. I. Bot. Gaz. 66: 117-142 (1918), II. ibid., 66: 318-353 (1918), III. ibid., 67: 27-64 (1919), IV. ibid., 67: 309-346 (1919), V. Jour. Arn. Arb. 1: 1-32 (1919), VI. ibid., 1: 67-97 (1919), VII. ibid., 1: 147-171 (1920), VIII. ibid., 1: 211-232 (1920), IX. ibid., 2: 1-25 (1920), X. ibid., 2: 65-90 (1920), XI. ibid., 2: 185-204 (1921), XII. ibid., 3: 61-125 (1921).

SCOGGAN, H. J. 1957. The Flora of Manitoba. Nat. Mus. Can. Bull. 140: 1-580.

SPETZMAN, L. A. 1951. Plant geography and ecology of the arctic slope of Alaska. Unpublished M.S. thesis, Univ. of Minnesota.

RYDBERG, P. A. 1899. The cespitose willows of Arctic America and the Rocky Mountains. Bull. N. Y. Bot. Gard. 1: 257-278.

—— 1901. In contributions to the botany of Yukon Territory, Pt. 4: An enumeration of the flowering plants collected by R. S. Williams and J. B. Tarleton. Bull. N. Y. Bot. Gard. 2: 149-87.

—— 1922. Flora of the Rocky Mountains and adjacent plains. 2nd Edition 1-1144. New York.

—— 1932. Flora of the prairies and plains of central North America. 1-969. New York.

SPORANGIA OF THE FERN GENERA ALLIED WITH POLYPODIUM AND VITTARIA[1]

KENNETH A. WILSON

The structure of the mature sporangium, particularly the nature and orientation of the annulus, has frequently been illustrated and has long been used as the principal taxonomic character of the families of the ferns (e.g., Lindley, 1830; Mohl, 1845; Mettenius, 1856; Sadebeck, 1898). The status of most of the families has remained relatively unchanged since the middle of the nineteenth century, and there appears to be general agreement about their distinctness and composition.

With the appearance of Bower's series of morphological papers and, ultimately, the publication of the three volumes of "The Ferns" (1923, 1926, 1928), the "family" *Polypodiaceae* was interpreted as being a polyphyletic taxon comaposed of heterogeneous groups. Bower's phylogenetic approach to the problem of fern classification and the evidence showing the diverse origins of the groups in the *Polypodiaceae* served as an impetus for a complete re-evaluation of this "family." This led to the appearance of four systems of classification of the ferns within a period of eleven years. They began with Christensen's scheme in the "Manual of Pteridology" (1938), which was fairly conservative. The authors of the other, more radical, systems are R. C. Ching (1940), R. E. Holttum (1947, 1949), and E. B. Copeland (1947). (For an outline of the four systems of fern classification, see A. G. Stokey, 1951.)

The confusion which now exists in the classification of the *Filicales* and more specifically in the large assembly of the *Polypodiaceae* may perhaps, in spite of cries of discouragement, prove to be valuable in itself. Comparatively little is known about the biology of the ferns. Our knowledge of their morphology is based to a large extent on Bower's works. Little new morphological work has been published since the 1930's, with the exception of Wagner's comprehensive study of *Diellia* (1952a). The present status of fern taxonomy demands that new research in this group be directed towards a more thorough understanding of the ferns themselves, as has been pointed out by Holttum

---

[1] Part of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

(1954) and Wagner (1954a). Only with the accumulation of new evidence can a truly phylogenetic system of classification be approached.

Only a few significant strides have been made in this direction. Among the contributions are the outstanding works of Manton (1950 *et seq.*) on the cytology of ferns, and of Stokey (1951 *et al.*) and Stokey and Atkinson (1952 *et seq.*) on the gametophyte generation. Morphological, anatomical, and cytological evidence has been used by Wagner (1954b) in unraveling the interrelationships of the Appalachian aspleniums. Haider (1954) has made a valuable contribution to filling the gap in our knowledge of the morphology of the mature leptosporangium.

The present study is limited to a consideration of the sporangium of genera of the *Polypodiaceae* and *Vittariaceae* as defined by Copeland in 1947. The systematic treatments of the plants that make up this assemblage vary considerably. Christensen (1938) placed these and a number of other groups in the *Polypodiaceae*, and treated these as the subfamilies *Vittarioideae, Dipteroideae,* and *Polypodioideae,* (which he said may be better dealt with as families). Ching (1949) considered them as comprising eight families: *Antrophyaceae, Vittariaceae, Loxogrammaceae, Cheiropleuriaceae, Dipteridaceae, Platyceriaceae, Polypodiaceae,* and *Grammitaceae* (*sic*). Holttum (1947) segregated them into the *Polypodiaceae* and *Grammitidaceae* and placed the *Vittarioideae* in the *Adiantaceae*. Copeland (1951), in his monograph of *Grammitis*, apparently on the additional strength of unpublished evidence from the gametophytes, recognized the *Grammitidaceae* and stated that "there is no reasonable doubt that the group should have family status."

Very little is known about the sporangia of most of these ferns. Bower (1915) described and illustrated the sporangia of *Dipteris, Cheiropleuria,* and *Platycerium*. He concluded that the sporangia of *Dipteris* and *Cheiropleuria* are closely alike, particularly in the four-rowed stalk, and that the three genera are related, although *Platycerium* is the most specialized. In 1928, Bower included descriptions of the sporangia of *Christiopteris, Neocheiropteris, Hymenolepis,* and *Pleopeltis*, and found them essentially similar (see also Bower, 1917). The sporangia of *Vittaria*, however, he described as having a four-celled stomium, with a two-celled, thin-walled epi- and hypostomium, and the sporangial stalk as "one-celled at the base, but more massive upwards." The sporangia of *Monogramme, Antrophyum, Hec-*

istopteris, and *Anetium* are all like that of *Vittaria*. Copeland (1947) listed these same sporangial characters in his description of the *Vittariaceae*.

Goebel (1924) placed great emphasis on the structure of the sporangium in determining relationships in the vittarioid complex. He reported that the sporangium of *Pleurogramme* (= *Cochlidium*) is so distinct that it can be immediately distinguished from those of the *Vittariaceae*. After an investigation of the sporangia of *Xiphopteris* and *Adenophorus* (= *Amphoradenium*) he concluded that, on the strength of the sporangial morphology in addition to other evidence, *Pleurogramme* should be removed from the *Vittariaceae* and placed with *Xiphopteris* and *Adenophorus*.

One of the few other references to the sporangium of a member of the *Grammitidaceae* was made by Copeland (1951), who described the sporangial stalk of *Grammitis* as being of "mostly a single row of cells."

Haider (1954), in his comparative survey of the mature sporangia of various fern families, illustrated the capsules of only nine members of the *Polypodiaceae*. He described the sporangium of the *Polypodiaceae* (*sensu* Copeland, 1947) as having two stomial cells with a several-celled epi- and hypostomium. Of most significance, an invagination occurs between the stomial cells; the epi-and hypostomial cells are swollen. (See, also, Goebel, 1924.) The sporangial stalk received only cursory mention in Haider's paper. His results show that the sporangia of *Dipteris* and *Cheiropleuria* are distinctly different from those of the other so-called *Polypodiaceae*, whereas those of *Platycerium* agree with them in all respects.

The structure of the mature sporangium has been of value in studies of ferns in families not included in the scope of this paper. For instance, Wagner (1952a), after comparison of davallioid, lindsaeoid, and asplenioid sporangia, concluded that those of *Diellia* closely resemble those of the *Aspleniaceae*. Schnarf (1904) had earlier pointed out the differences of the sporangia of *Asplenium*, *Phyllitis*, and *Ceterach* from those of *Athyrium* and *Diplazium*. One of the primary bases for the establishment of the family *Negripteridaceae* by Pichi-Sermolli (1946) was the structure of the sporangium.

Haider (1954) pointed out several interesting results of his comparative study. He wrote that the sporangia of the *Pteridaceae* (excluding the *Dicksoniaceae*) fall into two groups corresponding to Bower's Gymnogrammoid and

Pteroid ferns. The sporangia of the genera of the *Davalliaceae* agree closely with each other, while those of the genera of the *Blechnaceae* which he examined differ considerably one from the other.

Considerably less work has been done on the nature and the systematic value of paraphyses in comparative studies than on the sporangia. A valuable contribution to our knowledge of paraphyses was made by Pirard in 1947. Fifty-one different species of ferns were examined by her, and she reported that most of the structures interpreted by various authors as "transformed sporangia" have nothing to do with the spore-producing organs. However, *Vittaria scolopendrina* was shown to possess secretory structures which are truly transformed sporangia. Of value also in Pirard's paper is a systematic listing of the presence of paraphyses in the ferns as indicated in the literature by various authors.

The value of paraphyses in systematic studies and as a guide to fern phylogeny is not yet known. The Hawaiian relatives of the genus *Ctenopteris* have been segregated by Copeland (1947) as the genus *Amphoradenium* on the basis of the presence of clavate, glandular paraphyses within their sori. A study has been made of the paraphyses of *Polypodium virginianum* by Martens (1943, 1949) and Martens and Pirard (1943). Simple-stalked or branching glands were found in *P. virginianum*, and their presence was said to furnish a clear-cut distinction between that species and *P. vulgare*. Further studies indicated that these glands were in reality aborted or transformed sporangia (Martens and Pirard, 1943).

An unusual situation is presented by Copeland (1947), who, on the one hand, recognized the genus *Amphoradenium* on the single morphological basis of the paraphyses, yet, on the other hand, included with the genus *Polypodium* species with (1) no paraphyses, (2) filamentous paraphyses, (3) clathrate peltate paraphyses, and (4) stellate paraphyses.

ACKNOWLEDGEMENTS

During the course of this investigation I was greatly aided by the guidance of Dr. Warren H. Wagner, Jr.; I owe special thanks to him for his patient and helpful directions and criticisms. Dr. C. A. Arnold, Dr. Marston Bates, Dr. F. G. Gustafson, Dr. R. J. Lowry, and Dr. Rogers McVaugh have read the manuscript and offered valuable suggestions; I am indebted to them for their efforts in my behalf. Dr.

Rogers McVaugh has also generously made available to me the facilities of the Herbarium of the University of Michigan. Much of the material used in this investigation was collected during an expedition by me to Jamaica, B. W. I., in 1954. I am deeply grateful to Dr. Grady L. Webster, Professor H. H. Bartlett, and Professor Richard A. Howard for making this expedition possible. I am indebted also to Mr. George R. Proctor and Mr. C. B. Lewis, of the Institute of Jamaica, whose assistance made my trip more profitable. The Botanical Gardens of the University of Michigan has assisted me not only in helping finance the Jamaican expedition but also in supplying materials on which some of these studies are based. To Mrs. Nancy Bell Bates I owe special thanks for her aid in the preparation of the manuscript.

TERMINOLOGY

Much inconsistency has prevailed throughout the years with respect to the terminology used to designate the various parts of the sporangium. Haider (1954) reviewed the terminology and proposed a more precise definition of some of the loosely used and misused terms, and, in addition, introduced a few valuable new ones. (See also Renner, 1955.)

The annulus may be complete (i.e., a complete ring) and have all of its cells thickened, as in *Gleichenia*, or it may be complete but only partially indurated so that a few of its cells are thin-walled, as in *Loxsoma*. (Cf. Bower, 1923.) In either case, the term "annulus" refers to all of the cells in the "ring," whether or not they are indurated. The term "ring" has, in fact, frequently been used as a synonym for "annulus." The polypodiaceous sporangium has an incomplete ring; that is, the annulus is interrupted by the stalk. To differentiate the thin-walled cells of the annulus from the thick-walled cells, I follow Haider's example and call the series of thick-walled cells the "bow" (Haider's "Bogen") and the thin-walled region the "stomial region."

The "stomium" proper is found within the stomial region, and is characterized by the presence of cells which have thicker walls than those above or below it, although never as thick as the cells of the bow. As shown by Haider, in sporangia whch have more than two stomial cells, as in *Vittaria*, only two function in initiating the dehiscence of the capsule by separating from each other. These are distinguished from the other stomial cells as the "separation cells" (Haider's "Trenn-" or "Saumzellen"). The cells below the stomium are referred to as the "hypostomium," while the thin-walled cells between the bow and the stomium may be called the "epistomium."

The two sides of the sporangium are distinctly different in their cellular construction, and a series of terms has been used to differentiate them. Haider equated the terms in this manner: "Stielseite=proximale (basale)=infraanulare=bisuturale, Deckseite=distale (peripherische)=supraanulare=unisuturale Seite."

I question Haider's choice of "infraanulare—supraanulare" in preference to others. He does not explain how one can distinguish the "upper" and "lower" sides of the sporangium in the *Polypodiaceae*. The same problem would arise were we to select "stalk side—cover side." "Bisutural—unisutural" are also confusing terms and do not correctly portray the real condition in the sporangium. We are then left with "proximal" and "distal." These terms appear to be the most suitable. The proximal face of the sporangium includes the entire upper portion of the first capsular segment, while the distal face is composed of the second and third segments (Cf. Wilson 1958a and 1958b). Even these terms may be criticized on the same basis as the others, but I hesitate to suggest any new terms at this time. A really satisfactory designation for the capsular faces cannot be proposed until our knowledge of the morphology of the sporangia of the so-called "primitive leptosporangiate ferns" has been extended and correlated with facts concerning the sporangia of higher ferns.

MATERIAL AND METHODS

This comparative study of the mature sporangium is based on an examination of fifty-eight species of ferns from forty-nine different genera of the *Polypodiaceae* and *Vittariaceae* as defined by Copeland. His (1947) treatment of the genera of ferns is the most comprehensive of the recent revisions, and therefore Copeland is followed as a matter of convenience. The number of genera included in my study totals approximately 65 percent of all those included by him in the above-named families. Because of the intimate association of paraphyses with sporangia, these also have been included. It is to be regretted that it was not possible to study all genera in these families. The difficulties of obtaining material of the missing genera, in view of the fact that most of them are monotypic and frequently rare in collections, forced their exclusion. It is hoped that these will be added to the material contained herein as more complete collections become available.

The sporangia of all but two of the species examined are illustrated. A careful search was made for the presence of paraphyses in each species and, when present, these have also been illustrated. It may be significant to note that paraphyses have been found in many species in which they had not been reported, or were previously reported as being absent.

Except in a few cases where preserved material was available, all studies were made from herbarium specimens. Since, in drying, the sporangia shrink and become distorted it was not possible to study them directly from the herbarium sheets. However, it was found that by boiling the sori for about a minute in 5 percent sodium hydroxide and then carefully dissecting out the sporangia the cells of the stalk and capsule became clearly visible.

In order that my identifications may be verified, specimens of all material used are available at the Herbarium of the University of Michigan, or, in rare circumstances, in other indicated herbaria.

All illustrations are camera lucida drawings made from temporary water mounts of the sporangia. For each species both the proximal and distal face of the sporangium are illustrated. The stalk, because of its extreme length, is seldom shown in its entirety. When it is important, however, the stalks are fully illustrated. In other cases, the following system has been followed: the upper portion of two-rowed stalks is generally illustrated to include the base of the third row beneath the capsule. One-rowed stalks are shown from the bottom of the two- and three-rowed portion. Open lines at the lower end of the portion of the stalk shown indicate that the same condition exists in the stalk from its insertion to the portion illustrated. Thus, if the stalk is shown as ending in a single open row of cells, it is then one-rowed to its base, et cetera. Occasionally it has been difficult to illustrate the stalk correctly because of distortions in the material. However, when this was so, a correct illustration of the stalk may always be found in one of the two views of the sporangium.

With a knowledge of the ontogeny of the sporangium, each of the original sporangial segments may be distinguished in the illustrations (cf. Wilson, 1958a and 1958b). In view of the potential significance of the sporangium in comparative morphology it is felt that without an accurate illustration of each sporangial face no valid conclusions can be drawn. This, unfortunately, is a shortcoming of most illustrations of the sporangium. Haider, who criticized inaccuracies of earlier illustrations, himself fell short in figuring only one side and in incorrectly picturing the cell arrangement of many sporangial faces.

MORPHOLOGICAL OBSERVATIONS

There appears to be little constancy in the size of the sporangia. Differences in the dimensions of the capsule occur between genus and genus, but there seems to be no significance in this variation. Haider (1954) has pointed out that sporangia may vary in their size and shape within a single sorus. Of the genera included in this study, *Anarthropteris* (Pl. 5, figs. J_3 and J_5) and *Loxogramme* (Pl. 5, figs. E-I) possess the largest capsules, which measure up to 300 microns in diameter. However, within the genus *Loxogramme,* sporangial capsules of different sizes are to be found. *Loxogramme lanceolata* (Pl. 5, figs. I_1 and I_2) and *L. chinensis* (Pl. 5, figs. G_1 and G_3) have large capsules with a diameter of 275 to 300 microns, while those of *L. brooksii* (Pl. 5, figs. H_1 and H_3) range from 200 to 250 microns. *Grammitis* (Pl. 4, figs. A-C), *Cochlidium* (Pl. 4, figs. D_1 and D_2), and *Hecistopteris* (Pl. 5, figs. C_1 and C_3) are among those genera which have small capsules which measure only 100 to 150 microns in diameter. Most of the other genera studied have capsules with an average diameter of 250 microns.

In shape, the capsule of all genera except those of the *Vittariaceae* is ellipsoidal or biconvex. Those of the *Vittariaceae* are spherical. In some genera such as *Pessopteris* (Pl. 2, figs. C_1 and C_2), *Neocheiropteris* (Pl. 2, figs. F_1 and F_2), and *Prosaptia* (Pl. 4, figs. I and J) the capsule is greatly elongated, while in the sporangia of other genera the length of the sporangial face is only slightly greater than the width. Haider described the length-width ratio of the sporangium of *Pessopteris* as being 3:2; this agrees with my measurements.

THE SPORANGIAL FACES

The proximal and distal faces of the sporangium may be easily recognized. The proximal face may be distinguished by the characteristic four cells in the upper portion of Segment I (e.g, Pl. 1, fig. D_1). In addition, only one of the rows of the stalk leads into this face. On the other hand, two of the rows of the stalk lead into the distal face, and by following the line between the two rows Segments II and III may be easily located.

Except for *Dipteris* and *Cheiropleuria* the cell arrangement in the sporangial faces of the genera studied is essentially similar. Some genera have a greater number of cells contributing to the sporangial faces, but their arrangement reflects the ontogeny of the sporangium (e.g., *Ananthacorus*: Pl. 5, figs. D_1 and D_2). There appears to be no reason to doubt that the development of these capsules follows the same pattern of those of *Phlebodium* (Wilson, 1958a), *Xiphopteris*, and *Pyrrosia* (Wilson, 1958b). The great similarity of the cell arrangement in the sporangial faces in these genera indicates that this is so.

Dipteris (Pl. 1, figs. A_1 and A_3) and *Cheiropleuria* (Pl. 1, figs. B_1 and B_3) have a cell arrangement in the sporangial faces that distinguishes them not only from each other but also from all other sporangia studied. It is not possible for me to homologize the sporangial faces of these two genera with those of the other genera investigated. There is no doubt that their ontogeny is different. Bower (1915) suggested that they develop from the initial by an opposite, two-rowed segmentation, but he did not describe the development of the capsule. The differences of the sporangial faces of the two genera are striking, but, for a clearer understanding of their structure, the ontogeny of their sporangia should be studied in detail.

A few genera have sporangia which bear hairs arising from the cells of the sporangial faces. *Polypodium plumula* (Pl. 1, figs. E_1 and E_2) produces short hairs which arise from the cells of the distal face. A few sporangia of this species are naked and others may have up to five hairs, but more frequently each sporangium bears only two or three.

The hairs on the sporangia of *Pessopteris* have been frequently described. The two extremes have been figured here: one sporangium with thirteen hairs (Pl. 2, fig. C_1) and another with none (Pl. 2, fig. C_2).

The sporangium of *Ctenopteris exornans* bears an extremely long seta (Pl. 4, fig. H_2). Occasional sporangia may be found to be naked; less frequently they bear two setae.

THE ANNULUS

Dipteris (Pl. 1, figs. A_1 and A_3) and *Cheiropleuria* (Pl. 1, figs. B_1 and B_3) are the only two genera which have an oblique and complete annulus. All of the other genera studied have a vertical ring which is interrupted by the stalk. Furthermore, the sporangia of *Dipteris* do not have a well-defined stomial region: almost all cells of the ring are indurated, although the cells opposite the stalk are usually thinner-walled. Copeland (1947) described the stomium of *Dipteris* as "ill developed." *Cheiropleuria*, on the other hand, has a clearly differentiated stomial region.

The Bow

Although the number of bow cells varies within a single species, there is a general tendency for this variation to fall within a certain range, and usually one particular count occurs more frequently than any other. Wagner (1952a) reported the range and the average of the number of bow cells in the species he examined. Haider (1954), however, indicated the range and the most frequently occurring count of the cells rather than the average. Haider's method of recording the counts seems to be the better one; even though, except in unusual circumstances, the most frequently occurring count would probably not vary greatly from the mean. Table I presents the range and most frequent count (italics) of bow cells in ten sporangia of most of the species examined in this study.

Haider counted the bow cells of seven species of the *Polypodiaceae*, including *Platycerium bifurcatum* and *Cyclophorus* [*Pyrrosia*] *winkleri*, and concluded that "die Zahl der BZ [Bogenzellen] bei den *Polypodium*-Arten nahezu konstant 14 beträgt." As may be seen from Table I, there is a tendency for most species of the *Polypodiaceae* to have about fourteen bow cells, but there is no suggestion of constancy, even in the genus *Polypodium*.

The greatest number of bow cells was found in the sporangia of *Cheiropleuria*, in which the count of nineteen was found to occur as frequently as twenty-four. The sporangia with the smallest number of bow cells were those of *Grammitis graminea*; in this species the number ranged from seven to ten, with ten being the most common.

Colysis elliptica shows an unusual condition in the induration of the cells of the annulus. Frequently one of the cells of the hypostomium may be found to have its walls thickened in the same manner as the bow cells (Pl. 3, fig. E_1). Only rarely do two hypostomial cells become indurated (Pl. 3, fig. E_2). Most sporangia, however, are normal, and all hypostomial cells are thin-walled (Pl. 3, fig. E_4).

Table I

COMPARISON OF NUMBER OF BOW CELLS*

Dipteris conjugata	10 — *12* — 14
Cheiropleuria bicuspis	18 — *19* — *24* — 27
Platycerium andinum	17 — *18* — — 20
Polypodium plumula	*14* — 15
P. vulgare	12 — *15* — *17* — 19
Goniophlebium persicifolium	*12*
Thylacopteris papillosa	*12*
Dictymia attenuata	14 — *16* — 21
Pleopeltis thunbergiana	*13* — *14*
Microgramma lycopodioides	12 — *13* — *14* — 16
M. piloselloides	14 — *15* — 16
Solenopteris bifrons	13 — *14*
Marginariopsis wiesbaurii	14 — 15
Campyloneurum phyllitidis	14 — *15*
Pessopteris crassifolia	13 — *14* — 17
Phlebodium aureum	*13*
Eschatogramme furcata	12 — *13* — 15
Paltonium lanceolatum	13 — *14*
Neocheiropteris phyllomanes	*14* — 15
Lemmaphyllum microphyllum	*14* — 17
Weatherbya accedens	*14*
Belvisia spicata	*14* — *15*
Pyrrosia nuda	17 — *18* — 23
Pteropsis piloselloides	17 — *18* — 19
Microsorium punctatum	*14* — 15
M. scolopendria	*14*
Leptochilus axillaris	13 — *14* — 15
Colysis elliptica	14 — *16* — 17
Dendroglossa cantoniensis	11 — *14* — 15
Pseudodrynaria coronans	*14*
Drynaria propinqua	12 — *14*
Lecanopteris carnosa	11 — *13*
Crypsinus hastatus	*14* — 15
Grammitis graminea	7 — 8 — *9*
G. marginella	9 — *10* — 13
G. trifurcata	13 — *14*
Cochlidium graminoides	*9* — *10*
Scleroglossum minus	*12* — 13
Xiphopteris serrulata	8 — 9 — *10*
Calymmodon cucullatus	*12* — 13
Ctenopteris exornans	12 — *13* — 14
Amphoradenium sarmentosum	11 — *12* — 13
Prosaptia contigua	11 — *12* — 14
P. linearis	11 — *12* — 13
Loxogramme brooksii	13 — *14* — 15
L. chinensis	*13* — 15
L. lanceolata	*14* — *15* — *16* — 17
L. salicifolia	11 — *13*
L. conferta	*13* — 14

*The first and last figures represent the range in the number of bow cells per sporangium for each species, while the figure or figures in italics indicate the most frequent count.

Anarthropteris dictyopteris	14 — 15
Antrophyum reticulatum	13 — *14* — 15
Anetium citrifolium	*10* — 11
Polytaenium lineatum	12 — *14* — 15
Scoliosorus ensiformis	13 — *15* — 16
Hecistopteris pumila	17 — *20* — 23
Vittaria remota	17 — *20*
Ananthacorus angustifolius	13 — *14*
Vaginularia paradoxa	17 — *18* — 19

The Stomial Region

The greatest degree of variation in the structure of the capsule occurs in the stomial region. In *Dipteris* (Pl. 1, figs. A_1 and A_3) the stomial region is not differentiated from the bow, while *Cheiropleuria* (Pl. 1, figs. B_1 and B_3) possesses a well-defined stomial region with three stomial cells and usually three epistomial and three hypostomial cells.

The sporangia of all species of the *Polypodiaceae* and *Grammitidaceae* examined are remarkably similar in the structure of the stomial region. All have two stomial cells clearly separated from the bow by thin-walled epistomial cells and with a well-defined hypostomium. The epistomium is generally three-celled, although in some cases it was found to be two-celled (e.g., *Polypodium plumula*: Pl. 1, fig. E_1), or four-celled (e.g., *Polypodium vulgare*: Pl. 1, fig. D_1). The epistomium of *Platycerium* (Pl. 1, figs. C_1 and C_2) typically consists of four cells, while that of the species of *Loxogramme* (Pl. 5, figs. F-I) ranged from three cells (Pl. 5, fig. H_1) to as many as six cells (Pl. 5, figs. E_3 and I_1). The stomium of all sporangia examined in these two families was seen to have the characteristic invagination between the stomial cells described by Haider. Unfortunately, not all illustrations show this condition since many sporangia were drawn after the separation of the stomial cells. Nevertheless, examination of other sporangia showed this invagination clearly, and it is evident in the sporangia well before the cells of the bow become thickened. This condition may be clearly seen in the illustration of the proximal face of *Belvisia* (Pl. 2, fig. I_1). Other figures show the stomium from slightly different angles which frequently obscures this feature.

In sharp contrast to the stomial region of the above families, that of the members of the *Vittariaceae* has a four-celled stomium (e.g., *Scoliosorus*: Pl. 4, figs. N_1 and N_2), an epistomium of typically two cells, and a one- to three-celled hypostomium. Only in rare cases are there only three stomial cells present (e.g., *Vaginularia*: Pl. 5, fig. B_2). There is no invagination to be found between any of the stomial cells of this group.

THE SPORANGIAL STALK

The sporangial stalk was found to be composed of one, two, three, or four rows of cells. The stalks of *Dipteris* (Pl. 1, figs. A_1 and A_3) and *Cheiropleuria* (Pl. 1, fig. B_1 and B_3) are four-rowed, but they are not identical to each other. That of *Dipteris* is elongated and is formed by four regular rows of cells. (Only two of the rows may be seen in each view of the sporangium.) *Cheiropleuria*, however, has a more massive stalk which becomes constricted at the base of the capsule. The arrangement of cells does not always appear to be as regular as it is in *Dipteris*. The sporangial ontogeny of these two genera is in need of investigation, since earlier reports are questionable.

Three-rowed stalks (not figured) may be found in *Platycerium*, *Marginariopsis*, and *Pyrrosia* (Wilson 1958b), but they are rare. Generally their sporangial stalks are two-rowed except at the base of the capsule where they become three-rowed.

Two-rowed stalks are frequent and have been observed in all members of the *Polypodiaceae sensu stricto*. An unusual condition is seen in the stalk of *Dictymia* (Pl. 1, figs. H_1 and H_2), which has a single small cell at the base of the two-rowed stalk.

The sporangia of the ferns included by Copeland (1951) in the *Grammitidaceae* generally have a stalk which is one-rowed at the base, but there are a few notable exceptions. *Prosaptia contigua* (Pl. 4, figs. I_1 and I_2) has a stalk that is two-rowed almost at the very base. The basal one-rowed portion varies in length in different sporangia, but in general consists of a single basal cell. On the other hand, the stalk of *Prosaptia linearis* (Pl. 4, figs. J_1 and J_2) is one-rowed for most of its length and does not differ from the others in this family.

The species of *Loxogramme* possess a sporangial stalk which is usually one-rowed only at the base. Most frequently the one-rowed portion consists of two cells (Pl. 5, fig. F_1). The stalks of *L. brooksii* (Pl. 5, figs. H_1 and H_3) and particularly of *L. lanceolata* (Pl. 5, figs. I_1 and I_2) are very irregular. That of *L. lanceolata* may be two-rowed at the base, but the rows of cells do not conform to the sporangial segmentation that has been described in my earlier papers (Wilson 1958a and 1958b). The irregular arrangement of cells seems to indicate that vertical divisions may take place during stalk formation. Similar irregular stalks are found in *Anarthropteris* (Pl. 5, figs. J_3 and J_4). In this genus there is no doubt that vertical divisions do occur in the formation of the stalk : vertical walls have been found in the basal cell of young sporangia (Pl. 5, figs. J_1 and J_2). *Loxogramme lanceolata* and *Anarthropteris dictyopteris* are the only ferns examined that show evidence of vertical intercalary divisions in the stalk.

The sporangia of all species of *Vittariaceae* agree in having a sporangial stalk that is one-rowed at the base. This conforms with Bower's (1928) and Copeland's (1947) observations.

PARAPHYSES

Many of the species of ferns examined bore paraphyses. The most commonly encountered type was a simple hair composed of two to six cells. This type is found in *Eschatogramme* (Pl. 2, fig. D_2), *Paltonium* (Pl. 2, fig. E_2), *Leptochilus* (Pl. 3, fig. D_2), and many other genera (see especially Plate 3). The stalked clathrate scale was also frequently found (e.g., *Pleopeltis*: Pl. 1, fig. I_3; *Marginariopsis*: Pl. 2, fig. A_2). These clathrate paraphyses are either peltate (Pl. 1, fig. I_3) or laterally affixed (Pl. 2, fig. H_2), and frequently both types are found in the same sorus (Pl. 2, figs. I_3 and I_4).

Stellate paraphyses are associated with the sporangia of *Platycerium* (Pl. 1, fig. C_2), *Pteropsis* (Pl. 3, fig. A_3), and *Pyrrosia* (Wilson, 1958b). *Microgramma lycopodioides* bears branched filamentous paraphyses (Pl. 1, fig. K_2), while *M. piloselloides* has clathrate, laterally affixed ones (not figured).

Except for *Anetium* and *Polytaenium*, which bear no paraphyses, each genus of the *Vittariaceae* has a type entirely different from the others.

All species of *Loxogramme* bear multicellular, filiform paraphyses (Pl. 5, figs. E_2, F_2, G_2, H_2, and I_2). Those of *Anarthropteris* are long, multicellular, and composed of two or three rows of cells (Pl. 5, fig. J_4); Copeland (1947) suggests that they may be metamorphosed sporangia.

Still other types are found in *Dipteris* (Pl. 1, fig. A_2), *Cheiropleuria* (Pl. 1, fig. B_2), *Goniophlebium* (Pl. 1, fig.

F_4), *Solenopteris* (Pl. 1, fig. J_1), and *Ctenopteris* (Pl. 4, fig. H_3).

Aborted, tannin-filled sporangia in various stages of development were observed in *Polypodium plumula*, *Eschatogramme*, *Pseudodrynaria*, *Crypsinus*, *Selliguea*, and *Prosaptia contigua*.

DISCUSSION OF THE SIGNIFICANCE OF SPORANGIAL MORPHOLOGY TO FERN TAXONOMY

During the last several decades it has been the general practice to describe the sporangia of the so-called "advanced leptosporangiate ferns" as being simply of the "polypodiaceous type." With this, all sporangia which are stalked and possess an erect annulus were considered to be fundamentally similar. From the facts presented in the previous section, it is shown that the parts of the sporangia of different fern groups are by no means identical in their structure. The morphology of the sporangium can be used as a valuable guide to indicate generic interrelationships, and may serve in clarifying the status of problematic genera and species.

The sporangia of the vittarioid genera stand out as the most distinct and easily recognizable group among those included in this study. These sporangia are characterized by having four stomial cells, a thin-walled epi- and hypostomium, and a one-rowed sporangial stalk.

There has been very little disagreement with respect to the composition of the *Vittariaceae*. Ching (1940) was the only one who divided this assemblage into two families. This he did on the basis of the structure of the spores, but both types of spores he used as the basis of separation are known to occur in a single genus, as in *Vittaria*. On the basis of the number of bow cells in the sporangium, Ching's division receives some support. The genera which he places in the *Antrophyaceae* generally have about fourteen bow cells, while those he places in the *Vittariaceae*, *sens. str.*, have twenty. One may question, however, the significance of the number of bow cells in classification, since their number appears to be so variable. In all other respects the sporangia of the genera of the *Vittariaceae*, *sens. lat.*, are very similar to each other.

Another distinguishing characteristic of the *Vittariaceae*, as pointed out by Stokey (1951), is in the gametophyte, which she said is "sharply distinct from that of any other known higher fern." The morphological distinctness of the sporophyte was discussed by Goebel (1924).

Manton and Sledge (1954) reported that the *Vittariaceae* might be placed with *Adiantum*, as was suggested by Holttum (1947), "without doing violence to the cytology." However, very little is known about the sporangium of *Adiantum*. Haider (1954) illustrated the capsule of *A. peruvianum* and showed three stomial cells. (Unfortunately the stalk was not figured.) But three stomial cells are rare in vittarioid sporangia, and a single incomplete drawing is insufficient for adequate comparison. Surprisingly little is known about the gametophyte of *Adiantum* (Stokey, 1951). Much more work is needed in the pteroid ferns before we can arrive at any conclusion in this problem. Suffice it to say that Copeland's treatment of the *Vittariaceae* is well supported by the evidence from the sporangium.

The sporangia of *Dipteris* and *Cheiropleuria* do not show any indication that these genera are closely related or even remotely allied to the polypodioid ferns. A four-rowed condition of the stalks is not in itself evidence of relationship, particularly when these stalks differ from each other. The structure of the capsule of the one genus is different from that of the other. Haider (1954) has already stressed these differences. The removal of the two genera from the *Polypodiaceae*, and their placement in two separate families as done by Ching, is now supported by the structure of the sporangium as demonstrated in the present investigation. Evidence from the gametophyte as reported by Stokey (1945) and Stokey and Atkinson (1945a) also justifies this treatment. Wagner (1952b) found that the combination of characters in the sporophyte of *Cheiropleuria* supports the establishment of the family *Cheiropleuriaceae*. Manton (1954) reported that the "n" number of chromosomes is "c. 33." This is significantly different from that of the typical *Polypodiaceae* which ranges around thirty-seven. On the basis of this accumulated evidence, the recognition of the families *Dipteridaceae* and *Cheiropleuriaceae* is now strongly justified.

Ching placed *Platycerium* in the isolated family *Platyceriaceae*. The sporangial structure does not, however, justify this action. The sporangia of *Platycerium* do not differ in any fundamental respects from those of the other members of the *Polypodiaceae*. Haider has reported that there is "kein Zweifel, dass die Gattung mit *Polypodium* verwandt ist." I can only emphasize his conclusion. Stokey and Atkinson (1954b), in a study of the gametophytes of five species of *Platycerium*, also found no evidence to justify the family *Platyceriaceae*. Manton and Sledge (1954) have shown that cytologically this genus agrees with other members of the *Polypodiaceae*. Wagner (1952b) reported on other similarities of *Platycerium* to the polypodiaceous genera *Pleopeltis* and *Pyrrosia*. The evidence is unusually clear and detailed that *Platycerium* is rightly placed in the *Polypodiaceae*.

Most recent authors agree that the grammitid ferns are distinct from the *Polypodiaceae*. Whereas the sporangia of the members of the two groups are remarkably similar in the structure of the capsule, the one-rowed stalk clearly distinguishes the *Grammitidaceae* from the *Polypodiaceae*. The sporangia of both families have a capsule with an erect annulus which is interrupted by the stalk. In both, the stomial region is clearly differentiated and possesses two stomial cells and a thin-walled epi- and hypostomium. Both have a deep invagination between the two stomial cells. However, the stalk of the *Polypodiaceae* is two-rowed at the base, while that of the *Grammitidaceae* is one-rowed.

The problematic species *Polypodium plumula*, which shows some characters in common with the grammitid genus *Ctenopteris*, has a two-rowed stalk, and on this basis its inclusion in the *Polypodiaceae* is supported.

The significance of the single cell at the base of the stalk of *Dictymia* is uncertain. This may be the result of the orientation of the first oblique wall in the sporangial initial which may not quite reach the level of the receptacular cells. Additional investigations may indicate that the typical two-rowed polypodiaceous stalk may also sometimes occur in this genus. Nevertheless, the presence of a single small cell at the base of the stalk is at present not considered to be significant in this genus. An investigation of the nature of the first division of the sporangial initial would help clarify the problem. There seems to be no question on any other grounds about the position of *Dictymia* in the *Polypodiaceae*. Perhaps an exception may be found in the statement of Ching, who placed the genus *Dictymia* in the *Polypodiaceae* but commented: "The genus rather belongs to *Loxogrammaceae* with which it agrees very well in venation, habit and leaf texture." The significance of this statement is not clear to me, and such an association has not been suggested by others. Moreover, Ching's inclusion of *Anarthropteris dic-*

tyopteris in this genus is not supported by evidence from the sporangium.

The three-rowed stalk is rare in the *Polypodiaceae* and has been found only in a very few individual sporangia out of a two-rowed majority in three different species.

The sporangia of *Prosaptia contigua* are peculiar in the structure of their stalk. They do not agree with the typically grammitid stalk of *P. linearis*. This may be a result of abnormal development. The abundance of aborted sporangia is the sori of *P. contigua* indicates this may be the case.

The genus *Loxogramme* has turned out to be a problematic one from the standpoint of sporangial structure. It has been placed in the *Polypodiaceae* by Holttum, in the *Grammitidaceae* by Copeland, and in its own family, *Loxogrammaceae*, by Ching, who considered it closely related to the vittarioid ferns. Christensen (1938) treated it as "a distinct genus of very doubtful relationship, perhaps related to *Grammitis*, but in vegetative characters not unlike *Hymenolepis* [*Belvisia*] and *Paltonium*." A widely divergent view has recently been expressed by Nayar (1955) who suggested that *Loxogramme* be placed in the *Pteridaceae* and considered a derivative of the "*Syngrammoid*" ferns. The structure of the sporangia of *Loxogramme* does not agree entirely with either that of the *Polypodiaceae* or the *Grammitidaceae*. They differ from these families in having the basal one-rowed portion of the stalk composed of one or two cells and having generally five instead of three epistomial cells. Their sporangial stalk is difficult to interpret, and a study of the sporangial ontogeny is needed to clarify its structure. The stalks of *Loxogramme brooksii* and *L. lanceolata* only add to the confusion. I would tentatively suggest that *Loxogramme* may best be treated as a distinct family, but a more satisfactory treatment must await a comprehensive study of the genus.

The association of *Loxogramme* with *Syngramma* is dubious, at least from sporangial evidence. Nayar (1955) makes the following comparison: "The characteristic three-rowed stalk of sporangium, the average number of cells constituting the annulus [bow], and the stomium with protruding lip cells and separated from the stalk and annulus by unthickened cells, are also characters in common." The basal portion of the stalk of *Loxogramme*, however, is only one-rowed, and the three-rowed portion subtending the capsule cannot validly serve as a basis for comparison since this is characteristic of sporangia of the *Polypodiaceae, Grammitidaceae, Vittariaceae, Aspleniaceae etc.*, and reflects the ontogeny of the capsule (Wilson, 1958b). As has been shown, the number of bow cells is of questionable significance. Moreover, the sporangium of *Syngramma* has not been studied, nor have those of the other genera of the *Pteridaceae*.[2]

The gametophyte of *Loxogramme* is imperfectly known. Manton (1953) reported the chromosome number of the genus, but this still did not solve the problem of its relationship: cytological evidence indicates that it is not associated with the *Vittariaceae*, but places it in the polypodioid-grammitid complex; the chromosome numbers of the members of the *Polypodiaceae* and *Grammitidaceae* are not basically unlike.

The sporangia of Copeland's monotypic genus *Anarthropteris* present an equally perplexing problem. Copeland (1947) stated that "*Anarthropteris* seems most nearly related to *Loxogramme*," and placed it with the grammitid ferns. The sporangium is certainly not grammitid in its structure. The evidence of vertical intercalary walls during stalk development is unusual, although its significance is obscure. The primordial sporangium indicates that the first division is most likely transverse as in *Xiphopteris* (Wilson, 1958b). But again this is not conclusive evidence of relationship. The only resemblance of its sporangium to that of *Loxogramme* is in its stalk which, by a slight stretch of the imagination, might be compared to that of *L. lanceolata*. From the structure of the sporangium it appears that *Anarthropteris* does not belong either in the *Polypodiaceae* or the *Grammitidaceae*. Its association with *Loxogramme* is questionable. The actual affinities of this little known fern cannot be determined without further investigation.

On the basis of the structure of the paraphyses, there appear to be three major groups of genera in the *Polypodiaceae*. The first of these, including *Platycerium, Pyrrosia*, and *Pteropsis*, has stellate paraphyses and may be a closely related group of genera. Wagner (1952b) discussed the similarity of *Platycerium* to *Pyrrosia*, and Copeland (1947)

[2] Since this paper was prepared, a publication by A. Landmann (Beitrage zur Kenntnis der Verwandtschaftsverhaltnisse einiger Farngattungen Flora 125: 359-426. 1931) has come to my attention. Landmann described the sporangia of *Syngramma* as being short-stalked and possessing 2-4 elongated, narrow, brown stomial cells; a 2-3 celled epi- and hypostomium; and 15-20 bow cells. (The most common number of bow cells was 17 and 18.) On the basis of this description it seems even more doubtful that *Loxogramme* and *Syngramma* are closely related.

suggested that the affinity of *Pteropsis* is "manifestly to *Pyrrosia*."

Bower (1923) suggested that "it is but a step from . . . stellate hairs to a peltate scale with central attachment." It seems more likely in my opinion, however, that the peltate paraphyses are not derived from the stellate ones. The development of the stellate paraphyses (Wilson, 1958b) seems to be quite different from that of the peltate scale as described by Bower. *Pleopeltis, Marginariopsis, Lemmaphyllum, Neocheiropteris, Weatherbya,* and *Belvisia* all have peltate, clathrate paraphyses. The last three genera also have clathrate paraphyses which are laterally affixed; these are also found in *Microgramma piloselloides.* On this basis, these genera may represent, therefore, the second closely related group in the *Polypodiaceae.* Copeland (1947) also suggested this association.

The genus *Microgramma,* however, has species with different types of paraphyses. *Microgramma lycopodioides* has branched filamentous paraphyses. This suggests either that the genus is in need of revision or, as is more likely, the paraphyses are not always adequate indicators of relationship.

The third group might be composed of those genera having simple filamentous paraphyses. This would include *Eschatogramme, Paltonium, Microsorium, Leptochilus, Colysis, Dendroglossa, Pseudodrynaria, Lecanopteris, Selliguea, Arthromeris,* and *Phlebodium.* This assemblage of genera is not considered to be a closely related group by any author. Unbranched filamentous paraphyses may arise in many different ways, and without a precise knowledge of their origin they cannot point to interrelationships of species or genera.

The value of paraphyses as indicators of fern phylogeny is not known. What do the widely different types of paraphyses described in the species of *Polypodium* or *Microgramma* signify? Much more study is needed to solve this problem.

Alston (1956) suggested that *Stenochlaena* belongs in the *Polypodiaceae.* Copeland (1947) placed it in the *Blechnaceae,* while Holttum put it in the subfamily *Pteridoideae* of the *Dennstaedtiaceae.* Stokey and Atkinson (1952) found that its gametophyte has much in common with that of *Blechnum.* Manton and Sledge (1954) reported that the cytology of *Stenochlaena* does not conform very well with either Copeland's or Holttum's view. Cytological evidence gives support to Alston's placement of the genus in the *Polypodiaceae*. However, Haider (1954) examined the sporangia and said that in the structure of the stomial region they are very similar to those of the *Aspidiaceae*. The problem of the affinity of *Stenochlaena* thus also remains unsolved.

The sporangia of the rare Bornean fern *Holttumiella flabellifolia* are not known. Copeland reported that they are "apparently sessile." On the basis of this description and of the findings of the present investigation, there is some doubt about its placement in the *Polypodiaceae*.

Our knowledge of the sporangium of the genera of other fern families is meager. It is evident that the structure of the sporangium can contribute a great deal to our understanding of fern phylogeny. There is no doubt that the study of sporangial morphology can serve as important new evidence in fern taxonomy in a manner like that which has been demonstrated for the cytology and the gametophyte generation.

SUMMARY

The structure of the sporangia of fifty-eight species of ferns placed by Copeland in the *Polypodiaceae* and *Vittariaceae* is discussed and compared. It is shown that the structure of the sporangium can be used as a valuable guide in systematic studies of ferns.

On the basis of sporangial morphology, the *Vittariaceae* has been shown to be a distinct family. The families *Dipteridaceae* and *Cheiropleuriaceae* are justified by the sporangial structure. There is no evidence to support the recognition of a family, *Platyceriaceae*. The two-rowed stalk of the sporangia of the *Polypodiaceae* serves to distinguish them from those of the *Grammitidaceae* which are one-rowed. It is suggested that the genus *Loxogramme* be placed in a separate family. Both *Loxogramme* and *Anarthropteris* are in need of intensive investigation. Some probable taxonomic implications of paraphyses are discussed but their significance in phylogenetic studies remains obscure.

LITERATURE CITED

ALSTON, A. H. G. 1956. The subdivision of the Polypodiaceae. Taxon 5: 23-25.

BOWER, F. O. 1915. Studies in the phylogeny of the Filicales. V. *Cheiropleuria bicuspis* (Bl.), Presl, and certain other related ferns. Ann. Bot. 29: 495-529.

——. 1917. Studies in the phylogeny of the Filicales. VI. Ferns showing the "Acrostichoid" condition. Ann. Bot. 31: 1-29.

TABLE II
COMPARISON OF SPORANGIAL STRUCTURE WITH PROPOSED TAXONOMIC SYSTEMS[a]

SPORANGIA	GENERA[b]	CHRISTENSEN[c] *(1938)*	CHING *(1940)*	COPELAND *(1947)*	HOLTTUM *(1947, 1949)*	ASSEMBLAGE OF OTHER DISTINCTIVE CHARACTERS
Stalk 4-rowed; annulus complete; stomium undifferentiated.	*Dipteris*	Dipteridoideae	**Dipteridaceae**	Polypodiaceae	Polypodiaceae	Solenostelic stem; spores elliptic; gametophyte with thick midrib; $n = 33$.
Stalk 4-rowed; annulus complete; stomium well defined.	*Cheiropleuria*	Polypodioideae	**Cheiropleuriaceae**	Polypodiaceae	Polypodiaceae	Protostelic or solenostelic stem, spores tetrahedral; stipes nonarticulate; gametophyte narrowly cordate.
Stalk 2-rowed; annulus interrupted; stomium 2-celled.	*Platycerium*	Polypodioideae	Platyceriaceae	**Polypodiaceae**	**Polypodiaceae**	Dictyostelic stem; spores elliptic; stipes articulate; scales mostly clathrate; gametophyte cordate; $n = 36, 37$; leaf mainly reticulate-veined.
	Polypodium	Polypodioideae	**Polypodiaceae**	**Polypodiaceae**	**Polypodiaceae**	
	Goniophlebium	Polypodioideae	**Polypodiaceae**	**Polypodiaceae**	**Polypodiaceae**	
	Thylacopteris	—	—	**Polypodiaceae**	—	
	Pleopeltis	Polypodioideae	**Polypodiaceae**	**Polypodiaceae**	**Polypodiaceae**	
	Microgramma	Polypodioideae	**Polypodiaceae**	**Polypodiaceae**	—	
	Solenopteris	—	—	**Polypodiaceae**	—	
	Marginariopsis	Polypodioideae	**Polypodiaceae**	**Polypodiaceae**	—	
	Campyloneurum	Polypodioideae	**Polypodiaceae**	**Polypodiaceae**	—	
	Pessopteris	—	**Polypodiaceae**	**Polypodiaceae**	—	
	Phlebodium	Polypodioideae	**Polypodiaceae**	**Polypodiaceae**	—	

[a] Those families which are in bold face type are those treatments which are best favored by the evidence at present. Genera not specifically mentioned by an author are indicated by a dash.

[b] The genera are those included in this study and follow the treatment of Copeland (1947); synonyms and differing generic taxonomic treatments of the other authors are not indicated

[c] Christensen treats these fern groups as subfamilies of the Polypodiaceae in the very broad sense.

TABLE II (continued)

SPORANGIA	GENERA	CHRISTENSEN (1938)	CHING (1940)	COPELAND (1947)	HOLTTUM (1947, 1949)	ASSEMBLAGE OF OTHER DISTINCTIVE CHARACTERS
	Pseudodrynaria	Polypodioideae	Polypodiaceae	Polypodiaceae	—	
	Paltonium	Polypodioideae	Polypodiaceae	Polypodiaceae	—	
	Neocheiropteris	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Lemmaphyllum	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Weatherbya	—	—	Polypodiaceae	—	
	Belvisia	Polypodioideae	—	Polypodiaceae	Polypodiaceae	
	Pyrrosia	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Pteropsis	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Microsorium	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Leptochilus	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Colysis	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Dendroglossa	—	—	Polypodiaceae	—	
	Pseudodrynaria	Polypodioideae	Polypodiaceae	Polypodiaceae	—	
	Drynaria	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Lecanopteris	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Crypsinus	—	—	Polypodiaceae	—	
	Selliguea	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
	Arthromeris	Polypodioideae	Polypodiaceae	Polypodiaceae	Polypodiaceae	
Stalk 2-rowed; 1-celled at base; annulus interrupted; stomium 2-celled.	*Dictymia*	—	Polypodiaceae	Polypodiaceae	—	Dictyostelic stem; spores elliptic; stipes articulate; scales clathrate; leaf reticulate-veined.
Stalk 1-rowed; annulus interrupted; stomium 2-celled.	*Grammitis*	Polypodioideae	Grammitaceae	Polypodiaceae[d]	Grammitidaceae	Solenostelic stem; spores tetrahedral; stripes nonarticulate; scales nonclathrate;
	Cochlidium	Polypodioideae	Grammitaceae	Polypodiaceae[d]	Grammitidaceae	
	Scleroglossum	Polypodioideae	Grammitaceae	Polypodiaceae[d]	Grammitidaceae	

---

[d] The family Grammitidaceae was recognized by Copeland in 1951 and these genera were placed in it.

TABLE II (continued)

SPORANGIA	GENERA	CHRISTENSEN (1938)	CHING (1940)	COPELAND (1947)	HOLTTUM (1947, 1949)	ASSEMBLAGE OF OTHER DISTINCTIVE CHARACTERS
	Xiphopteris	—	—	Polypodiaceae[d]	**Grammitidaceae**	gametophyte elongate; n 36, 37; leaf mainly free-veined.
	Calymmodon	Polypodioideae	**Grammitaceae**	Polypodiaceae[d]	**Grammitidaceae**	
	Ctenopteris	Polypodioideae	**Grammitaceae**	Polypodiaceae[d]	**Grammitidaceae**	
	Amphoradenium	Polypodioideae	**Grammitaceae**	Polypodiaceae[d]	**Grammitidaceae**	
	Prosaptia	Polypodioideae	**Grammitaceae**	Polypodiaceae[d]	**Grammitidaceae**	
Stalk 1 row of 2 cells; annulus interrupted; stomium 2-celled.	*Loxogramme*	Polypodioideae	Loxogrammaceae	Polypodiaceae[d]	Polypodiaceae	Dictoyostelic stem; spores elliptic or tetrahedral; stipes nonarticulate scales clathrate; n 36.
Stalk irregular, 2- or 3-rowed; annulus interrupted; stomium 2-celled.	*Anarthropteris*	—	Polypodiaceae	Polypodiaceae[d]	—	Dictyostelic stem; spores elliptic; stipes nonarticulate; leaf reticulate-veined.
Stalk 1-rowed; annulus interrupted; stomium 4-celled.	*Antrophyum*	Vittarioideae	Antrophyaceae	**Vittariaceae**	Adiantaceae —	Protostelic or siphonostelic stem; spores elliptic or tetrahedral; stipes nonarticulate; scales clathrate; gametophyte elongate; n 30; laminar spicular cells; leaf mainly reticulate veined.
	Polytaenium	Vittarioideae	Antrophyaceae	**Vittariaceae**	Vittarioideae	
	Ananthocorus	Vittarioideae	Antrophyaceae	**Vittariaceae**	—	
	Anetium	Vittarioideae	Antrophyaceae	**Vittariaceae**	—	
	Hecistopteris	Vittarioideae	Vittariaceae	**Vittariaceae**	Vittarioideae	
	Vaginularia	Vittarioideae	Vittariaceae	**Vittariaceae**	—	
	Vittaria	Vittarioideae	Vittariaceae	**Vittariaceae**	Vittarioideae	
	Scoliosorus	—	—	**Vittariaceae**	—	

——. 1923. The Ferns. Vol. I. Analytical Examination of the Criteria of Comparison. 359pp. University Press, Cambridge, England.

——. 1926. The Ferns. Vol. II. The Eusporangiatae and other relatively primitive ferns. 344pp. University Press, Cambridge, England.

——. 1928. The Ferns. Vol. III. The Leptosporangiate Ferns. 306pp. University Press, Cambridge, England.

CHING, R. C. 1940. On natural classification of the family "Polypodiaceae." Sunyatsenia 5: 201-268.

CHRISTENSEN, C. 1938. Filicinae. In Fr. Verdoorn. Manual of Pteridology. Chapt. 20: 522-550. Martinus Nijhoff, The Hague.

COPELAND, E. B. 1947. Genera Filicum, the genera of ferns. 247pp. Chronica Botanica, Waltham, Mass.

——. 1951. *Grammitis*. Philipp. Jour. Sci. 80: 93-271.

GOEBEL, K. 1924. Archegoniatenstudien. XVI. Vittariaceen und Pleurogrammaceen. Flora **117**: 91-132.

HAIDER, K. 1954. Zur Morphologie und Physiologie der Sporangien Leptosporangiater Farne. Planta **44**: 370-411.

HOLTTUM, R. E. 1947. A revised classification of the Leptosporangiate ferns. Journ. Linn. Soc. (Bot.) **53**: 123-158.

——. 1949. The classification of ferns. Biol. Rev. **24**: 267-296.

——. 1954. The classification of ferns: The present position and some thoughts on future developments. Huitième Congr. Intern. Bot. Rapports & Communications. Sect. **2,4,5,6**: 5-8.

LINDLEY, J. 1830. An Introduction to the Natural System of Botany. 374pp. Longman, Rees, Orme, Brown and Greene, London.

MANTON, I. 1950. Problems of Cytology and Evolution in the Pteridophyta. 316pp. University Press, Cambridge, England.

——. 1953. The cytological evolution of the fern flora of Ceylon. Symp. Soc. Exper. Biol. VII, Evolution: 174-185.

——. 1954. Cytological notes on one hundred species of Malayan ferns. Appendix, in R. E. Holttum, A Revised Flora of Malaya. Vol. II. Ferns of Malaya. Botanic Gardens, Singapore.

MANTON, I., AND W. A. SLEDGE. 1954. Observation on the cytology and taxonomy of the Pteridophyte flora of Ceylon. Philos. Trans. Roy. Soc. London. B. **238**: 127-185.

MARTENS, P. 1943. Les organes glanduleux de *Polypodium virginianum* (*P. vulgare* var. *virginianum*). I. Valeur systématique et répartition géographique. Bull. Jard. Bot. Bruxelles **17**: 1-14.

——. 1949. Les organes glanduleux de *Polypodium virginianum*. III. Nouvelles données géographiques, systématiques et histologiques. Cellule **53**: 187-212.

MARTENS, P., AND N. PIRARD. 1943. Les organes glanduleux de *Polypodium virginianum* L. II. Structure, origine et signification. Cellule **49**: 385-406.

METTENIUS, G. 1856. Filices horti botanici Lipsiensis. Die Farne des botanischen Gartens zu Leipzig. 135pp. L. Voss, Leipzig

MOHL, HUGO VON. 1845. Morphologische Betrachtungen über das Sporangium der mit Gefässen versehenen Cryptogamen. In Vermischte Schriften botanischen Inhalts. L. F. Fues, Tübingen.

NAYAR, B. K. 1955. Studies in Polypodiaceae. III. *Loxogramme* (Bl.) Presl. Jour. Indian Bot. Soc. **34**: 395-407.

PICHI-SERMOLLI, R. 1946. Negripteridaceae e *Negripteris*, nuova famiglia e nuovo genere delle Filicales. Nuovo Giorn. Bot. Ital II. **53**: 129-169.

PIRARD, N. 1947. Sporanges, paraphyses, et organes connexes chez les fougères. Cellule **51**: 155-184.

RENNER, O. 1955. Bau und Funcktion des Ringes am Farnsporangium. Sitzs. Bayer. Akad. Wiss. math.-naturwiss. **1954**: 6-8.

SADEBECK, R. 1898. Pteridophyta. In Engler and Prantl. Die natürlichen Pflanzenfamilien 1(4): 1-91.

SCHNARF, K. 1904. Beiträge zur Kenntnis des Sporangienwandbaues der Polypodiaceae und der Cyatheaceae und seiner systematischen Bedeutung. Sitzs. Akad. Wiss. Wien, math.-naturwiss. **113**: 549-573.

STOKEY, A. G. 1945. The Gametophyte of *Dipteris conjugata*. Bot. Gaz. **106**: 402-411.

——. 1951. The contribution by the gametophyte to classification of the homosporous ferns. Phytomorphology **1**: 39-58.

STOKEY, A. G., AND L. R. ATKINSON. 1952. The gametophyte of *Stenochlaena palustris* (Brum.). Bedd. Phytomorphology **2**: 1-9.

——. 1954a. The gametophyte of *Cheiropleuria bicuspis* (Bl.) Presl. Phytomorphology **4**: 192-201.

——. 1954b. The gametophyte of five species of *Platycerium*. Phytomorphology **4**: 165-172.

WAGNER, W. H. JR. 1952a. The fern genius *Diellia;* its structure, affinities and taxonomy. Univ. Cal. Publ. Bot. **26**: 1-212.

——. 1952b. Types of foliar dichotomy in living ferns. Amer. Jour. Bot. **39**: 578-592.

——. 1954a. The evidence used in recent classifications of the ferns. Huitième Congr. Intern. Bot. Rapports & Communications. Sect. **2,4,5,6**: 9-15.

——. 1954b. Reticulate evolution in the Appalachian aspleniums. Evolution **8**: 103-118.

WILSON, K. A. 1958a. Ontogeny of the sporangium of *Phlebodium (Polypodium) aureum*. Amer. Jour. Bot. **45**: 483-491.

——. 1958b. Ontogeny of the sporangia in *Xiphopteris serrulata* and *Pyrrosia nuda*. Jour. Arnold Arb. **39**: 478-493.

PLATE I. Mature sporangia and paraphyses — Fig. A. *Dipteris conjugata* (Philippines: Gates 7663). — Fig. B. *Cheiropleuria bicuspis* (Ryukyu Is.: Walker & Tawada 6891). — Fig. C. *Platycerium andinum* (Peru: Klug 3872). — Fig. D. *Polypodium vulgare* ("in paeninsula Hel ad marem Balticum." Trela). — Fig. E. *Polypodium plumula* (Bermuda: Taylor 49-1163). — Fig. F. *Goniophlebium persicifolium* (Sumatra: Bartlett 8470). — Fig. G. *Thylacopteris papillosa* (Sumatra: Bartlett 6753b). — Fig. H. *Dictymia attenuata* (Australia: Simonds 1895). — Fig. I. *Pleopeltis thunbergiana* (Hawaiian Is.: Topping 3712). — Fig. J. *Solenopteris bifrons* (Colombia: Klug 1838). — Fig. K. *Microgramma lycopodioides* (Cuba: Jervis 1441B). In all cases the two faces of the sporangia are shown: paraphyses, when present, are also shown.

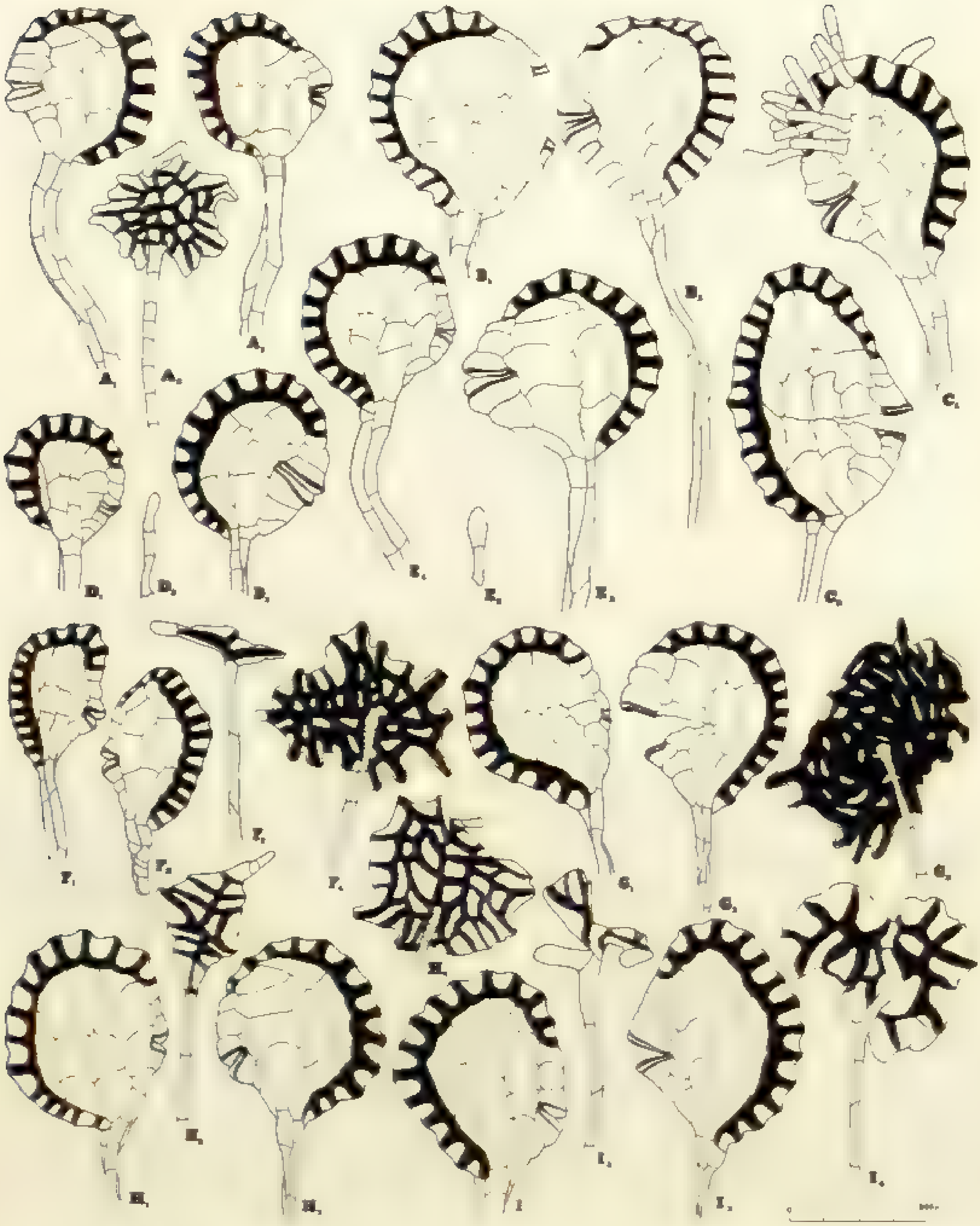


PLATE II. Mature sporangia and paraphyses. — Fig. A. *Marginariopsis wiesbaurii* (Costa Rica: Skutch 2637). — Fig. B. *Campyloneurum phyllitidis* (Univ. Mich. Bot. Gard. 14131). — Fig. C. *Pessopteris crassifolia* (Costa Rica: Scamman, March 1951). — Fig. D. *Eschatogramme furcata* (Haiti: Ekman 4714). — Fig. E. *Paltonium lanceolatum* (Dominica: Cooper III 92). — Fig. F. *Neocheiropteris phyllomanes* (China: Tsang 20875). — Fig. G. *Lemmaphyllum microphyllum* (China: Lau 835). — Fig. H. *Weatherbya accedens* (Sumatra: Boeea 6968). — Fig. I. *Belvisia spicata* (Sumatra: Bartlett 8004).

Plate III. Mature sporangia and paraphyses. —Fig. A. *Pteropsis piloselloides* (Indo-China: Clemens 3333). —Fig. B. *Microsorium punctatum* (Philippines: Copeland 1535). —Fig. C. *Microsorium scolopendria* (Hawaiian Is.: Scully 1017). —Fig. D. *Leptochilus axillaris* (Philippines: Steere). —Fig. E. *Collysis elliptica* (Okinawa: Walker & Tawada 5886). — Fig. F. *Dendroglossa cantoniensis* (China: Lau 3321). — Fig. H. *Drynaria propinqua* (Univ. Mich. Bot. Gard. 19978; Koelz 11716). —Fig. I. *Crypsinus hastatus* (China: Tak & Chow: Canton Christian College 13108). —Fig. J. *Lecanopteris carnosa* (Sumatra: Yates 2334). —Fig. K. *Selliguea feei* (Sumatra: Bartlett 7819). —Fig. L. *Arthromeris juglandifolia* (India: Duthie 6295).

Plate IV. Mature sporangia and paraphyses. — Fig. A. *Grammitis graminea* (Jamaica: Wilson & Murray 558). – Fig. B. *Grammitis trifurcata* (Jamaica: Wilson & Webster 534). Fig. C. *Grammitis marginella* (Jamaica: Wilson & Webster 609). Fig. D. *Cochlidium graminoides* (Jamaica: Proctor 5744; in the Herbarium of the Institute of Jamaica). – Fig. E. *Scleroglossum minus* (Philippines: Copeland PPE 78). Fig. F. *Calymmodon cucullatus* (Philippines: Steere). - Fig. G. *Amphoradenium sarmentosum* (Hawaiian Is.: Ozaki, preserved material only). — Fig. H. *Ctenopteris exornans* (Jamaica: Wilson & Rattenbury 649). Fig. I. *Prosaptia contigua* (Fiji; Degener 14857). Fig. J. *Prosaptia linearis* (Brit. N. Borneo: Topping 1715). – Fig. K. *Vittaria remota* (Jamaica: Wilson & Murray 584). Fig. L. *Anetium citrifolium* (Colombia: Haught 1886). Fig. M. *Antrophyum reticulatum* (Sumatra: Toroes 50). — Fig. N. *Scoliosorus ensiformis* (Mexico: Matuda 2907).

PLATE V. Mature sporangia and paraphyses. — Fig. A. *Polytaenium lineatum* (Jamaica: Wilson & Webster 468). Fig. B. *Vaginularia paradoxa* (Samoa: Yuncker 9070). — Fig. C. *Hecistopteris pumila* (Colombia: Haught 2080). Fig. D. *Ananthacorus angustifolius* (British Honduras: Gentle 3332). Fig. E. *Loxogramme salicifolia* (China: Tsang 26072). — Fig. F. *Loxogramme blumeana* (Sumatra: Yates 990). - Fig. G. *Loxogramme chinensis* (China: Lau 2413). — Fig. H. *Loxogramme brooksii* (Sumatra: Bartlett 7722). Fig. I. *Loxogramme lanceolata* (Philippines: Topping 429). Fig. J. *Anarthropteris dictyopteris* (New Zealand: Inverarity 1868).

THE SOMATIC CHROMOSOMES OF RUDBECKIA AND RELATED GENERA OF THE COMPOSITAE[1]

ROBERT E. PERDUE, JR.[2]

INTRODUCTION

The research reported in this paper is the outgrowth of a study that was directed primarily toward an understanding of the taxonomy and relationships of species of the genus *Rudbeckia*. Data on chromosome number and somatic chromosome morphology were obtained which reflect upon the relationships of species within the genus as well as upon relationships between *Rudbeckia* and related genera. While these data did not provide the primary basis for taxonomic judgment, they aided considerably in guiding the taxonomic approach and provided evidence which fully supports decisions based upon conventional morphological study. Study of the chromosomes of this genus indicated where the line should be drawn between 2 subgeneric groups and where the taxonomist should expect to find distinct morphological differences.

The fulfillment of the objective of the investigation called for a consideration of 3 additional genera, *Dracopis*, *Echinacea*, and *Ratibida*. Species of these three genera were at one time regarded as members of *Rudbeckia*. A number of them were originally described as species of *Rudbeckia;* others were transferred to that genus. Although most recent floristic manuals agree in treating *Echinacea* and *Ratibida* as separate genera, in the most recent edition of Gray's Manual, Fernald (1950) regarded *Dracopis* as a section of *Rudbeckia*. In the latest edition of Britton and Brown's Flora (Gleason, 1952), Cronquist treated *Dracopis* as a distinct genus. Battaglia (1952) expressed the opinion, based primarily on embryological data, that of these genera,

---

[1] Revised from a portion of a thesis submitted to the Department of Biology, Harvard University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. I am especially indebted to Dr. Reed C. Rollins under whose direction this study was conducted. A large portion of the work was completed during tenure as Associate Botanist, Texas Research Foundation, and was supported by a grant from the Caruth Foundation. During the early stages of the research, laboratory and greenhouse facilities were provided by Dr. Ronald Bamford, Department of Botany, University of Maryland. Grateful acknowledgement is extended also to the botanists who provided seed and plants for the cytological studies, both to those listed in the table of chromosome numbers and to those whose collections have not yet been used.

[2] U. S. Department of Agriculture, Agricultural Research Service, Crops Research Division, Beltsville, Maryland.

only *Echinacea* should be segregated from *Rudbeckia*. Morphologically these 4 genera can readily be distinguished from one another and these distinctions are supported by the cytological data presented in the present paper.

Rudbeckia is a genus of North America Compositae, Tribe Heliantheae. The 15 species form 2 very natural subgeneric groups, subg. *Rudbeckia* and subg. *Macrocline*, whose limits are morphologically very well defined, though a number of the characters which distinguish them are comparatively obscure. The morphological basis for the distinction of the 2 subgenera is discussed in detail in another paper (Perdue, 1958).

Rudbeckia subg. *Rudbeckia* includes 9 species, consisting of a total of 22 taxa (Perdue, 1957). The species are very distinct (morphological intergradation between species does not occur), so distinct that interspecific hybridization would not appear to be possible in most combinations even though the species were to be brought into contact. Most of the species of this subgenus occupy natural habitats in conjunction with 1 or more other species. Extensive field and herbarium studies have not revealed even the most remote suggestion of interspecific hybridization. Essentially, subg. *Rudbeckia* is a group of eastern North America species. Only a single taxon, *R. hirta* var. *pulcherrima*, is distributed generally beyond the eastern borders of the Great Plains. This common weed is found from southern Canada, through all the United States, into northern Mexico.

Rudbeckia subg. *Macrocline* includes 6 species, encompassing a total of 16 taxa (Perdue, 1958). In contrast to those of subg. *Rudbeckia*, the species of this group are very closely related. Morphological intergradation is not common, but this is apparently due to the restriction of the species to geographic areas well separated from the ranges of their close relatives. The occurrence of 2 species in the same habitat or even in the same county is rare. Several of the species of subg. *Macrocline* appear to be so closely related that hybridization might be expected were they to be brought together.

Although many species of *Rudbeckia* are well known, judging from the arrangement of species in floristic manuals the existence of 2 well-defined subgeneric groups has long gone unrecognized. This lack of recognition has been chiefly due to the existence in each subgenus of a single species with very narrow, grass-like leaves that are unlike those of any other species of the genus. The narrow-leaved

R. mohrii (subg. *Macrocline*) is distributed through a comparatively restricted area in western Florida and southern Georgia. The narrow-leaved *R. graminifolia* (subg. *Rudbeckia*) is a very narrow endemic restricted to a small area of western Florida within the geographic area of *R. mohrii.* Gray (1884) recognized the true relationships of most of the species of *Rudbeckia* but placed *R. mohrii* and *R. graminifolia* together and apart from their true relatives because of their unique, narrow leaves. The understandable failure to recognize the existence of the 2 subgeneric groups has persisted into our most recent floristic manuals.

MATERIALS AND PROCEDURE

A majority of the plants examined cytologically were grown in the greenhouse from seed. Other plants were collected in nature, potted and maintained in the greenhouse. Each lot of seed or of living plants was assigned an accession number. The culture numbers used in Table I reflect the accession numbers and in those cases in which 2 or more plants were grown from a single accession, they are distinguished by secondary numbers.

Considerable difficulty was experienced in germinating seed of most species of the 4 genera. Seed of the annuals (*Rudbeckia hirta, R. mollis, R. triloba* and *Dracopis amplexicaulis*) germinated without treatment in 5 to 7 days when placed on moist filter paper in a petri dish and maintained at room temperature. Seed of the other species failed to germinate after 2 weeks in petri dishes even after an initial over-night soaking in water. Difficulty in germinating seed of the perennial species appeared to be due to impermeability of the achene wall to moisture. When the achene walls were teased open with a needle, germination of seed of perennial and annual species occurred in 3 to 4 days. Removing the ovule completely from the achene did not decrease the time required for germination nor did it appear to increase the percentage of germination.

During the early stages of the work, several attempts were made to germinate seed on circles cut from ordinary paper towels rather than on filter paper. In each instance the cotyledons increased in size and turned green; the radicle of the embryo began to develop but soon turned brown and died. Apparently, a substance which acts as an inhibitor of root growth was present in the paper toweling.

About 5 to 7 days after the seed germinated, the young plants were of sufficient size to be handled. Twenty-five or more plants were transplanted from each petri dish to a large pot. Several weeks later, selected plants were transplanted to small individual pots.

Although seed could be germinated at any time of the year and at any stage after they matured, growth of young or mature plants was negligible during the winter. Murneek (1940) found that seedlings of a horticultural form of *Rudbeckia hirta* (as *R. bicolor* var. *superba*) grow very slowly during the fall and winter until about the middle of March, when the photoperiod increases to about 12 hours. At this time the leaves of the young rosette, extremely flat during the winter, assume a more upright position and vigorous growth begins. These observations seem to apply to all species of *Rudbeckia* that I have grown in the greenhouse. Although this factor was not studied closely, it appeared that the plants were essentially dormant, or at least very sluggish in growth, until the photoperiod reached a satisfactory length. Within a period of a few days after conditions became satisfactory for growth, leaves that had been flat or even drooping somewhat, raised slightly, and shortly new leaves began to develop. Root tips collected after this change were very vigorous and provided excellent material for study. Except on plants which became pot bound, vigorous root tips could be collected through the spring and summer up to the time when development of the flowering stalk was initiated. Root tips collected after this stage were few and most provided poor material for study.

The most satisfactory time of day for collection of root tips for cytological study was between 9 and 11 a.m., although vigorous material could be collected at any hour on comparatively cool days. Apparently, a daily cycle of significantly increased root growth does not occur in species of *Rudbeckia*.

Excised root tips were pretreated in colchicine and fixed in 1:3 acetic-alcohol. Squash preparations were made by a Feulgen-acetocarmine technique.

Slides were examined and suitable chromosome complements were photographed at a magnification of 1350x or 1425x. From each complement photographed, a diagram was made with a camera lucida, primarily for accurate identification of each negative. In these diagrams each chromosome was represented by a line conforming to the angle formed by the chromosome and in length proportional to it. In instances where it was considered that a constriction, observable to the eye, might not be clearly seen in the photograph, a short line showing the position of the constriction was placed across the line representing the chromosome. The diagrams were annotated as necessary to insure accurate interpretation of the photographs. These diagrams proved invaluable in properly interpreting certain photographs in which 2 or more chromosomes were close together or lying across one another.

Considerable difficulty was encountered in growing plants of subg. *Macrocline* to maturity; consequently voucher specimens were not obtained from many of the plants examined. Fortunately, all species and varieties of this subgenus are readily identified in the rosette stage and there is no doubt but that the determinations given are correct. Vouchers were obtained for most of the plants of subg. *Rudbeckia* examined. Available specimens will be deposited at the Gray Herbarium and in the herbarium of the Texas Research Foundation.

CHROMOSOME NUMBERS

During this study, chromosome numbers, obtained from mitotic metaphases in root tips, were determined for 88 plants representing all 6 species of *Rudbeckia* subg. *Macrocline*, 8 of the 9 species of *Rudbeckia* subg. *Rudbeckia*, and 4 species of the related genera *Dracopis*, *Echinacea*, and *Ratibida*. The only species of *Rudbeckia* not represented is *R. heliopsidis* (subg. *Rudbeckia*), a very rare species of the southeastern United States. For subg. *Macrocline* counts were made for a single variety of each species; for subg. *Rudbeckia*, counts were made for 14 of the 22 specific and subspecific taxa.

Chromosome numbers of *Rudbeckia*, *Dracopis*, and *Echinacea* previously reported in the literature are as follows:

Rudbeckia laciniata	n = 32-37	Fagerlind,	1946.
	2n = 76	Battaglia,	1946c.
R. laciniata var. flore pleno Hort.	2n = 38	Battaglia,	1946c.
R. bicolor (= *R. hirta*)	n = 19	Battaglia,	1946a.
R. flava (= *R. hirta*)	2n = 38	Battaglia,	1947.
R. hirta	n = 19	Battaglia,	1946a.
R. hirta var. meine Freude Hort.	n = 19	Battaglia,	1946a.
R. speciosa (= *R. fulgida* var.)	2n = 76	Battaglia,	1946b.
Dracopis amplexicaulis	n = 16	Battaglia,	1946a.
Echinacea purpurea	n = 11	Battaglia,	1946a.

Chromosome numbers determined during the present study, most of which are reported herein for the first time, are given in Table 1, along with culture numbers, and collector and place of collection.

TABLE I. CHROMOSOME NUMBERS IN RUDBECKIA AND RELATED GENERA

SPECIES	CULTURE NO.	2N	SOURCE
Rudbeckia subg. *Macrocline*			
R. californica var. *californica*	201-2	36	Above Rancheria Creek, ca. 1 mile east of Huntington Lake, Fresno, California. *C. H. Quibell.*
	202-2	36	Same source as 201-2.
	202-4	36	Same source as 201-2.
R. laciniata var. *laciniata*	4-2	72	Near Rock Hill Station, Bucks Co., Pennsylvania. *M. G. Henry.*
	4-3	ca. 72	Same source as 4-2.
	4-5	ca. 72	Same source as 4-2.
	4-8	102+	Same source as 4-2.
	28-1	54	Ca. 15 miles west of intersection of Routes 31 and 92, Mahnomen Co., Minnesota. *G. B. Ownbey.*
	28-2	36	Same source as 28-1.
R. maxima	225-1	36	Along Texas Route 64, 3.2 miles southwest of Myrtle Springs, Van Zandt Co., Texas. *R. E. Perdue, Jr.*
R. mohrii	205	36	0.9 mile west of junction of Routes 71 and 22, Wewahitchka, Gulf Co., Florida. *R. E. Perdue, Jr. 1399.*
	207-2	36	Same source as 205. *R. E. Perdue, Jr. 1400.*
	207-4	36	Same source as 205.
	208	36	Same source as 205. *R. E. Perdue, Jr. 1401.*
	214-1	36	Same source as 205.
R. nitida var. *texana*	224-1	36	1 mile southwest of Laporte, Harris Co., Texas. *R. E. Perdue, Jr.*
	224-2	36	Same source as 224-1.

	224-3	36	Same source as 224-1.
R. occidentalis var. *occidentalis*	57-1	36	Near Moran, Jackson Hole Wildlife Park, Teton Co., Wyoming. *C. L. Porter.*
	57-2	36	Same source as 57-1.
Rudbeckia subg. *Rudbeckia*			
R. fulgida var. *fulgida*	2-1	ca. 76	Near Naceville, Bucks Co., Pennsylvania. *M. G. Henry.*
	2-2	ca. 76	Same source as 2-1.
	6	ca. 76	Near Finland, Bucks Co., Pennsylvania. *M. G. Henry.*
	203-2	ca. 76	Salem Valley, 3 miles northeast of Ringold, Catoosa Co., Georgia. *R. E. Perdue, Jr. 1360.*
	253-1	38	About 2 miles northwest of St. Marks along road to Hyde Park, 1.6 miles from junction with Route 30, Wakulla Co., Florida. *R. E. Perdue, Jr. 1658c.*
	253-2	38	Same as 253-1. *R. E. Perdue, Jr. 1658d.*
R. fulgida var. *palustris*	55-2	38	3 miles northwest of Greeley, Reynolds Co., Missouri. *J. A. Steyermark.*
	236-1	38	Buffalo River region, 49 miles east of Fayetteville, near Ponca, Newton Co., Arkansas. *H. H. Iltis.*
	251-1	38	Along Turtle Creek near Upper Turtle Creek Road about 5 miles north of junction with Route 16, Kerr Co., Texas. *R. E. Perdue, Jr. 1861.*
	251-5	38	Same source as 251-1.
R. fulgida var. *speciosa*	40-1	ca. 76	*C. C. Deam.*
	40-2	77	*C. C. Deam.*
	72	ca. 76	Seed from a garden plant, the roots originally from Mitchell Co., Illinois.

			V. H. Chase.
	87	ca. 76	*E. Battaglia*
R. fulgida var. *umbrosa*	43-1	76	Seed from a garden plant. *C. C. Deam.*
	43-2	ca. 76	Same source as 43-1.
R. graminifolia	209	38	0.9 miles north of Route 22, 6.6 miles west of Wewahitchka, Gulf Co., Florida. *R. E. Perdue, Jr. 1408.*
	210	38	Same source as 209. *R. E. Perdue, Jr. 1408a.*
	211	38	Same source as 209. *R. E. Perdue, Jr. 1409.*
R. grandiflora var. *alismaefolia*	252-1	38	Near Route 146, 2 miles north of Seabrook, Harris Co., Texas. *R. E. Perdue, Jr. 1971.*
	252-4	38	Same source as 252-1.
R. grandiflora var. *grandiflora*	227-1	38	Along railroad right-of-way, near Route 70, 12 miles east of Hugo, Choctaw Co., Oklahoma. *R. E. Perdue, Jr.*
	227-2	38	Same source as 227-1.
	227-3	38	Same source as 227-1.
	227-5	38	Same source as 227-1.
R. hirta var. *angustifolia*	52-3	38	Navco, Mobile Co. Alabama. *G. N. Perdue.*
R. hirta var. *hirta*	18-1	38	Seed from herbarium specimen: about 3 miles west of Genesis, Tennessee. *F. W. W., R. E. S., and E. H. C. 14133.*
	22-1	38	Seed from herbarium specimen: 1.5 miles east of Tennessee City, Dickson Co., Tennessee. *R. E. S., F. W. W., and E. H. C. 14822.*
R. hirta var. *pulcherrima*	7-8	38	Harvard Forest, Petersham, Worcester Co., Massachusetts. *R. E. Perdue, Jr.*
	12-1	38	Avenel, Silver Spring, Maryland.

			D. S. Correll.
	12-2	ca. 38	Same source as 12-1.
	13-2	38	Seed from herbarium specimen: Benton Co., Tennessee. *T. Walker 16054.*
	13-3	38	Same source as 13-2.
	15-10	38	Along Route 50, just west of the bridge at Ocean City, Maryland. *R. E. Perdue, Jr.*
	15-11	38	Same source as 15-10.
	27-2	38	10 miles south of Grand Marais, Cook Co., Minnesota. *G. B. Ownbey.*
	30-1	38	Hamilton Co., Ohio. *E. L. Braun.*
	37-1	38	Illinois *H. E. Ahles.*
R. missouriensis	56-2	38	Massa Creek, south of Jonesburg, Warren Co., Missouri. *J. A. Steyermark.*
R. mollis	239	38	5.8 miles west of Ft. White (junction of Routes 27 and 47) along Route 27, Suwanee Co., Florida. *R. E. Perdue, Jr, 1663.*
	246	38	Near Route 20, 2.4 miles east of Hawthorne (junction of Routes 20 and 301), Putnam Co., Florida. *R. E. Perdue, Jr. 1817.*
R. subtomentosa	10-1	38	*C. C. Deam.*
	21-1	38	Seed from herbarium specimen: near Woodlawn School, Montgomery Co., Tennessee. *F. W. W., R. E. S., and E. H. C. 14415.*
	21-2	38	Same source as 21-1.
	35-3	38	Illinois. *H. E. Ahles.*
	45-1	38	*C. C. Deam.*
	46-1	38	Seed from a garden plant, original seed from 2 miles southeast of Mt. Carmel, Illinois, in Gibson Co., Indiana. *C. C. Deam.*
	46-2	38	Same source as 46-1.
	46-3	38	Same source as 46-1.

R. triloba var. *triloba*	1-4	57	*A. F. Blakeslee.*
	19-1	ca. 38	Seed from herbarium specimen: northeast of Morristown, Hamblen Co., Tennessee. *R. E. S., F. W. W., and E. H. C. 8830.*
	19-3	38	Same source as 19-1.
	20-1	38	Seed from herbarium specimen: bottoms of Turnbull Creek, near Craggie Hope, Cheatham Co., Tennessee. *R. E. S., E. H. C., and F. W. W. 14788.*
	26-1	ca. 57	Near Sturbridge, Worcester Co., Massachusetts. *R. E. Perdue, Jr.*
	26-2	57	Same source as 26-1.
	32-1	ca. 57	Hamilton Co., Ohio. *E. L. Braun.*
	32-2	ca. 57	Same source as 32-1.
	34-1	57	Illinois. *H. E. Ahles.*
	34-2	57	Same source as 34-1.
Dracopis amplexicaulis	126-1	32	Near Waco, McLennan Co., Texas. *M. P. Mauldin.*
	126-2	32	Same source as 126-1.
	126-6	32	Same source as 126-1.
Echinacea pallida	38	22	Illinois. *H. E. Ahles.*
	233-1	44	At junction of Coit and Huffines Road, ca. 2 miles west of Richardson, Dallas Co., Texas. *R. E. Perdue, Jr.*
	233-7	44	Same source as 233-1.
Ratibida columnaris	63-1	27	10 miles south of Scott City, Scott Co., Kansas. *L. & O. S. Fearing.*
	63-2	26	Same source as 63-1.
R. pinnata	31-2	28	Adams Co., Ohio. *E. L. Braun.*
	31-10	28	Same source as 31-2.

All species of subg. *Macrocline* are apparently diploid with a chromosome number of $2n=36$, except *R. laciniata* in which diploid, triploid, tetraploid, and possibly pentaploid plants were found. In reporting a tetraploid plant of *R. laciniata* as having 2n=76 chromosomes, Battaglia (1946c) was apparently misled by the fact that other *Rudbeckia* species that he studied do have a diploid number of 38.

All plants of *R. laciniata* var. *laciniata* from which chromosome counts were made were grown from seed. How well these plants would survive in nature is not known. Of the 6 plants examined, only the specimen with 102+ chromosomes did not grow vigorously in the greenhouse. There was no noticeable difference in vigor between other plants of the same culture. In this group of plants, only the triploid flowered. The pollen was highly variable in size and a large percent was aborted, as evidenced by its failure to take up a nuclear stain. An examination of pollen of numerous herbarium specimens of *R. laciniata* var. *laciniata* indicates that in nature well over a third of the plants have a large amount of aborted pollen that is highly variable in size. It appears that cytological instability, possibly due in part to polyploidy, is widespread in nature. Hybridization on the varietal level may have been a factor (Perdue, 1958).

In subg. *Rudbeckia* the diploid number is 38 and triploid and tetraploid plants also exist. The triploid nature of *R. triloba* var. *triloba*, a widespread plant of the eastern United States, is especially interesting. In this highly variable taxon, two extreme morphological forms can be distinguished between which intergradation is complete. Comparatively speaking, one form is a tall slender plant with small disks and pale-yellow rays. This type is most typical of collections from the southern states but is also common in the north. The second form has short stout stems, large disks, and dark orange-yellow rays. This form is rare in the south but is met fairly frequently in the north. The northern form resembles *R. triloba* var. *rupestris*, a very distinct variety collected only from several high mountains in a small area of western North Carolina.

The four triploid collections listed in Table I were grown from seed collected in the northern states and are fairly typical of the northern form. The two diploid collections from Tennessee are equally representative of the southern form. One can only speculate as to the origin of the cytogeographic pattern indicated by these data. As *R. triloba* is a highly distinct species, not closely related to any other species of *Rudbeckia*, it is unlikely that interspecific hybridization was a factor. On the other hand, it is quite possible that hybridization between var. *rupestris* and the typical southern form of var. *triloba* is responsible for the present existence of triploidy and the present morphological variation among the northern representatives of var. *triloba*.

R. fulgida is a highly polymorphic species with 7 varieties. Of the 4 varieties from which counts were obtained, tetraploid plants were found in all but one. It is perhaps more than coincidence that, for the species as a whole, the polyploid collections originated from localities more or less within the heart of the over-all area of distribution. In contrast, the diploid collections are all from areas that are at the periphery of the over-all distribution of the species. Although no locality data were available for the collection of var. *umbrosa*, this variety has so far been found only in an area that lies almost at the exact center of distribution of the species. *R. fulgida* is a very distinct species and it seems unlikely that its polyploid nature originated as a result of interspecific hybridization, but it may well have resulted from hybridization between varieties.

My counts agree with those reported by Battaglia (1946a) for *Dracopis amplexicaulis* ($2n=32$). A plant of *Echinacea pallida* from one source proved to be diploid ($2n=22$); plants from another source proved to be tetraploid ($2n=44$). The diploid number of this species agrees with the chromosome number reported by Battaglia for *E. purpurea*. In *Ratibida* apparent diploid numbers of 26 and 28 occur; one plant was aneuploid with 27 chromosomes.

CHROMOSOME MORPHOLOGY

Somatic chromosomes of the species of the 4 genera studied are comparatively numerous and though very variable in size they are quite large. The position of the primary constriction (centromere) is usually very clear and in well-spread figures can be observed in every chromosome. Secondary constrictions can occasionally be observed in species of *Rudbeckia*. Easily distinguished satellites appear only in chromosome complements of *Rudbeckia hirta* and *Ratibida*.

Morphology of the chromosomes of species of *Rudbeckia* and the 3 related genera was studied by use of the better photographs obtained from the plants listed in Table I. A number of these photographs are included as figures 1-23. This study is based upon a total of 37 photographs representing 18 species. There are included 6 species of *Rud-*

beckia subg. *Macrocline*, 8 species of *Rudbeckia* subg. *Rudbeckia*, 2 species of *Ratibida*, 1 species of *Dracopis* and 1 species of *Echinacea*.

With the exception of the chromosomes of *Echinacea pallida* and *Rudbeckia triloba*, all of the chromosome complements examined in the present study were diploid. The use of tetraploid complements of *Rudbeckia* species was impractical as there were usually many chromosomes that could not be accurately measured. As the data within each of the genera and subgenera are comparatively uniform, it is unlikely that analysis of polyploid complements would contribute anything new. For most of the species or varieties studied, 2 photographs were examined but in most cases these were from the same plant. For *Rudbeckia graminifolia* and *R. triloba*, single photographs were examined. Three photographs representing *Echinacea pallida* were studied.

The photographic records were made of cells in which the chromosomes were darkly stained and, with a few exceptions, sufficiently dispersed so that the length of each chromosome and the position of its primary constriction could be clearly seen. It was impossible to get perfect records in every instance, but there were never more than a few chromosomes in any photograph for which the length and constriction position could not be measured. From the negatives exposed at a magnification of 1350x or 1425x, photographic enlargements were prepared at a total magnification of approximately 4000 diameters. From these enlargements lengths of the chromosome segments were measured in millimeters. As the comparisons to be made are relative, the measurements are hereafter referred to as units.

Secondary constrictions were disregarded. In most cases they could not be seen. When they were apparent, they could usually be distinguished from the primary constriction. In a few cases, the 2 constrictions were equally prominent and it was necessary to compare the troublesome chromosome with the data from other photographs to determine which of the constrictions should be disregarded.

For each chromosome the total length was measured and from this a relative length was calculated by dividing the length of each chromosome by the average length of all of the chromosomes in its complement. This was designed primarily to eliminate variation in chromosome length between different materials resulting from slightly different treatments with colchicine, or differing response to the same colchicine treatment by different chromosome complements of the same root tip or collection of root tips from a single plant. Additional records made for each chromosome included measurements of the length of each of the 2 arms, and a value representing the position of the constriction obtained by dividing the length of the long arm by the length of the short arm. This method of obtaining a value for the constriction position was selected as it always yields a value of 1.0 or higher. Thus a value of 1.0 represents a chromosome with an exactly median constriction, whereas a value of 5.0 represents a chromosome which may be classified as subterminally constricted, the intermediate values representing chromosomes in which the constriction occurs at positions between these two extremes.

One of the major limitations in this study was the difficulty in obtaining sufficient data. When working with plants with such high chromosome numbers, it is difficult to obtain a large number of cells in which the chromosomes are sufficiently spread so that the length of each and the constriction position show up clearly. In studies of plants with lower chromosome numbers, where this difficulty is either not encountered or is not so great, this method of chromosome analysis could be carried much further.

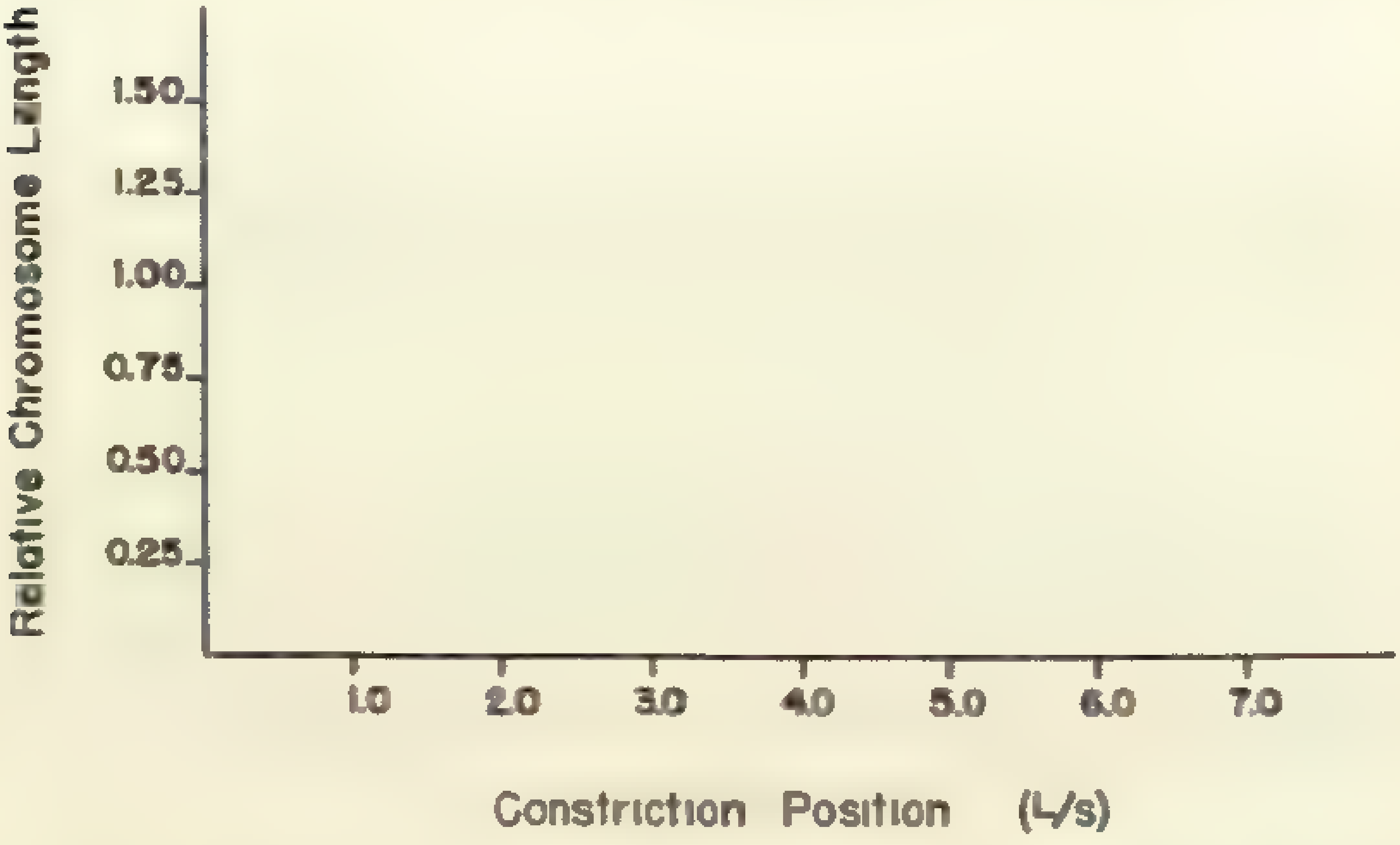
A number of errors were unavoidable even though good photographs were used and extreme care was exercised in making measurements. It is very difficult to get all the chromosomes in a cell in perfect focus in one photograph. Any chromosomes below or above the level of focus appears shorter than it does when in perfect focus. This affects the measurement of length and can affect the relative position of the constriction, especially in measurements of short chromosomes and in measurements of long chromosomes when only one end is out of focus. The error due to this source is believed to commonly be 0.5 unit and, as the error can involve both ends of a chromosome, the total error for a single chromosome can readily be 1.0 unit. In certain instances it was profitable to expose 2 or more negatives at different levels of focus in order to get more accurate measurements for the chromosomes lying above or below the level common to most members of the complement. Although the chromosome measurements were carefully made, there was some discrepancy between 2 independent sets of measurements from identical photographs. This type of error is much smaller than the type mentioned above and is not great enough to cause any appreciable concern. A third source of error is the differential shrinking of the chromosomes by colchicine. While this does not affect the relative position of the constriction it makes any comparisons of chromosome lengths difficult. In this study comparisons of chromosome lengths were for the most part unnecessary. During the course of the study, it was necessary to use two different microscopes, the optical system of one having a magnification of 1350x and that of the other a magnification of 1425x. This difference is so slight as to be relatively insignificant, especially since measurements of length played only an indirect part in interpretations of the data.

The data derived from the measurements of the chromosomes were organized in tabular form to show the total length of each chromosome, the relative length, the length of the long segment (L), the length of the short segment (S), and the value representing the position of the constriction (L/S).

The large number of chromosomes in each complement made a direct comparison of the tables very difficult. In this study, scatter diagrams proved most satisfactory for the demonstration of similarities or differences in karyotypes. This graphic method of presentation has several advantages. The data can be vividly presented without the need for setting up arbitrary classes for chromosome length or constriction position. The picture presented by each graph is as accurate as could possibly be obtained; facts, not possibly arbitrary interpretations, are presented. Furthermore, it is much easier to compare the chromosomes of one plant with those of another by study of the graphs than it is by study of the tables. Finally, patterns of variation in chromosome length or constriction position that can be observed in the tables or that are suggested by the tables are very clearly confirmed or denied by graphs.

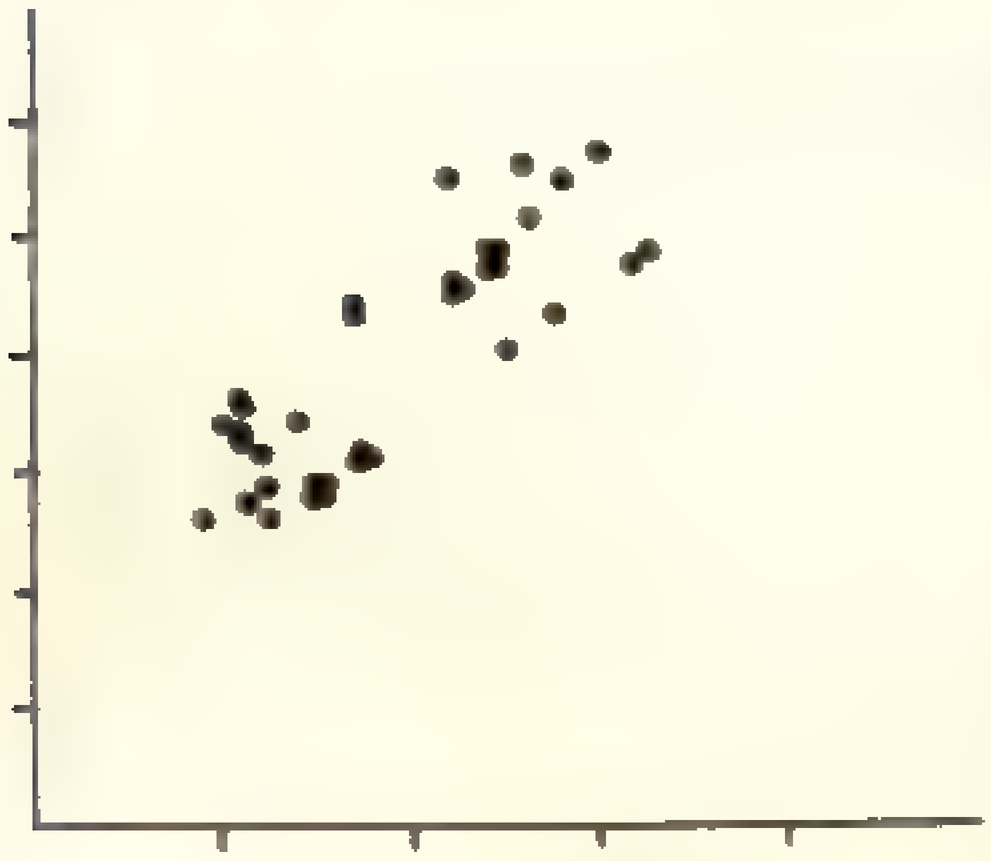
The data recorded in the tables were used to prepare the accompanying graphs. Graphs 1-12 pertain to species of *Rudbeckia* subg. *Macrocline* and Graphs 13-28 to species of *Rudbeckia* subg. *Rudbeckia*. *Dracopis* is represented by graphs 29 and 30, *Ratibida* by Graphs 31-34, and *Echinacea* by Graphs 35-37. Relative chromosome length is plotted along the vertical axis and L S, the value representing the position of the constriction, is plotted along the horizontal axis. Two or more chromosomes of a complement of equal length and with constrictions in the same position are represented on the graphs by the appropriate number of dots grouped closely around the correct point. This representation is judged to present a truer impression of the complement than would be obtained if only a single dot was used. For example, if a single dot is used to represent duplicate measurements, 20 chromosomes cannot be adequately portrayed on Graph 27 and 16 chromosomes cannot be adequately portrayed on Graph 28. The following diagram indicates the numerical measurements used along the ordinate and abscissa in Graphs 1 to 37.

Graphs 1-12 illustrate details of chromosome morphology for all 6 of the species of *Rudbeckia* subg. *Macrocline*. The species are similar in gross chromosome morphology and a very definite pattern is established for this subgenus. The chromosomes can be readily divided into 2 natural groups of 18 chromosomes each. One group includes comparatively small chromosomes more or less medianly constricted (L S values mostly 1.8 or less); the other includes comparatively large chromosomes the constrictions of which range from submedian to a condition approaching subterminal (L S values mostly 1.7 or greater). Differentiation of the chromosomes into 2 groups is not so distinct in the graphs representing *R. californica* (Graphs 1 and 2) but is very distinct in the graphs representing the other 5 species.

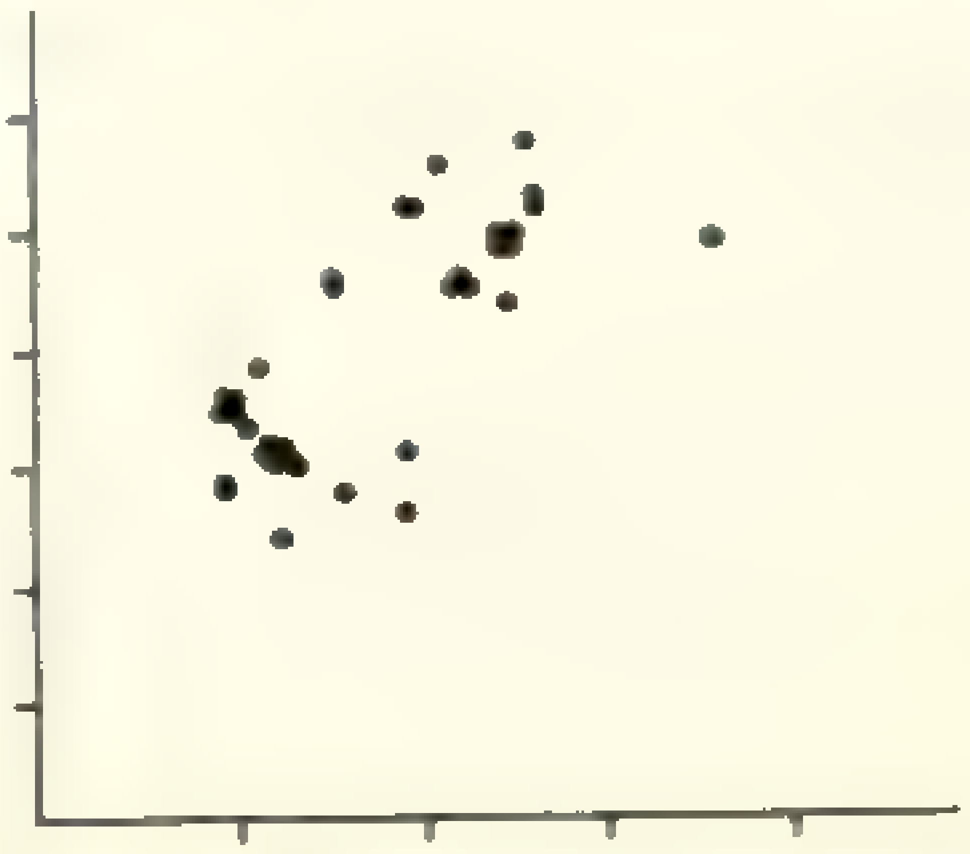


From the standpoint of general morphology and geographic distribution it is very clear that *R. californica* and *R. occidentalis* are more closely related to one another than either is to another pair of closely related species, *R. max-*

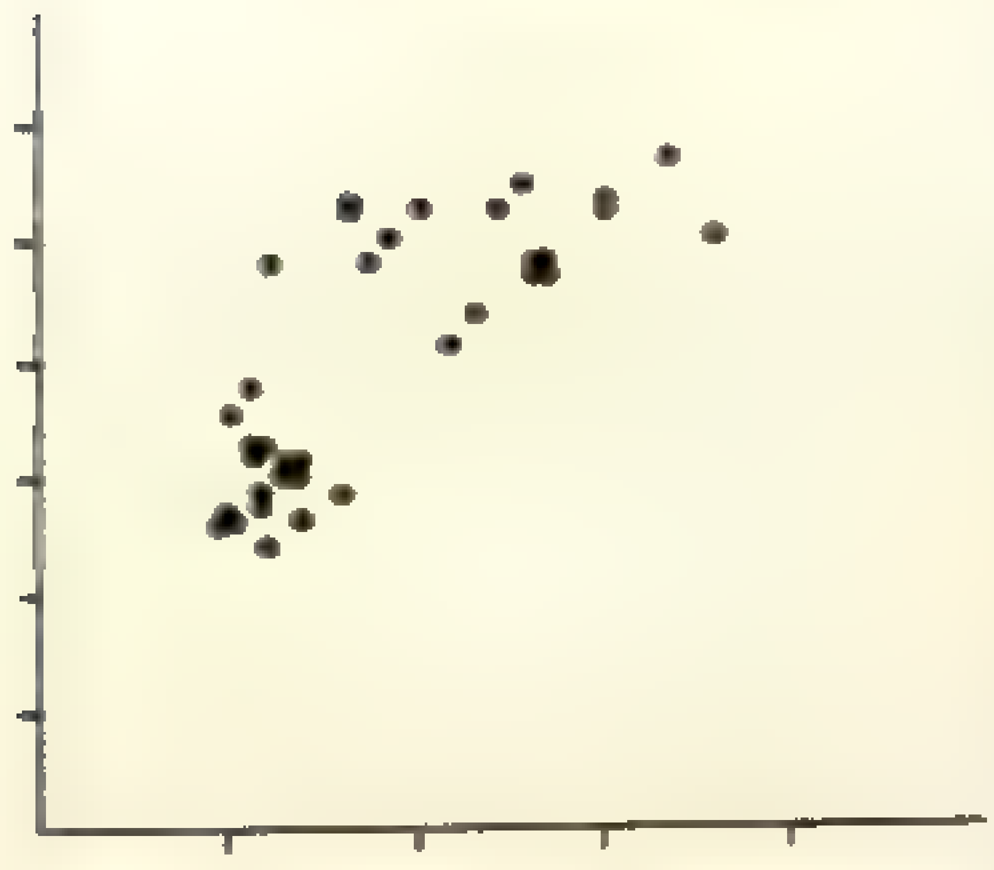
ima and *R. nitida*. The first 2 species are even more distantly related to *R. mohrii*, the morphological extreme of the subgenus. If significant differences do occur between individual species or species-groups within subg. *Macrocline* such differences would be expected to show up in a comparison of



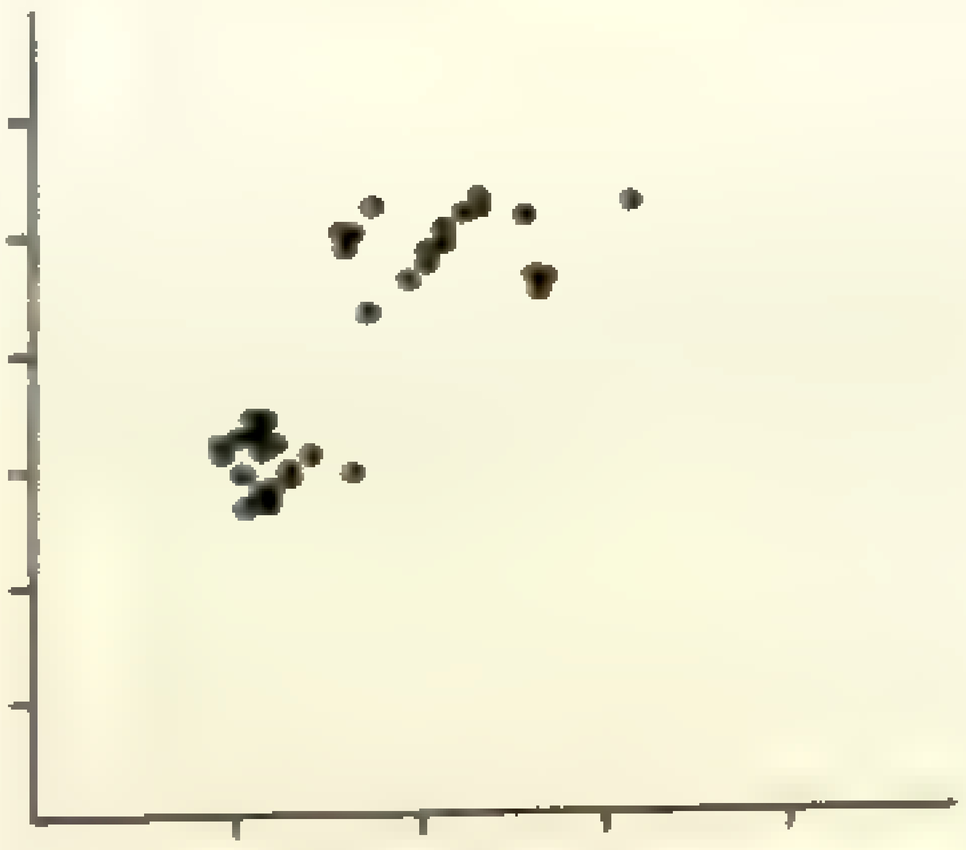
Graph I. Rudbeckia californica var. californica



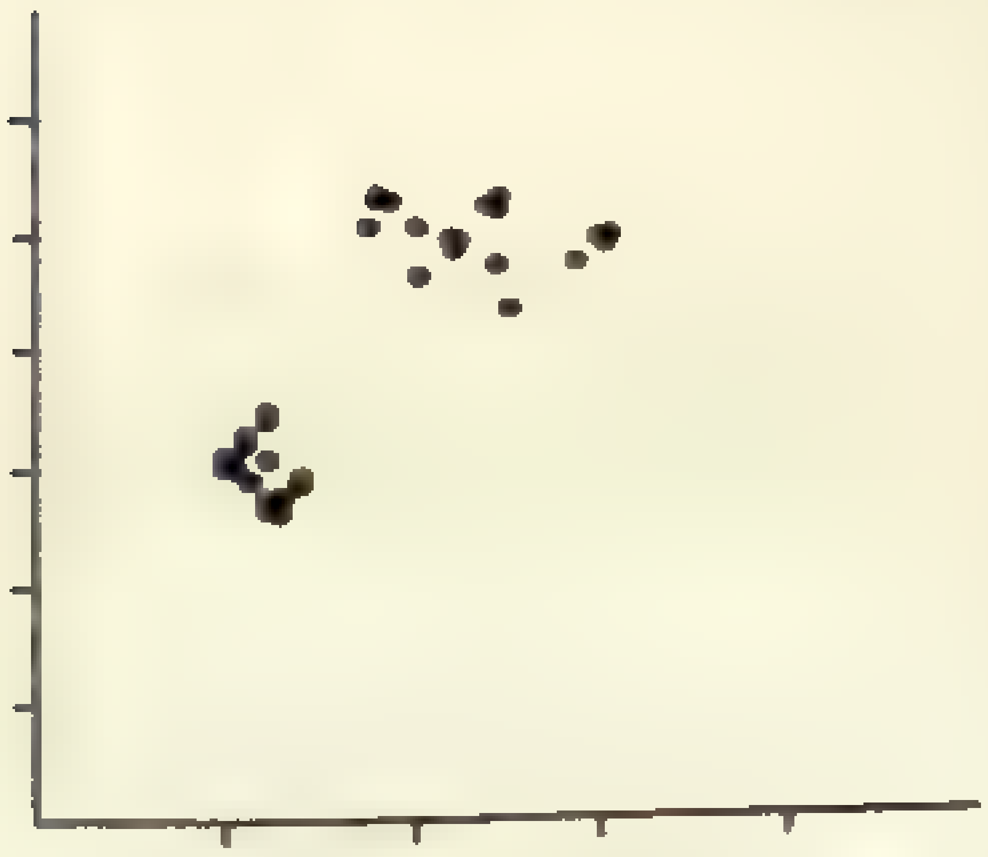
Graph 2. Rudbeckia californica var. californica



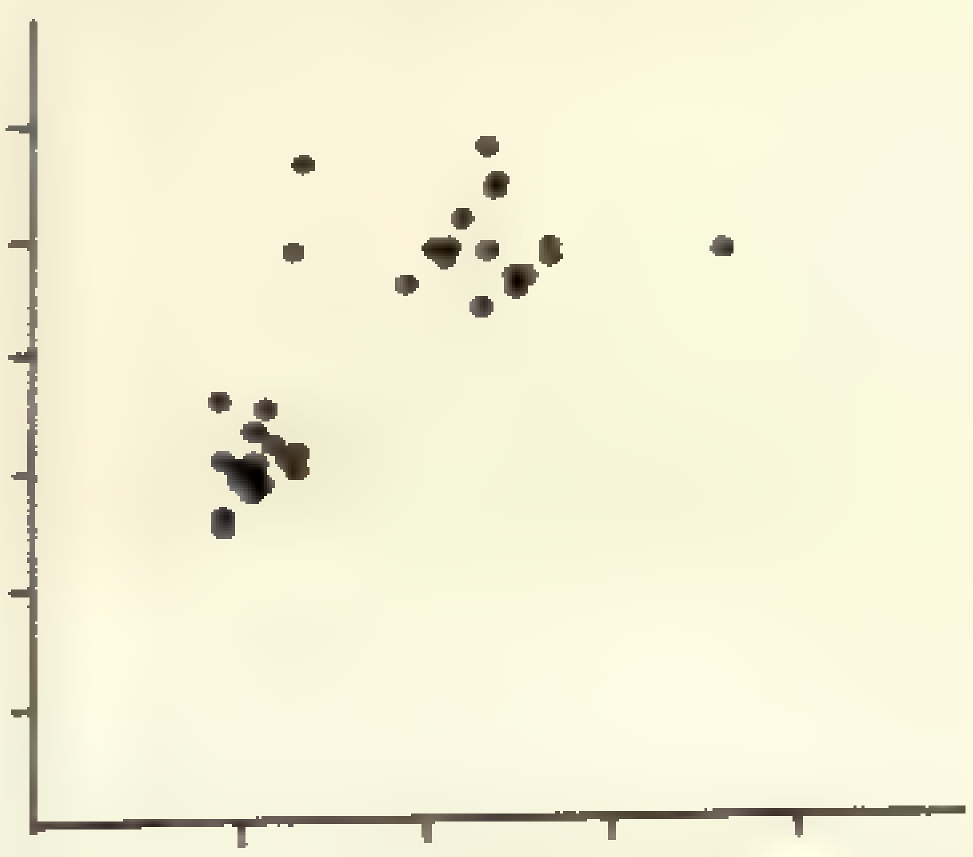
Graph 3. Rudbeckia occidentalis var. occidentalis



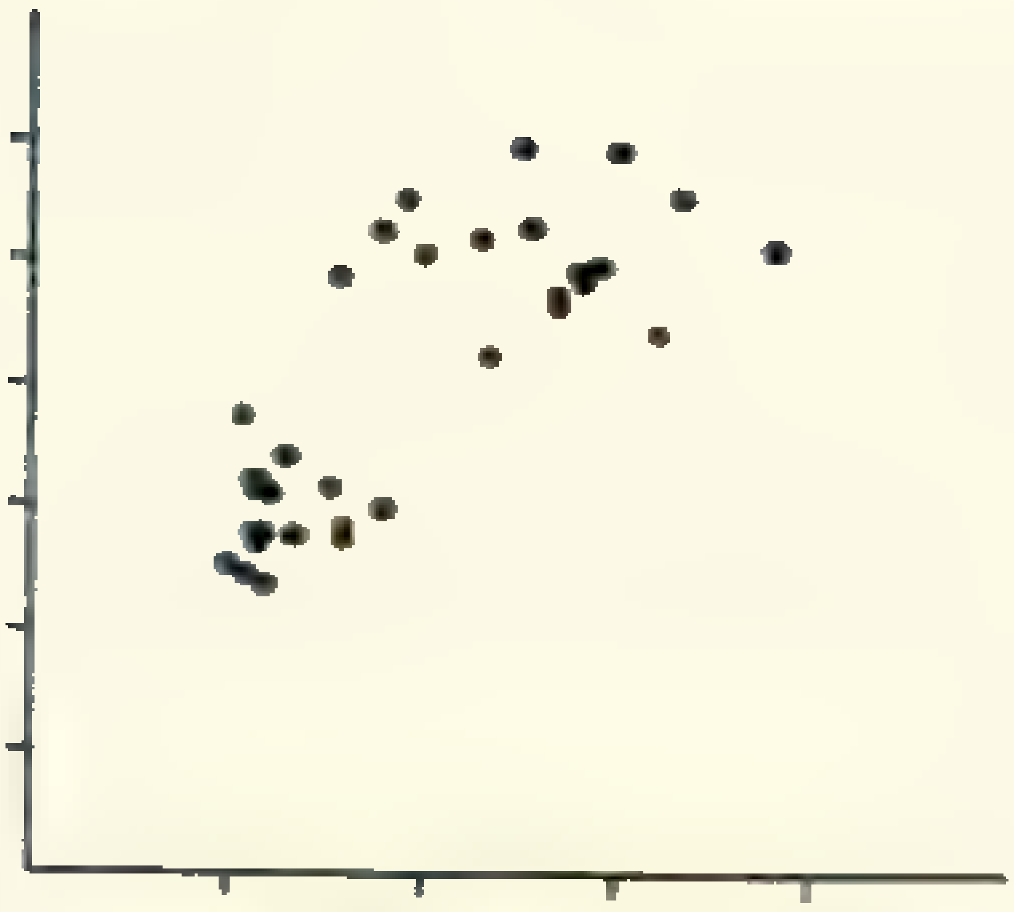
Graph 4. Rudbeckia occidentalis var. occidentalis



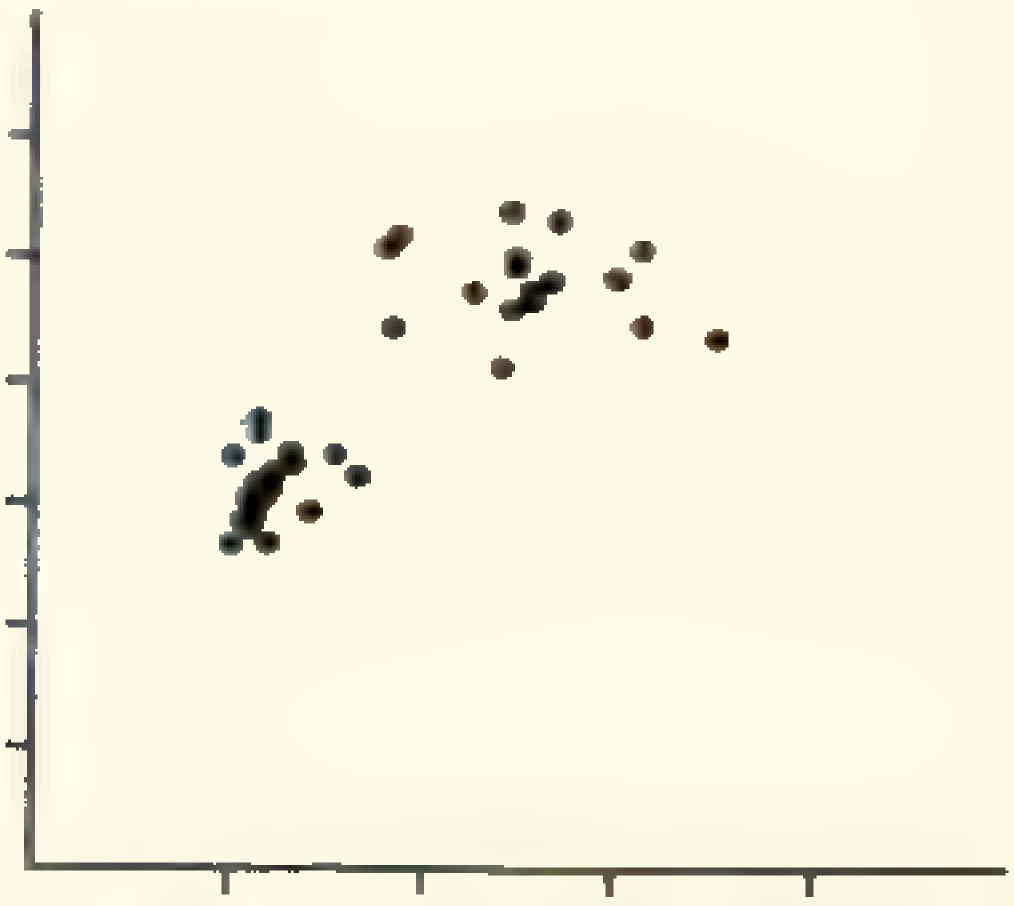
Graph 5. Rudbeckia laciniata var. laciniata



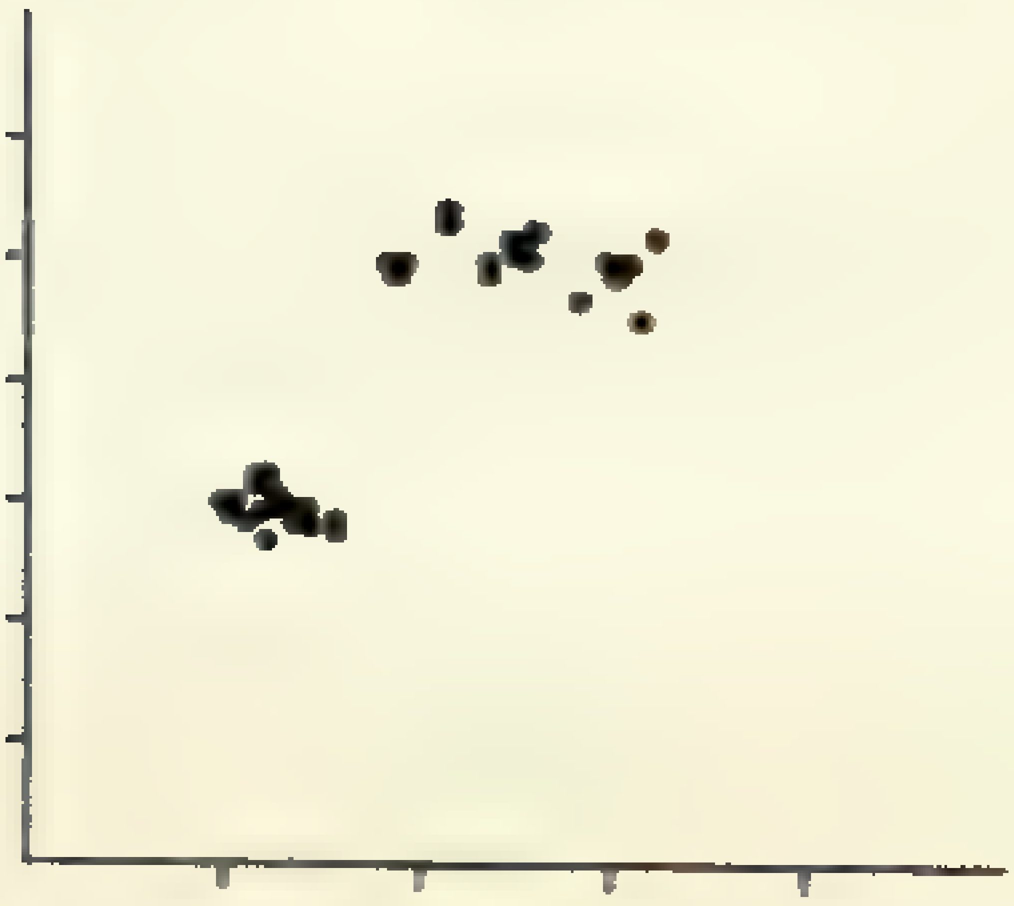
Graph 6. Rudbeckia laciniata var. laciniata



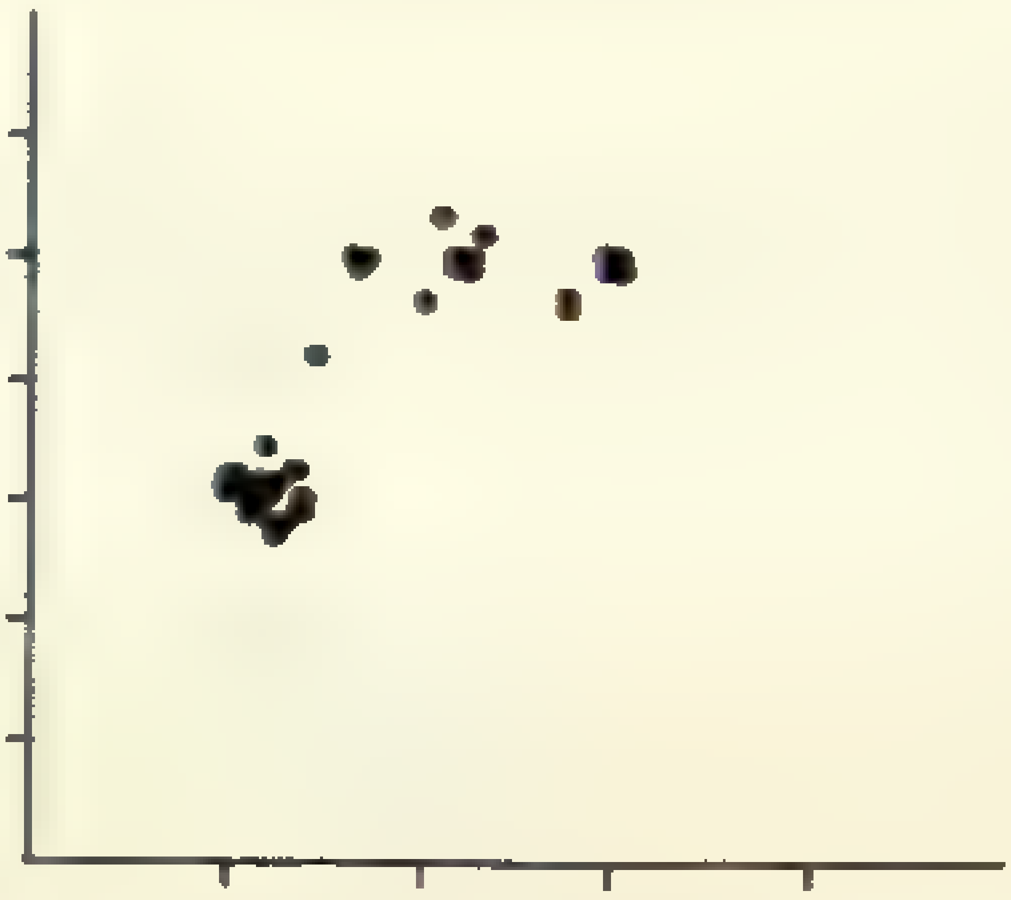
Graph 7. Rudbeckia maxima



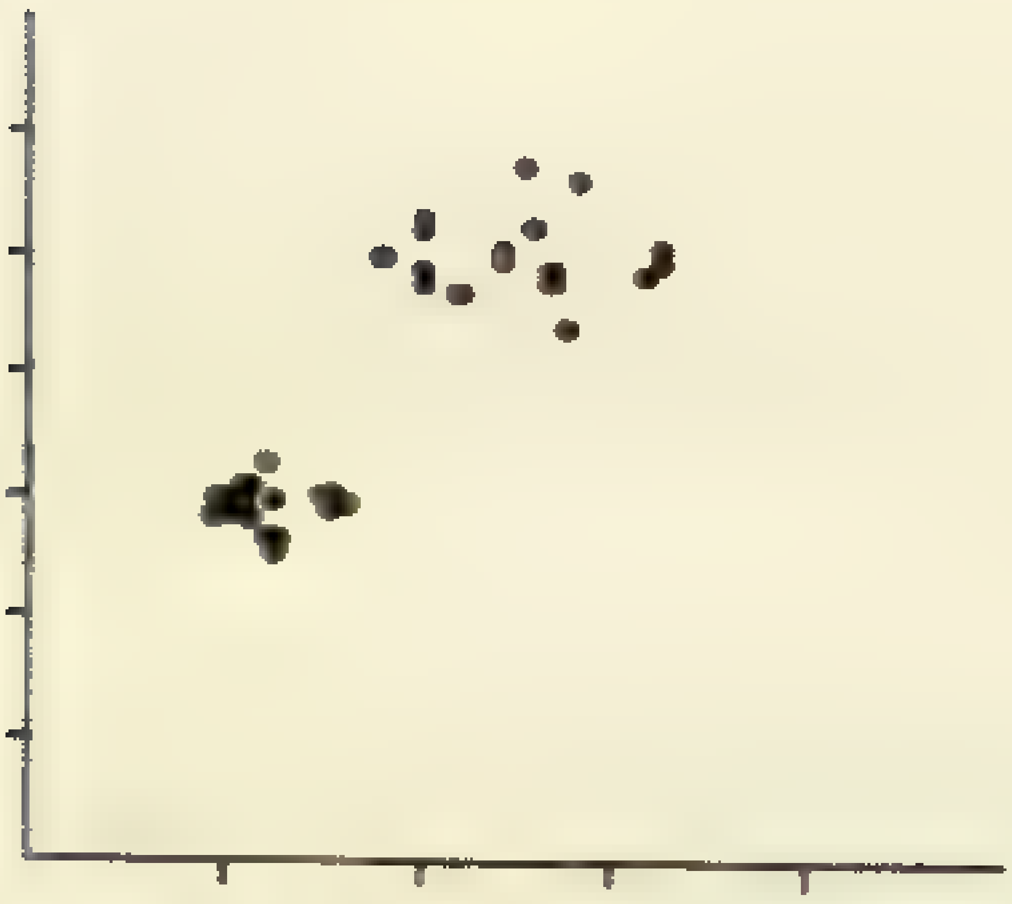
Graph 8. Rudbeckia maxima



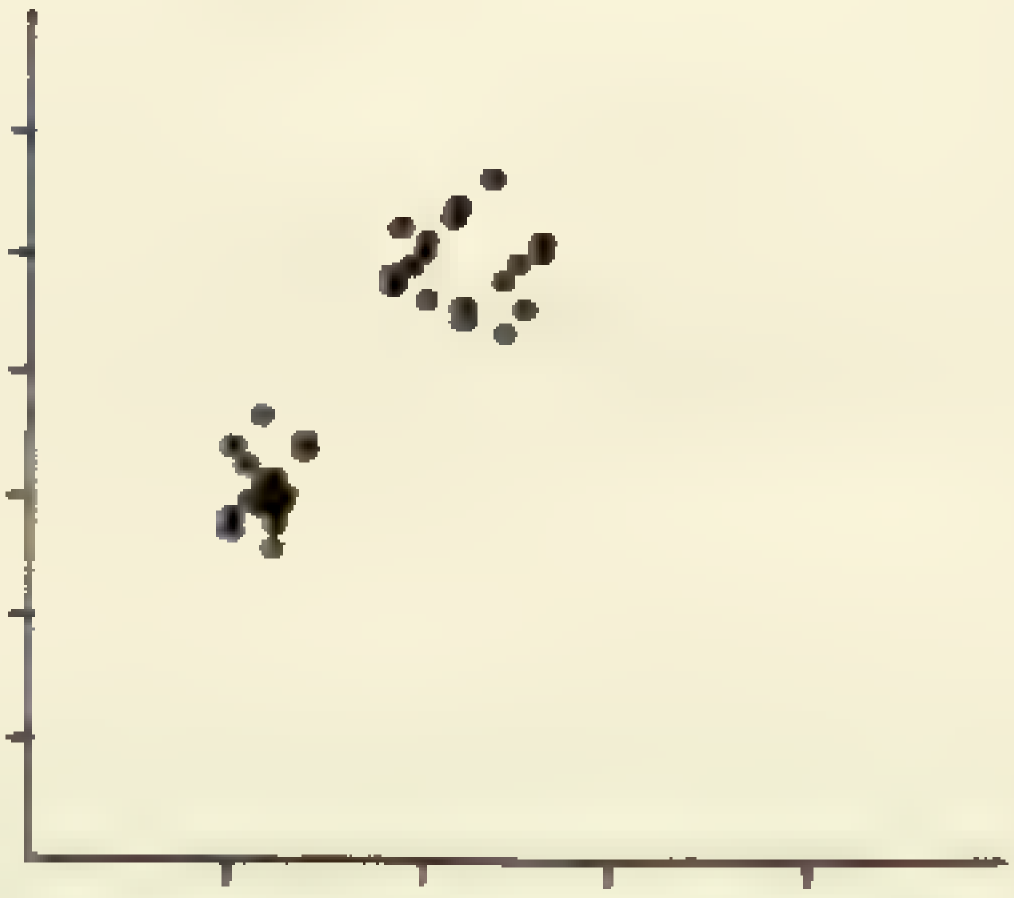
Graph 9. Rudbeckia nitida var. texana



Graph 10. Rudbeckia nitida var. texana

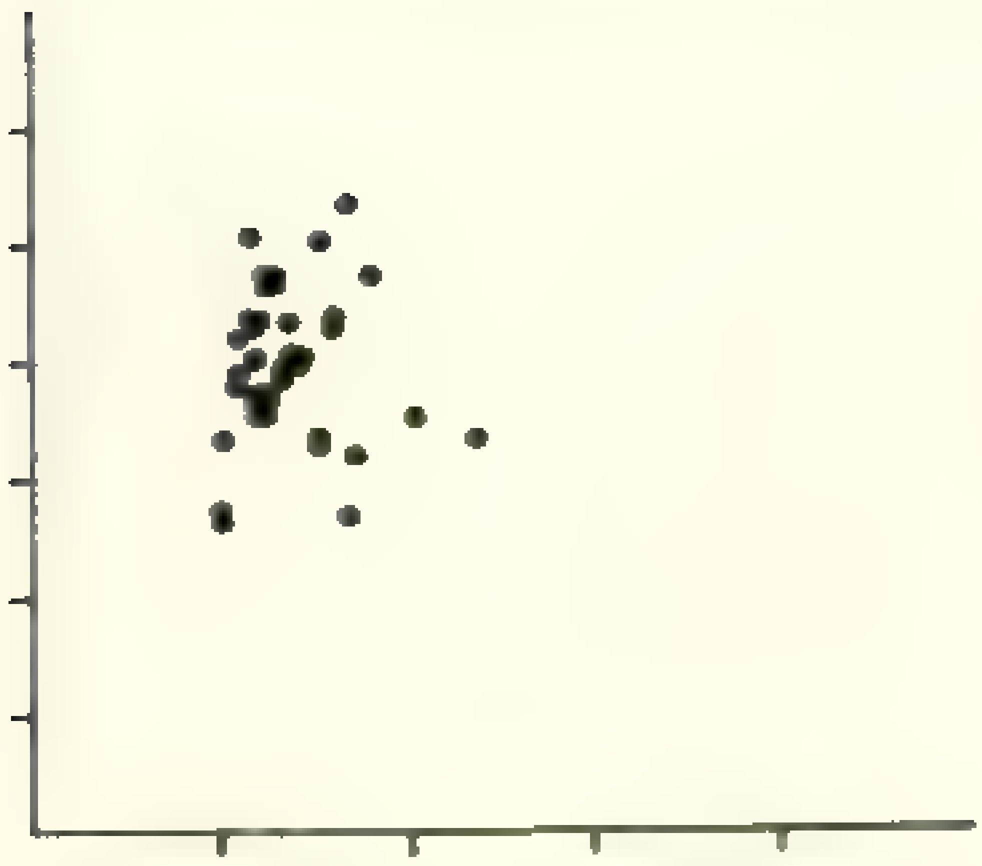


Graph 11. Rudbeckia mohrii

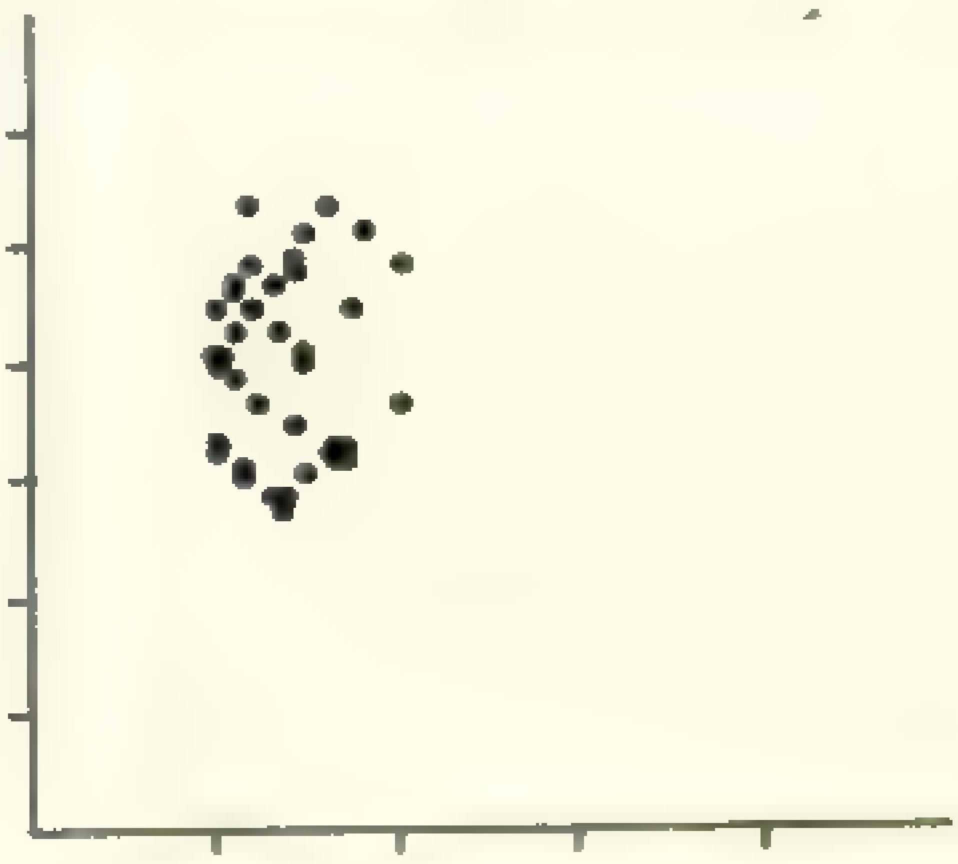


Graph 12. Rudbeckia mohrii

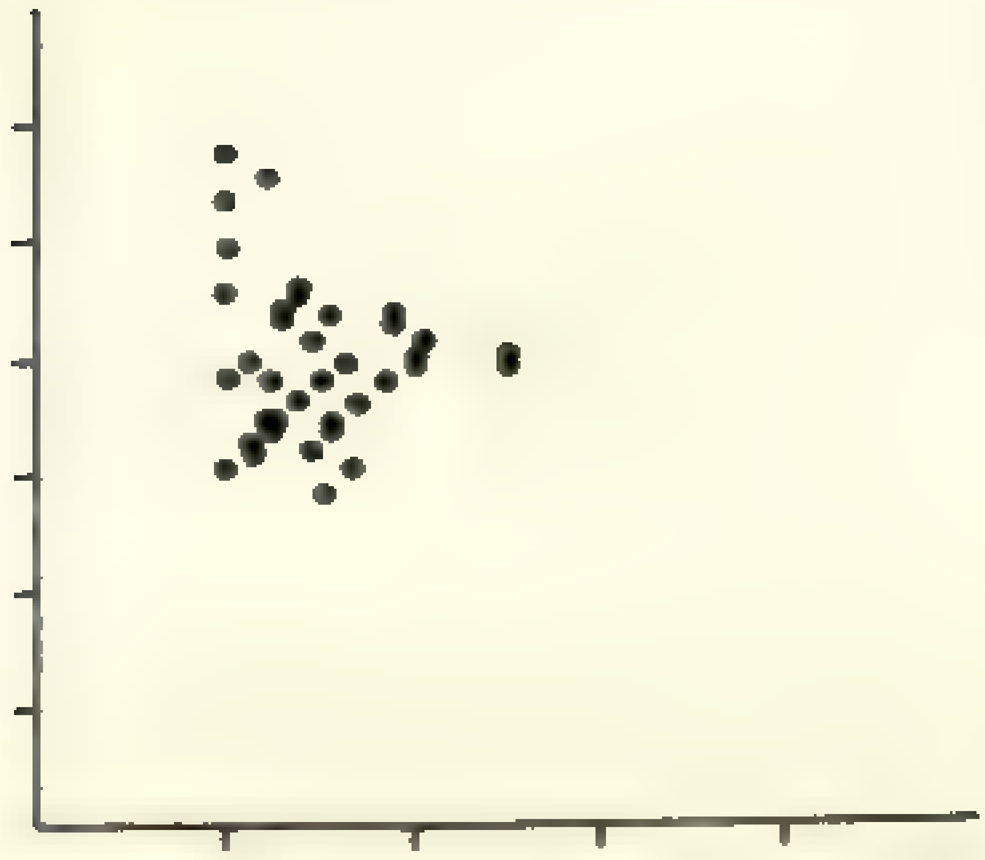
the chromosomes of *R. californica* and *R. occidentalis* on the one hand with those of *R. maxima* and *R. nitida* on the other. Either species pair might also be expected to show differences setting them apart from *R. mohrii.* From the graphs it is clear that such distinctions are not indicated



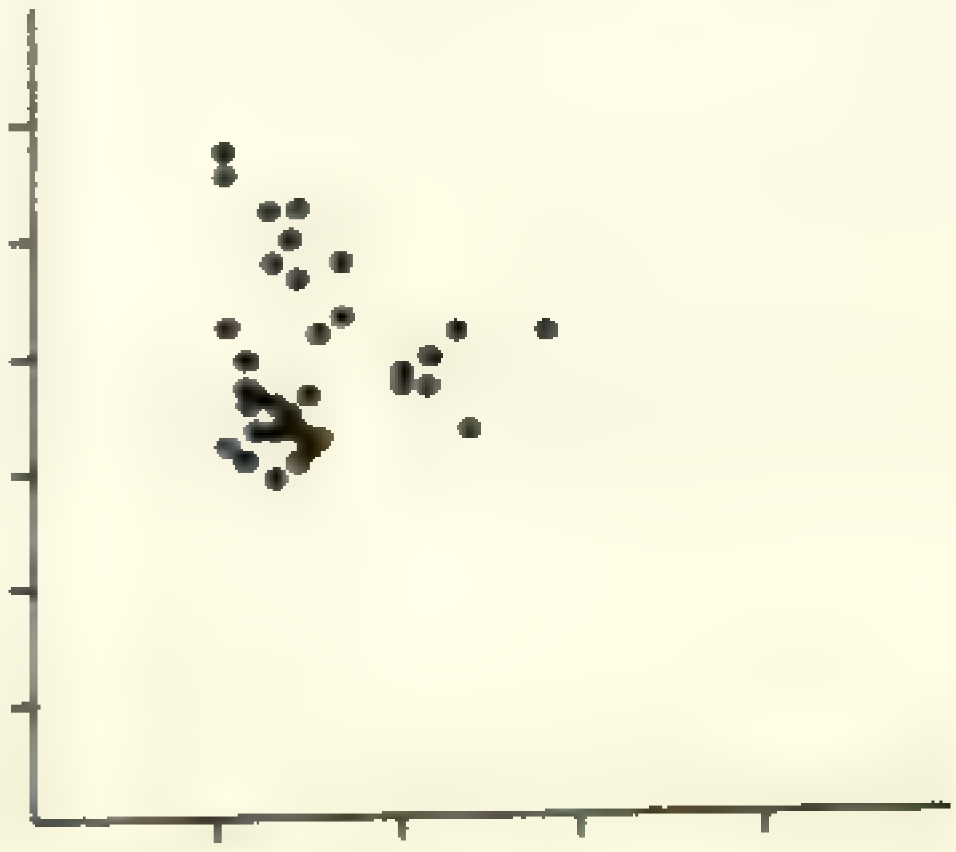
Graph 13. Rudbeckia hirta var. pulcherrima



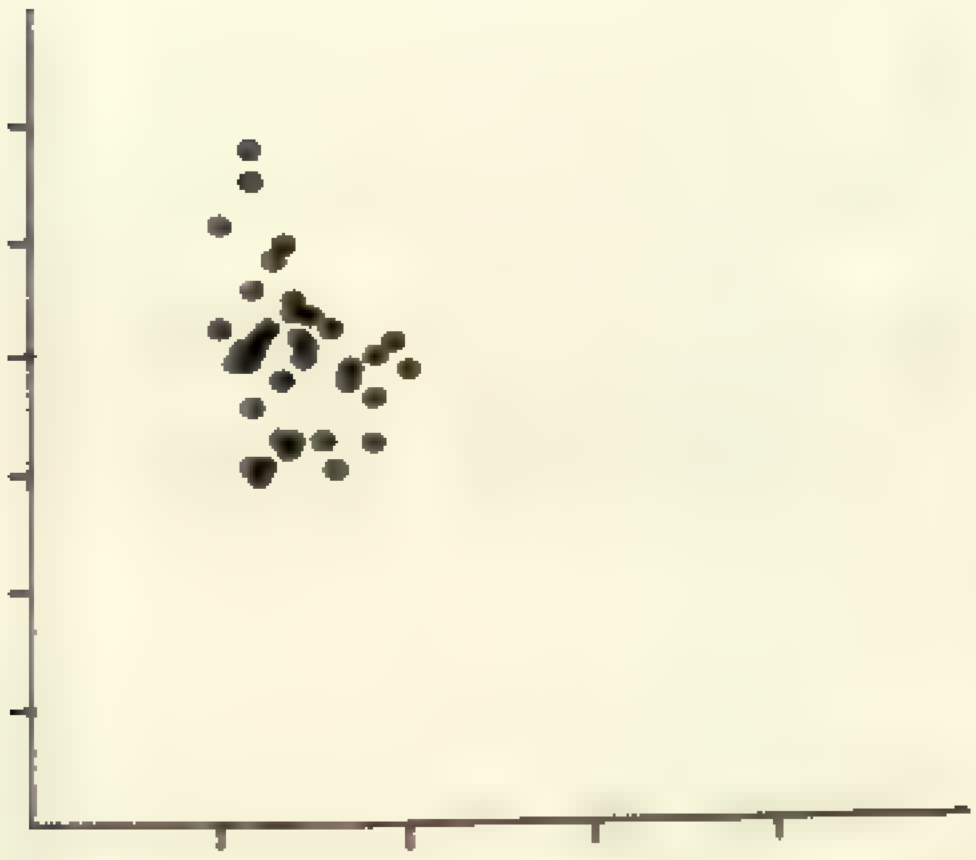
Graph 14. Rudbeckia hirta var. pulcherrima



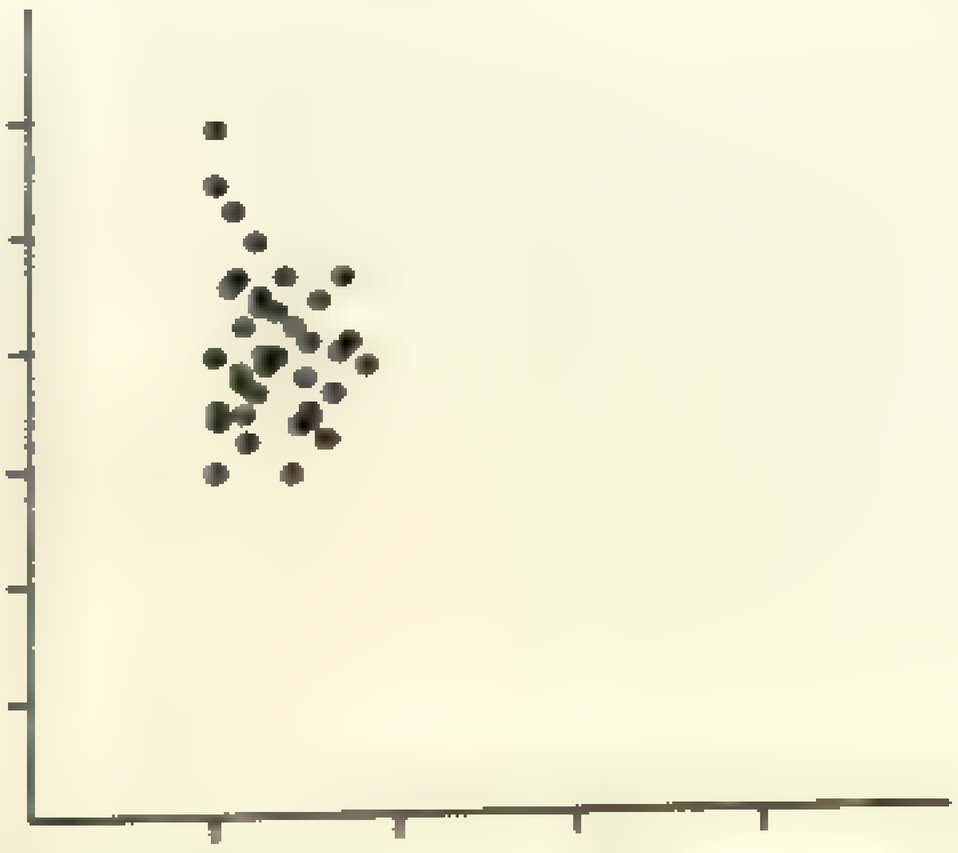
Graph 15. Rudbeckia missouriensis



Graph 16. Rudbeckia missouriensis



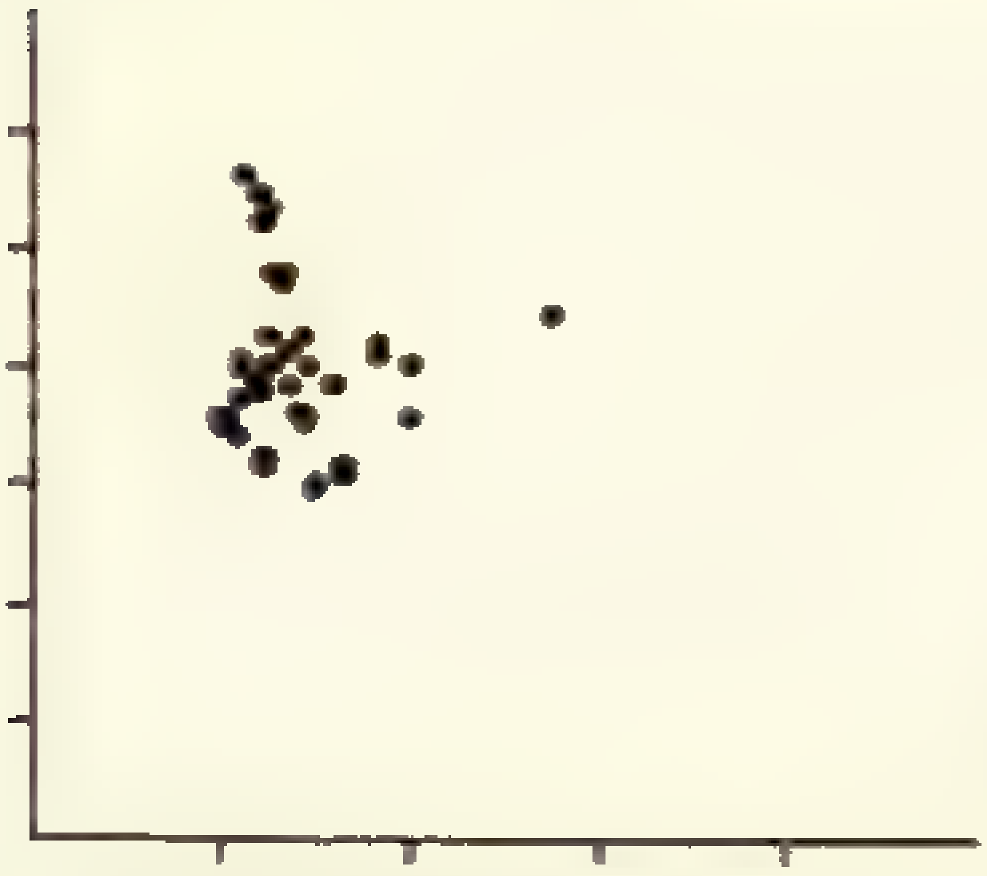
Graph 17. Rudbeckia fulgida var. fulgida



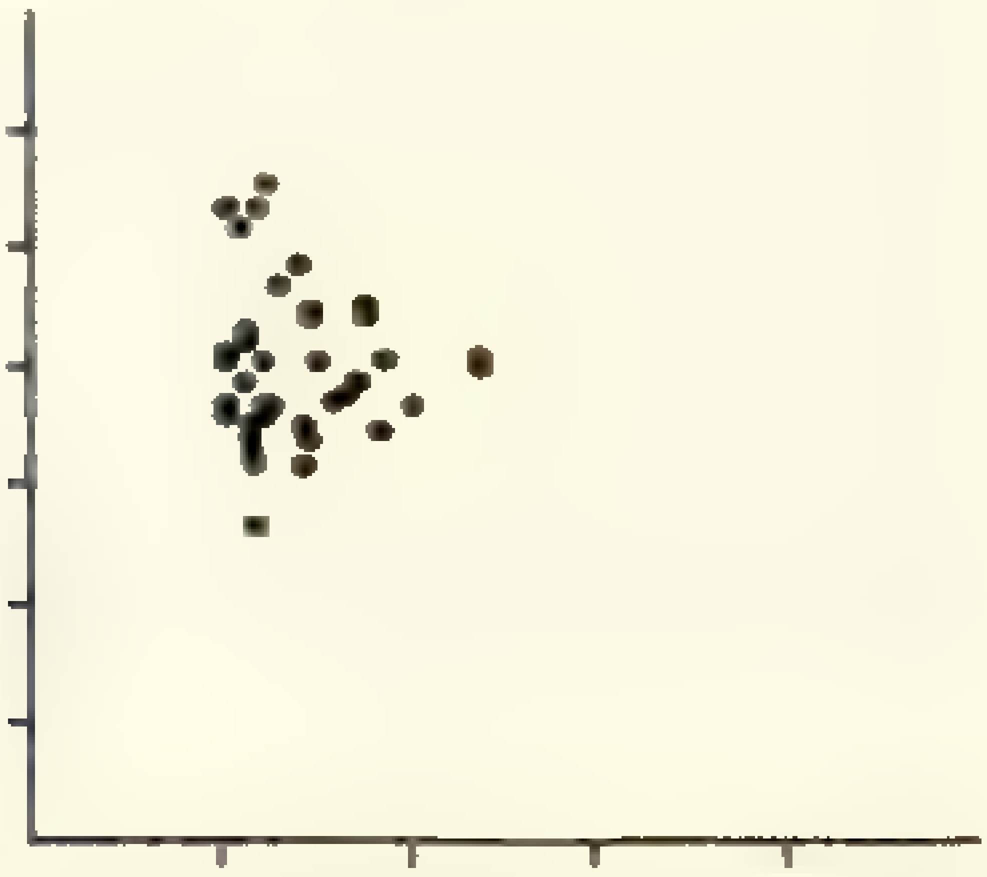
Graph 18. Rudbeckia fulgida var. fulgida

within subg. *Macrocline* and it is likely that additional data would show the same uniform pattern for all the species.

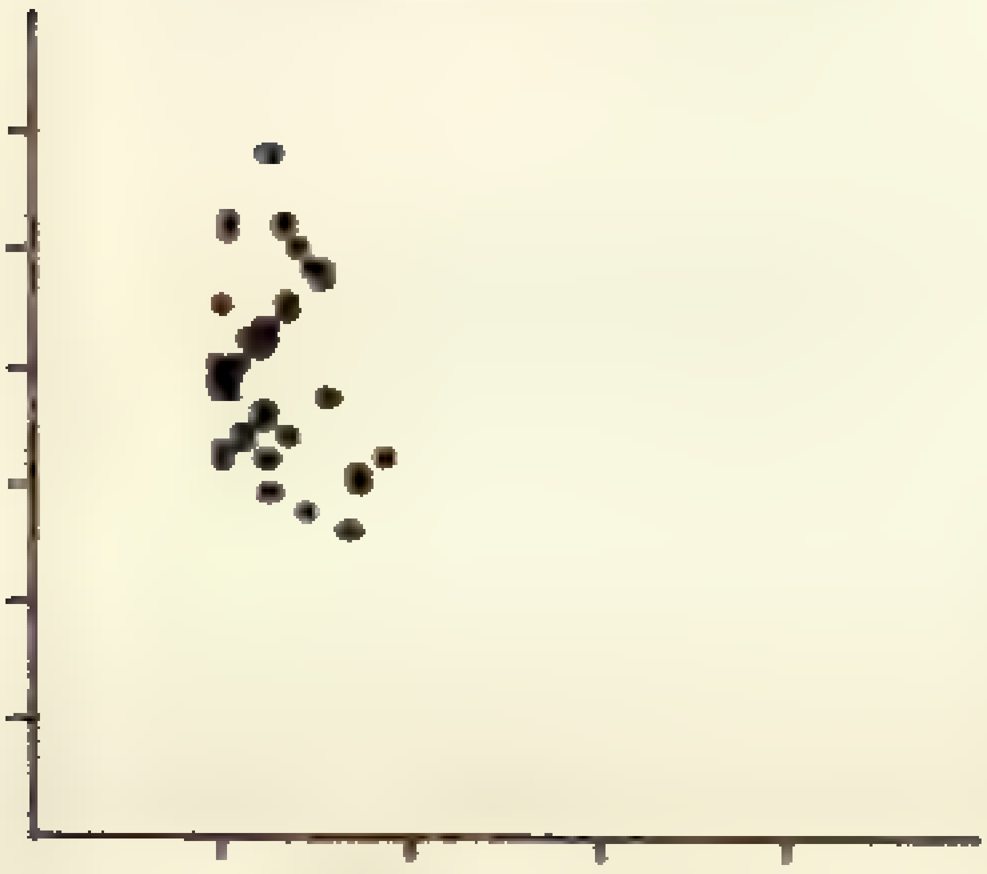
Details of chromosome morphology of 8 of the 9 species of *Rudbeckia* subg. *Rudbeckia* are portrayed in Graphs 13-28. More or less clumping of the dots is characteristic of



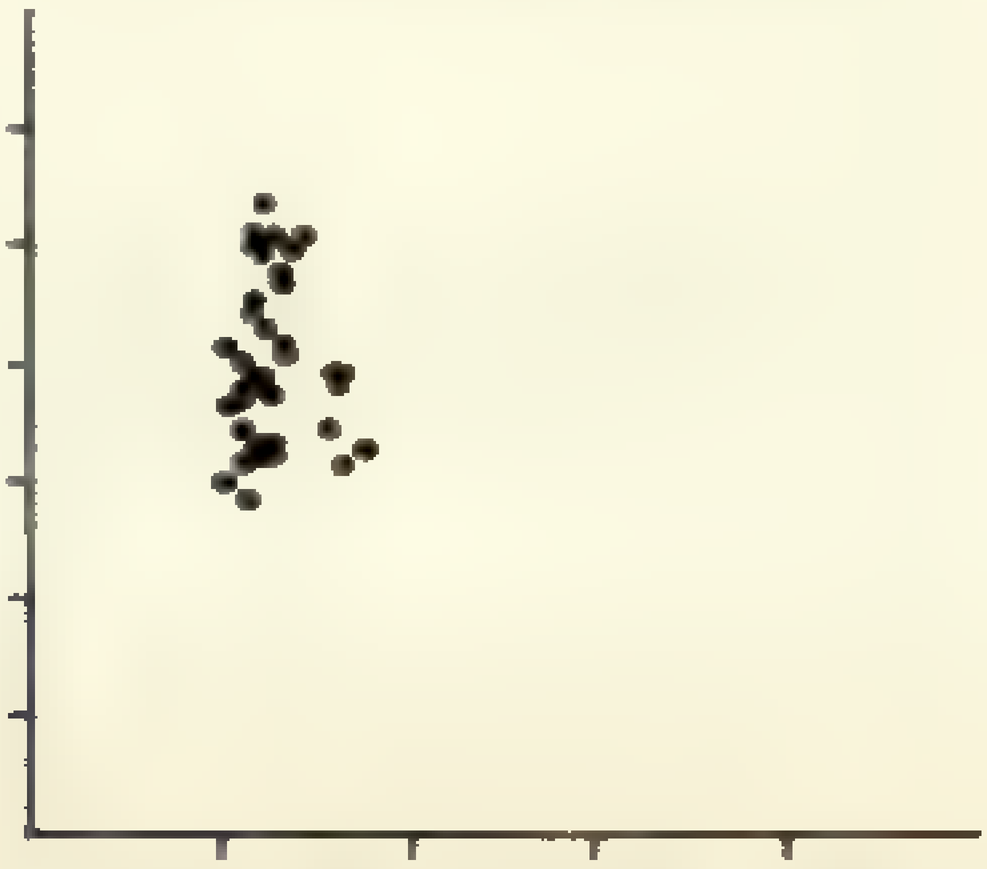
Graph 19. Rudbeckia fulgida var. palustris



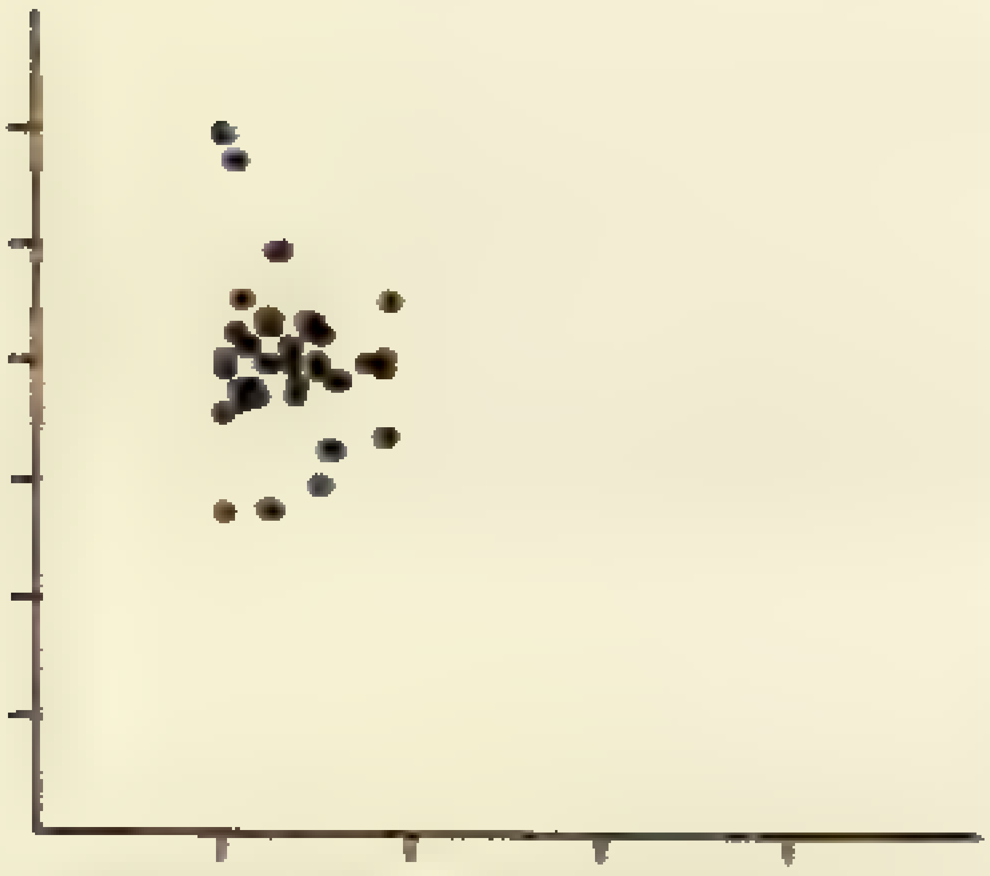
Graph 20. Rudbeckia fulgida var. palustris



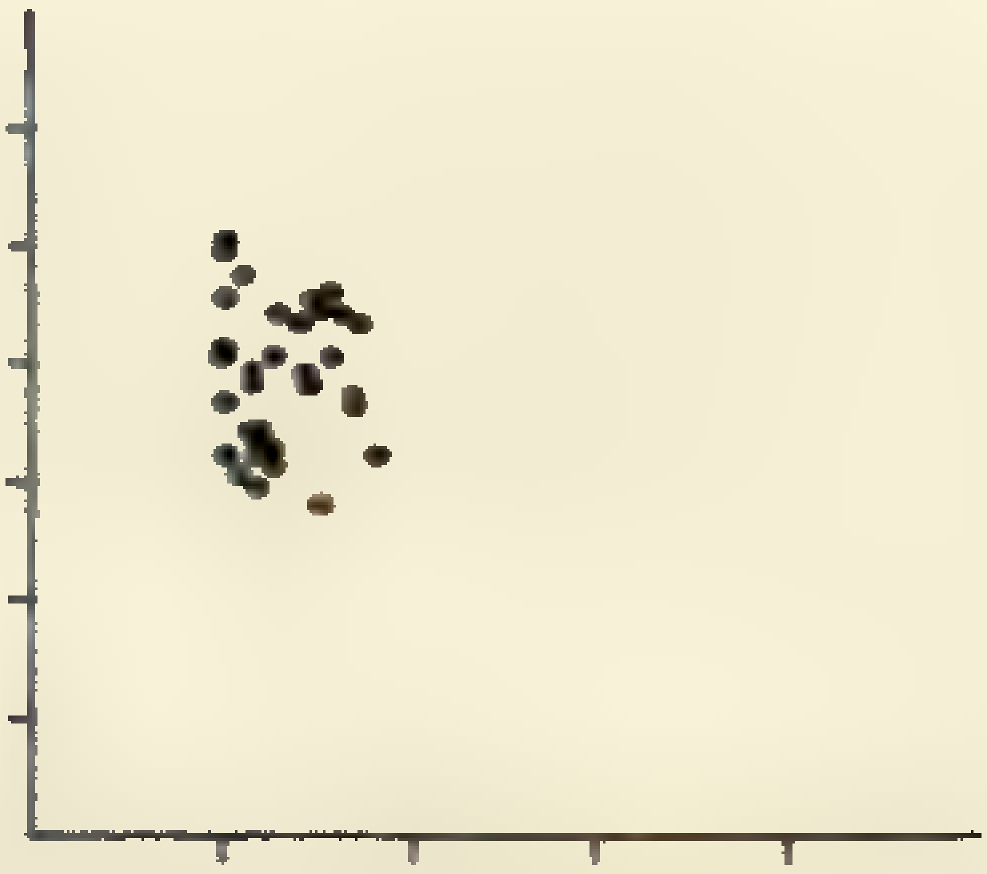
Graph 21. Rudbeckia mollis



Graph 22. Rudbeckia mollis

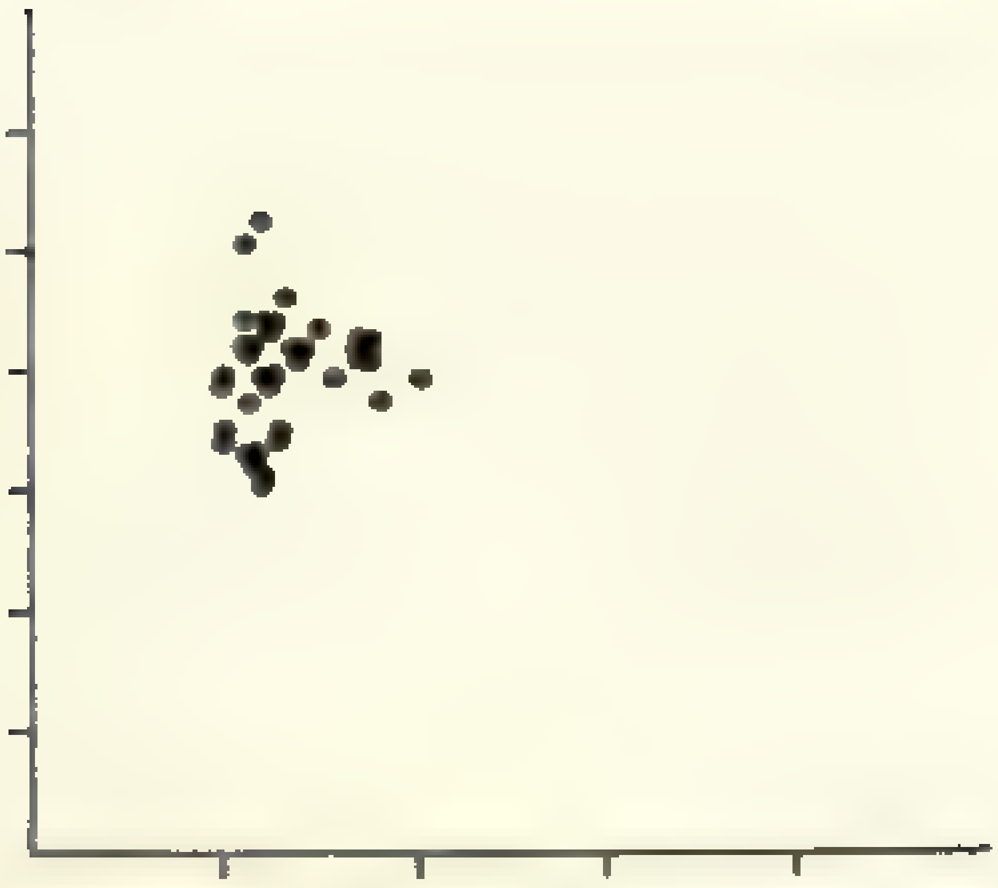


Graph 23. Rudbeckia grandiflora var. grandiflora



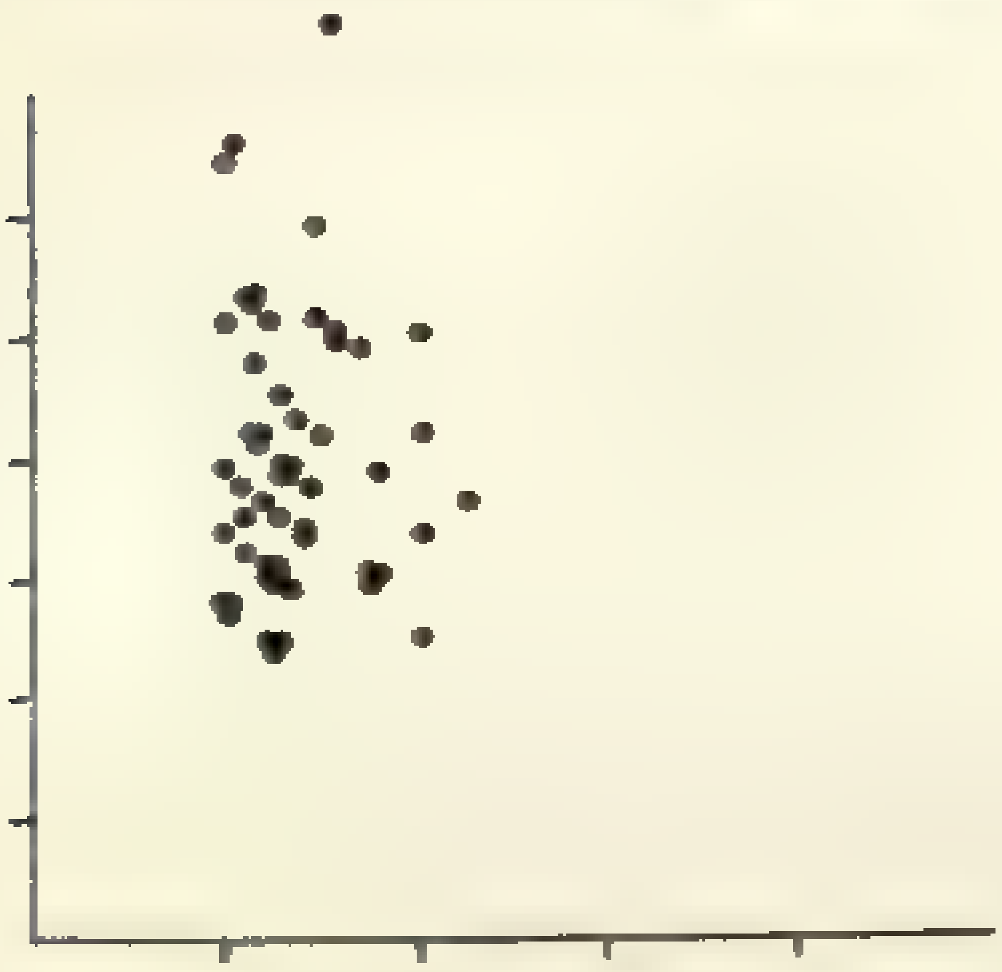
Graph 24. Rudbeckia grandiflora var. grandiflora

all species of this subgenus; that is, there is no separation of the chromosomes into groups on the basis of either length or constriction position. The constriction position varies from median to more or less submedian.

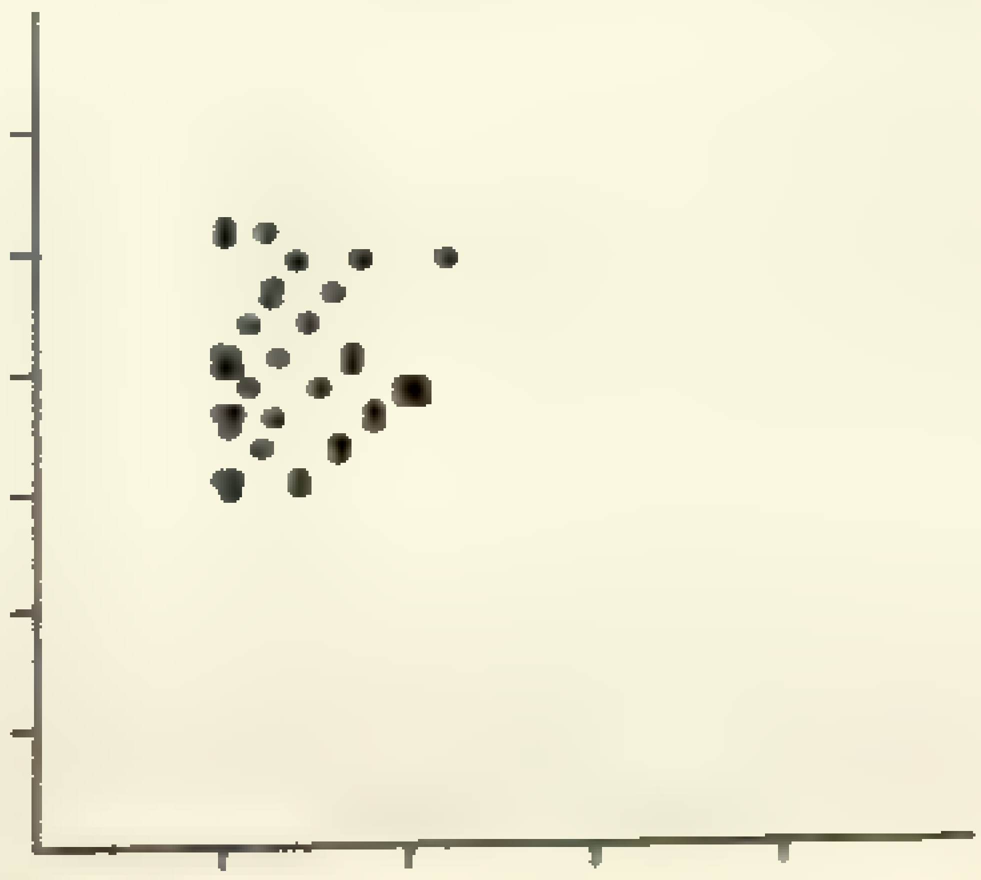


Graph 25. Rudbeckia subtomentosa

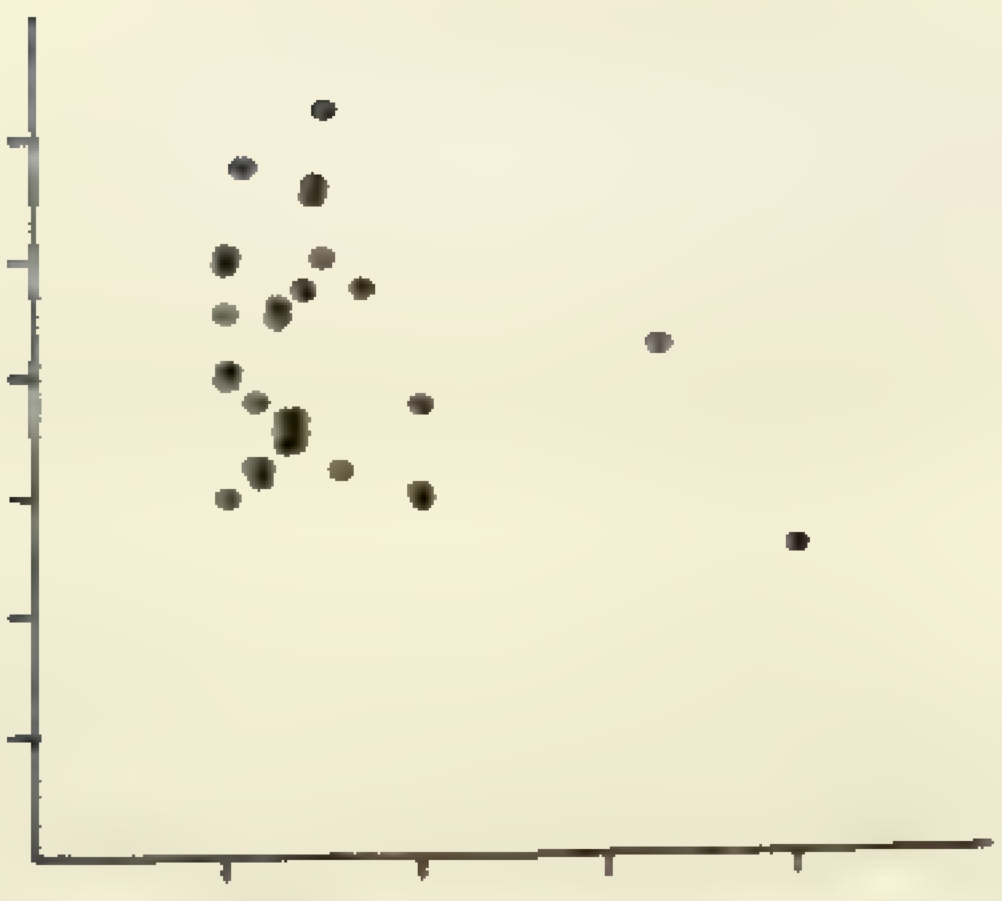
Graph 26. Rudbeckia subtomentosa



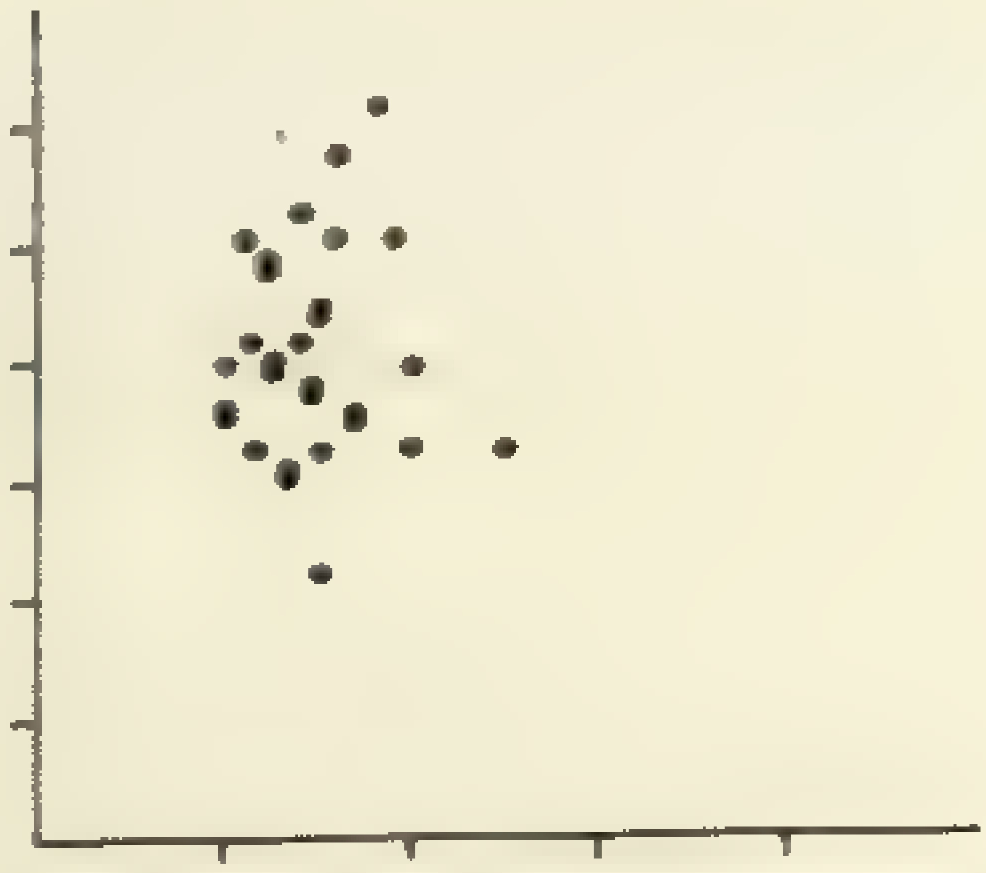
Graph 27. Rudbeckia triloba var. triloba



Graph 28. Rudbeckia graminifolia

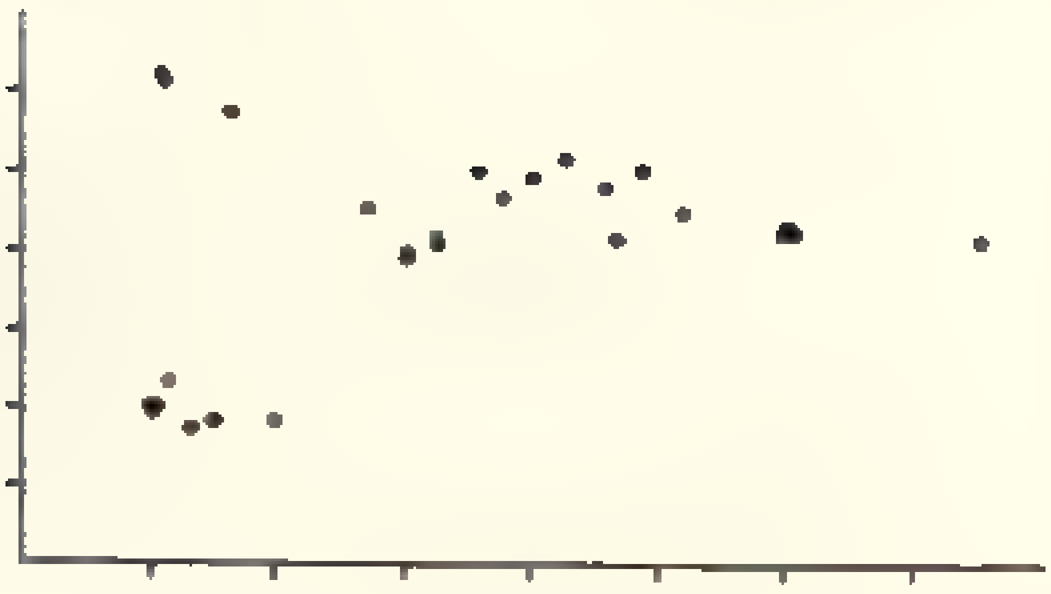


Graph 29. Dracopis amplexicaulis

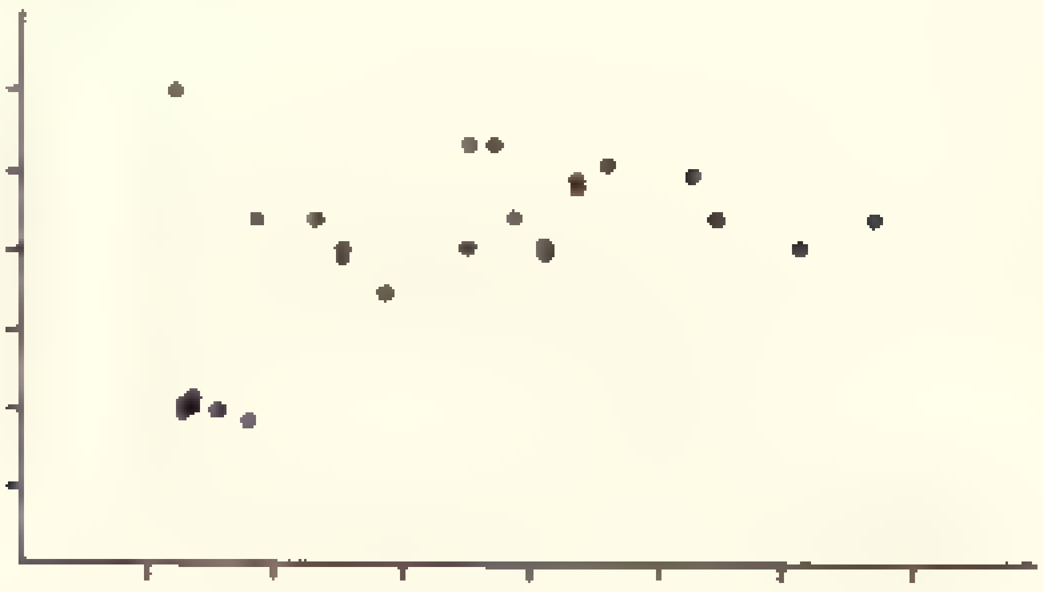


Graph 30. Dracopis amplexicaulis

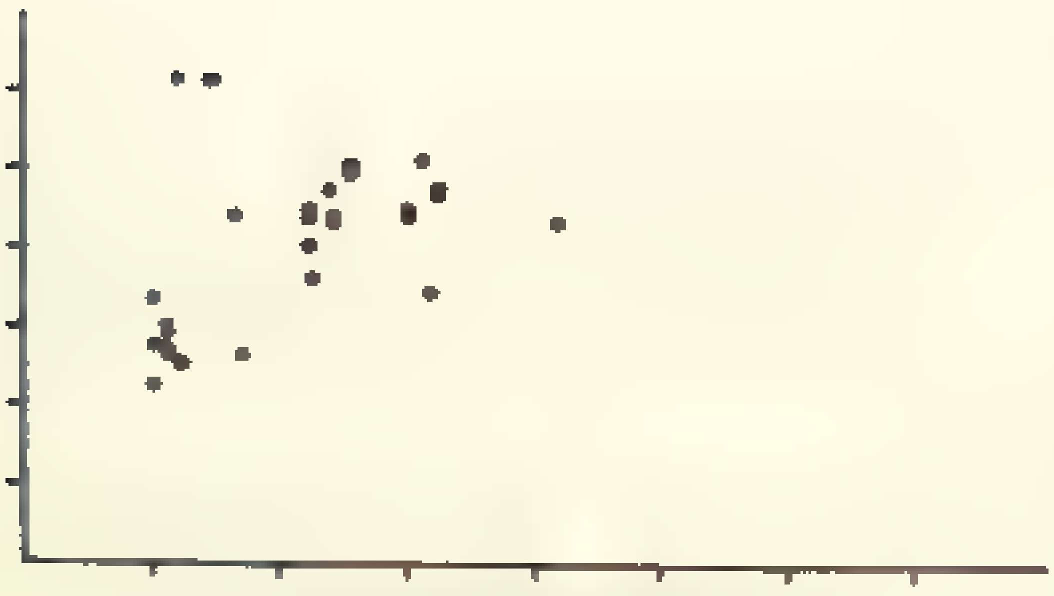
In contrast to the morphologically homogeneous subg. *Macrocline*, in which all of the species are fairly closely related, subg. *Rudbeckia* includes species and species groups that are much more diverse in their relationships. Examples of species that are highly distinct morphologically



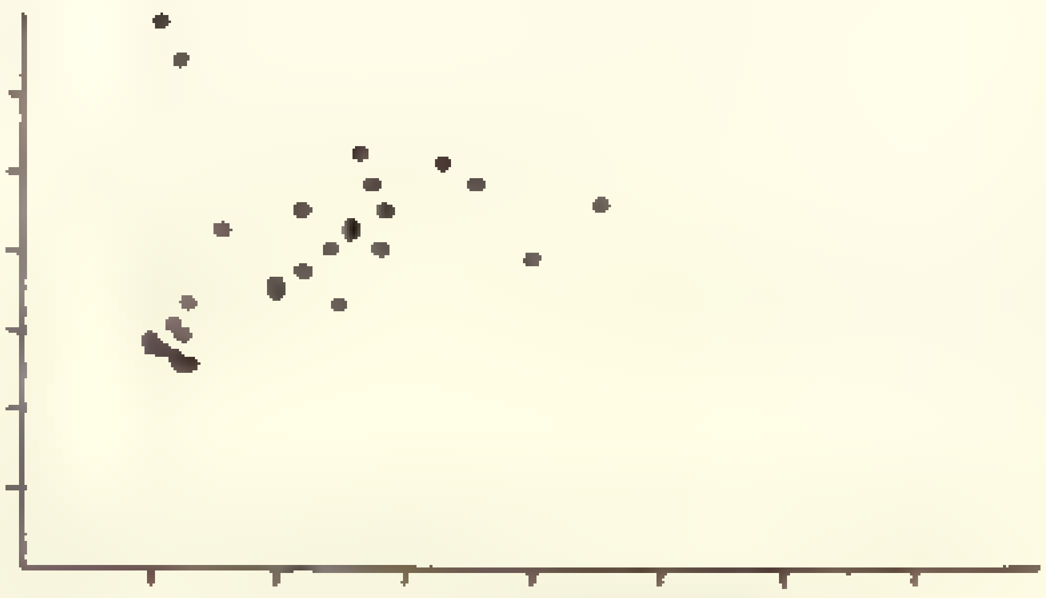
Graph 31. Ratibida columnaris



Graph 32. Ratibida columnaris



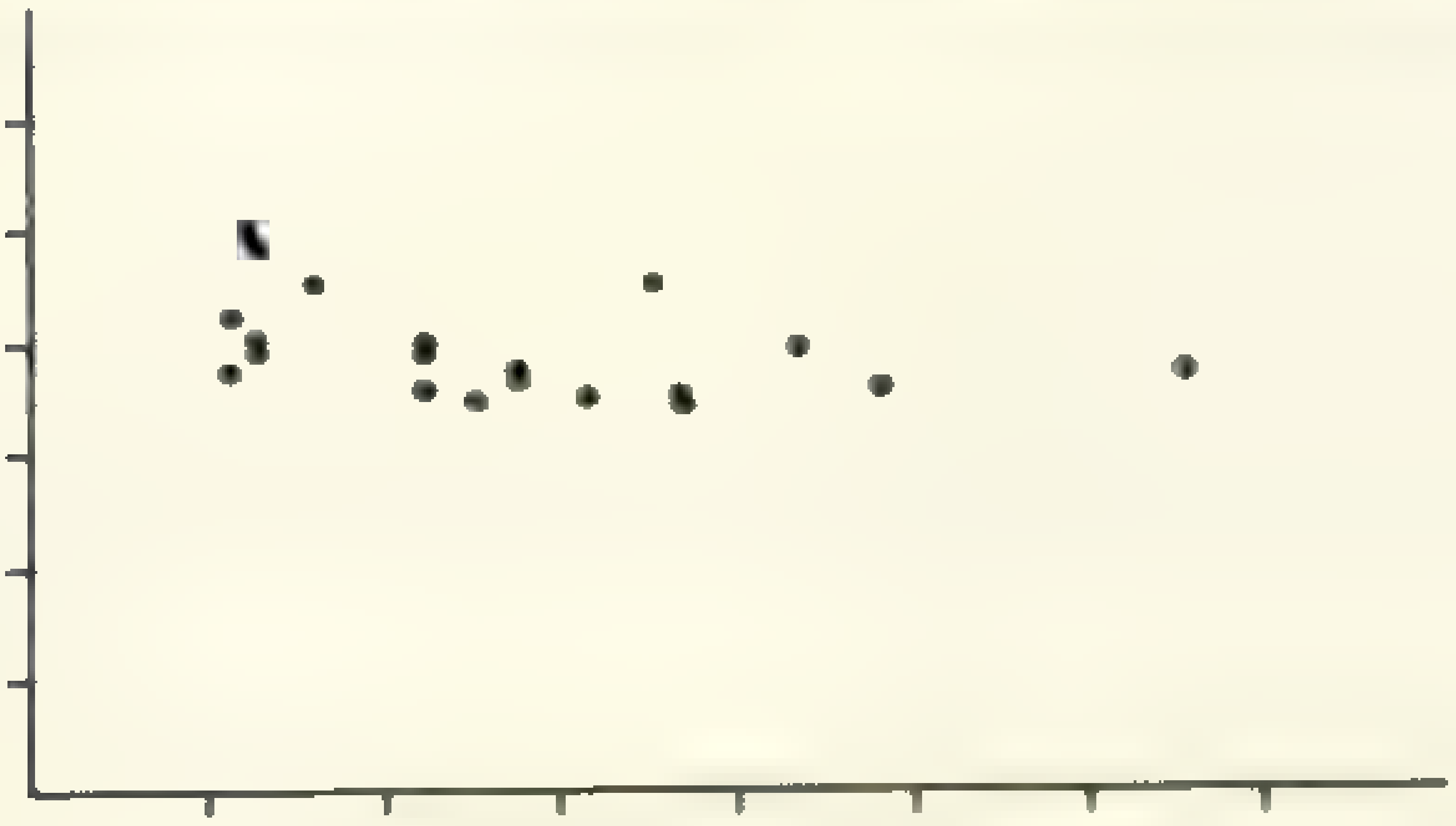
Graph 33. Ratibida pinnata



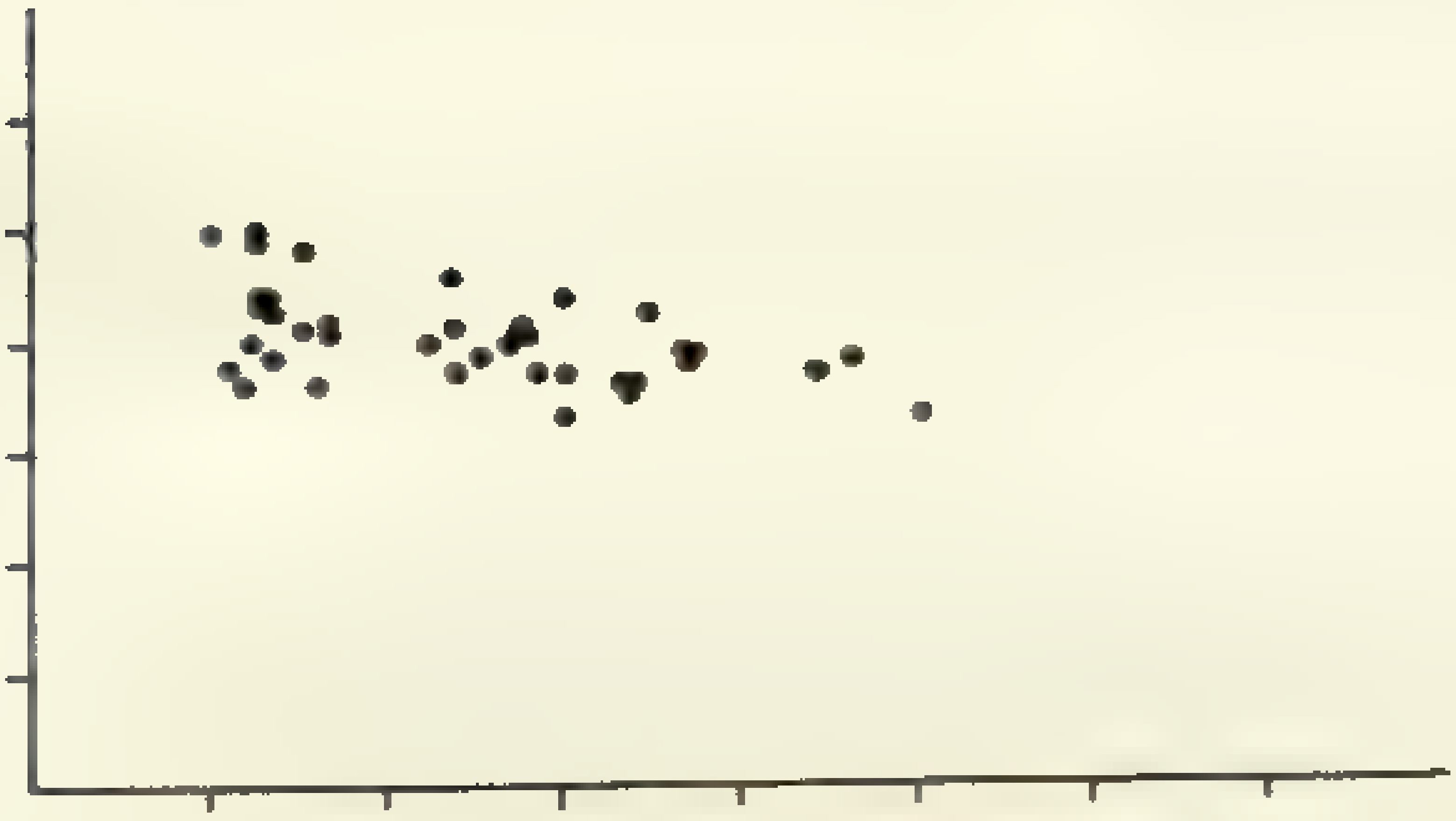
Graph 34. Ratibida pinnata

are *R. hirta* (Graphs 13 and 14), *R. triloba* (Graph 27), and *R. graminifolia* (Graph 28). *R. missouriensis* (Graphs 15 and 16) and *R. fulgida* (Graphs 17-20) are much more closely related to one another than to any other species. This is also true of *R. grandiflora* (Graphs 23 and 24) and *R. subtomentosa* (Graphs 25 and 26). The graphs do not indicate any differences of greater magnitude between the most distantly related species than between closely related species or between 2 varieties of the same species. Compare the 2 varieties of *R. fulgida* in Graphs 17-20. Even though the graphs indicate that the morphological patterns of the chromosomes of species of this subgenus are comparatively uniform, it is possible that significant differences could be established by study of additional material.

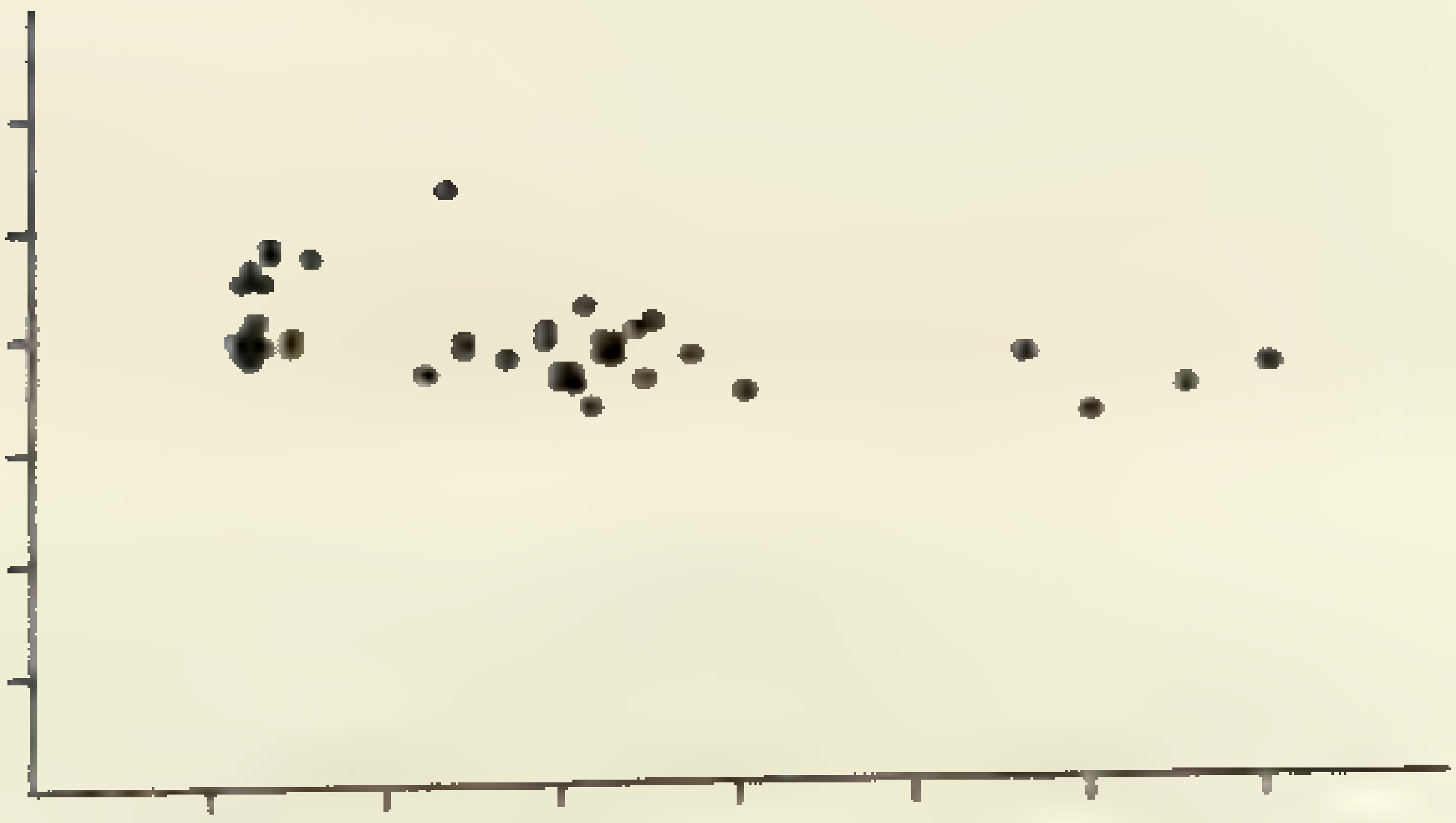
Graphs 29 and 30 represent the chromosomes of *Dracopis amplexicaulis,* the only species of the genus. Although the data for this species are so limited as to be very inconclusive, Graph 29 was derived from an excellent photograph (Fig. 19) and probably represents fairly accurately the pattern of chromosome morphology in this species. This graph suggests that the chromosomes can be separated into 2 groups. In the first group, consisting apparently of 1 pair, the chromosomes are more or less subterminally constricted (L S values of 3.25 and 4.00). In the second group the position of the constriction varies from median to submedian (L/S values of 2.0 or less). There is no separation



Graph 35. Echinacea pallida



Graph 36. Echinacea pallida



Graph 37. Echinacea pallida

of the members into groups on the basis of size. As evidenced by the illustrations (compare Fig. 19) the chromosomes are much smaller, on the average, than are those of any other of the species studied. This smaller size was apparent in all of the material examined.

Graphs 31-34 illustrate details of chromosome morphology of 2 species of the genus *Ratibida*. Dispersion of the dots is characteristic of this genus, the result of considerable variation in chromosome size and especially of variation in position of the constrictions. The chromosomes can be separated into 3 groups. The first group, consisting apparently of but a single pair, is relatively long and more or less medianly constricted (L/S values of 1.0-1.6). Another group of chromosomes is comparatively short, but also more or less medianly constricted (L/S values of 1.0-2.0). The third group includes chromosomes of median length that are constricted from the submedian position to the subterminal position (L/S values mostly greater than 2.0). Graphs 33 and 34 represent *Ratibida pinnata*, which has a chromosome number of 2n=28. Graph 32 represents *R. columnaris* (*R. columnifera* of manuals), which has a chromosome number of 2n=26. The constriction of one long chromosome could not be observed and this chromosome is not represented on the graph. An aneuploid plant of *R. columnaris* with 27 chromosomes is represented by Graph 31. The graphs clearly show that the aneuploid plant of *R. columnaris* differs by the presence of an extra, medianly constricted, small chromosome. The graphs further indicate that *R. pinnata* differs from *R. columnaris* in having 2 additional, small, medianly constricted chromosomes.

Graphs 35-37 all represent *Echinacea pallida*. A diploid plant with 22 chromosomes is portrayed in the first graph; a tetraploid plant with 44 chromosomes is represented by the last two. The chromosomes are more or less uniform in size as evidenced by the distribution of the dots in a more or less straight, horizontal line. There is great variation, however, in the position of the constrictions and on this basis the chromosomes can be easily separated into three distinct groups. One group is more or less medianly constricted (L/S values of 1.0-1.8), a second is constricted from submedianly to more or less subterminally (L/S values of 2.0-4.0), and the third is constricted in a position that is distinctly subterminal (L/S values of 4.0 or greater).

CONCLUSIONS

The two subgenera of *Rudbeckia* are sufficiently represented in the data presented so that definite conclusions can be drawn as to the differences in the patterns of morphology of their chromosomes. Interpretations based on the data presented for the other genera are inconclusive and must be regarded as tentative although they probably present a fairly accurate picture, especially for *Ratibida.* If minor exceptions are disregarded, definite patterns of chromosome morphology are clearly established in the major taxa considered, and uniformity is the rule within each of these groups. The most important conclusion to be drawn from the data presented is the fact that morphological differentiation of *Rudbeckia* into 2 distinct subgenera has been accompanied by visible differentiation in chromosome structure as well as by a change of chromosome number. These data support the recognition of subg. *Macrocline* and subg. *Rudbeckia* as 2 distinct very natural taxa, and they support the recognition of *Rudbeckia*, *Ratibida*, *Dracopis* and *Echinacea* as distinct genera. The genera and subgenera discussed can be distinguished from one another by the morphology of their somatic chromosomes as well as by their chromosome number.

The patterns of chromosome morphology exhibited by *Rudbeckia*, *Ratibida*, *Dracopis*, and *Echinacea*, based upon the material examined (limited as it may be for the last two genera), are compared in Table 2. For each genus or subgenus considered in this paper, the table lists the basic chromosome number, total number of species, and number of species examined in the present investigation. It also indicates the average chromosome length (a comparative value) for each group of species. Finally, the table describes briefly the visible morphological differences between the somatic chromosomes of the generic and subgeneric taxa.

The great taxonomic value of data of the type discussed in this paper cannot be denied. However, it should be pointed out that these data are only a step aside from conventional morphology. For the genera studied the information derived from the chromosomes is as much within the realm of morphology as are the characteristics of the achene. These are additional morphological characters, however, in importance, characters of the greatest magnitude.

The chromosome numbers of *Rudbeckia* subg. *Macrocline* (2n=36), *Ratibida pinnata* (2n=28), and *Dracopis* (2n=32) raise a question as to the possibility that the last genus was derived from a hybrid between the other two. If an egg cell of a species of *Ratibida* with n=14 was fertilized by pollen from a species of *Rudbeckia* subg. *Macrocline* with n=18, the resulting plant would have a chromosome number of 2n=32. Apomictic development would be neces-

TABLE 2. CYTOLOGICAL DIFFERENTIATION OF RUDBECKIA AND RELATED GENERA

Rudbeckia subg. *Rudbeckia*	*Rudbeckia* subg. *Macrocline*	*Dracopis*	*Ratibida*	*Echinacea*
$2n = 38$	$2n = 36$	$2n = 32$	$2n = 26, 28$	$2n = 22$
No. species: 9	No. species: 6	No. species: 1	No. species: 5	No. species: 5
No. species examined: 8	No. species examined: 6	No. species examined: 1	No. species examined: 2	No. species examined: 1 (2n and 4n races)
Average chromosome length: 16.87 units. Chromosomes not divided into natural groups as to length or constriction position.	Average chromosome length: 14.25 units. Chromosomes divided into two natural groups as to length and constriction position.	Average chromosome length: 8.56 units. Chromosomes divided into two natural groups as to constriction position.	Average chromosome length: 16.32 units. Chromosomes divided into three natural groups as to length and constriction position.	Average chromosome length: 15.94 units. Chromosomes divided into three natural groups as to constriction position.
Chromosomes medianly to sub-medianly constricted, L/S 1.0-1.7 (-2.5).	*Group 1.* Short chromosomes medianly to sub-medianly constricted, L/S mostly 1.0-1.8.	*Group 1.* Chromosomes medianly to sub-medianly constricted. L/S 2.0 or less.	*Group 1.* Long chromosomes medianly to sub-medianly constricted, L/S 1.0-1.6.	*Group 1.* Medianly to sub-medianly constricted. L/S 1.0-1.8.
	Group 2. Long chromosomes sub-medianly to more or less sub-terminally constricted, L/S mostly 1.7-3.3.	*Group 2.* Chromosomes more or less sub-terminally constricted. L/S 1.0-2.0. *(Data very inconclusive)*	*Group 2.* Short chromosomes medianly to sub-medianly constricted, L/S 1.0-2.0.	*Group 2.* Sub-medianly to sub-terminally constricted. L/S 2.0-4.0.
			Group 3. Chromosomes of medium length, sub-medianly to sub-terminally constricted, L/S mostly greater than 2.0.	*Group 3.* Strongly sub-terminaly constricted, L/S 4.0 or greater.

sary to the reproduction of such a plant and its establishment in nature. An examination of the chromosomes of the three genera, while not completely voiding the possibility, does not support a theory of hybrid origin for *Dracopis*. First, the chromosomes of *Dracopis* are conspicuously smaller than those of species of *Rudbeckia* and *Ratibida*. While the morphological patterns of the chromosomes of *Rudbeckia* subg. *Macroline* and *Ratibida* are somewhat similar, those of *Dracopis* are distinctly different from each of the other two. An intergeneric hybrid between species of *Rudbeckia* and *Ratibida* would also display a distribution of 3 more or less distinct groups of chromosomes and would be expected to have more chromosomes with subterminal constrictions. From these data a theory of the hybrid origin of *Dracopis* cannot be completely negated but it seems very unlikely unless the chromosomes of this species have changed considerably since the initial hybridization. Battaglia (1946a) reported that *Dracopis* is fully sexual, reproducing according to the *Fritillaria*-type of embryo-sac formation. This fact also argues against the possibility of hybrid origin of the genus.

BIBLIOGRAPHY

BATTAGLIA, E. 1946a. Ricerche cariologiche ed embriologiche sul genere *Rudbeckia* (Asteraceae). I-V: Il gametofito femminile e maschile di *R. bicolor* Nutt., *R. hirta* L., *R. hirta* L. var. meine freude Hort., *R. amplexicaulis* Vahl, e *R. purpurea* L. (= *Echinacea purpurea* Moench.). Nuovo Gior. Bot. Ital., n.s. 53:1-26.

——. 1946b. Ricerche cariologiche ed embriologiche sul genere *Rudbeckia* (Asteraceae). VI: Apomissia in *Rudbeckia speciosa* Wender. Nuovo Gior. Bot. Ital., n.s. 53:27-69.

——. 1946c. Ricerche cariologiche ed embriologiche sul genere *Rudbeckia* (Asteraceae). VII: Apomissia in *Rudbeckia laciniata* L. e anfimissia nella sua varietà a fiori doppi. Nuovo Gior. Bot. Ital., n.s. 53:437-482.

——. 1947. Ricerche cariologiche ed embriologiche sul genere *Rudbeckia* (Asteraceae). XII: Il gametofito femminile e maschile di *Rudbeckia flava* Greene, con particolare riguardo al suo comportamento di ibrido strutturale. Nuovo Gior. Bot. Ital., n.s. 54:560-567.

——. 1952. Utilizzazione di dati embriologici in funzione di una migliore conoscenza della sistematica del genere *Rudbeckia* (Compositae). Atti Soc. Toscana Sci. Nat. (Pisa). Ser. B. 59:217-221.

FAGERLIND, F. 1946. Sporogenesis, Embryosackentwicklung und pseudogame Samenbildung bei *Rudbeckia laciniata* L. Acta Horti Bergiani 14:39-99.

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co., New York.

GLEASON, H. A. 1952. The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. New York Botanical Garden, New York.

GRAY, ASA. 1884. Synoptical Flora of North America. Vol. 1. Pt. 2.

MURNEEK, A. E. 1940. Length of day and temperature effects in *Rudbeckia*. Bot. Gaz. **102**:269-279.

PERDUE, R. E., JR. 1957. Synopsis of *Rudbeckia* subgenus *Rudbekia* Rhodora **59**: 293-299.

——. 1958. Monograph of *Rudbeckia* subgenus *Macrocline*. Contrib. Tex. Research Found. (In press).

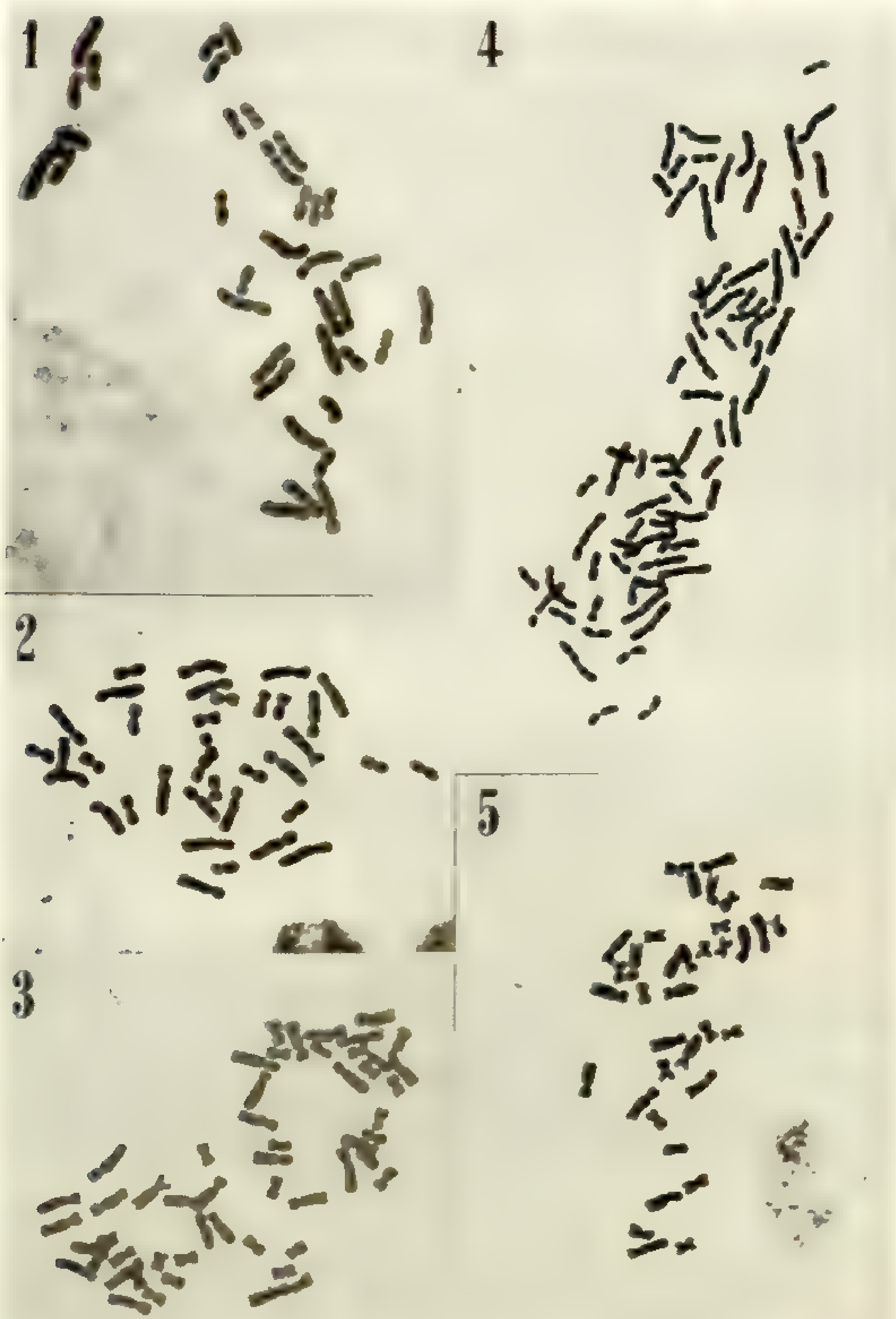


Fig. 1-5. Chromosomes of *Rudbeckia* species, mitotic metaphases from root tips. Fig. 1. *R. californica* var. *californica*, 2n=36 (1425x). Fig. 2. *R. laciniata* var. *laciniata*, 2n=36 (1370x). Fig. 3. *R. laciniata* var. *laciniata*, 2n=54 (1350x). Fig. 4. *R. laciniata* var. *laciniata*, 2n=72 (1350x). Fig. 5. *R. occidentalis* var. *occidentalis*, 2n=36 (1350x).

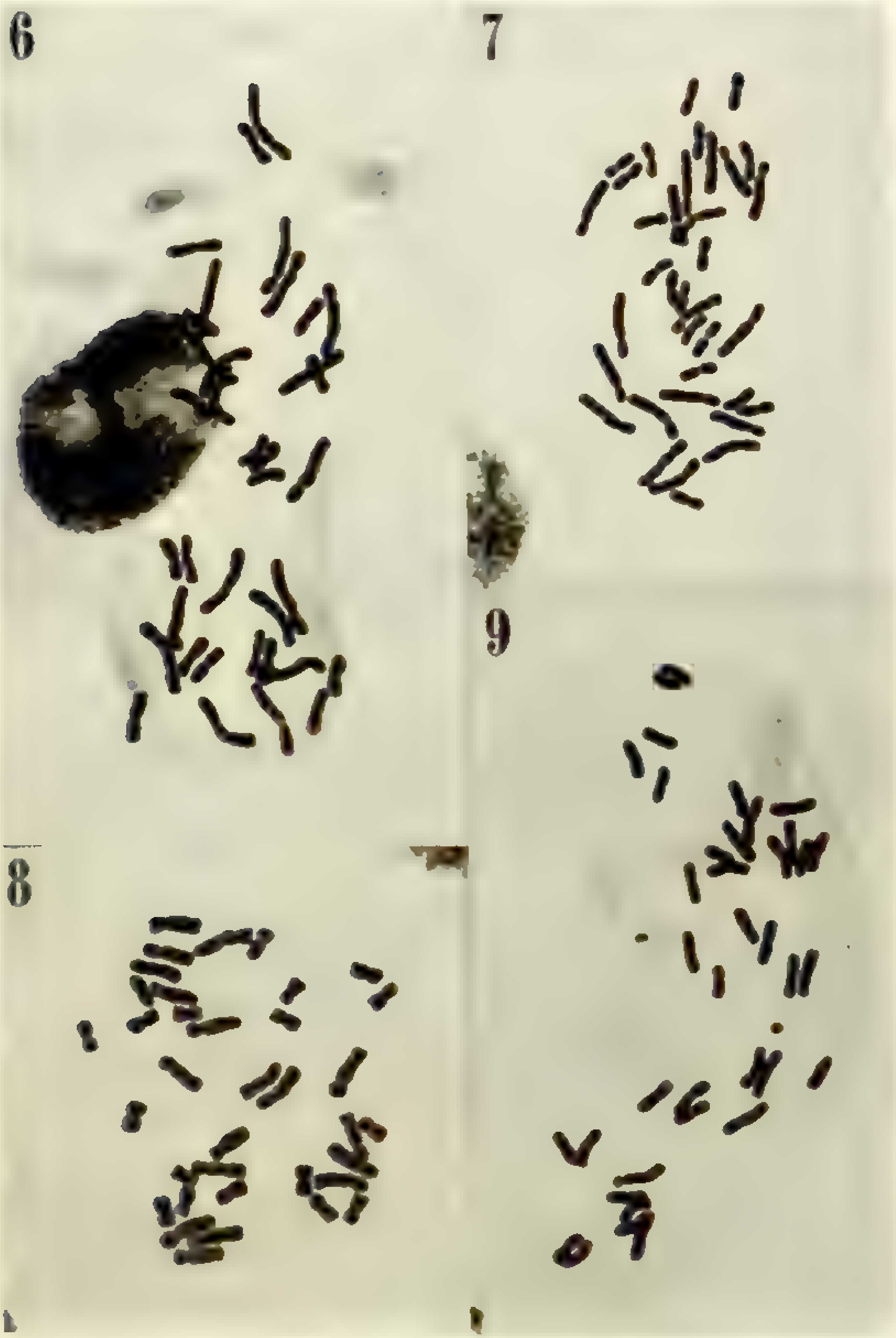


Fig. 6-9. Chromosomes of *Rudbeckia* species, mitotic metaphases from root tips. Fig. 6. *R. maxima*, 2n=36 (1350x). Fig. 7. *R. nitida* var. *texana*, 2n=36 (1350x). Fig. 8. *R. mohrii*, 2n=38 (1350x). Fig. 9. *R. hirta* var. *pulcherrima*, 2n=38 (1350x).

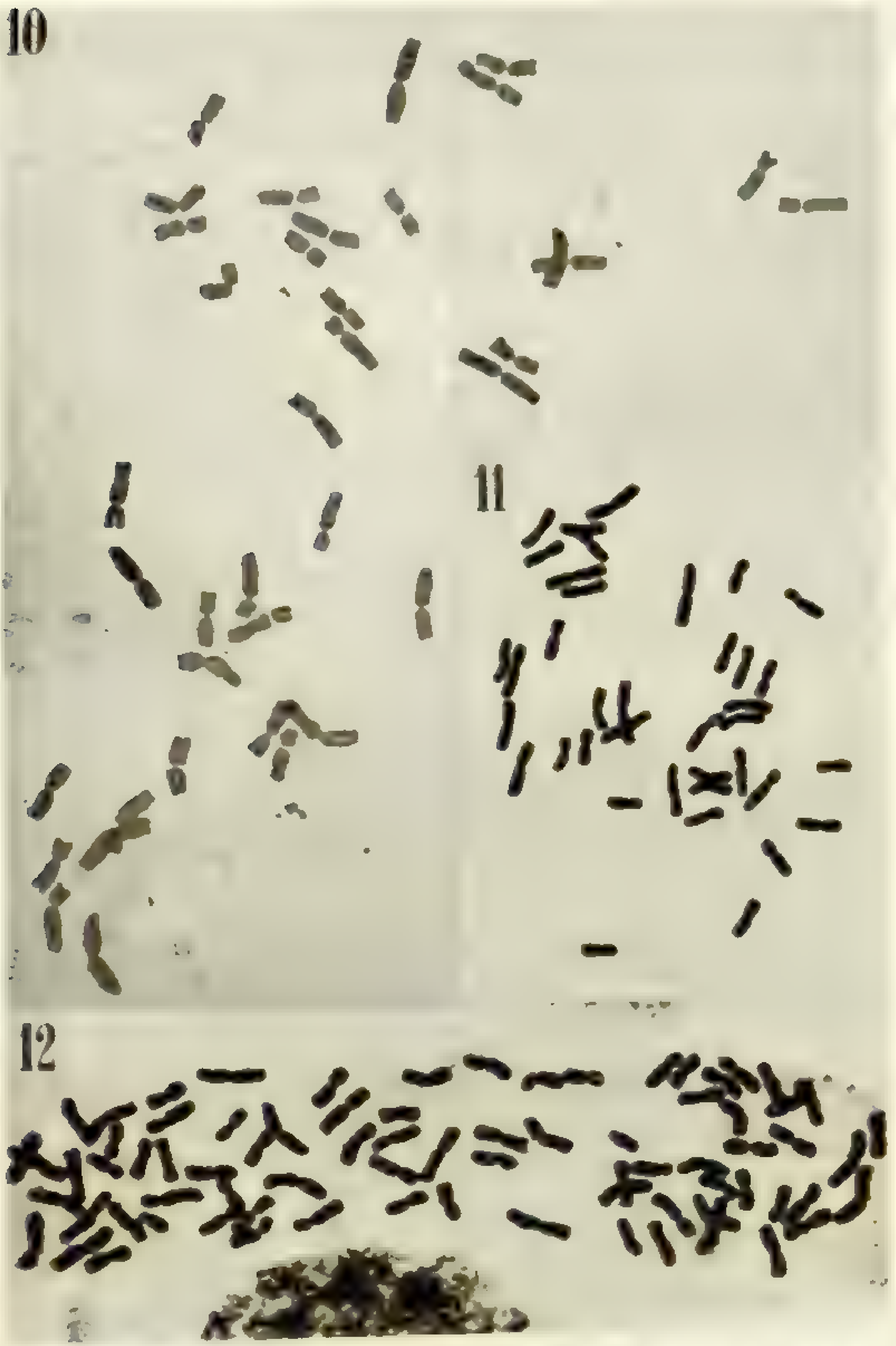


Fig. 10-12. Chromosomes of *Rudbeckia* species, mitotic metaphases from root tips. Fig. 10. *R. missouriensis*, 2n=38 (1425x). Fig. 11. *R. fulgida* var. *palustris* 2n=38 (1350x). Fig. 12. *R. fulgida* var. *speciosa*, 2n=77 (1425x).

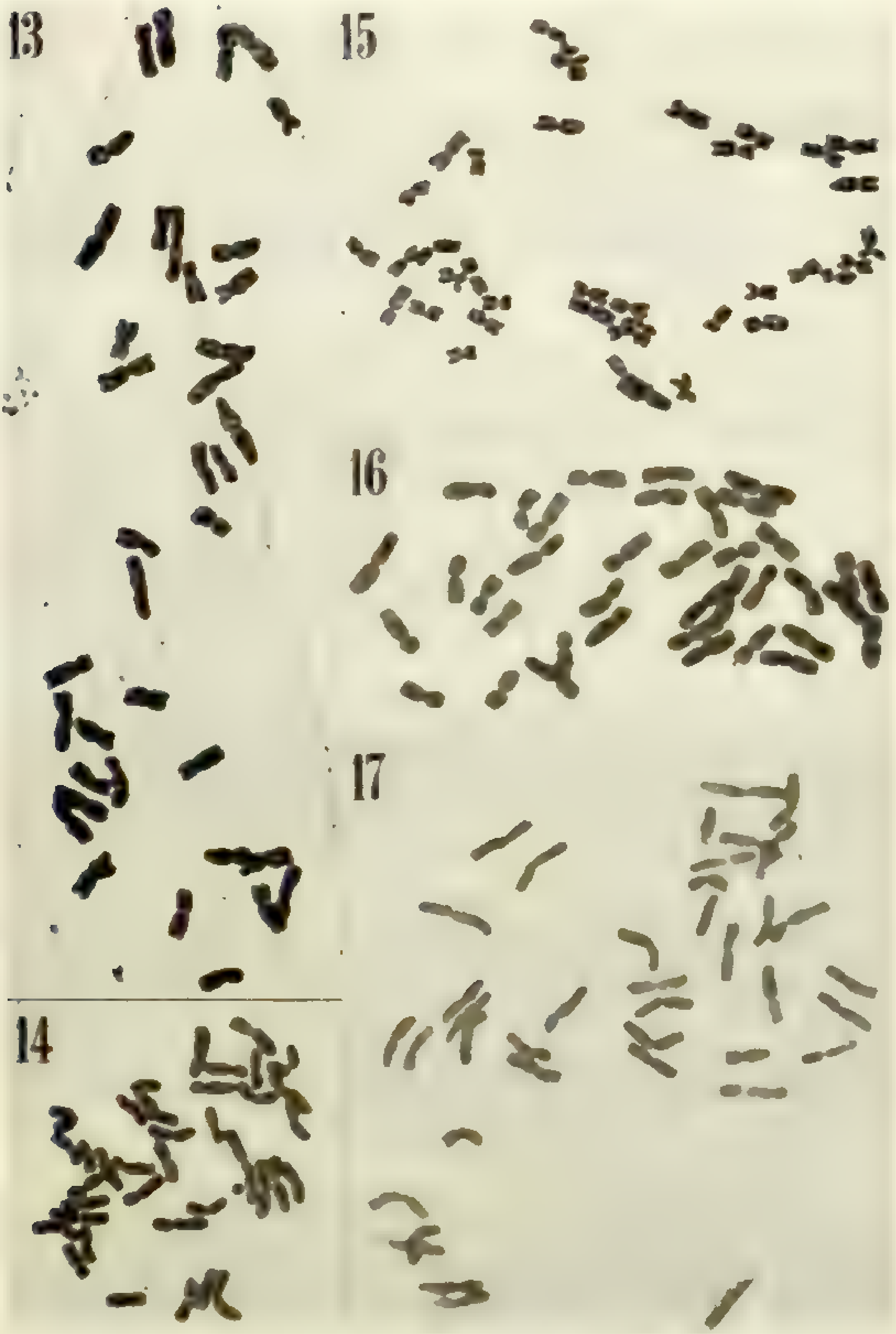


Fig. 13-17. Chromosomes of *Rudbeckia* species, mitotic metaphases from root tips. Fig. 13. *R. fulgida* var. *fulgida*, 2n=38 (1425x). Fig. 14. *R. graminifolia*, 2n=38 (1350x). Fig. 15. *R. mollis*, 2n=38 (1425x). Fig. 16. *R. subtomentosa*, 2n=38 (1425x). Fig. 17. *R. grandiflora* var. *grandiflora*, 2n=38 (1350x).

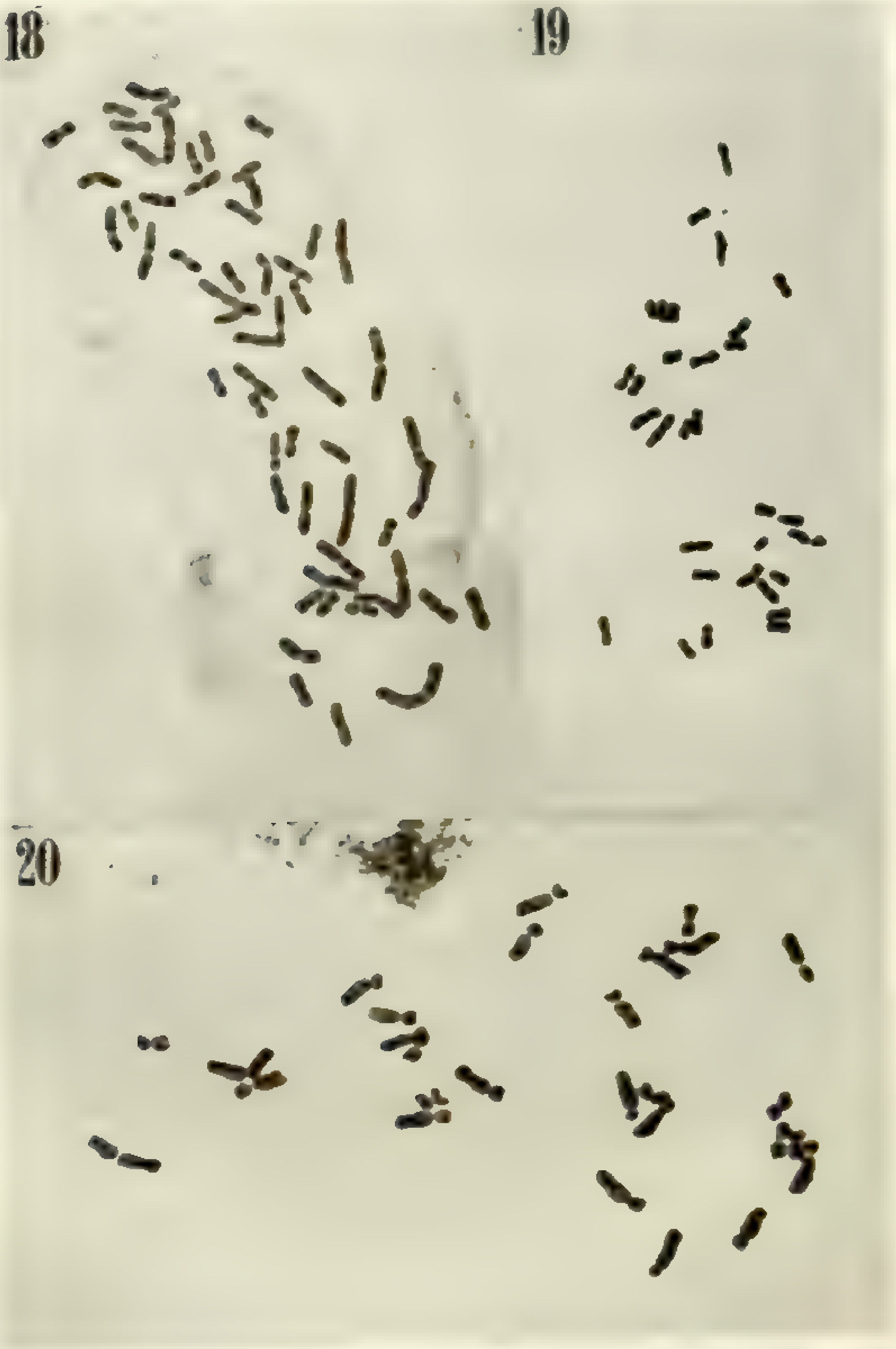
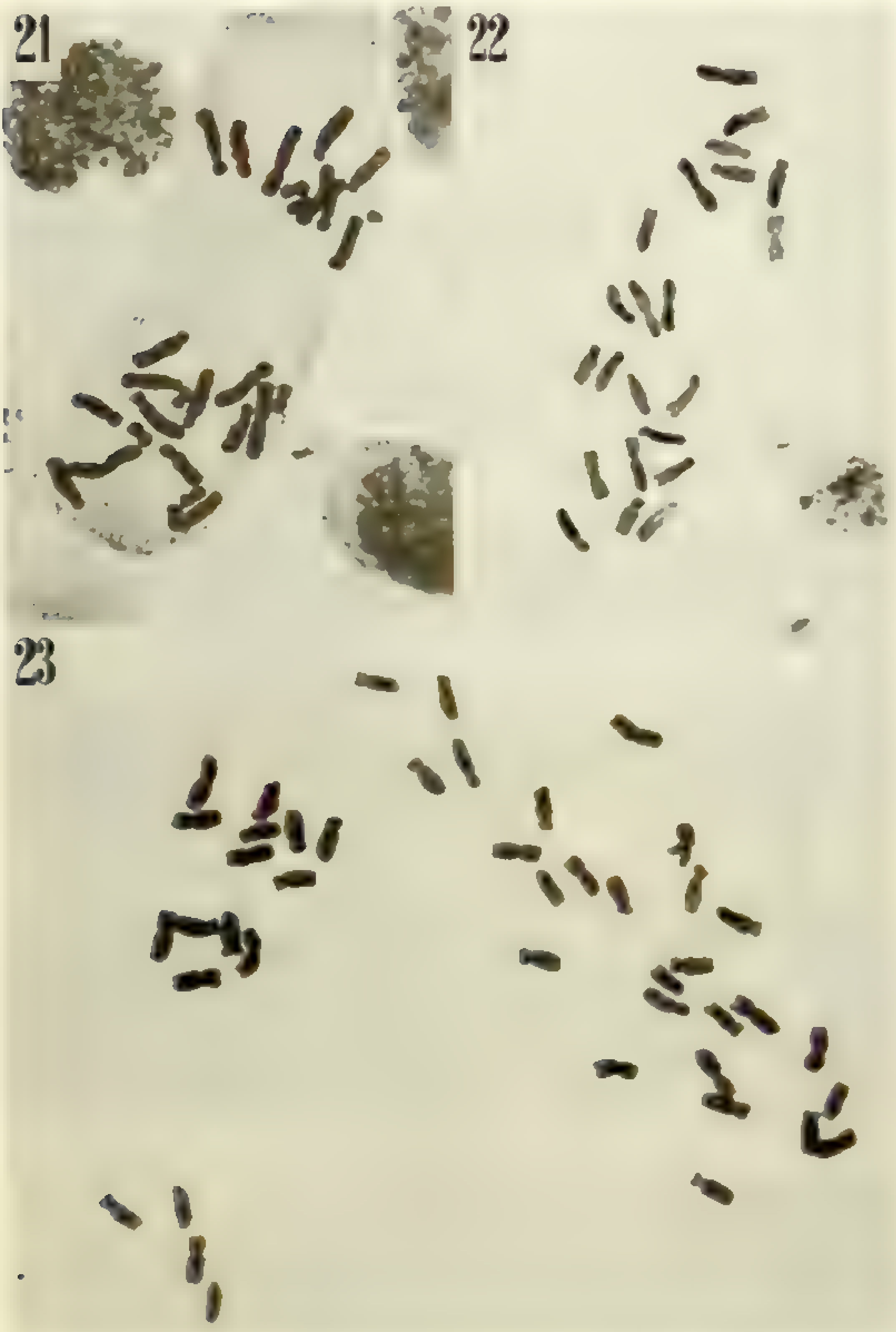


Fig. 18-20. Chromosomes of *Rudbeckia*, *Dracopis*, and *Ratibida* species, mitotic metaphases from root tips. Fig. 18. ***Rudbeckia triloba*** var. ***triloba***, $2n=57$ (1425x). Fig. 19. ***Dracopis amplexicaulis***, $2n=32$ (1350x). Fig. 20. ***Ratibida pinnata***, $2n=28$ (1350x).



Figs. 21-23. Chromosomes of *Ratibida* and *Echinacea* species: mitotic metaphases from root tips. Fig. 21. *Ratibida columnaris*, 2n=27 (1425x). Fig. 22. *Echinacea pallida*, 2n=22 (1425x). Fig. 23. *E. pallida*, 2n=44, (1350x).

CONTRIBUTIONS FROM THE GRAY HERBARIUM
OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXVI

A MONOGRAPHIC STUDY OF THE CYRILLACEAE

By

Joab L. Thomas

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

[redacted]

CONTRIBUTIONS FROM THE GRAY HERBARIUM
OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXVI

A MONOGRAPHIC STUDY OF THE CYRILLACEAE

By

JOAB L. THOMAS

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

1960

Issued May 27, 1960

The Lexington Press Inc., Lexington, Massachusetts

A MONOGRAPHIC STUDY OF THE CYRILLACEAE

BY

JOAB L. THOMAS

INTRODUCTION

The Cyrillaceae is a family of shrubs and small trees distributed on the Coastal Plain of southeastern United States, in middle America, including the West Indies, and in northern South America. The family, as recognized in the present treatment, is composed of three genera and thirteen species. Although the three genera are very distinct morphologically, the family appears to be a natural unit, and is easily distinguishable from related groups. On the basis of a study of fossil pollen it is evident that the Cyrillaceae is also an old family, with definite Cyrillaceous pollen occurring in deposits of Upper Cretaceous age (Steeves, 1959). The genera, also, have apparently been distinct at least since Upper Oligocene (Traverse, 1955).

In addition to a taxonomic revision of the three genera the present treatment includes studies of the morphology, geographic distribution, paleobotanical history, evolution, species relationships, and infraspecific variation. The study of herbarium material was supplemented by two summers of field work in southeastern United States, and a short period of time in Pinar del Rio and Oriente Provinces in Cuba. Special mass collections and detailed studies of the plants under field conditions proved to be invaluable, both in clarifying the taxonomy of the group and in interpreting the patterns of infraspecific variation.

Vegetative reproduction was found to be widespread in both *Cyrilla* and *Cliftonia*. The nature and effects of this phenomenon have been examined in some detail in these two genera, and some consideration has been given to the effects of similar phenomena in other plant groups. Previous workers concerned with the Cyrillaceae have either failed to recognize the occurrence of widespread asexual reproduction, or have failed to consider the effects of this phenomenon on the biology of the plants. This has resulted in a false and misleading picture of the variation, particularly in *Cyrilla*, where the effects of asexual reproduction are very pronounced.

Although considerable information has been obtained in the present study, there are several interesting problems in the Cyrillaceae which need further work. Additional field studies are needed on the ecology and infraspecific variation of several species of *Purdiaea* in eastern Cuba. Further work is also needed on the origin and development of root sprouts in *Cyrilla*, particularly morphogenetic studies of the early stages of bud formation. The cytology of the entire group is virtually unknown and deserves careful study.

ACKNOWLEDGEMENTS

I am deeply indebted to Professor Reed C. Rollins, Director of the Gray Herbarium, under whose guidance the research was carried out. His helpful suggestions and criticisms during the preparation of this work, and his assistance in obtaining funds for research and field work are greatly appreciated.

Dr. Robert C. Foster has answered many questions on nomenclature, and Mrs. L. Schwarten has given valuable assistance in the library. The Latin diagnosis was prepared by Mr. Leslie A. Garay. Dr. C. E. Kobuski has been very helpful in obtaining loans of herbarium specimens and in providing storage and work space in the Harvard University Herbarium. Helpful suggestions and criticisms have been offered by several other persons associated with the Herbarium, including Dr. C. E. Wood, Dr. K. A. Wilson, Dr. Arthur S. Barclay, Mr. George Argus, and Dr. W. P. Adams.

Professor Ralph H. Wetmore has shown a great deal of interest in the morphological studies and has offered many valuable suggestions. Professor Elso S. Barghoorn has given much assistance in the paleobotanical studies and has generously provided equipment for the preparation of photomicrographs.

Dr. R. K. Godfrey of Florida State University has kindly provided cytological material and several special mass collections of dried material. A summer of field study was made possible by a grant from the Fernald Fund For Study in Systematic Botany, provided through the generosity of Mr. F. W. Hunnewell of Wellesley, Massachusetts. Research during the summer of 1958 was supported by a National Institute of Health grant-in-aid through the Department of Biology, Harvard University.

I wish to extend special thanks to my wife, Marly Dukes Thomas, without whose assistance and understanding this study would not have been possible.

I am indebted to the curators of the following herbaria for the loan of specimens used in this work:

Arnold Arboretum (A); Chicago Natural History Museum (F); University of Florida (FLAS); Gray Herbarium (GH); Herbario de la Salle, Habana (LS); University of Michigan (MICH); Missouri Botanical Garden (MO); Université de Montréal (MT); New York Botanical Garden (NY); Estación Experimental Agronómica, Habana (SV); University of Texas (TEX); University of California (UC); United States National Museum (US).

HISTORY OF THE GENERA

CYRILLA

Cyrilla racemiflora was described by Linnaeus in 1767 from material sent to him by Dr. Alexander Garden, a resident of South Carolina. The name *Cyrilla* was given in honor of Dr. Domenico Cirillo, an Italian physician and professor at Naples. Michaux (1803) described a second species, *Cyrilla antillana*, apparently from material collected in the West Indies, but no specimen or locality was cited. A few years later, however, Poiret (1812) noted that the characteristics used to distinguish the two species intergraded to such an extent that he could not separate them, and concluded that they must be varieties of the same species. This seems to have established a precedent, for in the years to follow ten more species were described in this genus, and in most cases later workers found the species difficult to segregate due to numerous intermediate forms which seemed to link one species to another. Botanists who were familiar with this genus in the field were particularly aware of these intermediate forms.

Rafinesque (1840) noted that the various collections of *Cyrilla* from the United States showed considerable variation in leaf size and shape, but stated that he had found in the fruits "... characters for three distinct, blended species." Subsequent authors agreed that these species were blended, and two of the three species were not recognized in any later works, the names seldom appearing even as synonyms. The third species, *Cyrilla parvifolia* Rafinesque, has been recognized by several workers, although the authorship is usually attributed to Shuttleworth (1896) who described a similar plant under the same name. Sargent (1921) reduced *Cyrilla parvifolia* to a variety of *C. racemiflora*, stating that the plants of the variety "... afford no morphological characters by which it can be distinguished specifically from that species." One additional species in the United States, *Cyrilla arida*, was described by Small (1924) from material collected in the southern lake region of Florida.

N. E. Brown (1901) described a new South American species of *Cyrilla*, *C. brevifolia*, from material collected in British Guiana. However, Gleason (1931), after studying additional collections from this area, stated that "... the differences between this species and the following (*C. racemiflora*) are slight and scarcely entitle it to specific rank."

Three additional species of *Cyrilla* have been described from eastern Cuba: one by P. Wilson (1902) — *Cyrilla cubensis*, and two by Urban (1926) — *C. nitidissima* and *C. nipensis*. These species have been recognized in most subsequent treatments of the group, but at least one worker, Carabia (unpublished)[1], concluded that all of the representatives of *Cyrilla* growing in Cuba belonged to the original Linnaean species, *C. racemiflora*.

In spite of widespread disagreement as to the validity of the various species of *Cyrilla*, Mattick (1935) recognized nine of the above species, excluding the two Rafinesque species only. This treatment was also followed by Uphof in Engler and Prantl (1942). Yet there was still considerable disagreement in the literature, and some authors (e. g. Lawrence, 1951) continued to refer to *Cyrilla* as a monotypic genus. The situation was accurately summarized by Gleason (1952) as follows: "The genus is by some considered to be monotypic, by others as many as ten species are recognized."

CLIFTONIA

In contrast to *Cyrilla*, *Cliftonia* has been treated as a monotypic genus by every author who has dealt with the group. However, it is such a striking and unusual looking plant that it has been described as a new genus on several different occasions. It was originally described by Lamarck (1791) as a species of *Ptelea*, *P. monophylla*. The original description was based on fruiting material only, and apparently the winged fruit of *Cliftonia* was the characteristic which caused Lamarck to include it in the genus *Ptelea*. Fourteen years later Gaertner f. (1805) described a new genus and species, *Cliftonia nitida*, unaware that it was the same as Lamarck's species of *Ptelea*. Britten (1905) pointed out that the name *Cliftonia* was given in honor of D. G. Clifton, Chief Justice of West Florida, and not Francis Clifton, the English physician, as was stated by Sargent (1892). Four years after Gaertner's description of *Cliftonia*, this taxon was again described as a new genus and species, *Mylocaryum ligustrinum*, by Willdenow (1809). A fourth generic name for this taxon, *Walteriana*, was published in synonomy by Endlicher (1841) from the manuscript of Fraser.

There was considerable confusion in the nomenclature of *Cliftonia* for several years as various combinations of the above names were used by different authors. Finally Britton (1889) pointed out by implication that the correct combination was *Cliftonia monophylla*. He did not make the combination, however, and the first author to use the correct combination was Sargent (1892), who attributed

---

[1] This appears on annotation labels which read, "Revision of Cuban Plants – det. J. P. Carabia, 1942." Apparently this information has not been published.

the combination to Britton. In recent years there has been little confusion in either the nomenclature or the taxonomy of *Cliftonia*.

PURDIAEA

The genus *Purdiaea* and a single species, *P. nutans*, were described by Planchon (1846) from material in the Hooker Herbarium. It was named in honor of Purdie who collected it in New Granada (Colombia). The second species of *Purdiaea* was described by A. Richard (1853) as a new genus and species, *Costaea cubensis*, from material collected in Cuba by Valenzuela. For unexplainable reasons, most subsequent authors adopted the later name *Costaea*, treating the older name *Purdiaea* as a synonym. The correct combination *Purdiaea cubensis* was first made by Urban (1926).

A third species, *Purdiaea stenopetala*, was described by Grisebach (1860) from the collections of Charles Wright in Oriente Province, Cuba. Three additional species from eastern Cuba *(P. velutina, P. microphylla*, and *P. shaferi)* were described by Britton and Wilson (1915) from the extensive collections of Shafer in Oriente Province.

From collections of *Purdiaea* in Peru made by Weberbauer, Gilg (1931) described a new genus and species, *Alloiosepalum weberbaueri*. Mattick (1935) noted that Gilg had later become aware that his new genus was actually a species of *Purdiaea* but was prevented by his death from making the transfer. Mattick made the transfer to the genus *Purdiaea*, recognizing it as a distinct species, *P. weberbaueri.*

The latest treatment of the group is a revision of the Cuban species of *Purdiaea* by Marie-Victorin which was edited and published posthumously by J. Brunel in 1948. In that treatment, four species *(P. ekmanii, P. moaensis, P. nipensis, P. ophiticola)* and three varieties *(P. cubensis* var. *albosepala, P. nipensis* var. *alaini, P. ophiticola* var. *parvifolia)* were described as new.

CYRILLOPSIS

The genus *Cyrillopsis* Kuhlmann (1925) was included in the Cyrillaceae by Mattick (1935) and Uphof in Engler and Prantl (1942). This genus is excluded from the Cyrillaceae in the present treatment on the basis of wood anatomy, pollen morphology, and several aspects of the flower structure (discussed below). It is suggested that this genus possibly belongs to the Celastraceae.

ECONOMIC IMPORTANCE

Members of the Cyrillaceae are of only minor economic importance. Both *Cyrilla* and *Cliftonia* are occasionally cultivated as ornamentals in southeastern United States, but are seldom cultivated outside of this area except in botanic gardens. These plants can be grown considerably north of their natural range. *Cliftonia* has been grown as far north as Delaware and southern New Jersey; *Cyrilla* as far north as Massachusetts (Rehder, 1940). A specimen of *Cyrilla* has been in cultivation at the Arnold Arboretum in Jamaica Plain, Massachusetts since 1926. Although the plant is somewhat dwarfed and the reproductive structures do not develop normally, it is a very attractive shrub and flowers abundantly each year.

The bark of *Cyrilla* is rich in phenolic compounds, and there are a few reports in the literature of the use of this bark as a styptic or astringent (Sargent, 1892). According to Elliott (1821) the bark of *Cyrilla* can also be used as ". . . a serviceable application to wounds or ulcers, where the indication is to cicatrize them."

In some areas of southeastern United States *Cyrilla* is valued in the production of honey. The glandular, secretory petals, the long flowering period, and the large number of flowers produced each year combine to make this plant an unusually good source of nectar. The honey is known locally as "titi" honey, in reference to the colloquial name for *Cyrilla.*

MATERIALS AND METHODS

The plant materials used in the morphological studies were primarily from my own collections, although herbarium material was used in a few instances. A list of all collections used, giving the area from which they were collected and the herbarium in which the collections were deposited, is included in the appendix.

Floral buds were fixed in either Carnoy's solution with chloroform, or Formalin-Acetic acid-Alcohol. Those fixed in Carnoy's solution were transferred after two to five hours into 70% ethyl alcohol; those fixed in FAA were stored in the same solution. The buds were dehydrated in a normal-butyl alcohol series, embedded in paraffin and sectioned with a rotary microtome. The sections were stained with either safranin and fast green or crystal violet, and mounted in damar.

Stems and older wood were softened in hot water and sectioned, without embedding, with a sliding microtome.

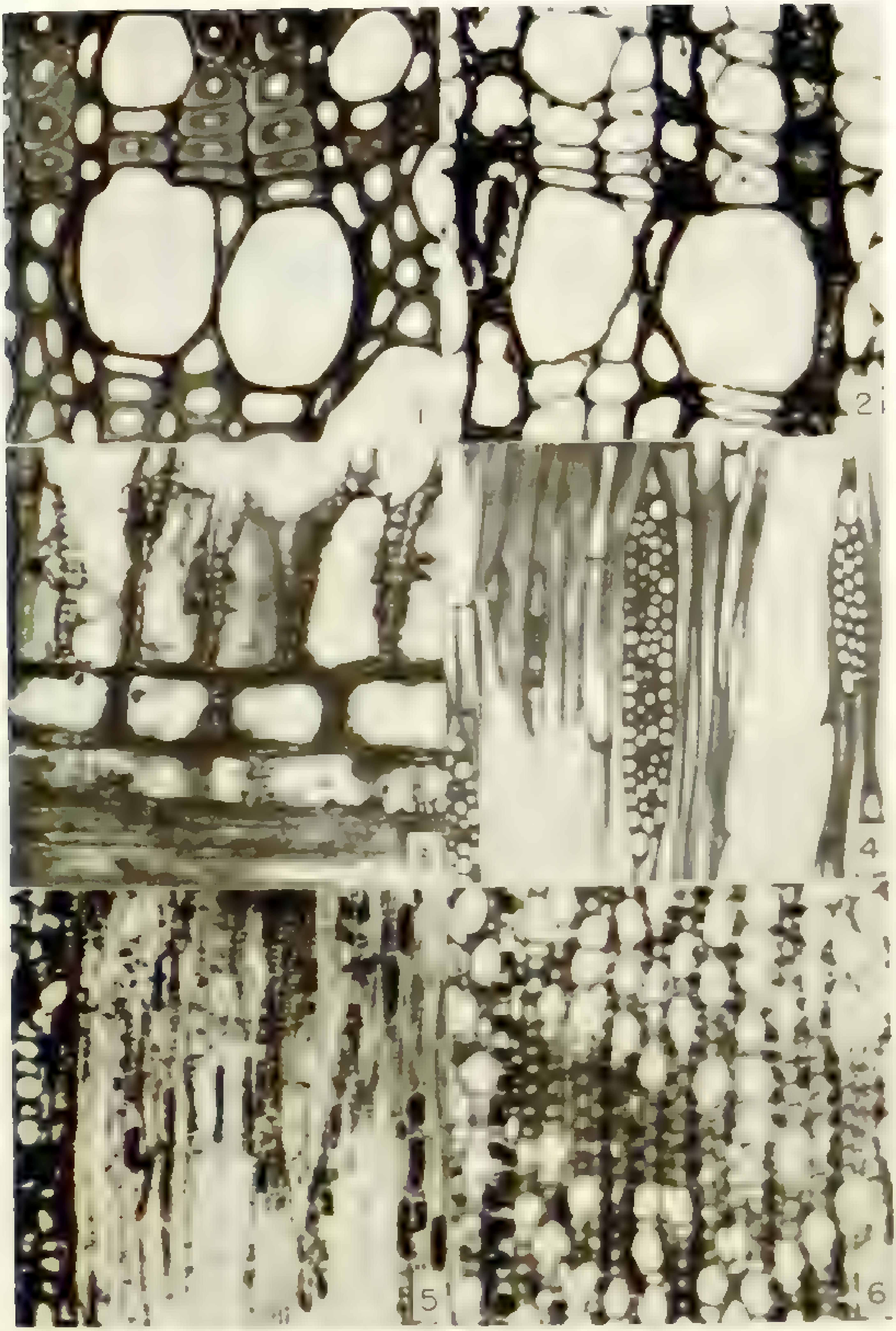
Wood sections were stained with Heidenhain's Haematoxylin and safranin, and mounted in diaphane.

The leaf preparations were made by hand sectioning with a razor blade. In a few cases leaves fixed and stored in FAA were used, but it was found that satisfactory preparations could be made from dried material. The dried leaves were softened in warm water, with a little detergent added, for approximately two hours before sectioning. The sections were mounted, unstained, in glycerin.

VEGETATIVE MORPHOLOGY

STEM. — In *Cyrilla* and *Cliftonia* the young stems are glabrous and are usually angled or ridged. The ridges tend to form a spiral pattern around the stem with each ridge evident for a distance of approximately two nodes, ending at the base of a leaf. The ridges become less prominent as the stem increases in diameter, and by the end of the second growing season the stems are more or less terete. In *Purdiaea* the external morphology of the stem varies considerably from one species to another, ranging from the small, delicate, somewhat vine-like stems in *P. parvifolia*, to the robust, rigidly erect stems of *P. velutina*. The robust stems are usually more sharply ridged than the smaller stems, but in all members of the Cyrillaceae the young stems are angled to some extent. The stems of *Purdiaea velutina* and *P. moaensis* are always densely pubescent near the end. In other species, such as *Purdiaea cubensis* and *P. nutans*, the stems are always glabrous, whereas in *P. nipensis* the stems may be either glabrous or puberulent.

Cork formation begins early in the stems of all three genera. Although the periderm layer is relatively thin in young stems, it often becomes quite thick and spongy in older stems, especially in *Cyrilla*. It is apparently this feature which accounts for the common name "Leatherwood" which is often applied to *Cyrilla* and occasionally to *Cliftonia* in the southeastern United States. A single layer of phelloderm is developed in the young stems of *Cyrilla*, *Cliftonia* and probably of *Purdiaea*, although it has not been verified in the latter genus. The primary cortex contains numerous thick-walled parenchyma cells with wide lumina (Metcalfe and Chalk, 1950). The cortex, however, is rapidly destroyed by the periderm which develops rather early in the innermost layers of the cortex. The primary vascular system of the stem is a eustele with numerous primary vascular bundles surrounding the pith. The primary xylem is com-



Figs. 1–6. Wood anatomy of the Cyrillaceae. Fig. 1. *Cliftonia monophylla*, transverse section of mature wood showing a growth ring. Fig. 2. *Cyrilla racemiflora*, transverse section of mature wood showing a growth ring. Fig. 3. *Cyrilla racemiflora*, radial section through a ray. Note irregularly thickened cell walls. Fig. 4. *Cliftonia monophylla*, tangential section of mature wood showing an unusually large multiseriate ray. Fig. 5. *Purdiaea nutans*, radial section through a young stem. Fig. 6. *Purdiaea nutans*, transverse section through the same stem shown in Fig. 5. Figs. 1–4, magnification ca. [illegible] ×. Figs. 5–6, magnification ca. 115 ×.

posed of spirally-thickened tracheids in the protoxylem with a rapid transition in the metaxylem to tracheids with bordered pits, fiber-tracheids, and vessels (Fig. 5). The pith is 5-angled in transverse section. It is composed of relatively thick-walled, parenchymatous cells, many of which are filled with densely-staining phenolic compounds.

MATURE WOOD. — Growth rings, present in all three genera, consist of from two to five rows of fiber-tracheids which are thicker-walled and usually somewhat smaller in radial dimensions than the fiber-tracheids in the "spring wood" (Figs. 1 and 2). The vessels are usually abruptly smaller and fewer in number near the end of a growing season than earlier in the season. In the tropical representatives the growth rings are obscure, and in some preparations it is difficult indeed to designate a definite growth ring. This, of course, is expected in a tropical or sub-tropical tree growing along stream margins where there is little seasonal fluctuation in either temperature or moisture.

The vessel elements are small with a tangential diameter of 25-50 micra for *Cyrilla* and *Cliftonia* (Metcalfe and Chalk, 1950). No old wood of *Purdiaea* has been seen, but the vessel size in the young stem is comparable to that in *Cyrilla* and *Cliftonia* at a similar stage of development (Fig. 6). In *Cyrilla* the vessels are solitary; in *Cliftonia* pore multiples occur, particularly in the late wood; and in *Purdiaea* pore multiples occur sporadically throughout the secondary xylem of the young stems. The vessels are numerous in all three genera, more so in *Cliftonia* and *Purdiaea* than in *Cyrilla*. The vessel elements are thin-walled and somewhat angular in cross-section. The end walls are oblique, and there is considerable overlap of consecutive elements in the vessel (Fig. 7). This phenomenon accounts for most of the apparent tangential pairs of vessels seen in transverse section of *Cyrilla*. The perforation plates are scalariform, consisting of numerous small bars (Fig. 8). There is an average of 30-40 bars per end wall, but as many as 65-70 have been counted in some preparations of both *Cyrilla* and *Cliftonia*. The intervascular pitting is rather variable, even in a single plant. Scalariform, transitional, and opposite intervascular pitting have been seen in a single preparation, although transitional to opposite pitting is by far the most common type. The mean length of the vessel elements in *Cyrilla* and *Cliftonia* is approximately 0.8 mm., with a range of 0.6 to 1.0 mm. (Bailey and Tupper, 1918). Dark-staining deposits occur frequently in older vessels, but

FIGS. 7–9. Wood anatomy of the Cyrillaceae. Fig. 7. *Cyrilla racemiflora*, tangential section of mature wood, showing the upright cells on the ends of rays. Fig. 8. *Cliftonia monophylla*, radial section of mature wood, showing a typical vessel end wall with 30–40 scalariform bars. Fig. 9. *Cliftonia monophylla*, radial section of mature wood, showing the intervascular pitting of tracheids and fiber-tracheids. Note that in the fiber-tracheids the pit aperture extends only slightly beyond the pit border. Figs. 7–9, magnification ca. 360 ×.

no tyloses have been seen in any members of the Cyrillaceae.

The imperforate tracheary elements are primarily fiber-tracheids in the older wood, but some tracheids occur in both *Cyrilla* and *Cliftonia* (Fig. 9). The fiber-tracheids produced early in a growing season have relatively thin walls; those produced late in the season have moderately thick walls. Small, circular-bordered pits are abundant on both the radial and the tangential walls (Figs. 4 and 9). The mean length of the fiber-tracheids is approximately 1.0 mm. with a range of 0.6 to 1.3 mm. (Bailey and Tupper, 1918).

The rays are heterogeneous and may be either uniseriate or multiseriate (Fig. 4). The uniseriate rays are usually only 3-5 cells high, but may be up to 12 cells high. Those with 3-5 cells are usually composed of only upright or square cells, whereas those containing 8 or more cells are composed primarily of procumbent cells. The multiseriate rays contain mostly procumbent cells, but there are usually upright cells on each end, often forming wings (Fig. 7). Most of the multiseriate rays are 4-6 cells wide and 20-30 cells high, although exceptionally large rays up to 8 cells wide and 50-60 cells high have been observed. The cell walls in the rays are usually very irregular, with conspicuous thick and thin areas. This is particularly striking in the upright cells on the ends of multiseriate rays. Occasionally some of the multiseriate rays in *Cyrilla* broaden on the periphery external to the cambium. This characteristic is particularly noticeable in some of the fossil preparations of *Cyrilla* from the Brandon Lignite in Vermont (Spackman, 1949).

The xylem parenchyma is relatively abundant and diffuse in *Cyrilla* usually occuring as apotracheal strands. It is less abundant in *Cliftonia*, where it is more often found adjacent to vessel elements.

The nodes are unilacunar in all members of the Cyrillaceae. There is some evidence from the external ridges on the stem that the vascular traces leave the stele approximately two nodes below the level at which they enter a leaf, but this has not been verified by anatomical studies.

LEAVES. — The leaves are simple, entire, estipulate, and moderately to heavily coriaceous. They are highly variable in size and shape in *Cyrilla* and *Purdiaea*, but rather uniform in *Cliftonia*. In a few species of *Purdiaea* the leaves are approximately the same size and shape in all of the specimens seen; but these are poorly collected species, and future collections will undoubtedly show a much wider range of variation. The high degree of variation in the leaves of *Cyrilla* is discussed in detail below in the section on variation in *C. racemiflora.* In general, the leaves of *Purdiaea* range in length from 1-1.5 cm. in *P. microphylla*, to 11-12 cm. in *P. moaensis;* those of *Cyrilla* range from 2-15 cm. long and those of *Cliftonia* range from 3-6 cm. long.

The venation is pinnate in *Cyrilla*, *Cliftonia*, and the South American species of *Purdiaea*. In all other species of *Purdiaea*, however, the leaves have one to five pairs of strongly arcuate, lateral veins which run longitudinally, more or less parallel to the margin of the leaf. The midvein is prominent beneath in all members of the Cyrillaceae. In most species of *Purdiaea* the lateral veins are prominent beneath and impressed or prominent above; whereas in *Cliftonia* the lateral veins are scarcely if at all prominent on either surface. In *Cyrilla* there is considerable variation in the degree of prominence of the lateral veins.

There is a fairly heavy layer of cuticle on both surfaces of the leaves, particularly in the more coriaceous leaves of *Purdiaea* and the leaves of the subtropical representatives of *Cyrilla*. The cuticle on the lower surface is often irregularly ridged in *Cliftonia*. Stomata are fairly abundant and confined to the lower surface in all three genera. The guard cells are not flanked by any specialized accessory cells, but by normal epidermal cells. Below the upper epidermis there are two layers of rather compact, columnar, palisade cells in *Cyrilla* and *Purdiaea*, and one to two layers of more loosely arranged palisade cells in *Cliftonia*. According to Solereder (1899) the mesophyll in *Cyrilla* and *Cliftonia* consists solely of palisade tissue, but in all of the preparations that I have seen (which include samples from the United States, Cuba, and South America) there is a well-developed, spongy mesophyll of loosely arranged, more or less isodiametric cells, with numerous large air spaces. These air spaces are particularly large and numerous in leaves of *Cliftonia* which have only a single layer of palisade cells. In these leaves the mesophyll region occupies approximately 2 3 of the cross-sectional diameter of the leaf. In some leaves of *Cliftonia* there is a gradual transition between the columnar cells of the palisade layer and the more isodiametric cells of the mesophyll.

Druses are abundant in the leaves of all three genera. Solitary crystals have been seen in *Purdiaea* and *Cyrilla* and were reported in *Cliftonia* by Beauvisage (1920). The vascular bundles in the veins are surrounded by a sheath of thick-walled sclerenchymatous cells. In the midvein of *Cyrilla* and *Cliftonia*, and in the midvein and large, lateral veins of *Purdiaea*, the metaxylem is composed of cells with relatively thick, secondary walls. The tracheary elements in the smaller veins have spirally-thickened, secondary walls.

There are no stipules in any members of the Cyrillaceae, but extending over the axillary buds and laterally to each side there are several bright red, ligulate, glandular structures. A pair of similar structures is also found at the base of the bracts, occasionally at the base of the bracteoles, and rarely even at the base of the sepals. The nature of these structures is unknown. The similarity between the structures at the base of the bracts and those in the axils of leaves may be merely superficial. The position of these peculiar structures is suggestive of bud scales in the leaves, but they are more suggestive of vestigial stipules at the base of the bracts where they always occur in pairs, one on either side of the bract.

ROOTS. — The roots of *Cyrilla* and *Cliftonia* are woody, much branched, and quite shallow. They are composed of a diffuse network of branches with no primary or tap root. The major branches bend abruptly a few inches under the ground and run horizontally, more or less parallel to the surface of the ground. They tend to remain parallel to the surface even when the plants are growing on small mounds or in depressions. Numerous smaller branches which are fibrous in texture run both horizontally and vertically into the soil. Along the length of the horizontal roots numerous adventitious shoots arise, forming large vegetative clones. (The nature and development of these adventitious shoots are discussed in detail below.)

The primary vascular system in the roots of *Cyrilla*, the only genus in which the roots have been examined anatomically, is a triarch protostele (Fig. 19). Cambial activity begins early, and growth rings are present in all but extremely small roots. The vessels are solitary, small, and angular in cross section, with relatively thin, secondary walls. The perforation plates are scalariform, consisting of 25-50 bars per end wall. Vessel pitting is transitional to opposite, the pits being rather small. The imperforate tracheary elements consist of both tracheids and fiber-tracheids, with secondary walls varying from quite thin in the tracheids to relatively thick in some of the fiber-tracheids. The rays are heterogeneous, and may be either multiseriate or uniseriate. The multiseriate rays are usually only 2-3 cells wide in younger roots, occasionally becoming 4-5 cells wide in older roots. The uniseriate rays are 3-10 cells high, consisting of both procumbent and upright cells. Xylem parenchyma is rather scanty and apparently apotracheal, usually occurring in vertical strands which are adjacent to a ray. The outer layer of the bark of young roots consists of a layer of spongy, relatively thin-walled cork cells. Just inside the cork cells there is a layer, several cells thick, of parenchymatous cells, many of which contain densely-staining phenolic compounds. Small lenticels occur infrequently in the roots.

PUBESCENCE. — Although both *Cyrilla* and *Cliftonia* are glabrous, most species of *Purdiaea* are to some degree pubescent, particularly on the reproductive structures. The degree of pubescence is highly variable in some species of *Purdiaea*, occasionally varying from glabrous to pubescent in a single species. In *Purdiaea cubensis* and *P. nipensis* this variation occurs within a small geographic area.

Two different types of trichomes have been found in *Purdiaea*. In *Purdiaea velutina*, *P. moaensis*, and *P. shaferi* the racemes and, in the latter two species, the young stems are clothed with long, silky, usually appressed trichomes; whereas in most of the other species the trichomes are short and more rigidly erect. The long trichomes have a small, bulbous base usually composed of 6-8 cells, and a long, unicellular, non-septate "blade". The blade is terete, pointed, and relatively thick-walled. The small trichomes do not have a multicellular base, the entire structure being a single, elongate epidermal cell. They are pointed, thick-walled, and covered externally with an irregular layer of cutin.

FLORAL MORPHOLOGY

RACEMES. — The flowers are borne in either terminal or axillary racemes which vary in length from 2-3 cm. in *Purdiaea microphylla* to 25 cm. in some populations of *Cyrilla racemiflora*. Flowering proceeds progressively from the base to the apex of the racemes. The rachis is ridged, each ridge extending for approximately two nodes and ending at the base of a pedicel. The pedicel is also ridged, strongly so in *Cyrilla*, where there are fine, sharp ridges that extend the full length of the pedicel. Each ridge terminates at the base of a bracteole or a sepal. The rachis and pedicel are glabrous in *Cyrilla* and *Cliftonia*, but are often puberulent or pubescent in *Purdiaea*. The pedicel is articulate at the base in all members of the family.

BRACTS. — The bracts which subtend the flowers of the Cyrillaceae are highly variable in size, shape, and texture. In *Cyrilla* they are lanceolate, medially thickened, and usually claw-shaped, varying in length from 5-30 mm. In *Cliftonia* the bracts are spatulate and slightly concave with relatively little variation in size. In *Purdiaea* the bracts, at maturity, vary in size and shape progressively from the base to the apex of a raceme. Characteristically, the bracts near the base of the raceme are long and lanceolate; those further up the racemes become increasingly shorter and more deltoid. The long, basal bracts often attain a maximum length of more than twice that of the short, deltoid, apical bracts.

There is but one vein in the bracts and bracteoles of *Cyrilla* and *Cliftonia*, whereas those of *Purdiaea* have several prominent, longitudinal veins, and usually a distinctly visible, reticulate pattern of smaller veins. In *Purdiaea* and *Cliftonia* the bracts are articulate at the point of attachment to the peduncle; and in the latter genus they are deciduous, usually shedding well before anthesis. A pair of bracteoles is borne in varying positions on the pedicel in *Cyrilla* and *Cliftonia*. The bracteoles are of the same texture as the bracts, and in *Cyrilla* they are approximately the same shape. In *Cliftonia* the bracteoles are usually lanceolate and quite different from the spatulate bracts. There are no bracteoles in *Purdiaea*.

SEPALS.— All members of the Cyrillaceae have, as a rule, five sepals, although six sepals are rarely encountered in *Cyrilla*, and as many as eight have been reported for *Cliftonia* (Sargent, 1892). In *Cyrilla* and *Cliftonia* the sepals are deltoid, usually thickened medially, and are equal in size. Rarely the sepals are laterally united at the extreme base in *Cyrilla*. This phenomenon occurs with greater frequency in some populations than in others, but apparently it is always sporadic in occurrence, and is without geographical or ecological significance.

In *Purdiaea* the sepals are highly specialized and quite different from those found in *Cyrilla* and *Cliftonia*. Sepals provide the most valuable taxonomic characters in *Purdiaea* and, because of their specialization, require a rather detailed description. The sepals are arranged on the receptacle in a tight, somewhat compressed spiral, and are inserted in a quincuncial manner. That is, two are exterior, two are interior, and one has one edge exterior and one interior. A similar type of sepal insertion is found in the Theaceae, Clethraceae and Hypericaceae. The quincuncial type of sepal insertion is greatly exaggerated in *Purdiaea*, with the two exterior sepals completely enclosing the two interior sepals, and all but one edge of the middle sepal. The size and shape are often quite different in three of the five sepals, and it is therefore necessary to describe them individually. They are numbered for convenience, according to their position in the spiral. The lowermost of the two exterior sepals is number 1; the other exterior sepal is number 2; the middle sepal which has one exterior and one interior edge is number 3. The two interior sepals are usually the same size and shape, and thus are not numbered, being referred to simply as the "interior sepals". In a similar way, the first two sepals which enclose the other three are referred to collectively as the "exterior sepals".

The exterior sepals are approximately equal in length in *Purdiaea stereosepala*, *P. stenopetala*, and *P. moaensis*. However, in all of the other species, the first sepal is clearly longer and usually broader than the second sepal. In fact, in *P. nutans*, *P. cubensis*, and *P. nipensis* the first sepal is as much as twice as long as the second sepal at maturity. The third sepal is usually somewhat asymmetrical. The edge which extends laterally between the two exterior sepals is rounded, whereas the other edge which is completely enclosed by the exterior sepals is flattened. The flattened margin is usually ciliate, even in species in which the other margin is glabrous. Also, the surface of the enclosed portion of the third sepal is often more densely pubescent than the surface which is exposed. The interior sepals are approximately equal in size in all species, and are considerably smaller than the outer three. They are very narrow, lanceolate, and somewhat thickened basally. The ventral surface is adjacent to the ovary, and the sepals are usually concave, following the shape of the ovary. The interior sepals are characteristically more densely pubescent than the other three sepals. Moreover, the interior sepals are always pubescent, even in species in which all other parts are glabrous.

The sepals of all the Cyrillaceae are persistent in fruit. Those of *Purdiaea* increase considerably in overall dimensions during the maturation of the fruit, whereas those of *Cyrilla* and *Cliftonia* attain near maximum size soon after anthesis. In the latter two genera there is a single, very small, and obscure vein which extends longitudinally for the entire length of the sepal. In *Purdiaea*, there are several, more or less prominent, longitudinal veins and a well-developed, reticulate system of smaller veins.

In *Cyrilla* the sepals are composed of more or less isodiametric parenchyma cells. They are 6-7 cells thick near the middle, gradually tapering laterally to only two cells thick along the edge. The dorsal and ventral surfaces are covered with a thin, irregular layer of cutin. The cutin fills the spaces between the epidermal cells, and stands out from the surface in numerous microscopic ridges.

PETALS. — The corolla consists of 5 (rarely 6) petals which are delicate, and membranaceous. In *Cyrilla* and *Cliftonia* they are white or pinkish-white; in *Purdiaea* they range from deep pink to violet. The venation of the petals is quite different in the three genera. In *Purdiaea* there are numerous small, longitudinal veins which branch repeatedly, covering the entire petal. In *Cliftonia* there are one large central vein and two smaller side veins which extend the full length of the petal, branching only a few times. In *Cyrilla* there is only one vein which runs the full length of the petal, and usually there are 1-2 pairs of very small lateral veins which arise near the middle of the petal.

The petals of *Cyrilla* are morphologically quite distinct from those of the other two genera due to a characteristic median and basal thickening. This thickened area is composed of fairly thick-walled, glandular cells, filled with densely-staining compounds. These cells are nectariferous, secreting a sweet, sticky "honey" which is very attractive to bees. In this thickened region the petals are 8-10 cells thick, but lateral to this on either side they taper abruptly to 3 cells in thickness. There is a thin layer of cutin on both surfaces of the petals. As in the sepals, the cutin protrudes in numerous microscopic ridges. The outer walls of the epidermal cells are also cutinized and thickened, more so on the dorsal than on the ventral surface.

ANDROECIUM. — The stamens of *Cliftonia* and *Purdiaea* are in two whorls with five stamens in each whorl. The stamens in the outer whorl are opposite the sepals; those in the inner whorl, opposite the petals. In *Cyrilla*, only the outer whorl is present. The stamens of the two whorls are approximately equal in *Purdiaea*, but in *Cliftonia* those of the outer whorl are considerably longer than those of the inner whorl. The anthers are versatile in all members of the Cyrillaceae. The filaments are attached near the middle, on the dorsal side in *Cyrilla* and *Cliftonia*, but on the ventral side in *Purdiaea*. The filaments of *Cyrilla* and *Purdiaea* are narrow, terete, and subulate; those of *Cliftonia* are laterally expanded and petaloid below the middle, narrowing abruptly above the middle, becoming terete and subulate. The filaments of all members of the family are vascularized by a single, longitudinal trace.

In *Cyrilla* and *Cliftonia* the anthers are ovoid and shed their pollen by means of longitudinal slits. In *Purdiaea*, on the other hand, the anthers are quite different. They are oblong with a caudate base, and shed their pollen by means of terminal pores. The filament is folded back on itself in bud, and the anthers develop in an inverted position. When the flowers open the filament straightens, rotating the anthers through 180 degrees, placing the pores in an apical position and the cauda in a basal position. It is interesting to note that in *Cyrilla* and *Cliftonia* where the filaments are attached on the dorsal side of the anthers, the two lobes of the anthers are free below the point of attachment; whereas in *Purdiaea*, where the filaments are attached on the ventral side, the anther lobes are free above the point of attachment (after the filaments have straightened at anthesis).

The developmental morphology of the anthers was studied in detail in *Cyrilla* only. They are composed of two pairs of elongate microsporangia. The tissue of the partition between the two sporangia of each pair remains intact and the sporangia do not become confluent. The outer layer of the anther wall becomes flattened and stretched during the growth and development of the anther, but the cells usually remain intact and uniformly adjacent in mature anthers. Occasionally fibrous bands develop in the cells of the anther wall.

The endothecium is well-developed, becoming elongate at maturity with conspicuous fibrous bands extending laterally from the inner walls. There is a middle layer of highly vacuolate cells, usually three cells in width, between the endothecium and the tapetum. The two inner rows of cells in this layer become flattened and crushed during the development of the microspore mother cells. The inner layer persists more or less intact through meiosis; but it, too, breaks down during the maturation of the pollen grains.

The tapetal layer is easily distinguishable from the sporogenous tissue even at an early stage because of a consistent difference in the shape of the cells comprising the two tissues. The cells of the tapetal layer are more columnar than those of the sporogenous tissue, the latter being more or less isodiametric. Typically, the cells are densely cytoplasmic in both of these tissues. The tapetum persists more or less intact through meiosis but rapidly disappears during the subsequent development of the microspores.

In early stages the archesporial cells are seen as a plate of tissue, usually 2-3 cells wide and approximately 25 cells long in longitudinal section, and 3-4 cells across in transverse section. The primary sporogenous cells undergo occasional divisions, giving rise to a slightly larger number of microspore mother cells. The divisions of the microspore mother cells are of the so-called simultaneous type (Maheshwari, 1950). That is, the first and second meiotic divisions are completed before cytokinesis begins. With cytokinesis a tetrad of microspores is formed in the shape of a tetrahedron. The tetrads break up soon after cytokinesis, with the beginning of exine formation.

POLLEN. — All pollen preparations used in this study were prepared by acetolysis, and are in the pollen reference collection at Harvard University. A detailed description of the acetolysis procedure used is given by Traverse (1955).

The pollen of *Cyrilla* has received considerable attention since this genus was found to be one of the most abundant elements in the Brandon Lignite. A brief description of the pollen of the Cyrillaceae was given by Erdtman (1952), and a more detailed description of *Cyrilla* pollen by Traverse (1955).

His description of the pollen of *Cyrilla racemiflora* is as follows:

> Tricolporate and tetracolporate pollen grains with very wide longitudinal furrows, which are seen in polar view to narrow toward the poles, producing a Y-shape. As seen at polar view there is a characteristic overhang of exine at the edge of the furrow . . . Transverse furrows elliptical, constricted at the contact with the longitudinal furrow. Margos and bow-shaped longitudinal costae very prominent. Psilate sculpture. Size ca. 25 micra. Thickness of exine: ca. 2.7 micra.

The pollen grains of *Purdiaea* and particularly those of *Cliftonia* are very similar to those of *Cyrilla* (Figs. 10-16). The wide, longitudinal furrows narrowing to produce a Y-shape in polar view; the characteristic manner in which the exine overhangs the edge of the furrow; and the prominent, bow-shaped, longitudinal costae are found in the pollen of all members of the Cyrillaceae. The pollen of *Purdiaea* is readily distinguishable from that of *Cyrilla* and *Cliftonia* by several characters. The grains of *Purdiaea* are usually smaller (ca. 16 micra in diameter at the polar axis). They are much more angular, usually having a 3-lobed appearance in polar view due to a slight depression of the surface between the poles (Fig. 15). Also the exine and intine in *Purdiaea* are thinner than in *Cyrilla* and *Cliftonia* and the sculpturing is much less prominent than in the latter gen-

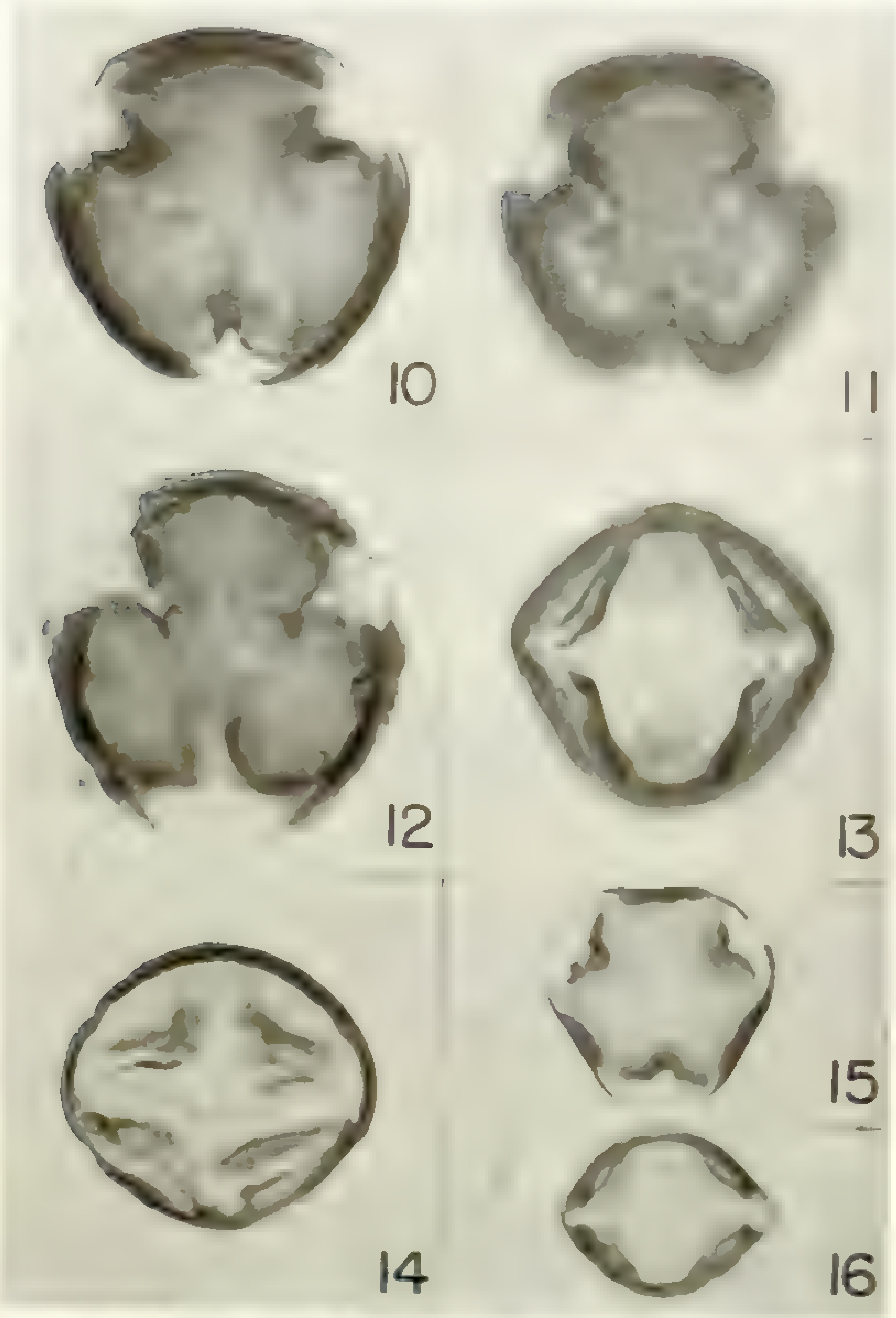


Fig. [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] Fig. [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] shown in Fig. 10. Fig. 12. [illegible] [illegible] [illegible] [illegible] Fig. 13. [illegible] [illegible] [illegible] [illegible] Fig. [illegible] [illegible] [illegible] [illegible] [illegible] Fig. [illegible] [illegible] [illegible] [illegible] and central focus. Fig. 16. *Purdia*[illegible] [illegible] [illegible] [illegible] [illegible] Fig. 10-16, magnification ca. 1000 X.

era, being quite fine and reticulate, visible only under very high magnification. The separation of *Cyrilla* and *Cliftonia* on the basis of pollen is much more difficult. The pollen grains of *Cyrilla* are generally more rounded and have a thinner ektexine though a thicker total exine. They have a slightly more prominent exine sculpturing. Also the exine usually overhangs the edge of the furrow to a greater extent in *Cyrilla* than in *Cliftonia*. These distinguishing characteristics are all variable, and the two genera occasionally overlap. However, on the basis of a combination of these characters more than 90% of the pollen grains of these two genera can be distinguished with accuracy.

The close similarity of the pollen grains of all members of the Cyrillaceae is of considerable significance, particularly in view of the fact that the genera are so distinct, and, indeed, quite dissimilar in several characteristics. There is some evidence from the fossil record that the morphology of the pollen of this group has remained rather constant. In the Magothy Formation of the Upper Cretaceous (discussed below) several grains of cyrillaceous pollen have been found. These grains are very similar to those of *Cyrilla* and *Cliftonia*, strikingly so considering the age of the deposit.

Pollen studies have also added further evidence to a close relationship between the Cyrillaceae and the Ericales. The only group which has pollen that closely resembles that of the Cyrillaceae is the genus *Clethra*. The pollen of *Clethra* is larger than that of the Cyrillaceae, but the grains are similar in several characteristics. Possibly the pollen of the Ericaceae and the Pyrolaceae would show a closer resemblance to that of the Cyrillaceae were it not for the fact that in these families the pollen remains in terads.

In the Aquifoliaceae and the Celastraceae, on the other hand, the pollen is quite unlike that of the Cyrillaceae as was pointed out by Erdtman (1952). An examination of the pollen of *Cyrillopsis* has added further evidence for excluding this genus from the Cyrillaceae. The pollen of *Cyrillopsis* is similar to that found in some members of the Celastraceae, but quite unlike that of the Cyrillaceae.

GYNOECIUM. — The ovary is 2-5-locular with pendulous ovules, one in each locule of *Cliftonia* and *Purdiaea*, three in each locule of *Cyrilla*. The ovules are anatropous in *Cyrilla* and *Cliftonia*, but in *Purdiaea* they are attached to the funiculus in an orthotropous manner, and could thus be described as pendulous-orthotropous. In all of the Cyrillaceae there is a central column of vascular tissue which extends longitudinally from the receptacle to near the apex of the ovary. Copeland (1953) has shown in his illustration of *Cyrilla* and *Cliftonia* that this vascular bundle divides near the apex of the ovary with a single trace extending into each locule. A similar type of development is also found in *Purdiaea.* In *Cliftonia* and *Purdiaea* the funiculus is attached directly to a small column of tissue surrounding this trace. In *Cyrilla* the trace passes into a short placental arm which branches twice to give rise to three ovules per locule.

There is a column of elongate parenchyma cells extending from the ovule to the apex of the style. According to Copeland (l.c.) this column of cells broadens at the apex in *Cyrilla* and *Cliftonia* forming the stigmatic surface. In *Purdiaea* there is a single, elongate style which is not lobed at the apex. The style is composed of a thin layer of epidermal cells enclosing 4-5 columns of elongate, parenchyma cells, similar to those leading from the ovule to the stigma in *Cyrilla.* These columns do not fuse; and if the epidermal layer is removed they readily separate into discrete intact strands, each leading from the apex of the style to an ovule.

In the ovules of *Cyrilla* and *Cliftonia* there is a single integument, and a thin, short-lived nucellus. The nucellus usually disappears shortly after tetrad formation during megasporogenesis. Copeland predicted the existence of a tenuinucellate condition in this group although his material was too old to show any nucellus. In later stages of megasporogenesis, there is a fairly well-developed integumentary tapetum.

The embryo sac begins development relatively early. An expanding tetrad of megaspores is usually present before the microspore mother cells of the same bud have begun to enlarge prior to meiosis. Subsequent development in the embryo sac is slower, however, and the male and female gametophytes mature at approximately the same time in a given flower. The mature embryo sac is 8-nucleate, although one of the antipodals is occasionally either difficult to discern or missing. This phenomenon was also noted by Copeland (1953).

Intermediate stages of seed development have not been seen, but the mature seed is apparently devoid of a seed coat. Planchon (1846) practically described this situation in *Purdiaea* in his original description of the genus. In his description of the seed he says: " . . . integumento tenuissimo subfloccoso albicante, albumini carnoso adhaerente . . . ".

Similarly Gilg (1896) describes the seed of the Cyrillaceae as having seed coats not clearly differentiated (" . . .undeutlich abgegliederte Samenschale. . ."). Copeland interpreted the fruit of *Cyrilla* as a 2-seeded caryopsis, thus intimating that the seed coat is fused to the ovary wall. However, in fruits in which no seeds develop (parthenocarpy is of common occurrence in the Cyrillaceae) the structure of the ovary wall is the same as it is in fruits which do contain seeds. There is no evidence in the latter of any extra layer which could be interpreted as a seed coat. The cells of the outer layer of the endosperm are somewhat differentiated, but this layer is composed entirely of thin-walled cells and is clearly a part of the cellular endosperm and not a seed coat. This unusual characteristic of seeds without a seed coat is found in all members of the Cyrillaceae and serves as a reliable character by which this family can be distinguished from related families.

CYTOLOGY

Considerable effort was made to obtain chromosome counts in the Cyrillaceae from preserved material, but with little success. Although several fixing and preserving solutions were used none was found which kept the material in useable condition for periods longer than a few days. In material of *Cyrilla racemiflora* from northern Florida a few metaphase II configurations were found in which the chromosomes could be counted with accuracy. The number that was found in most cells was $n = 20$ Unequal distributions were apparently quite frequent in this collection, however, for numbers ranging from 18 to 22 were obtained in several cells. In one pair of daughter cells, one cell contained 19 chromosomes and the other, 21 chromosomes. Several bridge formations were observed and there was considerable variation in the size of the chromosomes. Possibly the discrepancy in chromosome number was due partially to chromosome fragments rather than to unequal divisions.

More cytological work is badly needed in this group, not only on *Cyrilla* but also on *Cliftonia* and *Purdiaea* which have never been studied cytologically. On the basis of my experience with preserved material, it seems advisable that cytological work in this group be attempted only if living material is readily available.

ADVENTITIOUS SHOOTS

Reproduction in both *Cyrilla* and *Cliftonia* is primarily by means of retoños[2], that is, vegetative sprouts from horizontally positioned, underground roots. As discussed above, the root systems of *Cyrilla* and *Cliftonia* are shallow, and the major branches grow in a horizontal direction, parallel to the surface of the ground. Along the length of these horizontal roots numerous retoños arise. These develop underground and, as they emerge from the soil, resemble normal seedlings.

Propagation by means of retoños accounts for the vast majority of individuals or apparent individuals of *Cyrilla* and *Cliftonia* throughout the range of these genera. Hundreds of shrubs and small trees of *Cyrilla* have been examined in populations along the coastal plain of southeastern United States from Virginia to eastern Texas, and in the Provinces of Pinar del Rio and Oriente in Cuba. In every case, exposure of the root systems revealed that the plants were interconnected with several and often numerous other "individuals" near by. Thus, what appears superficially to be a population composed of separate individuals is usually a large clone.

The total area covered by one of these clones has been found, in many instances, to be quite extensive. For example, in southeastern Virginia, near the North Carolina border (Thomas 458), I excavated an area approximately 15 feet wide and 30 feet long, containing over 50 bushes of *Cyrilla*, and found that all of these bushes were part of a single clone. In numerous other areas, by tracing the root systems from one bush to the next, I have found clones which extended for even greater distances.

Since the root systems in *Cyrilla* remain interconnected, it is a simple matter to demonstrate in the field that these various "individuals" are part of a clone. The clone described above (Thomas 458) included several large shrubs that were up to eighteen feet tall with a trunk diameter of three or more inches below the first branch. The entire system was still interconnected, thus indicating that the plants in a clone remain interconnected for several years.

It is difficult, on the other hand, to determine the parent plant of a clone. In a situation such as the one described above, in which the clone is large and contains several large

[2] The term "retoño", used by the Mexicans to denote sprouts from the roots as well as sprouts from underground stems, was adopted by Lloyd (1911) and has been used by subsequent authors to denote vegetative shoots which develop from roots. Due to the awkwardness of the English equivalent, the term retoño will be used here to refer to this phenomenon, that is, the situation in which vegetative shoots originate from underground roots.

shrubs of approximately the same size, it is virtually impossible to select the parent plant. In certain areas one can find small clones in which there is a single, large bush and a number of smaller ones more or less, radiating from it. Clones such as this are exceptional, however, and even in these one cannot be certain that the supposed parent plant did not originate from the roots of other bushes that once grew in the area. Numerous clones were found which seemed to be composed entirely of young retoños, but these could usually be traced to old stumps in the vicinity. This is common along highway right-of-ways that are clear-cut periodically.

In some plant groups the formation of retoños is related to disturbance or injury. In Guayule (*Parthenium argentatum*), for example, Lloyd (1911) has shown that there is a direct correlation between disturbance and the formation of retoños. The ratio of retoños to seedlings was found to vary greatly with the habitat, although both seedlings and retoños can be found in practically any habitat in which the species grows. On stony slopes, where there is evidence of disturbance, the retoños were found to be more abundant than the seedlings, whereas on more level and less disturbed soil just the reverse was true. Apparently, in Guayule the so-called normal retoños are formed only when the end or a portion of the root is exposed. "Induced retoños", on the other hand, can be stimulated to develop by injuring the root system or by severing it from the plant. Also, in Guayule the retoños become separate and independent soon after they emerge from the root of the parent plant. As the retoño develops, the proximal part of the root connecting it with the parent plant undergoes little or no further growth and soon dies. The distal portion of the root continues to grow and forms the equivalent of a tap root for the developing retoño. The retoño, however, is distinguishable from a seedling by the shape of the taproot and its position in the soil (Muller, 1946).

In *Cyrilla* there is no apparent correlation between disturbance or injury and the formation of retoños. They form regularly on unexposed roots 3 to 8 inches underground in areas which show no evidence of disturbance. They develop in such large numbers under these conditions that it is difficult to believe that injury or disturbance could be an important factor. It is true that large clones of *Cyrilla* are unusually abundant in cut-over areas, but this is more likely to be a result of the ability to colonize rapidly (by means of vegetative sprouts) than a result of disturbance caused by the cutting.

One of the most striking examples of rapid colonization by *Cyrilla* of a cut-over area was seen in the Sierra de Moa in Oriente Province, Cuba. A large part of the vegetation of this area was second growth following extensive lumbering operations which were terminated approximately fifteen years ago. One of the dominant elements of this second growth, particularly on the moist sites, was *Cyrilla*. One area near the town of Moa was of particular interest in this connection. On a rather gentle slope, 350-400 feet above sea level, an area of roughly 500 acres showed signs of having once supported a sizeable pine forest, as evidenced by numerous tree stumps. However, in the summer of 1957, the area was covered by a fairly dense growth of *Cyrilla*. An examination of several of these plants in different parts of the region indicated that the colonization by *Cyrilla* had been the result of vegetative propagation. Moreover, the presence of hundreds of young retoños indicated that the colony was still expanding rapidly. There was little evidence of recent disturbance in the area and the young retoños were developing from unexposed roots. There was some evidence of erosion, but the area appeared to have been more or less stable for several years, and colonization by vegetative means was continuing.

ANATOMY OF DEVELOPING RETOÑOS. — The development of vegetative shoots from roots is a fairly common phenomenon, especially among the dicotyledons, and has been recognized for several centuries. It was first pointed out by Hieronymus Tragus in 1546 in *Convolvulus arvensis*. Since then the number of species recognized as reproducing by this method has continued to increase. Irmisch (1857) listed 42 species, Warming (1877) 87 species, and Wittrock (1884) 132 species which reproduce vegetatively. The most comprehensive treatment of this subject was made by Beijerinck (1887) who referred to 246 different genera in which one or more species are known to propagate by means of root sprouts. In many of these, however, the anatomy and developmental morphology have not received detailed study.

The present study of the origin and early development of adventitious buds within the roots was made on material of *Cyrilla racemiflora* collected in Virginia and North Carolina. Several roots bearing young retoños were collected in late May and early June, and fixed and stored in Formalin-Acetic Acid-Alcohol. The material was softened for four to

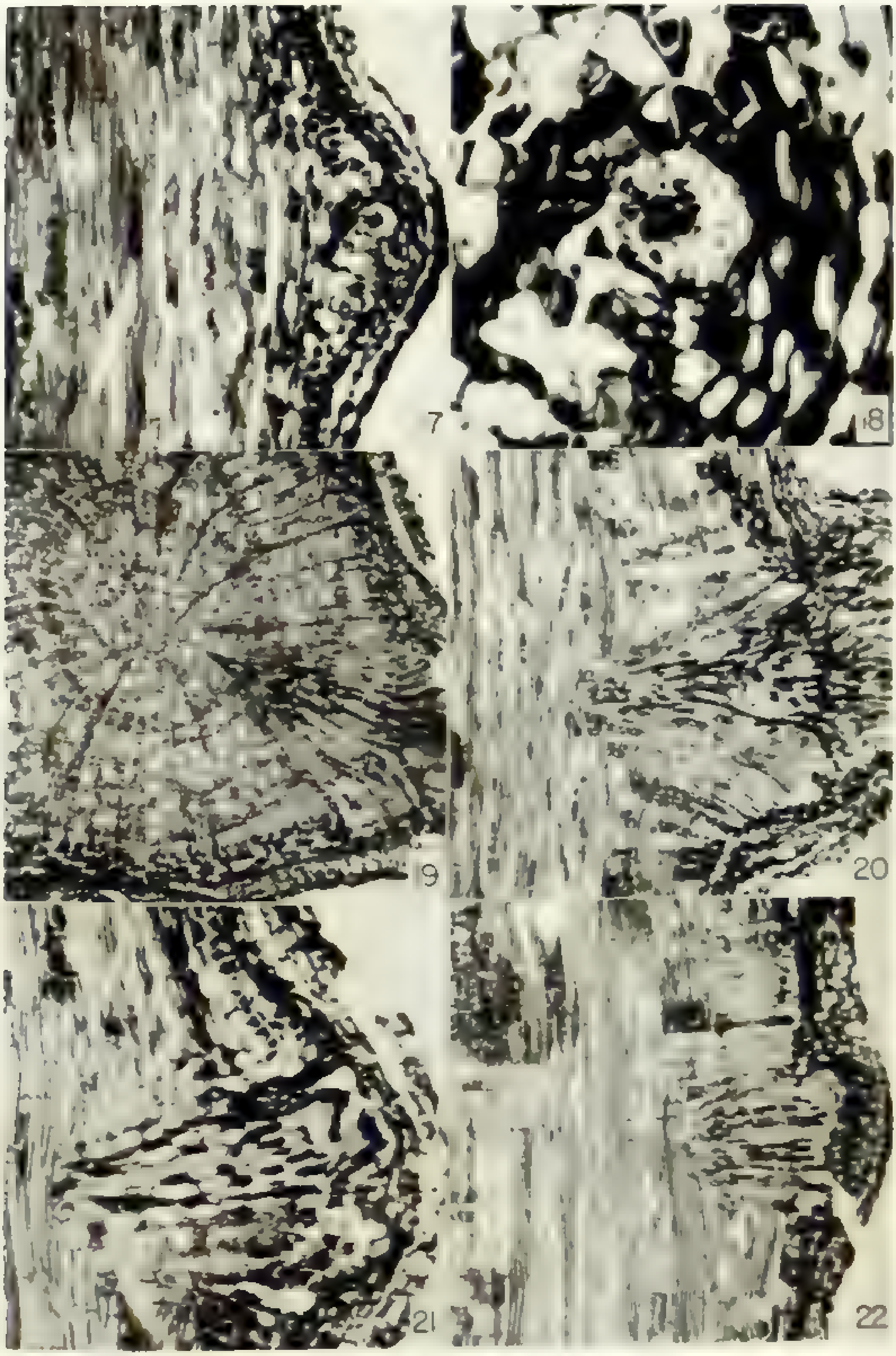


Fig. 17–22. Anatomy of developing retoños in *Cyrilla racemiflora*. Fig. 17. An early stage in the development of a retoño. This section passes approximately through the center of the bud. Fig. 18. An enlargement of the bud shown in Fig. 17. Fig. 19. Transverse section through a root bearing a retoño that has just emerged from the root. Fig. 20. Radial section through a root bearing a retoño that has just emerged. Fig. 21. Radial section through a bud 2-3 years old. Fig. 22. Radial section of a root showing a retoño at an intermediate stage of development. Fig. 17, 19, 20, and 22, magnification ca. 100 ×. Fig. 18 and 21, magnification ca. 450 ×.

five weeks in concentrated hydrofluoric acid, embedded in paraffin, and sectioned with a rotary microtome. The sections were cut at a thickness of ten micra, and stained in safranin and fast green.

In sectioning roots from which very young retoños were emerging, I was fortunate enough to pass through several buds in various stages of development. An examination of these buds added a great deal of valuable evidence, particularly in interpreting early stages in the ontogeny of the adventitious buds. In early stages the bud consists of a rounded cluster of small, densely cytoplasmic, meristematic cells. A recognizable pith of darkly-staining, tanniniferous cells develops during the early stages of bud formation. At the earliest stages seen the bud is located in the region of the phellogen or cork cambium and apparently originated either directly from the phellogen or from recent derivatives of the phellogen. Thus, the origin of the adventitious bud must be exogenous. (A median section of the bud in an early stages of development is shown in Fig. 17, and an enlargement of the same bud is shown in Fig. 18).

The evidence that adventitious buds continue to originate in roots that have undergone two or more seasons of cambial activity is a further indication of an exogenous origin of the buds. The pericycle is destroyed soon after the initiation of cambial activity, thus eliminating the possibility of any subsequent buds originating endogenously from the pericycle.

Adventitious buds have not been seen in roots lacking secondary tissues, and therefore it is not known whether buds ever develop in the primary body of the root. Since all the young buds that have been seen apparently originated in the vicinity of the phellogen, it is conceivable that adventitious buds are formed only after the development of a secondary dermal system.

During the early stages of bud development a noticeable swelling appears on the root, external to the bud (Fig. 17). This swelling becomes more extreme in later stages, as cells derived from the bud begin to elongate at right angles to the long axis of the secondary xylem in the root (Fig. 21). In still later stages radial rows of parenchymatous cells can be seen extending laterally on each side of the developing shoot (Fig. 20). These rows of parenchyma cells are not derivatives of the bud, but develop from the cambium of the root, leaving a gap in the stele.

An unusual aspect of the development of these retoños is the long period of time between the initiation of the bud and its emergence from the root. In every case that has been examined the bud has remained within the root for three or more years before emerging. During this three-or four-year period the developing shoot increases considerably in size. The rate of growth in diameter of the bud increases as it grows outward, and as a result the developing shoot becomes somewhat obconical in shape (Figs. 19 and 20).

During the first three or four years of development the rate of growth in the shoot is just sufficient to keep pace with the growth of the secondary body of the parent root. As the bud increases in cross-sectional diameter, procambial cells begin to differentiate basipetally, eventually establishing vascular connections with the stele of the root. (An intermediate stage in this process is shown in Fig. 22). The establishment of vascular connection and the emergence of the adventitious shoot from the root occur at approximately the same time. It seems likely that the shoot must establish these connections before it can emerge from the root.

By the time the young shoot has emerged it already has a rather large cross-sectional area of procambial cells that are blocked out, and a relatively large area of differentiated primary xylem. The differentiation of the primary xylem and the development of a cambium is a rapid process in the young shoot once it has emerged. There is also a deflection of some secondary xylem from the root into the shoot. Fig. 20 shows a radial section through the base of a young shoot collected during the middle of the growing season of the year that it emerged from the root. This photomicrograph shows the deflection of secondary xylem from the root into the shoot and also the well-developed primary xylem in the shoot. It also shows that the tissues of the young retoños can be traced well into the stele of the root. A transverse section of a root bearing a shoot at approximately the same stage of development as the preceding one is shown in Fig. 19.

Again, the tissues of the shoot can be traced well into the stele of the root, and the age of the retoño is indicated by the number of growth rings in the root. The tissues of the retoño can be traced through three or possibly four growth rings in the root. This bud must have originated soon after the initiation of cambial activity. There are, however, definite radial rows of secondary xylem in the root, internal to the tissues of the developing shoot.

Occasionally two adventitious buds are found in close proximity. Fig. 22 shows a transverse section through a root containing two buds developing quite close together. (Although one of the buds cannot be seen at this level it became visible in later sections, approximately 70 micra deeper at the position indicated by an arrow). These two buds apparently originated at approximately the same time and developed at the same rate. This simultaneous development of two buds in close proximity may be of significance in later studies, particularly in connection with the possibility of hormonal control of the development of these adventitious buds.

In summary, the retoños of *Cyrilla* originate exogenously as adventitious buds in the region of the phellogen, develop at a rate that is just sufficient to keep pace with the secondary growth of the parent root during a period of three to four years, and finally emerge as a vegetative shoot. The factor, or factors, which controls the origin and development of these buds is not known. On the basis of this limited anatomical study it seems that the buds must establish vascular connections with the stele of the parent root before they emerge from the root. Further studies are needed on the origin and development of retoños, including comparative anatomical studies on other groups, and particularly morphogenetic studies to determine the nature and source of the stimulus that initiates the buds, and the possibility of hormonal control of their subsequent development.

PHYLOGENY

In the history of phylogenetic classifications involving the Cyrillaceae most authors have considered the relationships of the family to be with either the Ericales or the Celastrales, and it has been shifted back and forth between these two groups many times. Jussieu (1789), the first to attempt a natural or phylogenetic classification of *Cyrilla*, included it in his Ericae. Lindley (1836) placed *Cyrilla* and a second genus, *Cliftonia*, which had been described after Jussieu's treatment, in the Celastraceae. Torrey and Gray (1838) also included these two genera in the Celastraceae, but added a note saying that the relationships seemed closer to the Ericaceae and that these genera probably should be considered as a sub-group of that family. Endlicher (1840) included the Cyrilleae in his supplement, indicating that they were related to the Ericaceae. The following year, however, he changed their position and included the Cyrilleae as a sub-group within his Ilicineae (Endlicher, 1841). Five years later Planchon (1846) described the genus *Purdiaea*, stating that it was closely related to *Cliftonia* and *Cyrilla*, but also pointed to relationships with *Clethra*, *Pyrola*, and, oddly enough, *Sarracenia*. In his classification, however, Planchon placed *Purdiaea* and the ericaceous genus *Elliottia* along with *Cyrilla and Cliftonia* in his Cyrilleae, which he included in the Ericaceae. This treatment of the Cyrilleae as a sub-group of the Ericaceae was followed by Walpers (1847) and Agardh (1858). Even Lindley (1847), who was the first to include *Cyrilla* and *Cliftonia* in the Celastraceae, revised his treatment and recognized the Cyrillaceae as a separate family related to the Olacaceae and the Ericaceae. Chapman (1860) also gave family status to the Cyrillaceae and placed it near the Aquifoliaceae and the Styracaceae, but in his treatment these familes were also placed near the Ericaceae. Bentham and Hooker (1876) placed the family Cyrillaceae near the Ilicineae, but also emphasized a relationship with the Olacaceae, indicating further that the apparent relationship between *Purdiaea* and *Clethra* was merely a superficial resemblance. This opinion was based primarily on the work of Decaisne.

With very few exceptions this treatment of Bentham and Hooker has been followed in the major botanical works up to the present day. The following are among those whose treatment of this group essentially agrees with that of Bentham and Hooker: Durand (1888); Gilg, in Engler and Prantl (1892); Mohr (1901); Dalla Torre and Harms (1900-1907); Brown (1901); Small (1903, 1913, 1933); Bessey (1915); Wettstein (1935); Mattick (1935); Uphof in Engler and Prantl (1942); Fernald (1950) and Gleason (1952). One interesting exception to the above is the work of Baillon (1892), in which he separated the Cyrillaceae from the Ericaceae, but left the genus *Purdiaea* in the latter family. This is one of the few times in which one of the three genera of the Cyrillaceae has been treated in a family separate from the other two.

The more recent workers concerned with the Cyrillaceae, however, have pointed to further evidence of the relationship between the Cyrillaceae and the Ericaceae and related families. Marie-Victorin (1948) was of the opinion that the present family is clearly related to the Ericales, and that the problem at hand is primarily that of the position of the Cyrillaceae within the Ericales. Copeland (1953) presented further evidence from comparative morphology, particularly of the reproductive parts, in favor of a close relationship between the Cyrillaceae and Ericales, although he stated that this conclusion did not necessarily negate the former association of the Cyrillaceae with the Aquifoliaceae. He also cited the work of Heimsch (1942) on the comparative anatomy of the Terebinthales and Gruinales of Wettstein (1935).

Heimsch concluded, on the basis of wood anatomy, that the Cyrillaceae did not belong in this group. The wood of the Cyrillaceae is more primitive than that of the other groups in Wettstein's Terebinthales and Gruinales, but is in many respects similar to the wood of the Ericales. As further aspects of the total biology of the Cyrillaceae have been studied, the evidence for a close relationship with the Ericales has become increasingly strong, and in my opinion the Cyrillaceae should be included in that order. The following is a summary of the anatomical and morphological features of the Cyrillaceae which are also found in the Ericales: primitive wood structure with small vessels having oblique end walls and scalariform perforation plates; rays uniseriate and multiseriate, heterogeneous; imperforate tracheary elements primarily fiber tracheids; parenchyma, apotracheal; crystals and tannin deposits common; unilacunar nodes; 5-angled pith; leaves alternate, entire, simple, coriaceous, and estipulate; flowers in axillary or terminal racemes, flower parts in 5's; sepals inserted in a quincuncial manner, persistent; anthers inverted in bud, dehiscing by terminal pores; glandular nectariferous disk at the base of the ovary; ovary 2-5-loculed; ovules with a single integument; pollen grains tricolporate, with wide longitudinal furrows, longitudinal costae, psilate sculpturing, and with the exine overhanging the furrow margins.

PALEOBOTANICAL HISTORY

The Cyrillaceae has a rather lengthy paleobotanical history. Cyrillaceous pollen grains have been found in the Upper Cretaceous Magothy formation from a well drilling near Brookhaven, Long Island (Steeves, 1959). These pollen grains are not assignable to any of the living representatives of the Cyrillaceae, but in view of the age of the deposit this is not surprising. However, the grains are very similar to those of *Cyrilla and Cliftonia*, and definitely belong to the Cyrillaceae. In some characteristics these ancient pollen grains appear intermediate between those of *Cyrilla* and *Cliftonia* and possibly represent a stage in the history of this family before these two genera became distinct.

The most thoroughly documented paleontological record of this family is the occurrence of *Cyrilla* in the flora of the

Brandon Lignite of Vermont. This rich, fossil flora consists of numerous fruits, seeds, fragments of leaves, an abundance of pollen and spores, and a large amount of well-preserved wood including both stems and roots. The Brandon Lignite is one of very few deposits of Tertiary age in northeastern North America (Barghoorn and Spackman, 1949). For this reason our knowledge of the flora of the Northeast during this period is rather meagre, and the flora of the Brandon Lignite is highly significant.

The composition of this flora long remained a mystery, and until 1949 only three of the different woods had been tentatively identified. These were described as *Pityoxylon microsporosum Brandonianum* Knowlton, *Laurinoxylon brandonianum* Jeffrey and Chrysler, and a third very doubtful member which was tentatively placed in the genus "*Betuloxylon*". A most important clue to a real understanding of the nature of this flora was the discovery by Barghoorn and Spackman (1949) that the most abundant wood in the deposit, the puzzling "*Betuloxylon*", was actually the wood of *Cyrilla*. With this discovery, other elements began to fall into place. The *Pityoxylon* of Knowlton was found to be a member of the genus *Gordonia* in the Theaceae, and the *Laurinoxylon brandonianum* of Jeffrey and Chrysler was tentatively assigned to the genus *Persea* in the Lauraceae. These three elements can be found growing together at the present time along the margins of acid swamps on the Coastal Plain of southeastern United States.

Further evidence of the occurrence of these plants in the Brandon Lignite was presented by Traverse (1955) in a study of the fossil pollen, spores, and other micro-fossils of the deposit. Pollen of both *Cyrilla* and *Gordonia* was found to be very abundant, that of *Cyrilla* being second only to *Quercus* in order of abundance in the deposit. The pollen of *Persea*, like that of other members of the Lauraceae, does not preserve, and thus does not occur in the deposit. However, fossil cupules were found which apparently belong to that genus.

The identification of the *Cyrilla* wood in the deposit was rather difficult, due primarily to the unspecialized nature of the wood anatomy of that genus. A reliable identification was possible, however, due in part to the great abundance of the wood of *Cyrilla* in the deposit (49.8%). Because of this abundance of remarkably well-preserved wood, relatively good preparations were obtainable. These showed several aspects of the anatomy including radial, tangential, and transverse, nodal sections of the stem. Detailed studies of these sections, and comparisons of them with equivalent sections of living material of *Cyrilla* were made by Barghoorn and Spackman (1949), and were illustrated by Spackman (1949). Though not identical in every detail, the living and fossil material were found to be remarkably similar. And in view of the age of the deposit, estimated by the above authors to be Upper Oligocene, the close similarity between the two is indeed remarkable.

One extremely puzzling feature of the Brandon deposit is the absence of fruiting material of *Cyrilla*. Throughout its present range, *Cyrilla* is found to produce abundant fruits each year. Even a cultivated bush in the Arnold Arboretum in Jamaica Plain, Massachusetts, approximately 600 miles north of the present range of the genus, produces abundant fruits each year. Yet no fruits of *Cyrilla* have been found in the Brandon Lignite.

One explanation for this may be related to the structure of the fruit and the seed. In *Cyrilla* the ovary wall of the mature fruit is the functional seed coat. The seed itself is composed of an elongate embryo, surrounded by a mass of cellular endosperm, but with no seed coat. Moreover, germination of the seed involves a breakdown of the ovary wall which occurs readily under moist conditions. This would tend to lessen the chances of fruits being preserved. Nevertheless, if *Cyrilla* fruits were produced at or near the site of deposition as abundantly as they are produced throughout the range of the genus today, one would expect some fruits to have been preserved in the deposit.

The determination of the age of this deposit has also been a rather difficult matter. The stratigraphy of the entire vicinity of the Brandon formation is very confusing, and gives little insight into the age of the deposit. The conclusions as to the age of the Brandon Lignite were based primarily on the degree of "modernization" of the flora. This technique consists of comparing the fossil flora with the living flora of the same area, and plotting the percentages of exotic or extinct taxa in the fossil flora against geologic time. Reid (1920) employed this technique in studying the Pliocene floras of Europe. His plot yielded a curve which showed a range from over 90% exotic species at the beginning of the Pliocene to less than 10% at the end of this period. Similarly, Barghoorn (1951) has developed a curve for the Tertiary floras of North America, and a certain amount of control was added by including several floras for which fairly reliable dates were available from other evidence. On the basis of this curve the Brandon Lignite was placed in the latter part of the Upper Oligocene.

The Barghoorn curve also shows a sharp rise during the Oligocene which correlates with the climatic deterioration during the Tertiary. Thus at the time of deposition of the Brandon Lignite a rapid "modernization" of the flora of northeastern North America had already begun.

On the basis of present-day distributions of the various elements found in the Brandon Lignite, it would seem that this flora was decidedly warm temperate or sub-tropical. The above authors have designated the general region of the Coastal Plain of southern Georgia and Florida as the nearest present-day equivalent of the climatic and ecological conditions that must have characterized the Brandon area at the time of the deposit. The extreme abundance of *Cyrilla* wood in the formation indicates that there must have been fairly extensive, shallow swamps bordered by *Cyrilla* thickets, comparable to the *Cyrilla* thickets commonly found on the Coastal Plain of southern Georgia and northern Florida today. The abundance of roots as well as stems in the deposit further indicates that these thickets probably consisted of large, vegetative clones of *Cyrilla*, as is true of the *Cyrilla* thickets at the present time. Thus, there is some evidence that the capacity of vegetative reproduction may have developed quite early in this genus.

The pollen of *Cyrilla* in the deposit was found by Traverse (1955) to be rather variable, particularly in size. He states that the range of variation is conceivable within a single species of *Cyrilla*, particularly when one takes into consideration that anthers containing immature pollen are commonly found in the deposit. It is possible, nevertheless, that more than one species of *Cyrilla* was present. In fact, on the basis of this variation, Traverse described a new species, *Cyrilla barghoorniana*. Although the genus, as it is represented in the present-day flora, is composed of a single species, it is quite conceivable that there were two or more species of *Cyrilla* present during the Upper Oligocene. It seems equally plausible, however, to assume that there was then, as now, a single variable species.

In this connection the paleobotanical history of *Cyrilla* seems to have some bearing on the lack of speciation in this genus. The effects of the climatic deterioration during late Tertiary on plants such as *Cyrilla* is in striking contrast to its effects on some of the more northern elements that were not as sensitive to low temperature. Some of these latter examples remained north as the climate became colder. Various races and species were destroyed, divided, or isolated by the subsequent glaciation. Many of these divided populations were apparently able to survive in refugia for long periods of time, during which they were geographically isolated from other such populations of the same species. Moreover, environmental conditions were obviously changing, giving rise to various differences in selection pressure toward gene combinations that were best adapted for survival under conditions prevalent in a given refugium. These conditions, which are thought to be favorable for speciation, were in large part avoided by the more subtropical elements which would tend to retreat early in the face of a cooling climate.

The indication that vegetative reproduction may have developed quite early in the history of *Cyrilla* could also be an important factor in interpreting the evolutionary history of this group. One can only speculate as to what effects vegetative reproduction may have had on *Cyrilla* in the past, but in view of the effects of this phenomenon on the group at the present time it seems probable that vegetative reproduction has played an important role in the history of the genus. One of the effects of a reduced rate of genetic recombination will be a tendency toward a more static group in terms of evolution. The clear evidence that the wood anatomy and pollen morphology of *Cyrilla* have undergone so little change since the Upper Oligocene indicates that this group has been rather static for several million years. The term static is not intended to imply genetic homogeneity or complete evolutionary stagnation. So long as the capacity for some genetic recombination is retained, the group will have some degree of evolutionary potentiality. On the other hand, the evolutionary history of such a group should be quite different from one in which there is a rapid rate of sexual union and recombination. The latter situation would more likely give rise to a dynamic, rapidly-evolving group.

Geographic Distribution

The geographic distribution of the Cyrillaceae is totally within the New World. *Cyrilla racemiflora*, by far the most wide-spread species, occurs over an area which includes most of the range of the entire family. This species is distributed as follows (Map 11) : along the Coastal Plain of southeastern

United States; in Oaxaca, Mexico and British Honduras; in the Greater and Lesser Antilles and Trinidad; in British Guiana, Venezuela, northern Brazil, and western Colombia. There is one species of *Purdiaea* which occurs in Venezuela, Colombia, and Peru; and ten species which occur only in Cuba and the Isle of Pines. The third genus, *Cliftonia*, is quite narrowly distributed, occurring only on the Coastal Plain of Georgia, Florida, Alabama, and Mississippi. Thus the family is distributed in the sub-tropical or warm-temperate areas surrounding the Caribbean Sea and the Gulf of Mexico, with northward extentions on the Coastal Plain of southeastern United States, and southward extensions on the mountains of northern South America.

There is little evidence, however, on which a definite center of origin for the group can be postulated. The fossil record of the Cyrillaceae indicates that the group is a very old one, and that it has had representatives in North America since the Upper Cretaceous. The occurrence of *Cyrilla* pollen and wood in deposits of Oligocene age in Brandon, Vermont, indicates that this genus has been distinct for several million years, and that it was once distributed considerably north of its present range. Of the three genera in the Cyrillaceae, *Purdiaea* shows the highest degree of morphological similarity to the Ericales, and seems to be the most primitive. In *Purdiaea* there are fairly clear lines of specialization which seem to indicate that the one South American species is more primitive than the Cuban species. Thus a very tenuous thread of evidence suggests that the group may have originated in South America, but this is certainly in the realm of speculation.

However, the center of diversity of the group at the present time seems to be in eastern Cuba. Nine of the eleven known species of *Purdiaea* are endemic to Oriente Province, and in this same area one finds the highest degree of local variation in *Cyrilla racemiflora*.

According to Croizat (1952) the Cyrillaceae did not originate in the New World, but rather came from South Africa. The evidence for this view is apparently based on a supposed relationship between the Cyrillaceae and two genera of uncertain affinities, *Crypteronia* and *Heteropyxis* (treated as the Crypteroniaceae and the Heteropyxidaceae by the above author). Croizat contends that these three groups are surviving relicts of a larger group which originated in South Africa and was subsequently divided into three major parts as follows: the Cyrillaceae migrated to the West Indies, the Crypteroniaceae migrated to Malaysia, and the Heteropyxidaceae remained in Africa. In the words of the above author: "We believe, then, that Cyrillaceae, Crypteroniaceae, and Heteropyxidaceae belong to the same archetypal node, or 'genorheitron', and that the mainsprings of their dispersal are to be accounted for by migrations effected to Malaysia and a now crumbled range in West Indies from South Africa. Migrations of the sort are conventional."

So far as I can determine, the relationship between the Cyrillaceae and the two taxa mentioned above is, at best, a superficial resemblance. These groups have flowers borne in slender racemes with the flower parts in fives. The fruits are similar also, being small, globose, and with a persistent style. A more critical examination of *Crypteronia*, however, reveals that the flowers and fruits of this group are quite unlike those of the Cyrillaceae. Moreover, the leaves of *Crypteronia* are opposite, whereas those of the Cyrillaceae are alternate. I have not seen material of *Heteropyxis*, but the description of this genus does not indicate a close relationship with the Cyrillaceae.

In view of the well-known relationship between the flora of eastern United States and eastern Asia, particularly in regard to the more primitive woody taxa, it would not be surprising if fossil or even living representatives of the Cyrillaceae were found in eastern Asia. At present, however, there is no evidence that members of the Cyrillaceae have ever occurred in the Old World.

ASEXUAL REPRODUCTION AND VARIATION IN CYRILLA RACEMIFLORA

Vegetative reproduction, operating within a species, will tend to influence the degree of variation found within populations and between different populations in a variety of ways. The effects on the variation will depend upon the degree to which sexual reproduction has been replaced by asexual reproduction, the nature of the populations, and the nature of the species concerned.

Cyrilla racemiflora is a very polymorphic species, a feature which is particularly apparent when the various extreme forms from different geographical areas are compared. On the other hand, local populations tend to be rather uniform for the most part, with certain important exceptions which will be described below. Moreover, the variation from one population to the next, though often striking from the point of view of the extremes, is usually graded, and characteristically there are numerous intermediate forms. Different ecological variants show very clear preferences for a certain type of environment, but this is obvious in the extreme habitats only. In the intermediate habitats the various forms are usually thoroughly intermixed, and the overall picture is rather complex. This complex intergradation becomes very pronounced in areas such as the mountains of eastern Cuba, particularly the Sierra de Moa, where there is a high degree of habitat variation over a relatively small geographical area. Here one finds several ecological variants, the extremes of which are quite distinct morphologically and often form large uniform populations occupying discrete ranges or micro-ranges. For this reason several of these variants have been described by earlier authors as separate species or subspecies. A careful examination of these populations in the field, however, particularly the various intermediate populations, shows that they compose a single, large, intergrading system of variation. A few collections of the extreme forms give a false picture of the situation as a whole.

The common occurrence of complex variation patterns in conjunction with apomixis has long been recognized. The variation patterns themselves as well as the various factors involved in the development of this variation are both multiform and complex. In general the degree of intergradation within a system of variation is directly related to the amount of gene exchange within and between populations. In some instances barriers to gene exchange become quite rigid, thereby insuring variation patterns of a discontinuous nature (Gustafsson, 1947b). This is particularly striking in plant groups in which apomixis has become obligate. For example, in the genus *Alchemilla* (Rothmaler, 1936, 1941), the species of certain sections have apparently lost all capacity for sexual reproduction. The variation pattern is characterized by numerous distinct populations or groups of populations. Each of these forms a discrete unit, termed "microspecies" by some authors. These units are readily separable from other such units, and thus form a discontinuous pattern of variation. Moreover, according to Turesson (1943) these "microspecies" are not rigidly uniform, but are rather polymorphic themselves and segregate, in response to different environmental conditions, into what he refers to as "agamotypes." Other apomictic genera, which in certain areas exhibit a variation pattern similar to that described above, include *Crataegus*, *Hieracium*, *Poa*, *Tarax-*

acum, and several others of the familiar and "difficult" genera (Gustafsson, 1947).

A similar situation is found in the genus *Parthenium* in which two species, *P. argentatum* and *P. incanum*, are facultatively apomictic. Rollins (1944, 1950) has shown that, in *Parthenium argentatum* particularly, numerous different apomictic populations are readily dstinguishable from other such populations. There is a limited amount of intergradation between some of these populations, but they remain relatively stable, even though the species is only facultatively apomictic. However, it was clearly shown here that the relationship between these apomictic populations and the species as a whole is of a different order from the relationships between the various species in the genus. Moreover, the variation pattern found in the apomictic populations of these two species, although discontinuous, is explainable in terms of the variation found in the sexual members plus the effects of polyploidy and introgressive hybridization between the two species.

Similarly, the role of vegetative reproduction is undoubtedly of great significance as part of the mechanism involved in the origin of a variation pattern such as that found in *Cyrilla racemiflora*. As described above, this species propagates and spreads extensively by vegetative shoots which arise from horizontally situated, underground roots. By this method large clones are developed which usually remain interconnected by means of the root system. Self-incompatibility has not been demonstrated experimentally in *Cyrilla*, but evidence from field observations points clearly in this direction. The plants produce abundant flowers and fruits each year, but a high percentage of the fruits is parthenocarpic. In certain areas, however, a few plants can be found which produce a much higher percentage of seeds. In fact, Copeland (1951), in studying the morphology of the reproductive organs of *Cyrilla*, reported that the fruits of *Cyrilla* always contain two seeds. Careful examination of the areas in which there is a high percentage of seed development has shown that there are always at least two different individuals growing in close proximity. Usually this is found in the vicinity of two adjacent clones. Individual clones that are isolated from other individuals by a mile or more seldom, if ever, produce seeds, although the plants will flower and fruit profusely each year. Throughout the range of the genus the plants are visited regularly by bees, but in most situations pollen transfer is probably limited to a single clone. Apparently self-pollination is sufficient to stimulate the development of fruits, but fertilization of the ovule is accomplished only by pollen from a different individual. It is conceivable that an occasional self-pollination could result in the fertilization of an ovule and the development of seeds, but certainly the available evidence points to a high degree of self-incompatibility.

The formation of large clones will tend to produce more uniform local populations, although in self-incompatible species, which tend to have more heterozygous populations, this will not be so pronounced as in species capable of self-fertilization. And, as a clone of a self-incompatible species increases in size, the plants toward the center become increasingly seed sterile due to the lack of pollen from a different individual. The overall effect of mutations and recombinations will also be somewhat different in species capable of both sexual and asexual reproduction, in contrast to species reproducing by sexual methods only. The presence of asexual reproduction will tend to preserve mutant forms in two ways: 1. The "swamping effect" of sexual reproduction will be lessened, due to a decreased rate of sexual union and recombination; and 2. Homozygotes that would be eliminated for one reason or another in a purely sexual system could be maintained almost indefinitely and even spread by asexual means.

Thus the combination of these factors found in *Cyrilla* would tend to produce wide-ranging, heterozygous, and genetically variable populations, capable of sexual reproduction but free from many of its limitations. Moreover, this combination of factors will tend to produce, in a varied environment, local populations with a relatively high degree of adjustment to the habitat. In a genetically heterogeneous group of this type, gene combinations that are well adapted to the local environment can be "mass produced" by vegetative means. In this manner different populations will segregate according to habitat preference. In a region characterized by a high degree of ecological variation one would expect to find a correspondingly high degree of local variation among the populations occupying these different sites. On the other hand, with sexual reproduction still operative, there will be a certain amount of interbreeding between populations. This will tend to maintain the genetic heterogeneity of the group and also give rise to various intermediate forms which will, in some cases, occupy intermediate habitats. Thus if the various ecological segregates show morphological differences, the group would then be quite polymorphic, and the different morphological forms would be more or less segregated according to habitat, with occasional intergradations on the periphery.

TRENDS OF SPECIALIZATION IN PURDIAEA

There are several trends of specialization in *Purdiaea* which indicate that the South American species, *P. nutans*, is the most primitive species in the genus. The characteristics of *P. nutans* which are considered to be primitive are the following: leaves with uniformly pinnate venation; racemes which show a zone of transition from a vegetative to a reproductive shoot; and flowers with large, scarious, unequal exterior sepals.

The first character listed, leaves with uniformly pinnate venation, is found in *P. nutans* only. In all other species there are two or more pairs of prominent, lateral veins which run more or less longitudinally. In *Purdiaea cubensis* these longitudinal, lateral veins arise all along the midvein and are only slightly more prominent than the smaller, pinnate lateral veins. These specialized, lateral veins become quite prominent in other species of *Purdiaea,* forming an almost linear sequence of increasing prominence as follows: *Purdiaea nipensis, P. stenopetala, P. stereosepala, P. moaensis, P. velutina, P. shaferi, P. ekmanii.* Correlated with this increase in prominence is a tendency for these specialized veins to originate near the base of the midvein. Thus, in *Purdiaea* there is a series of venation patterns beginning with a simple, pinnate venation in *Purdiaea nutans*, and ending in a highly modified pattern with several prominent, lateral veins that originate near the base of the leaf and are almost parallel.

The largest break in this line of specialization occurs between *Purdiaea nutans* and *P. cubensis*, where the venation pattern changes from simple pinnate to modified pinnate as described above. However, the difference between the two patterns is not as great as it might seem. The lateral veins in the leaves of *Purdiaea nutans* are rather strongly arcuate and if extended would run more or less parallel to the leaf margin. The specialized lateral veins in the leaves of *Purdiaea cubensis* differ from this only in being longer and slightly more prominent. The smaller, lateral veins, and indeed most other aspects of the leaves of *Purdiaea cubensis*, are very similar to those of *P. nutans*.

There is a similar line of specialization in the transition from a vegetative to a reproductive shoot. In *Purdiaea nutans* there is a definite zone at the base of the racemes where a gradual transition from a vegetative shoot to a reproductive shoot occurs. In this zone there is a change in the morphology of the shoot axis, and often a transition from leaves to large bracts to smaller bracts. A similar zone is found in *P. cubensis*. A zone of transition is also evident in some collections of *Purdiaea nipensis* and *P. moaensis*, although the zone is much smaller and more obscure than in *P. cubensis*. In other collections of these species, however, the transition from a vegetative to a reproductive shoot is abrupt. In all other species of *Purdiaea*, this transition is usually quite abrupt.

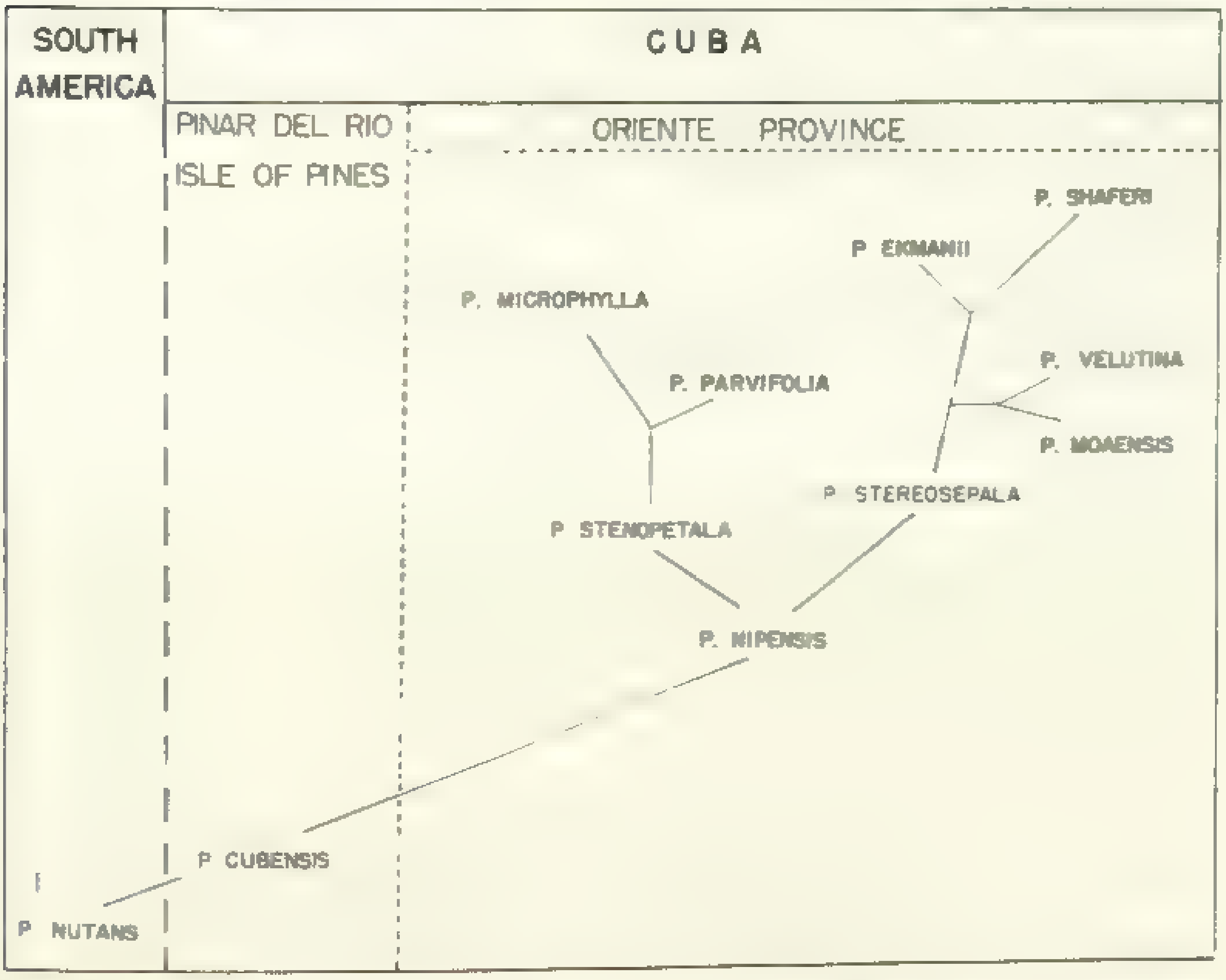


FIG. 23. Species relationships and present geographical distribution in the genus *Purdiaea*. Further explanation in text.

The texture of the sepals also shows a similar line of specialization. In *Purdiaea nutans* and *P. cubensis* the sepals are scarious and quite delicate; whereas in *P. moaensis*, *P. velutina*, and particularly *P. stereosepala*, the sepals are more foliaceous, or even coriaceous in the latter species. Again, *Purdiaea nipensis*, with sepals that are scarious-foliaceous, is somewhat intermediate between *P. cubensis* and the other Cuban species. Generally, there is a correlation between the texture of the sepals and the size relationship of the exterior sepals . The species with more scarious sepals also have very unequal exterior sepals; and species with more coriaceous sepals tend to have equal exterior sepals. There are some exceptions to this, particularly in *Purdiaea velutina* and *P. moaensis*. The texture of the sepals is about the same in these two species, but in the former the exterior sepals are clearly unequal, whereas in the latter they are approximately equal.

A secondary line of specialization is indicated in *Purdiaea parvifolia* and *P. microphylla*. As the names suggest, these species are characterized by very small leaves. They also have smaller stems, shorter racemes, and smaller floral parts than other species in the genus. These species occur in exposed and usually drier sites in the mountains, and have apparently become specialized, through reduction, for these habitats.

As is true of most plant groups, species of *Purdiaea* which show a high degree of advancement in one structure do not necessarily show a corresponding degree of advancement in every other structure. The degree of correlation is high, however, and the trends in specialization are rather clear.

On the basis of these lines of specialization, a tentative evolutionary sequence along with species relationships is indicated in Fig. 23. The geographical areas shown in this illustration represent the present distribution of the species and are not intended to suggest the areas in which speciation may have occurred. The length of lines separating the different species is intended to indicate the degree of morphological divergence between the various species.

SYNOPSIS OF THE GENERA

Purdiaea: Sepals unequal, the exterior sepals considerably larger than the interior sepals; petals lavender or violet; stamens 10, anthers inverted in bud, becoming erect at anthesis, dehiscing through terminal pores; fruit 3-5-ribbed, style elongate, unbranched.

Cliftonia: Sepals equal; petals spatulate, white or pinkish-white; stamens 10, anthers erect, dehiscing through longitudinal slits, filaments broad and petaloid below the middle, becoming terete and subulate above; fruit distinctly 3-5-winged, style sub-sessile, 3-5-lobed, massive.

Cyrilla: Sepals equal, petals white, thickened and glandular medially and below the middle; stamens 5, anthers dehiscing through longitudinal slits, filaments terete, subulate; fruit longitudinally bisulcate or trisulcate, style short, 2-3-lobed.

Purdiaea Planchon in Hook. Lond. Journ. Bot. 5: 250, 1846. Type: *P. nutans* Planch.

Costaea A. Rich. Fl. Cub. Fanerog. 2:75, 1853. Type: *C. cubensis* A. Rich.

Alloiosepalum Gilg, Notizbl. Bot. Gart. Berlin **11**, 102:97, 1931. Type: *A. Weberbaueri* Gilg.

Evergreen shrubs or small trees, bark light gray or brown; leaf scars prominent, triangular, diamond shaped to more or less rounded; stems glabrous or occasionally pubescent toward the ends; branches usually forming a zigzag pattern due to sympodial growth, with each shoot terminated by an inflorescence. Leaves coriaceous, dark green above, pale beneath; simple, alternate, entire, sessile, estipulate, articulate at the base, usually crowded toward the ends of branches; ovate, elliptic, obovate, spatulate, or oblanceolate; apex truncate, rounded, obtuse, acute, or abruptly acuminate. Venation pinnate or with two or more lateral veins arising near the base of the midvein and running more or less parallel to the margin of the leaf. Inflorescence a terminal raceme; pedicel articulate at the point of attachment to both the rachis and the receptacle. Bracts oblong or lanceolate near the base of the raceme, those toward the apex of the raceme becoming smaller and ovate to reniform. Sepals scarious to foliaceous, persistent; increasing in length considerably during the maturation of the fruit; glabrous to velutinous; inserted in a quincuncial manner; unequal, the exterior sepals considerably larger than the interior sepals, the first sepal equal to or as much as twice as long as the second and third sepals. Petals 5, pink to violet; ovate to oblong; apex acute, acuminate, or rounded; glabrous or rarely puberulent on the dorsal surface; coalescent at the point of attachment to an hypogynous disk. Stamens 10, the anthers oblong, caudate, versatile, with poricidal dehiscence; distinctly 2-lobed, the two lobes free above the point of attachment of the filaments; the two thecae of each lobe becoming confluent at anthesis; the anthers extrorse in bud, becoming inverted and introrse at anthesis by the inflection of the apex of the filament. Filaments subulate, adnate basally to the base of the petals at the point of attachment of the hypogynous disk. Ovary superior, ovoid to subglobose, usually 5-lobed and 5-loculed (rarely 3-4), each locule containing a single, pendant ovule. Fruit indehiscent; ovoid to subglobose, glabrous to velutinous, the indumentum usually denser near the apex; 1- to 5-seeded, the seed composed of a straight, cylindrical embryo, surrounded by a mass of cellular endosperm; no seed coat present, the ovary wall serving as the functional seed coat; style 1, persistent, attenuate.

KEY TO THE SPECIES

A. Leaves pinnately veined .... 1. *P. nutans.*

A. Leaves with two or more lateral veins running more or less parallel to the leaf margin.

B. Leaves extremely thick and coriaceous, 0.4-0.6 mm. thick at maturity, venation quite prominent on both sides, the lateral veins forming a loose prominent network .... 11. *P. ekmanii.*

B. Leaves not over 0.2 mm. thick.

C. Leaves 0.5-1.3 cm. long, 0.4-0.8 cm. broad, usually abruptly acuminate .... 6. *P. microphylla.*

C. Leaves 2 cm. long or longer.

D. Exterior sepals less than 2 mm. broad at anthesis, leaves with revolute margins .... 5. ***P. parvifolia.***

D. Exterior sepals more than 2 mm. broad at anthesis, leaves usually without revolute margins.

E. First and second sepal approximately equal in length.

F. Young shoots velutinous below the base of the peduncle, peduncle ca. 2 mm. in diameter at the base .... 8. *P. moaensis.*

F. Young shoots glabrous or nearly so below the base of the peduncle, peduncle 1.0 mm. or less in diameter at the base.

G. First sepal rounded at the apex, thickened at the base, usually asymmetrical, with the inner margin flattened, the outer margin flaring outward above the middle; finely pubescent, particularly below the middle .... 7. *P. stereosepala.*

G. First sepal with an acute or rarely obtuse apex; only slightly thickened basally; symmetrical; finely pubescent on a conspicuous dark area near the base, glabrous or nearly so above this area .... 4. ***P. stenopetala.***

E. First sepal clearly longer than the second sepal.

H. First leaves of a shoot developing into cataphylls, densely clothed with appressed, silky trichomes .... 9. *P. velutina.*

H. First leaves of a shoot foliaceous, no cataphylls formed.

I. First sepal elliptic-oblong; leaves with fine, reticulate venation clearly visible .... 2. ***P. cubensis.***

I. First sepal ovate, leaves without fine, reticulate venation.

J. Peduncle 2.5-3 mm. in diameter at the base, densely clothed with silky, velutinous trichomes. Leaves broadly elliptic-obovate with 6-8 prominent lateral veins .... 10. *P. shaferi.*

J. Peduncle ca. 1 mm. in diameter at the base, finely pubescent to puberulent. Leaves obovate-oblanceolate to spatulate, 2-4 prominent lateral veins .... 3. ***P. nipensis.***

1. **Purdiaea nutans** Planchon in Hook. Lond. Journ. Bot. 5: 251, 1846. Type: not seen.[2]

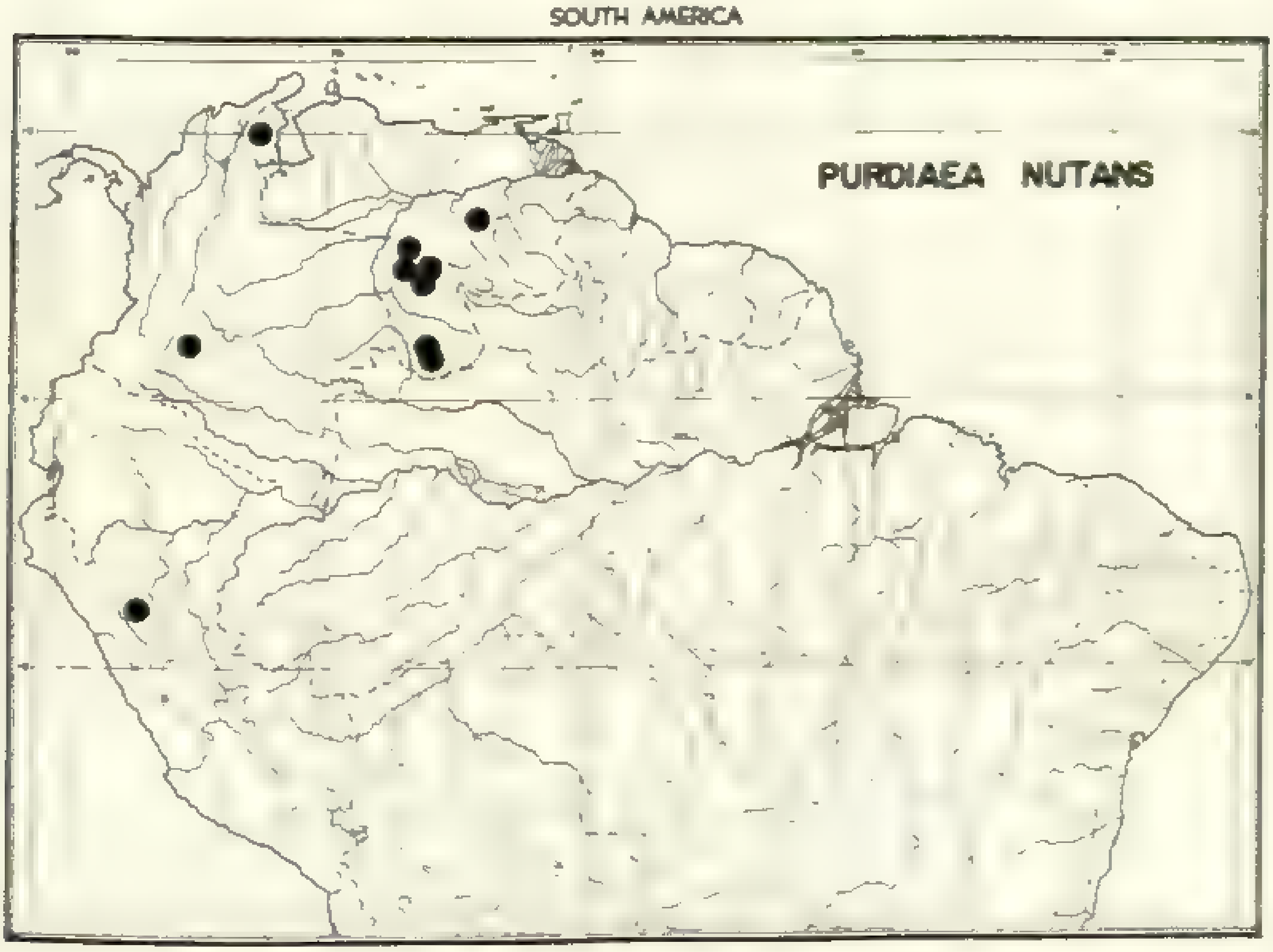
Alloiosepalum weberbaueri Gilg, Notizbl. Bot. Gart. Berlin **11, 102**:97, 1931.

Purdiaea weberbaueri (Gilg) Mattick, Notizbl. Bot. Gart. Berlin **12, 393**:398, 1935.

Shrub or small tree up to 6 or 7 meters tall; bark light gray or brown; stems glabrous. Leaves dark green, shining above, pale beneath; 2-5 cm. long, 1-2 cm. broad, obovate, oblong, or oval; apex obtuse or rounded, mucronulate; base cuneate, narrowly sessile; midvein prominent beneath, depressed above, secondary veins much weaker, uniformly pinnate, bending upward slightly at the margin; smaller reticulate veins distinct beneath, less so above. Racemes 2.5-5.5 cm.

[2] The original description was based on material in the Hooker Herbarium collected by Purdie in New Granada (Colombia).

long, suberect to pendulous; a zone of transition from a vegetative to a reproductive shoot near the base of the peduncle: rachis attenuate, ca. 1.0 mm. in diameter at the base, tapering to 0.5 mm. in diameter at the apex; villous, tomentose, or glabrous: pedicel 2-5 mm. long, those at the base of the raceme longer than those at the apex; villous to glabrous, the indumentum corresponding to that on the peduncle; the articulation at the point of attachment with the receptacle usually swollen: bracts lanceolate or occasionally lanceolate-elliptic; up to 19 mm. long near the base of the raceme, 10-13 mm. long near the apex; glabrous or rarely pubescent along the midvein near the base; borne on a small protuberance of the peduncle, distinctly articulate at the base. Sepals scarious, very unequal, variable in size; the first sepal 14-17 mm. long, 7-10 mm. broad at anthesis, up to 19 mm. long, 12 mm. broad at maturity, considerably longer than the second sepal; broadly ovate; apex acute or occasionally obtuse or rounded, mucronulate; glabrous or nearly so: second sepal 8-12 mm. long, 6-7 mm. broad at anthesis, up to 13 mm. long, 8 mm. broad at maturity; apex obtuse or acute, occasionally mucronulate; glabrous or nearly so: third sepal 7-9 mm. long, 3-4 mm. broad at anthesis; asymmetrical, the inner margin flattened and cilliate, the outer margin rounded and glabrous; interior sepals 4.5-5.5 mm. long, 1-1.5 mm. broad at anthesis, up to 6.5 mm. long, 2.5 mm. broad at maturity; lanceolate; margin strongly ciliate. Petals 9-11 mm. long, 3-4 mm. broad at anthesis; apex obtuse or acute, glabrous; violet in color. Anthers 3.5-5 mm. long, rather variable in size in a single flower; bright yellow: filaments 4.5-6 mm. long; subulate; glabrous. Ovary ovoid, 3-locular (rarely 4- to 5-locular); glabrous or tomentose. Fruit 2-2.5 mm. long, ovoid, tapering from near the middle to the apex; 3-5-ridged. Style



ca. 5.5 mm. long at anthesis, becoming 7 mm. long at maturity; glabrous; attenuate.

DISTRIBUTION: Northern South America, dense forests or "elvan woodlands" of higher elevations.

REPRESENTATIVE SPECIMENS SEEN: VENEZUELA. **State of Amazonas:** Cerro Huachamacari, Rio Cunucunuma; along South Escarpment at 1500 m. alt., *Maguire, Cowan, and Wurdack 29803* (US, NY); vicinity Summit Camp at 1500 m. alt., *Maguire, Cowan, and Wurdack 30011* (US, NY); Summit Camp at 1500 m. alt., *Maguire, Cowan, and Wurdack 30211* (US, NY, MO); Cerro de la Neblina, Rio Yatua; West Cumbre Camp at 5800 feet alt., *Maguire, Wurdack, and Bunting 36956* (NY); along west escarpment, 1700-1800 m. alt., *Maguire, Wurdack, and Bunting 37083* (US, NY, F). Summit of Mount Duida; alt. 7100 feet, *Tate 611* (US, NY); alt. 5500-6000 feet, *Tate 425* (NY). Rio Ventuari; Serrania Paru, Rio Paru, Cano Asisa, *Cowan and Wurdack 31074* (US, NY, UC). **State of Zulia:** Helechal Perija; alt. 2000 m., *Gines 2022* (US).

COLOMBIA. **Department of Huila:** Cordillera Oriental; Rio Ambrica, near confluence of Quebrada la Trinidad, *Fosberg and Holdridge 19567* (US, NY). Without locality; *Bruckmüller* (NY).

PERU. **Department of Amazonas:** Chachapoyas; entre Chachapoyas y Taulia, *Raimondi 2054* (GH); Molinopampa, *Weberbauer 4332* (GH).

Purdiaea nutans is the only species of *Purdiaea* which occurs in South America. It is found in dense forests or "elvan woodlands" of higher elevations, usually 1500-2000 meters above sea level. It is sparsely distributed, seldom if ever occurring in large stands or populations. The most distinctive and probably the most primitive species in the genus, *Purdiaea nutans* is most closely related to *P. cubensis*. It is easily distinguishable from the latter species, and indeed, all other species of *Purdiaea* by several characters. *Purdiaea nutans* is the only species in which the leaves have uniformly pinnate venation. Its large flowers are distinctive, being the largest in the entire Cyrillaceae. The broadly ovate first sepal and the pendulous racemes also serve to distinguish this species from *Purdiaea cubensis*.

A relatively wide-ranging species, *Purdiaea nutans* shows a minor degree of variation in several characters. The leaves, bracts, and sepals are usually somewhat smaller on specimens collected at high elevations than on specimens collected at lower elevations in the same geographic area. The petals, also, are variable in size, but in contrast to the above structures, a wide range of variation can be found on a single plant. Occasionally a size range comparable to that known from the entire species can be found on a single specimen. Similarly, the degree of pubescence on the rachis and the pedicel is rather variable, but this variation has no apparent geographic or altitudinal significance. Specimens varying from glabrous to pubescent to tomentose are found throughout the range of the species, with the exception of the two collections from Peru. The apex of the first sepal is also rather variable in shape, varying from acute to obtuse or rounded.

Purdiaea weberbaueri (Gilg) Mattick was described from specimens collected in Peru and was segregated from *P. nutans* on the basis of its glabrous racemes and more acute exterior sepals. However, it falls well within the variation pattern of *P. nutans* and is included in that species in the present treatment. Several collections of *P. nutans* have been made in recent years in Colombia and Venezuela. These collections, which were not available when *Purdiaea weberbauri* was described, have made possible a much better understanding of the variation pattern in the present species. As discussed above, the degree of pubescence on the racemes and the shape of the sepal apex are among the more variable characters of *Purdiaea nutans*. The variation in these characters is graded, with many intermediates between the extreme forms. Several specimens of *Purdiaea nutans* are indistinguishable from the type of *P. weberbauri*. There are, in fact, collections of *P. nutans* which accord with the original description of *P. weberbauri* better than the type collection of that species. In the latter collection the first three sepals have ciliate margins and the third sepal is finely puberulent on the inner edge of the ventral surface. There are specimens of *P. nutans* in which the first three sepals are glabrous. Future collections of *Purdiaea nutans* from Peru will undoubtedly show more variation in the degree of pubescence in the plants from that area.

2. **Purdiaea cubensis** (A. Rich.) Urban. Fedde. Repert. Spec. Nov. 22:366, 1926. Type: not seen.[4]

Costaea cubensis A. Rich. Fl. Cub. Fanerog. 2:75, 1853.
Purdiaea monodynama Griseb. Cat. Plant. Cub. 53, 1866.
Purdiaea cubensis (A. Rich.) Urb. var. *albosepala* Marie-Victorin, Contrib. Inst. Bot. Univ. Montréal, 63:61, 1948.

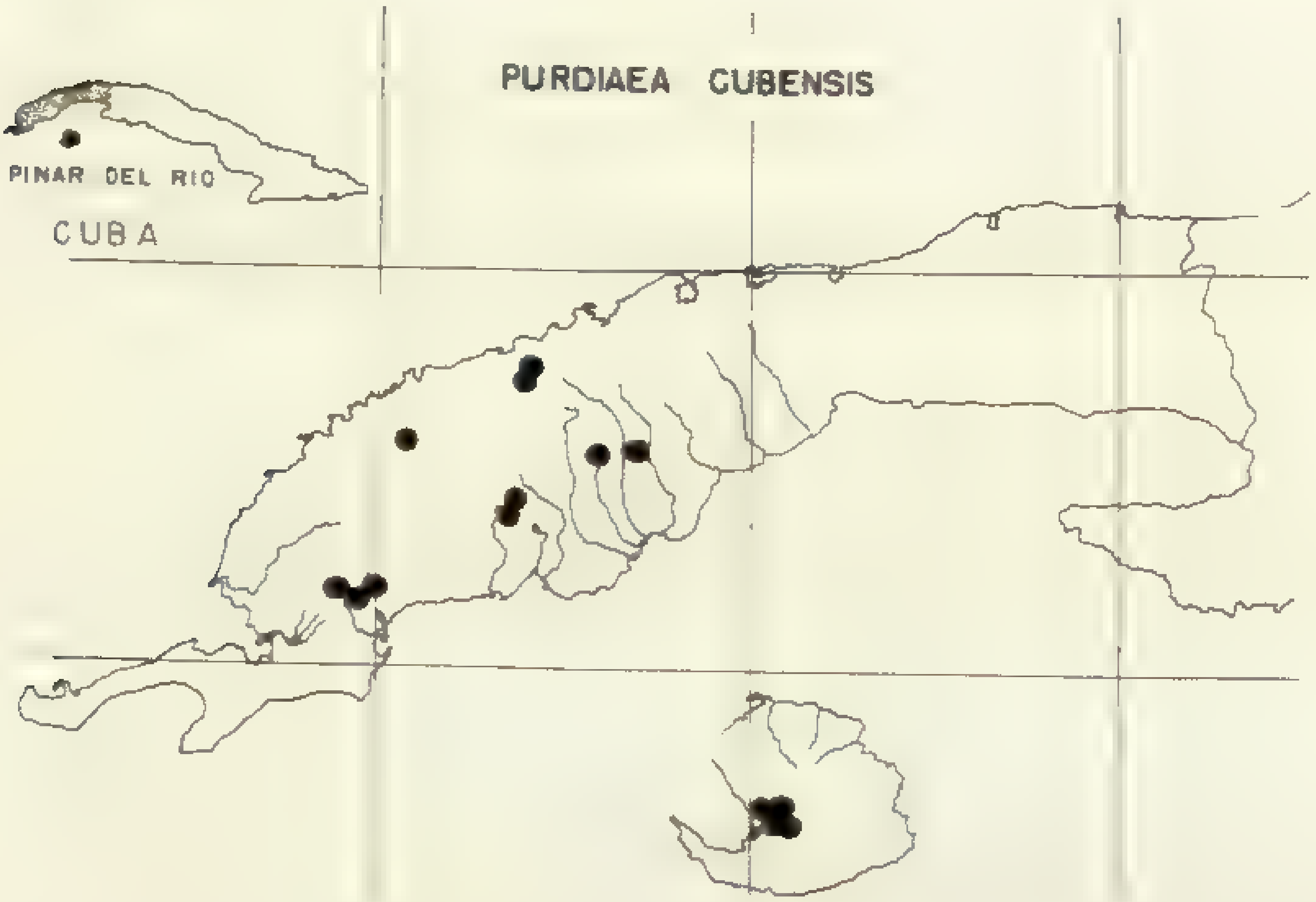
Shrub up to 4 meters tall, stems smooth or scaly, glabrous; leaf scars prominent, triangular. Leaves dark green above, pale beneath, somewhat crowded toward the ends of branches, 3-7 cm. long, 1.5-3.5 cm. broad, obovate to elliptic; apex rounded or obtuse; base narrowly sessile: midvein prominent on both surfaces; 4-6 longitudinal lateral veins arising along the length of the midvein and running more or

---

[4] The original description of *Costaea cubensis* was based on material collected in "Sierra de Marcos Guerra" by José Maria Valenzuela.

less parallel to the margin of the leaf, prominent above, less so beneath; smaller lateral veins freely branching, pinnate, forming interconnections between the midvein and the longitudinal lateral veins. Racemes 5-12 cm. long, erect: rachis glabrous or puberulent; subulate: pedicel 3-4.5 mm. long, glabrous or puberulent. Bracts oblong, 7-10 mm. long, 2-3 mm. broad near the base of the raceme, becoming ovate, 2-4 mm. long, 1-2.5 mm. broad near the apex of the raceme; glabrous or nearly so, occasionally with a finely ciliate margin; articulate at the base. Sepals light pink to white; scarious; very unequal: first sepal oblong to ovate-oblong, 12-14 mm. long, 6-8 mm. broad at anthesis, up to 16 mm. long, 10 mm. broad at maturity; apex obtuse, rarely acute; glabrous or finely pubescent near the base, often with a ciliate margin: second sepal ovate, 6-8 mm. long, 2-5 mm. broad at anthesis, 9-10 mm. long, 5-6 mm. broad at maturity; apex obtuse, mucronulate, glabrous or finely pubescent toward the base; margin ciliate: third sepal approximately the same length as the second sepal at anthesis, often slightly larger than the second sepal at maturity; interior margin flattened, strongly ciliate; exterior margin rounded, glabrous or finely ciliate: fourth and fifth sepal lanceolate, 4-6 mm. long at anthesis, up to 10 mm. long at maturity; pubescent, margin ciliate; midvein conspicuous. Petals 5-7 mm. long, 2-4.5 mm. broad, ovate to ovate-oblong; apex abruptly acuminate, glabrous; deep pink or violet. Anthers 2-2.7 mm. long, weakly caudate: filaments 2.5-3 mm. long; narrow, slightly subulate. Ovary subglobose to globose, 1-1.5 mm. in diameter at anthesis; 5-lobed, glabrous or pubescent: style subulate, 4.5-5 mm. long at anthesis, up to 7 mm. long at maturity. Fruit 2-2.5 mm. in diameter, subglobose to globose; strongly 5-angled; glabrous or pubescent.

DISTRIBUTION: Pine barrens of Pinar del Rio Province, Cuba and the Isle of Pines.



REPRESENTATIVE SPECIMENS SEEN: CUBA. **Prov. Pinar del Rio:** *Wright 2204* (UC, GH, MO); *Carabia 3940* (NY); Pinares near Loma, Marcos Guerra, N. W. of S. Diego, *Léon and Charles 4887* (NY, MT, LS); Galalon to San Pedro Del Caimito, *Shafer 11950* (US, NY); Pinar del Rio City, between Laguna Maguina and Laguna de Junco, *Ekman 17905* (NY); Herradura, *Van Hermann 5851* (SV, 2 sheets); Sabanas de Santo Tomas, *Acuña 11210* (SV); between Mina de Oro and Playa del Soldado, *Killip 43900* (US, LS); pinelands between Pinar del Rio and Surnidero, *Roig 3150* (US, GH). Santa Catalina; *Van Hermann, 3242* (UC, SV); *Caldwell and Baker 7073* (F); cerro de Cabras; *Léon 17758* (LS); *Britton, Britton, and Cowell 9796* (NY); *Marie-Victorin, Léon, Alain, and Carabia 17758* (MT); *Léon 3395* (NY, MT, LS); on Guane Road, *Britton, Britton, and Gager 7289* (US, NY, F). La Cajalbana; *Acuña 16439* (SV); *Ekman 70480* (NY); La Palma, *Alain and Acuña 1169* (LS).

ISLE OF PINES: Vicinity of Los Indos; *Marie-Victorin and Léon 17864* (MT); *Jennings 326* (US. NY, GH); *Britton, Britton, and Wilson 14202* (GH, F, US, NY, MO); *Killip 44042* (NY, LS); *Léon and Marie-Victorin 17864* (LS); *Marie-Victorin and Alain 88* (LS); *Calvius and Elfameli 7978* (SV); *Léon, Marie-Victorin, and Carabia 18860* (LS).

Purdiaea cubensis, a very distinctive species of the pine barrens and savannas of western Cuba and the Isle of Pines, is seldom if ever confused with any other species of the genus. In common with all species of *Purdiaea* from Cuba, the leaves of *P. cubensis* have a venation pattern characterized by two or more pairs of prominent lateral veins which arise from the midvein, curve abruptly, and run longitudinally, parallel to the margin of the leaf. In the leaves of *Purdiaea cubensis*, however, there is a fine, densely reticulate pattern of smaller veins, which is distinctly visible on both surfaces of the leaf. This characteristic reticulum is not found in the leaves of other species of *Purdiaea* from Cuba. A similar reticulate pattern is found in the leaves of *Purdiaea nutans*, but in that species the lateral veins are pinnate, and do not run parallel to the margin of the leaf. The large, delicate oblong-elliptic exterior sepals also serve to distinguish *Purdiaea cubensis* from all other species in the genus.

Purdiaea cubensis is most closely related to *P. nutans* and is discussed under that species. Among the Cuban species, *Purdiaea cubensis* seems most closely related to *P. nipensis*. This relationship is obscure, however, and *Purdiaea nipensis*, in contrast to *P. cubensis*, is clearly related to other Cuban species.

In spite of its bicentric distribution, *Purdiaea cubensis* exhibits only minor morphological variation. The material from the Isle of Pines was segregated by Marie-Victorin (1948) as *Purdiaea cubensis* var. *albosepala*, but there seem to be no constant characters by which the material from these two areas can be distinguished. According to the above author, the plants from the Isle of Pines have white sepals, whereas those from Pinar del Rio have pink or rose-colored sepals. Very few specimens have label data giving the color of the sepals, but in at least two collections from the Isle of Pines (*E. P. Killip 44042* and *43900*) the sepals are described as varying from pink to white. In a few other collections from this area (notably *Jennings 326*) the sepals have remained distinctly pink on the dried material, although sepal color in *Purdiaea* usually fades upon drying. I have not seen *P. cubensis* in the field, but in all of the species of *Purdiaea* which I have seen in the field, sepal color was rather variable. In *Purdiaea velutina*, for example, the color of the sepals was found to vary from white to deep pink in plants growing only a few feet apart.

The average leaf size in *Purdiaea cubensis* is usually slightly larger in the collections from the Isle of Pines than in collections from Pinar del Rio, but there is a high degree of overlap in the measurements, and several collections can be assigned to the above variety only if the area from which they were collected is known. For these reasons it seems that the material of *Purdiaea* from the Isle of Pines does not warrant varietal status, and variety *albosepala* is not recognized in the present treatment.

There are a few collections of *Purdiaea cubensis* from Pinar del Rio which have noticeably smaller than average leaves (*Van Hermann 3243* and *Caldwell and Baker 7073.*) There is also some variation in the shape of the exterior sepals. One specimen in particular (*Roig 3150*) has sepals that are narrower and more pointed than those found in other collections of this species. These are apparently ecological variants, although there is little information available on the effects of different ecological factors on any of the species in this genus.

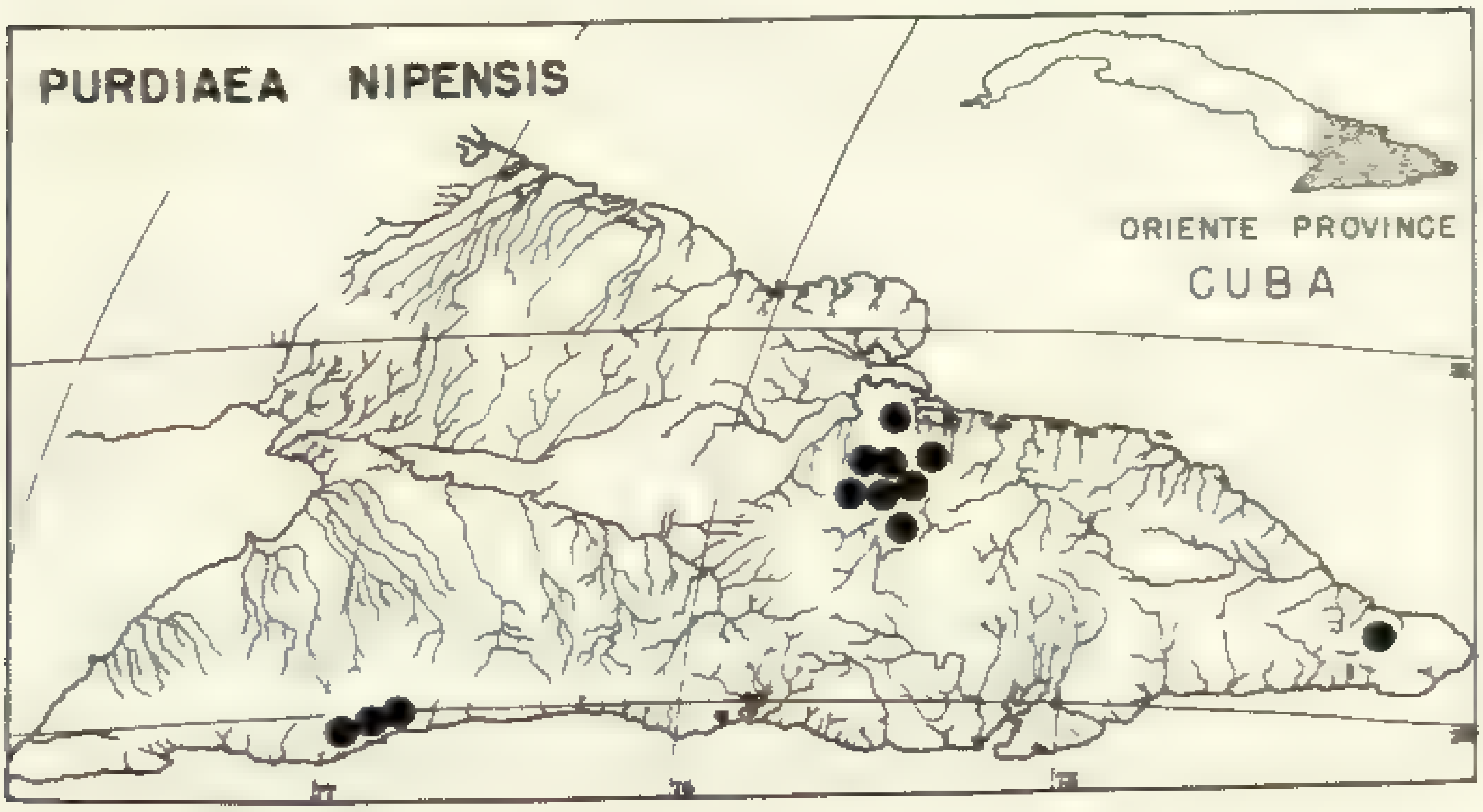
3. **Purdiaea nipensis** Marie-Victorin & Léon, Contrib. Inst. Bot. Univ. Montréal, 63:55, 1948. Type: *Léon, Marie-Victorin, Clément, and Alain 19837*

Purdiaea nipensis Marie-Victorin var. *alaini* Marie-Victorin, Contrib. Inst. Bot. Univ. Montréal 63:56, 1948.

Shrub with light gray bark, young shoots puberulent to glabrous; light brown, becoming gray with age. Leaves highly variable in size, 2.5-10 cm. long, 1-1.5 cm. bread; obovate, obovate-spatulate, or obovate-oblanceolate; apex acute, obtuse, or emarginate, often mucronulate;

base attenuate or cuneate; midvein and 2-6 longitudinal lateral veins prominent beneath, weak above; 2 longitudinal lateral veins often arising near or slightly above the middle of the leaf; smaller reticulate veins distinct beneath, less so above. Racemes 3.7-7 cm. long, erect to pendulous: rachis pubescent or puberulent, attenuate; ca. 1 mm. in diameter at the base tapering to 0.3 mm. in diameter at the apex; zigzag in shape, often strikingly so toward the apex: pedicel 1-2 mm. long, 0.3-0.5 mm. in diameter at anthesis, pubescent: bracts lanceolate, ca. 6 mm. long near the base of the raceme, becoming ovate-lanceolate to ovate, ca. 2 mm. long toward the apex of the raceme; pubescent below the middle, glabrous above. First sepal 9-11 mm. long, 4.5-6 mm. broad at anthesis, up to 15 mm. long, 9 mm. broad at maturity; considerably longer than the second sepal; ovate to somewhat deltoid; apex acute to acuminate, rarely slightly obtuse; base obtuse, truncate, or slightly cordate; scarious; glabrous or nearly so, rarely puberulent near the base: second sepal 7-7.5 mm. long at anthesis, up to 9 mm. long at maturity; apex acute or rounded; base truncate or rounded; dorsal surface puberulent near the base, ventral surface pubescent below the middle: third sepal approximately the same length as the second sepal; asymmetrical, the exterior edge rounded, the interior edge flattened; dorsal surface glabrous, or occasionally puberulent near the base; ventral surface pubescent below the middle, glabrous above: interior sepals 3.5-4 mm. long, 1-1.5 mm. broad at anthesis, 5-6 mm. long at maturity; lanceolate; apex acuminate; glabrous or puberulent on the dorsal surface, pubescent on the ventral surface; margin ciliate; midvein prominent on the dorsal surface. Petals ovate, 6-7 mm. long, 2.5-3.5 mm. broad, apex rounded; glabrous. Anthers 2.7-2.8 mm. long, weakly caudate, with a small glandular tip terminating the cauda: filaments ca. 4 mm. long, subulate. Ovary globose, 5-ribbed, glabrous or pubescent: style 3.5-4 mm. long at anthesis, ca. 5 mm. long at maturity. Fruit globose, 5-ribbed, glabrous or pubescent.

DISTRIBUTION: Mountains and stream valleys of Oriente Province, Cuba.



REPRESENTATIVE SPECIMENS SEEN: CUBA. **Prov. Oriente:** Sierra de Nipe; Arroyo seco between Woodfred and La Mina, *Léon, Marie-Victorin, Clément, and Alain 19837* (Type: GH. Isotypes: LS, 2 sheets; SV; MT); *Léon, and Alain 20414* (MT, Type of *P. nipensis* var. *alaini*); Cayo del Rey, Cuabales de la Loma de Bio, *Carabia 4059* (NY, LS); En el charrasco, Cayo Rey, *Lopez 1839* (LS); *Ekman 9485* (NY); Bosque de La Plancha, *Léon and Alain 19110* (LS); Cajo La Plancha, sur la limonite granuleuse, *Léon and Alain 19111* (LS, MT); Chemin de la mine Woodfred, *Léon and Alain 19147* (MT, LS); *Léon, Marie-Victorin, and Alain 19837* (LS); Alto de la Bandera, *Léon, Marie-Victorin, Clément, Alain 19754* (LS); Falda Norte Loma Mensura, *M. Lopez 2824* (SV, LS); Charrascales de Arroyo Potrero, *Lopez 2824* (SV, LS); *Marie-Victorin, Carabia 4059* (MT); South of lumber camp, alt. 600-700 m., *C. V. Morton and Acuña 3051* (US); along trail Piedra Gorda to Woodfred, 400-500 m. alt., *Shafer 3110* (US, NY); Minas de la Nicaro, Ocujal, *Acuña, Alonzo, and Piña 18781* (SV). Sierra de Cristal; Bosques humedos de El Prado, *Alain, Acuña, and Lopez 5391* (SV, LS); *Alain, Lopez 4694* (LS). Sierra de Maestra: Pico de La Bayamesa, 4800 ft., *Lopez 2304* (SV, LS); between Pico Turquino and La Bayamesa, alt. 1350 m., *Morton and Acuña 3755* (US); Banks of Arroyo Corjo, near Nagua, Pico Turquino, *Ekman 14738* (NY, LS). Vicinity of Toa; Orillas de un arroyo, Km. 20 al Sur de Sabanilla, Via Azul, *Alain and Morton 5159* (LS); Nuevo Pinar, Alcarraza arriba, *Clément 5107* (LS); same locality, *Clément and Carlos 5107*, (LS). Without locality; ***Wright 2205*** **(GH, UC)**.

This species, known from three rather isolated mountain ranges in eastern Cuba, is the most probable connecting link between *Purdiaea cubensis* and the other Cuban species of *Purdiaea*. Although the relationship between these two species is rather distant there are two points of similarity which seem significant. In the leaves of both species two or more of the longitudinal lateral veins consistently arise near the middle of the leaf. This occurs sporadically in other species but usually the longitudinal lateral veins arise near the base of the leaf. The other point of similarity is the very unequal exterior sepals, with the first sepal almost twice as long as the second sepal. This extreme size difference between the two exterior sepals is not found in any of the other species of *Purdiaea* from Oriente Province (although it is found in *P. cubensis* from Pinar del Rio and *P. nutans* from South America). In general aspect, and in most characteristics, however, *Purdiaea nipensis* is more like the other Cuban species, all of which are endemic to Oriente Province. It is most closely related to *P. stenopetala*, but the two species are readily distinguishable because of the longer and very unequal exterior sepals in *P. nipensis*.

Purdiaea nipensis is one of the more variable species in the genus, and future collections and field observations in eastern Cuba may necessitate the establishment of one or more geographical varieties. The material from the Sierra de Maestra has longer and more obovate leaves, and somewhat more acuminate sepals than the material from the Sierra de Nipe. Similarly, in the collection from extreme eastern Cuba, south of Sabanilla *(Alain and Morton 5159)* the leaves are even longer and more elliptic and the sepals are more foliaceous than those of collections from other parts of the range. The collections from the Sierra de Maestra and Sabanilla are few in number, however, and are insufficient to show the variation pattern of the plants from these areas.

Purdiaea nipensis var. *alaini* Marie-Victorin, on the other hand, occurs in the Sierra de Nipe, apparently sympatric with other representatives of the species which are not assigned to this variety. The variety does differ from the type in having slightly broader leaves and more acuminate sepals, but this difference falls well within the range of variation found in other collections from this area, and there are many intermediates between the two forms. For this reason var. *alaini* is not retained in the present treatment.

NOTES: Some confusion has arisen as to which sheet of the type collection represents the holotype. In the specimen citations following the original description of the species, Marie-Victorin (1948) cited the type as follows: "Arroyo Seco, entre Woodfred et la Mine, Sierra de Nipe. 6 Avril, 1941. *Léon, Victorin, Clément and Alain 19837.* (TYPE dans l'herbier de Colegio de la Salle, La Habana, Cuba)". To my knowledge there is but one specimen on which the label data conforms to this citation. This specimen, now in the Gray Herbarium, is stamped "EX HERBARIO DE LA SALLE; HABANA, CUBA". In the herbarium of the College of La Salle in Havana there are two sheets bearing collection number 19837, but the name of one of the collectors, Clément, is not listed. One of these sheets, marked as TYPE, has the locality designated as "Cayo de las Mujeres, falda Oeste de la Loma Mensura, Sierra de Nipe, Mayari, Oriente", and is dated April 6, 1941. The other sheet is dated April 4, 1941, and has the locality designated as: "Camino de la Mina — Woodfred, Sierra de Nipe, Oriente". The other two isotypes cited above bear a full complement of collectors, Léon, Victorin, Clément, and Alain; both are dated April 6, 1941, and the locality data, though not the same, apparently refer to the same area. The locality is apparently the same for all five of these specimens, and so far as I can tell the material on the five sheets is identical. It seems logical to assume, therefore, that the sheet in the Gray Herbarium does represent the holotype since it is the only sheet that conforms in habitat data to the original citation, and since this sheet apparently was in Havana at the time of the citation.

4. **Purdiaea stenopetala** Grisebach in Goett. Abh. 9:45, 1860. Type: *Wright 341*

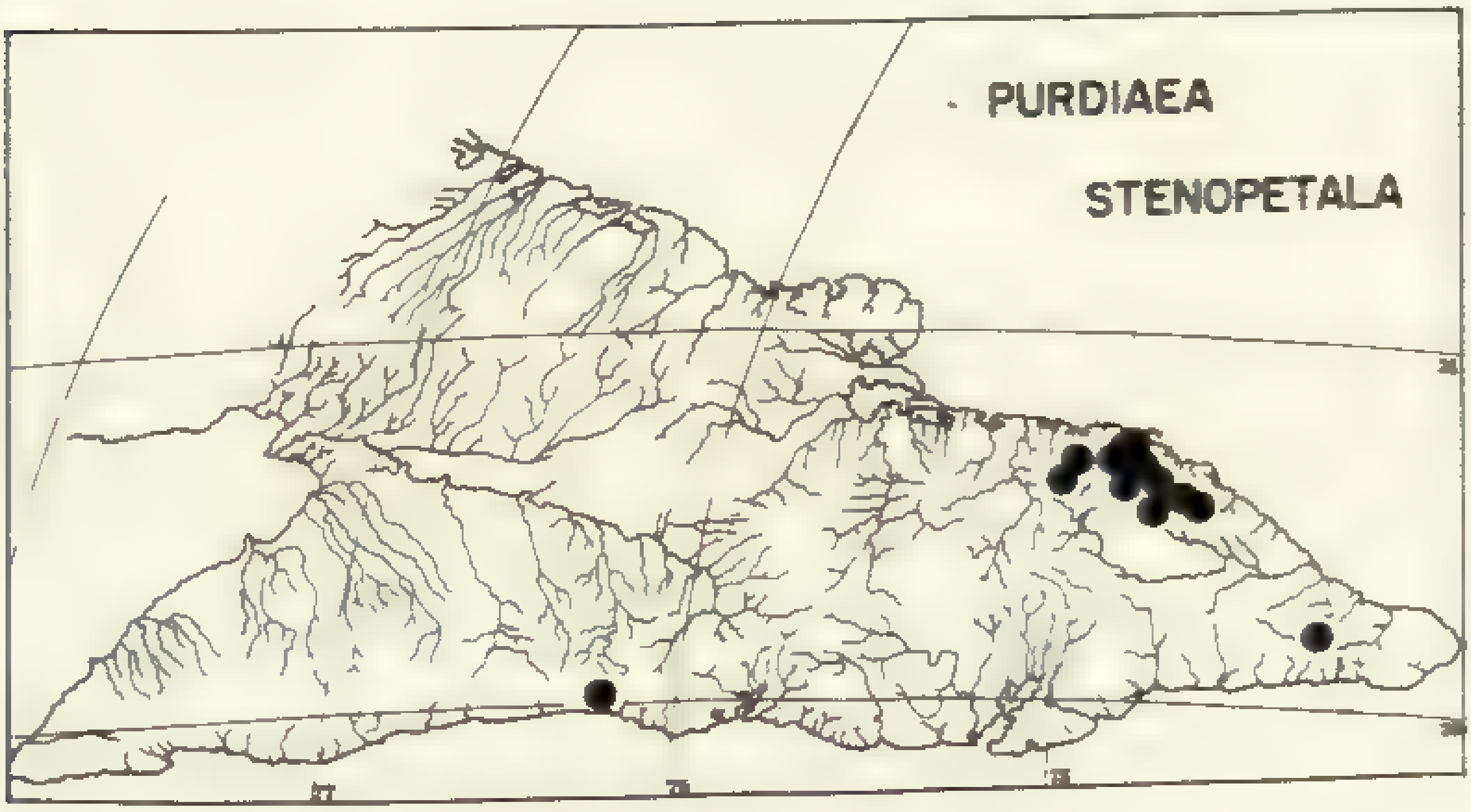
Purdiaea ophiticola Marie-Victorin, Contrib. Inst. Bot. Univ. Montréal, 63:56, 1948.

Shrub with light gray bark, stems glabrous, smooth, light brown becoming gray with age. Leaves dark green above, pale beneath, 2.5-8 cm. long, 1-2 cm. broad; obovate, obovate-oblanceolate, or spatulate; apex obtuse, truncate, or slightly emarginate and mucronulate; base attenuate, narrowly sessile; midvein and 2-4 longitudinal lateral veins running parallel to, and very near, the leaf margin; smaller secondary veins more or less distinct beneath, less so above. Racemes 5-6 cm. long at mid-anthesis, up to 7.5 cm. long at maturity, usually more or less pendulous. Rachis glabrous, puberulent or pubescent; attenuate, ca. 1.5 mm. in diameter at the base, tapering to ca. 0.5 mm. in diameter at the apex, ridged. Pedicel 1-1.5 mm. long, 0.5 mm. in diameter, glabrous or pubescent, distinctly articulate at the point of attachment to the rachis and the receptacle. Bracts ovate-lanceolate or lanceolate, 4-5 mm. long near the base of the raceme, becoming ovate to reniform, 1-1.5 mm. long near the apex of the raceme; articulate at the base; glabrous or pubescent, the indumentum corresponding to that of the peduncle. Sepals highly variable in size, scarious in bud becoming more foliaceous at maturity; the first sepal 5-7.5 mm. long, 3.5-4 mm. broad at anthesis, up to 12 mm. long, 7 mm. broad at maturity; ovate or ovate-deltoid; apex acute or obtuse; base truncate or cordate; finely pubescent on a conspicuous, dark area near the base of the sepal, glabrous, or nearly so above this area: second sepal approximately the same size as the first sepal with a narrower and more acute apex; usually pubescent on both surfaces below the middle, glabrous or nearly so above: third sepal equal to or slightly shorter than the second sepal; apex acute, base truncate; asymmetrical, the interior margin flattened and ciliate, the exterior margin rounded and glabrous: interior sepals lanceolate, apex acute or acuminate, base obtuse; ca. 4 mm. long at anthesis, up to 6.5 mm. long at maturity; pubescent on both surfaces, densely so below the middle; the two sepals more or less opposite and enclosing the fruit. Petals 5-6 mm. long, 2-3 mm. broad, oblong; apex acute or obtuse; glabrous or occasionally with a weakly ciliate margin near the base; deep violet in color. Anthers 2-2.7 mm. long, slightly caudate; filaments 2.5-3 mm. long, subulate. Ovary subglobose, ca. 1.5 mm. in diameter at anthesis; 5-angled, glabrous or pubescent. Style persistent, subulate, ca. 3 mm. long at anthesis, becoming 5-6.5 mm. long at maturity; glabrous, exserted. Fruit subglobose to ovoid, usually strongly 5-keeled, 2.5-3.2 mm. in diameter at maturity.

DISTRIBUTION: Mountains of Oriente Province, Cuba.

REPRESENTATIVE SPECIMENS SEEN: CUBA. **Prov. Oriente:** *C. Wright 341* (isotypes: MO, 2 sheets; GH, 2 sheets; NY, 2 sheets; UC). Vicinity of Moa; sur la limonite humide de la plage, *Marie-Victorin 21433* (MT, type of *Purdiaea ophiticola* Marie-Victorin; isotypes: MT, GH, LS); *Acuña 12528* (US, SV); Playa Vaca, *Acuña 12527* (US, SV); *Acuña 12529* (US, SV); *Bucher 19* (NY); *Bucher 1173f* (SV); *Bucher 11044* (SV); Petit ruisseau de chemin Aviation, *Clément 3557* (MT, LS); *Clément 3559* (MT, 2 sheets; LS, 2 sheets); *Léon, Marie-Victorin, and Clément 20669* (MT, LS); Pinares de Moa, *Marie-Victorin and Clément 2592* (LS); entre la vallée du Rio Cayoguan et la vallée à l'est, vers la mine Delta, *Marie-Victorin and Clément 3666* (GH, MT, LS); *Clément 3672* (MT, LS); Sobre la meseta, Alt. 400 m., *Marie-Victorin, Clément, and Alain 21786* (LS). Rio Cabanas; Charrascos, *Léon, Marie-Victorin, and Clément 20736* (LS); plateau entre le Rio Cabana et le Rio Moa, *Marie-Victorin and Clément 21786* (MT, 2 sheets; GH). Cayo Chiquito; *Clément, Alain, and Chrysogone 3802* (MT); *Clément, Alain, and Chrysogone 3803* (LS). Charrascal del Coco; Lugares secos, *Léon, Alain, Clément, and Chrysogone 22598* (LS); *Léon, Alain, Clément, and Chrysogone 22615* (LS); *Léon, Clément, Alain, and Chrysogone 4718* (LS). Rio Jicotea; *Léon, Clément, Howard 20143* (MT, LS); *Léon, Clément, and Howard 20144* (MT, 2 sheets; LS); Pinares, *Léon, Clément and Howard 20174* (LS, MT); Rio Yagrumaje; *Alain, Clément and Chrysogone A. 953* (LS); *Clément 3611* (MT, LS); Pinares, *Clément, Alain and Chrysogone 6854* (LS); Charrascos, *Marie-Victorin, Clément, and Alain 21787* (LS). Cananova; La Esmeralda, *Clément, Alain, and Chrysogone 6926* (LS); Cerro de Miraflores, *Léon 21098* (MT, LS); *Léon 21146* (MT, LS); *Léon 21154* (MT, LS). Yamuri Arriba; to Bermejal, *Shafer 8456* (US; NY, 2 sheets); Sierra de Moa; alt. 800 m. approx., *Alain 3430* (LS).

In reproductive as well as vegetative structures, *Purdiaea stenopetala* is the most variable species in the genus. The leaves vary in size from 2.5-8 cm. and in shape from obovate



to obovate-oblanceolate to spatulate, with the apex varying from obtuse to truncate to slightly emarginate. The obovate leaves usually have an obtuse apex, and as the leaves become more spatulate the apex becomes more abruptly truncate or emarginate. The variation within the complex is graded, and it is possible to find leaves of varying size and shape within one geographic area.

The sepals are also variable, the first sepal ranging from 5-7.5 mm. in length at anthesis. Moreover, the exterior sepals often nearly double in length between anthesis and maturity. The ontogenetic increase in size is not always so extreme, however, and as a result the sepals are even more variable in size at maturity than at anthesis. Failure to recognize this variation in the ontogeny of the sepals has, in the past, led to some confusion in the taxonomy of this variable group.

The pubescence on the rachis also varies in *Purdiaea stenopetala*. The extreme forms may be glabrous or pubescent, but again there is gradation with many intermediates between the extremes.

Marie-Victorin (1948) divided this group into two species: *Purdiaea stenopetala* represented only by the type collection (*Wright 341*); and *P. ophiticola*, a new species, represented by all of the other collections in this complex. The latter species was differentiated from the former on the basis of the two most variable characteristics in the complex: sepal size and leaf shape. Oddly enough, there is little if any size difference in the sepals between the type material of the two "species", if the stage of development is taken into consideration. In some of the other collections, however, there is considerable variation in this character. The leaves of the two types do differ in shape, but there are numerous intermediate forms between the two, and occasionally a single specimen can be found on which some leaves resemble those of one type and other leaves resemble those of the other type.

No character or combination of characters has been found by which this complex can be divided into discontinuous groups. Thus, until more is known about the nature of the variation in this group it seems that the entire complex should be considered a single, variable species. Precise field observations and population studies of this species are badly needed for a better understanding of the variation in this interesting group.

The species most closely related to *Purdiaea stenopetala* are *P. nipensis* and *P. parvifolia*. The relationship is discussed under those species. *Purdiaea stenopetala* also resembles *P. stereosepala* in the shape and venation of the leaves and in general aspect.

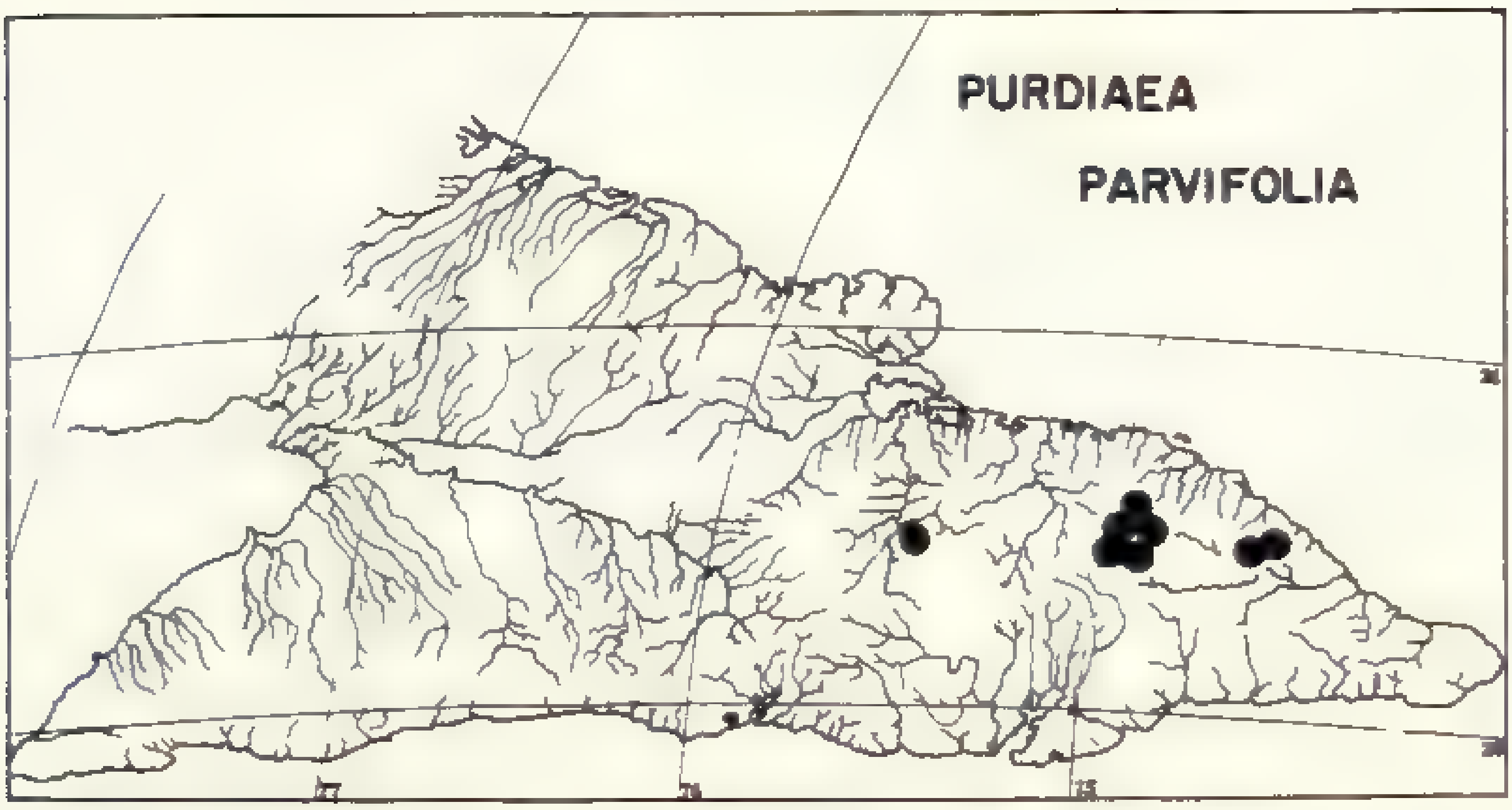
5. **Purdiaea parvifolia** (Marie-Victorin) Thomas, comb. nov. Type: *Shafer 8179*

Purdiaea ophiticola var. *parvifolia* Marie-Victorin, Contrib. Inst. Bot. Univ. Montréal, **63**:57, 1948.

Shrub 3-4 meters tall, bark light gray; young stems pubescent or velutinous, the indumentum usually closely appressed. Leaves dark green, shining above, paler beneath; obovate to obovate-spatulate, apex obtuse, rounded, truncate to slightly emarginate; mucronulate; base attenuate, narrowly sessile; 2-4 cm. long, 0.5-1 cm. broad; the first leaves produced often clothed with appressed trichomes: midvein prominent beneath, impressed above; 2-4 longitudinal lateral veins running near, and parallel to, the margin of the leaf, obscure on both surfaces; smaller reticulate veins distinct above on immature leaves, obscure on mature leaves. Racemes 1.2-2.5 cm. long, erect or pendulous. Rachis attenuate, ca. 1.0 mm. in diameter at the base, tapering to 0.2 mm. in diameter at the apex; pubescent or velutinous. Pedicel 1-1.5 mm. long, ca. 0.3 mm. in diameter, pubescent or velutinous, the indumentum corresponding to that of the peduncle. Bracts ovate-lanceolate, ca. 3.5 mm. long at the base of the raceme, becoming ovate to ovate-deltoid, ca. 1.0 mm. long toward the apex of the raceme: velutinous below the middle, margin ciliate. Sepals 1.8 mm. broad at anthesis, up to 7 mm. long, 3 mm. broad at maturity; ovate-lanceolate; apex acute, obtuse, or rarely somewhat rounded; glabrous or puberulent toward the base near the margin; margins ciliate: second sepal approximately the same length or only slightly shorter than the first sepal; narrower with a more acute apex; pubescent toward the base: third sepal usually symmetrical, ca. 2/3 as long as the first and second sepal in bud, the three sepals approximately equal shortly after anthesis; interior sepals lanceolate, apex acute or acuminate; 3-3.5 mm. long, 0.7-1 mm. broad at anthesis, 3.5-4 mm. long, 1-1.5 mm. broad at maturity; pubescent or velutinous on both surfaces; margin ciliate. Petals oblong, 3.5-4 mm. long, 2.5-3 mm. broad; apex obtuse or acute; usually puberulent near the base on the dorsal surface, particularly in bud. Anthers 1.5-1.8 mm. long, weakly caudate: filaments 2-2.3 mm. long, subulate, glabrous. Ovary globose, ca. 1.2 mm. in diameter at anthesis, weakly 5-ribbed; glabrous or pubescent; style 1.5-2 mm. long at anthesis becoming 2-2.5 mm. long at maturity. Fruit globose, 5-ridged, pubescent or glabrous, the indumentum concentrated along the ridges.

DISTRIBUTION: Mountains of northern Oriente Province, Cuba.

SPECIMENS SEEN: CUBA. Prov. Oriente: Vicinity of Sierra de Moa; "Dense shrub, 6 ft. erect; Capsules pinkish." *Shafer 8179* (type: NY; isotypes: US, GH); *Shafer 8196* (US, GH, NY, F); *Shafer 8233* (NY); along the Piloto Road, ca. 3000 ft. alt., on red, sandy soil, *Thomas 522* (GH); *Thomas 523* (GH); Summit, *Thomas 524* (GH); *Thomas 525*



(GH); *Thomas 526* (GH); Camp San Benito; Shrub 6-15 ft., very common in higher altitudes (2500-3100 ft.), *Shafer 4057* (US, NY, GH); Vicinity of Toa; La Magdalene, Charrascos de Peña Prieta, Alt. approx. 750 m., *Alain 3618* (LS, SV); Bosque charrascoso, cumbre del Pico Galano, Sierra del Frijol, La Alagria, Alt. approx. 1200 m., *Alain 3711* (LS).

This species was originally described as *Purdiaea ophiticola* var. *parvifolia* Marie-Victorin, but now that abundant flowering and fruiting material is available it is readily apparent that this taxon is a distinct species. Although *Purdiaea parvifolia* is closely related to *P. stenopetala*, it is easily separated from that species on the basis of several morphological characters. In *Purdiaea parvifolia* the leaves are smaller, more obscurely veined, and have revolute margins; the stems are more densely pubescent; and the exterior sepals are shorter, narrower, and more lanceolate. The petals of *Purdiaea parvifolia* also differ from those of *P. stenopetala*, being shorter but relatively broader, and puberulent on the dorsal surface near the base. *Purdiaea parvifolia* also resembles *P. microphylla* and is discussed under that species.

In contrast to most of the species in the genus, *Purdiaea parvifolia* is seldom if ever found as scattered individuals growing along stream banks. In the Sierra de Moa, certainly, it occurs as large populations, extending over several acres. Though it is abundant in these areas, it does not occur in dense stands, but grows in a very rich, mixed vegetation. The soil in this area is dark red with a high iron content. The entire area is quite moist, but *Purdiaea parvifolia* is usually found in the more exposed and relatively drier places.

There is little variation within a given population of this species, but there is a small degree of clinal variation particularly in leaf size. As would be expected, the leaves are somewhat smaller on specimens collected at higher elevations than on those collected at lower elevations, but the difference between the most extreme forms is not particularly striking. There is also some variation in size and shape of the external sepals, although this seems to have little or no correlation with elevation. Future collections of flowering and fruiting material of *Purdiaea parvifolia* from the Sierra de Cristal and in the vicinity of Toa will possibly show more significant geographic variation in this species.

The material available from these regions differs somewhat from the material from Sierra de Moa in the size and shape of the leaves; but there are only one or two collections from each area, and all of the material is sterile.

6. **Purdiaea microphylla** Britton and Wilson, Bull. Torrey Club 42:389, 1915. Type: *Shafer 8265*

Shrub 1-2 meters tall; bark light gray; young twigs thin, ascending, puberulent or glabrous. Leaves rigid, coriaceous, dark green above, pale beneath, 0.5-1.3 cm. long, 0.4-0.8 cm. broad, obovate, oval, or elliptic, apex usually abruptly accuminate, rarely obtuse; narrowing abruptly below the middle to a narrowly sessile base; mid-vein prominent beneath, obscure above, 2-4 longitudinal lateral veins, faintly visible beneath, usually not showing above in mature leaves (venation more prominent in immature leaves). Racemes erect, 1-2 cm. long: rachis pubescent to puberulent, attenuate; ca. 0.8 mm. in diameter at the base tapering to 0.2 mm. in diameter at the apex: pedicel 1 mm. long, 0.4 mm. in diameter, pubescent. Bracts 0.5-1 mm. long 0.4-0.8 mm. broad, deltoid to reniform, apex obtuse or rounded; base obtuse, sessile; pubescent on both surfaces. Sepals unequal, standing apart above the middle, not enclosing either the flower or the fruit; first sepal 2.5-2.8 mm. long at anthesis, ca. 3 mm. long, 2.5 mm. broad at maturity; ovate-elliptic to rounded, apex obtuse or rounded; glabrous or nearly so on both surfaces: second sepal 2.5-2.7 mm. long, 2.2-2.4 mm. broad at anthesis, usually slightly shorter than the first sepal; obovate, apex obtuse, acute, or acuminate; base rounded; distinctly 3-veined; finely pubescent on the periphery, glabrous near the middle: third sepal often longer than the first and second sepals, up to 13 mm. long, 2 mm. broad at anthesis; slightly asymmetrical, the interior edge flattened and ciliate, the exterior edge rounded and glabrous; apex acuminate or acute; base obtuse: interior sepals 1.6-1.8 mm. long, 1.4-1.5 mm. broad at anthesis, the two often unequal; ovate, apex acute; conspicuously thickened medially and basally; pubescent on both surfaces; margin ciliate. Petals ca. 3.5 mm. long, 3.0 mm. broad at anthesis, obovate-oblong, apex truncate; glabrous; violet in color. Anthers ca. 2 mm. long, slightly caudate: filaments 2.5-3 mm. long, subulate.

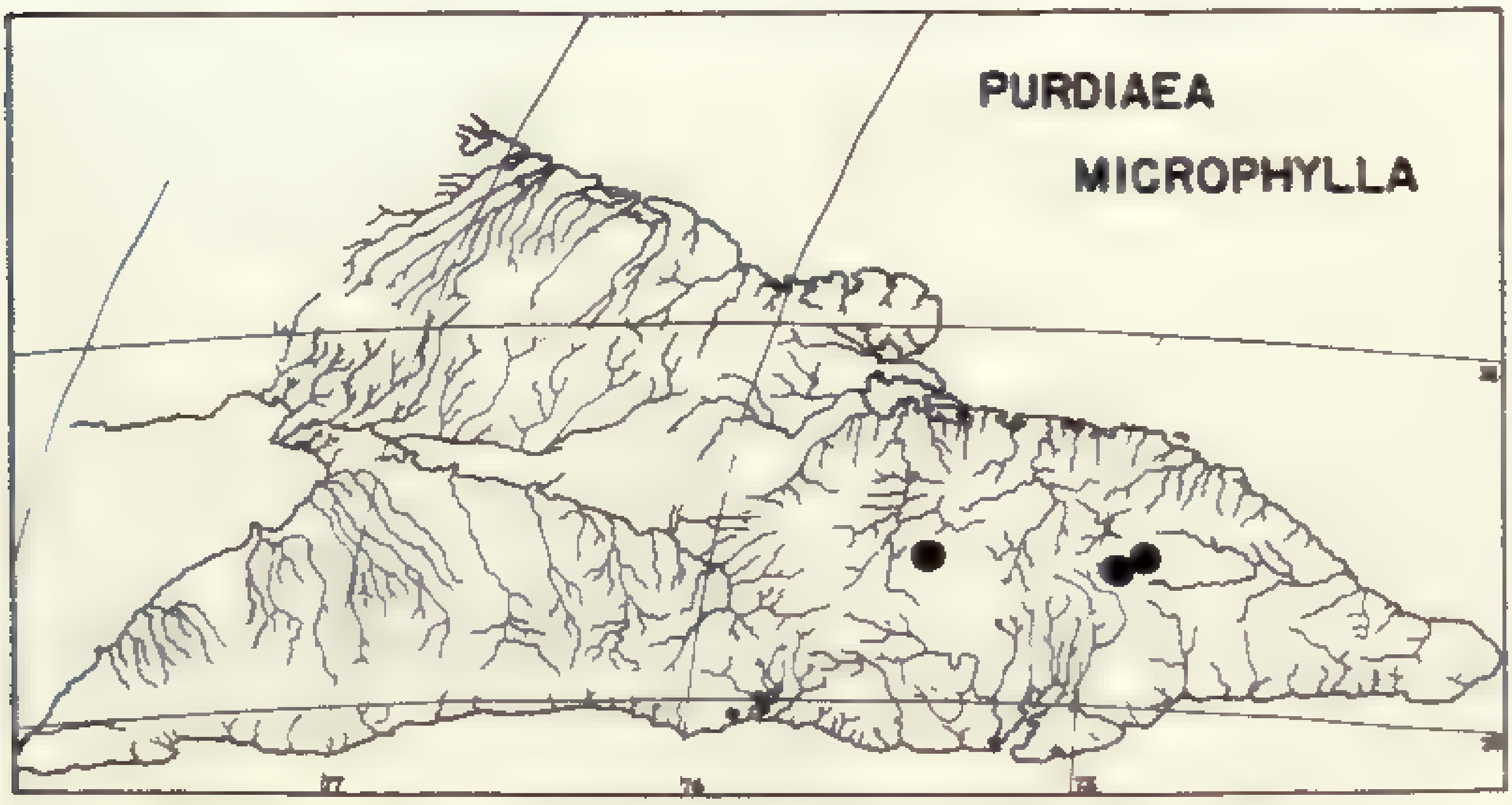
Ovary subglobose, 0.7-0.9 mm. in diameter at anthesis, more or less sharply 5-ridged; pubescent to hirsute, the indumentum often forming longitudinal striations. Style persistent, attenuate, ca. 1.5 mm. long, glabrous. Fruit subglobose, 1.5 mm. in diameter, 5-ridged, not enclosed by the persistent sepals.

DISTRIBUTION: Mountains of northern Oriente Province, Cuba.

SPECIMENS SEEN: CUBA. **Prov. Oriente:** Vicinity of Sierra de Moa; Camp La Gloria, *Shafer 8265* (type: NY; isotypes: NY, LS); Shrub 4 ft., rocky bank of river, vicinity of Camp San Benito, 900 m. altitude, *Shafer 4095* (US; NY, 2 sheets; F); Charrasco, en las cumbres de la Sierra de Moa, *Alain 3387* (LS).

Because of its extremely small leaves, *Purdiaea microphylla* is a very distinctive species. It is closely related to *P. parvifolia* which also has small leaves, but the two are easily separated even in sterile material, by the larger, revolute, obovate-spatulate leaves in the latter species. The leaves of *P. microphylla* are ovate, with an abruptly acuminate apex, and are much smaller than those of *P. parvifolia.*

The flowers of *Purdiaea microphylla* also afford several characters by which this species can be distinguished from other species in the genus. The sepals are open or slightly reflexed in bud, and remain so after anthesis. Thus neither the bud nor the fruit is enclosed by the sepals. The sepals of *Purdiaea microphylla* are the smallest in the genus, and show the least amount of differentiation between the exterior and the interior sepals. In all other species of *Purdiaea* the interior sepals are quite different from the exterior sepals. In the present species however, the interior sepals are ovate, with a length-width ratio approximately the same as that of the exterior sepals. Moreover,*Purdiaea microphylla* is the only species in which one of the interior sepals is



noticeably larger than the other. The unusual petals of *Purdiaea microphylla* are almost square, being only slightly longer than they are broad, with an abrupt truncate apex.

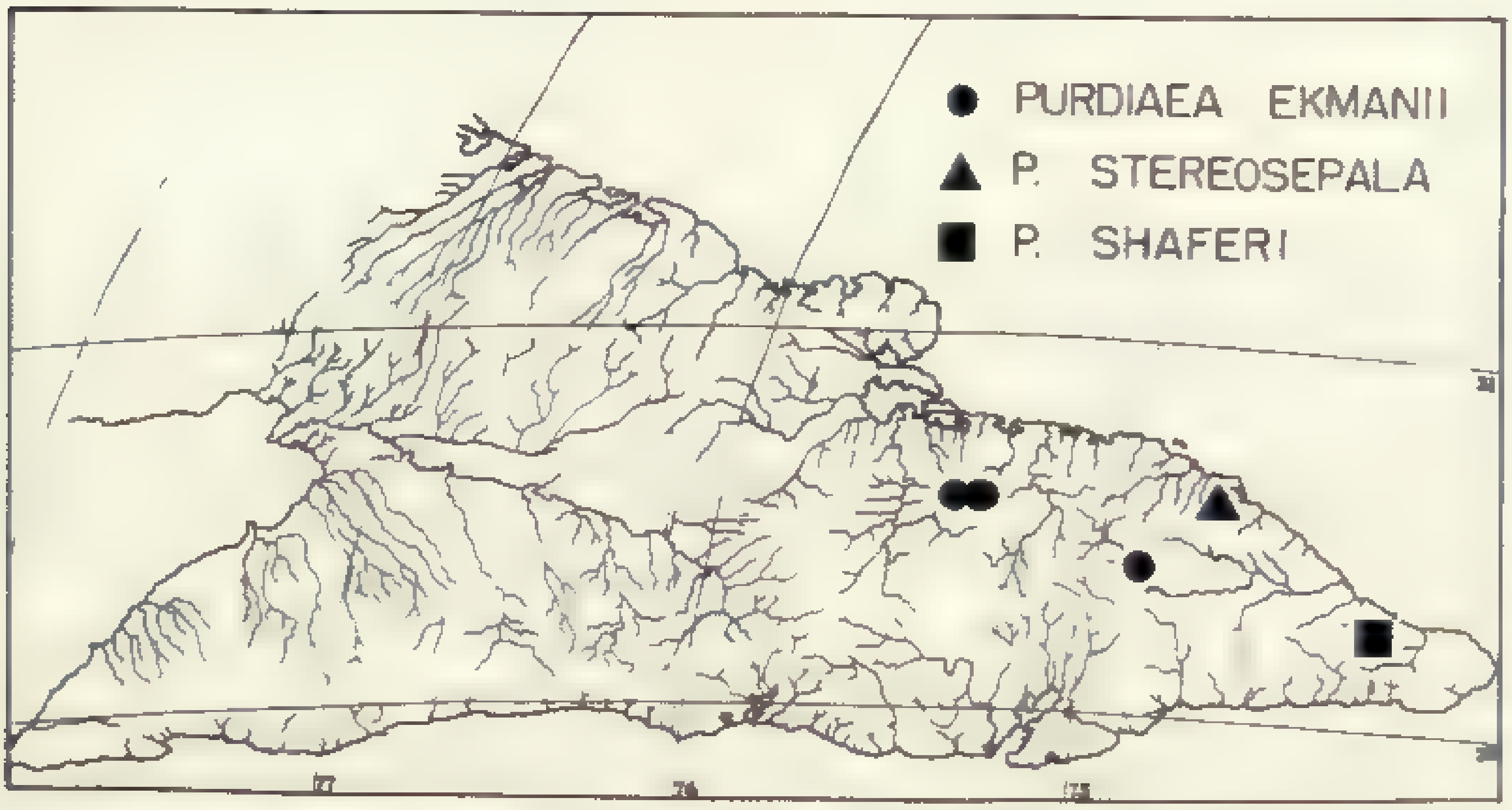
The variation within this species is very poorly known, there being but one collection, of a single sheet, with flowering material *(Alain 3387)*. The variation in the leaves of the available collections is within the range of variation found on a single specimen. Although this species apparently occupies the same general area as *Purdiaea parvifolia*, I was unable to locate it during my brief stay in the Sierra de Moa. Future field work in this area will probably reveal that the two species are ecologically, if not geographically, isolated to a certain extent.

7. **Purdiaea stereosepala** Thomas, sp. nov. Type: *Thomas 516*

Shrub or small tree 4-5 meters tall; stems smooth, glabrous, light brown, becoming gray with age; leaf scars prominent, more or less diamond shaped. Leaves dark green above, pale beneath; obovate to obovate spatulate; apex emarginate, truncate or occasionally rounded, mucronulate; base attenuate; 4-6.5 mm. long, 1.5-2 mm. broad: midvein prominent beneath, impressed or slightly prominent above; 6 prominent lateral veins running longitudinally, more or less parallel to the margin of the leaf; the first two arising at the base of the midvein and extending ca. 1/2 the length of the leaf; the next two arising just above the first two and extending ca. 2/3 the length of the leaf; the fifth and sixth arising alternately, well above the other four, extending the entire length of the leaf, usually connecting with the midvein at the apex: shorter pinnate lateral veins forming interconnections between the midvein and the longitudinal lateral veins. Racemes 6-7 cm. long, erect or occasionally bending near the apex: rachis attenuate, 1-1.2 mm. in diameter at the base, tapering to 0.3 mm. in diameter at the apex, villous or velutinous, the trichomes ca. 0.5 mm. long: pedicel ca. 2 mm. long, 0.2-0.5 mm. in diameter. One to 3 large bracts near the base of the raceme, 5-7 mm. long, 2-2.5 mm. broad; ovate with a rounded apex, pubescent below the middle: the remaining bracts reniform, 1-2.2 mm. long, 1-2 mm. broad, pubescent below the middle, margin strongly ciliate. Sepals rigid, scarious-foliaceous at anthesis, foliaceous at maturity; thickened basally, meeting along the lateral margins, and occasionally at the apex; first sepal ca. 8 mm. long, 6 mm. broad at anthesis, becoming 11 mm. long, 9 mm. broad at maturity, slightly asymmetrical, the side toward the rachis flaring somewhat, the side away from the rachis flattened; ovate, apex rounded, rarely somewhat obtuse; base truncate; finely pubescent on both surfaces particularly below the middle; margin ciliate: second sepal approximately the same size as the first sepal; usually symmetrical: third sepal often slightly longer than the second sepal at anthesis, becoming equal to or slightly shorter and narrower than the second sepal at maturity; decidedly asymmetrical, the interior edge flattened and pubescent, the exterior edge rounded and glabrous or nearly so; interior sepals lanceolate to lorate, apex rounded, 5-7 mm. long, 1-1.5 mm. broad; thickened basally; pubescent on both surfaces, margins ciliate. Petals 6-6.5 mm. long, ca. 3 mm. broad, ovate oblong; apex obtuse; dorsal surface pubescent on the lower 1/3, glabrous above, ventral surface glabrous. Anthers oblong, 3 mm. long, caudate, the cauda acuminate, ca. 0.4 mm. long: filaments 2.5 mm. long, subulate. Ovary globose, 5-ribbed, velutinous; style persistent, attenuate, 4.5 mm. long at anthesis, becoming 5-5.5 mm. long at maturity. Fruit globose, 5-ribbed, velutinous above the middle, ca. 3 mm. in diameter.

Frutex vel arbor, 4-5 m. alta; ramis planis glabrisque; foliis 4-6.5 cm. longis, 1.5-2 cm. latis, obovatis vel obovato-spatulatis, apice sive emarginatis sive truncatis, interdum rotundatis cum mucronulo in medio; venis lateralibus utrinque ternis, cum margine foliorum plus minusve parallelis; racemis 6-7 cm. longis; rhacide sursum attenuato, villoso; bracteis racemi basin versus ovatis, magnis, supra reniformibus minoribusque; sepalis rigidis, per anthesin scarioso-foliaceis, post anthesin foliaceis, basi incrassatis, margine sese tangentibus; sepalis exterioribus per anthesin ca. 8 mm. longis, 6 mm. latis, post anthesin 11 mm. longis, 9 mm. latis, aequalibus, ovatis, pubescentibus; sepalo tertio asymmetrico, margine interiori pubescenti, margine exteriori glabro; sepalis interioribus pubescentibus, lanceolatis vel loratis, apice rotundatis, basi incrassatis, 5-7 mm. longis, 1-1.5 mm. latis; petalis ovato-oblongis, ca. 6-6.5 mm. longis, 3 mm. latis anthera oblonga; filamentis subulatis; ovario globoso, 5-loculato; stylo pertinaci, subulato.

DISTRIBUTION: Known only from the type locality.



SPECIMENS SEEN: CUBA. **Prov. Oriente:** Vicinity of Moa; Rocky shores of Rio Cayoguan, *Thomas 516* (Type: GH).

This distinct new species is the fifth species of *Purdiaea* known from the vicinity of Moa, and is the ninth species from northern Oriente Province, Cuba. It is closely related to *Purdiaea moaensis* and *P. velutina*, and more distantly related to *P. stenopetala* and *P. shaferi*. *Purdiaea stereosepala* is readily distinguishable from other species by several characters. As alluded to by its name, the sepals are rigid and thickened. The exterior sepals are coarse and foliaceous, and meet along their lateral margins and often at the apex. The first sepal is asymmetrical, flaring outward on the side toward the rachis, slightly flattened on the side away from the rachis.

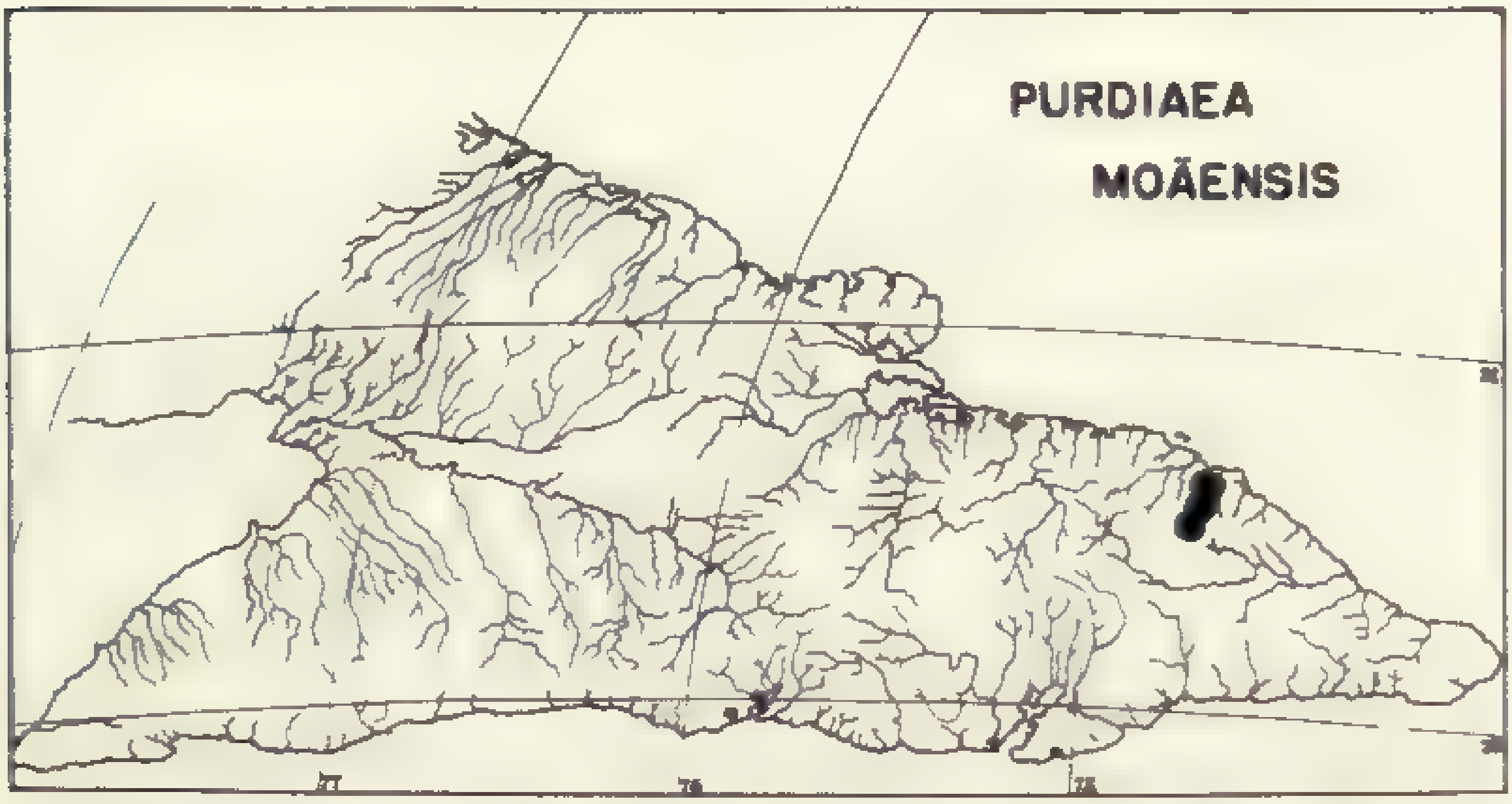
Purdiaea stereosepala also differs from closely related species by its smooth, glabrous vegetative shoots, and well-differentiated, villous rachis. This characteristic is also found in *P. shaferi*, but in the latter species the external sepals are scarious, and very unequal in length — quite unlike those of the present species. Also, the indumentum on the peduncle is different in the two species. In *Purdiaea stereosepala* the trichomes are unicellular and erect, whereas in *P. shaferi* the trichomes are multicellular, quite long, and usually somewhat appressed.

The pattern of leaf venation in the present species, with prominent, longitudinal lateral veins arising well above the base of the midvein, suggests some relationship with *Purdiaea nipensis;* although the leaves of *P. stereosepala* are more coriaceous, more obovate, and have a more broadly sessile base.

8. **Purdiaea moaensis** Marie-Victorin, Contrib. Inst. Bot. Univ. Montréal 63:60, 1948. Type: *Marie-Victorin, Clément, and Alain 21788*

Shrubs or small trees up to 4 meters tall, 4-5 cm. in diameter; bark light gray or brown; young stems pubescent to velutinous toward the ends, becoming glabrous with age. Leaves crowded toward the ends of branches, dark green, shining above, pale beneath, more or less broadly sessile; elongate-elliptic, elliptic-obovate to somewhat spatulate; apex obtuse or rounded, mucronulate; 6-12 cm. long, 1-2.3 cm. broad, the upper leaves of a shoot glabrous, the lower leaves often pubescent, grading off abruptly into velutinous cataphylls at the base of the shoot: midvein prominent beneath, smooth or occasionally somewhat depressed above; 4-5 lateral veins arising near the base of the midvein running more or less parallel to the margin of the leaf, prominent beneath, less so above. Smaller secondary veins arising at increasingly greater angles toward the apex of the midvein, forming interconnections between the midvein and the prominent, longitudinal lateral veins; midvein broadening at the base below the level at which the lateral veins arise. Racemes rigidly erect, 7-9 cm. long at mid-anthesis, becoming 12-13 cm. long at maturity; transition from vegetative to reproductive shoot fairly abrupt, rarely a short zone of transition evident. Rachis robust, ca. 2 mm. in diameter at the base tapering to ca. 1.0 mm. in diameter at the apex; ridged, densely clothed with long, velutinous trichomes up to 1.5 mm. long. Pedicel short, ca. 1.5 mm. long, 0.5 mm. in diameter, velutinous, the articulate base and apex obscured by the indumentum. Bracts lanceolate, up to 10 mm. long, 3 mm. broad near the base of the raceme, becoming smaller and rounded, 2-3 mm. long, 1.2-2 mm. broad near the apex of the raceme. Sepals prominently veined, the three outer sepals approximately equal in length; first sepal 6-8 mm. long, 5-6 mm. broad at anthesis, 9-11 mm. long, 7-7.5 mm. broad at maturity; ovate, apex acute or obtuse; pubescent on both surfaces, particularly toward the base; margin ciliate: second sepal slightly narrower than the first sepal; ovate, apex obtuse, rarely acute, margin ciliate, dorsal surface pubescent below the middle, becoming puberulent above; ventral surface glabrous or nearly so above the middle, becoming puberulent to pubescent below. Third sepal narrow, somewhat asymmetrical, the interior edge flattened basally, puberulent, the exterior edge rounded, glabrous; apex acute, margins ciliate: interior sepals lanceolate; apex acute to acuminate; somewhat shorter and much narrower than the exterior sepals; dorsal and ventral surfaces densely pubescent, a ridge of conspicuously longer trichomes evident along the midvein on the dorsal surface; margin strongly ciliate. Petals oblong, apex rounded or obtuse, 6-7 mm. long, 2-2.5 mm. broad, violet in color. Anthers bright yellow, oblong, 3-3.5 mm. long, 0.5-0.7 mm. broad, distinctly caudate, the cauda bearing a small, spheroid, glandular tip. Ovary 5-lobed, subglobose, densely clothed with long silky trichomes. Fruit rounded to ovoid, velutinous, particularly near the apex: style persistent, 5-6.5 mm. long at anthesis, becoming ca. 8 mm. long at maturity, exserted.

DISTRIBUTION: Vicinity of Moa, Oriente Province, Cuba.



SPECIMENS SEEN: CUBA. **Prov. Oriente:** Vicinity of Moa; Rio Yagrumaje; Punta Gorda, *Marie-Victorin, Clément, Alain 21788* (type: MT; isotypes: LS, SV); *Acuña 12532* (US, SV); *Alain, Clément, Chrysogone 3866* (LS); con braiteas solas, *Clément 3640* (LS, MT); d'en haut, arbusto muy alto, casi arbol, *Clément 3641* (LS, MT); *Thomas 502* (GH); *Thomas 505* (GH).

This species is known from only one locality, a small river near the town of Moa. The plants are fairly abundant along the rocky shores of this stream, however, and future collectting will undoubtedly show that the species is more widely distributed.

Purdiaea moaensis is closely related to *P. velutina*, and the two species are occasionally confused, particularly in sterile material. In both of these species the first leaves produced on a shoot develop into cataphylls, densely clothed with long, silky, appressed trichomes. These peculiar structures are not found in any of the other species in the genus. In *Purdiaea moaensis* the cataphylls are smaller and less conspicuous than those of *P. velutina*, and in the former species the cataphylls are usually shed shortly after flowering begins. In *Purdiaea velutina* the cataphylls are very conspicuous structures and usually persist during most of the flowering period. In both species the cataphylls are closely spaced on the stem, and in early stages are somewhat strobiloid in appearance. Marie-Victorin (1948) in discussing *Purdiaea velutina* described this species as having an "... énorme bourgeon d'inflorescence où les bractées velues composent un espèce de strobile argenté ...".

Purdiaea moansis also resembles *P. stereosepala* and *P. shaferi* in having very prominently veined, coriaceous leaves, and densely pubescent racemes. The present species is usually distinguishable from related ones, however, by its elongate-elliptic to elliptic-obovate leaves. It is distinguishable from *Purdiaea velutina* and *P. shaferi* in having exterior sepals that are approximately equal in length; and is distinguishable from *P. stereosepala* in having scarious exterior sepals and densely pubescent vegetative shoots.

The leaves of *Purdiaea moaensis*, although distinguishable from those of other species in the genus, are quite variable in size and shape, even on a single individual. On one fairly sizeable shrub (*Thomas 505*) I found leaves varying in shape from elongate-elliptic to elongate-spatulate. On this same shrub the mature leaves varied in length from six to eleven cm. The flowers, on the other hand, are relatively uniform on an individual plant, and show little variation from one plant to the next in the few collections of flowering material available.

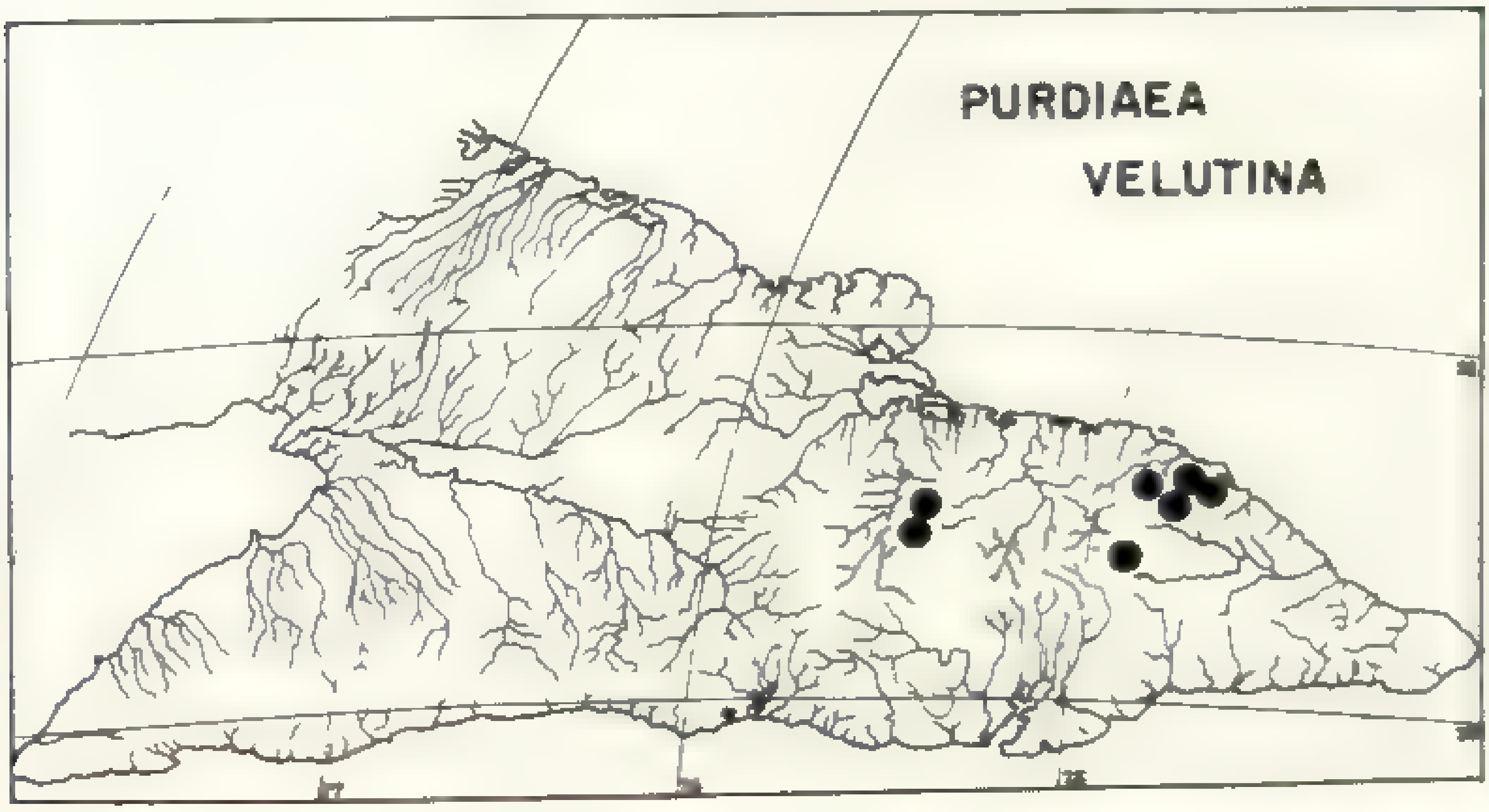
9. **Purdiaea velutina** Britton and Wilson, Bull. Torrey Club **12**:389, 1915. Type: *Shafer 4474*

Shrub or small tree up to 4 meters tall, 3-6 cm. in diameter; bark light gray, scaly; stems velutinous, particularly toward the ends; robust, growing in a zigzag pattern. Leaves dark green, shining above, pale beneath; 4-9.5 cm. long, 2.2-3 cm. broad, obovate-oblanceolate to spatulate; apex broad, rounded, mucronulate or slightly emarginate; base more or less broadly sessile: midvein prominent on both surfaces, broadening considerably near the base; 4-6 longitudinal secondary veins arising at or near the base of the midvein, running more or less parallel to the leaf margin; smaller pinnate lateral veins prominent above the middle, forming interconnections between the midvein and the prominent longitudinal lateral veins. The first leaves of a shoot developing into a dense cluster of velutinous cataphylls. Racemes 3-5.5 cm. long at mid-anthesis, becoming up to 7.5 cm. long at maturity; rachis ridged, attenuate, 1.5-2 mm. in diameter at the base, tapering to 0.7-1.2 mm. in diameter at the apex; densely clothed with long, silky trichomes up to 1.5 mm. long: pedicels short, 1-2.5 mm. long, ca. 0.5 mm. in diameter, often partially enclosed by the subtending bract; velutinous, the indumentum corresponding to that of the rachis. Bracts near the base of the raceme lanceolate to ovate-lanceolate, ca. 5 mm. long, those near the apex of the raceme ovate to reniform, ca. 2.5 mm. long. Sepals several-veined, scarious-foliaceous; white, pink, or rose-colored, unequal: first sepal 11-12 mm. long, 5-6.5 mm. broad at anthesis, becoming 14-17 mm. long, 6-8 mm. broad at maturity; ovate, ovate-elliptic or elliptic; apex acute, rarely slightly obtuse; dorsal surface clothed with fine, silky trichomes below the middle; ventral surface finely pubescent toward the base, glabrous or nearly so above; margins sparsely ciliate: second sepal clearly shorter than the first, 7-9 mm. long, 4-5 mm. broad at anthesis, becoming 9-11 mm. long, 5-6 mm. broad at maturity; ovate, apex acute; more densely pubescent than the first sepal, especially on the dorsal surface: third sepal slightly longer and narrower than the second sepal, somewhat asymmetrical, the interior edge flattened, particularly near the base; puberulent or pubescent near the flattened margin on the dorsal surface, pubescent or velutinous on the lower half of the ventral surface; margins ciliate: interior sepals lanceolate with an acuminate apex; 3-4 mm. long, 0.8-1 mm. broad at anthesis, becoming 5-8 mm. long, 1.0-1.5 mm. broad at maturity, dorsal and ventral surfaces velutinous with a ridge of conspicuously longer trichomes along the full length of the midvein on the dorsal surface; margin strongly ciliate. Petals ovate to ovate-oblong, ca. 7.5 mm. long, 3.5-4 mm. broad, violet in color. Anthers oblong, 4-4.5 mm. long. Ovary subglobose, velutinous, 5-lobed; style ca. 7 mm. long at anthesis, becoming up to 9 mm. long at maturity, exserted.

DISTRIBUTION: Mountains and lowlands of northern Oriente Province, Cuba.

REPRESENTATIVE SPECIMENS SEEN: CUBA. **Prov. Oriente:** Vicinity of Toa; Rio Yamaniguey to Camp Toa, on compact red iron ore, *Shafer 4474* (type: NY); Vicinity of Moa; Charrascos, Rio Jaragua, *Clément, Alain 4020* (LS); *Clément, Alain, and Chrysogone 4020* (LS); Rio Cayoguan, zone riparienne, près du pont de la mine Delta, *Marie-Victorin and Clément 21789* (LS; MT, 3 sheets; GH); *Marie-Victorin, Clément and Alain 21789* (LS); *Marie-Victorin, Clément and Alain 21790* (MT); *Marie-Victorin, Clément, Mr. and Mrs. Bucher 2609* (LS);

along shores of Arroyo Jicotea, between Punta Gorda and Moa, *Thomas 506* (GH); *Thomas 507* (GH); *Thomas 508* (GH); Camp San Benito; margin of rocky river, small tree to 15 ft., *Shafer 4092* (US, F, NY); *Shafer 4094* (US, NY, F); Camp La Gloria; tree 10-12 feet, *Shafer 8261* (NY).



This species is known from both the mountains and the lowlands of northern Oriente Province. It usually occurs as widely-scattered individuals along the rocky banks of small rivers and arroyos.

Purdiaea velutina is closely related to *P. moaensis* and more distantly to *P. stereosepala*. These relationships are discussed under the latter species. In general aspect and particularly in the silky pubescence on the rachis, *Purdiaea velutina* is similar to *P. shaferi*, but these two species are quite different in sepal structure and in the size and shape of the leaves. *Purdiaea velutina* is also similar to *P. ekmanii* in leaf venation, and the discovery of fertile material of the latter species will probably show that these two species are closely related.

The present species is rather uniform in its distinctive characters such as the structure of the sepals, the venation pattern in the leaves, and the structure of the cataphylls. However, there is some variation in several characters. The leaves are rather variable in shape and even more variable in size. The mature leaves may be obovate-oblanceolate to spatulate and range from four to nine centimeters in length. The degree of prominence of the small, lateral veins which arise above the middle of the leaf is also rather variable. As in most species of *Purdiaea* the sepals, particularly the third sepal, vary in the degree of pubescence. The sepals also show a rather diverse range of color, often varying from white to bright pink in plants that are only a few yards apart.

Purdiaea velutina is a very beautiful shrub, and would likely be a popular ornamental in areas with a warm climate if the plant were better known. The dark green, shining leaves, the silvery, strobiloid cluster of cataphylls, the long racemes of flowers with lavender petals, bright yellow stamens, and persistent sepals which vary in color from white to rose, are features which make this an unusually attractive shrub.

10. **Purdiaea shaferi** Britton and Wilson, Bull. Torrey Club 42:389, 1915. Type: *Shafer 4285*

Shrub 2-3 meters tall, stems glabrous, light brown, becoming gray with age. Leaves 4.5-9.5 cm. long, 2.5-4.5 cm. broad, broadly elliptic-obovate; apex mucronulate, rounded or emarginate; base broadly sessile: midvein and 6-8 longitudinal, lateral veins prominent on both surfaces; a rather coarse reticulum of smaller veins prominent beneath, obscure above. Bracts near the base of the raceme lanceolate, 6-8 mm. long, 2-2.5 mm. broad, velutinous below the middle, pubescent to puberulent above. Racemes ca. 5 cm. long, erect; rachis robust, 2.5-3 mm. in diameter at the base, tapering to 1.0 mm. in diameter at the apex, densely velutinous, the trichomes silky, 0.5-0.8 mm. long: pedicel 1.5 mm. long, 0.7 mm. in diameter; velutinous. Sepals scarious, very unequal: first sepal broadly ovate to ovate-oblong, 12-14 mm. long, 7-8 mm. broad at anthesis; apex rounded or acute, apiculate; base cuneate-attenuate; pubescent toward the base, the trichomes appressed, silky: second sepal 8-9 mm. long, 4.5-5 mm. broad at anthesis; ovate, apex acute; base cuneate-attenuate: third sepal approximately the same length as the second sepal; asymmetrical, the interior edge flattened: interior sepals lanceolate, 5-6 mm. long, 2 mm. broad; velutinous, margin ciliate, apex acuminate. Petals elliptic, ca. 5 mm. long, 2.5-3.2 mm. broad, mucronulate, glabrous. Anthers 2.5-3 mm. long, caudate, the cauda small and pointed: filaments ca. 3 mm. long, strongly subulate. Ovary globose-ovoid, hirsute; style attenuate; fruit unknown.

DISTRIBUTION: Known only from the type collection.

SPECIMENS SEEN: CUBA. **Prov. Oriente:** Vicinity of Baracoa; Pinelands back of town, *Shafer 4285* (type: NY).

This poorly known species has not been re-collected since the original collection by Shafer in 1910. *Purdiaea shaferi* is quite similar in vegetative structures to *Purdiaea ekmanii*. This relationship is discussed under the latter species. The present species also resembles *Purdiaea moaensis* and *P. velutina* in several characters including the silky trichomes on the rachis, the rigidly erect, robust stems, and the very prominent, longitudinal, lateral veins in the leaves. *Purdiaea shaferi* is also similar to *P. velutina* in having unequal exterior sepals. The present species is easily distinguished from *Purdiaea moaensis* and *P. velutina*, however, by its large, broadly ovate leaves, glabrous stems, and particularly the absence of cataphylls, which are so characteristic of the former species. The one available specimen of *Purdiaea shaferi* is in bud, just prior to anthesis, and there is no evidence of any cataphylls on the specimen. This is the stage at which the cataphylls are most prominent in *Purdiaea velutina* and *P. moaensis*.

11. **Purdiaea ekmanii** Marie-Victorin, Contrib. Inst. Bot. Univ. Montréal **63**:61, 1948. Type: *Ekman 15981*

Shrub, apparently small; branches robust, light gray to brown, glabrous. Leaves crowded toward the ends of branches, giving a rosette appearance; 4-6 cm. long, 2.5-3.5 cm. broad, broadly obovate; apex obtuse or rounded, mucronulate; base abruptly cuneate, more or less broadly sessile; glabrous, coriaceous, rigid, ca. 0.4 mm. thick; venation strongly prominent on both surfaces, the midvein becoming broad near the base; 6-8 prominent, longitudinal lateral veins arising near the base of the midvein; leaf scars conspicuous, 4-5 mm. broad. Flowers and fruits unknown.

DISTRIBUTION: Mountain tops, Sierra de Cristal and Sierra de Moa, Oriente Province, Cuba.

SPECIMENS SEEN: CUBA. **Prov. Oriente:** Sierra de Cristal; In low, rocky arthrostylidium thickets which cover the top, 1100-1325 meters, *Ekman 15981* (Photograph of type: NY; isotypes: LS, NY); *Alain and Lopez 4824* (LS). Sierra de Moa; Charrascos, alt. 800 m. approx. *Alain 3365* (LS).

Although this species is known from sterile material only, the leaves are quite distinct and are not comparable to those of any of the known species. Its robust, glabrous stems and thick, heavily coriaceous leaves are most like those of *Purdiaea shaferi*, and the discovery of fertile material of the present species along with further collections of *P. shaferi* will probably reveal that the two are closely related. In view of the variation found in the leaves of other species of *Purdiaea*, it is possible that *P. ekmanii* and *P. shaferi* are geographical varieties of the same species. The evidence for this is insufficient at present, however, and a critical treatment of this group must await further collections and field work.

Cliftonia Banks ex Gaertner f. Fruct. 3:246, 1805. Type: *C. monophylla* (Lam.) Britton ex Sarg.

Mylocaryum Willd. Enum. Hort. Berol. 454, 1809.
Walteriana Fras. ex Endl. (in synonymy) Gen. 1413, 1841.

Shrubs or small trees, leaves simple, alternate, entire, estipulate, glabrous; oblanceolate-elliptic or obovate-oblanceolate. Flowers in terminal or axillary racemes: bracts obovate-spatulate or spatulate, one subtending each pedicel: bracteoles lanceolate or oblanceolate, two borne on each pedicel: sepals 5 (6-7) imbricate in bud, small, deltoid, persistent. Petals as many as the sepals, spatulate to obovate-elliptic: stamens 10 in two whorls of 5, the outer whorl opposite the sepals, the inner whorl shorter and opposite the petals: filaments flattened and petaloid below the middle, terete above: anthers versatile, dehiscing through longitudinal slits: ovary borne on a glandular, hypogynous disk; ovary 3-5-locular, each locule containing a single ovule: stigma massive, subsessile: fruits winged, indehiscent; endosperm cellular, embryo straight, elongate.

The genus is composed of a single species, *Cliftonia monophylla.*

Cliftonia monophylla (Lam.) Britton ex Sargent, N. Amer. Silva 2:7, 1892. Type: not seen, presumably in the Lamarck Herbarium, Paris

Ptelea monophylla Lam. Illus. 1:336, 1789.

Cliftonia nitida Gaertn. f. Fruct. 3:247, 1805.

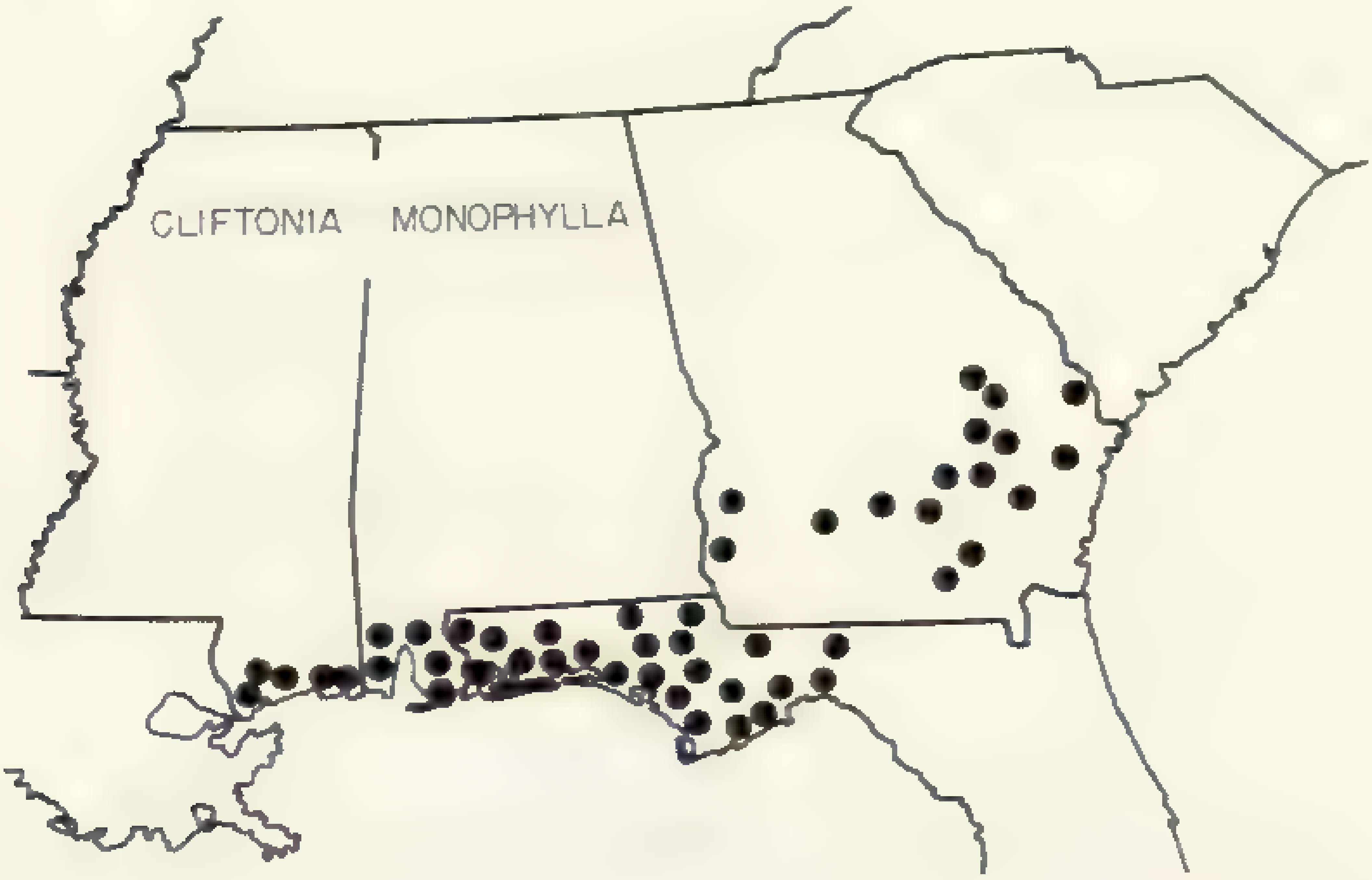
Mylocaryum ligustrinum Willd. Enum. Hort. Berol. 454, 1809.

Cliftonia ligustrina (Willd.) Sims ex Spreng. Syst. 2:316, 1825.

Evergreen shrubs or small trees usually 4-5 meters tall, 6-12 cm. in diameter, branching near the base, rarely becoming 12 meters tall, 30 cm. in diameter. Bark reddish brown or gray, thick and spongy on the trunks of older trees. Young stems dark red, smooth, becoming gray and scaly after 1-2 years. Leaves simple, alternate, entire, estipulate, short-petioled, sub-coriaceous or coriaceous; light green, shining above, pale, glaucous beneath; oblanceolate-elliptic or rarely obovate-oblanceolate, apex acute or slightly emarginate, 3-6 cm. long, 1-2 cm. broad. Flowers in terminal or axillary racemes, glabrous. Rachis 4-8 cm. long, 0.5-0.8 mm. in diameter near the base, attenuate, ridged, each ridge terminating in a small, concave mound at the base of a bract. Pedicels 3-5 mm. long, 0.3-0.4 mm. in diameter, articulate at the point of attachment to the rachis. Bracts 2.5-5 mm. long, 0.5-1.0 mm. broad, white or occasionally pinkish, usually turning brown above the middle; membranaceous, the texture only slightly coarser than that of the petals, obovate-spatulate or spatulate, apex rounded, slightly concave and thickened basally, midvein obscure; articulate at the base, caducous, shedding well before anthesis. Two bracteoles borne alternately on the pedicel, 1-2 mm. long, 0.2-0.4 mm. broad, lanceolate or rarely oblanceolate, usually shedding shortly after anthesis. Sepals 5 (rarely 6-7), white or pinkish, imbricate in bud, 0.5-0.7 mm. long, 0.6-0.8 mm. broad, deltoid, apex acute or rounded; persistent, membranaceous at anthesis, becoming foliaceous at maturity. Petals 5 (6-7), white or pinkish, imbricate in bud, spatulate to obovate-elliptic, occasionally weakly clawed near the base, 3.5-5.5 mm. long, 1.5-2.5 mm. broad, distinctly 3-veined, the veins running longitudinally. Stamens 10 in two whorls, the outer whorl 3.5-4 mm. long, opposite the sepals, inserted lower on the receptacle than the inner whorl; the inner whorl 2.5-3 mm. long, opposite the petals; filaments laterally expanded and petaloid below the middle, narrowing abruptly, becoming terete and subulate above; the expanded lower portion 0.6-1.0 mm. broad; a single conspicuous vein running the length of the filament; anthers versatile, attached slightly below the middle, dehiscing by means of longitudinal slits. Ovary borne on a small, slightly concave, glandular disk which secretes a sticky fluid at anthesis; ovary ovoid or oblong, 3-5-angled, 3-5-locular, each locule containing a single, pendulous ovule; stigma massive, sub-sessile, 2-5-lobed, the lobes corresponding to the number of locules. Fruit 2-5-winged, dry, indehiscent, usually devoid of seeds, but as many as 5 may develop in a fruit. Seeds consisting of an elongate embryo with short cotyledons, surrounded by a mass of cellular endosperm; seed coats lacking.

DISTRIBUTION: Coastal Plain of Southeastern United States.

REPRESENTATIVE SPECIMENS SEEN: UNITED STATES. **Alabama:** Baldwin County: Route 31, 4 miles east of Bay Minette, *Coker* (NY); Escambia County: 2 miles south of Atmore, *Blanton 1* (F, MT, NY, UC, US); Mobile County: Spring Hill, along a water course, *Graves 540* (MO). **Florida:** Bay County: Lynn Haven, St. Andrew's Bay, *Banker 3477* (NY); Calhoun County: Rt. 71, 1 mile north of Blountstown, *S. C. Hood, 1566* (FLAS); Clay County: Green Cove Springs, *W. A. Murrill* (FLAS); Escambia County: Bayou Marcus Creek, west of Pensacola, *R. K. Godfrey 54590* (FLAS, UC); Franklin County: swamps and ponds in the pine barrens, Apalachicola, *Chapman Herbarium 2004a* (US); Gadsden County: ad. fluv. "Little R." prope Quincy, *Rugel* (MO, NY); Gulf County: north of Port Saint Joe, *Small, DeWinkeler, and Mosier 11229* (NY); Holmes County: 2 miles S. W. of Bonifay, *Ford*



3537 (FLAS); Jefferson County: Tyty Bay, *Harper 131* (US); Liberty County: *Demaree 10143* (MO, UC); Okaloosa County: near Laurelhill, *Palmer 38632* (MO, UC); Santa Rosa County: east bank of the Blackwater River, across from the town of Milton, *Webster and Wilbur 3582* (US); Wakulla County: 35 miles S. W. of Tallahassee, along Road 319, *Deam 57745* (NY); Walton County: near De Funiak Spring, *Curtiss 6381* (MO, NY, UC, US); Washington County: east of Holmes Creek and north of Highway 280, *Ford 3764* (FLAS). **Georgia:** Appling County: S. W. of Baxley, *Steyermark 63344* (F); Chandler County: 10 miles N. W. of Rosemary Church, *Hermann 10123* (F, NY, US); Clinch County: 5.2 miles N. E. of Homerville, *McVaugh 5294* (UC); Coffee County: Seventeen Mile Creek, *Harper 692* (F, MO, NY, US); Early County: along Temple Branch, 5 miles north of Blakely, *Thorne 6818* (MT); Emanuel County: pine barrens near Graymont, *Harper 811* (MO, NY, US); Irwin County: along Alapaha River, 3 miles W. of Irwinville, *Hermann 10054* (F, MO, NY, US); Liberty County: swamp in and about the Alatamaha River, *Small* (F, NY); Randolph County: along west side of Nochaway Creek, *Thorne and Muenscher 7898* (NY); Tatnall County: sandhills 3 miles W. of Reidsville, *Cronquist 4938* (FLAS, MO, NY, US); Toombs County: thickets along creek, near Lyons, *Palmer 38281* (F, MO, MT, US); Ware County: 2 miles east of Millwood, *Pyron and McVaugh 1503* (F); Wayne County: 1 mile south of Rt. #341 on State Road #23, *Duncan 1990* (UC); Worth County: vicinity of Poulan, *Pollard and Maxon 539* (NY, US);. **Mississippi:** Harrison County: along ravines in pine woods, Pass Christian,*A. B. Langlois* (F, NY, UC); Jackson County: pinelands east of Pascagoula, *Small, Mosier, and Matthaus 12808* (NY).

This species occurs only on the Coastal Plain of southern Georgia, Alabama, Mississippi, and northern Florida. In this area *Cliftonia monophylla* is found growing side by side with *Cyrilla racemiflora*, but the former species has a much narrower ecological tolerance, growing only in very wet, sandy, acid soils. In contrast to *Cyrilla racemiflora*, *Cliftonia monophylla* shows very little intra-specific variation from one population to the next. There is a very minor degree of variation in the size and shape of the stamens and petals, but a range of variation comparable to that found throughout the range of the species can usually be found on a single individual. Thus in general aspect and in most characteristics *Cliftonia monophylla* is rather uniform throughout its limited geographic range. In view of the age of the genus, the narrow geographic distribution, and the lack of any appreciable variation, it seems likely that *Cliftonia* is only a relict form in the present-day flora.

Cyrilla Garden ex L. Mantissa Plant. 1:5, 1767. Type: *C. racemiflora* L.

Itea L'Hérit. Stirp. Nov. 1:137, 1785.
Andromeda Marsh. Arbust. Amer. 9, 1785.

Shrubs or trees, leaves alternate, entire, estipulate, short-petioled, dark green above, paler beneath. Flowers white or pinkish white, borne in slender, axillary racemes. Pedicels ascending in bud, laterally spreading at anthesis, borne in the axils of persistent bracts: 2 lanceolate, persistent bracteoles on each pedicel. Sepals 5, ovate-lanceolate to deltoid, acute, thickened medially and basally, coriaceous. Petals 5, oblong-lanceolate to oblong-elliptic, thickened and glandular on the inner surface below the middle, inserted on a small, glandular disk at the base of the ovary. Stamens 5, opposite the petals; anthers versatile, dehiscing by means of longitudinal slits; filaments terete, subulate. Ovary superior, sessile, 2-4-loculed: ovules pendulous, anatropous, 3 in each locule: style short, persistent, 2-4-lobed. Fruit dry, indehiscent, often devoid of seeds; not more than one seed in each locule. Seeds devoid of a seed coat; embryo cylindrical, radicle superior.

The genus is composed of a single species, *Cyrilla racemiflora.*

Cyrilla racemiflora L. Mant. 1:50, 1767. Type: in the Linnaean Herbarium. (Photograph of type: GH)

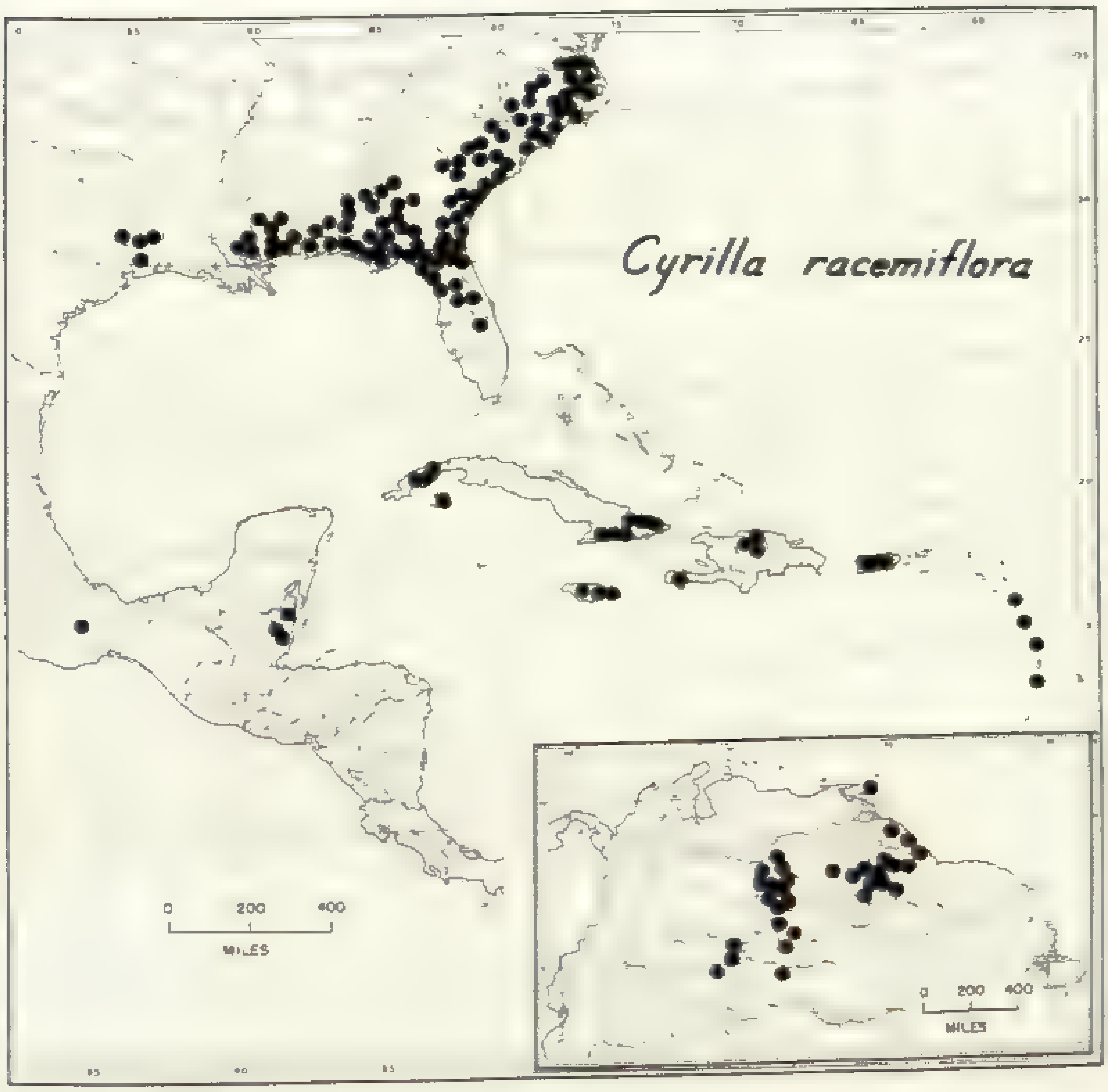
Itea Cyrilla L'Héritier, Stirp. Nov. 1:137, 1785.
Andromeda plumata Marshall, Arbust. Amer. 9, 1785.
Itea caroliniana Lam. Encyclop. Méthod. 3:315, 1789.
Cyrilla caroliniana Michx. Fl. Bor.-Am. 1:158, 1803.
C. antillana Michx. l.c.
C. polystachia Raf. Autik. Bot. 8, 1840.
C. parvifolia Raf. l.c.
C. fuscata Raf. l.c.
C. parvifolia Shuttl. Bull Torrey Club 23:101, 1896. (A later homonym.)
C. perrottetii Briq. Ann. Conserv. Jard. Bot. Genève 232, 1900.
C. brevifolia N. E. Brown, Trans. Linn. Soc. Ser. 2, 6:22, 1901.
C. cubensis P. Wilson, Mem. Torrey Club 16:77, 1902.
C. racemiflora L. var. *parvifolia* Sargent, Jour. Arnold Arb. 2:166, 1921. Based on *C. parvifolia* Shuttl.
C. arida Small, Bull. Torrey Club 51:383, 1924.
C. nipensis Urb. Fedde Repert. 22:365, 1926.
C. nitidissima Urb. l.c.
C. racemiflora L. var. *subglobosa* Fernald, Rhodora 46:46, 1944.

Shrub or small tree, rarely a large tree up to 25 m. high, 1-1.25 m. in diameter; usually branching at or near the base; bark light gray or brown, becoming rather thick and spongy with age; stems rigid or rarely vinelike, smooth or scaly, leaf scars prominent. Roots shallow, running horizontally, a few inches beneath the surface of the ground. Leaves simple, alternate, entire, estipulate, short-petioled, sub-coriaceous to heavily coriaceous, dark green, shining above, pale beneath; often clustered toward the ends of branches; 2-15 cm. long including the petiole, 0.4-4.5 cm. broad; obovate, obovate-oblong, oblanceolate, or oblanceolate-elliptic; apex acute, obtuse, rounded, or emarginate; often apiculate; midvein prominent beneath, prominent or depressed above; numerous lateral veins freely branching, forming a dense reticulate pattern, usually prominent beneath, either prominent or obscure above. Flowers in slender, glabrous, erect or pendulous racemes, borne near the ends of branches, in the axils of leaves or leaf-scars of the previous growing season: rachis 4-26 cm. long, ca. 1.0 mm. in diameter, articulate at the point of attachment to the rachis, ascending in bud, laterally spreading at anthesis, persistent. Bracts lanceolate, concave, thickened basally, persistent, 0.4-4.1 cm. long, 0.2-0.6 mm. broad, longitudinally traversed by a single, obscure vein. Two bracteoles borne above the middle of the pedicel, ascending in bud, spreading after anthesis, alternate or opposite, 0.4-1.3 mm. long, 0.2-0.4 mm. broad, lanceolate, persistent, somewhat thickened basally. Sepals 5 (rarely 6), free or occasionally coalescent laterally at the extreme base; persistent, ovate-lanceolate to deltoid, apex acute, medially and basally thickened, 0.7-1.8 mm. long, 0.4-0.9 mm. broad; imbricate in bud. Petals 5 (rarely 6), white or pinkish white, inserted on a small, glandular disk; oblong-lanceolate to oblong-elliptic, slightly concave; apex acute, obtuse or rounded; membranaceous laterally and above the middle, thickened and glandular on the inner surface medially and below the middle. Stamens 5, opposite the petals, 1.4-2.5 mm. long, shorter than the petals; filaments terete, subulate; anthers versatile, attached near the middle on the dorsal side; 2-lobed, the lobes free below the point of attachment to the filament, united above; usually a small apical protuberance between the two lobes; pollen shed through longitudinal slits. Ovary superior, sessile, 2-3, rarely 4-locular, ovules pendulous, anatropous, 3 in each locule; stigma 2- to 4-lobed, corresponding to the number of locules. Fruit dry, indehiscent, subglobose, globose, ovoid, ovoid-oblong, or obpyriform; longitudinally bisulcate or trisulcate, 1.6-4.9 mm. in diameter, often devoid of seeds, but with as many as 4 seeds developing; not more than one developing in each locule; seeds pendulous, elongate, devoid of a seed coat; endosperm cellular, abundant; embryo elongate, cylindrical, the cotyledons short, inferior, the radicle superior.

DISTRIBUTION: Coastal Plain of Southeastern United States; Middle America; Northern South America.

REPRESENTATIVE SPECIMENS SEEN: UNITED STATES. **Alabama.** Escambia County: *McCullough, Blanton 16* (MT, NY, UC, US); Mobile County: Spring Hill, *Bush 43* (NY, US); Conecuh County: 3 miles west of Evergreen, *Crawford and Harvill 5738* (TEX); Russell County: 2 miles W. of Phoenix City, *Duncan 9627* (MO); Lee County: Auburn, *Earle and Baker* (MO, NY, US); Baldwin County: Fairhope, *Jack 3040* (A); Montgomery County: Vicinity of Montgomery, *G. McCarthy s.n.* (A); Barbour County: 3 miles north of Eufaula, *Wiegand and Manning 1869* (GH). **Florida.** Wakulla County: swamps, *W. W. Ashe s.n.* (NY); Seminole County: from Wagner to Oviedo, *M. F. Baker* (FLAS); Okaloosa County: near Crestview *Blanton 6576* (MO, US); Franklin

County: near Apalachicola, *Curtiss 1774* (F, MICH, NY, US); Duval County: near Jacksonville, *Curtiss 4280* (NY, SV, UC, US); Levy County: Gulf Hammock, *J. H. Davis* (FLAS); Gulf County: 3 mi. N. of Indian Pass, *Ford 3245* (FLAS); Holmes County: east bank of Choctawhatchee River at bridge of Highway #2, *Ford 3473* (FLAS); Jefferson County: swamps, *A. S. Hitchcock s.n.* (F, MO); Gadsden County: 3 mi. s.w. of Quincy, *G. M. Hocking s.n.* (FLAS); Escambia County: Bayou San Marcus, west of Pensacola, *Kral and Godfrey 6029* (MT); Baker County: McClenny, *Lighthipe 588* (FLAS, NY); Osceola County: Lake Wilson, *McFarlin 5660* (A, MICH, TEX); Alachua County: S. of Cox Bridge, *Murrill 407* (US); Columbia County: Lake City, *Nash 2218* (F, GH, FLAS, MICH, MO, NY, SV, US); Calhoun County: along stream, Rock Bluff, *O'Neill 6158* (MO); Indian River County: Indian River, *E. Palmer 325* (F); Leon County: small creek near Tallahassee, *E. J. Palmer 35198* (A, NY); Highlands County: between Avon Park and Sebring, *J. K. Small, J. W. Small, J. B. DeWinkeler 11486* (GH, MICH, MO, NY, TEX). **GEORGIA.** Upson County: S. E. of Woodbury, *Cronquist 5502* (FLAS, GH, NY, UC, US); Tattnall County: 7 miles W. of Claxton, *Duncan 2727* (FLAS, GH, UC, US); Early County: 10 mi. S. of Blakely, *Hardin 147* (FLAS, MICH, TEX); Sumpter County: Leslie, *Harper 1392* (A, F, MO, NY, US); Thomas County: near Thomasville,



Small (F, NY); Baker County: along Ichawaynochaway Creek, across bridge from Field Station, *Thorne and Ford 1953* (US); Wilcox County: 12 miles N. W. of Abbeville, *Wilbur and Webster 2714* (GH, US); Bulloch County: 6 mi. N. W. of Statesboro, *Wilbur and Webster 2764* (GH, US). **LOUISIANA.** Washington Parish: 10 mi. W. of Bogalusa, *Brown 5631* (A); St. Tammany Parish: vicinity of Covington, *Arsène 12234* (US); near Akita Springs, *Pennell 4194* (NY); Tangipahoa Parish: 1 mile W. of Robert, *D. S. Correll and H. B. Correll 9302* (GH, NY). **MISSISSIPPI.** Stone County: south of Wiggins, *L. G. Brenner* (MO); Jackson County: Ocean Springs, *Demaree 28118* (TEX); Harrison County: Rt. 49, Bayhead, N. of Saucier, *Hood 4646* (FLAS); Jones County: Ellisville, *Tracy 3373* (NY); Forrest County: 2 miles S.E. of Hattiesburg, *Webster and Wilbur 3377* (GH, US). **NORTH CAROLINA.** Perquimans County: along river, Hert Ford, *Bartley and Pontius 491* (NY); Anson County: 7 mi. s. of Lilesville near Jones Creek, *Boyce 1037* (GH); Craven County: Riverdale, *Brown 2359* (TEX); Halifax County: Weldin, *Canby* (F); Martin County: low pocosin woods near Jamesville, *Correll 1857* (A); Hyde County: moist woods near Swanquarter, *Correll 1765* (A); Harnett County: Buie's Creek, *Foust* (NY); Moore County: 1/2 m. S. of High Falls, *Fox 2539* (GH); Gates County: on Rt. 158, 2 1/2 miles E. of Chowan River, *Fox and Whitford 350,* (UC); Onslow County: Euelaville, *Godfrey 4467* (US); New Hanover County: shrub savannah at Carolina Beach, *Godfrey and Shank 4208* (GH, US); Robeson County: near Pembroke, *Heller 14015* (MO); Greene County: Snow Hill; *L. F. and F. R. Randolph 774* (GH); Richmond County: 3 mi. N. of Hoffman, *Wiegand and Manning 1869* (GH); Pitt County: 1 mi. E. of Grimesland, *Wiegand and Manning 1868* (GH); Columbus County: 1.5 mi. N.E. of Nakina, *Wilbur 4210* (GH); Pamlico County: 2 mi. E. of Hobucken, *Wilbur 3897* (GH); Bladen County: east rim of White Lake, *Woods* (UC). **SOUTH CAROLINA.** Aiken County: lakes near Graniteville, *Eggert* (MO, US); Georgetown County: 10 miles northwest of Georgetown, *Godfrey and Tryon 736* (GH, MO, NY, UC, US); Clarendon County: 3 mi. S.W. of Manning, *Godfrey and Tryon 932* (GH, NY, US); Charlestown County: 6 mi. N.W. of McClellanville, *Godfrey and Tryon 1130* (GH, NY, US); Lexington County: vicinity of Batesburg, *McGregor 622* (US); Richland County: swamp, Columbia, *Taylor* (F); Chesterfield County: Sugarloaf Mountain, *L. F. Ward* (US); Berkeley County: 4 mi. S. of Bonneau, *Wiegand and Manning 1870* (GH). **TEXAS.** Hardin County: Saratoga, *Bailey 948* (US); Newton County, 5 miles east of Kirbyville, *Cory 49791* (NY, UC, US); Tyler County: Woodville, *G. L. Fisher* (F, US); Jasper County: Jasper, *Stark 8570* (FLAS, TEX, UC, US); Polk County: in Big Thicket, *B. C. Tharp* (MICH, MO, TEX). **VIRGINIA.** Southampton County: Franklin, *Eggleston 4917* (MO, NY); Dinwiddie County: woods west of Winfred's Mill, *Fernald and Long 13676* (GH); Norfolk County: eastern side of Great Dismal Swamp, north of Wallaceton, *Fernald and Long 13676* (GH, MO); Nansemond County: east of Cox Landing, *Fernald and Moore 15113* (GH, MO, US).

MEXICO. **Oaxaca:** near Totontepec, *E. W. Nelson 794* (US). BRITISH HONDURAS. **El Cayo District:** Rio Privacion, *Bartlett 11788* (F, MICH);

Mountain Pine Ridge, *Lundell 6883* (MICH); Temash River, *Schipp 1356* (F, GH, MICH, MO, NY). CUBA. **Prov. Oriente.** Sierra de Maestra: summit of Pico Turquino, *Acuña 6750* (NY); Loma del Gato, *Acuña 9834* (SV); alto de Comejin, *Ekman 9353* (NY); alto de la Valenquela, *Lopez 2256* (LS, SV, US); Cordillera de la Gran Piedra, *Lopez 2766* (LS, SV); Aserradero de Fresneda, *E. E. Smith 256* (SV); Jiquarito Mt., *Taylor 502* (NY); Vicinity of Moa: Pinares, *Acuña 12523* (SV, US); cerca de Cayo Fortuna, *Alain 3311* (LS); arroyito, en el camino de Cayo Chiquito, *Clément 3645* (LS, MT); Rio Yagrumajes, *Clément and Alain 3872* (LS); Rio Cayoguan, cerca del puente de la Mina Delta, *Clément, Alain, and Chrysogone 4000* (LS); edge of pine woods near airfield, *Howard 6205* (GH, NY, US); 15 kms. S.W. of Compania de Moa mill, *Howard 5857* (GH, NY, US); Bosque de la Breña, *Leon and Clément 23303* (LS); Charrascal del Coco, *Léon, Clément and Alain 22620* (LS); chemin de Cayoguan, *Léon, M.-Victorin and Clément 20831* (LS, MT); entre le Rio Caboños et le Rio Moa, *M.-Victorin and Clément 21780* (MT); Bosque de Centeno, *M.-Victorin, Clément and Alain 21784* (LS, MT); vicinity of Camp San Benito, *Shafer 4067* (NY); alluvial valley of Rio Yamaniguey, *Shafer 4236* (NY, US); Camp La Gloria, *Shafer 8032* (GH, NY, US); Sierra de Nipe: Pinar Mayari, Arroyo Naranjo, *Carabia 3621* (NY); Cayo del Rey, Rio Canapu, *Carabia 4087* (MT, NY); in carrascales, *Ekman 2168* (NY); cabezades del Arroyo Guaro, *Léon 19171* (LS); Cerro de Miraflores, *Léon 21135* (LS, MT); chemin de la mine Woodfred, *Léon and Alain 19171* (LS, MT); Cayo de Monte, al pie de la Mensura, *Léon, M.-Victorin, Clément, Alain 19925* (LS); Vicinity of Baracoa: banks of Rio Janco, *Léon 11755* (US); Cabuebaje, Finca la Maria, *Thomas 501* (GH). Prov. Pinar del Rio: Loma de Cajalbana, Le Palma, *Alain and Clément 1461* (LS); banks of Rio de las Vueltas, foot of Cajalbana, *Léon and Charles 4931* (LS, NY); Sierra del Rosario, *Alain and Ponce de Léon 103,* (LS); dry sandy soil, Herradura, *Shafer 436* (NY, SV); along stream, vicinity of Herradura, *Britton, Britton, Earle and Gager 6490,* (NY); Sierra de Cabra, on Guane Road, *Britton, Britton and Gager 7211* (NY, US); Rangel, Loma Pelada, *Léon 12534* (MT); Arroyo del Sumidero, *Shafer and Léon 13627* (MO, NY, US); Bahia Honda, *Léon 17088* (LS, MT). ISLE OF PINES. near Nueva Gerona, *Curtiss 490* (F, MO, NY, SV, US); Rio del Indos, *Jennings 436* (GH, NY, US); savanes de Los Indos, *M.-Victorin and Alain 93* (GH, MT); Arroyo del Hatillo, *Léon and M.-Victorin 17825* (LS); San Juan, *Roig and Cremata 1814* (NY).

WEST INDIES. **JAMAICA.** St. Thomas: crest of Gossamer Peak, *Maxon 9249* (GH, US); Prospect Hill, *Thompson 7947* (F, NY); Portland: southeast slope of Caledonia Peak, *Proctor 15549* (GH); St. Andrews: New Haven Gap, vicinity of Cinchona, *Britton 192* (NY); near Cinchona, *Harris 9117* (F, GH, NY, US); mist forest on track to Old England, *West and Arnold 690* (FLAS, GH); Gordon Town, *Hart 890* (F, US); 2 miles northwest of Hardwar Gap, *Webster and Wilson 4937* (GH); Trelawny: 4 miles west of Troy, *Maxon 2879* (NY, US); Crown Lands, near Troy, *Harris 8725* (F, NY). **HAITI.** Massif du Nord, Pors-Margol, *Ekman 2813* (US); Massif de la Hotte, western group, near Dutreuil, *Ekman 10764* (US); road from Camp No. 1 to

La Barriere Couchant, *Nash and Taylor 1107* (NY); Riviere Glacu, *Holdridge 2226*, (US). **DOMINICAN REPUBLIC.** Prov. Monti Cristi: Mancion, Lagunas de Cenobi, *Ekman 12877* (GH, US). Prov. Santiago: road to Loma Bajita, Jicome, *Valeur 726* (F, GH, MICH, MO, NY, US); en los alrededores del Pico del Gallo, *J. Jiminez 2515*, (US). **PUERTO RICO,** in sylvis montanis ad Sta. Isabel, *Sintenis 6167* (F, GH, MO, NY, SV, US); El Duque, Sierra de Naguabo, *Shafer 3657* (F, GH, MO, NY, US); Rio de Maricao, *Britton and Cowell 4220* (NY, US); Maricao, *Sargent 502*, (US); San Sebastian, *Sargent 353* (US); El Verda, Luquillo Mountains, *Blomquist 11907* (TEX); near Mayaguez, *Heller 4582* (F, GH, MICH, MO, NY, SV); Mt. Ategrillo, *Britton, Stevens and Hess 2611* (NY, US). **GUADELOUPE.** Souprière, *Questel 1666* (US); Source du Galion, Chemin Souprière, *Stehle 387* (US). **DOMINICA.** Solfatara area near Soufrière, *Howard 11782* (GH, US); Soufrière, *Lloyd 16* (NY). **ST. VINCENT.** in elfin woodland, Letchwood Valley, *Beard 614* (GH, MO, NY, UC).

SOUTH AMERICA. **BRITISH GUIANA.** Mt. Roraima: summit, *Tate 401* (NY); Ipelemorita, Arapos River, *Jenman 35* (US); Camp River, *Jenman 1861* (NY); Pomeroon District, Mora Landing, Moruka River, *Cruz 1882* (F, GH, MO, NY, US); upper Mazaruni River, *Cruz 2080* (GH, MO, NY, UC, US); Ituni Road, Mackenzie, Demerara River, *Fanshawe 5242* (NY); Rockstone, *Gleason 486* (GH, NY, US); Kaieteur Plateau, *Maguire and Fanshawe 23106* (F, NY, US). **COLOMBIA.** Rio Kananari, Cerro Isibukuri, *Schultes and Cabrera 15058* (US); Rio Kuduyari, Cerro Yapoboda, Vaupés, *Schultes and Cabrera 14472* (US). **VENEZUELA.** State of Bolivar: Sarven-tepui, *Wurdack 34099* (NY); Plato arriba da Auyantepui, *Vareschi and Foldats 4954* (NY); Sororopantepui, *Steyermark 60147* (F); Mount Roraima, *Steyermark 58763* (F, NY, US); Cerro Guaiquinima, Rio Paragua, *Maguire 32867* (NY); Churi-tepui, *Wurdack 34214* (NY); State of Amazonas: Maroa, Rio Guainia, *Williams 14242* (F, US); summit of Cerro Duida, *J. A. Steyermark 58353* (F, NY); Cerro Yavi, *Phelps and Hitchcock 42* (NY); Cerro de la Nablina, Rio Yatua, *Maguire, Wurdack, and Bunting 37164* (F, NY); Cerro Sipapo, *Maguire and Politi 28478* (NY, US); Serrania Yutaje, Rio Manapiare, *Maguire and Maguire 35506* (NY); Cerro Moriche, Rio Ventuari, *Maguire, Cowan and Wurdack 30946* (MO, NY); Cerro Yapacana, Rio Orinoco, *Maguire, Cowan and Wurdack 30664* (F, NY); Cerro Huachamacari, Rio Cunucunuma, *Maguire, Cowan and Wurdack 30216* (NY, UC, US); Serrania Paru, Rio Paru, Cano Asisa, Rio Ventuari, *Cowan and Wurdack 31231* (NY). **BRAZIL.** Prope San Carlos, ad Rio Negro, *Spruce 2999* (GH, NY); Rio Curicuriari, middle course, Rio Negro, *Schultes and Lopez 9718* (GH, US); Mt. Roraima, on savannas, *Tate 231* (NY); Mt. Roraima, summit, *Tate 387* (NY).

An extraordinary degree of variation is found in the genus *Cyrilla.* It is so variable, in fact, that on the basis of various extreme forms, eleven species and several varieties have been described by previous authors. However, on studying the material in the field over a wide geographic and ecological range, and on bringing together for examination most of the major collections, it has become apparent that the genus *Cyrilla* should be considered as a single species, *C. racemiflora*.

Several aspects of the nature of the variation in *Cyrilla* are discussed above under the section on asexual reproduction and variation in *Cyrilla racemiflora*. The following discussion of the variation in this group is primarily descriptive.

There are several patterns of variation within this species, but there are no real gaps or discontinuities separating one pattern from the next. Instead, the different patterns of variation are connected by intermediate forms. Studies were made of many of the complex variation patterns that occur within and between populations of this species throughout most of its geographical range. These studies have been based on mass collections in a few instances, but primarily on herbarium material. The use of mass collections or similar sampling methods for studying the variation within a given population was found to have certain limitations due to the widespread occurrence of vegetative reproduction in the group. Within a population of *Cyrilla*, particularly a small population, there will usually be relatively few biological individuals. Thus in examining the variation found in such a population one is more often than not dealing with the ecological variation within a single clone. Moreover, large populations of *Cyrilla* are exceptional. It usually occurs as scattered groups of bushes which frequently can be shown to be a single clone. This sporadic occurrence of clones is particularly characteristic along stream banks and wooded areas. The larger populations are usually found in open fields, cut-over hillsides, or along highway right-of-ways — areas where young sprouts from the roots will not be shaded or crowded out by other competition. Populations under these conditions are often somewhat weedy in nature.

The occurrence of large clones proved to be of some advantage, however, in studying the variation found in a single individual. The variation that may occur within a single genotype can be assessed more accurately by studying a large clone than by studying a single plant. The mass collections used are of two types: those in which material was collected from a number of plants that were known to constitute a single clone; and those in which no two collections were made within 60 feet of each other. In the latter type it was still not possible to be certain that each sample collected represented a different individual, thus limiting their value as random samples of a population. Familiarity with the plant under field conditions made it possible in many instances to select different individuals by their appearance, but certainly samples of this type are not random. Nevertheless, with the large number of herbarium specimens available, in addition to special collections made during two summers of field work, the sampling at worst should be of significance.

In studying the variation in *Cyrilla,* primary emphasis has been placed on the size, shape, and texture of the leaves. There were several reasons for this: 1) most of the species which have been described have been segregated on the basis of leaf size or shape; 2) leaves are the most variable part of the plant; and 3) leaf length proved to be a very convenient basis on which to compare other, less variable characteristics.

Geographically, three areas were of particular interest in studying the variation in the group: eastern Cuba, northern South America, and southeastern United States. These areas will be considered individually.

EASTERN CUBA

The highest degree of local variation in *Cyrilla* was found in the mountains and stream valleys of northern Oriente Province, particularly in the Sierra de Moa. Here, within an area of 10 square miles, one can find individuals that closely resemble those found throughout the range of the species. A glance at the divergence in leaf size and shape, shown in Fig. 24, will give some idea of the degree of variation found in the leaves of plants from this region. The leaves shown in this plate were taken from specimens collected within a small geographical area in the Sierra de Moa. They represent, as nearly as was posible to determine, average, mature leaves. In each case, the leaves shown with the adaxial side up were selected as being average for the specimen, and those with the abaxial side up were selected to show some of the variation that occurs among the mature leaves of a given specimen. The arrangement of the leaves was intended primarily to show two obvious trends of variation from the average leaves shown at the top to the small form in row A, and the large form in row B.

The effects of the environment are rather clear in the extreme forms. Moisture and shade seem to be the most important ecological factors influencing leaf size in *Cyrilla.* The large-leaved forms, shown in the lower third of row B are invariably found growing along stream margins and

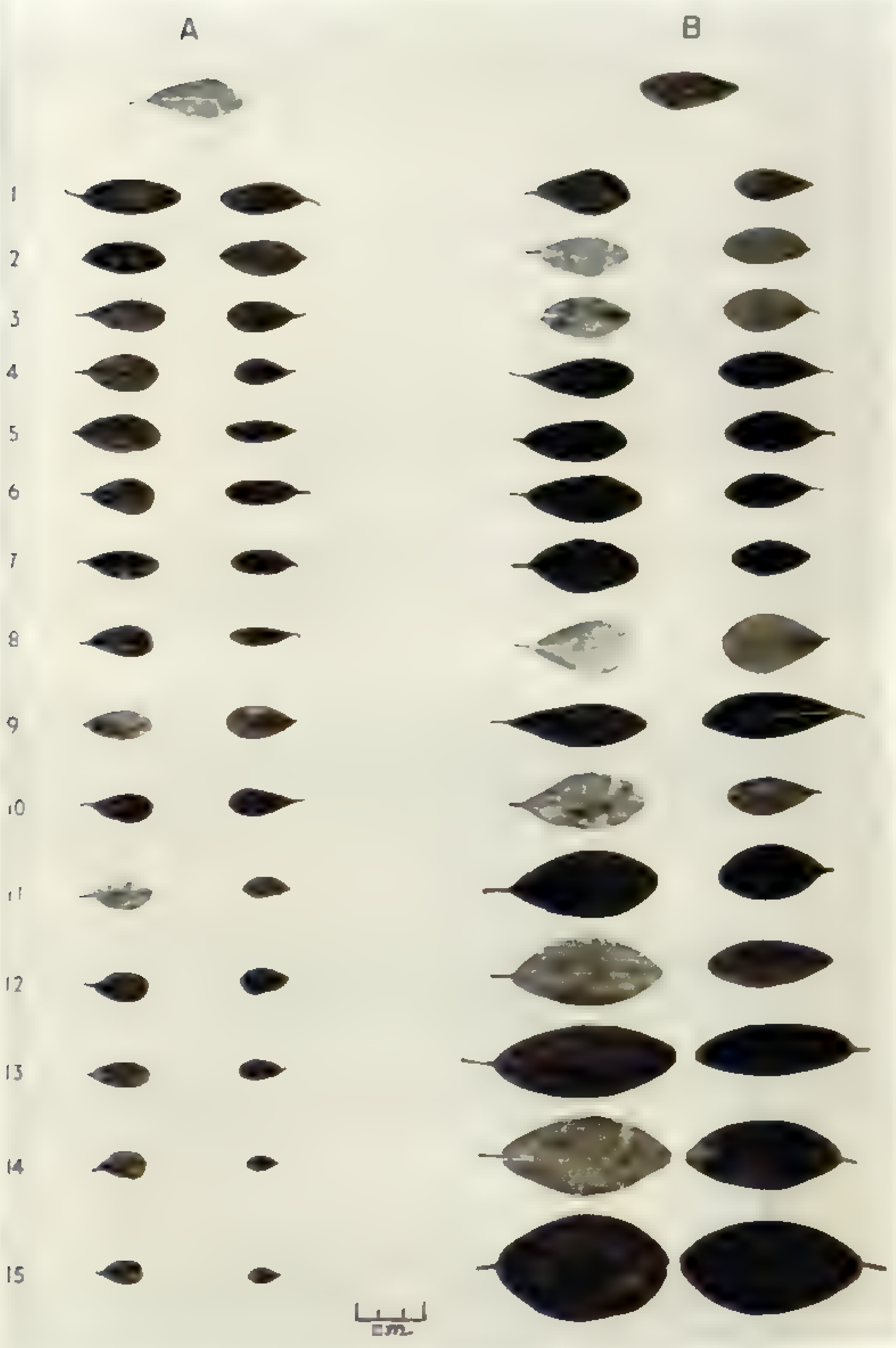


Fig. 21. Leaf variation in *Cyrilla racemiflora* from the Sierra de Moa, Oriente Province, Cuba. The leaves to the left in each row are shown with the adaxial side up, those to the right with the abaxial side up. Further explanation in text.

in partial shade. The extremely small-leaved forms, shown in the lower third of row A are found on much drier sites, usually on open hillsides or exposed sites on the tops of mountains. The intermediate forms however, are intermixed, although the tendency is toward an increase in leaf size with a corresponding increase in moisture and shade in the environment. No attempt has been made to actually measure the amount of available moisture or light, or to evaluate separately the influence of moisture and shade. Differences in altitude seem to have little effect on leaf size in *Cyrilla.* In the Sierra de Moa both large and small-leaved plants can be found from the foot of a mountain to within a few hundred feet of the summit.

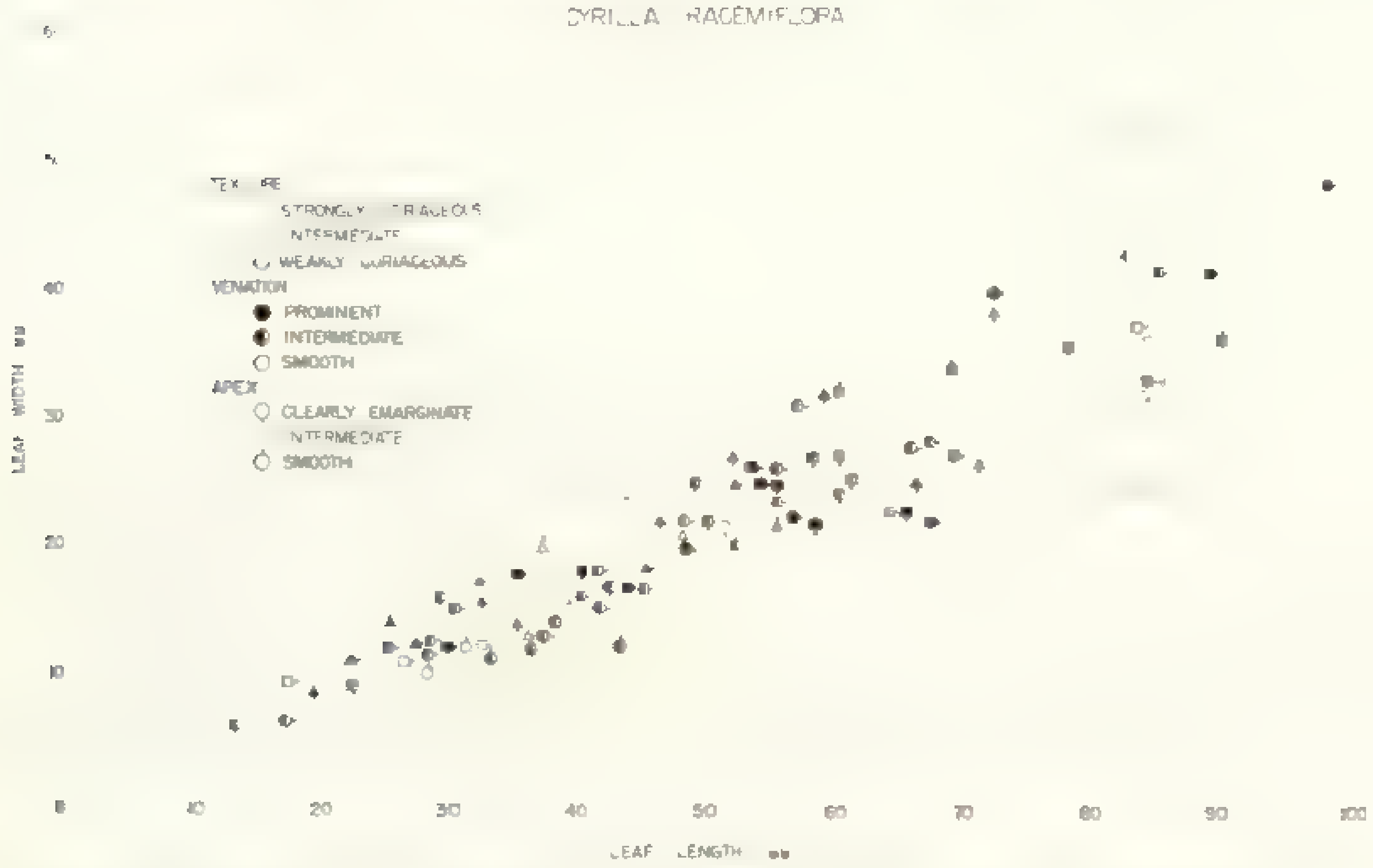


FIG. 25 Scatter diagram showing the relationship between leaf size and leaf texture, venation, and apex. All plants used in preparing this diagram were collected in the Sierra de Moa, Oriente Province, Cuba. Each point plotted represents average mature leaves of a separate collection. Further explanation in text.

The relationship of leaf size to three other leaf characters is shown in Fig. 25. Here the texture, the venation, and the shape of the apex are shown for each leaf length plotted. In preparing this diagram, a series of patterns was first made containing leaves that were typical of each character that was to be plotted. Each specimen was then compared with the pattern and plotted accordingly. In scoring the various leaf characters, only the older mature leaves were used. This was particularly important in Cuba and areas south of there where *Cyrilla* is evergreen, and leaves frequently remain on the plant for more than one year. In these areas after the leaves have attained full size they slowly become more coriaceous with increasing age. Also, in some populations the surface venation becomes more obscure in older leaves.

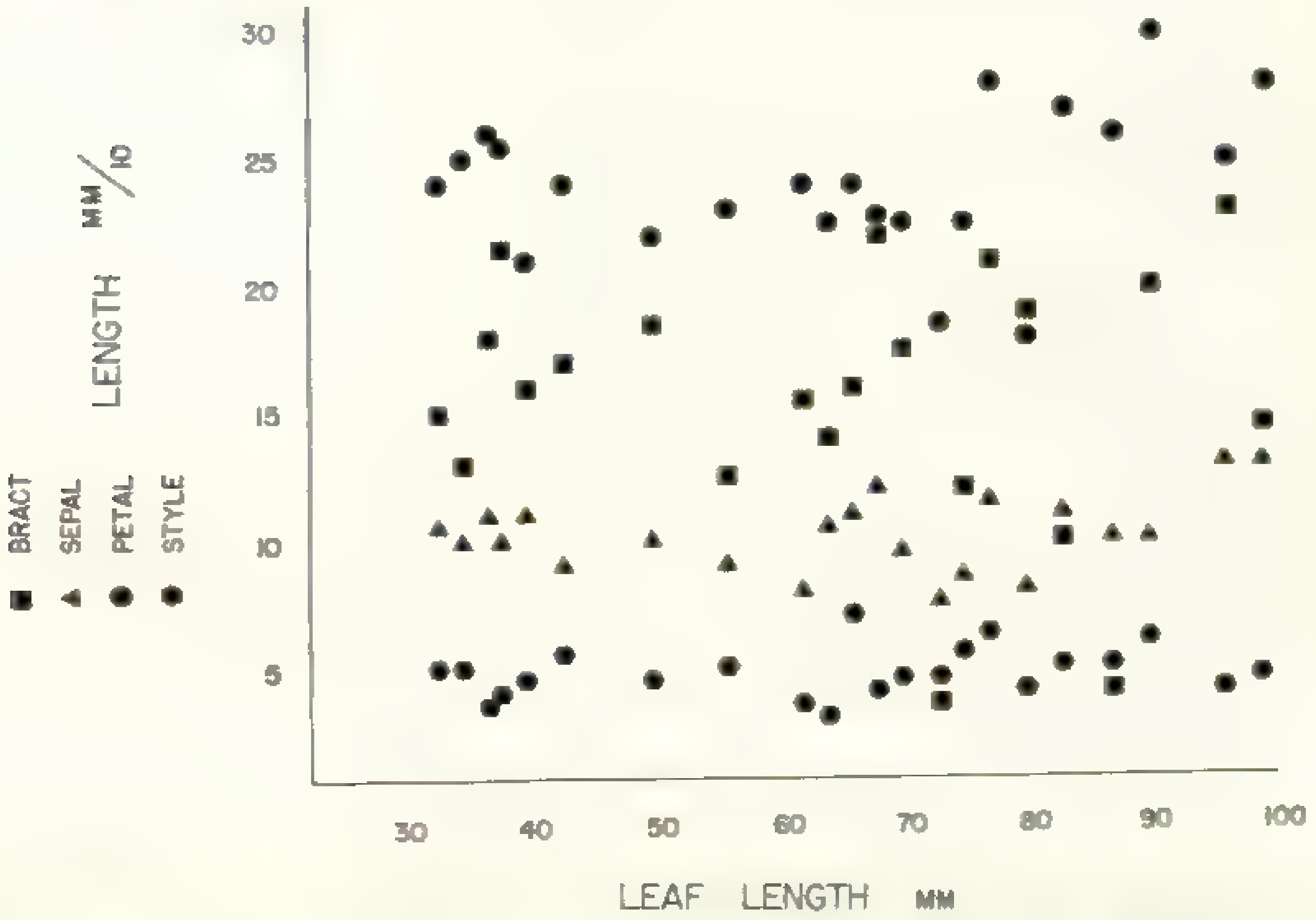


FIG. 26. Scatter diagram showing the relationship between the length of the leaves and the length of the bracts, sepals, petals, and style of plants collected in eastern Cuba. Each vertical series of points represents the average of several measurements from a single collection. Further explanation in text.

It is apparent from the diagram (Fig. 25) that the various characters plotted vary more or less independently, and that the system intergrades completely so far as these leaf characters are concerned. There is a slight correlation between coriaceous leaves and prominent venation, but there is a great deal of overlap. The intermediate forms tend to predominate over the extremes in most of the characters scored, but the various combinations of characters are thoroughly intermixed throughout the range of leaf length. The specimens used in this diagram include four named species: *Cyrilla cubensis*, *C. nipensis*, *C. nitidissima*, and *C. racemiflora*. The first three species listed were segregated from *Cyrilla racemiflora* primarily on the basis of the leaf characters used in this diagram.

In Fig. 26 the lengths of four of the floral parts are plotted in relation to leaf length for plants of the same area. The measurements of the floral parts were taken at anthesis, and each measurement plotted represents the average of several measurements made on each plant. Each vertical row of points represents floral measurements of a different individual, positioned along the abscissa according to leaf length. Two very prominent aspects of the variation in *Cyrilla* are illustrated in the graph. With the obvious exception of the bracts, the floral parts are relatively uniform in size, in contrast to the leaves which are highly variable. The variation in size of the bracts is not of great significance here because they are so highly variable in a single clone and even along a single raceme. The style, sepals, and petals, however, are quite uniform in size in a given individual. These floral parts also tend to be relatively uniform in size throughout a population, and in most areas from one population to another. Moreover, the variation in these structures is apparently independent of leaf length.

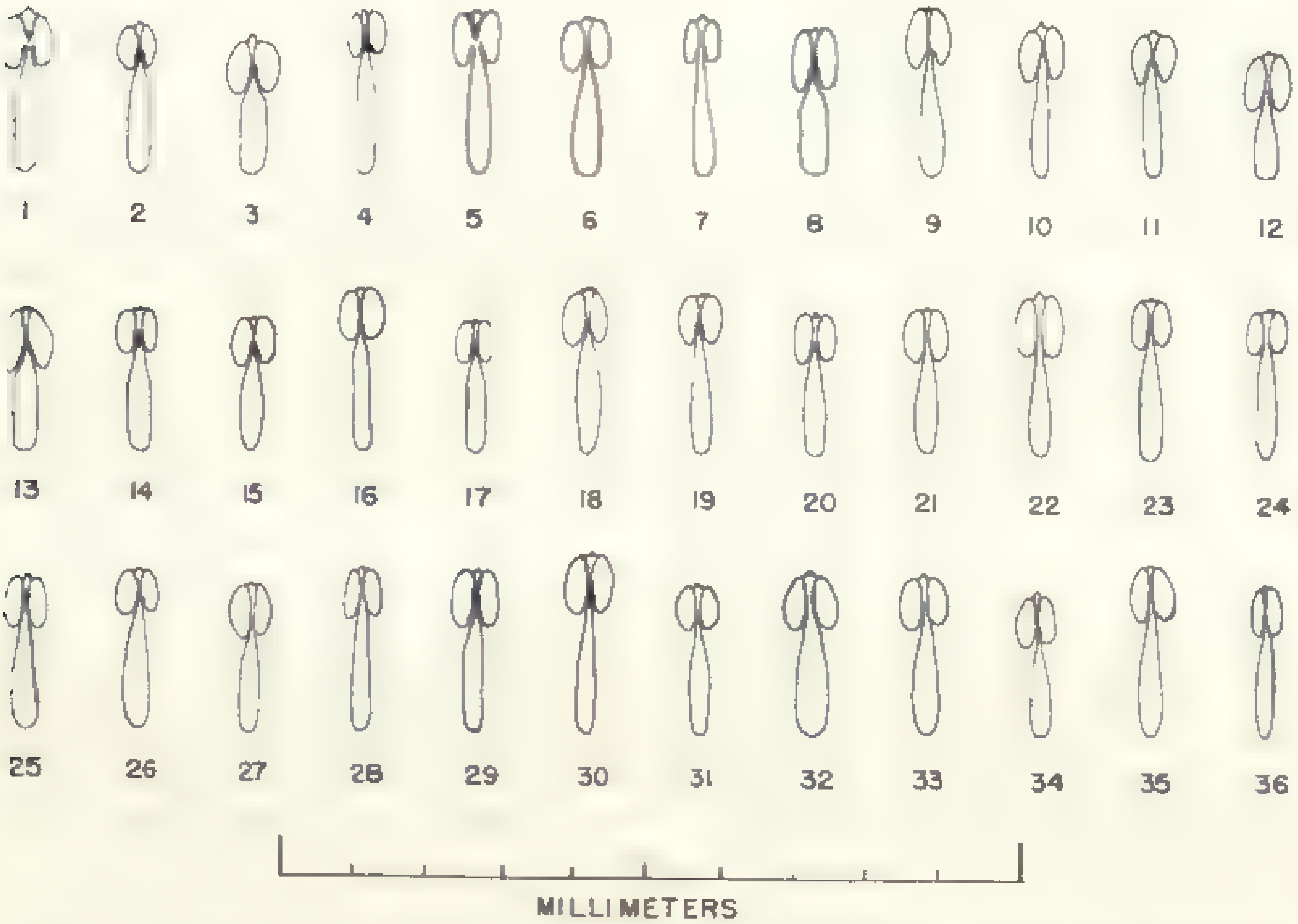


Fig. 27. Micro-projector drawings of representative stamens from plants collected in the Sierra de Moa, Oriente Province, Cuba.

In order to illustrate some of the variation of the floral parts other than that of length, drawings were made of representative stamens and petals from the specimens used in Fig. 26. These outline drawings, made by means of a microprojector, are shown in Figs. 27 and 28. The most salient aspect of the variation in the petals is in the shape of the apex. This varies from slightly acuminate to acute to almost rounded. Less striking is the variation in over-all shape, most of the petals being more or less elliptic or ovate-elliptic. The stamens are even more uniform in the material from the Sierra de Moa, the most obvious variation being found in the length of the filaments and the size of the anther sacs. One interesting aspect of the gross morphology of the stamens is the mucronate tip which is formed on the connective tissue between the two anther sacs. This small structure is rather variable in both size and shape, even among plants within a single population. The extent to which the connective tissue is developed between the two pairs of anther sacs is also rather variable. Formerly, this was thought to be of taxonomic significance, and was used by Small (1924) as one of the specific characters in distinguishing "*Cyrilla arida*" from "*C. parvifolia*". An examination of this development on a population basis, however, has shown that anthers comparable to those found in "*Cyrilla arida*" can be found in populations of "*C. parvifolia*", and, indeed, in other variants that have been assigned to still other species.

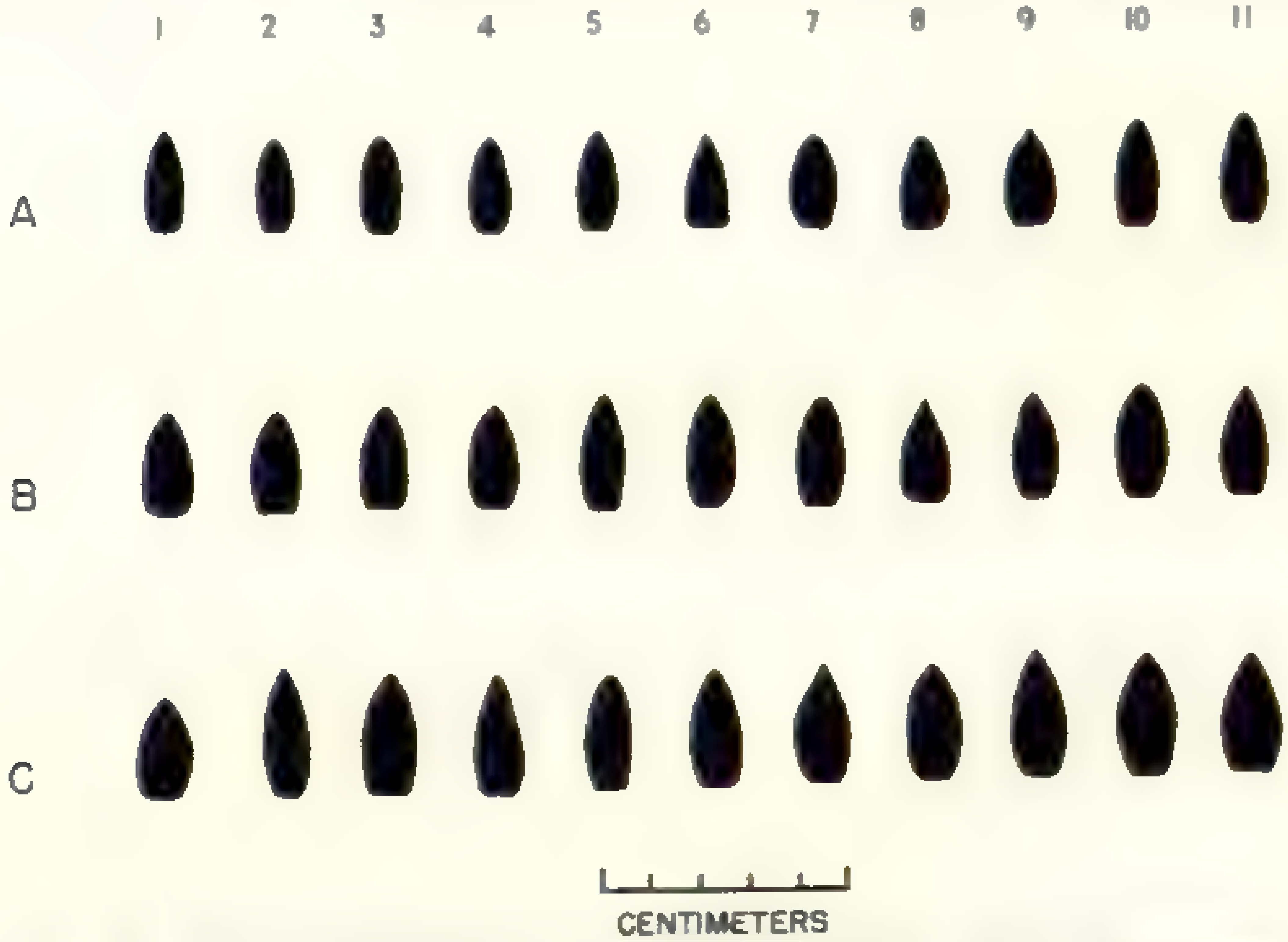


FIG. 28. Micro-projector drawings of representative petals from plants collected in the Sierra de Moa, Oriente Province, Cuba.

Another character that shows an interesting variation pattern between different populations of *Cyrilla* in the Sierra de Moa is the size and particularly the shape of the fruits. Fig. 29 is a photograph of fruits from plants of this area selected to show the extremes of diversity. The fruits were arranged to show four different trends of variation in shape. The extreme forms of the four trends are, in each case, shown at the bottom of the rows.

The degree of divergence in the size and shape of the fruits shown in this photograph is quite remarkable. It should be mentioned, however, that the fruits used in this photograph do not represent random samples. The extreme forms, shown at the bottom of each row, occur very rarely and were included only to illustrate more clearly the different trends in the variation of the fruits. The fruits characteristic of most plants from the Sierra de Moa are shown in the upper part of each row. These four trends are evident, however, and in less extreme form can be found in collections from South America and the United States, as well as Cuba.

Although each of the extreme forms appears to be quite different from the other, there is a complete intergradation. The intergradation is particularly striking when the different forms are observed in the field. The discontinuities that may be apparent in a few isolated collections disappear when the plants are studied in the field. The different patterns of variation are seen to form one larger system of variation that is graded and continuous,

The variation in size and shape of the fruits has no apparent correlation with the variation found in the leaves. Likewise, on the basis of a rather limited number of observations in the field and certain collections in which both flowering and fruiting material were obtained from the same individual, variation in size and shape of the fruits seems to be independent of any corresponding variation in the flowers. The relationship of fruit size to leaf length is illustrated in Figs. 30 and 31, in which average leaf length is plotted against fruit diameter, using the fruits shown above in Fig. 29. In Fig. 30, the diameter of the fruit is measured perpendicular to the plane of the style. Measuring the fruit diameter in the other plane, that is parallel to the plane of the style, gives essentially the same picture (Fig. 31). There is somewhat less size difference in the fruit diameter in this plane, so that points are more bunched, but the lack of correlation with leaf length is quite evident in either case.

Another aspect of the fruits of *Cyrilla* which is variable in the Sierra de Moa is the number of stigma lobes (which corresponds to the number of carpels). In most collections outside of this area the fruits are predominantly two-car-

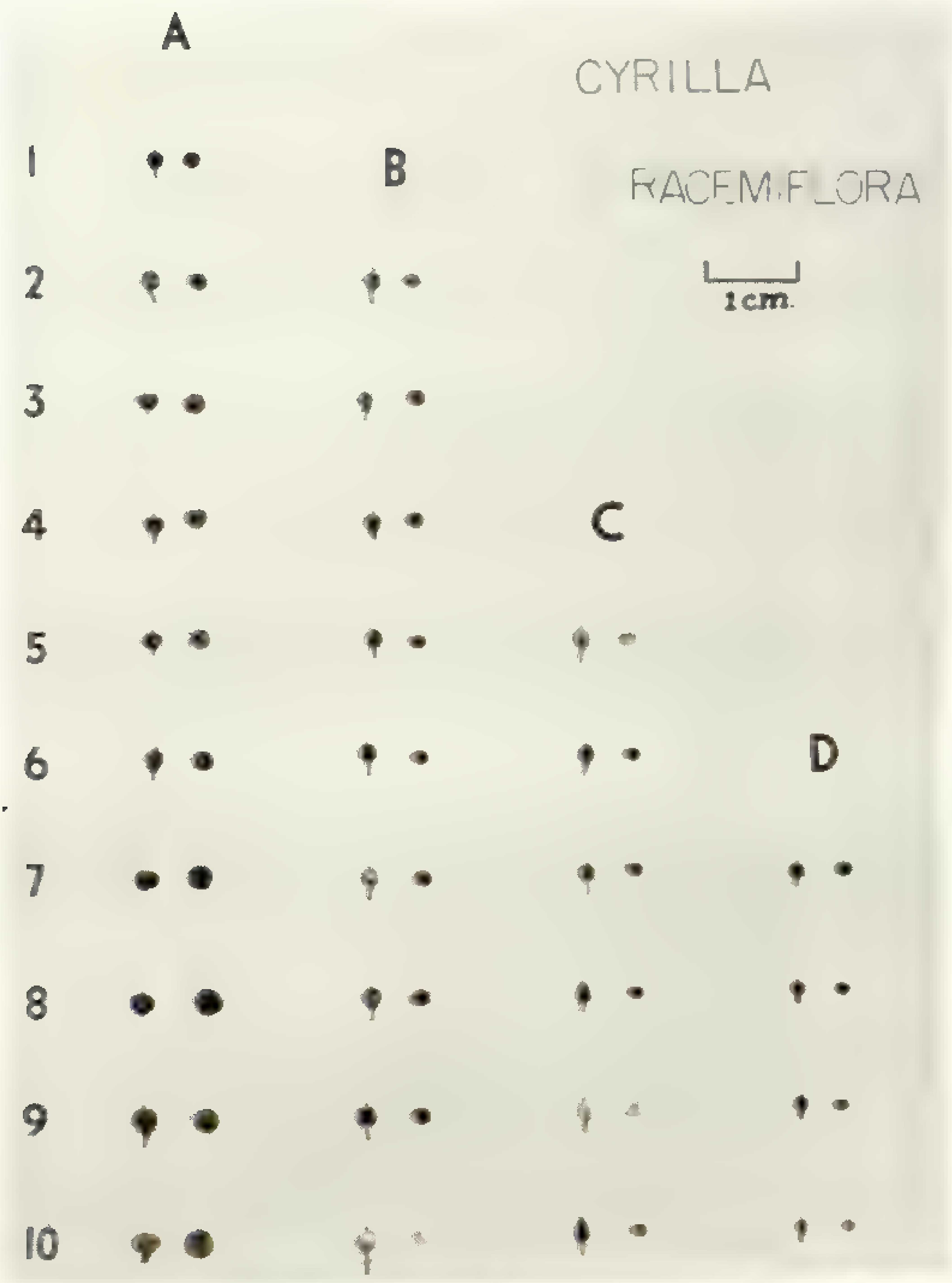
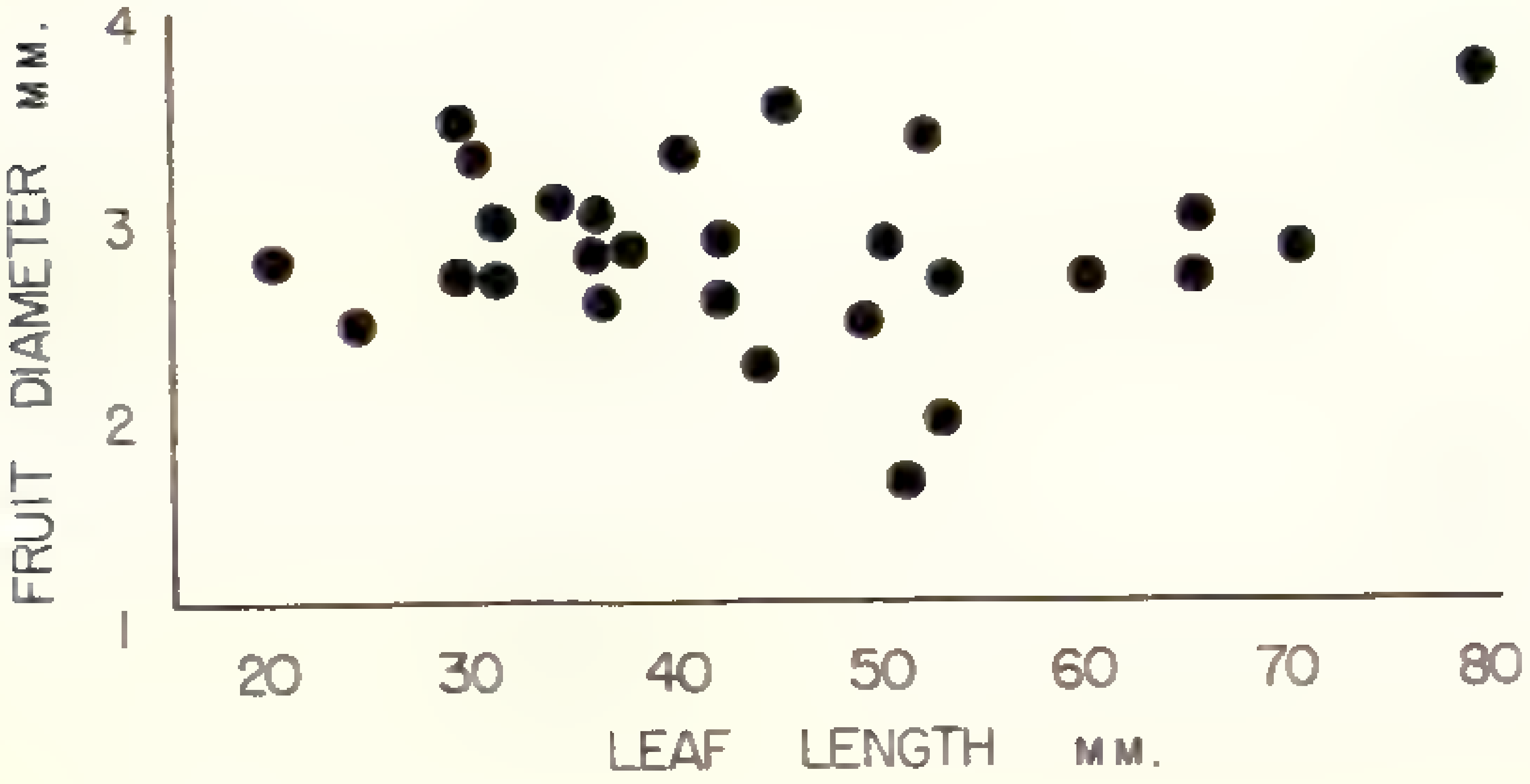


FIG. 29. *Cyrilla racemiflora.* Variation in the size and shape of fruits from the Sierra de Moa, Oriente Province, Cuba. Further explanation in text.

pellate with two stigma lobes. In the Sierra de Moa, however, there are many populations in which three-carpellate, and occasionally even four-carpellate fruits, are of frequent occurrence. There are usually several two-carpellate fruits on each raceme even here, but in some populations three-carpellate fruits occur more frequently than two-carpellate ones.



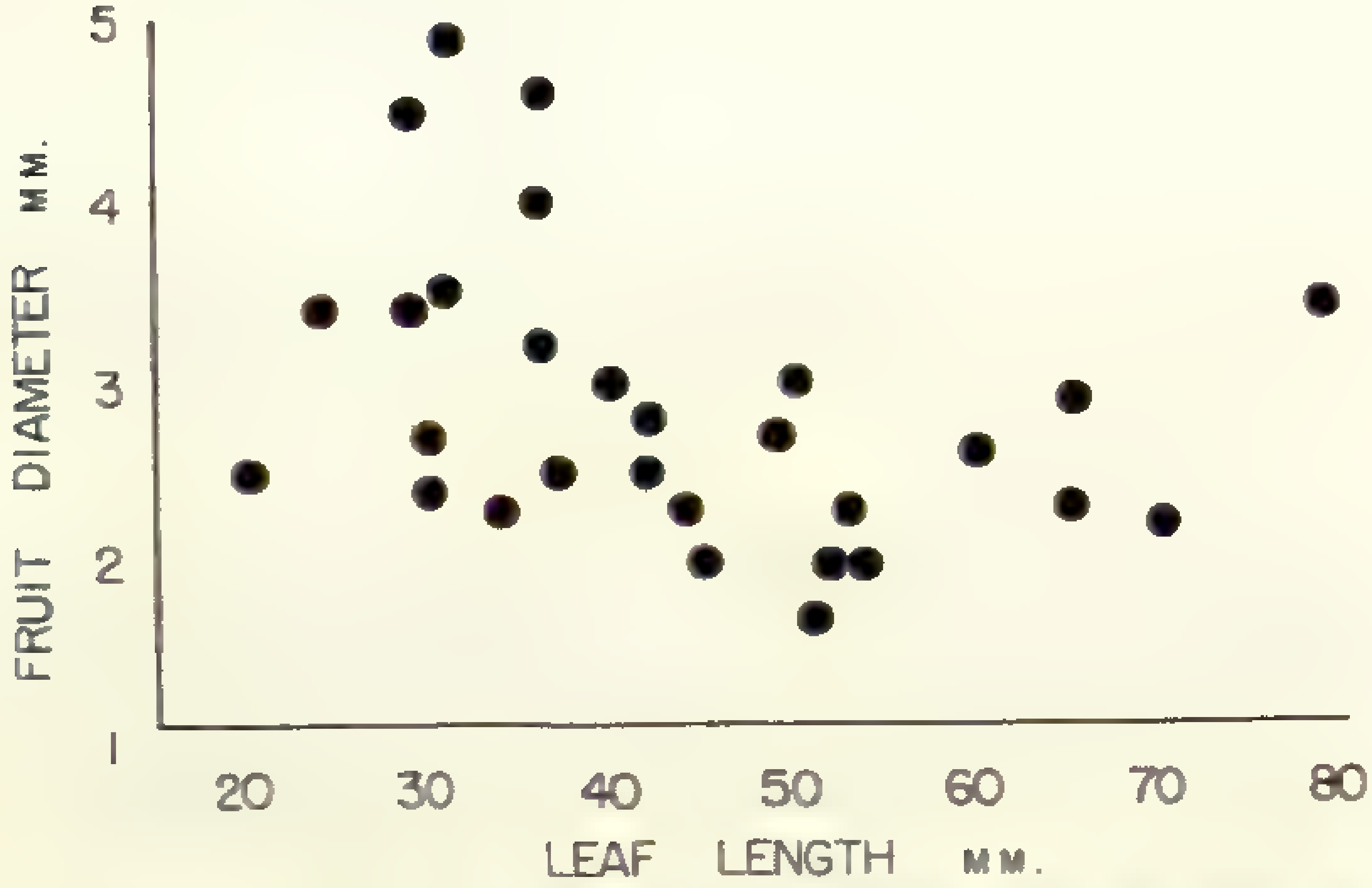


FIG. 30-31. Scatter diagrams showing the relationship between leaf length and fruit diameter. The fruits used in this diagram are illustrated in Fig. 29. In Fig. 30 the fruit diameter was measured perpendicular to the axis of the style. In Fig. 31 the fruit diameter was measured parallel to the axis of the style.

SOUTH AMERICA

In South America the variation in leaf size and shape is not as extreme as that found in Cuba, but there is a great deal of similarity between some of the patterns of variation found in the two areas. A series of representative leaf types from South America is shown in Fig. 32, to illustrate more clearly some of the differences as well as similarities in the variation patterns between the two areas. As pointed out above, in the Sierra de Moa there are two rather clear trends of variation shown in the two rows of leaves in Fig. 21. In the South American material over-all trends similar to these can be seen in alternate rows of Fig. 32. However, each row illustrates a pattern of variation in itself which is fairly clear in the rather extensive collections available from this region.

I have not done field work in South America and must therefore rely upon secondary sources of information for ecological or habitat data. Label data for most of the collections used in preparing Fig. 32 included approximate altitude. This information, along with the collection numbers and the collectors is given in the appendix. As in the material from the Sierra de Moa, altitude alone is not the primary ecological factor affecting leaf size or shape. The apparent effects of altitude are more pronounced in South America than in Cuba, but the altitudinal range in which *Cyrilla* has been collected is almost twice as great in South America as it is in Cuba. The extremely large-leaved forms were collected at lower elevations almost exclusively, and the small-leaved forms were collected primarily at higher elevations. The intermediate forms, which are by far more common in the collections than the extremes, are found intermixed in a rather complex array of sizes and shapes at all elevations. There is no gradual transition from larger to smaller leaf forms with increasing elevation, so the variation pattern does not correspond to a cline. So far as can be determined, the degree of exposure and the amount of available moisture in the environment are the most important ecological factors involved in segregating the various populations according to leaf size and shape. This was apparent in both Cuba and southeastern United States where I have had the opportunity to study the plants in the field, and the available evidence indicates that a similar situation obtains in the mountains of South America.

The importance of environmental influence on leaf form seems to be particularly significant in some areas of South America. In certain collections of the extremely small-leaved, prostrate forms one can occasionally see a transition toward the development of larger leaves. This is particularly noticeable in some of the collections from the higher elevations on open savannas, but can also be seen in plants from lower elevations. *Maguire and Politi 27643* and *Ma-*

guire 32807 are examples of the former, and *Albert S. Pinkus 91* is an example of the latter. Similarly in collections of extremely large-leaved forms many of the intermediate or transitional leaf forms can be found on a single individual.

There is also notable variation in the flowers of *Cyrilla* in South America. In fact there is more variation in size of the floral parts in this area than anywhere else in the range of the species. In Fig. 33 average measurements of certain floral parts are plotted against leaf length in the same manner as in Fig. 26, so that each vertical series of points represents floral measurements of a separate individual. Again the bracts are extremely variable, but as was mentioned above, this variability is of little significance due to a high degree of variation within a single individual. The variation shown in the other floral parts is of significance, however, as the size of these parts tends to be very uniform in a given individual. The variation in petal length is particularly noticeable in the collections from South America, ranging from 19 to 35 mm. in length. Outline drawings of representative petals from plants used in this figure are shown in Fig. 34.

The variation in the petals of the South American material is of interest because petal size was one of the specific characters used in distinguishing "*Cyrilla brevifolia*" N. E. Brown from *C. racemiflora.* The distinguishing characters used in segregating this species were its large petals; small, ovate leaves; and short, compact racemes (the term compact refers to the spacing of the pedicels on the rachis). It is conceivable that detailed field observations on this variant will reveal that it should be given the rank of subspecies or variety, but on the basis of the available evidence such a designation seems unwarranted and would be of little or no value to an understanding of the species. This variant intergrades in all of its diagnostic characters with other forms, apparently in the same geographic area. In fact, in the available collections from this area there are far more forms that are intermediate for these diagnostic characters than forms that are "typical" of the variant.

As shown in Fig. 33, larger petals and sepals are also found in plants with larger leaves. Moreover, when raceme length and compactness are compared with leaf length, these characters also are seen to intergrade. Certain aspects of the interrelationship of these characters are shown graphically in Fig. 35. Here raceme length is plotted against leaf length, with the degree of compactness of the raceme indicated by the shape of the symbol used in plotting the two

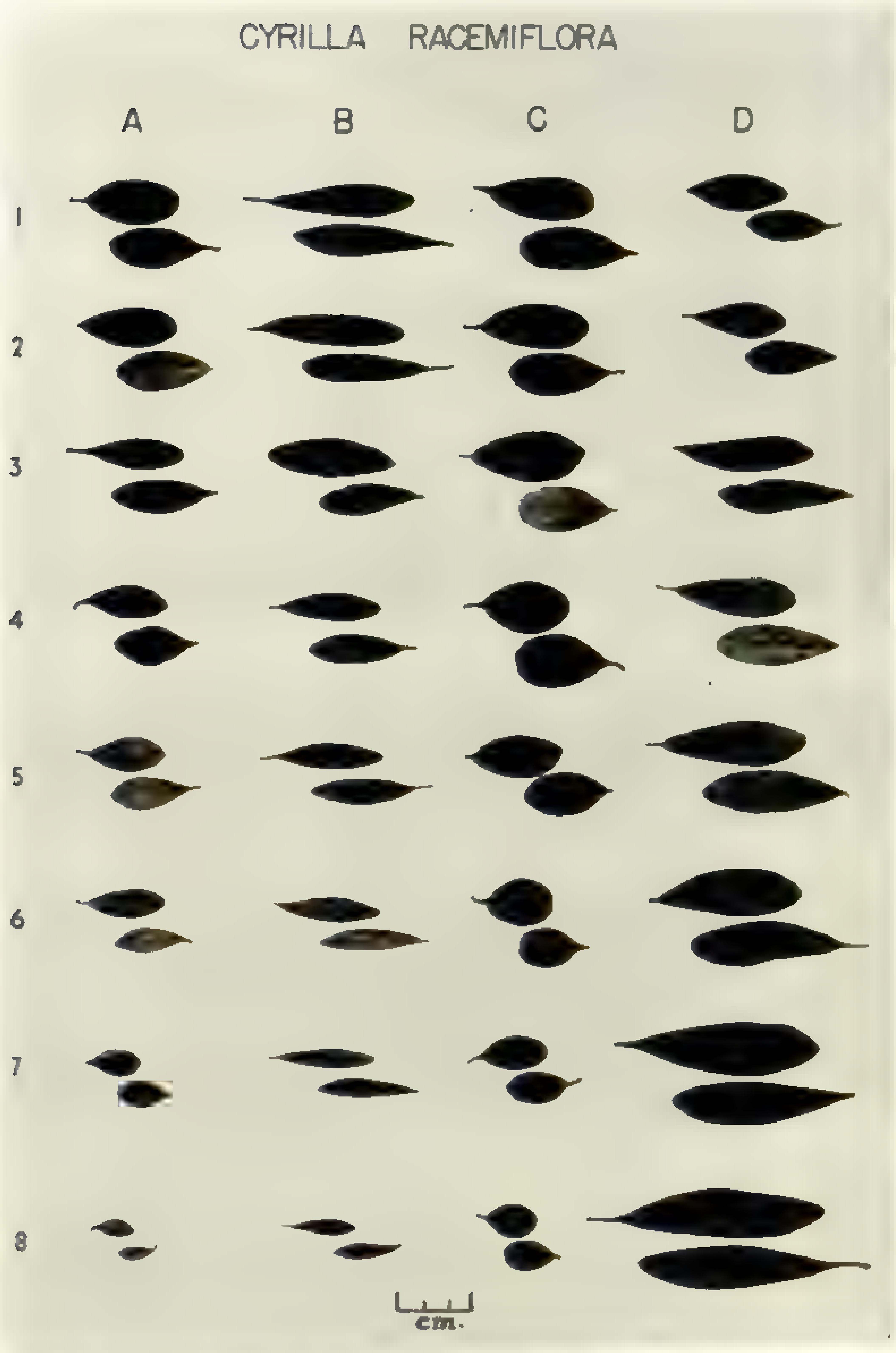


FIG. 32. Leaf variation in *Cyrilla racemiflora* from northern South America. Further explanation in text.

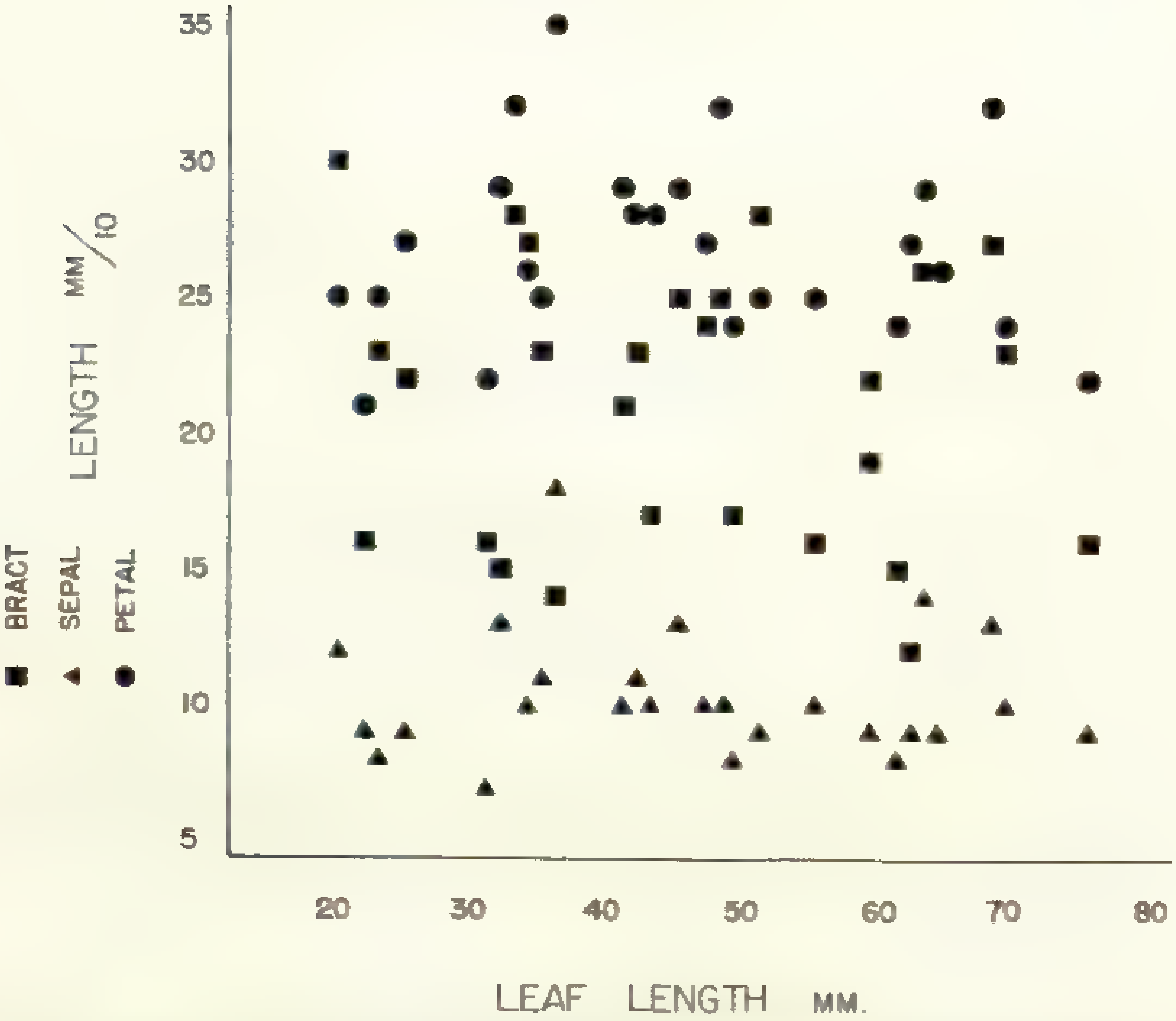


FIG. 33. Scatter diagram showing the relationships between the length of the leaves and the length of the bracts, sepals, and petals of plants collected in northern South America. This diagram was prepared in the same manner as Fig. 26 above.

coordinates. The degree of compactness of the racemes is represented by an arbitrary value between one and four, with one representing the most compact and four representing the most open or least compact raceme. It is evident in this figure that the relationship between raceme length and leaf length is approximately linear. Thus, with an increase in leaf length there is generally a corresponding increase in raceme length. A similar relationship is also shown between the length and the degree of compactness of the racemes. Generally, as the racemes become longer the distance between the pedicels increases. This, of course, is what one would expect in an indeterminate raceme, where there is differential internodal elongation. It is evident that the differences in the length of the racemes are due primarily to differences in internodal elongation in the raceme. It is not surprising, therefore, that one should find a high degree of correlation between these characters. In populations in which the leaves tend to undergo greater elongation, the racemes also tend to undergo greater elongation, which in

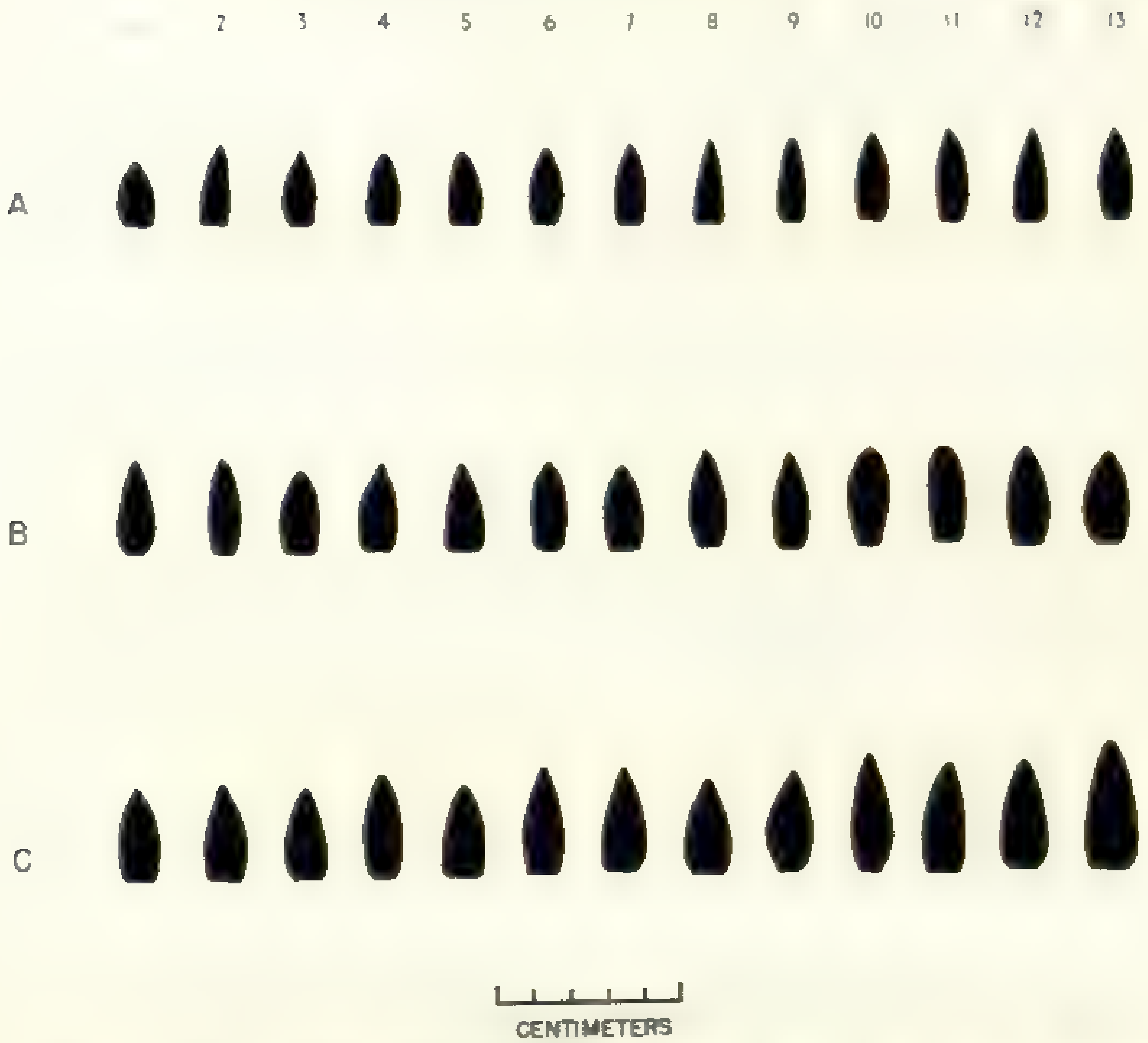


FIG. 34. Micro-projector drawings of representative petals from plants collected in northern South America. Note that the petals show a greater size range on the plants from South America then on the plants from eastern Cuba (Fig. 28).

turn gives rise to a wider spacing of the individual flowers on the raceme. A similar correlation is found between these characters throughout the geographic range of *Cyrilla*.

A somewhat different relationship is illustrated in Fig. 36, in which petal length is plotted against leaf length with the degree of compactness of the raceme shown as in Fig. 35. It is evident from this graph that the variation in petal length is more or less independent of leaf length and raceme density. It is also evident that the extremely large petals, which are correlated with small leaves and dense racemes in the variant described above, are also found in plants with long leaves and less compact racemes.

SOUTHEASTERN UNITED STATES

The third area in which *Cyrilla* shows a high degree of local variation is in southeastern United States. Here one finds a pattern of leaf variation much like that shown above for Cuba and northern South America. Again, the effects of different ecological conditions are fairly clear in the ex-

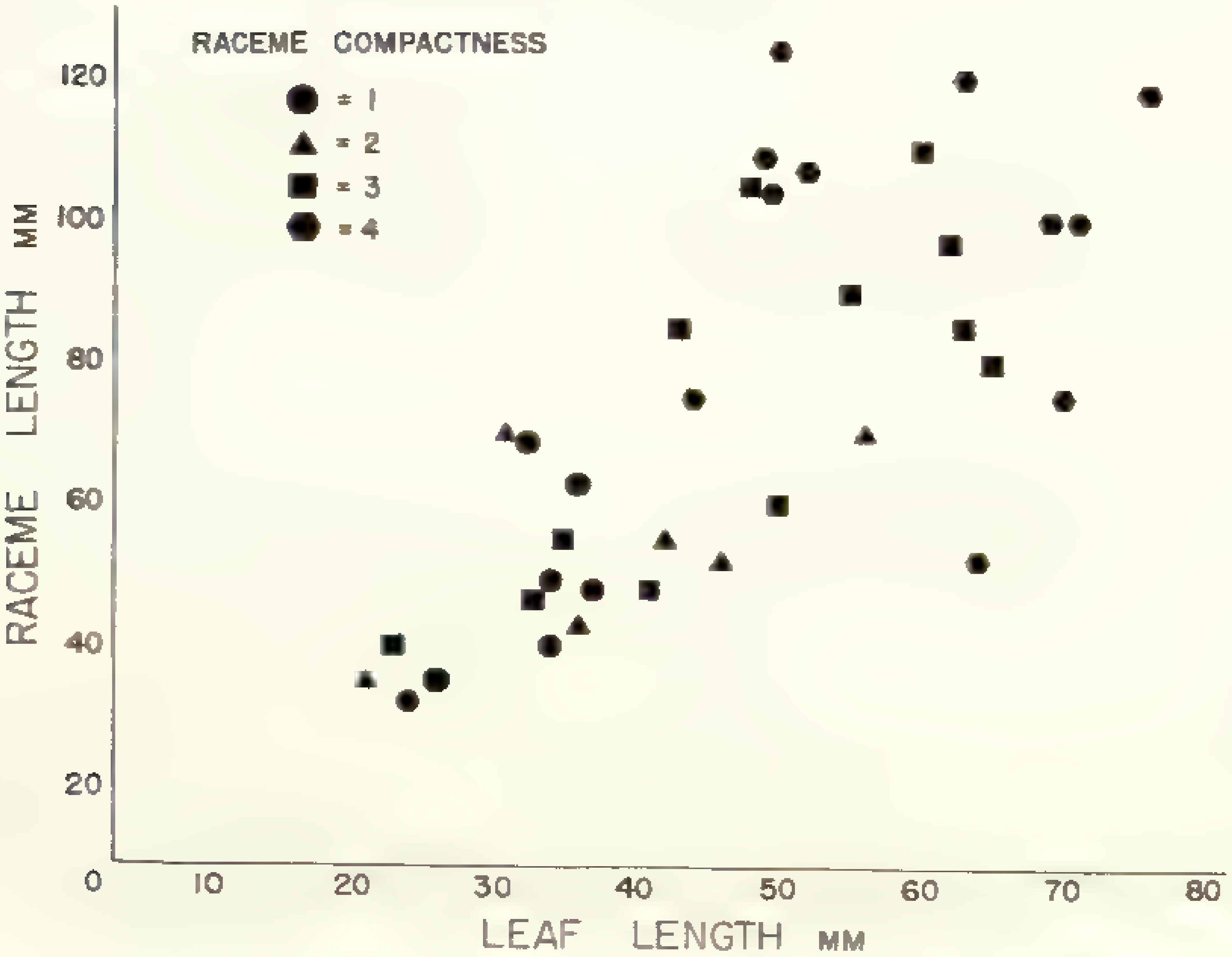


FIG. 35. Scatter diagram showing the relationship of leaf length and raceme length to raceme compactness in plants from northern South America. Further explanation in text.

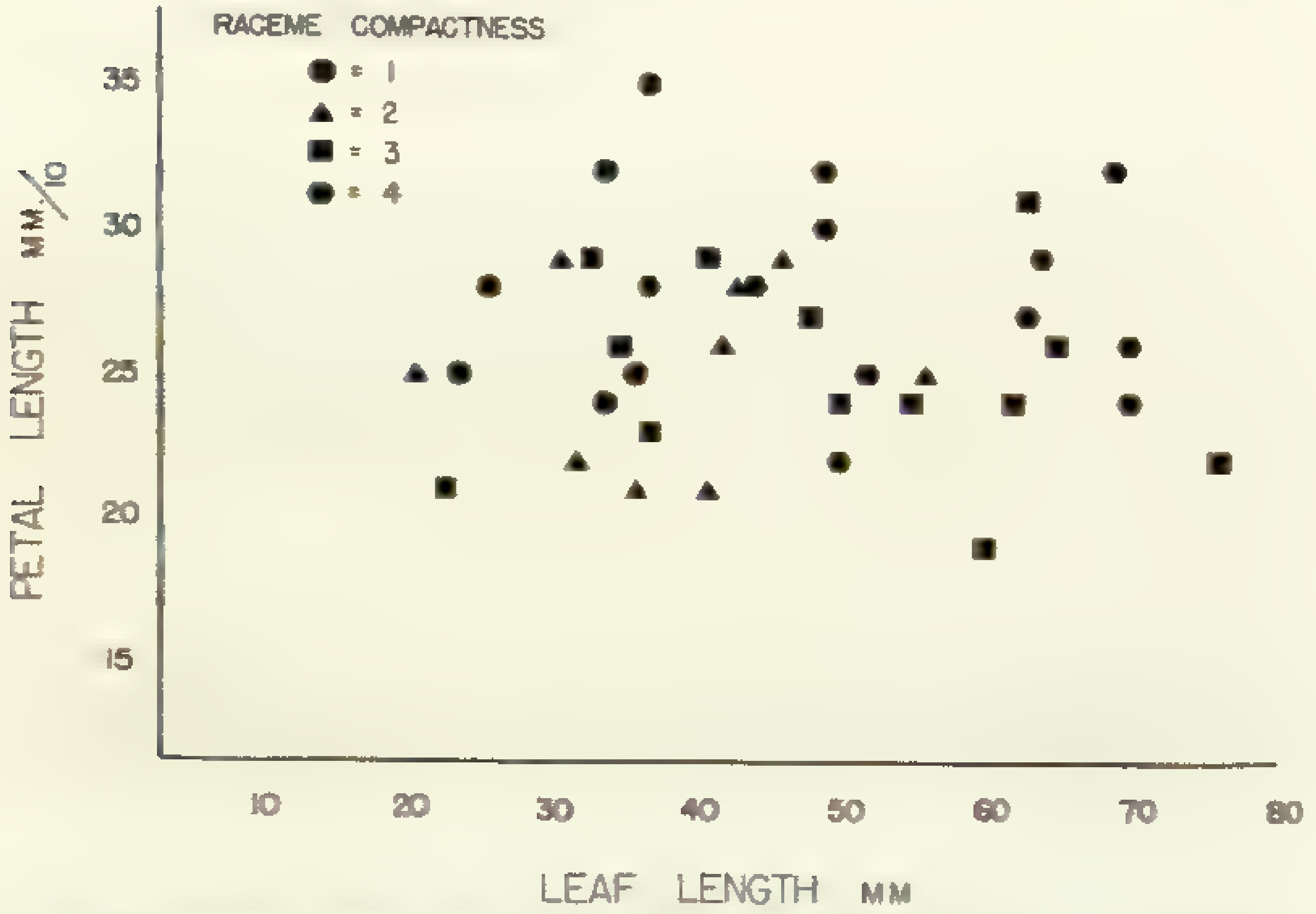


FIG. 36. Scatter diagram showing the relationship of leaf length and petal length to raceme compactness in plants from northern South America. Further explanation in text.

treme forms. The extremely large-leaved form is found in fairly dense swamps, usually in partial shade; whereas the extremely small-leaved form is found in drier and more exposed sites. The intermediates tend to shade off toward the extremes, but are frequently intermixed. The relationship between leaf length and the length of certain floral parts of plants from this region is shown in Fig. 37. This figure was prepared in the same manner as Figs. 26 and 33 above.

The area in the United States that is most interesting from the standpoint of local variation in *Cyrilla* is northern Florida. Here the two extremes of leaf size overlap geographically. The two forms usually maintain a fair degree of ecological separation, but they intergrade completely in certain local populations, and there is evidence of considerable gene exchange throughout the area of overlap. Because of this ecological separation, however, the two forms appear superficially to be distinct species and have been recognized as separate species by some authors. The small-leaved form was described as a separate species, *Cyrilla parvifolia*, by Rafinesque (1840) and again by G. V. Nash (1896). This species was said to differ from *C. racemiflora* by its lower habit, smaller leaves, shorter racemes, and globose fruits. In the extreme forms they also differ in flowering time, although there is usually some overlap in this respect. Population studies on these two different forms have revealed that the variation pattern is not discontinuous, and that they intergrade completely in some areas.

One particularly interesting population which shows a complete intergradation of the two extremes was seen between Wewahitchka and Port St. Joe, near the point where Florida Route 71 crosses the Intercoastal Waterway. On the north side of the waterway there is a relatively undisturbed evergreen, shrub-tree swamp; just to the south of the waterway there is an old levee of white sand, apparently thrown up years ago when the canal was dredged. This levee is rolling, and grades off to an open, undisturbed, pine flatwoods. A fairly sizeable population of the large-leaved plants was found growing in the evergreen, shrub-tree swamp, and a somewhat larger population of the small-leaved plants was growing in the open, pine flatwoods. On the artificial levee between the two populations there was an extremely variable population which showed numerous stages of intermediacy between the two populations on either side.

Although the plants in the variable population were pretty

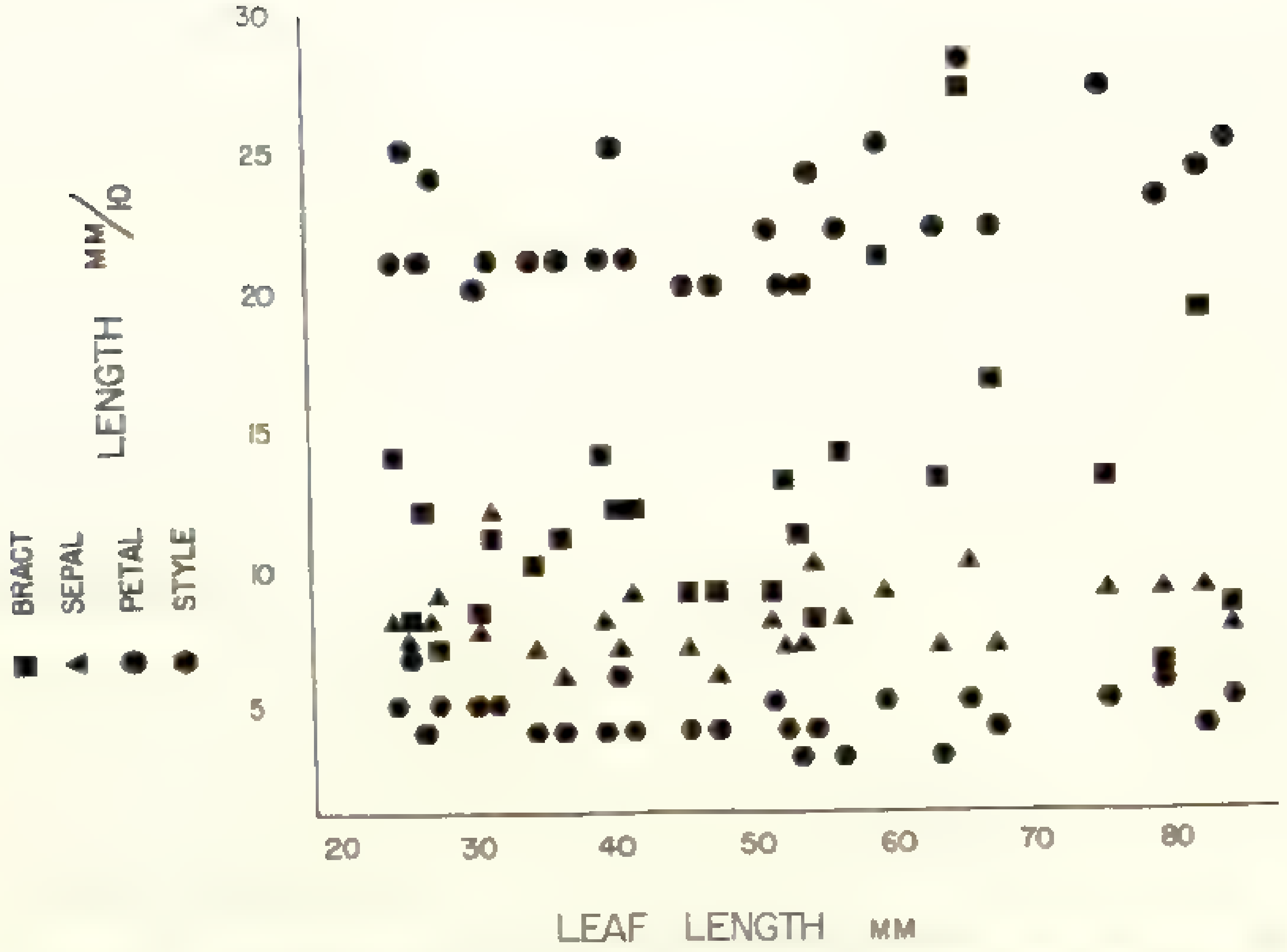


FIG. 37. Scatter diagram showing the relationships between the length of the leaves and the length of the bracts, sepals, petals, and styles of plants collected in Southeastern United States. This diagram was prepared in the same manner as Fig. 26 and 33 above.

well intermixed, there was a noticeable tendency for the larger-leaved plants to be nearest the channel and for the smaller-leaved plants to be nearest the pine flatwoods. The analysis of these populations given below was based on collections made in the following manner. A sizeable collection was made from a single individual which appeared to be representative of the population growing in the swamp, and a similar collection was made from an individual which appeared to be representative of the population in the pine flatwoods. Then a large mass collection was made in the intermediate population on the levee.

The two extreme populations were compared first in order to evaluate the differences. A plot of leaf length against leaf width for the two populations, shown in Figs. 40 and 41, reveals that the degree of correlation of these two measurements is very similar in the two populations. Thus, one is justified in using the measurement of length, only, to obtain a crude value for leaf size in the two populations. In evaluating leaf size in the plants from these populations every mature leaf on a shoot was measured. The mean and standard deviation were derived in order to evaluate the total variation found in a single individual. The mean values for

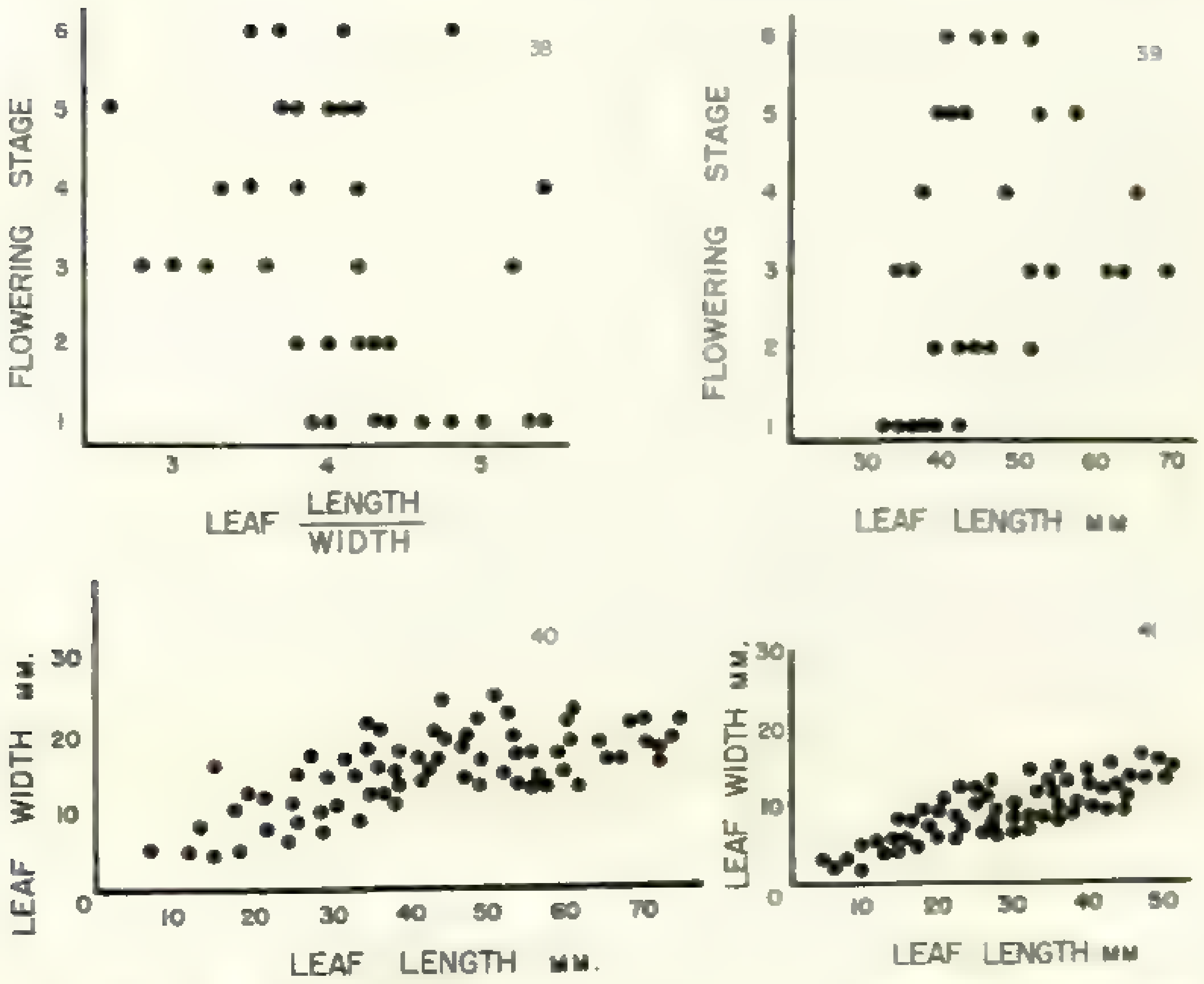


FIG. 38-41. The relationships between the leaf length and leaf width, and between leaf length and flowering stage for plants collected near Port St. Joe, Florida. Fig. 38 and 39 were prepared from plants collected in the intermediate population on the artificial levee. Fig. 40 was prepared from plants of the "large-leaved" form collected in the shrub-tree swamp. Fig. 41 from plants of the "small-leaved" form collected in the pine flatwoods. Further explanation in text.

leaf length were found to differ less between the two populations than was expected, and the standard deviation was quite high in each case. For the population in the swamp, the mean leaf length was 44.6 mm. with a standard deviation of 15.7; whereas in the collections from the pine flatwoods, the mean was 28.06 mm. with a standard deviation of 10.5. There is clearly a large overlap in leaf size between the two populations, but they are significantly different.

These two populations also differed significantly in flowering time, the large-leaved population being at mid-anthesis, while the small-leaved population was not yet in flower. The flowering time in *Cyrilla* extends over a relatively long period of time, beginning at the base of the raceme and progressing toward the apex. Because of this it is possible to recognize several arbitrary stages during the time of flowering. In comparing the populations under consideration, four arbitrary stages of flowering were recognized between the two extremes. In this manner flowering stage and leaf length can be compared and contrasted in the intermediate population from the artificial levee. One aspect of this relationship is shown in Fig. 39 in which flowering stage is plotted along the ordinate and leaf length along the abscissa. The intermediacy and discordance of the two characters are quite apparent in this diagram. Plants in late stages of flowering have small leaves, and conversely plants in early flowering stages often have large leaves. Similar results are obtained by using leaf length-width ratio as the abscissa (Fig. 38).

In this area it is apparent that the two different forms occupying two different habitats were, to a certain extent, thrust together by the intervention of man in dredging the Intercoastal Waterway. The interbreeding of two populations that resulted from this has given rise to a highly variable, intermediate population. In terms of plant generations, this population was relatively young and there had not been sufficient time for any appreciable blending of the various extremes. The fact that the intermediate population tended to be graded toward the two extremes indicates that some backcrossing had occurred, but the different forms were intermixed for the most part.

In other areas, however, one can find more uniform populations in various stages of intermediacy between the two extreme forms. One such population was found in Walton County, Florida, approximately 3 miles west of Santa Rosa, near Highway 98. In this area the plants showed some variation in flowering time and leaf size, although the variation here was considerably less than that found in the plants from the intermediate population described above. The population as a whole appeared more like the small-leaved form, although it was clearly intermediate between the extremes, and a few individuals were found which appeared more like the long-leaved form. Eastward from this area the population was more or less continuous along the highway and in surrounding fields for several miles. In this large population the variation pattern was graded from west to east. The plants to the east had increasingly smaller leaves and a later flowering period; those to the west had larger leaves and an earlier flowering period. Throughout this large zone of intergradation, various intermediate forms were intermixed to some extent, but in general the intergradation was continuous.

A similar situation was observed in a population near the Alabama-Florida line on United States Highway 90. This population was also intermediate, but in this area the variation pattern was more like the large-leaved form. Likewise, the variation pattern in the plants from this area was graded from west to east in a manner similar to that described above. The intergradation was not so evenly graded in this area as in the population near Santa Rosa, possibly because the former population was not continuous, but rather broken up into numerous smaller populations. Nevertheless, the tendency toward larger leaves and earlier flowering time was apparent in plants growing west of this area.

The habitat seems to be highly significant in determining the over-all character of these intermediate populations. The extreme variation found in the population on the artificial levee along the Intercoastal Waterway indicates that the effects of the habitat must be primarily that of selecting well-adapted gene combinations, and secondarily that of ecological modification of a given genotype.

The other named species of *Cyrilla* from the United States is *Cyrilla arida* Small. This species was described from plants collected from Highlands County, in south-central Florida. According to Small (1924) this species " . . . differs from *C. parvifolia* in the narrower sepals and petals and the notched anthers, as well as in the vine-like branches."

At the time this species was described, it was thought to be geographically isolated from the *Cyrilla* in northern Florida, but subsequent collections have revealed that scattered populations of *Cyrilla* occur in several areas between central and northern Florida, (Map 11). Apparently there was also some confusion as to the habitat of "*Cyrilla arida*". It was said to grow high up on dunes of dry, white sand. I have made an intensive search in the vicinity of the type locality, between Avon Park and Sebring, Florida, and have found no plants of *Cyrilla* growing out on the sand dunes. In this area, as elsewhere in Florida, *Cyrilla* occurs only in low moist areas.

It seems likely that the designation of "*Cyrilla arida*" as a distinct species was due in part to this confusion in habitat and distribution. The petal and sepal shape, as well as all other characteristics of this "species", fall well within the variation pattern found in plants of *Cyrilla* from northwest Florida. The notched anthers, as mentioned above, occur in collections of *Cyrilla* throughout its geographic range. Plants with small, "vine-like" branches are also found in other areas. Moreover, this character is not found in all of the collections from Highlands County, Florida. In short, the small-leaved representatives of *Cyrilla* in south-central Florida are not significantly different from the small-leaved representatives in northern Florida, and the latter intergrade with the large-leaved forms in the same area.

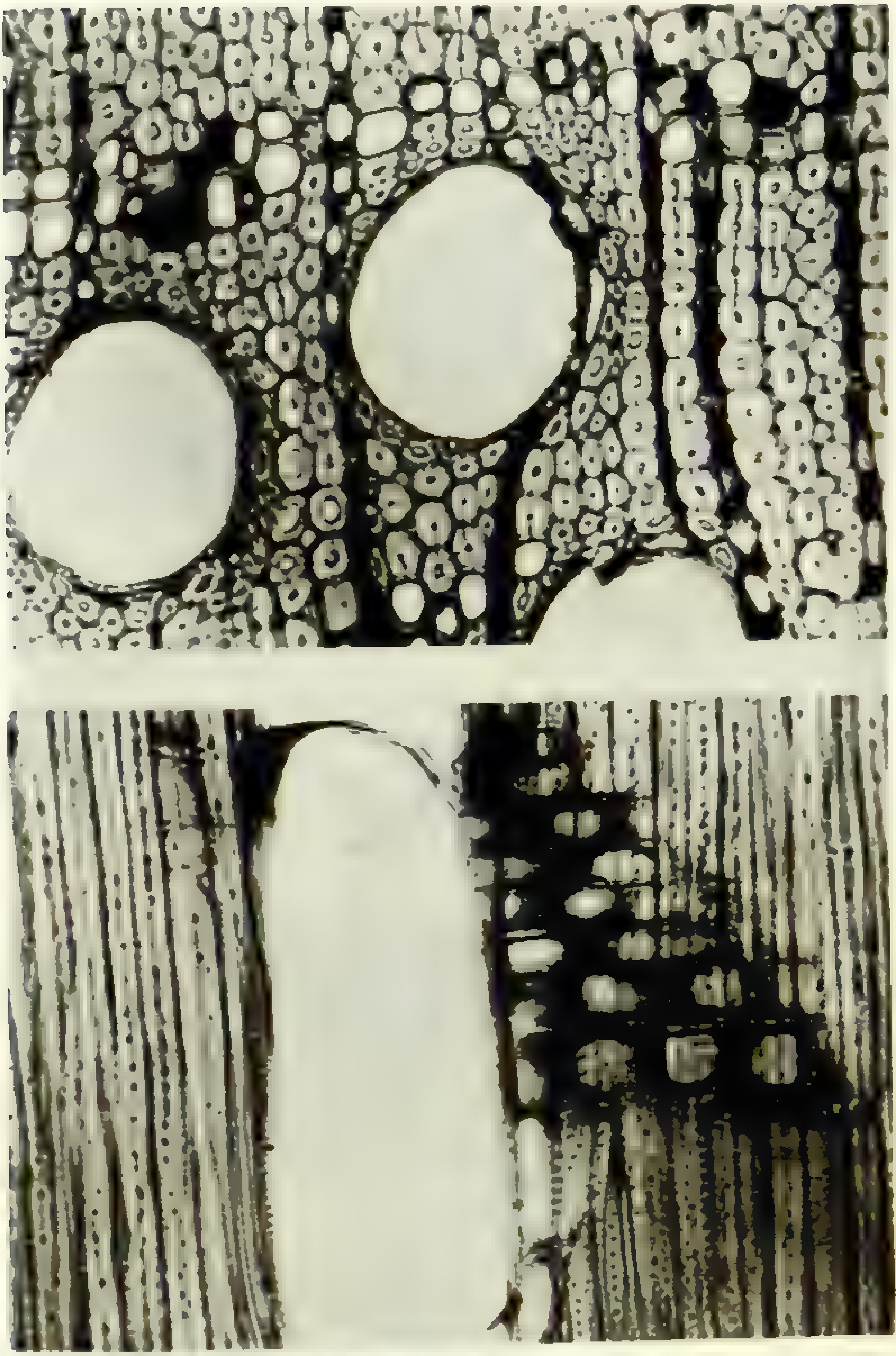
CYRILLOPSIS

The genus *Cyrillopsis* Kuhlmann, which was included in the Cyrillaceae by Mattick (1935) and Uphof (in Engler and Prantl, 1942) is excluded from the present treatment. This is done primarily on the basis of the structure of the fruit, the pollen, and the wood anatomy. Although no mature fruits of *Cyrillopsis* have been seen, it is readily apparent from the immature fruits that the structure is unlike that of members of the Cyrillaceae. The fruits of *Cyrillopsis* are elongate, flat, and asymmetrical in shape, and contain seeds with well-developed seed coats. Seed coats are not developed by members of the Cyrillaceae. The pollen grains of *Cyrillopsis* are also very different from those of the Cyrillaceae. As mentioned above in the section on pollen morphology, the pollen grains of *Cyrillopsis* are similar to those of some members of the Celastraceae, but show none of the structural features that are characteristic of members of the Cyrillaceae.

Anatomically, *Cyrillopsis* differs from members of the Cyrillaceae in having much more advanced wood structure. As shown in Fig. 42 and 43 the vessel elements of *Cyrillopsis* are short and broad. The end walls of the vessel elements are completely perforate, and fall into the category of group III or group IV vessels according to the classification of Bailey and Tupper (1918). The imperforate tracheary elements are composed of libriform fibers and very thick walled fiber-tracheids. No tracheids have been observed in the wood of *Cyrillopsis.*

The present genus also differs from members of the Cyrillaceae by several other characters, including its exserted stamens with non-versatile anthers and filaments that are imbricate in bud; its persistent, cup-shaped disk on which the anthers, but not the petals, are borne, and its leaf venation with alternating strong and weak lateral veins.

Superficially *Cyrillopsis* resembles the genus *Itea*, of the Saxifragaceae. The resemblance is so close, in fact, that an occasional sheet of *Itea virginica* is found misidentified as *Cyrillopsis paraensis.* However, the morphology of the flower and particularly the fruit is unlike that of members of the



FIGS. 42–43. Wood anatomy of *Cyrillopsis paraensis*. Fig. 42. Transverse section of mature wood. Note the large vessels, extremely thick-walled fibers, and abundant xylem parenchyma. Fig. 43. Radial section of mature wood showing the vessel end wall. Magnifications ca. 144 ×.

Figs. 44–45. Habitats of *Cyrilla racemiflora*. Fig. 44. Pine flatwoods near Covington, Louisiana. Fig. 45. Cypress swamp near Ponchatoula, Louisiana.

Saxifragaceae, but does show certain similarities to members of the Celastraceae. Also, the leaf venation and the pollen morphology indicate a possible relationship with the Celastraceae. The wood anatomy, on the other hand, is more advanced than that found in most members of the Celastraceae. Additional collections of plants with mature fruits, and further study are needed before this genus is assigned to the proper family, but provisionally I would suggest that *Cyrillopsis* should be included in the Celastracaee.

SPECIES EXCLUDED

Cyrilla aquatica Roxb. Pl. Corom. 2:47, 1795 = *Limnophila racemosa* Benth. in Wall. Cat. n. 3907.

Cyrilla indica Koen. ex Wight and Arn. Prod 1:364, 1834 = *Vahlia oldenlandoides* Roxb. Hort. Beng. **86**: Fl. Ind. 2:89, 1832.

Cyrilla oldenlandoides Koen. ex Wight and Arn. l.c. — *Vahlia oldenlandoides* Roxb. l.c.

Cyrilla paniculata Nutt. in Am. Journ. Sc. 5:290, 1822 — *Ardisia pickeringia* Torr. and Gray ex D. C. Prod. Syst. Veg. 8:124, 1844.

Cyrilla spinosa Spreng. Nov. Prov. Hort. Hall. 15, 1831 = *Bursaria spinosa* Cav. Icon. Descrip. Plant. 4:30, 1797.

Cyrilla viscosa Koen. ex Wight and Arn. Prod. 1:364, 1834 = *Vahlia viscosa* Roxb. Hort. Beng. **86**: Fl. Ind. 2: 89, 1832.

Cyrilla pulchella L'Hérit. Stirp. Nov. 147, 1785 = *Achimenes coccinea* Pers. Syn. Plant. 2:165, 1807.

BIBLIOGRAPHY

AGARDH, J. G. 1858. Theoria Systematis Plantarum. 107.

BAILLON, H. 1892. Histoire des plantes **11**: 143. 193.

BARGHOORN, E. S. 1950. Geological and botanical study of the Brandon Lignite and its significance in coal petrology. Econ. Geol. 45. **4**: 344-357.

———. 1951. Age and environment: A survey of North American Tertiary floras in relation to paleoecology. Jour. Paleontol. 25. **6**: 736-744.

——— AND W. SPACKMAN. 1949. A preliminary study of the flora of the Brandon Lignite. Am. Jour. Sci. **247**: 33-39.

BEAUVISAGE, L. 1920. Étude anatomique de la famille des Ternstroemiacées. Tours, 470 pp.

BEIJERINCK, M. W. 1887. Beobachtungen und Betrachtungen über Wurzelknospen und Nebenwurzeln. Verhandel. K. Akad. Wetensch. Amsterdam, 146 pp.

BENTHAM, G. AND J. D. HOOKER. 1876. Genera Plantarum. 1226.

BESSEY, C. E. 1915. The phylogenetic taxonomy of flowering plants. Ann. Missouri Bot. Gard. **2**: 109-164.

BRITTEN, J. 1905. Note on the history of *Cliftonia*. Jour. Bot. **43**: 282-284.

BRITTON, N. L. 1899. Index to recent American botanical literature. Bull. Torrey Club **16**: 309-310.

———. 1915. Studies of West Indian plants IV. Bull. Torrey Club 5. **42**: 388-389.

———. 1920. Descriptions of Cuban plants new to science. Mem. Torrey Club **16**: 77-78.

BROWN, N. E. 1901. Report on two botanical collections from Mt. Roraima in British Guiana. Trans. Linn. Soc. ser. 2, **6**: 22.

CHAPMAN, A. W. 1860. Flora of the Southern United States. New York, 621 pp.

COPELAND, H. F. 1953. Observations on the Cyrillaceae particularly on the reproductive structures of the North American species. Phytomorphology **3**:405-411.

CROIZAT, L. 1952. Manual of Phytogeography; or, An Account of Plant Dispersal Throughout the World. The Hague, 587 pp.

DE CANDOLLE, A. 1855. Géographie Botanique Raisonée. Paris, 2 vols., 1365 pp.

DALLA TORRE AND HARMS. 1900-1907. Gen. Siphon. 288.

DURAND, T. 1888. Index Generum Phanerogamarum. Bruxelles, 722 pp.

ELLIOTT, S. 1821. A Sketch of the Botany of South Carolina and Georgia. 294.

ENDLICHER, S. 1840. Genera Plantarum. 1413.

———. 1841. Enchiridion Botanicum. 578.

———. 1842. Gen. Plant. Suppl. **2**:86.

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. Stockholm, 539 pp.

FERNALD, M. L. 1950. Gray's Manual of Botany (eighth edition). Boston, 1632 pp.

GILG, E. 1892. The Cyrillaceae. In Engler and Prantl, Die Natürlichen Pflanzenfamilien (first edition). 3. **5**:179-182.

GILG, E. 1931. Über eine neue Gattung der Ochnaceae (?), Alloiosepalum, aus Peru. Notizbl. Bot. Gart. u. Mus. Berlin-Dahlem, 11, **102**:97-99.

GLEASON, H. A. 1931. Botanical results of the Tyler-Duida expedition. Bull. Torrey Club **58**:383.

———. 1952. The New Britton and Brown Illustrated Flora. **2**:498.

GRISEBACH, A. H. 1860. Cyrilleen. Erlaut. ausgew. Pfl. d. trop. Amer. in Abh. Kön. Ges. d. Wiss. Göttingen **9**:45.

GUSTAFSSON, Å. 1946. Apomixis in higher plants. I. The mechanism of apomixis. Lunds Univ. Årsskr. Avd. 2, **42**(3) :1-66.

———. 1947a. Apomixis in higher plants. II. The causal aspects of apomixis. Lunds Univ. Årsskr. Avd. 2, **43**: (2) :71-178.

———. 1947b. Apomixis in higher plants. III. Biotype and species formation. Lunds Univ. Årsskr. Avd. 2, **44**: (2) :183-370.

———. 1948. Polyploidy, life form and vegetative reproduction. Hereditas **34**:1-22.

HEIMSCH, C., Jr. 1942. Comparative anatomy of the secondary xylem in the "Gruinales" and "Terebinthales" of Wettstein with reference to taxonomic grouping. Lilloa **8**:83-198.

HITCHCOCK, A. S. 1935. Manual of the grasses of the United States. U. S. Dept. Agri. Misc. Publ. 200, 1040 pp.

HULTÉN, E. 1937. Flora of the Aleutian Islands. Stockholm, 397 pp.

IRMISCH, T. 1857. Über die Keimung und die Erneuerungsweise von *Convolvulus sepium* und *C. arvensis*, so wie über hypokotylische Adventivknospen bei Krautartigen phanerogamen Pflanzen. Botanische Zeitung 15:433-448.

JUSSIEU, A. L. 1789. Genera Plantarum Secundum Ordines Naturales Disposita. Paris, 498 pp.

KUHLMANN, J. G. 1925. Contribuição para o conhecimento de algumas plantas novas. Archiv. Jard. Bot. Rio de Janeiro 4:357.

LAMARCK, J. B. 1791. Encyclopédie Méthodique. 2:144.

LAWRENCE, G. H. M. 1951. Taxonomy of Vascular Plants. New York, 823 pp.

LAWRENCE, W. E. 1945. Some ecotypic relations of *Deschampsia caespitosa*. Am. Jour. Bot. 32:298-314.

LINDLEY, JOHN. 1836. Natural System of Botany. 2:119.

————. 1847. The Vegetable Kingdom (second edition). 445.

LLOYD, F. E. 1911. Guayule (*Parthenium Argentatum* Gray), A Rubber-Plant of the Chihuahuan Desert. Carnegie Inst. Publ. 139, 213 pp.

MAHESHWARI, P. 1950. An Introduction to the Embryology of Angiosperms. New York, 453 pp.

MARIE-VICTORIN, FRÈRE. 1948. Nouvelles études taxonomiques sur la flore de Cuba. Contrib. Inst. Bot. Univ. Montréal 63:49-62.

MATTICK, FR. 1935. Die Gattung *Purdiaea* Planchon (*Costaea* Richard, *Alloiosepalum* Gilg). Notizbl. Bot. Gart. u. Mus. Berlin-Dahlem 12, 113:395-401.

METCALFE, C. R. AND L. CHALK. 1950. Anatomy of the Dicotyledons. London, 2 vols., 1500 pp.

MICHAUX, A. 1803. Flora Boreali-Americana, vol. I. Paris, 340 pp.

MOHR, C. T. 1901. Plant life of Alabama. Cont. U. S. Nat. Herb. 6:601.

MULLER, C. H. 1946. Root Development and Ecological Relations of Guayule. Tech. Bull. U. S. Dep. Agr. 923, 114 pp.

PLANCHON, J. E. 1846. Description d'un genre nouveau voisin du *Cliftonia* . . . Hook. Lond. Jour. Bot. 5:250.

POIRET, J. L. M. 1812. Encyclopédie Méthodique, Supplement 2:436.

PRIESTLY, J. H. AND C. F. SWINGLE. 1929. Vegetative propagation from the standpoint of plant anatomy. Tech. Bull. U. S. Dep. Agr. 151, 99 pp.

RAFINESQUE, C. S. 1840. Autikon Botanikon. 8.

REHDER, A. 1940. Manual of Cultivated Trees and Shrubs, (second edition). New York, 996 pp.

REID, E. M. 1920. A comparative review of Pliocene floras, based on the study of fossil seeds. Quart. Geol. Soc. London 76:145-161.

RICHARD, A. 1853. Flora Cubana, en Ramon de la Sagra, La isla de Cuba, 3:75.

ROLLINS, R. C. 1949. Sources of genetic variation in *Parthenium argentatum* Gray (Compositae). Evolution 3(4):358-368.

————. 1950. The nature and occurrence of apomixis in *Parthenium* (Compositae). Proc. Seventh Int. Bot. Cong., Stockholm 326.

ROTHMALER, W. 1935. Systematische Vorarbeiten zu einer Monographie der Gattung *Alchemilla* (L.) Scop. emend. III. Notizen über das subgenus *Aphanes* (L.). Fedde, Repert, spec. nov. regni veget. **38**:36-43.

————. 1941. Systematiche Vorarbeiten . . IX. über *Alchemilla* Arten aus Osteuropa und Asien. Fedde, Repert. spec. nov. regni veget. **50**:245-255.

SALISBURY, E. J. 1942. The Reproductive Capacity of Plants. London, 244 pp.

SARGENT, C. S. 1892. Silva of North America, vol II. 1-8.

————. 1921. Notes on North American trees. VIII. Jour. Arnold Arb. **2**:166.

SHUTTLEWORTH, R. 1896. In Nash, Notes on some Florida plants. II. Bull. Torrey Club **23**:101-102.

SMALL, J. K. 1903. Flora of the Southeastern United States. New York, 1370 pp.

————. 1913. Flora of the Southeastern United States (second edition). New York, 1394 pp.

————. 1933. Manual of the Southeastern Flora. New York, 1554 pp.

SOLEREDER, H. 1899. Systematische Anatomie der Dicotyledonen. 240-241.

SPACKMAN, W. 1949. The flora of the Brandon Lignite: geological aspects and a comparison of the flora with its modern equivalents. Unpublished Ph.D. Thesis, Biology Department, Harvard University, Cambridge, Massachusetts.

STEEVES, M. W. 1959. Pollen and spores of the Raritan and Magothy (Cretaceous) Formations of Long Island. Unpublished Ph.D. Thesis, Biology Department, Harvard Univ., Cambridge, Massachusetts.

TORREY, J. AND A. GRAY. 1838. The Flora of North America, vol. I. 256.

TRAVERSE, A. 1955. Pollen analysis of the Brandon Lignite of Vermont. U. S. Dept. of the Interior, Bureau of Mines Report of Investigation 5151, 107 pp.

TURESSON, G. 1943. Variation in the apomictic microspecies of *Alchemilla Vulgaris* L. Bot. Not. **1943**: 413-427.

UPHOF, J. C. 1942. The Cyrillaceae. In Engler and Prantl, Die Natürlichen Pflanzenfamilien (second edition). **20b**:1-12.

URBAN, I. 1926. Sertum antillanum XXVII. Fedde, Repert. spec. nov. regn. veget. **22**:365-367.

WALPERS, G. G. 1847. Repertorium Botanices Systematicae, vol. VI. 422.

WARMING, E. 1877. Smaa Biologiske og morfologiske Bidrag. Botanisk Tidsskrift **10**:52-63.

WETTSTEIN, R. 1935. Handbuch der Systematischen Botanik. (fourth edition). Deuticke. Leipzig and Wien. 1152.

WITTROCK, V. B. 1884. Om rotskott, etc. Bot. Not. 1884: 21-37.

APPENDIX

KEY TO COLLECTION NUMBERS OF LEAVES USED IN FIG. 24

Top leaves — Thomas 515

A-1. M. Lopez Figueiras 1902
2. Thomas 532
3. Acuña 13174
4. Shafer 4181
5. Alain 3547
6. Howard 5857
7. Léon, Marie-Victorin, Clément 20753
8. Léon, Marie-Victorin, Clément 20832
9. Montero 21148
10. Ankerman 11790
11. Morton, Acuña 3068
12. Léon, Clément, Alain, Chrysogone 4693
13. Howard 6013
14. Shafer 4109
15. Shafer 4054

B-1. Morton, Acuña 3205
2. Thomas 528
3. Thomas 504
4. Acuña 13173
5. Clément, Alain, Chrysogone 6798 A 894
6. Marie-Victorin, Clément, Alain 21610
7. Clément, Alain 3884
8. Thomas 521
9. Marie-Victorin, Léon 21312
10. Thomas 503
11. Clément, Alain Chrysogone 3829
12. Thomas 512
13. Thomas 520
14. Thomas 513
15. Clément 3643

KEY TO COLLECTION NUMBERS OF FRUITS USED IN FIG. 29

A-1. Alain 3749. 2. Clément 2486. 3. Léon, Bucher, Marie-Victorin 20753. 4. Marie-Victorin and Clément 21780. 5. Acuña 13171. 6. Léon, Marie-Victorin and Clément 20832. 7. Léon, Marie-Victorin and Clément 20831. 8. Léon, Marie-Victorin and Clément 20831. 9. Acuña 13174. 10. Shafer 4181.

B-1. Morton and Acuña 3068. 2. Clément, Alain and Chrysogone 6798, A894. 3. Shafer 4054. 4. Clément 2486. 5. Léon and Alain 19172. 6. Thomas 503. 7. M. Lopez Figueiras 1902. 8. M. Lopez Figueiras 1601. 9. Thomas 513.

C-1. Thomas 503. 2. Marie-Victorin and Léon 21312. 3. Thomas 521. 4. Shafer 3575. 5. Thomas 529. 6. Clément 4426.

D-1. Morton and Acuña 3250. 2. Clément 3547. 3. Acuña 13173. 4. Shafer 8083.

KEY TO COLLECTION NUMBERS OF LEAVES USED IN FIG. 32

	Collection	*Altitude* (Meters)
A-1.	Tate 231	1280
2.	Cowan, Wurdack 32131	2000
3.	Pinkus 155	2194
4.	Cardona 208	2000-2200
5.	Maguire, Cowan, Wurdack 30216	1800

6. Cardona 2042	1800
7. Steyermark 59790	2200
8. Wurdack 34214	2200-2300
B-1. Maguire, Politi 28478	1676
2. Williams 14242	127
3. Steyermark 58353	1820-2075
4. Tamayo 3117	
5. Pinkus 77	1280
6. Maguire, Cowan, Wurdack 30178	1800
7. Maguire, Politi 27523 b	1500
8. Steyermark 58140	1700-1980
C-1. Steyermark 60112	2255
2. Cardona 929	1740
3. Maguire, Wurdack, Bunting 37037	1700
4. Steyermark 58763	2255-2620
5. Tate 1045 (not originally numbered)	2164
6. Steyermark 58803	2560-2620
7. Tate 401	summit of Roraima
8. Tate 387 A	
D-1. Cardona 2696	2100
2. Phelps, Hitchcock 402	1700
3. Maguire, Cowan, Wurdack 30640	1000
4. Maguire, Cowan, Wurdack 30946	1250
5. Schultes, Cabrera 14472	450
6. Gleason 486	
7. De La Cruz 3467	
8. Spruce 2999	

KEY TO THE COLLECTION NUMBERS OF STAMENS USED IN FIG. 27

1. Howard 6013. 2. Léon, Clément, and Howard 20117. 3. Léon, Clément, Alain, Chrysogone 4693. 4. Léon, Alain 19173. 5. Léon, Howard, Clément 20117. 6. Clément, Alain, and Chrysogone 4117. 7. Carabia 4087. 8. Morton and Acuña 3250. 9. Marie-Victorin, Clément, Alain 21610. 10. Léon 11755. 11. Clément, Alain 3872. 12. Clément, Alain, and Chrysogone 3864. 13. Léon 19171. 14. Clément 3645. 15. Clément 2000. 16. Montero 21135. 17. Clément, Nestor, and Chrysogone 7407. 18. Léon, Alain 19171. 19. Thomas 512. 20. Thomas 509. 21. Thomas 503. 22. Thomas 504. 23. Clément 3643. 24. Alain 3350. 25. Clément, Alain, and Chrysogone 7407. 26. Léon, Clément, and Nestor 5441. 27. Clément, Alain, and Chrysogone 3872. 28. Clément, Alain, and Chrysogone 4002. 29. Thomas 510. 30. Thomas 521. 31. Thomas 520. 32. Thomas 532. 33. Thomas 527. 34. Thomas 528. 35. Thomas 515. 36. Carabia 4087.

KEY TO THE COLLECTION NUMBERS OF PETALS USED IN FIG. 28

A-1. Thomas 515. 2. Clément and Alain 3872. 3. Thomas 503. 4. Thomas 512. 5. Léon, Clément, Nestor, and Chrysogone 3872. 6. Clément, Alain, and Chrysogone 4002. 7. Clément, Alain, and Chrysogone 3872. 8. Clément 3645. 9. Thomas 510. 10. Marie-Victorin, and Alain 21610. 11. Thomas 509. 12. Léon 19171. 13. Thomas 504.

B-1. Thomas 511. 2. Thomas 520. 3. Thomas 515. 4. Carabia 4087. 5. Clément, Nestor, and Chrysogone 7407. 6. Morton and Acuña 3250. 7. Thomas 504. 8. Clément and Alain 3872. 9. Thomas 513. 10. Alain 3350. 11. Clément 3643. 12. Clément, Alain, and Chrysogone 3829. 13. Léon and Alain 19171.

C-1. Thomas 521. 2. Clément 2000. 3. Carabia 4087. 4. Clément, Alain, and Chrysogone 4117. 5. Montero 21135. 6. Thomas 532. 7. Léon, Howard, and Clément 20117. 8. Léon 11755. 9. Howard 6013. 10. Léon, Clément, Alain, and Chrysogone 4693. 11. Howard 5857. 12. Léon, Clément, and Howard 20117. 13. Léon and Alain 19173.

KEY TO THE COLLECTION NUMBERS OF PETALS USED IN FIG. 34

A-1. Irwin 103. 2. Steyermark 59684. 3. Maguire and Politi 27523. 4. Maguire and Fanshawe 23106. 5. Lasser 1476. 6. Cardona 1133. 7. Phelps and Hitchcock 339. 8. Maguire, Cowan, and Wurdack 30664. 9. Pinkus 91. 10. Phelps and Hitchcock 402. 11. Tate 1189. 12. Maguire, Phelps, Hitchcock, and Bunting 31717. 13. Pinkus 190.

B-1. Tate 1015. 2. Maguire and Politi 28207. 3. Ducke 160. 4. Maguire 32867. 5. Maguire, Cowan, and Wurdack 30946. 6. Wurdack 34214. 7. Maguire 32807. 8. Phelps and Hitchcock 42. 9. Maguire, Wurdack, and Bunting 36936. 10. Maguire, Cowan, and Wurdack 30216. 11. Pinkus 100. 12. Maguire, Cowan, and Wurdack 30112. 13. Cardona 2042.

C-1. De La Cruz 3467. 2. Steyermark 58253. 3. Shultes and Lopez 9718. 4. Maguire and Politi 27523. 5. De La Cruz 1822. 6. Tate 615. 7. Cardona 929. 8. Pinkus 190. 9. Steyermark 60112. 10. Tate 693. 11. Maguire and Maguire 35122. 12. Wurdack 34099. 13. Steyermark 58826.

PLANT MATERIALS USED IN MORPHOLOGICAL STUDIES

Species and Collection	Geographical Area	*Parts Studied*						
		root	stem	leaves	flowers	fruits	pollen	mature wood
Cyrilla racemiflora								
Thomas 458	Virginia	x		x	x		x	
470	N. Carolina	x	x		x			
472	N. Carolina	x		x	x		x	
483	S. Carolina			x	x			
492	Florida			x	x			
500	Cuba			x	x	x	x	
503	Cuba			x	x	x		
533	Florida			x	x			

PLANT MATERIALS USED IN MORPHOLOGICAL STUDIES

Species and Collection	*Geographical Area*	*Parts Studied*						
		root	stem	leaves	flowers	fruits	pollen	mature wood
Harvard Wood Collection								
H-19068								x
H-24138								x
H-24139								x
H-24671								x
H-24691								x
Purdiaea cubensis								
Acuña 16439	Cuba			x	x		x	
microphylla								
Alain 3387	Cuba			x	x		x	
moaensis								
Thomas 505	Cuba		x	x	x	x	x	
nipensis								
Lopez 2563	Cuba			x	x	x		
nutans								
Maguire, Cowan, Wurdack 30211	Colombia		x	x	x	x	x	
parvifolia								
Thomas 525	Cuba			x	x	x	x	
stereosepala								
Thomas 516	Cuba			x	x	x		
velutina								
Marie-Victorin, Clément 21789	Cuba			x	x	x	x	
Thomas 508				x		x		
Cliftonia monophylla								
Thomas 379	Florida			x		x		
Thomas 380	Florida		x	x		x		
Thomas 576	Mississippi		x	x		x		
Godfrey 52959	Florida				x		x	
Harvard Wood Collection								
H-24134								x
H-24135								x
H-24136								x
Cyrillopsis paraensis								
Ducke 20629	Brazil			x		x		
Ducke 33826	Brazil				x			
Harvard Wood Collection								
H-24137								x

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXVII

THE MAIDENHAIR FERNS (ADIANTUM) OF COSTA RICA

By

Edith Scamman

A REVIEW OF THE GENUS DENNSTAEDTIA IN AMERICA

By

Rolla Tryon

THE LEPTOSPORANGIUM OF THE NEW ZEALAND FERN ANARTHROPTERIS DICTYOPTERIS

By

Kenneth A. Wilson

OBSERVATIONS ON THE LEAVES OF PELLAEA ANDROMEDIFOLIA

By

Alice F. Tryon

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.
1960

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXVII

THE MAIDENHAIR FERNS (ADIANTUM) OF COSTA RICA

By

Edith Scamman

A REVIEW OF THE GENUS DENNSTAEDTIA IN AMERICA

By

Rolla Tryon

THE LEPTOSPORANGIUM OF THE NEW ZEALAND FERN ANARTHROPTERIS DICTYOPTERIS

By

Kenneth A. Wilson

OBSERVATIONS ON THE LEAVES OF PELLAEA ANDROMEDIFOLIA

By

Alice F. Tryon

Published by
THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.
1960

Issued June 30th

Manufactured

by

The Lexington Press, Inc., Lexington, Massachusetts

THE MAIDENHAIR FERNS (ADIANTUM) OF COSTA RICA

EDITH SCAMMAN

Costa Rica, although a small country, is very rich in ferns, and contains a greater number of species than any other country in Central America. The high mountains of the interior and the rushing streams and rivers flowing down the slopes to both Atlantic and Pacific Oceans afford a great variety of habitats and climates, ideally suited for an abundance of fern life.

Many species from Mexico and Guatemala in the north extend into Costa Rica, as well as more tropical species native to Panama and South America on the southern border. Beside the species known to be more or less common and widely distributed throughout Central America along the coasts at lower elevations, many rare ferns endemic to the mountain regions and great central plateau have been discovered and described by early botanists.

The purpose of my four trips to Costa Rica, usually during the months of February and March, in 1951, 1953, 1955, and 1956, was to add to the collection of ferns from that country already in the Gray Herbarium. Accordingly, I spent more of my time in the interior, visiting regions of historic interest to botanists, such as La Palma, La Hondura, Vara Blanca, Las Nubes, Valley of the Reventazón, slopes of Irazú and Barba. Staying in Cartago during my first season, I tried to go everywhere the crowded buses would take me into the little villages and then following the cart-roads up into the hills. The Pan American Highway, recently extended over the high cerros and so-called "páramos", offered an opportunity to collect in regions formerly reached only by horseback.

It was my good fortune during my first trip to meet Dr. Leslie R. Holdridge of the staff of the Interamerican Institute of Agricultural Sciences at Turrialba. The Holdridges kindly offered me their home in San José as headquarters for my later visits to Costa Rica, and the days spent in 1955 and 1956 at their finca in a low-altitude forest on the Puerto Viejo and Sarapiquí rivers proved to be most fruitful. Weekend picnics and all-day collecting trips with the Holdridges in their jeep, wherever I desired to go, enabled me to visit many regions fascinating to a fern enthusiast. My collections could not have been obtained without Dr. Holdridge's knowledge of tropical forests and his help in innumerable ways.

As comparatively little has been written recently about the ferns in any single Central American country, it has seemed worthwhile to present the results of a study of a single genus of wide distribution as a guide to future collectors and fern lovers who may visit that beautiful land.

Costa Rica is divided into seven provinces, and I have arranged the specimens cited under them — Limón on the Atlantic, Guanacaste and Puntarenas on the Pacific, and Heredia, Alajuela, San José and Cartago in the interior of the country.

The habitat and altitude given for each species refer only to the specimens seen from Costa Rica. Only in cases where no specimen has been seen from there have the habitat and altitude been noted from another country mentioned.

For inspiration, encouragement, and valuable assistance in the preparation of this paper I am greatly indebted to Dr. Rolla M. Tryon of Harvard University, and for the help afforded by his manuscript on the Ferns of Peru. He has also generously provided me with the use of many of the drawings already prepared by Mrs. Bernadette Velick for his Peruvian work. Other excellent drawings were made especially for this paper by Mr. John Gumppenberg.

ADIANTUM

The Adiantums are terrestrial ferns of shady ravines and rocky river banks in moist forests. Although the genus is found in other parts of the world, Tropical America is the home of the majority of species of Maidenhair. Of the twenty-eight species enumerated here from Costa Rica, many grow along the banks of streams and rivers at low elevations, while a few are found only in cloud forests in the mountains at high altitudes.

Rhizomes are thick and short-creeping or slender and long-creeping; stipes and rachises are firm, dark, usually polished, erect or less often pendulous; blades are 1- to 6-pinnate; pinnules vary greatly in size and shape, are usually glabrous, sessile or stalked, often articulate at the base of the stalk and sometimes deciduous. The genus is especially characterized by the separate or continuous marginal sori, with the sporangia borne on the under side of the modified and reflexed marginal indusium.

KEY TO SPECIES

a. Ultimate segments (pinnae or pinnules) borne on long slender stalks, blade once or bipinnate . . . . b.

  b. Blade once pinnate, sometimes taking root at the apex, pinnae broadly lunate to fan-shaped, green beneath, several oblong sori borne on the lobed outer margin . . . . c.

c. Sterile margins entire or with obscure, rounded "teeth", veins often ending in the indefinite sinus, segments not articulate .... 22. *A. philippense.*

c. Sterile margins sharply serrate, each vein ending in a tooth, segments articulate .... 23. *A. deflectens.*

b. Blade once to bipinnate, not rooting, ultimate segments ovate-acuminate, glaucous beneath, several oblong to linear sori on each entire margin .... 3. *A. Seemannii.*

a. Ultimate segments sessile to short-stalked, or if rather long-stalked then the blade tri- to quadripinnate . . . . d.

d. Ultimate segments definitely to rather long-stalked, the dark color of the stalk stopping abruptly at the segment base, usually articulate by a sharp clean break . . . . e.

e. Rachis and pinna-rachises glabrous, atropurpureous to ebeneous . . . . f.

f. Ultimate segments glaucous beneath, small (about 0.5-1.5 cm. long), coriaceous, cuneate; rhizome long-creeping .... 24. *A. andicola.*

f. Ultimate segments green beneath; or if in no. 27 sometimes glaucous then trapeziform and large (about 3-5 cm. long) . . . . g.

g. Sori borne on the convex outer edge of the fertile segments . . . . h.

h. Segments orbicular-flabellate, the sterile ones with margins with indefinite teeth, sori oblong-lunate to linear, rhizome scales blackish or with narrow brown margins .... 18. *A. Braunii.*

h. Segments mostly trapeziform to rhombic-oblong, sori roundish to short-oblong . . . . i.

i. Rhizome scales small, distinctly bicolorous (center blackish, margins brown) and long-ciliate; margins of sterile segments serrulate .... 25. *A. tenerum.*

i. Rhizome scales large, concolorous, bright brown and only slightly ciliate; margins of sterile segments subentire or only faintly denticulate .... 26. *A. princeps.*

g. Sori borne on the upper and outer edges of the segments; apex of fertile segments sterile and acute to acuminate .... 27. *A. trapeziforme.*

e. Rachis and pinna-rachises densely puberulent, brown, blade scandent, its rachis and pinna-rachises strongly flexuous; segments suborbicular-cuneate, puberulent beneath .... 28. *A. Feei.*

d. Ultimate segments sessile to very short-stalked, or definitely stalked and the dark color of the stalk passing into the segment-base . . . . j.

j. Blade gradually reduced to the apical ultimate segment . . . . k.

k. Sterile margins of segments sharply serrate, each vein ending in a tooth; rhizome slender, long-creeping, its scales light brown .... 17. *A. Capillus-Veneris.*

k. Sterile margins of the segments with each vein ending in a sinus between the definite or indefinite teeth . . . . l.

l. Pinnae subsessile, the lower as well as the upper with the inner upper pinnules overlying the rachis, inner upper pinnule of lower pinnae divided into two ultimate segments .... 19. *A. concinnum.*

l. Pinnae, or at least the basal or lower ones, definitely stalked, their inner upper pinnules not or hardly overlying the rachis . . . . m.

m. Rhizome stout, very short-creeping, stipes closely clustered, ultimate segments cuneate to cuneate-flabellate, sori orbicular to suborbicular .... 20. *A. Raddianum.*

m. Rhizome slender, rather long-creeping, stipes at intervals, ultimate segments mostly orbicular to suborbicular, sori oblong to lunate, occasionally with yellow wax .... 21. *A. Poiretii.*

j. Blade with a more or less conform terminal pinna, or lacking a truly apical segment . . . . n.

n. Blade pedate or digitate-pedate; the ultimate branches once pinnate, puberulent .... 16. *A. patens.*

n. Blade pinnate . . . . o.

o. Blades commonly 4- to 5-pinnate at the base, leaves very large, segments deeply incised-lobed .... 15. *A. pectinatum.*

o. Blade once pinnate or bipinnate . . . . p.

p. Blade once pinnate . . . . q.

q. One long sorus along each edge of the pinna, occasionally this interrupted . . . . r.

r. Veins somewhat anastomosing toward the edge; pinnae cordate, stalked, the fertile lanceolate-ovate .... 1. *A. Wilsonii.*

r. Veins all free; pinnae sessile or with a very short petiolule, usually opposite, the lowermost with a broad truncate to subcordate base, the fertile long-triangular .... 2. *A. macrophyllum.*

q. Several short, oblong-arcuate or long-oblong sori along each margin of the pinna . . . . s.

s. Segments green, usually shining on both sides, the sterile ones or portions deeply and unevenly biserrate, rhizome creeping, with appressed scales, the stipe bases approximate .... 4. *A. obliquum.*

s. Segments dull, usually glaucous beneath, sterile ones or portions evenly serrate, rhizomes often long-creeping, with spreading scales, the stipe bases usually well-spaced .... 5. *A. petiolatum.*

p. Blade bipinnate . . . . t.

t. Stipe and rachises clothed with numerous wide-spreading subulate-filiform scales, pinnules glaucous beneath; indusium with a broad membranous border .... 13. *A. decoratum.*

t. Stipe and rachises glabrous, puberulent to short-scaly; indusium usually with a narrow membranous border . . . . u.

u. Terminal pinna larger than the few laterals and usually broadest at the base . . . . v.

v. Segments green, sterile ones unevenly biserrate .... 4. *A. obliquum.*

v. Segments glaucous . . . . v'.

v'. Sterile segments evenly serrate .... 5. *A. petiolatum.*

v'. Sterile segments biserrate .... 6. *A. caryotideum.*

u. Terminal pinna about the same size as the laterals and usually narrowed at the base . . . . w.

w. Pinnules nearest the long acuminate terminal segment of the pinna greatly reduced, less than half as long as the longest pinnule . . . . x.

x. Sori several, roundish to oblong, on the upper and outer edges of the fertile pinnules . . . . y.

y. Pinna-rachises puberulent, rhizome moderately stout, long-creeping, pinnules long-triangular or trapeziform .... 10. *A. Kalbreyeri.*

y. Rachis and pinna-rachises scaly or pubescent-scaly . . . . z.

z. Rhizome long-creeping, the stipe-bases distant, fertile pinnules with the sterile tips mostly turned toward the apex of the pinna and acute .... 11. *A. tetraphyllum.*

z. Rhizome usually short-creeping, often knotted, the stipe bases adjacent, fertile pinnules with the sterile tips mostly straight and obtuse .... 12. *A. fructuosum.*

x. One, rarely two, long sori on the upper edge of the fertile pinnules, rarely another on the outer edge .... 14. *A. pulverulentum.*

w. Pinnules nearest the terminal segment usually not greatly reduced, about half as long as the longest pinnule . . . . aa.

aa. Rhizome rather short-creeping, sterile pinnules coarsely and often unevenly serrate .... 7. *A. villosum.*

aa. Rhizome cord-like, very long-creeping, sterile pinnules finely and evenly serrate . . . . bb.

bb. Pinnules herbaceous and glaucous, midvein usually distinct, indusia-bearing margins flat, oblong sori usually on the lower as well as the upper edge of pinnules .... 8. *A. latifolium.*

bb. Pinnules coriaceous, green, midvein not present, indusia-bearing margins revolute, sori on the upper and outer edges of pinnules. .... 9. *A. serratodentatum.*

1. **Adiantum Wilsonii** Hook. Sp. Fil. **2**: 6, pl.72A. 1851

This species is one of the few Adiantums, and the only one in Costa Rica, with veins somewhat anastomosing, only uniting toward the edges. The fronds are always simply pinnate with a large terminal pinna and from 2-6 subsessile lateral ones on each side, these ovate-acuminate, and somewhat rounded at the base. The midrib is median and distinct, and the sori linear and continuous on both margins nearly to the apex.

Mexico to Panama, to Colombia; West Indies.

In wet forests at low elevations from near sea level to 200 m.

Specimens seen: LIMON: La Colombiana Farm of United Fruit Co., *Standley 36785, 36864* (US); Ontario Farm, Reventazón, *Lankester 950* (US). HEREDIA: Plains of Río Hondo, *Cook & Doyle 575* (US). ALAJUELA: Llanuras de San Carlos, *Brade 473* (NY).

2. **Adiantum macrophyllum** Sw. Nov. Gen. Sp. Prod. 135. 1788

A beautiful fern, distinctive and widely distributed. The blade is once pinnate, with large, equal-sided, opposite pinnae, the lower-most ones with a broad truncate to subcordate base. The young fronds are reddish in color and are striking when seen in the forest and on banks of streams.

Mexico to Panama, to Bolivia and Brazil; West Indies.

Generally distributed, usually on banks of rivers in wet forests at 100 to 1400 m. on both the Atlantic and Pacific slopes. Among the many collections seen, all of the provinces of Costa Rica are represented.

Representative specimens: LIMON: Tsâki, Talamanca, *Tonduz 9458* (GH, NY, US); Forêts de Shirores, Talamanca, *Pittier & Tonduz 9201* (US); Jiménez, Llanos de Santa Clara, *J. D. Smith 5076* (GH, NY, US); La Lola, cacao finca, near Río Madre de Dios, *Scamman 7066* (GH). HEREDIA: Confluence of Río Puerto Viejo and Sarapiquí, *Pittier 7500* (US); Finca La Selva, Río Puerto Viejo, *Scamman & Holdridge 7450* (GH). ALAJUELA: San Ramón, *Tonduz 17598* (US); Alajuela, *J. D. Smith 6869* (US). SAN JOSE: Vicinity of El General, *Skutch 3898* (GH, US). CARTAGO: Peralta, *Lankester 591* (GH, US); El Muñeco, south of Navarro, *Standley 33479* (US); Dulce Nombre, *Standley 35901* (US); Río Reventazón, Turrialba, *Scamman 6103, 7632* (GH); Río de las Vueltas, Tucurrique, *Tonduz 12809* (US). GUANACASTE: near Hacienda Santamaría and source of Río Liberia, *Dodge & Thomas 6332* (GH, US); Los Ayotes near Tilarán, *Standley & Valerio 45523* (US); La Tejona, north of Tilarán, *Standley & Valerio 45851* (US). PUNTARENAS: Río Naranjo, *Maxon 657* (US).

3. **Adiantum Seemannii** Hook. Sp. Fil. **2**: 5, pl. 81 A. 1851

This attractive fern was discovered by Seemann, on one of his voyages, at San Lorenzo, Veraguas, Panama, on the Pacific side of Central America. It has been confused in herbaria with *Adiantum platyphyllum* Sw., and often so labelled, but it is very distinct. The latter is found only in South America. The black portion of the stalk of *Adiantum platyphyllum* extends well into the midrib of the segment and the sterile margins are subentire, not incised-serrate, as in *A. Seemannii.*

Mexico to Panama and Colombia.

PLATE 1. Fig. 1-7. Fig. 1. *A. Wilsonii:* a pinna, × ½. Fig. 2. *A. macrophyllum:* a pinna, × ½. Fig. 3. *A. Seemannii:* a central pinna, × ½. Fig. 4. *A. obliquum:* a pinna, × 1. Fig. 5. *A. petiolatum:* a pinna, × 1. Fig. 6. *A. caryotideum:* a pinna, × ¾. Fig. 7. *A. villosum:* A. base of a pinna, × 1; B. apex of a pinna, × ½.

In humid forests and deep ravines at low altitudes from 150 to 700 m. on both the Atlantic and Pacific slopes.

Specimens seen: 1901-1905 *Wercklé* (US). LIMON: Talamanca, *Tonduz 8580* (US); Los Diamantes, Rubber Plant Station, *Scamman 6099* (GH). HEREDIA: La Emilia, Llanuras de Santa Clara, *J. D. Smith 6866* (GH, US). CARTAGO: Río Reventazón below Turrialba, *Skutch 4673* (GH, US); Turrialba, *Maxon 149* (US), *Scamman 6098, 7073, 7633, 7939* (GH). GUANACASTE: Naranjos Agrios, *Standley & Valerio 46537* (GH, US); Arenal, May 21, 1927, *Valerio* (US); Matambú, Nicoya Peninsula, *Cook & Doyle 692* (US). PUNTARENAS: Vallée du Diquís, *Pittier 11952, 11968* (US).

4. **Adiantum obliquum** Willd. Sp. Pl. **5**: 429. 1810

This species is rather similar to the following one, *A. petiolatum*, and often confused with it, especially as both may occur in two forms — once pinnate and bipinnate. Throughout the range the once pinnate form is more common; it has the blades broadly linear to elongate-triangular with few pairs of alternate pinnae, these ovate-lanceolate and usually more acute at the tip than those of *A. petiolatum*. In both species the terminal pinna of the bipinnate blades is larger than the few laterals and broadest at the base. The segments of *A. obliquum* are green on both sides, not glaucous.

Mexico to Panama, to Bolivia and Brazil; West Indies.

In forest ravines and on the banks of streams from sea level to 600 m. This species seems to be rare in Costa Rica and the few collections which have been seen are mostly bipinnate.

Specimens seen: HEREDIA: Finca La Selva, *Scamman & Holdridge 7937* (GH). CARTAGO: Turrialba, *G. P. DeWolf 218* (GH). GUANACASTE: Tilarán, *Standley & Valerio 45012* (GH); Carrillo, *Pittier 1167* (US). PUNTARENAS: Jesús María, *Lankester 615* (US).

5. **Adiantum petiolatum** Desv. Berl. Mag. **5**: 326. 1811

Adiantum Kaulfussii Kze. Linnaea **21**: 221. 1848.

The pinnae and pinnules of this species are dull and glaucous beneath and are usually oblong in shape rather than ovate-acute; the sterile margins are evenly serrate. It is much more common than *A. obliquum*.

Mexico to Panama, to Bolivia and Brazil; West Indies.

In wet forests and on rocky river banks, usually from 50 to 300 m.

Representative specimens: LIMON: Tsâki, Talamanca, *Tonduz 9485* (US); Hamburg Finca, Río Reventazón below Cairo, *Standley & Valerio 48687* (US); Siquirres, *Wercklé 595* (US); La Lola near Río Madre de Dios, *Scamman 7068, 7070* (GH); Los Diamantes, Rubber Plant Station, *Scamman 7071* (GH). HEREDIA: Río Toro Amarillo, Llanuras de Santa Clara, *J. D. Smith 6867* (GH, US); Río Hondo, Plains of Santa Clara, *Cook & Doyle 504* (US); Confluence of Río Puerto Viejo and Sarapiquí, *Pittier 7499* (US); Finca La Selva, Río Puerto Viejo, *Scamman & Holdridge 7451, 7452, 7938* (GH). ALAJUELA: San Mateo, Feb. 1900, *Biolley* (US). SAN JOSE: Cerro Turrubares, Orotina, *Jimenez 610* (US). CARTAGO: Vicinity of Turrialba, *Maxon 178* (US). GUANACASTE: Nicoya, *Cook & Doyle 677* (US); Carrillo, *Wercklé 17434* (GH, US); Río Liberia, *Dodge & Thomas 7868* (GH). PUNTARENAS:

Buenos Aires, *Pittier 10557* (US); Between El General and Buenos Aires, *Holdridge 7069* (GH); Vallée du Diquís, *Pittier 11966* (US); Plaines de Surubres de Puntarenas, Côte du Pacific, *Pittier 2685* (US).

6. **Adiantum caryotideum** Christ, Bull. Soc. Bot. Genève II, **1**: 230. 1909
Type from Costa Rica, 1904, ***Wercklé.***

Rhizome long-creeping, nodose; stipe and rachises glabrous, black ebeneous; blade bipinnate with the terminal pinna larger than the few laterals and broadest at the base. The pinnules are on short but definite stalks and glaucous beneath, with long lunate sori, adjacent but separate, on the upper and outer edges. The sterile margins are biserrate.

The length of the petiolules helps to distinguish this species from bipinnate fronds of *A. obliquum* and *A. petiolatum.*

Mexico to Panama; along rivers from sea level to 300 m.

No specimen seen from Costa Rica.

7. **Adiantum villosum** L. Syst. Nat. ed. 10, **2**: 1328. 1759

In this species, as in the two following, the pinnules nearest the terminal segment of the pinna are not greatly reduced. The pinnules are dark green, lustrous and oblong to narrowly rhombic with the oblong or linear sori usually extending around the acuminate or acute tip. The margins of the sterile segments are coarsely serrate. The rhizome is strongly nodose and rather short-creeping.

Mexico to **Panama, to Peru and Brazil; West Indies.**

Along banks of forest ravines from sea level to 650 m.

Specimens seen: LIMON: Along Banana River above R. R. Bridge, *W. W. & H. E. Rowlee 465* (US). ALAJUELA: Cataratas de San Ramón, *Brenes 13562* (NY). GUANACASTE: Vicinity of Tilarán, *Standley & Valerio 45012* (US); Nicoya, *Cook & Doyle 658* (US), Matambú, Nicoya Peninsula, *Cook & Doyle 713* (US). PUNTARENAS: Caldera, Jan. 1926, *Lankester* (US).

8. **Adiantum latifolium** Lam. Encycl. **1**: 43. 1783

The rhizome is slender and very long-creeping, with the stipes well spaced. The pinnules are herbaceous, glaucous beneath, the fertile ones oblong-lanceolate, acute or acuminate with the sori usually on the lower as well as the upper edge; the sterile segments are often rounded at the apex, evenly serrate or denticulate. In this species the midvein of the pinnules is usually quite distinct.

Tropical America.

In wet thickets and on the banks of streams from near sea level to 1100 m.

Representative specimens: Cocos Island (Pacific): *R. E. Snodgrass & E. Heller 967* (GH, US); June 11, 1929, *A. K. Fisher* (GH, US); *Valerio 2224* (US); *A. Stewart 226* (US). LIMON: La Colombiana Farm of United Fruit Co., *Standley 36704* (US); Port Limón Oct. 20, 1911, *A. S. Hitchcock* (US); Zent, *Tonduz 14561* (US); Siquirres, *Scamman 6102* (GH); La Lola, near Río Madre de Dios, *Scamman 7665* (GH). HEREDIA: Confluent of Puerto Viejo and Sarapiquí, *Pittier 7285* (US), Finca La Selva, Río Puerto Viejo, *Scamman & Holdridge 7449* (GH). ALAJUELA: Canton de San Carlos, *Austin Smith 1482* (NY); La Palma de San Ramón, *Brenes 5790* (NY); Boca Machado, Vallée de San Juan

Nicaragua, *Pittier 9632* (US). CARTAGO: Turrialba near Río Reventazón, *Scamman 6100, 7064* (GH).

9. **Adiantum serratodentatum** Willd. Sp. Pl. 5: 445. 1810

This species can be recognized by the many small oblong to rhombic pinnules, usually rounded at the apex, rigid to coriaceous, with the few sori borne on revolute margins on the upper and outer edges, but not on the lower. The terminal pinna is little reduced at the base. The sterile margins are usually finely serrate.

Guatemala to Panama, to Brazil; West Indies.

In open grass lands and thickets in low to middle altitudes. Only one specimen has been seen from Costa Rica, but it is not uncommon in Panama. PUNTARENAS: Buenos Aires, *Pittier 4850* (US).

10. **Adiantum Kalbreyeri** C. Chr. Ind. Fil. 28. 1905

Adiantum pilosum Bak., Ann. Bot. 5: 207. 1891, not Fée, 1850-52.

This differs from all the other bipinnate species of Costa Rica in its puberulent pinna-rachises.

Costa Rica to Peru.

This species seems to be rarely collected, usually at middle elevations, in the interior, in wet forests about 900 to 1500 m.

Specimens seen: CARTAGO: Pejivalle, *Standley & Valerio 46879* (GH, US); El Muñeco, Río Navarro, *Standley & Torres 51070* (US); Navarrito, *Lankester 735* (US).

11. **Adiantum tetraphyllum** Willd. Sp. Pl. 5: 441. 1810

It seems to be difficult to separate this species from *A. fructuosum* without the rhizomes which many herbarium specimens lack. However typical *A. tetraphyllum* has the sterile apex of the pinnules acute and almost falcate.

Generally distributed throughout tropical America.

In wooded ravines and dense forests from 50 to 1500 m.

Representative specimens: LIMON: Tsâki, Talamanca, *Tonduz 9442* (US); La Lola, cacao finca, *Scamman 7075* (GH); Los Diamantes, Rubber Plant Station, *Scamman 6105* (GH); near Río Madre de Dios, *Pittier 10256* (US). HEREDIA: Finca La Selva, Río Puerto Viejo, *Scamman & Holdridge 7453, 7940* (GH); Vara Blanca, *Skutch 3633* (US). ALAJUELA: San Ramón, *Tonduz 17599* (US), Río Grande, San Ramón, *Brenes 18875* (GH); Zapote on the road to Villa Quesada, *Scamman 7637* (GH). CARTAGO: Tucurrique, *Tonduz 12779* (US); Tuis, *Tonduz 11313* (US); Juan Viñas, Reventazón Valley, *Cook & Doyle 211* (US); Turrialba, *G. P. DeWolf 22* (GH), *Scamman 7074, 7636* (GH). GUANACASTE: Boca Culebra, on the Pacific, *Pittier 12019* (US); Los Ayotes, near Tilarán, *Standley & Valerio 45368* (US). PUNTARENAS: Vallée du Diquís, *Pittier 12052* (US).

12. **Adiantum fructuosum** Spreng. Syst. Veget. 4: 113. 1827

Apart from the difference in the rhizomes mentioned in the key the chief character distinguishing this species from the preceding is in the sterile tips of the pinnules, which are usually obtuse and straight instead of acute and turned toward the apex of the pinna.

Mexico to Panama, to Peru and Brazil; West Indies.

In moist forests from 100 to 1100 m.

PLATE 2. Fig. 8-13. Fig. 8. *A. latifolium:* base of a pinna, × 1. Fig. 9. *A. serratodentatum:* base of a pinna, × 1. Fig. 10. *A. Kalbreyeri:* base of a pinna, × 1. Fig. 11. *A. tetraphyllum:* apical portion of a pinna, × 1. Fig. 12. *A. fructuosum:* a pinna, × ½. Fig. 13. *A. decoratum:* A, a pinna, × 1; B, scales on rachis, × 4.

Representative specimens: LIMON: Port Limón, *Cook & Doyle 415, 416* (US). HEREDIA: La Concepción, Llanuras de Santa Clara, *J. D. Smith 6864* (US). ALAJUELA: Río Surubres near San Mateo, Feb. 1906, *Biolley* (GH, US); Zapote on the road to Villa Quesada, *Scamman 7635* (GH). SAN JOSE: Vicinity of El General, *Skutch 2306* (GH, US). GUANACASTE: El Arenal, *Standley & Valerio 45239* (US); La Colonia Carmona, *Jimenez 390* (US). PUNTARENAS: Between Golfo Dulce and Río Terraba, *Skutch 5256* (US).

13. **Adiantum decoratum** Maxon & Weatherby, Am. Jour. Bot. **19:** 165. 1932

"Stipe conspicuously shaggy with very numerous, wide-spreading, subulate-filiform scales, these extending freely to the rachises throughout." So wrote the authors of this species, and this characteristic is sufficient to distinguish it from all other related ones. The rhizome is short-creeping and coarsely nodose. The segments are oblique, rhombic-oblong to lanceolate, membrano-herbaceous, dark green above, glaucous beneath with oblong adjacent sori on the upper and outer margins. The sterile pinnules are unequally serrulate at the upper margin and apex.

Mexico to Panama.

In moist ravines in forests from 50 to 800 m. on the Pacific slope **(except the specimen from Turrialba).**

Specimens seen: ALAJUELA: Capulín, Río Grande de Tárcoles, *Standley 40174* (US); Gorge of Machuca River, near San Mateo, *Biolley 2017* (US), Río Machuca, *Biolley 17392* (GH, US). SAN JOSE: Hills above Río Paquita, *Dodge & Goerger 9876* (US); Cerro Turrubares, Orotina, *Jimenez 602* (US); Cangrejal de Aserrí (Pacific), April, 1906, *Biolley* (US). CARTAGO: Turrialba, *Scamman 6101* (GH). GUANACASTE: Matambú, Nicoya Peninsula, *Cook & Doyle 693* (US); Nicoya, *Cook & Doyle 655* (US), *Tonduz 13766* (GH, US); Garza, *Holdridge 7631* (GH).

14. **Adiantum pulverulentum** L. Sp. Pl. 2: 1096. 1753

It is a relief in this group of Adiantums to find a species as easily recognizable as this one. It is characterized by the single long sorus borne on the upper margin of the pinnules. Rarely a shorter sorus occurs on the outer edge. The rachis and pinna-rachises are pubescent-scaly and the pinnules slightly stellate-scaly beneath.

Mexico to Panama, to Brazil; West Indies.

In shaded ravines in forests from 600 to 1300 m.

Specimens seen: 1901-1905, *Wercklé* (US). SAN JOSE: San Marcos, *Pittier 7722* (US); Cangrejal de Aserrí (Pacific slope) April, 1906, *Biolley* (US). CARTAGO: Juan Viñas, Reventazón Valley, *Cook & Doyle 203* (US); Livingston on Reventazón, *W. W. Rowlee & H. E. Stork 610* (US); Turrialba, *Scamman 6097, 7077, 7634* (GH).

15. **Adiantum pectinatum** Kze. ex Ettingsh. Farnkr. 85, t.45, fig. 14-16 **1865**

This is the largest of the Adiantums, the fronds sometimes becoming 2 m. tall. The blade is broadly deltoid-ovate to deltoid-circular, 4- to 5-pinnate, rarely 6-pinnate. The segments are numerous and small, deeply incised-lobed with the roundish sori borne at the apex of the

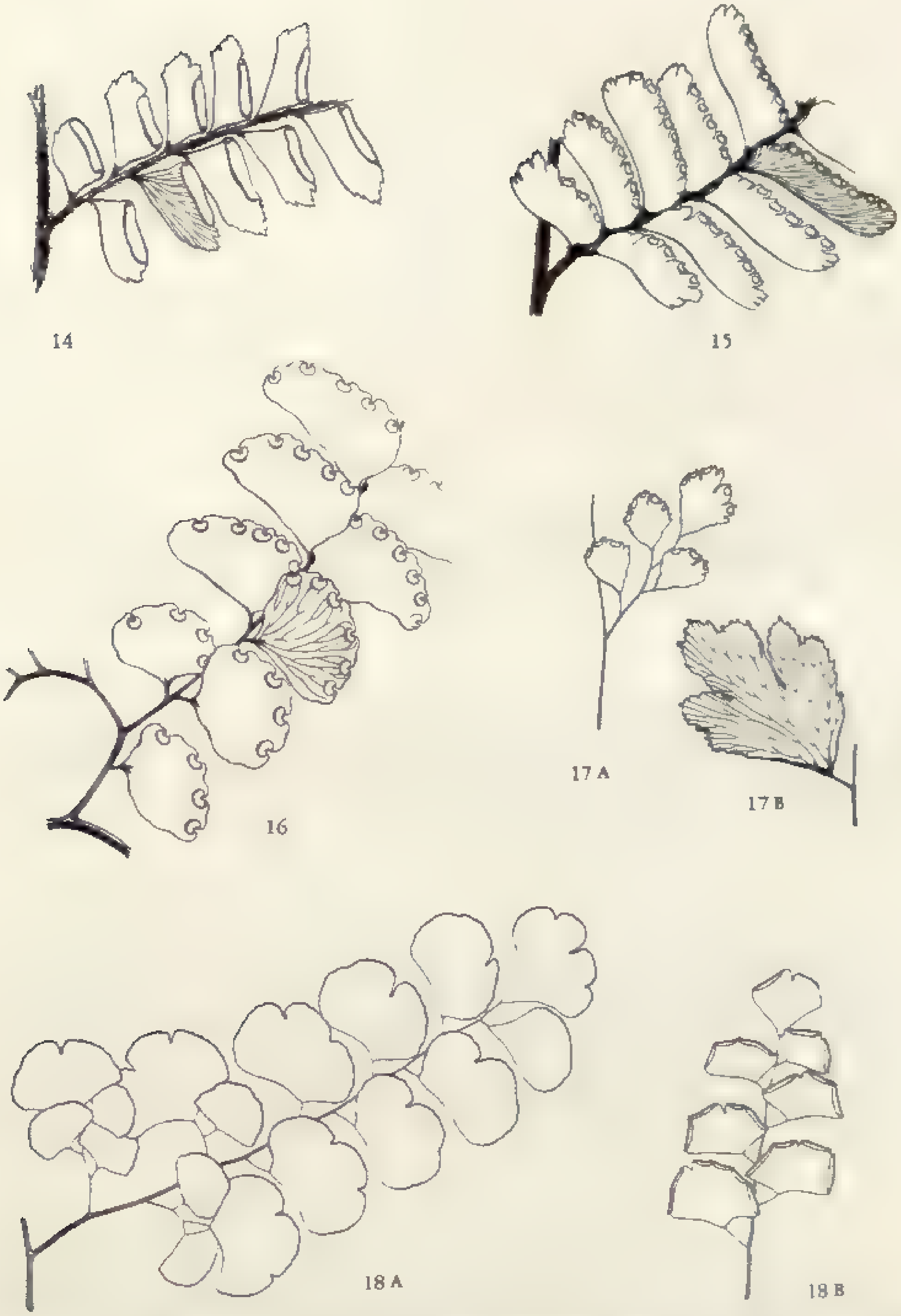


PLATE 3. Fig. 14-18. Fig. 14. *A. pulverulentum:* base of a pinna, × 1. Fig. 15. *A. pectinatum:* base of a pinna, × 1. Fig. 16. *A. patens:* base of a pinna, × 1. Fig. 17. *A. Capillus-Veneris:* A, a small pinna, × 1; B, a sterile segment, × 2. Fig. 18. *A. Braunii:* A, a sterile pinna, × $\frac{3}{4}$. B, apex of a fertile pinna, × $\frac{3}{4}$.

lobes on the upper and sometimes outer edge. They have conspicuous veins and are glabrous or have a few stellate scales beneath.

Costa Rica, where it is rare, to Argentina and Brazil.

In wet forests from low to middle elevations, 80 to 500 m. in Costa Rica.

Specimens seen: ALAJUELA: Capulín on the Río Grande de Tárcoles, *Standley 40171* (GH, US). SAN JOSE: Llano Grande de Puriscal, *Jimenez 835* (US); San Luis de Turrubares, *Valerio 1729* (US); Río Turrubares, *Brade 437* (NY).

16. **Adiantum patens** Willd. Sp. Pl. 5: 439. 1810

The frond is pedately tripartite and resembles, in the manner of division of the blade, *A. pedatum* — the beautiful and beloved Maidenhair of North America. It is smaller and has fewer branches; the stipe and rachises are reddish brown and glossy, slightly puberulent. The lunate or reniform-orbicular sori are borne in rounded sinuses on the upper and outer edges of the segments.

Mexico to Costa Rica; Venezuela to Colombia, to Bolivia.

Rocky slopes in mountains from 1000 to 1900 m. in the region of Costa Rica known as the Meseta Central.

Specimens seen: Nov. 1886, *J. J. Cooper* (GH, US); 1906, *Wercklé* (US). ALAJUELA: Alajuela, 1887, *A. Alfaro* (US). SAN JOSE: San José, *Valerio 205* (US), *Brade 154* (NY); San José to Escasú, *Pittier 48* (US); La Urica, *Pittier 913* (US); Río Torres, *Tonduz 8066* (US); La Verbena, Alajuelita, *Tonduz 8798* (US); Tablazo, *Biolley 107* (US); Santa María de Dota, *Standley 42375a* (US); Pozo Azul de Pirrís, *Lankester 1170* (US). CARTAGO: Dulce Nombre, *Quiros Calvo 1158* (NY).

17. **Adiantum Capillus-Veneris** L. Sp. Pl. 2: 1096. 1753

Blade bi- to tripinnate with the pinnae stalked, the segments not articulate. The sterile margins are sharply serrate with a cartilaginous border, each vein ending in a tooth; a striking characteristic which distinguishes this well-known and widely distributed species from many of the Adiantums.

Temperate and tropical America, also in parts of Europe, Asia and Africa.

Mexico and Guatemala from sea level to 1500 m. No specimen seen from Costa Rica, but as it may be expected to occur there, it is included in the key.

18. **Adiantum Braunii** Mett. ex Kuhn, Linnaea 36: 75. 1869

Blade deltoid in shape, tri- to quadripinnate; stipe glabrous, reddish ebeneous, the color of the stalk usually stopping at the base of the segments, but not articulate. Ultimate segments orbicular-flabellate with prominent nerves, the upper and outer borders deeply and bluntly lobed, the sterile margins with indefinite teeth. The fertile pinnules are usually smaller than the sterile, and the sori oblong-lunate to linear, subcontiguous; the indusium is brown and hard when dry.

Mexico to Costa Rica; Venezuela to Colombia and Ecuador.

On moist shady banks in the mountains, 1100 m., rare in Costa Rica.

Specimens seen: SAN JOSE: San José, *Brade 16673* (US); La Verbena près Alajuelita, *Tonduz 8802* (US).

19. **Adiantum concinnum** Willd. Sp. Pl. 5: 451. 1810

The blade is lance-oblong in shape, usually drooping, bi- to tripinnate, with subsessile pinnae, both the lower and upper with the inner upper pinnules overlying the rachis; sori roundish to reniform.

A distinguishing character of this species is the division of the inner upper pinnule of the lower pinnae into two ultimate segments.

Mexico to Panama, to Venezuela and Peru; West Indies.

On moist cliffs and shaded roadside banks, common in some localities, from 400 to 1400 m.

Representative specimens: Nov. 1886, *J. J. Cooper* (GH, US). HEREDIA: La Paz, a waterfall, *Scamman & Holdridge 7936* (GH). ALAJUELA: Grecia, *Hunnewell 16482* (GH); La Granja, *Scamman 6095* (GH). SAN JOSE: San José, Río Tiribi, *Biolley 103* (GH, US); San José, Sept. 1887, *E. S. Hyde* (GH, NY, US); El General, *Skutch 2913, 3949* (GH, US); Aserrí, *Scamman 6094* (GH); Finca Ortuna, Desamparados, *Scamman & Holdridge 7935* (GH); Santiago, *A. Alfaro 8068* (GH, NY, US). CARTAGO: Orosi, *Scamman 7063* (GH). GUANACASTE: Las Delicias below Hacienda Santamaría, *Dodge & Thomas 6288, 6291* (GH).

20. **Adiantum Raddianum** Presl, Tent. Pterid. 158. 1836

Adiantum cuneatum Langsd. & Fisch. Ic. Fil. 25. t. 26. 1810, not Forst. 1786.

Adiantum Werckleanum Christ, Bull. Herb. Boiss. II, 4: 1093. 1904. Hab. Costa Rica, *Wercklé*.

This is a complex species with slight variations, some fronds with glabrous segments, others slightly glandular beneath. There is also considerable variation in the shape and size of the segments. The chief differences between this species and the next one — *A. Poiretii* — are shown in the key. The blade is usually tripinnate, rarely bipinnate or quadripinnate, the stipes dark reddish brown to blackish, with the pinnae definitely stalked and the ultimate segments cuneate to broadly cuneate-flabellate.

A specimen of Wercklé's collection determined by Christ seen in New York and other specimens so labelled in the U. S. National Herbarium do not appear to differ fundamentally from forms of *A. Raddianum*, so they have been included under this species.

Tropical America.

In high country on banks of streams, in oak forests from 1700 to 2200 m.

Specimens seen: 1906, *Wercklé* (US). ALAJUELA: Zarcero, July 13, 1937, *Austin Smith* (GH). SAN JOSE: Potreros of Rancho Redondo, *Dodge & Thomas 7887* (GH); Rancho Redondo, on slope of Volcán Irazú, *Scamman 7630* (GH); Cerro de Piedra Blanca, above Escasú, *Standley 32518* (GH, US); Between Aserrí and Tarbaca, *Standley 41396* (US); Vicinity of Santa María de Dota, *Standley 43119* (US); Near Quebradillas north of Santa María de Dota, *Standley 42904* (GH, US); Tablazo, *Brade 147* (NY, US).

21. **Adiantum Poiretii** Wikstr. Vet. Akad. Handl. 1825: 443. 1826

A. thalictroides Willd. ex Schlechtd. Adumbr. Pl. pt. 5: 53. 1832.

The blade is deltoid in outline, usually tripinnate; the stipes vary from light to dark reddish brown to atropurpureous; the ultimate seg-

PLATE 4. Fig. 19-23. Fig. 19. *A. concinnum:* a basal pinna, × ¾. Fig. 20. *A. Raddianum:* A, a pinna, × ¾; B, a sterile segment, × 1½. Fig. 21. *A. Poiretii:* A, a lower pinna, × ¾; B, a sterile segment, × 1½. Fig. 22. *A. philippense:* a leaf, × ⅓. Fig. 23. *A. deflectens:* A, a leaf, × ¾; B, a sterile pinna, × 1½.

ments are suborbicular to subcuneate, lobed, and the sori oblong to lunate.

Mexico to Costa Rica, to Chile and Argentina; Hispaniola.

This species grows on moist shady banks, rocky hillsides, and slopes of volcanos at high elevations, from 1500 to 3000 m. in Mexico and Guatemala. The single collection from Costa Rica does not indicate the habitat or altitude.

Specimen seen: SAN JOSE: 5 miles northeast of Coronado, *M. A. Chrysler & W. E. Roever 5339* (US).

22. **Adiantum philippense** L. Sp. Pl. 2: 1094. 1753

A charming fern easily recognized by its once pinnate blade occasionally rooting at the tip with the oblong-lunate, dimidiate pinnae on fairly long petiolules and with the uppermost pinna cuneate-flabellate. The sori are oblong-linear, close together and sometimes contiguous. The segments are not articulate.

Mexico to Panama, also Cuba, and northern South America. Widely distributed in Africa, Asia, and Australia.

Among rocks on banks of creeks and streams and near waterfalls, from 100 to 650 m.

In Costa Rica it has been rarely collected and all the specimens seen are from the Pacific slope. ALAJUELA: Aguacate, *C. Hoffmann 754* (NY, US); Canyon, Río Grande de Tárcoles, Oratina, *W. W. & H. E. Rowlee 200* (US); Machuca River near San Mateo, *Lankester 611* (US). GUANACASTE: Vicinity of Tilarán, *Standley & Valerio 46570* (US). PUNTARENAS: Río Surubres, *Brade 318* (NY), Plaines de Surubres, Puntarenas, *Pittier 2666* (US); Río Jesús María, route de Puntarenas, *Pittier 490* (US).

23. **Adiantum deflectens** Mart. Ic. Crypt. Brasil. 94. 1834

This delicate little fern, somewhat related to *A. philippense*, is very distinct from that species since the sterile margins are sharply serrate, each vein ending in a tooth. The margins of the fertile pinnae have sharply incised lobes on one or both sides of the sori. The segments are articulate with a clean break at the junction with the stalk.

Guatemala, Honduras, Panama; Guianas to Colombia, to Peru and Brazil.

No specimen has been seen from Costa Rica, but it is included here as it doubtless may be found there.

24. **Adiantum andicola** Liebm. Dansk. Vid. Selsk. Skrift. V, 1: 266 (seors 114). 1849

Adiantum glaucophyllum Hook. Sp. Fil. 2: 40. 1851.

Adiantum Cooperi Baker, Journ. Bot. 25: 25. 1887.

Blade deltoid, 3- to 5-pinnate, ultimate segments flabellate-cuneate, rather small, coriaceous, green above, glaucous beneath, veins prominent; sori at apex of lobes, roundish-reniform.

Adiantum Cooperi was described by Baker from a collection from Costa Rica by J. J. Cooper. He refers to it as "allied to *A. glaucophyllum* Hook., from which it differs by its much larger, fewer, less crowded segments, not at all glaucescent beneath." The size of the segments varies widely in different collections of *A. andicola*. A scrap of the type collection of Cooper's seen in the New York Botanical

Garden Herbarium does not seem distinct enough to warrant calling it a separate species.

Mexico to Panama, to Colombia.

Along shady banks and in oak forests on slopes of volcanos, at high altitudes from 1700 to 3000 m.

Specimens seen: 1901-1905, *Wercklé* (US). ALAJUELA: La Ventolera, southern slope of Volcán Poás, *Standley 34699* (GH, US). SAN JOSE: Cerro de Piedra Blanca above Escasú, *Standley 32490* (US); Vicinity of Santa María de Dota, *Standley 41664* (GH, US); Finca Guayabillos, July, 1936, *Dodge & Goerger* (GH); Laguna de la Escuadra, northeast of El Copey, *Standley 42013* (US); Las Nubes, *Scamman & Holdridge 7941* (GH). CARTAGO: Slopes of Volcán Irazú, near Hotel Robert, *Williams & Molina 13862* (GH), *Scamman 6104* (GH); near Sanatorio Durán, *Scamman 7062* (GH); Cervantes, *Lankester 665* (US); Reventado, *Lankester 693* (US); Río Birrís, southern slope of Volcán Irazú, *Standley 35418* (US).

25. **Adiantum tenerum** Sw. Nov. Gen. Sp. Prod. 135. 1788

Adiantum trapezoides Fée, Gen. Fil. 117. 1852. (See Morton, Am. Fern Jour. **45**: 113-115, 1955, for discussion of this and the following species).

Rhizome short-creeping with many bicolorous, ciliated scales. Stipes and rachises dark purplish brown, polished, blades deltoid-ovate, 3- to 5-pinnate, with segments quite variable, rhombic-oblong to flabellate-cuneate, sori retuse-oblong and numerous. The ultimate segments are jointed at the base of the stalks and definitely articulate by a sharp clean break, easily falling when dry.

Florida, Mexico to Panama to Venezuela; West Indies.

Cool ledges, shaded banks, old walls, rarely collected in Costa Rica. In Mexico from 300 to 2000 m.

Specimens seen: Costa Rica, Nov. 1886, *J. J. Cooper* (GH, US); 1901-1905, *Wercklé* (US).

26. **Adiantum princeps** Moore, Gard. Chron. n. ser. 4: 197, fig. 43, 44. 1875

Adiantum trapezoides of recent authors, not Fée.

A large fern 1-1.3 m. high, the stipes almost black, very shiny, segments larger than those of *Adiantum tenerum*, generally rhomboid in shape, but variable, articulated at the junction with the stalk. The margins of the sterile segments that are subentire or only faintly denticulate, and the concolorous brown scales distinguish this species from *A. tenerum.*

Mexico (common in western Mexico) to Fanama; Colombia.

Along moist shady river banks from 100 to 1200 m.

Specimens seen: HEREDIA: Banks of Río Virilla, *P. H. Allen 572* (GH). ALAJUELA: Gorges of Machuca, near San Mateo, *Biolley 2021* (US), Río Machuca, *Biolley 17387* (US), *Lankester 610* (US). SAN JOSE: El Rodeo, *Hunnewell 16484* (GH). GUANACASTE: Vicinity of Tilarán, *Standley & Valerio 45695* (US); La Colonia Carmona, *Jimenez 389* (US). PUNTARENAS: Puntarenas, Jan. 1926, *Lankester* (US).

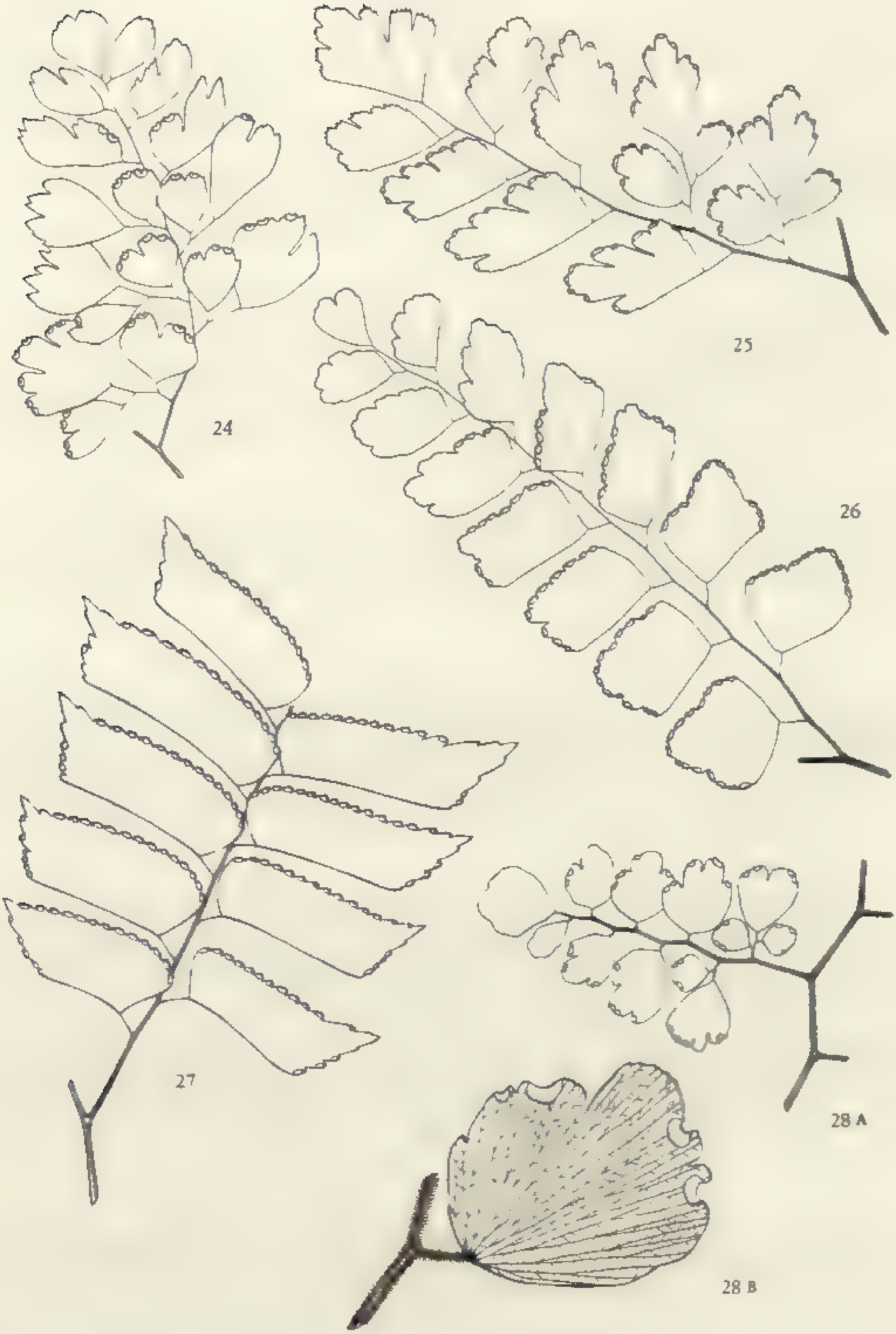


PLATE 5. Fig. 24-28. Fig. 24. *A. andicola:* an upper pinna, × 1. Fig. 25. *A. tenerum:* a pinna, × ¾. Fig. 26. *A. princeps:* a pinna, × ¾. Fig. 27. *A. trapeziforme:* base of a pinna, × ¾. Fig. 28. *A. Feei:* A, a pinna, × 1; B, a fertile segment, × 3.

27. **Adiantum trapeziforme** L. Sp. Pl. **2:** 1097. 1753

Blade quadripinnate with large glabrous pinnules, bright green above, sometimes glaucous beneath; stipe naked, polished, blackish; the ultimate segments long-stalked, mostly trapeziform, acute to acuminate at tip; sori numerous, contiguous, on the upper and outer edge.

A striking and beautiful *Adiantum* with the shining almost black stalks extending to the base of the green segments, but not articulate.

Mexico to Panama to Brazil; West Indies.

In forested ravines, on the banks of creeks and rivers from 80-1000 m. on the Pacific slope.

Specimens seen: ALAJUELA: Gorges of Río Machuca, near San Mateo, *Biolley 2018* (US), Río Machuca, *Biolley 17393* (US), Surubras near San Mateo, *Biolley 17* (GH, US); Vicinity of Capulín on Río Grande de Tárcoles, *Standley 40180* (GH, US); Río Grande, *A. Alfaro 46* (US). SAN JOSE: El Rodeo, *Pittier 1623* (US), *Hunnewell 16485* (GH). GUANACASTE: Garza, *Holdridge 7638* (GH); Nicoya, *Cook & Doyle 676, 680* (US).

28. **Adiantum Feei** Moore ex Fée, Mém. Foug. **7:** 29. pl. 24, fig. 1. 1857

Adiantum flexuosum Hook. Second Cent. Ferns pl. 61. 1861. (See Morton, Am. Fern Jour. **45:** 117, 1955).

This fern is distinct from all other Adiantums by its scandent blade and zigzag rachis and pinna-rachises spreading at a right angle. The densely tomentose brown stalks stop abruptly at the base of the small rigid, puberulent, suborbicular-cuneate segments.

Mexico to Panama, on mountain slopes, 1350 to 2400 m. Very rare.

The only specimen seen or reported from Costa Rica is labelled: "Costa Rica and Veragua", (Panama) collected by Warscewicz, no. 32 (NY, US).

Other species of *Adiantum* described from Costa Rica are the following. As no specimens have been seen and the types have not been available, these names cannot be placed; they are undoubtedly synonyms of some of the species treated.

A. heteroclitum Christ, Bull. Herb. Boiss. II, **4:** 1094. 1904. Costa Rica, 1903, *Wercklé.*

A. orosiense Christ, Repert. Sp. Nov. **8:** 17. 1910. Costa Rica, Orosi, finca de D. Valverde, 1900 m., *Brade 16816;* Carrillo, 400 m. 18 jun. 1909, *Brade 314.*

A. palmense Christ, Bull. Soc. Bot. Genève II, **1:** 230. 1909. Costa Rica.

A. subtrapezoideum Christ, Bull. Herb. Boiss. II, **4:** 1094. 1904. Costa Rica, Nicoya, *Pittier 13768.* — GRAY HERBARIUM, HARVARD UNIVERSITY.

NOTE. — On a recent visit in Paris where he saw the type specimens in Christ's herbarium, Dr. Tryon has determined *A. orosiense* to be a synonym of **A. Kalbreyeri,** *A. palmense* of **A. andicola,** and *A. subtrapezoideum* of **A. princeps.**

A REVIEW OF THE GENUS DENNSTAEDTIA IN AMERICA

Rolla Tryon

Some twenty species of *Dennstaedtia* are currently recognized in the Americas; however, there has been no recent survey of them and several have not been adequately defined. The treatment of the genus by Maxon[1] is an excellent one but includes only four (two of his species I place together) of our ten tropical species. During preparation of an account of *Dennstaedtia* in Peru, it become apparent that to treat the genus adequately it would be necessary to consider all of the American species. I have found reasons to maintain only eleven of the species previously recognized; however, these conclusions are sometimes tentative, for a number of problems remain which must be studied in the field and with more adequate collections.

Most of the species of *Dennstaedtia* are of common occurrence and of these I have cited only a selection from the many specimens examined. I have not cited any specimens of the well known and distinctive *D. punctilobula*. A few species are rare and in their treatment I have cited all of the material I have seen. The specimens in the Gray Herbarium and the United States National Herbarium have formed the principal basis for this study. I am indebted to Conrad V. Morton for the loan of material and also to Bassett Maguire of the New York Botanical Garden for making certain specimens available for my study. Mr. Richard van Frank has taken the photographs.

I have considered all of the names that seemed pertinent to the nomenclature of the species and some others that are rather widely used in the literature or in the herbarium. I have not listed combinations made under segregates of *Dennstaedtia*, none of which is currently considered seriously: *Patania* Presl, *Sitolobium* Desv., *Adectum* Link and *Litolobium* Newm.

THE GENUS DENNSTAEDTIA

The definition of *Dennstaedtia* has, through the years, been increasingly clarified. Species were often originally described in such genera as *Polypodium*, *Dicksonia*, *Deparia* and *Microlepia*. Most of these have been transferred to

---

[1] Maxon, W. R. Pteridophyta in Sci. Surv. Porto Rico and the Virgin Islands, 6^3: 491-494. 1926.

Dennstaedtia. The genus is particularly close to *Microlepia* and the relation of these two genera will be discussed. Other related genera, with hairs on the rhizome, are *Oenotrichia* and *Leptolepia* of the Old World; they seem distinct from *Dennstaedtia* but I have not especially considered them.

In relation to *Microlepia*, I have surveyed the species of it and of *Dennstaedtia* readily available to me, which included 12 American species, 54 Old World species and one pan-tropic one. On the basis of this study it is evident that the two genera are indeed closely related and evidently intergrade. However, of the 67 species studied, nearly all clearly belong in either one genus or the other, and the species that would tend to unite the genera are few. These major groups of species are each sufficiently homogeneous and distinct so that it does not seem a justifiable course, or a practical one, to unite them. I have assessed the genera and maintained them on the basis of their soral characters and a thorough revision of all species of *Microlepia* and *Dennstaedtia* may support this course. Such a study may indicate, however, that other and better characters exist and should be used either to unite the two genera or to maintain them.

In *Dennstaedtia* the sorus is marginal, the indusium being formed of an inner (true) indusium and an outer indusium which is the opposed leaf tissue, modified in form and texture; these are fully joined (connate) beyond the margin of the segment to form a reflexed saucer-, purse- or cup-shaped, or globular or cylindrical whole indusium; or they are joined as far as the margin and extend separately beyond it to form a moderately to strongly bilabiate indusium.

The following species described in or sometimes transferred to other genera I would place in *Dennstaedtia: D. pilosella* (Hook.) Moore, *Microlepia stenoloba* Prantl, *Saccoloma Werckleі* Christ and *D. Wilfordii* Moore. The last species is not maintained in *Dennstaedtia* with any great confidence. It does not appear to be a *Microlepia* and, although perhaps rightly segregated as the genus *Coptidipteris* by Nakai & Momose, I would prefer to retain it in *Dennstaedtia* until its removal is suggested by a study of broad scope. The American *Saccoloma Werckleі* has recently been placed in *Microlepia* on the basis of several similarities with *Microlepia Hookeriana*. The generic (soral) characters presented here separate the two species and I am inclined to regard their similarities as due to convergent evolution. Each is a 1-pinnate species in a genus of species with decompound leaves and the sorus has perhaps been modified in each case by the alignment of adjacent sori along an entire margin, so that neither species has a sorus quite typical for its genus. *Saccoloma Wercklei* is closely related, in its pubescence, to several American species (nos. 7-10) and in its sorus especially to one of these, *D. arborescens* (Compare figs. 32 and 38). The indusium of *M. Hookeriana* shows a relation to the form sometimes present in *M. pilosula* where the edges of the indusium attached to the leaf tissue may be attenuated toward the margin of the segment.

In *Microlepia* the sorus is abaxial, borne well back of, or near, the margin of the segment, the indusium is fully attached (rarely only partially) to the leaf tissue along its sides, these sometimes approaching and rarely reaching the margin; it is usually half cup-shaped, with the sides and apex extended rather equally, or rarely the sides are attenuated well beyond the apex toward or to the margin.

I would place the following critical species in *Microlepia*: *Dennstaedtia concinna* Rosenst. (*illegit.*), *Microlepia dennstaedtioides* Copel., *Microlepia melanorhachis* Rosenst., and *Dennstaedtia resinifera* (Bl.) Mett. In *Dennstaedtia concinna* the sorus is rather close to the margin and only a moderate degree of modification of it and of the indusium would make it, by definition, a *Dennstaedtia*. In *Microlepia jamaicensis* and a species from New Caledonia (Rosenst. Fil. Nov. Caled. exsicc. 131) the sides of the indusium are only partially attached to the leaf tissue. If some of the species listed above are placed in the genus I suggest, nomenclatural changes are necessary. I am not willing to make these, without a greater familiarity with the species, except in the case of the single American one.

SPECIES IN DENNSTAEDTIA

The species of *Dennstaedtia* have been difficult to define. This difficulty, I believe, is due more to the fragmentary nature of most herbarium specimens than to an inherent lack of defining characters. Most, if not all, of the remaining problems exist where there is a lack of sufficient information. The leaves of *Dennstaedtia* are usually large and the specimens prepared from them commonly consist of such a part as may readily be accommodated on an herbarium sheet and they are not often accompanied by notes on the portion of the lamina represented or its shape. There is considerable uncertainty involved in relating these pieces to a whole lamina so that one may compare characters of comparable portions of the leaf. There are so few collections that provide data on the shape of the lamina that, although evidently an important character, it has not been possible to emphasize it. When a sufficient number of adequate specimens exists it will also be possible to know if specific characters are to be found in the petiole and rhizome. There may be differences between juvenile and adult leaves of the same species and there is a possibility that the juvenile type may persist in large leaves.

The key presents the species as less well defined than they actually are. A key that utilized lamina shape and characters of the basal pinnae more prominently would reflect the difference between the species to better advantage but would be impractical to use with most specimens. A major difficulty in the construction of the key, and one that will hardly fail to pass unnoticed by its users, is that of the characters available for a practical key some are variable and others, although constant, are not unique. The identification of a single fragment then often depends on a combination of its characters and will not always be either easy or perhaps possible.

GEOGRAPHY AND RELATIONSHIP OF THE SPECIES

The American species of *Dennstaedtia* have, with the exception of *D. punctilobula* and *D. Wercklei*, large and complex leaves. The lamina is frequently 1-1.5 (-2) m. long and the petiole is of similar length. The leaves are borne singly on an extensively creeping rhizome and the species often form large and conspicuous colonies. They grow predominantly in moist and usually shaded places. The tropical species are most frequent in forests but also grow along forest margins, or in clearings and other open habitats.

The most pronounced group within the American representatives of the genus is formed by species 7-11 which share the characters of enlarged sterile vein tips and a closely crispate, persistent pubescence on the under surface of the axes. Of these five species, *Dennstaedtia Sprucei* and *D. Wercklei* each have one or more unique characters. The former species is known only from Ecuador and Peru, the latter from Costa Rica, Colombia and Peru. The other three species of this group are more closely related and the problems of their definition are discussed under their treatments. All three are known to bear proliferous buds in the axils of the pinnae and are the only American species that have such buds. *D. arborescens* is distributed from Mexico to Panama, the Greater Antilles, and in the Andes south to Bolivia. *D. dissecta* has a similar range but is more widely distributed in northern South America and extends, in the south, to southern Brazil. *D. obtusifolia* is the most widely distributed of the three; its range is similar to that of *D. dissecta* except that it also occurs throughout the Lesser Antilles and is the only species of the genus in that area.

Dennstaedtia globulifera and *D. bipinnata* are evidently related, sharing a similar type of pubescence and decurrent herbaceous wings on the minor axes. Both species are distributed widely in tropical America, from Mexico to Panama, the Greater Antilles, northern South America to Bolivia. The former, *D. globulifera*, has a wider range in the south, extending to Argentina, Uruguay, and Brazil; while the latter, *D. bipinnata*, extends north to Florida.

The three species, *Dennstaedtia cicutaria*, *D. distenta* and *D. glauca* are not clearly closely related but do share characters of pubescence and of slender sterile vein tips. *D. cicutaria* is the most widely distributed of the three, growing from Mexico to Panama, the Greater Antilles, and in South America southward to Bolivia and southern Brazil. *D. distenta* has a relatively restricted range from Mexico to Panama; Jamaica and Hispaniola. *D. glauca*, the only species of Chile, also occurs from northwestern Argentina to southern Peru.

Dennstaedtia punctilobula, the only species of temperate to boreal regions, has no close relations with the other American species. Rather, it is related to certain species of eastern and southeastern Asia. It occurs in eastern and midwestern United States, north to Newfoundland. The gland-tipped trichomes on the lamina are distinctive among the American species.

The occurrence of six of the American species in Central America and Mexico and also in the Greater Antilles, but not the Lesser Antilles, lends emphasis to the well known floristic affinity between those two regions.

KEY TO THE SPECIES

a. Axis of the penultimate segments, as in figs. 8, 9, lacking perpendicular herbaceous wings on the upper surface or perpendicular wings present but the one on the basiscopic side not decurrent onto the axis of the next order; trichomes on the under surface of the pinnules, when present, whitish to brownish and usually subopaque. b.

b. Sterile vein tips, on the upper surface, slender, as in fig. 17, not enlarged, ending well back of the glabrous margin; tertiary axes glabrous to sparsely or densely pubescent beneath with straight to tortuous, more or less spreading trichomes. c.

c. Trichomes on the under surface of the pinnules gland-tipped, or many of them so, fig. 2. .... 1. *D. punctilobula.*

c. Trichomes on the under surface of the pinnules not gland-tipped, or absent.[2] d.

d. Pinnae alternate, the lower ones stalked, with the basal pinnules not or scarcely reduced, as in fig. 4. e.

e. Many or most of the sori borne in a sinus, fig. 5; pinnules more or less pubescent beneath, fig. 5; lamina deltoid. (Trichomes usually abundant on the under surface of the pinnules, some of them short, acicular, rigid, or rarely these absent and only larger, sometimes lax and subtortuous ones present; cells of the trichomes, except sometimes the lower ones, mostly several times longer than broad). .... 2. *D. cicutaria.*

e. All or most of the sori terminal on lobes, fig. 13; lamina ovate- or deltoid-lanceolate. ....4. *D. glauca.*

d. Pinnae opposite or rarely subopposite, the lower ones sessile, each with a pair of usually much reduced basal pinnules, fig. 6 (a detached pinna). (Major axes straw colored on the under surface; trichomes sparse, rarely absent, to usually rather abundant on the under surface of the pinnules, rather tortuous, their cells mostly about twice as long as broad, or shorter; lamina ovate to perhaps deltoid). ....3. *D. distenta.*

b. Sterile vein tips, on the upper surface, enlarged, as in fig. 30, clavate to punctate, or rarely (in *D. obtusifolia*) slender; tertiary axes glabrate to usually subappressed ascending pubescent beneath with the trichomes more or less curled. (Pinnae subopposite to alternate, the lower ones subsessile or less often short stalked). f.

f. Lamina pinnate-pinnatifid or more complex. (Basal pinnules of the lower pinnae more or less reduced, often strongly so, as in fig. 6, a detached pinna). g.

g. Sterile veins ending well back of the glabrous margin, as in fig. 30. h.

---

[2] Rarely, specimens of *D. obtusifolia* have slender sterile vein tips and are also glabrate; they may be separated from *D. cicutaria* by the subopposite, nearly sessile lower pinnae with reduced basal pinnules, from *D. glauca* by the sori borne predominantly in a sinus, from *D. distenta* by the major axes that are brownish beneath.

h. Pinnules 1-pinnate to pinnate-pinnatifid, figs. 23, 25-28, apical segments of the pinna separate or nearly so to the prolonged apex, the separate ones closest to the tip obtuse; obtuse pinnules on the apical pinnae deeply pinnatifid; lamina deltoid. i.

i. Mature sori, at least the basal acroscopic ones on an ultimate segment, mostly 1.0-1.5 mm. broad and about half as thick, fig. 24. .... *7. D. dissecta.*

i. Mature sori mostly 0.5-1.0 mm. broad and about as thick, fig. 29. .... **8. *D. obtusifolia.***

h. Pinnules entire to deeply pinnatifid, figs. 31, 33-35, apical segments of the pinna confluent back of the prolonged apex, the separate ones closest to the tip acute; obtuse pinnules on the apical pinnae entire to lobed, lamina evidently ovate. .... **9. *D. arborescens.***

g. Sterile veins nearly reaching the persistently pubescent margin, fig. 37 .... **10. *D. Sprucei.***

f. Lamina 1-pinnate, the pinnae entire, fig. 39. (Sterile veins ending well back of the glabrous margin) ...... 11. *D. Wercklei*

a. Axis of the penultimate segments bordered on each side, on the upper surface, by a pronounced herbaceous wing perpendicular to the plane of the segment, fig. 21, the wing on the basiscopic side decurrent onto the axis of the next order either as an herbaceous wing, fig. 22, or as a pronounced ridge; trichomes on the under surface of the pinnules wholly clear brown or tan, rarely subopaque or whitish. (Trichomes relatively straight and rather rigid, with all or many of their cells several times longer than broad; pinnae alternate, rarely subopposite, the lower stalked with the basal pinnules not or scarcely reduced, as in fig. 4; sterile vein tips, on the upper surface, slender, fig. 17, to rarely clavate, ending well back of the glabrous margin). j.

j. Basal segments of the pinnules of the central pinnae usually subopposite to nearly opposite, rather or quite equal in size, the inferior not or slightly ascending, fig. 14, (apical pinnae with the basal pinnules similar, the basal segments of the pinnules of the basal pinnae may be alternate); leaf tissue usually dull, sometimes shining above, dull beneath, the surface of the upper epidermis (dry) minutely pebbled by the individual epidermal cells; sori globular, fig. 16, to less often subglobular, rarely cylindrical; lamina deltoid. .... 5. *D. globulifera.*

j. Basal segments of the pinnules of the central pinnae definitely alternate, quite unequal in size, the inferior ascending to strongly ascending, fig. 18, (apical pinnae with the basal pinnules similar, the basal segments of the pinnules of the basal pinnae may be less unequal and the inferior less ascending); leaf tissue usually shining, rarely dull, above and beneath, the surface of the upper epidermis (dry) minutely striate to sometimes nearly smooth; sori cylindrical to subcylindrical, fig. 20, rarely globular; lamina ovate to lanceolate-ovate. .... 6. *D. bipinnata.*

1. **Dennstaedtia punctilobula** (Michx.) Moore, Ind. Fil. xcvii. 1857. FIGS. 1-2.

Nephrodium punctilobulum Michx. Fl. Bor.- Am. 2: 268. 1803. Holotype: Canada. "*Polypodium punctilobulum*", Hb. Michaux, P. (D. C. Eaton, Can. Nat. 13: 28. 1870, comments on the identity of the type).

The gland-tipped trichomes on the lamina (Fig. 2) distinguish this species from all other American ones. It is related, rather, to certain species of eastern and southeastern Asia, especially to *D. appendiculata*, and *D. scabra* but also to *D. pilosella* and *Microlepia stenoloba* (this last species has not been transferred to *Dennstaedtia*).

The named forms, f. *cristata*, f. *nana*, f. *Poyseri* and f. *schizophylla*, are fully treated in Gray's Manual of Botany, ed. 8.

In the eastern portion of its range this species grows in a variety of habitats, especially in open pastures, in meadows, in woods, on rocky hillsides, streams banks and moist road banks; from Indiana westward it becomes restricted to sandstone cliffs.

Newfoundland southwestward through the southern parts of Ontario, Indiana and Illinois, to Iowa (US), Missouri and Arkansas, and southward to Georgia and Alabama (US).

I do not believe it is necessary to cite specimens of this well known and distinctive species.

2. **Dennstaedtia cicutaria** (Sw.) Moore, Ind. Fil. xcvii. 1857. FIGS. 3-5.

Dicksonia cicutaria Sw. Schrad. Jour. 1800^2: 91. 1801. Holotype: Jamaica, *Swartz*, S-PA, fragment and photographs US!.

Dicksonia rubiginosa Kaulf., Enum. Fil. 226. 1824. Holotype: Rio de Janeiro, Brazil, Hb. Mertens.

Dicksonia apiifolia var. *dissecta* Desv. Mém. Soc. Linn. Paris 6: 318. 1827. Holotype: none cited, presumably Brazil, *Raddi*.

Dicksonia angustidens Presl, Tent. Pterid. 136. 1836. Based, indirectly, on *Dicksonia apiifolia* var. *dissecta* Desv.

Dicksonia umbrosa Liebm. Vid. Selsk. Skr. V, 1: 262 (reprint 101). 1849. Holotype: Colipa to Misantla, Mexico, March, *Liebmann*, C; isotype, US!.

Dennstaedtia rubiginosa (Kaulf.) Moore, Ind. Fil. xcvii. 1857.

Dicksonia decomposita Christ, Bull. Soc. Bot. Belg. 35: 180. 1896. Holotype: Costa Rica, *Tonduz 8644*, P; isotype, "*Tonduz in Pittier 8644*", US!.

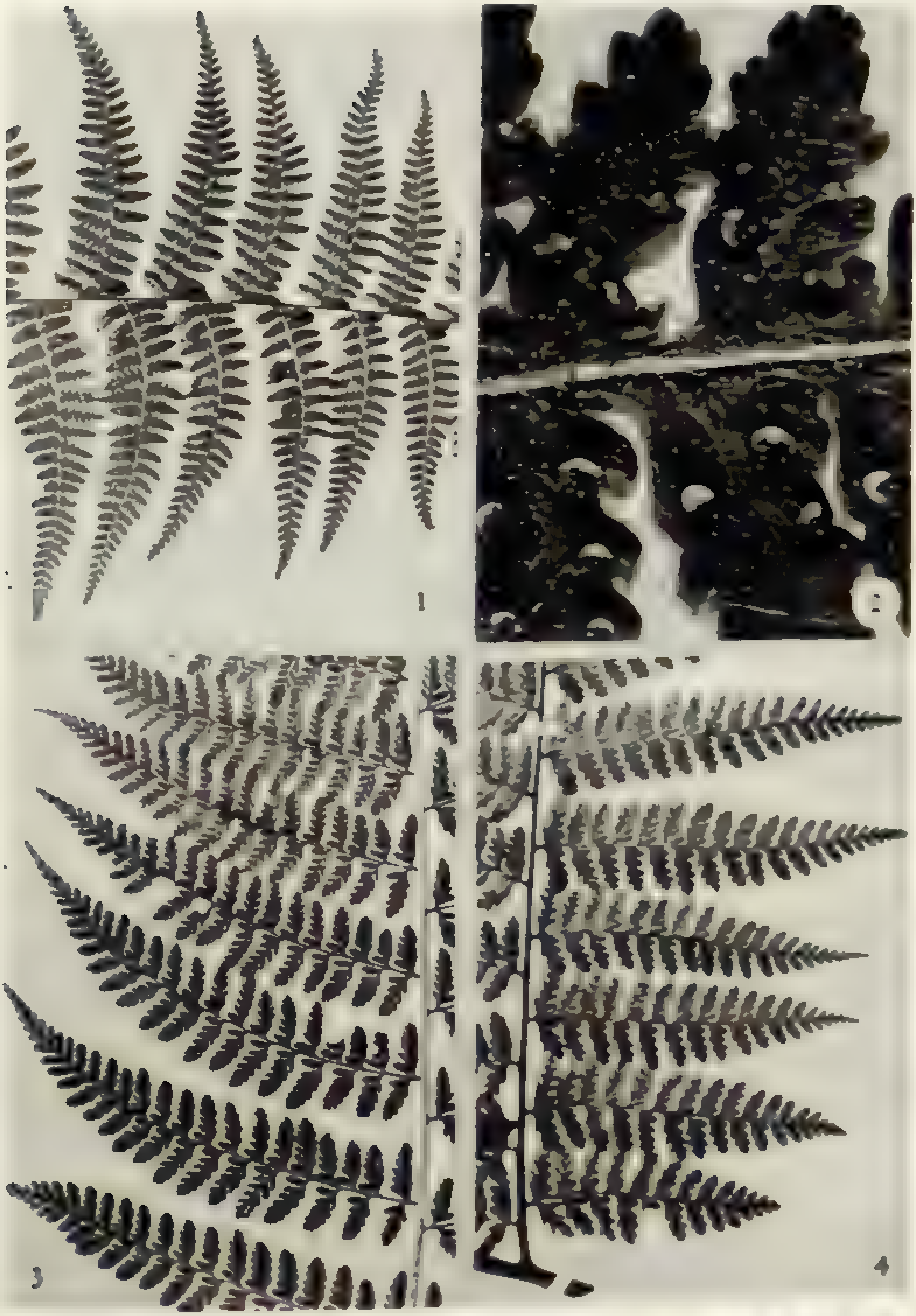


PLATE 1. *Dennstaedtia punctilobula*. Fig. 1, central portion of a lamina, × ½, Massachusetts, *Stevens in 1892*; Fig. 2, sori, × 10, Quebec, *Marie-Victorin 2734*. *Dennstaedtia cicutaria*. Fig. 3, central portion of a pinna, × ½, Haiti, *Leonard 4956*; Fig. 4, basal portion of a pinna, × ½, Panama, *Maxon 4967*.

Dennstaedtia decomposita (Christ) Christ, Bull. Herb. Boiss. II, 5: 732. 1905.

Dennstaedtia cicutaria is apparently most closely related to *D. distenta* and *D. glauca.* It may be distinguished from the first, *D. distenta*, by its alternate rather than opposite or subopposite pinnae, by its stalked, rather than sessile, lower pinnae each bearing a basal pair of little or scarcely reduced pinnules, rather than strongly reduced ones. In addition, the major axes of *D. cicutaria* are usually brownish while those of *D. distenta* are usually straw colored. The pubescence is also different; the cells of the trichomes of *D. cicutaria* are mostly several times as long as broad (except sometimes the lower ones) while those of *D. distenta* are mostly about twice as long as broad. The differences from *D. glauca* are discussed under that species.

The pubescence of *D. cicutaria* is usually dimorphic and the presence of short, one-celled, acicular trichomes is characteristic. However, sometimes these are absent and only the larger, multicellular trichomes are present.

I have not been able to maintain *D. rubiginosa* although it has traditionally been recognized as a species. The only difference between it and *D. cicutaria* that I have found is in the distribution and abundance of the trichomes on the under surface of the pinnules. In *D. rubiginosa* they are only on the axes and veins while in *D. cicutaria* (*sens. str.*) they are also on the leaf tissue. This is correlated to a certain degree with the abundance of trichomes. The more pubescent specimens have them on the leaf tissue and the less pubescent (or glabrate) ones have them only on the axes or also on the veins. However, the correlation between abundance and distribution is only a general one and there is a complete gradation from one extreme to the other. These characters do not seem to be important ones, especially since other species of *Dennstaedtia*, for example *D. distenta*, exhibit a similar variation in extent and abundance of trichomes. The two extremes do not have distinct ranges and they are often collected in the same local area. Local field studies are needed to determine if *D. rubiginosa* and *D. cicutaria* (*sens. str.*) may be correlated with differences in habitat.

Wet forests, river and stream banks, moist wooded hillsides and open places, borders of forest, clearings and moist thickets, 100-2600 m.

Central Mexico to Panama; Greater Antilles; Venezuela and Colombia to Bolivia and southern Brazil.

PLATE 2. *Dennstaedtia cicutaria*. Fig. 5, sori, × [illegible]. Mexico, *Conzatti & Gonzales* [illegible]. *Dennstaedtia distenta*. Fig. 6, basal portion of a lower pinna (detached), × ½. Mexico, *Pringle* [illegible]. Fig. 7, upper pinnae, × ½. Jamaica, *Maxon* [illegible]. Fig. 8, base of penultimate segments and base of pinnules (upper surface), × [illegible]. Mexico, *Pringle* [illegible]. Fig. 9, base of penultimate segments and base of pinnule, × 5. Mexico, *Copeland 69*.

Representative specimens: **Mexico:** SAN LUIS POTOSÍ: *Pringle 3824* (GH, US). VERACRUZ: *Conzatti & Gonzales 573* (GH, US); *Copeland 70* (GH, US); *Fink 9* (GH, US); *Purpus 2936* (GH, US); *Seaton 463* (GH, US); *C. L. Smith 2222* (GH). MICHOACÁN: *Hinton 16254* (US). OAXACA: *Conzatti 3164* (US); *Makrinius 488* (US). CHIAPAS: *Ghiesbreght 367* (GH); *Purpus 7228* (US). **Guatemala:** *J. D. Smith 1542* (GH), *2426;* (GH, US); *Steyermark 51849* (US), *51849a* (GH); *Türckheim II 1328* (GH). **British Honduras:** *Schipp S-802* (GH). **Honduras:** *Ames 143* (US); *Yuncker 4592* (US). **Nicaragua:** *C. F. Baker 2469* (GH, US); *Maxon et al. 7530* (GH, US). **Costa Rica:** *Holm & Iltis 884* (US); *Pittier 7729* (US); *Scamman 5893, 7022, 7023, 7611, 7612* (GH); *Tonduz 8631* (GH, US). **Panama:** *Maxon 4967* (GH, US). **Cuba:** *Britton & Wilson 5250* (GH, US); *Caldwell & Baker 7110* (GH, US); *Ekman 4355, 16633* (US); *Morton & Acuna 3633* (GH, US); *Shafer 533* (GH, US); *Wright 3946* (GH, US). **Jamaica:** *Clute 227* (US); *Howard & Proctor 15074* (GH); *Maxon 8801, 8975, 10044, 10292, 10374, 10431* (GH, US); *Maxon & Killip 408, 1254, 1486* (GH, US); *Orcutt 6243* (GH); *Proctor 4151* (US); *Wilson & Webster 504* (GH). **Hispaniola.** HAITI: *Ekman H2094, H7176* (US), *H8591* (GH, US); *Eyerdam 453, 454* (GH); *Leonard 4956, 8092, 9259* (GH, US); *Leonard & Leonard 13742, 14522* (GH, US). DOMINICAN REPUBLIC: *Ekman H3194* (US), *H11803* (GH, US); *Fuertes 1516* (GH, US). **Porto Rico:** *Britton et al. 4526* (GH, US), *6451* (US); *Heller & Heller 921* (US); *Sintenis 2711* (GH, US). **Venezuela:** *Chardon 183* (US); *Fendler 58* (GH). **Colombia:** *Barkley & Gutiérrez 1902* (GH); *Karsten 17* (US); *Killip 7849* (GH, US); *Killip & Smith 17000, 18855, 19030* (GH, US); *Pennell et al. 8605* (GH, US); *H. H. Smith 1070* (GH, US). **Ecuador:** *Eggers 14355* (US); *Haught 3094* (GH, US); *Rimbach 32* (GH, US); *Sydow 656* (US). **Peru:** *Killip & Smith 22440, 23072, 23699* (GH, US); *Klug 3553* (GH, US); *Mexia 6128, 8218* (GH, US); *Spruce 4339* (GH); *Tryon & Tryon 5372* (BM, F, GH, U, US, USM). **Bolivia:** *Buchtien 3379* (GH, US), *3607* (US); *Cárdenas 859* (GH, US). **Brazil.** SANTA CATHARINA: ***Haerchen*** (Ros. exsicc. *173*) (US). PARANÁ: *Dusén 15288* (GH). SAO PAULO: *Luederwaldt 21350* (GH). RIO DE JANEIRO: *Claussen 121* (US). MINAS GERAES: *Claussen 2114* (US); *Mexia 4846, 4866* (GH, US). BAHIA: *Blanchet 305* (GH).

3. Dennstaedtia distenta (Kze.) Moore, Ind. Fil. 306. 1861. FIG. 6-10.

Dicksonia distenta Kze. Analect. Pterid. 39. 1837. Holotype: Jalapa, Mexico, May, 1829, *Schiede;* isotype, NY!.

Dicksonia antillensis Jenm. Jour. Bot. 24: 267. 1886. Holotype: Jamaica, *Morris.* (I have accepted Jamaican specimens collected and identified by Jenman, NY!, as authentic).

266-21355 *Dennstaedtia antillensis* (Jenm.) C. Chr. Ind. Fil. 216. 1905.

"*Dennstaedtia mexicana* Rosenst." has never been properly published but has been used by some authors, for example, Matuda, Anal. Instit. Biol. México 27: 66. 1956. See note by Morton, Am. Fern Jour. 48: 124. 1958.

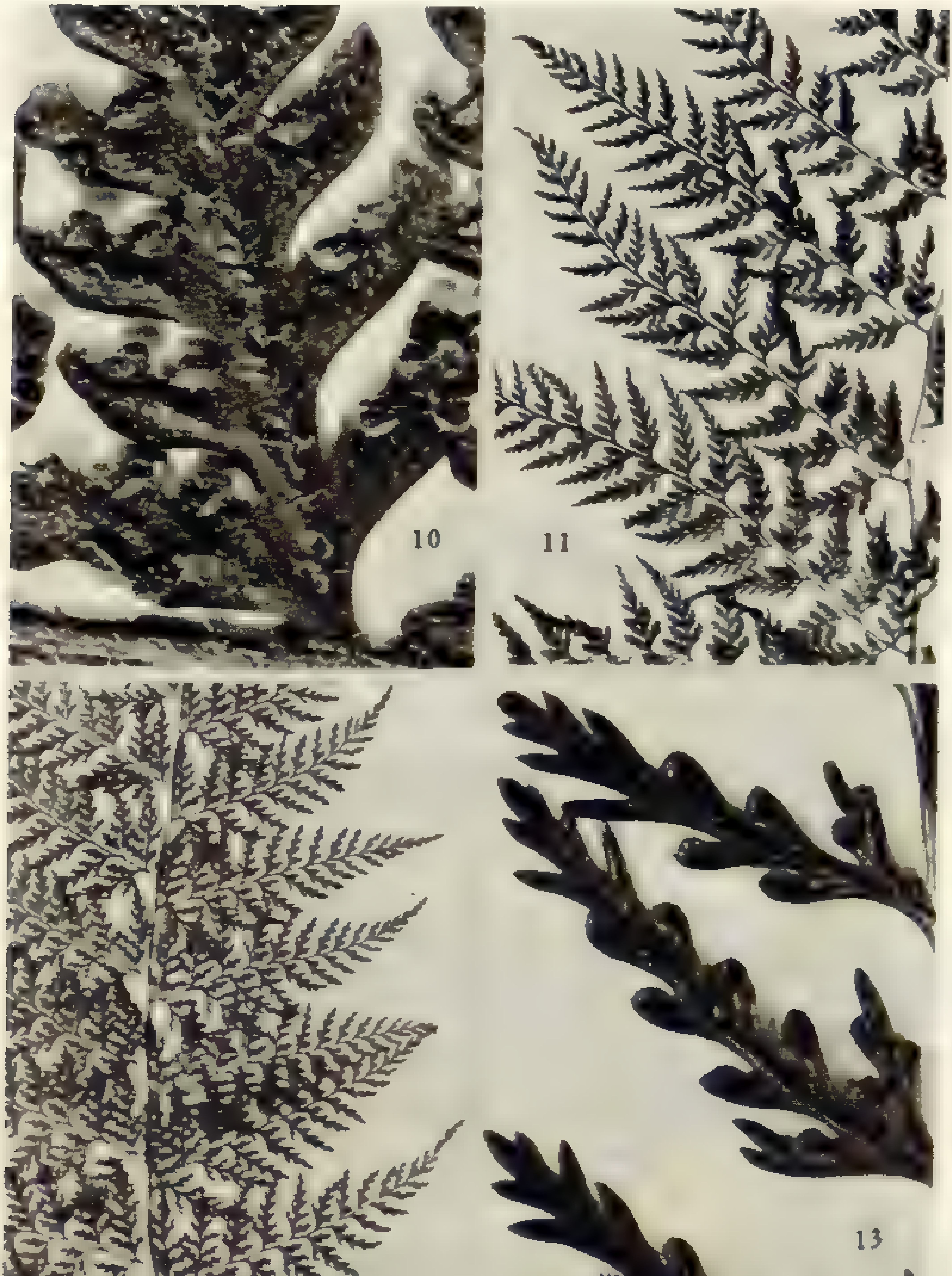


PLATE 3. *Dennstaedtia distenta:* Fig. 10, sori, × 10, Mexico, *Mexia 9057*. *Dennstaedtia glauca:* Fig. 11, central portion of a large pinna. × ½. Argentina. *Lillo 2658;* Fig. 12, central portion of a pinna, × ½, Chile, *Morrison 17076;* Fig. 13, sori, × 5, Argentina, *Schreiter 5783*.

Dennstaedtia distenta is evidently most closely related to the previous species, *D. cicutaria*, and the principal differences are discussed under that treatment. Especially in specimens that are abundantly pubescent on the under surface of the pinnules, there are both short and long trichomes and some of intermediate length. The major axes are usually straw colored beneath and in this character the species shows a relation to the following, *D. glauca*.

The material from Jamaica, Fig. 7, and Hispaniola previously considered to be a distinct species is a glabrate form with narrow lobes. These characters occur in a few specimens from Mexico and Central America although most of the continental material is pubescent and has broader lobes. Since several of the other species have, within the range of *D. distenta*, a similar distribution — Mexico and Central America and the Greater Antilles — it does not seem justifiable to recognize *D. antillensis* unless definite differences between it and *D. distenta* can be established.

Banks of streams and brooks, and other wet places, or in wet woods; 100-2500 m. usually above 1000 m. in Mexico, elsewhere confined to mountains, 1200-2850 m.

Western and central Mexico to Panama; Jamaica and Hispaniola.

Representative specimens: **Mexico:** CHIHUAHUA: *LeSueur 1132* (GH, US). SONORA: *Gentry 1395* (GH, US). DURANGO: *Sanchez 736* (US). SINALOA: *Gentry 7300* (GH, US). SAN LUIS POTOSÍ: *Cottam 10462* (US). VERACRUZ: *Bourgeau 2343, 2605* (GH, US); *Copeland 69* (GH, US). HIDALGO: March 21, 1938, *Copeland* (GH). MÉXICO: *Hinton 3637* (GH), *3776, 4046* (US), *7372* (GH, US). MICHOACÁN: *Arsène 6044, 6098* (GH, US). GUERRERO: *Hinton 14046* (GH, US), *14187* (GH); *Mexia 9085* (GH, US). OAXACA: *Conzatti 2232* (GH); *Pringle 10253* (GH, US). CHIAPAS: *Little & Sharp 9877* (US); *Purpus 9196* (GH, US). **Guatemala:** *Skutch 741* (US); *J. D. Smith 1542* (US); *Standley 67466, 85831, 85852* (US); *Steyermark 42386* (GH, US); *Türckheim II 2196* (US). **Salvador:** *Tucker 726* (US). **Costa Rica:** *Chrysler 5473* (US); *Standley & Valerio 49449* (GH, US). **Panama:** *Killip 5175* (US). **Jamaica:** *Maxon 9913* (GH, US), *9914* (US); *Sherring* (US). **Hispaniola.** HAITI: *Ekman H7980* (US).

4. **Dennstaedtia glauca** (Cav.) C. Chr. ex Looser, Rev. Hist. Geog. Chile **69:** 184. 1932. FIG. 11-13.

Davallia glauca Cav. Descr. Pl. 278. 1802. Holotype: Cordillera de Planchon, Chile, *Neé*, MA. (Looser, *loc. cit.*, and C. Chr. Dansk. Bot. Ark. **9**^{3}:28. 1937, discuss the identity of the type).

Dicksonia Lambertiana Remy, Gay Fl. Chil. **6:** 523. 1853. Holotype: Chile, Hb. Bonpland, P.

Dennstaedtia Lambertiana (Remy) Christ, Farnkr. 312. 1897.

Dennstaedtia glauca is the only species of the genus in Chile. In adjacent countries where *D. cicutaria* also occurs, the two species may be separated by the following characters. The under surface of the pinnules of *D. glauca* is glabrous or nearly so, the sori are borne predominantly on lobes and the lamina is ovate- to deltoid-lanceolate. The under surface of the pinnules of *D. cicutaria* is pubescent (rarely glabrate), the sori are borne predominantly in sinuses and the lamina is deltoid. The major axes of *D. glauca* are usually straw colored while those of *D. cicutaria* are usually brownish.

In canyons, ravines, stream borders and other locally wet places, 700-3200 m.

Chile, northeast to adjacent Argentina, north to Bolivia and southern Peru.

Representative specimens: **Peru:** *Herrera 279* (GH, US); *Vargas 2320* (US). **Bolivia:** *Cárdenas 153* (GH). **Argentina.** TUCUMÁN: *Lillo 1491, 2658* (GH); *Schreiter 4351, 5783* (GH); *Venturi 4204* (GH). CATAMARCA: *Castillon 1474* (GH). LA RIOJA: Jan. 25, 1928, *Castellanos* (GH). **Chile:** *Looser 346* (GH, US), *637* (GH); *Mexia 7872* (GH, US); *Morrison 17076* (GH, US).

5. **Dennstaedtia globulifera** (Poir.) Hieron. Bot. Jahrb. 34: 455. 1904. FIGS. 14-16.

Polypodium globuliferum Poir. Lam. Encycl. 5: 554. 1804. Holotype: Santo Domingo, Plumier, Fil. t. 30.

Dicksonia altissima Sm. Rees Encycl. 11. 1808. Based on *Polypodium globuliferum* Poir.

Dicksonia punctulata Poir. Lam. Encycl. Suppl. 2: 475. 1811. Holotype: Hb. Desfontaines, P.

Dicksonia tenera Presl, Del. Prag. 1: 189. 1822. Holotype: Rio de Janeiro, Brazil.

Dicksonia exaltata Kze. Bot. Zeit. 8: 59. 1850. Holotype: Plumier, Fil. t. 30.

Dennstaedtia tenera (Presl) Mett. Ann. Sci. Nat. V, 2: 261. 1864.

Dicksonia Lagerheimii Sod. Crypt. Vasc. Quit. 50. 1893. Holotype: Volcán El Corazón, 2000-2800 m., Ecuador, *Sodiro;* isotype or authentic specimen, NY! US (fragment)!

Dicksonia globulifera (Poir.) O. Ktze. Rev. Gen. Pl. 3^2: 378. 1898.

Dennstaedtia exaltata (Kze.) Hieron. Bot. Jahrb. 34: 454. 1904.

Dennstaedtia Lagerheimii (Sod.) C. Chr. Ind. Fil. 217. 1905.

Dennstaedtia Tamandarei Rosenst. Hedwigia 56: 359. 1915. Syntypes: Brazil, *Legru in 1913;* Brazil, *Tamandaré 5421.* Rosenst. Fil. Bras. exsicc. marked "n. sp. original", *"Tamand" & Brade 5421,* NY!.

Dennstaedtia Bradeorum Rosenst. Repert. Sp. Nov. 22: 3. 1925. Holotype: Costa Rica, *Brade 634;* isotype, NY!, US!.

Dennstaedtia globulifera is closely related to the next species, *D. bipinnata,* in the characters mentioned in the key. Of these, perhaps the most important is the character of the perpendicular herbaceous wings that border the axes of the penultimate segments and are decurrent onto the next axis. The differences between the two are discussed under *D. bipinnata.*

The distinctive characters of the basal segments of the pinnules (nearly opposite, rather equal is size and the inferior not or slightly ascending) may be developed only in certain portions of the lamina. They are present in the central portion of basal pinnae and progessively more basal portions of the pinnae above. In the apical pinnae, where the pinnules are not large enough to have basal segments, the same characters are developed in the basal pinnules. The apical portions of the pinnae and the basal portions of the lower pinnae may have the basal segments of the pinnules similar to those in *D. bipinnata.*

Wet forests, moist shaded hillsides, forest borders, stream banks, canyons, and ravines, 200-2300 m.

Eastern and central Mexico to Panama; Greater Antilles; Venezuela and Colombia south to Bolivia, Argentina, Uruguay and southern Brazil.

Representative specimens: **Mexico.** TAMAULIPAS: *Sharp 5077* (US). SAN LUIS POTOSÍ: *Pringle 3824* (GH, US). VERACRUZ: *Bourgeau 1941, 2342* (GH, US); *Conzatti & Gonzales 613* (GH, US); *Copeland 72* (GH, US); *Fink 14, 140* (GH, US); *Purpus 6192* (GH, US); *Spence 64* (GH). HIDALGO: Nov. 27, 1937, *Kenoyer* (GH): *Kenoyer & Crum 4108* (GH). MORELOS: *Lyonnet 2801* (US); *Rose & Painter 6879* (GH, US). **Guatemala:** *Skutch 973* (GH); *J. D. Smith 2709* (GH, US); *Standley 58877, 78350, 81027* (US); *Turckheim II 1328* (US). **Honduras:** *Williams & Molina 14486* (GH); *Yuncker et al. 6216* (GH, US). **Nicaragua:** *Grant 982* (US); *Standley 8753* (GH, US). **Costa Rica:** *Brade 634* (NY, US); *Haupt 42* (GH, US); *Scamman & Holdridge 7896* (GH); *Standley 43336* (US). **Panama:** *Killip 5252, 5487* (US); *Maxon 4969, 5725* (GH, US). **Cuba:** *Clément 1185* (US); *Ekman 14359* (US); *Howard 5198* (GH, US); *Jack 7037* (US), *7272, 7937* (GH, US). **Jamaica:** *Webster & Goldberg 20* (US), *23* (GH, US), *92* (US). **Hispaniola.** HAITI: *Ekman H3117, H5598* (US); *Holdridge 1981* (US); *Leonard 3768, 4026* (GH, US). DOMINICAN REPUBLIC: *Ekman H11634, H11778* (US); *Miller 1222* (US); *Turckheim 3075* (GH, US). **Porto Rico:** *Hioram 256* (US). **Venezuela:**

PLATE 4. *Dennstaedtia globulifera:* Fig. 14, basal portion of a central pinna, × ½, Colombia, *H. H. Smith 1118;* Fig. 15, central portion of a pinna, × ½, Argentina, *Rodriguez 1033;* Fig. 16, sori, × 5, Cuba, *Howard 5193. Dennstaedtia bipinnata:* Fig. 17, a sterile pinnule (upper surface), × 8, Jamaica, *Hunnewell & Griscom in 1936.*

Linden 140 (GH). **Colombia:** *Holton 70* (GH); *Killip & Smith 19111* (GH, US); *H. H. Smith 1118* (GH, US); *Triana 48* (US). **Ecuador:** *Camp E-3462* (GH, US); GALAPAGOS ISLANDS: *Stewart 882, 883, 959* (GH, US). **Peru:** *Killip & Smith 24648* (US), *25473* (GH, US). **Bolivia:** *Buchtien 3382* (GH, in part); *Cárdenas 2853* (US); *Herzog 2232* (US); *Steinbach 8939* (GH, US). **Argentina.** JUJUY: *Lillo 3123* (GH). SALTA: *Rodriguez 1033* (GH). TUCUMÁN: *Lillo 2875* (GH); *Venturi 255, 2516, 6136* (GH, US). CHACO: *Schulz 714* (GH). MISIONES: *Gozalbo 38* (GH); *Hindobro 5435* (GH); *Rodriguez 664* (GH). **Paraguay:** *Hassler 6842* (GH), *12244* (US); *Morong 571* (US). **Uruguay:** *Osten 6541* (US). **Brazil.** RIO GRANDE DO SUL: *Leite 154* (GH). SANTA CATHARINA: *Dusén 11806* (US); *Luederwaldt 705* (GH). PARANÁ: *Annies* (Ros. exsicc. 56) (US); *Dusén 16388* (GH). RIO DE JANEIRO: *Regnell II 59* (US); *L. B. Smith 2246* (GH, US); *L. B. Smith & Brade 2278* (GH, US). MINAS GERAES: *Regnell II 322c* (US).

6. **Dennstaedtia bipinnata** (Cav.) Maxon, Proc. Biol. Soc. Wash. **61:** 39. 1938. FIGS. 17-22.

Dicksonia bipinnata Cav. Descr. Pl. 174. 1802. Holotype: Porto Rico, *Ventenat*, MA; isotype, Hb. Willd. B, fragment US!. (Maxon, *loc. cit.*, discusses the Hb. Willdenow specimen accepted as an isotype).

Polypodium bacciferum Poir. Lam. Encycl. 5: 554. 1804. Holotype: Port-de-Paix, Santo Domingo, Plumier, Fil. t. 31 and the identical Plumier, Amer. t. 45.

Dicksonia adiantoides Humb. & Bonpl. ex Willd. Sp. Pl. 5: 488. 1810. Holotype: Caripe, Venezuela, *Humboldt & Bonpland*, Hb. Willd., B, fragment US!.

Dicksonia globuligera Desv. Mém. Soc. Linn. Paris **6:** 317. 1827. Based on *Polypodium bacciferum* Poir.

Dennstaedtia adiantoides (Humb. & Bonpl. ex Willd.) Moore, Ind. Fil. xcvii. 1857.

Dennstaedtia bipinnata is most closely related to the previous species, *D. globulifera.* In addition to the differences brought out in the key, the texture of the lamina is usually different, that of *D. bipinnata* being typically coriaceous to firmly herbaceous, while that of *D. globulifera* is usually softly herbaceous. The apex of the ultimate segments of *D. bipinnata*, (Figs. 17, 20) is shallowly to deeply toothed or laciniate, the more pronounced teeth being acute to subacute, while those of *D. globulifera* (Fig. 16) are entire to usually shallowly and bluntly (rarely subacutely) toothed. In *D. bipinnata* the trichomes on the under surface of the pinnules are more often deciduous than those in *D. globulifera* (or perhaps not as abundant) and they most often occur in the axils of the tertiary segments and of the pinnules.

The South American specimens (Fig. 18) are usually of a firmer texture and more deeply laciniate than those from

PLATE [illegible]. *Dennstaedtia [illegible]*. Fig. 18, basal portion of a central pinna, × ½, Bolivia, *R. S. Williams* [illegible]. Fig. 19, basal portion of an upper pinna (detached), × ½, Cuba, *Maxon* [illegible]. Fig. 20, sori, × 10, Peru, *Mexia* [illegible]. Fig. 21, portion of penultimate segment (upper surface), × 8, Mexico, *Ghiesbreght* [illegible]. Fig. 22, base of penultimate segment (pinnule) and portion of pinna-rachis (upper surface), × 8, Jamaica, *Hunnewell & Griscom* in [illegible].

Central America and the West Indies (Fig. 19). This variant is not sufficiently distinctive, however, to deserve recognition.

Wet forests or forest borders, road banks, rocky slopes and open habitats, sea level to 2000 m.

Southern Florida; central Mexico to Panama; Greater Antilles; Trinidad to Colombia, south to Peru and Bolivia.

Representative specimens: **United States.** FLORIDA: Palm Beach Co., May 14, 1926, *Small et al.* (GH, US). **Mexico.** HIDALGO: *Kenoyer 710* (GH, US); *H. E. Moore 3402* (GH). CHIAPAS: *Ghiesbreght 356* (GH); *Münch 155* (US). **Guatemala:** *Heyde & Lux 4667* (GH, US). **Honduras:** *Standley 18621, 55545* (US); *Thieme 5639b* (GH, US). **Salvador:** *Standley 19760, 20207* (GH, US). **Costa Rica:** *Pittier 6925, 7494, 10347* (US); *Scamman 5892, 7018, 7019, 7608* (GH); *Scamman & Holdridge 7895* (GH); *Skutch 3031* (GH, US); *Standley & Valerio 45186, 45895* (US). **Panama:** *Killip 4538* (US), *5003* (GH, US); *von Wedel 718* (US). **Cuba:** *Britton & Shafer 2096* (US); *Clément 1419, 5224* (US); *Eggers 4938* (US); *Hioram 6299, 6404* (GH); *Linden 1747* (GH); *Maxon 3960, 4144, 4400* (GH, US); *Morton & Acuña 3613* (GH, US); *Pollard & Palmer 174* (US); *Shafer 7868, 8499* (GH, US); *Wright 895* (GH), *962* (GH, US). **Jamaica:** *Maxon 10330* (US), *10368, 10371 10385,* (GH, US); *Orcutt 5770* (GH). **Hispaniola.** HAITI: *Ekman H8199* (GH, US); *Leonard 7919* (GH, US); *Leonard & Leonard 12149, 14324* (GH, US). DOMINICAN REPUBLIC: *Abbott 1592* (GH, US); *Ekman H11466* (US); *Fuertes 1554* (GH, US); *Valeur 739* (GH, US). **Porto Rico:** *Britton 5214* (GH, US); *Britton & Marble 446* (US); *Britton et al. 6189* (US); *Eggers 35* (US); *Garber 77* (GH); *Sintenis 401* (GH, US), *2391* (US). **Trinidad:** *Broadway 6020, 7265* (US); *Fendler 157* (GH). **Venezuela:** *Fendler 448* (GH); *Moritz 109* (US). **Colombia:** *Seifriz 157* (US); *H. H. Smith 2431* (GH, US). **Ecuador:** *Haught 3368* (GH, US). **Peru:** *Killip & Smith 22651* (GH, US), *22875, 26799, 27796* (US); *Mexia 6127* (GH, US); *Spruce 4890* (NY). **Bolivia:** *Buchtien 313, 3378* (US); *Herzog 321* (US); *Krukoff 10331* (GH, US); *Steinbach 3036* (GH); *R. S. Williams 1259, 1267* (GH, US).

7. **Dennstaedtia dissecta** (Sw.) Moore, Ind. Fil. 305. 1861. FIGS. 23-25.

Polypodium dissectum Sw. Prod. 134. 1788, not Forst. 1786.

Dicksonia dissecta Sw. Schrad. Jour. 1800^2: 91. 1801. Holotype: Jamaica, *Swartz*, S-PA, photograph and fragment US!.

Dicksonia cornuta Kaulf. Enum. Fil. 227. 1824. Holotype: Brazil, "ex Spreng.".

Dicksonia Millefolium Desv. Mém. Soc. Linn. Paris 6: 318. 1827. Holotype: Hb. Desv., P, photograph GH!.

Dennstaedtia cornuta (Kaulf.) Mett. Ann. Sci Nat. V, 2: 260. 1864.

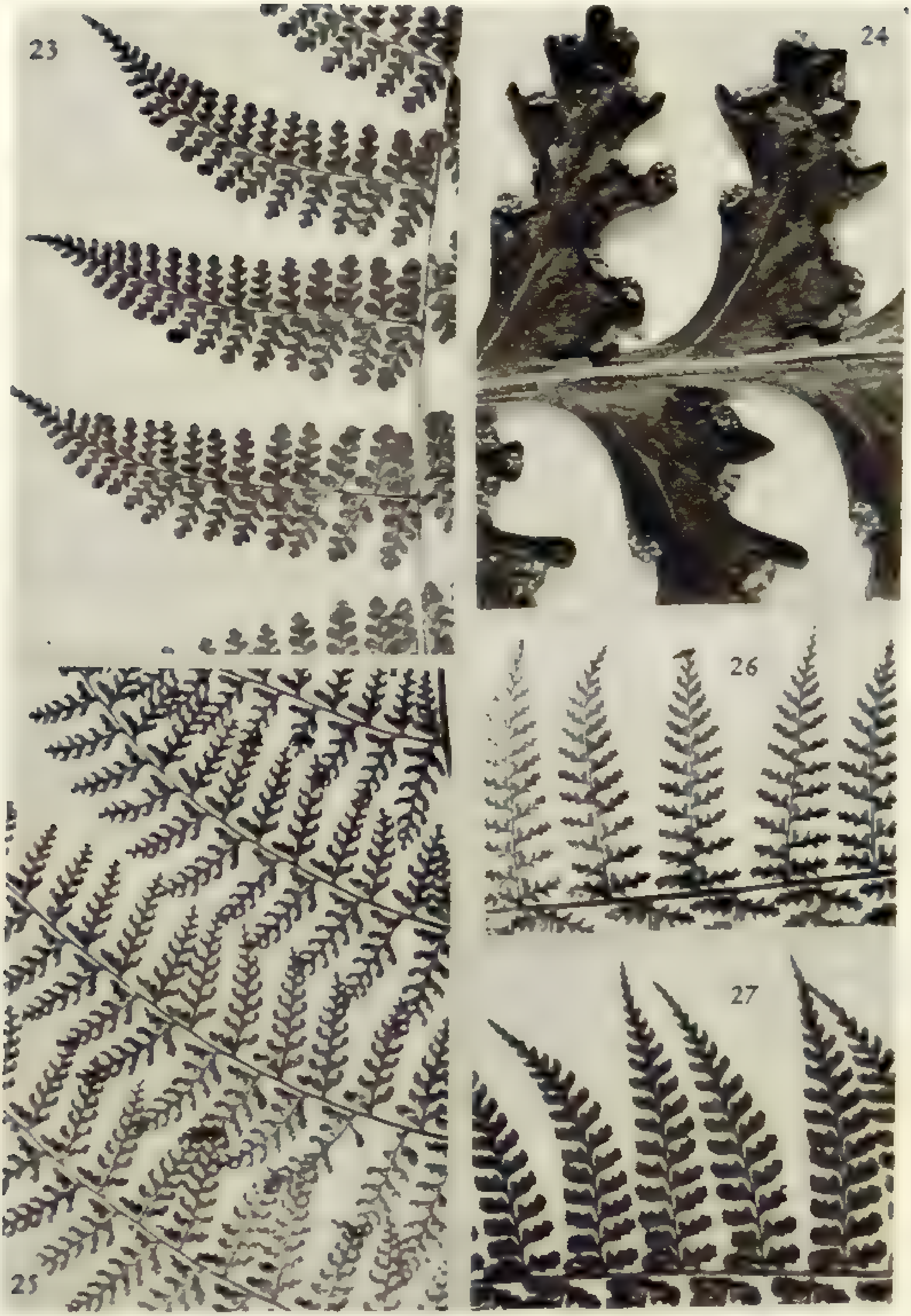


PLATE 6. *Dennstaedtia dissecta:* Fig. 23, central portion of a pinna, × ½. Haiti. *Leonard 4740;* Fig. 24, sori, × 5. Guatemala, *Turckheim 8629;* Fig. 25, upper pinnae, × ½. Costa Rica, *J. J. Cooper. Dennstaedtia obtusifolia:* Fig. 26, central portion of a pinna, × ½. Tobago, *Broadway in 1911*, Fig. 27, central portion of a pinna, × ½. Panama, *Killip 12141.*

The shape and size of the mature sori distinguish *D. dissecta* (Fig. 24) from *D. obtusifolia* (Fig. 29). In the key I have expressed this difference in terms of the breadth and the thickness. There is a simular relation of breadth and length, although this is not as constant. However, it may be useful for identification of immature specimens. In *D. dissecta* the sorus is about twice as broad as long, while in *D. obtusifolia* it is about as broad as long. The basal acroscopic sori of a segment are especially distinctive in *D. dissecta*; the apical ones may resemble those of *D. obtusifolia*. I have not been able to discover any means of identifying sterile specimens of these species, but fortunately they are few.

The close relation of *D. dissecta* and of *D. obusifolia*, their similar ranges and the occurrence of at least a few mixed collections[3] suggest that perhaps they are variants of a single species. However, *D. dissecta* is not known from Cuba, Porto Rico or the Lesser Antilles, while *D. obtusifolia* occurs in all of those areas.

Scamman 7609 and *7610* from Costa Rica have proliferous buds in the axils of the pinnae.

Wet forests, shady woods and forest openings, 30-2600 m.

Southern Mexico to Panama; Jamaica and Hispaniola; Trinidad to Colombia, south to Bolivia and southern Brazil.

Representative specimens: **Mexico:** VERACRUZ: *Copeland 71* (GH, US). CHIAPAS: *Ghiesbreght 368* (GH). **Guatemala:** *Heyde & Lux 3212* (GH, US); *Munch 151* (US); *Turckheim 8629* (GH, US), *II 2367* (US). **British Honduras:** *Schipp S-921* (GH). **Nicaragua:** *Standley 10919* (US). **Costa Rica:** *Maxon 305* (US); *Maxon & Harvey 8053* (US); *Pittier 63* (GH); *Scamman 7021, 7609, 7610* (GH); *Standley 37173, 51247, 51258* (US). **Panama:** *Cornman 1195* (US); *Killip 5175* (GH). **Jamaica:** *Clute 108* (US); *Hart 162* (US); *Maxon 9828* (GH, US); *Orcutt 5139* (GH); *Underwood 3155* (US); *Wilson 532* (GH). **Hispaniola.** HAITI: *Ekman H7527, H7528, H10185* (US); *Leonard 4279, 4740* (GH, US). **Trinidad:** *Lockhart* (GH). **Venezuela:** *Fendler 59* (GH); *Moritz 283* (GH, US). **Colombia:** *Killip & Smith 16057* (GH, US); *Linden 1043* (US); *Pennell 4424, 7602* (GH, US); *Stubel 438* (US). **Ecuador:** *Eggers 15313* (US); *Rimbach 105* (GH, US). **Peru:** *Killip & Smith 24546* (US); *Macbride 4844* (US); *Mexia 8248* (GH, US). **Bolivia:** *Bang 2423* (GH, US); *Herzog 2260* (US); *Rusby 127* (US). **Brazil:** RIO GRANDE DO SUL: *Leite 3048* (US). SANTA CATHARINA: *Luederwaldt 1821* (US). PARANÁ: *Dusén 14116* (US). SAO PAULO: *Brade 8351* (US). RIO DE JANEIRO: *Glaziou 1232* (US).

8. **Dennstaedtia obtusifolia** (Willd.) Moore, Ind. Fil. 306. 1861. FIGS. 26-29.

Dicksonia obtusifolia Willd. Sp. Pl. 5: 483. 1810. Holo-

---

[3] *Maxon 9475* and *9901*, *Maxon & Killip 1189* from Jamaica, and *Leite 3048*, Brazil, are all *D. dissecta* at US and *D. obtusifolia* at GH.

type: Caracas, Venezuela, *Bredemeyer*, Hb. Willd., B, photograph US!.

Dicksonia ordinata Kaulf. Enum. Fil. 226. 1824. Holotype: Porto Rico, *Ventenat*. (Kze. Farnkr. t. 106b is evidently drawn from the holotype).

Dennstaedtia ordinata (Kaulf.) Moore, Ind. Fil. 306. 1861.

Dennstaedtia producta Mett. Ann. Sci. Nat. V, 2: 260. 1864. Syntypes: Colombia, *Lindig 329*, B, photographs and fragment US!, P, photograph GH!; Colombia, *Lindig 333*, B, GH!, NY!, US!.

Dicksonia incisa Fée, Mém. Fam. Foug. 11:94, t. 25, fig 1. 1866. Holotype: Guadeloupe, *L'Herminier in 1864*; authentic specimen, *L'Herminier 172 in 1862*, P, photograph GH!.

Dicksonia cicutarioides Fée, Mém. Fam. Foug. 11: 95, t. 25, fig. 2. 1866. Holotype: Guadeloupe, *L'Herminier in 1864*.

Dennstaedtia incisa (Fée) Kuhn, Linnaea 36: 146. 1869.

Dicksonia scandens Baker, Jour. Bot. 15: 162. 1877, not Bl. 1828; illustrated in Ic. Pl. t. 1605. Holotype: Andes of Quito, Ecuador, *Sodiro*, K, photograph and fragment US!

Dicksonia pubescens Baker, Jour. Bot. 19: 203. 1881, not Schkuhr, 1809. Holotype: Antioquia, Colombia, *Kalbreyer 1859*, K, photograph and fragment US!.

Dennstaedtia Sodiroi Diels, Nat. Pflanz. 1^4: 218. 1899. Based on *Dicksonia scandens* Baker.

Dennstaedtia obtusifolia var. *protrusa* Christ, Prim. Flor. Costar. 3: 38. 1901. Holotype: Costa Rica, *Tonduz 11785*, P, isotype, GH!, US!.

Dennstaedtia cicutarioides (Fée) Hieron. Bot. Jahrb. 34: 454. 1904.

Dicksonia cicutaria var. *deparioides* Rosenst. Hedwigia 43:214. 1904. Holotype: Toledo, São Paulo, Brazil, *Ulbricht 73*, PA!

Dennstaedtia pubescens (Baker) C. Chr. Ind. Fil. 218. 1905.

Dennstaedtia deparioides (Rosenst.) Rosenst. Hedwigia 46: 71. 1906.

Dennstaedtia Kalbreyeri Maxon, Proc. Biol. Soc. Wash. 51: 40. 1938. Based on *Dicksonia pubescens* Baker.

Dennstaedtia obtusifolia is most closely related to *D. dissecta* and their distinguishing characters and problems of separation are discussed under the latter treatment.

This species and *D. ordinata* have commonly been maintained as distinct but I have been unable to find any reliable characters by which to separate them. Three other species have been less often recognized as distinct from *D. obtusi-*

folia. Dennstaedtia producta Mett. is an unusually laciniate form. *Dennstaedtia incisa* (Fée) Kuhn is a form with especially small and narrow lobes. *Dennstaedtia Kalbreyeri* Maxon I can interpret only as an unusual variation of *D. obtusifolia* with a fine, stiff and abundant pubescence, and the pinnules nearly at right angles to the pinna-rachis and with very uniform tertiary segments. The type of *D. Kalbreyeri* has some trichomes on the under surface of the costa that resemble (although they are longer) those usually occurring in *D. obtusifolia.* Another specimen (*Cuatrecasas 9382,* US) has the aspect of *D. Kalbreyeri* and the typical pubescence of *D. obtusifolia.*

Fée (*loc. cit.*, t. 25. fig. 2) illustrates a specimen of this species with proliferous buds in the axils of the pinnae.

Wet forests, forest clearings, wet banks and hillsides, sea level to 2100 m.

Guatemala to Panama; Greater and Lesser Antilles; Trinidad to Colombia, south to Peru, Paraguay and southern Brazil.

Representative specimens: **Guatemala:** *Türckheim 1053* (GH), *8629* (US). **Honduras:** *Ames 105* (US). **Nicaragua:** *C. F. Baker 2468* (US); *Levy 453* (GH). **Costa Rica:** *Scamman & Holdridge 7899, 7900* (GH); *Skutch 5357* (US); *Tonduz 11785* (GH, US); COCOS ISLAND: *Pittier 16230* (GH); *Snodgrass & Heller 952* (GH). **Panama:** *Killip 2832* (GH), *12141* (GH, US). **Cuba:** *Clément 1178* (GH, US), *1497, 1557, 1609* (GH); *Ekman 3937* (US); *Pollard & Palmer 165* (GH, US); *Wright 895* (GH, US). **Jamaica:** *Clute 292* (US); *Maxon 8836* (GH, US); *Wilson & Murray 581* (GH). **Hispaniola.** HAITI: *Leonard & Leonard 12280* (GH, US). DOMINICAN REPUBLIC: *Abbott 320* (US), *486* (GH, US); *Ekman H11473* (GH, US); *Howard & Howard 9394* (GH, US). **Porto Rico:** *Britton & Cowell 1023, 2205* (US); *Scamman 6524* (GH); *Sintenis 1789* (US), *5443* (GH, US), *6536* (US). **Guadeloupe:** *Duss 4184, 4341* (US); *L'Herminier 172* (GH); *Stehlé 1464* (US). **Dominica:** *Lloyd 900* (US). **Martinique:** *Duss 1685, 4164* (GH, US), *4686* (US). **St. Lucia:** *Box 469, 470* (US); *Proctor 17905* (GH). **St. Vincent:** *H. H. Smith 1723* (GH, US). **Grenada:** *Broadway 1862* (GH). **Tobago:** *Broadway 4219* (GH, US), *9223* (GH). **Trinidad:** *Britton et al. 1353* (GH, US); *Broadway 5354* (GH), *5914* (US), *9961* (GH,US); *Fendler 84* (GH, US). **Venezuela:** *Fendler 374* (GH); MARGARITA ISLAND: *Johnston 185* (GH, US), *Miller & Johnston 160* (GH, US). **Colombia:** *Lindig 333* (GH, NY, US); *Pennell 4472* (US), *8918* (GH, US); *Pennell et al. 8665* (GH, US). **Ecuador:** *Hitchcock 21764* (GH, US); *Stübel 947* (US). **Peru:** *Kanehira 160* (US); *Killip & Smith 22647* (GH, US), *23915, 24916* (US); *Schunke 154* (US). **Paraguay:** *Hassler 6840, 12244* (GH). **Brazil.** RIO GRANDE DO SUL: *Leite 3048* (GH). SANTA CATHARINA: *Spannagel* (Ros. exsicc. *241*) (US). PARANÁ: *Dusén 14678* (GH, US). SAO PAULO: *Luederwaldt 21351* (GH). RIO DE JANEIRO: *Glaziou 5256* (US).

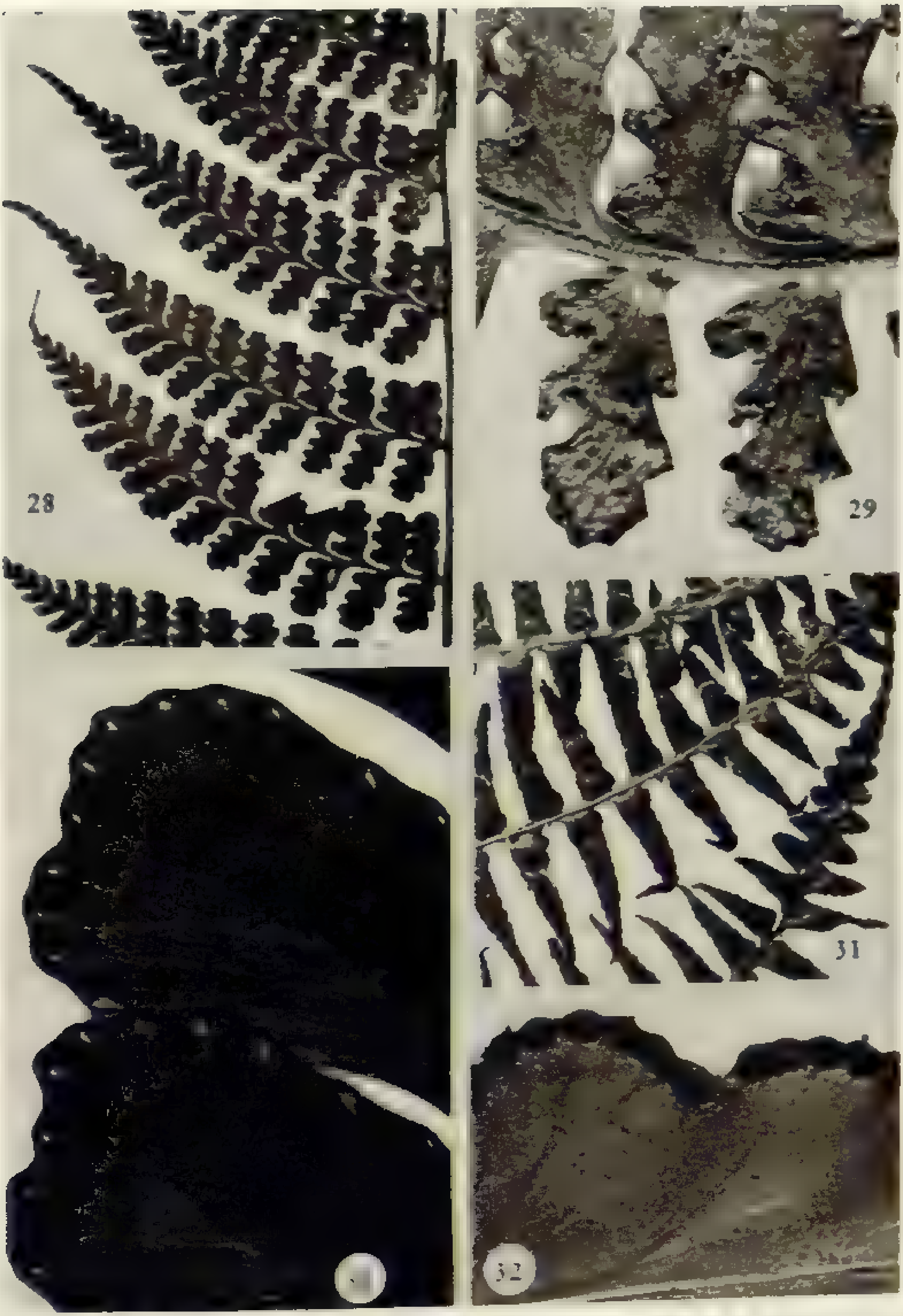


PLATE 7. *Dennstaedtia obtusifolia*: Fig. 28, central portion of a pinna, × ½, Nicaragua, *C. F. Baker 2458*. Fig. 29, sori × 5, Porto Rico, *Scamman 6124*. *Dennstaedtia arborescens*: Fig. 30, portion of a sterile pinnule (upper surface), × 5, Bolivia, *Buchtien 1791*. Fig. 31, portions of upper pinnae, × ½, Costa Rica, *Scamman 7020*. Fig 32, sori, × 5, Costa Rica, *Maxon & Harvey 8006*.

9. **Dennstaedtia arborescens** (Willd.) Ekman ex Maxon, Proc. Biol. Soc. Wash. 43: 88. 1930. FIGS. 30-35.

Davallia arborescens Willd. Sp. Pl. 5: 470. 1810. Holotype: Santo Domingo, Plumier Fil. t. 6.

Davallia concinna Presl, Rel. Haenk. 1: 66. 1825, not Schrad. 1818. Syntypes: "Chile, 1790, *Haenke*", 2 sheets PR, photographs GH!, US!. The species is not known from Chile; Presl, Epim. Bot. (reprint) 102, was undoubtedly correct in citing the Haenke collection as from Peru.

Dicksonia macrophylla Desv. Mém. Soc. Linn. Paris 6: 317. 1827. Based on *Davallia arborescens* Willd.

Dicksonia Paronii Hook. Sp. Fil. 1: 74. 1844. Based on *Davallia arborescens* Willd., not *Dicksonia arborescens* L'Hérit. The specimen cited is *Dennstaedtia Sprucei*.

Dicksonia concinna (Presl) Hook. Sp. Fil. 1: 74. 1844.

Deparia Mathewsii Hook. Sp. Fil. 1: 85, t. 30B. 1844. Holotype: Peru, *Mathews 1782*, K, photograph and fragment US!; isotype, US!.

Dicksonia consanguinea Kl. Linnaea 20: 445. 1847. Holotype: Puerto Cabello, Columbia, *Karsten*.

Dicksonia recognita Kze. Bot. Zeit. 8: 57. 1850. Holotype: Plumier, Fil. t. 6.

Patania triangularis Presl, Epim. Bot. (reprint) 261. 1852. Holotype: Colombia, *Linden 1042*, PR; isotype, GH!.

Dennstaedtia concinna (Presl) Moore, Ind. Fil. xcvii. 1857.

Dennstaedtia macrophylla (Desv.) Moore, Ind. Fil. xcvii, 1857.

Dennstaedtia Paronii (Hook.) Moore, Ind. Fil. 307. 1861.

Dennstaedtia consanguinea (Kl.) Moore, Ind. Fil. 305. 1861.

Dicksonia adiantoides var. *coronata* Sod. Rec. Crypt. Vasc. Quit. 23. 1883. Holotype: Ecuador, *Sodiro; Corazón, Sodiro*, US!, K, photograph US! and Canzacoto, *Sodiro*, NY! are presumably authentic.

Dicksonia coronata (Sod.) Sod. Crypt. Vasc. Quit. 48. 1893.

Dennstaedtia coronata (Sod.) C. Chr. Ind. Fil. 216. 1905.

Dennstaedtia Mathewsii (Hook.) C. Chr. Ind. Fil. 218. 1905.

Dennstaedtia grossa Christ, Bull. Herb. Boiss. II, 6: 192. 1906. Holotype: Navarro, Costa Rica, *Wercklé 9*, P; authentic specimens collected by *Wercklé*, NY!, US!.

Maxon (*loc. cit.*) has discussed the application of Willdenew's name and the confusion that led to the inappropriate epithet. The Plumier plate is not an entirely satisfactory match for material recently collected in Hispaniola, or elsewhere, but unless it can be shown that it represents a different species it seems best to accept its identity as Maxon determined it.

Some forms of *D. arborescens* with deeply pinnatifid pinnules and some of the previous species, *D. obtusifolia*, with 1-pinnate pinnules are rather similar and fragmentary specimens may be difficult to identify.

In the shape and size of the ultimate segments, *D. arborescens* is the most variable of the American species. The three principal variations are illustrated in Figs. 31, 33 and 34. The form with broadly obtuse segments illustrated in Fig. 33 may occur in both fertile and sterile pinnae, or the sterile ones may be truncate, as in Fig. 35. It is with some uncertainty that I treat these all as one species and do not give them some intraspecific status.

My conclusion that *D. arborescens* should be considered a polymorphic species is based on the following considerations. *Dennstaedtia Sprucei*, a distinctive species, exhibits some of the variability in shape and size of the ultimate segments that *D. arborescens* does. Some specimens, Fig. 36, are similar to those of *D. arborescens* in Fig. 33; others are substantially the same as those of *D. arborescens* in Fig. 31. None of the forms has a distribution that would favor its recognition. There are no other characters (or at least I have found none) to support those of size and shape of the ultimate segments. Finally, complete intergradation exists between the forms, although these intermediate specimens are not as numerous as the others. The lack of a distinctive geographic range and the parallel variation in *D. Sprucei* indicate, I believe, that no geographic subspecies or varieties are involved in the variation of *D. arborescens*. However, adequate field studies may bring out facts of correlation with habitat or local geography that may result in a reevaluation of this conclusion.

This species has, more often than the two preceeding ones, proliferous buds in the axils of the pinnae. They are not, however, common. Evidently they are readily detached and leave no observable scar; thus it is not possible to determine if specimens formerly bore them.

Wet forests, ravine banks, forest borders; 100-1500 m. in Central America, 1200-2200 m. in the Greater Antilles and 400-2800 m. in South America.

Southern Mexico to Panama; Cuba, Jamaica and Hispaniola; Venezuela to Colombia, south to Bolivia.

Representative specimens: **Mexico.** CHIAPAS: *Münch 60* (US). **Guatemala:** *Hatch & Wilson 114* (US); *Salvin* (GH). **Costa Rica:** *Maxon & Harvey 8006* (GH, US); *Scamman 7020, 7897, 7898* (GH); *Standley 44096* (GH, US). **Panama:** *Cornman 1226* (GH, US); *Maxon 4968* (GH, US); *Pittier 5338* (GH, US). **Cuba:** *Ekman 5499, 7145, 7146* (US). **Jamaica:** *Chrysler 2055* (GH, US). **Hispaniola.** HAITI: *Ekman H1682, H3122, H5446* (US), *H7633* (GH). **Venezuela:** *Fendler 60* (GH, US); *Moritz 386* (US). **Colombia:** *Killip & Hazen 8987* (GH, US); *Killip & Smith 19970, 20414, 20462* (GH, US); *Linden 1042* (GH); *H. H. Smith 1072, 2218* (GH, US). **Ecuador:** *Mexia 7208* (GH, US); *Rimbach 66* (US). **Peru:** *Macbride 4176, 4842* (F, US); *Mathews 1782* (US); *Killip & Smith 24642* (F, GH, US); *Spruce 4346* (GH). **Bolivia:** *Buchtien 314, 3593* (GH, US); *R. S. Williams 1243* (GH, US).

10. **Dennstaedtia Sprucei** Moore, Ind. Fil. 308. 1861.
Holotype: Ecuador, *Spruce 5350;* isotype, GH!, C, photograph and fragment US!. FIGS. 36-37.

Dicksonia Sprucei (Moore) Baker, Jour. Bot. 15: 162. 1877.

This is one of the most distinctive species; the sterile veins that nearly reach the margin of the segment and the persistently pubescent margin (Fig. 37) are unique characters among the American species. Specimens have sometimes been identified as *D. Pavonii*, but that name is based on *Davallia arborescens* (=*Dennstaedtia arborescens*) rather than the specimen of *D. Sprucei* (Peru, *Ruiz & Pavon*) cited and illustrated by Hooker (Sp. Fil. 1: 74, t. 26A).

Wet forests and moist open places, 1500-2000 m.

Ecuador and Peru.

Specimens seen: **Ecuador:** *Mille 165* (US); 1873, *Sodiro* (NY); *Spruce 5350* (GH). **Peru:** *Killip & Smith 25848* (GH, US); *Soukup 1826* (GH, US).

-06296

11. **Dennstaedtia Wercklei** (Christ) Tryon, comb. nov.
FIGS. 38-39.

Saccoloma Wercklei Christ, Bull. Herb. Boiss, II, 4: 1100. 1904. Holotype: Costa Rica, *Wercklé 320*, P, photograph and figures in Am. Fern. Jour. 48: pl. 13 and 14. 1958.

Dennstaedtia arcuata Maxon, Am. Fern Jour. 35: 22, 1945. Holotype: Colombia, *Killip 5565*, US!; isotype: GH. (Paratypes: Colombia, *Dryander 2446*, GH!, US!, *Juzepczuk 6570*, US!; Peru, *Bryan 674*, US!).

Microlepia Wercklei (Christ) Kramer, Am. Fern Jour. 48: 116. 1958.

The 1-pinnate lamina with entire, slightly auriculate pinnae is sufficient to distinguish *D. Wercklei* from all other species. The closely crispate pubescence on the under sur-

PLATE [illegible]. *Dennstaedtia arborescens:* Fig. 33, central portion of a pinna × ½, Haiti, *Ekman H7633;* Fig. 34, pinnules, × ½ Panama, *Pittier* [illegible]. Fig. 35, pinnules, × ½, Colombia, *Daniel 1899. Dennstaedtia Sprucei:* Fig. 36, pinnules × ½, Peru, *Soukup* [illegible]. Fig. 37, portion of a sterile pinnule, upper surface, × [illegible], Peru, *Killip & Smith* [illegible]. *Dennstaedtia Werckleana:* Fig. 38, sori × [illegible], Colombia, *[illegible] 2446.* Fig. 39, central pinnae × ½, Colombia, *[illegible] 2446.*

face of the costa and the enlarged sterile vein tips relate this species to *D. dissecta*, *D. obtusifolia*, *D. arborescens* and *D. Sprucei*.

Kramer (*loc. cit.*) has discussed and illustrated the previously obscure *Saccoloma Wercklei* and has (in herb.) identified *D. arcuata* as conspecific with it.

Forests, about 2000 m.

Costa Rica, Colombia and Peru.

Specimens seen: **Colombia:** *Dryander 2446* (GH, US); *Juzepczuk 6570* (US); *Killip 5565* (GH, US). **Peru:** *Bryan 674* (US).

DUBIOUS AND EXCLUDED NAMES

Some of the following names are undoubtedly based on specimens of *Dennstaedtia* but, not having seen the types, I have not been able to place them in synonymy. From some portion of the protologue, it is reasonably certain that none of them could be the correct name for any of the species recognized in this treatment. Other names are included that have been placed in *Dennstaedtia* but are referable to another genus.

Dennstaedtia apiifolia (Sw.) Moore, Ind. Fil. xcvii. 1857. *Dicksonia apiifolia* Sw. Schrad. Jour. **1800**^{2}: 91. 1801. = MAXONIA APIIFOLIA.

Dennstaedtia divaricata (Sod.) C. Chr. Ind. Fil. 217. 1905. *Dicksonia divaricata* Sod. Crypt. Vasc. Quit. 48. 1893. Holotype: Volcán Pululahua, 2000 m., Ecuador, *Sodiro*.

Dennstaedtia erosa (Kze.) Moore, Ind. Fil. 306. 1861. *Dicksonia erosa* Kze. Linnaea **9**: 88. 1834. Holotype: Pampayaco, Peru, July, 1829, *Poeppig*. The petiole and upper surface of the rachis are described as scaly and this would exclude it from *Dennstaedtia;* however, the description may be erroneous for the name has been applied to specimens of *Dennstaedtia arborescens*.

Dennstaedtia fluminensis (Fée) C. Chr. Ind. Fil. 217. 1905. *Microlepia fluminensis* Fée, Crypt. Vasc. Brésil **1**: 151, t. 51, fig. 1. 1869. Holotype: Brazil, *Glaziou 2378*. = MICROLEPIA sp.

Dennstaedtia grandifrons Christ, Prim. Flor. Costar. **3**: 38. 1901. Holotype: Costa Rica, *Tonduz 11931*, P.

Dennstaedtia lindsayiformis (Fée) C. Chr. Ind. Fil. 217. 1905. *Microlepia lindsayiformis* Fée, Crypt. Vasc. Brésil **1**: 152, t. 51, fig. 2. 1869. Syntypes: Brazil, *Glaziou 2379, 3332*. = MICROLEPIA SPELUNCAE?

Dennstaedtia Munchii Christ, Bull. Herb. Boiss. II, **5**: 732. 1905. Holotype: Chiapas, Mexico, *Munch 137*, P.

Dennstaedtia Orbignyana Kuhn, Linnaea **36**: 146. 1869; Chaetopt. 348. 1882. Holotype: Bolivia, *D'Orbigny 278*, B.

Dennstaedtia Pearcei (Baker) C. Chr. Ind. Fil. 218. 1905. *Dicksonia Pearcei* Baker, Ann. Bot. **5**: 197. 1891. = LOXSOMOPSIS PEARCEI.

Dennstaedtia rubicaulis Christ, Bull. Herb. Boiss. II, **5**: 258, 732. 1905. = HYPOLEPIS sp.

Dennstaedtia vagans (Baker) Diels, Nat. Pflanz. 1^{4}: 218. 1899. *Dicksonia vagans* Baker, Jour. Bot. **15**: 162. 1877. Holotype: Andes of Quito, Ecuador, *Sodiro*, K. — GRAY HERBARIUM, HARVARD UNIVERSITY.

THE LEPTOSPORANGIUM OF THE NEW ZEALAND FERN ANARTHROPTERIS DICTYOPTERIS

KENNETH A. WILSON

Anarthropteris was described as a genus by Copeland (1947) and includes only *A. Dictyopteris* (Mett.) Copel. a fairly common epiphytic or epipetric New Zealand fern which has also been reported from the New Hebrides (Dobbie, 1951). The genus was considered by Copeland to be most closely related to *Loxogramme* and the two genera were grouped by him with the grammitid ferns. A survey of the mature sporangia of polypodioid and grammitid genera disclosed that the sporangial structure of *Anarthropteris* did not conform with that of either the polypodioid or the grammitid ferns, and it was, in fact, considerably different from those of *Loxogramme* (Wilson 1959). Of considerable morphological interest, however, was the structure of the sporangial stalk which was very irregular in its cellular arrangement and suggested that longitudinal intercalary divisions had taken place during the ontogeny of the stalk. Since no vertical divisions had been observed in the sporangial stalk cells of the polypodioid genera *Phlebodium* (Wilson, 1958a), and *Pyrrosia*, or the grammitid genus *Xiphopteris* (Wilson, 1958b), it was felt that a study of the ontogeny of the sporangia of *Anarthropteris* would be highly desirable.

It was my good fortune to be able to obtain material from New Zealand through the generous efforts of Mrs. Lenette R. Atkinson. The plant material of *Anarthropteris Dictyopteris* was collected in the Waitakere Range, north of Auckland, New Zealand, by Lenette R. Atkinson and Marguerite Crookes in December, 1957, and preserved in F. P. A. (formalin-propiono-alcohol). Young sori were embedded in paraffin, sectioned at 15 microns, and stained in Conant's quadruple stain. Other young sori were cleared in sodium hydroxide (5%) and stained in tannic acid and iron chloride following the methods described in earlier papers on sporangial ontogeny. An herbarium specimen of the plant material was prepared and has been deposited in the Gray Herbarium of Harvard University. All illustrations were made with the aid of a camera lucida.

MORPHOLOGICAL OBSERVATIONS

The sporangium of *Anarthropteris Dictyopteris* develops from a single superficial cell of the receptacle which becomes swollen and then is divided by a more or less horizontal wall on a level well above that of the surface of the adjacent receptacular cells (fig. 1). The second wall is horizontal and is intercalated in the lower cell of the sporangial initial and is produced on a level with the surface of the neighboring receptacular cells. This second division produces Segment *O* and separates a basal cell from the sporangial primordium. The sporangial primordium is therefore two-celled at this stage, and consists of the proximal Segment *O* and a distal cell, the "mother initial" (fig. 2).

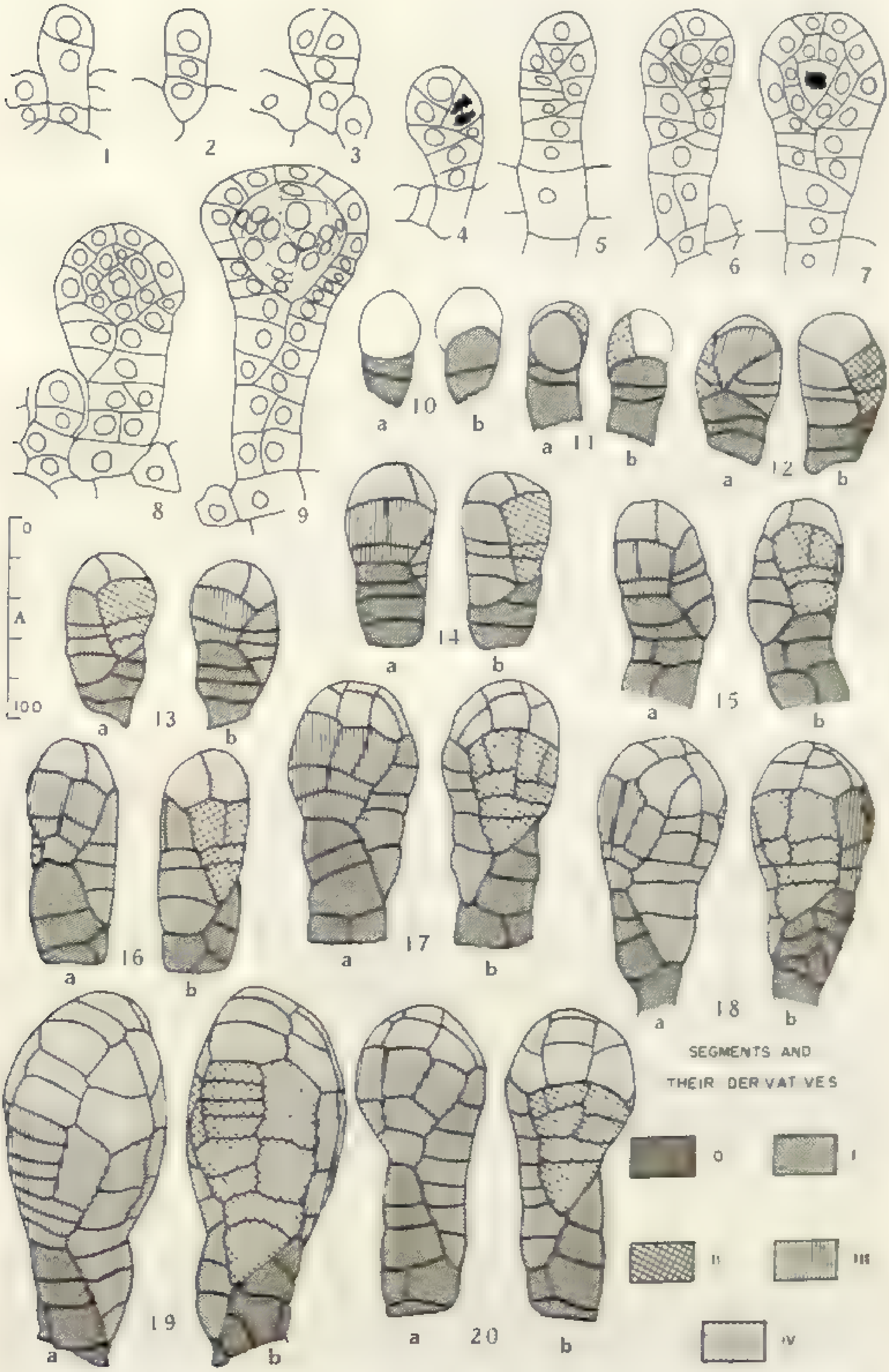
The mother initial divides by the formation of three oblique walls which produce Segments I, II and III, that contribute to the jacket layer of the capsule and to the three-rowed portion of the stalk subtending the capsule (figs. 3, 4). Segment *O* may become divided by the intercalation of a horizontal wall before the formation of Segment I (fig. 10), or it may remain undivided until after Segment I is produced (fig. 3).

Soon after the formation of Segment I, II and III, the mother initial, which now has the form of an inverted three-sided pyramid (fig. 4), divides and produces a horizontal wall which cuts off the cap cell, Segment IV, of the sporangium (fig. 5). This division results in the complete enclosure of the mother initial by its daughter cells. Following this, the enclosed tetrahedral mother initial divides in the same order and in the same manner as it did in producing Segments I, II, III, and IV, so that it becomes enclosed by still another layer of cells, the tapetal initials (figs. 6, 7).

The division of the tapetal initials to produce the two layered tapetum is accompanied by divisions in the central cell which eventually give rise to the spore mother cells (figs. 7-9).

Even before the formation of the tapetal initials, intercalary divisions have begun to take place within the various segments of the sporangial initial. In fact, intercalary divisions have begun to take place before the formation of segment IV (fig. 4).

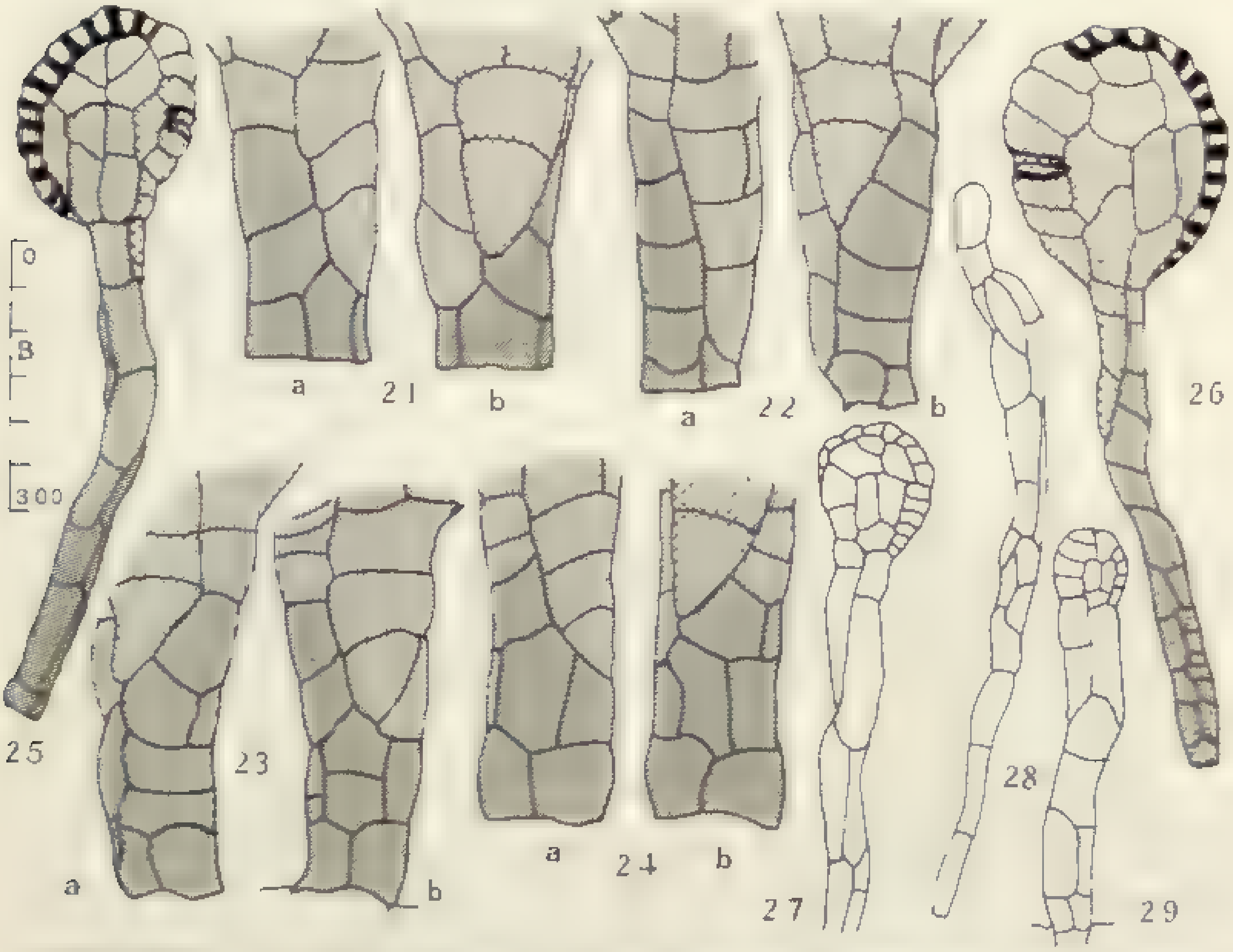
The divisions that take place in Segments I, II, III follow the general sequence described for *Xiphopteris serrulata* and for *Phlebodium aureum* (Wilson 1958a, 1958b). Segment I, then, when mature is composed of a tetrad of cells in its distal portion which forms part of one of the lateral faces of the capsule. Beneath these four cells is a row of three or four cells that form part of the stalk (figs. 18a, 25). Segment II is the segment in which the stomium forms,



FIGS. 1-20. Sporangial ontogeny in *Anarthropteris Dictyopteris.* 1-9, Internal segmentation; 10-20, Superficial segmentation. (Both sides of each sporangial primordium are illustrated and designated by the letters "a" and "b.") Figs. 1-24 drawn to scale "A," figs. 25-29 drawn to scale "B"; both scales in microns.

and in addition to contributing cells to the stomial region of the annulus, this segment also contributes cells to each face of the capsule as well as to the sporangial stalk (figs. 19b, 25, 26). Segment III contributes cells to the formation of the bow, to each of the sporangial faces, and to the sporangial stalk (figs. 25, 26). The cap cell, Segment IV, becomes subdivided and differentiated so as to form part of the bow, a portion of the epistomium, and also a portion of both sporangial faces (figs. 25, 26).

There seems to be no definite regularity in the divisions that take place in Segment *O*. Although the first two or three divisions in this stalk-forming segment are as a general rule transverse, the subsequent divisions may result in the intercalation of transverse walls, longitudinal walls, or at times even oblique walls. Vertical divisions may take place early in the ontogeny of the sporangium. Longitudinal walls have been seen in the lower cell of Segment *O* during the period of the formation of the tapetal initials (fig. 6). There is no precise sequence or pattern in the intercalation of the vertical walls. Most frequently the basal cell becomes divided by a longitudinal wall, or at other times two or more divisions



FIGS 21-29. Sporangial ontogeny in *Anarthropteris Dictyopteris*. 21-24. Various types of segmentation in the sporangial stalk; 25, Mature sporangium, proximal face; 26, Mature sporangium, distal face; 27, 29, Aborted sporangia; 28, Mature paraphysis.

may take place in this cell (figs. 8, 9, 15-26). Similar divisions may occur in other cells of Segment *O*, so that one or more cells of this sporangial segment may be subdivided by longitudinal walls. Occasionally the divisions that take place are oblique rather than vertical (figs. 8, 18). In some instances, after the vertical or oblique divisions have taken place, additional horizontal walls are formed which subdivide the cells (figs. 23b, 26).

Although most of the vertical or oblique divisions occur in the cells of Segment *O*, the lowermost cells of Segment I also rarely divide in a similar fashion (figs. 22a, 23b).

Mixed among normal young and mature sporangia are found both paraphyses and elongated, aborted, tannin-filled sporangia in various stages of development (figs. 27, 29). Even these aborted sporangia show the longitudinal walls in the cell of the stalk.

The paraphyses of *Anarthropteris* develop well before the sporangia are initiated. Unfortunately none of the material available was young enough to permit a study of their ontogeny. From an examination of the mature paraphyses it is not possible for me either to support or reject the interpretation that they represent transformed sporangia.

DISCUSSION

The study of the ontogeny of the sporangium of *Anarthropteris Dictyopteris* serves once again to emphasize the conclusion reached in the studies of the development of the sporangia of *Phlebodium aureum* (Wilson, 1958a) *Xiphopteris serrulata*, and *Pyrrosia nuda* (Wilson, 1958b), that the stalk of the sporangium is not produced by the activity of a tetrahedral apical cell as has been repeatedly described in the text-books of morphology during the last several decades (see, Bold, 1957; Foster and Gifford, 1959). Instead the sporangial stalk results from cells intercalated in the first-formed segments of the sporangial primordium.

The subdivision of the capsular segments of *Anarthropteris* follows the same pattern as that of *Phlebodium*, *Xiphopteris* and *Pyrrosia*, and in all, Segment I contributes to a portion of the stalk and a part of the proximal face of the capsule, Segment II to the stomial region and the stalk, and Segments III and IV to the rest of the annulus. The proximal face is formed from cells of Segments I, II, III and IV, and the distal face from those of Segments II, III and IV.

The first division of the sporangial initial is vertical or only slightly inclined and the wall is produced above the level of the surface of the adjacent receptacular cells. This same type of division occurs in the sporangial initial of *Xiphopteris serrulata*, and as a result of the position of the first-formed wall the sporangial stalk of *Xiphopteris* is one-rowed. But the stalk of *Anarthropteris* is irregular, and at different levels varies from one cell to three cells or pehaps even more. Morphologically the sporangial stalk of *Anarthropteris* is basically single-rowed at the base. This row, however, becomes complicated by the various longitudinal and oblique divisions that take place in the cells of the stalk. Contrary to Bower (1923) who reported that the "stalk-cell may undergo longitudinal cleavages, thus giving rise to the three-rowed stalk so common in Leptosporangiate Ferns," the longitudinal cleavages do not give rise to the common three-rowed stalk, but rather lead only to producing irregular stalks — the three-rowed portion remains undisturbed in *Anarthropteris* and subtends the capsule.

Very similar irregularities have been drawn to my attention by Alice F. Tryon in the two- or three-rowed stalks of *Jamesonia* which undergo longitudinal divisions and later cell enlargements that tend to make the interpretation of the sporangia very difficult.

Longitudinal divisions within the cells of the sporangial stalk apparently do not add regular rows to it but rather increase the number of cells in it in a very irregular manner.

The systematic position of *Anarthropteris* is still a matter of speculation. Whether the fundamentally one-rowed stalk of the sporangium indicates a relationship to the Grammitidaceae is by no means clear. Superficially there is a resemblance to *Loxogramme*, as was suggested by Copeland (1947), but so little is known about either genus that this affinity is far from certain. The sporangium of *Anarthropteris* is unique and differs from those of polypodioid and grammitid ferns in the irregularly divided one-rowed stalk. The gametophyte is not yet known, and the chromosome number of $n=37$ (Brownlie, 1958) does not help very greatly in indicating any relationship. The taxonomic position of *Anarthropteris* cannot be established with any degree of satisfaction without additional studies.

LITERATURE CITED

Bold, H. C. 1957. Morphology of Plants. xxiii + 669 pp. Harper, New York.

Bower, F. O. 1923. The Ferns. Vol. I. Analytical Examination of the Criteria of Comparison. ix + 359 pp. University Press, Cambridge, England.

Brownlie, G. 1958. Chromosome numbers in New Zealand ferns. Trans. Roy. Soc. New Zealand 85: 213-216, pl. 17. 1958.

COPELAND, E. B. 1947. Genera Filicum, the genera of ferns. xvi + 247 pp. Chronica Botanica, Waltham, Mass.

DOBBIE, H. B. 1951. New Zealand Ferns. Fourth ed. Revised and edited by M. Crookes. 406 pp. Whitcombe and Tombs, Auckland, New Zealand.

FOSTER, A. F., AND E. M. GIFFORD, JR. 1959. Comparative Morphology of Vascular plants. xi + 555 pp. Freeman, San Francisco.

WILSON, K. A. 1958a. Ontogeny of the sporangium of *Phlebodium (Polypodium) aureum*. Am. Jour. Bot. **45**: 483-491.

————. 1958b. Ontogeny of the sporangia in *Xiphopteris serrulata* and *Pyrrosia nuda*. Jour. Arnold Arb. **39**: 478-493.

————. 1959. Sporangia of the fern genera allied with *Polypodium* and *Vittaria*. Contrib. Gray Herb. **185**: 97-127.

OBSERVATIONS ON THE JUVENILE LEAVES OF PELLAEA ANDROMEDIFOLIA

ALICE F. TRYON[1]

The apogamous species of *Pellaea*, section *Pellaea* (Tryon 1957) are usually wide ranging and are morphologically distinct from the sexual types. A species in California, *Pellaea andromedifolia*, has apogamous members which are scarcely distinguishable from the sexual ones and have a limited and disjunct range. The sexual plants are diploid ($n = 29$) and the apogamous are probably polyploid although the count is not yet confirmed. Other apogamous races or varieties of this section are all polyploid (Tryon and Britton 1958). The most reliable differences that have been found in herbarium material of the two types are the number of spores in the sporangium and the corresponding differences in spore size. The apogamous plants occur within the range of the more widely distributed sexual phase. They have been identified from Baja California and in southern California in San Diego and Riverside counties and from Butte, Lake and Humboldt counties in northern California. The material with which this paper is concerned is the apogamous race collected among serpentine rocks on a grassy hillside with scattered oak trees. The plants grew in both sunny situations and in the shade, from crevices of large rocks (west of Redway, Humboldt county, California, *Tryon & Tryon 5556*, GH).

Spores from this collection and also from a collection of the sexual race were sown on soil in terra cotta pots which were placed in glass covered dishes and watered from below. Spores from apogamous plants germinated in ten days, while those from sexual plants germinated in eighteen days. The first sporelings were observed on the apogamous prothallia in three months. No sporelings were observed on the sexual prothallia at this time but they were then flooded with water and sporelings were evident two months later. During a vacation period the cultures were neglected, and although the apogamous plants remained vigorous, the sexual ones were lost.

The lamina of the adult leaf of *Pellaea andromedifolia* is elongate-triangular, 6-40 cm. long, imparipinnate, usually tripinnate (less often bipinnate or quadripinnate). There are about ten or twelve "pairs" of pinnae, usually alternate,

---

[1] For the use of specimens in the Gray Herbarium and for facilities in the greenhouse and culture chambers of the Biological Laboratory of Harvard University, I am most grateful.

up to 14 cm. long with 8-50 segments. The sterile ultimate segments are entire or ternate and usually ellipsoidal or ovate in form. The open venation of the sterile segment is unequally dichotomous with a central vein and nearly equally dichotomous ultimate veins (Fig. A). The margins of the sterile segments are slightly crenulate and the small crenations roughly correspond to the vein ends. The petioles of the adult leaves are straw colored to ruddy brown and dark brown only at the base or in spots or streaks above the base.

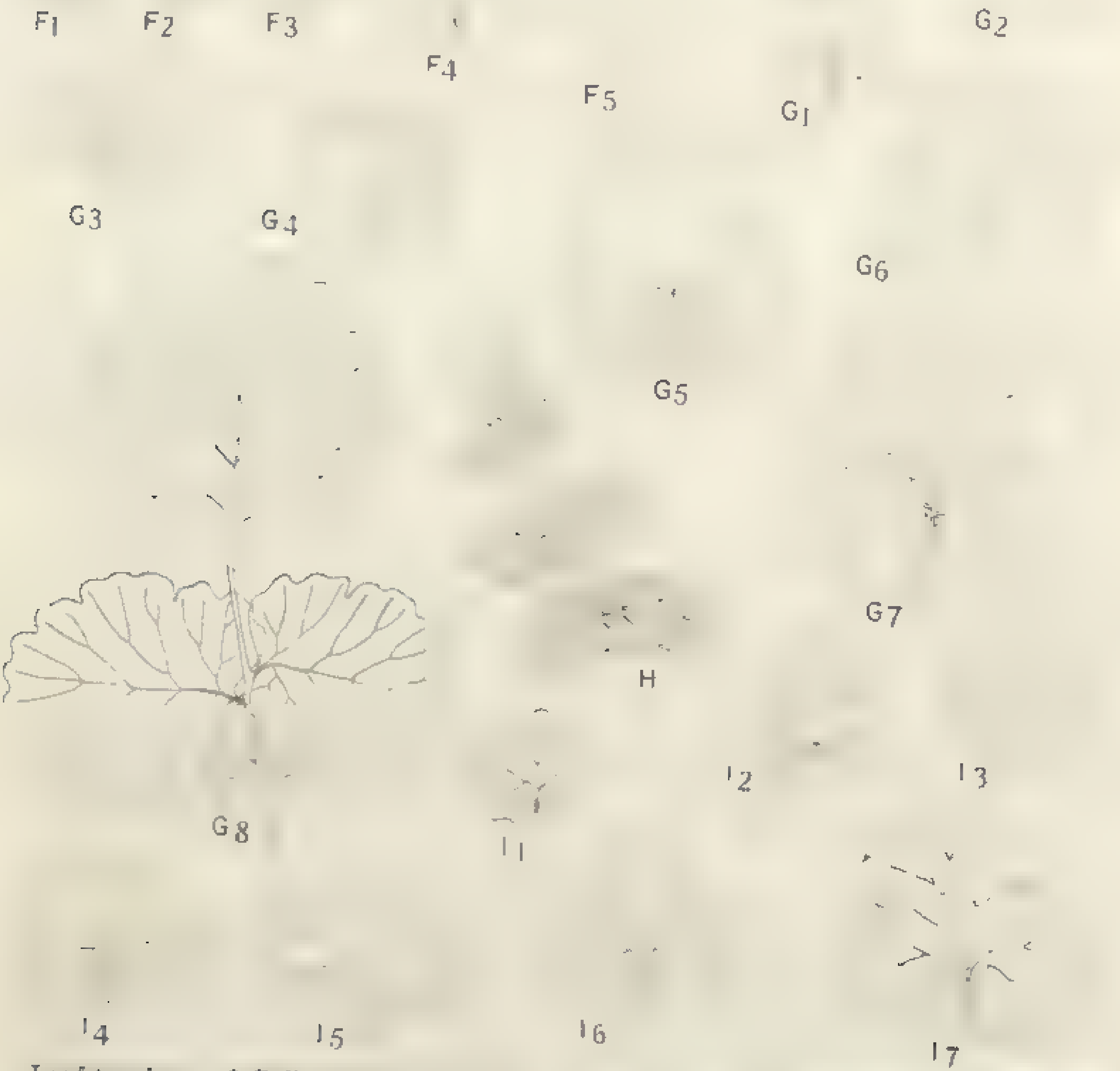
The juvenile leaves were examined on some 150 plants of *Pellaea andromedifolia* of different ages, varying from those with a single leaf on the prothallus to those with twelve leaves. Each series (Figs. D, E, F, G, I) illustrates the smallest to the largest leaves on a single plant. The intermediate stages are arranged from the sequences observed on several plants and may not be in strict order, but this will not affect the general conclusions. The illustrations were prepared from tracings of the leaves.

The initial leaf is small, usually slightly longer than the lobes of the prothallus (Fig. B 1, 2). The petiole arises from the cushion of the prothallus and is slightly longer than to twice as long as the lamina. The petioles of the first leaves are dark brown or blackish near the base. This color extends progressively farther up the petiole and in later juvenile leaves the petioles are wholly dark, the color obscuring the first dichotomy of the vascular system of the leaf. The lamina is broader than long and cordate. It has two large lobes, each with a pair of less developed lobes, or four nearly equal lobes which are shallowly bifid.

The vascular strand from the petiole divides into two equal branches near the apex of the petiole, usually in the expanded base of the lamina but sometimes at the apex of the petiole (Fig. C 1, 2). The two principal veins each divide equally in the base of the lamina. The subsequent branches again divide in the mid-portion of the lamina, resulting in eight, nearly equal, ultimate veins which end short of the margin (Fig. B 1; D 1). After the initial leaf, some four to seven additional leaves are formed which resemble the first but with a general increase in size and subsequent extension and branching of the veins. The central sinus becomes deeper and the two lateral sinuses deepen also (Figs. D 2-6; E 3-6; F 2-5; G 2-4). There is a marked resemblance between each of these lobes and the lamina of the initial leaf which gives the impression that they are parts of a repeated or duplicated system. Up to this point the leaves are quite unlike the adult leaf. An abrupt change of form occurs usually between the sixth to the ninth leaf when a terminal lobe, demarked by strong lateral sinuses, is developed, having an unequally dichotomous venation with a pronounced central vein (Fig. D 9, 10; E 9; G 5, 6). This stage seems to be the forerunner of the adult condition, and the series of leaves which follow appear more like the adult sterile leaf. The first leaf of the adult type is compound with three distinct pinnae borne on short, dark colored stalks, and each of these pinnae has a central vein and ultimate dichotomous veins (Fig. G 7). In later leaves the stalk of the terminal pinna elongates and rachis develops (Fig. G 8). Subsequent leaves bear additional pinnae along the rachis and these in turn become compounded (Fig. H). As the pinnae increase in size, the marginal lobes become less prominent crenations.

Leaf-tracings of Pellaea andromedifolia. - Fig. A. Pinna of adult leaf. × 1½. — Fig. B. Separate plants with initial leaves attached to prothallia. × 3. Fig. C. Juvenile leaves showing position of first vascular dichotomy. × 3. Figs. D and E. Sequences of juvenile leaves from individual plants. × 3.

Variations from the above sequence were noted. In some plants the initial leaf was only bilobed, or the four-lobed type had one or more lobes of larger proportions; or more than four lobes were formed (Fig. E 1). It was observed that occasionally among the first formed leaves there is one of a more advanced form which is often attached at the base of the prothallus near the soil. These are noticeably larger (Fig. B 3) than the usual type; the petiole may be short and rigid, and the lamina has a terminal lobe with a prominent central vein. The initial leaves of this kind are usually succeeded by those with two or four lobes and equally dichotomous venation but some plants were noted with more than one leaf of this advanced form (Fig. I 2, 3).



Leaf-tracings of Pellaea andromedifolia Figs. F. G. I. Sequences of leaves from individual plants. × 3. Fig. H. A twelfth leaf with the adult form, × 1½.

In *Pellaea andromedifolia* the sequence of juvenile leaves proceeds from an equally dichotomous plan of venation and lobing through an abrupt transition to one of pinnate arrangement with distinct pinnae and unequal dichotomy of the principal veins. The recognizable, repeated form and sequence in these leaves is evidence that there is an inherent pattern in the juvenile leaves. The variations from the normal sequence which have been observed may be a response to certain nutritional states.

Other investigations which have been made on juvenile leaves of ferns are mainly concerned with phylogenetic relationships or physiological processes. Some of these that are pertinent to the observations on *Pellaea* are reviewed. The work of R. Orth (1938), on the morphology of juvenile leaves of 17 species of ferns native to Germany, shows that in each species there exist certain patterns and that these can be classified in four groups. On the basis of the four-lobed initial leaves, *Pellaea andromedifolia* belongs to the same group as *Pteridium aquilinum* and is similar to it in general form. Orth illustrated the sequence of leaves on a single plant for a few species but most of his examples are drawn from selected stages. Comparisons are drawn with the adult form in each species and the variations in different parts of the same adult leaf are considered.

In his studies on *Diellia*, W. H. Wagner (1952a) draws comparisons with the aspleniaceous genera illustrated by Orth and remarks on the limitations of the system of classification based on the initial leaves. The three species of *Diellia*, illustrated by Wagner, have the first leaf entire with a single unbranched vein, or two-lobed with equal dichotomous venation and these would be placed in two different groups in Orth's classification. The form of the sporeling leaves in *Diellia* is different from that in *Pellaea andromedifolia* in having a simple lamina with few irregular lobes. The compound condition is reached after the ninth or tenth leaf and the venation progresses from a simple or equally dichotomous condition to a reticulate one. Wagner (1952b), using a technique of mass sampling, illustrates comparative series of juvenile leaves in *Polypodium virginianum* and *P. aureum*. The series of the former resembles that illustrated by Orth for the closely related *P. vulgare* more than it does the series in *P. aureum* — thus, characters of the juvenile leaves support those of other parts of the plant in showing the relationships of these three species.

Phylogenetic conclusions have been drawn on the basis of the form and vein pattern in juvenile leaves and it is of interest to examine these since there are two essentially opposed points of view. It was proposed by F. O. Bower (1923) that an understanding of the evolution of the fern leaf and its architecture will be found, in part, in the comparison of the juvenile and adult leaves of the same plant. He draws such comparisons and illustrates the sequence of leaves in *Anemia adiantifolia*, *Osmunda regalis*, and *Cyathea insignis*. There are marked differences in form between the series shown for each species; however, the initial leaf in each case has equally dichotomous veins and shows a progressive change to unequal dichotomy with the development of the central vein in the major segments. Bower (1923, p. 88) concludes: "Comparison of the juvenile leaves of other Ferns supports the view that equal dichotomy was the prior, and probably the original state in the construction of the leaf, and that some form or another of dichopodium of the main veins is a state derivative from it".

The most recent work in which phylogenetic conclusions are drawn, in part, from juvenile leaf form is that of W. H. Wagner (1952c), and his conclusions are quite opposed to those of Bower. Foliar dichotomy, including vascular dichotomy, is considered to be a modification of ancestral pinnately-organized leaves. Wagner (1952c, p. 591) states, "Foliar dichotomy in living ferns appears to represent de novo dichotomy rather than retained psilophytalean dichotomy". One of the sources of difficulty in a comparison of the theories of Bower and Wagner is a matter of terminology and this is apparent in reference to the juvenile leaves. The leaves which Wagner describes as midribless and midribbed are referred to by Bower as equally dichotomous and sympodially dichotomous respectively. The terms pinnate and dichotomous have been applied as opposing terms; however, the former refers to a kind of arrangement and the latter to a type of branching.

Wagner uses the juvenile leaves in *Osmunda cinnamomea* as evidence for his theory on the derived dichotomous condition. He notes that in a few leaves a "papillate" structure is formed between the lateral segments of the young leaves. These are interpreted by Wagner (1952c, p. 579) in terms of his midribless and midribbed condition: "intermediate conditions, i. e., with 'papillae' are occasionally found, the 'papillae' presumably analogous to abortive apices of leaves in the Gleicheniaceae". He reports that in nine species: "Intermediates have been found so far in one form or other". In this last statement it is not entirely clear what is meant by "intermediates" for only three of the examples are papillate. Of these three, a series of sporeling leaves is illustrated only in *Osmunda cinnamomea* and here the papillate condition is preceded by leaves of the two- or four-lobed form with equally dichotomous venation.

Among the physiological investigations, morphogenetic studies by R. H. Wetmore (1953, 1954) have been made on juvenile leaves of *Todea barbara, Osmunda cinnamomea, Cyrtomium falcatum* and *Pteridium aquilinum* var. *latiusculum*. In these the juvenile leaf form was changed through variation of the sugar concentration in the media upon which the plants were grown. On media containing a low sucrose concentration (0.1%) the first several leaves on each plant were all of the two-lobed type. On media containing a higher sucrose concentration (0.5%) the initial leaf and those following, prior to the production of a more complex type, were nearly all three-lobed, and the two-lobed type was rare. Wetmore (1954, p. 34) reports on this experiment: "Never was a two-lobed leaf evident on media containing 1 percent and 2 percent sucrose. Here the normal sequence was quickly dispensed with and pinnate leaves of the adult nature were the regular type". Wetmore examined the meristematic centers of juvenile leaves and indicated that the shape of the leaf is determined by meristematic activity along the margins and at the apex of the leaves. The two-lobed leaves result largely from marginal extension of the meristem, and when this is supplemented by apical cell division, the three-lobed or pinnate leaf is formed. He concludes that the sequence of development as observed in sporeling leaves is influenced by the carbohydrate concentration and that it is difficult to see a recapitulatory sequence.

Regenerated tissue on excised sporeling leaves was reported by E. W. Brown (1918) in *Phegopteris polypodioides (Thelypteris Phegopteris)*. The new, induced tissue formed a prothallial-like structure from which four leaves were produced. The first two were most complex, having three lobes each with a strong central vein, and these were followed by a leaf with two lobes and equally dichotomous veins and a final leaf which was entire with a single vein. The nutritional state was considered as a possible factor in this sequence. Whatever the cause, the example does illustrate a sequence of leaves in reverse order of that found in the juvenile leaves of normal plants and that the potential for each of these forms also exists in regenerated tissue.

The prothallus and sporeling leaves of *Pteris longifolia* were studied by H. G. Albaum (1938) in an investigation related to growth substances and metabolism. Albaum indicated that upon the initiation of the first leaf the center of growth is transfered from the prothallus to the meristematic areas of the leaf. A successful test was made for growth substance and experiments were conducted, using 3-Indole acetic acid, which controlled the production of sporeling leaves.

In conclusion, it has been shown that the sequence of juvenile leaves in *Pellaea andromedifolia* proceeds from a two- or four-lobed lamina with equally dichotomous veins to a more complex type with the initiation of a terminal segment and a prominent central vein formed by unequal dichotomy. In this series as well as in those illustrated by Orth, Wagner and Bower, certain characteristics are apparent in the juvenile leaves which may supplement those of the adult leaves in understanding the relationships of ferns. The juvenile leaves have been examined in relatively few species of ferns. It is evident from such studies as have been made that a synoptical survey would be worthwhile. There is, however, no reason to believe that in the juvenile leaves there is any evidence to be derived in support of theories pertaining to the evolution of the fern leaf. The studies by Wetmore show that, within the juvenile plant, the potential for the production of a leaf of either simple or more complex form may be influenced by variations in the nutritional state.

LITERATURE CITED

ALBAUM, H. G. 1938. Inhibitions due to growth hormones in fern prothallia and sporophytes. Amer. Journ. Bot. **25**:124-132.

BOWER, F. O. 1923. The Ferns. Vol. I. Analytical Examination of the Criteria of Comparison. 359 pp. University Press. Cambridge, England.

BROWN, E. W. 1918. Regeneration in Phegopteris Polypodioides. Bull. Torr. Bot. Club, **45**:391-397.

ORTH, R. 1938. Zur Morphologie der Primärblätter einheimischer Farne. Flora **133**:1-55.

TRYON, A. F. 1957. A revision of the fern genus Pellaea section Pellaea. Ann. Mo. Bot. Gard. **44**:125-193.

TRYON, A. F. AND D. M. BRITTON. 1958. Cytotaxonomic studies on the fern genus Pellaea. Evolution **12**:137-145.

WAGNER, W. H. 1952a. The fern genus Diellia; its structure, affinities and taxonomy. Univ. Cal. Publ. Bot. **26**:1-212.

———— 1952b. Juvenile leaves of two Polypodies. Amer. Fern Jour. **42**:81-85.

———— 1952c. Types of foliar dichotomy in living ferns. Amer. Jour. Bot. **39**:578-592.

WETMORE, R. H. 1953. Carbohydrate supply and leaf development in sporeling ferns. Science **118**:578.

———— 1954. The use of "in Vitro" cultures in the investigation of growth and differentiation in vascular plants. Brookhaven Symp. Biol. **6**:22-40.

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

EDITED BY

REED C. ROLLINS AND ROBERT C. FOSTER

NO. CLXXXVIII

CYTOTAXONOMIC AND EVOLUTIONARY STUDIES IN THE NORTH AMERICAN SPECIES OF GUTIERREZIA (COMPOSITAE)

BY

OTTO T. SOLBRIG

THE SOUTH AMERICAN SECTIONS OF ERIGERON AND THEIR RELATION TO CELMISIA

BY

OTTO T. SOLBRIG

PUBLISHED BY

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

1960

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXVIII

CYTOTAXONOMIC AND EVOLUTIONARY STUDIES IN THE NORTH AMERICAN SPECIES OF GUTIERREZIA (COMPOSITAE)

By

Otto T. Solbrig

THE SOUTH AMERICAN SECTIONS OF ERIGERON AND THEIR RELATION TO CELMISIA

By

Otto T. Solbrig

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

Issued December 13, 1960

Manufactured
by
The Lexington Press, Inc., Lexington, Massachusetts

CYTOTAXONOMIC AND EVOLUTIONARY STUDIES IN THE NORTH AMERICAN SPECIES OF GUTIERREZIA (COMPOSITAE)[1]

Gutierrezia is an American genus of *Compositae-Astereae* found in western America, Mexico, and southern and western South America. The genus is poorly known botanically. Several species have been described, but no intensive taxonomic study of them has ever been made. Morphological and cytological studies are also lacking.

The principal objective has been to study the genus from various approaches, such as cytology, morphology, distribution, ecology, including detailed investigations of populations in nature. Unfortunately the problem of transportation to the different localities where *Gutierrezia* grows, as well as lack of time, has prevented the author from studying all species with the same degree of intensity. This applies particularly to the South American representatives, which had to be excluded from this study for these reasons.

This work is therefore not primarily a systematic study, although a taxonomic revision of the North American species is attempted. Nevertheless it is hoped that this study, incomplete as it is, will help to clarify the taxonomy of the genus and furnish some information about the life-history of its species.

ACKNOWLEDGMENTS

Professor Lincoln Constance gave invaluable help during the course of this investigation and the preparation of the manuscript. Hours of conversation relating to subjects botanical and otherwise gave me a better and wiser understanding of science. Professor Herbert G. Baker's advice was very helpful in providing other dimensions and outlooks to the problems encountered and so was the help received from Professor G Ledyard Stebbins, Jr. To all three of them I express my sincere thanks.

A large number of persons have aided this work in various ways. Drs. H. Arnott, R. Bacigalupi, Marion S. Cave, D. S. Correll, F. W. Gould, R. H. Miller, R. Ornduff, P. Raven, Helen Sharsmith, L. Shinners, B. C. Tharp, G. W. Thomas, R. K. Vickery, Jr., U. T. Waterfall, W. A. Weber, Messrs. J. Swanson and E. C. Twisselmann and Miss Francia Chisaki obtained seeds or living material of *Gutierrezia* and or provided other information or help towards a better understanding of the problems. I am very grateful to all of them.

A "James Gowey Fellowship in Botany" from the University of

---

[1] Revised from a thesis submitted, in partial fulfillment of the requirements for the degree of Doctor of Philosophy, to the Graduate Division of the University of California, Berkeley.

California, Berkeley, permitted me to devote full time to research during the last year of graduate work. Grants in aid from the "Associates in Tropical Biogeography" and the "Patent Fund" of the University of California made field work in Mexico, South America, and the United States possible.

I have studied material from the following herbaria, to whose curators I wish to express my appreciation for making this possible: Academy of Natural Sciences of Philadelphia; California Academy of Sciences; Chicago Natural History Museum; Gray Herbarium and Arnold Arboretum of Harvard University; Jepson Herbarium, University of California; Missouri Botanical Garden; New York Botanical Garden; Pomona College; Rancho Santa Ana Botanical Garden; Rocky Mountain Herbarium, University of Wyoming; Southern Methodist University; United States National Herbarium; University of California, Berkeley; University of California, Los Angeles; University of New Mexico; University of Washington; and Washington State University.

HISTORY OF THE GENUS

The genus *Gutierrezia,* with the one species, *G. linearifolia,* was described in 1806 by Lagasca. It is dedicated to a member of the Spanish noble family Gutierrez. The type-material is unknown, since no specimens named by Lagasca exist and the original description is so general that it fits several modern species. Lagasca indicated the type locality only as "Hab. in *N. H.*" (Habitat in "Nova Hispania"?). The only other use of the name *G. linearifolia* Lag. known to me is that by Hooker and Arnott (1835) for plants collected by Darwin in South America. The description and the localities given suggest that they referred to what we know today as *G. Gilliesii.* Asa Gray (1884) noted that, "*G. linearifolia* Lag., the original species (of which no specimen named by Lagasca is extant) . . . may with the highest probability be referred to a Chilean species, the *Brachyris* [*Gutierrezia*] *paniculata* D.C." This species is closely allied to *G. Gilliesii* and its characters correspond to Lagasca's description.

Pursh (1814) described specimens collected by Lewis "on the plains of the Missouri" as *Solidago sarothrae.* Nuttall (1818), unaware of Lagasca's paper, described the new genus *Brachyris* and the species *B. euthamiae* based on material collected by himself and on *Solidago sarothrae.* A second species of *Brachyris, B. divaricata,* was described by the same author in 1841. Sprengel (1825) changed *Brachyris* into *Brachyachyris;* he stated no reason for this change, but it is supposed that it was purely etymological[2].

De Candolle (1836) was the first to study the totality of the material then known. He accepted Nuttall's *Brachyris,* dividing it into two sections, *Eubrachyris* and *Amphiachyris.* Under *Eubrachyris* he placed *B. euthamiae* Nutt. and five species newly described by himself; in *Amphiachyris* he placed another new species, *B. dracunculoides* DC. In addition he established the genus *Hemiachyris,* with one species, *H. texana* DC., and the genus *Odontocarpha* for a new species from Chile, *O. Poeppigii,* and placed this last genus in the tribe *Vernoniae,* its clearly asteroid characters notwithstanding.

Hooker and Arnott (1841) recognized that *Gutierrezia* and *Brachyris* were congeneric and further remarked, "We are far from certain if the *B. paniculata, euthamiae, californica* and *texana* are not all forms of the *G. linearifolia* Lag." This seems to indicate that Lagasca's species was not included among those specifically named. If this is so, the original material must come from South America, since, aside from the species indicated above, no other North American species fit the original description.

Torrey and Gray, in the "Flora of North America" (1841-43), did not include in their treatment of *Gutierrezia, Amphiachyris dracunculoides,* which had been elevated to generic rank by Nuttall (1841). However, they did include *Gutierrezia texana* (DC.) T. & G. In their study they recognized fewer species than did De Candolle; Asa Gray's treatment in the "Synoptical Flora" (1884) does not differ appreciably from that of 1841.

Hoffmann, in his monograph of Compositae (1897), for Engler's "Pflanzenfamilien", divided *Gutierrezia* into three sections, *Brachyris, Amphiachyris,* and *Hemiachyris.* His characterization of the sections is similar to that of De Candolle, who had described *Hemiachyris* as a genus.

No monographic study of *Gutierrezia* has been attempted since De Candolle, and the North American species were treated for the last time by Gray in 1884. Nevertheless, more than 50 species have been described from North and South America since then by various authors, particularly E. L. Greene, R. Philippi, J. Lunell, P. A. Rydberg, and more

---

[2] In the original description Nuttall derived the name *Brachyris* from *Brachys:* short, and *Achyris:* chaffy scale.

recently S. F. Blake, A. Nelson, and A. L. Cabrera. The genus has been studied on several occasions for different local floras; the various authors differ in their treatments, but they coincide in placing in synonymy a large number of the described taxa.

CYTOLOGY AND GENETICS

The investigation of chromosome number and morphology as an aid to taxonomy and evolutionary understanding is a well known technique. The analysis of artificially obtained interspecific hybrids has also been used widely enough to necessitate no introductory emphasis. Both of these approaches have been used in the present investigation.

CROSSES AND RESULTS

Plants were grown in the greenhouse of the Department of Botany of the University of California at Berkeley in the spring and fall of 1956, from seed obtained partly by the author and partly by various correspondents. The seeds were germinated in two-inch pots and the plants were later transferred to four-inch pots. A second transplantation was performed, usually a year later, to eight-inch pots. Several plants were grown from each seed collection. In the fall of 1957 a large number of the plants were transplanted to the experimental area of the University of California Botanical Garden in Strawberry Canyon.

To perform crosses, the maternal plants were decapitated with a razor blade just before the tubular flowers opened, and were then washed for several minutes with a thin jet of luke-warm water from a plastic squeezing-bottle. The washing was repeated twice a day until the stigmas came out. To avoid accidental pollination by insects, the heads were covered with a net of cheesecloth. The heads were pollinated by hand and pollination was also effected by tying together heads from the parent plants under the cheesecloth net.

All the crosses were done reciprocally between both parents and were repeated several times in each case. Control tests were run with unpollinated decapitated heads which did not set seed in any case, and with non-decapitated heads covered with the cheesecloth net, which did set some seed. This was taken as an indication of self-compatibility.

A few words about seed setting in *Gutierrezia* species might be appropriate here. It has been observed that a large amount of *Gutierrezia* seed collected in the field does not germinate. This might be due to a lack of optimal conditions in the laboratory, but since morphological examinations indicated a large amount of shrunken and apparently inviable seed, it seems likely that the species of *Gutierrezia* are poor seed producers. It is assumed that poor pollination is accountable for this, but it is likely also that the physiological balance needed for seed production is very delicate and easily upset. The possibility therefore exists that the failure of the crosses attempted is attributable to physiological and not genetical causes.

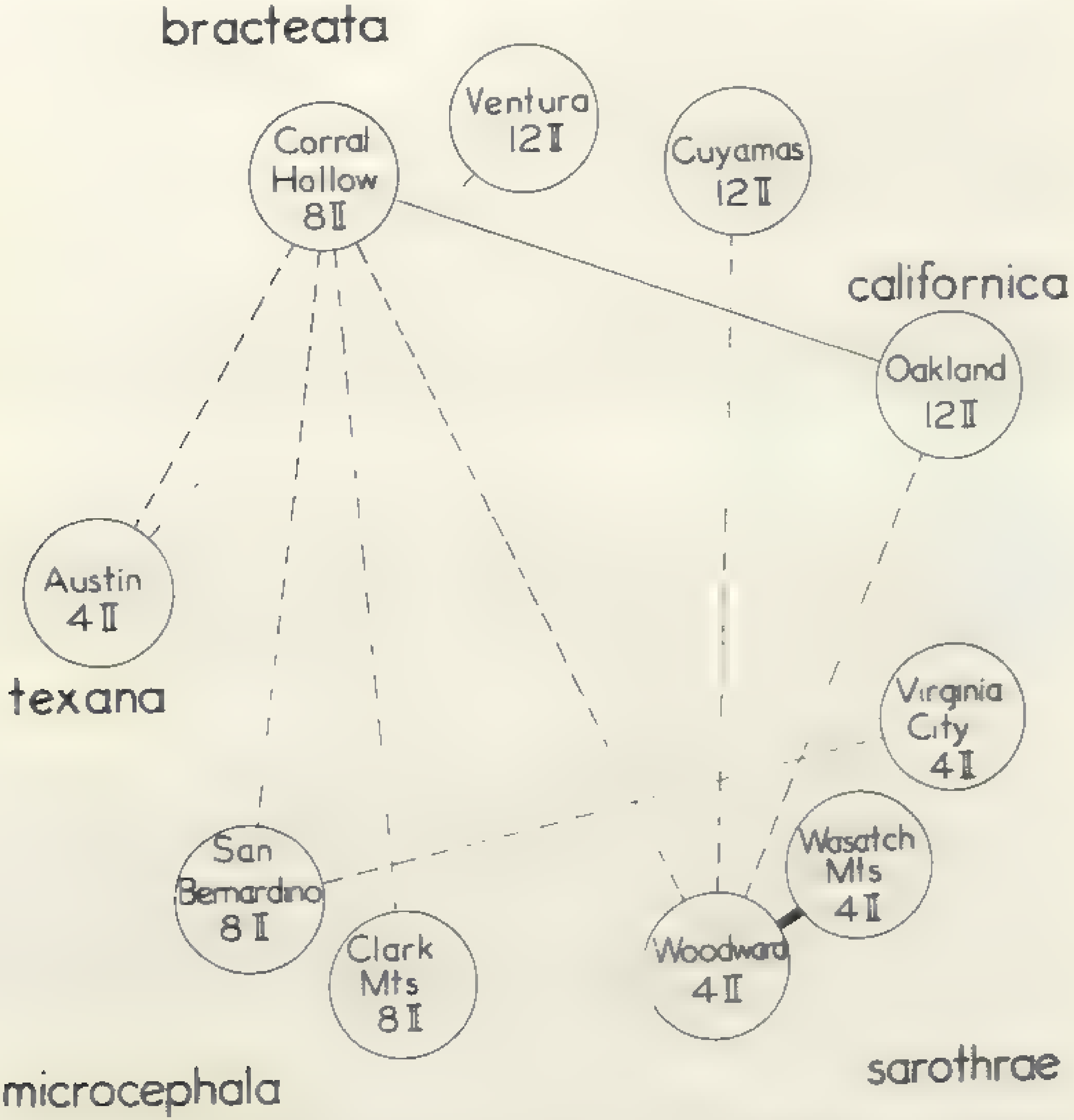


FIG. 1. Attempted artificial crosses between species of *Gutierrezia*. A thick full line represents a presumably fertile cross; a thin full line indicates a sterile hybrid; a dotted line indicates that no hybrid was obtained.

In figure 1 are depicted the crosses attempted and the results obtained. As can be seen, in only one case was a cross between two different levels of ploidy successful. The hybrid plant obtained from several attempted crosses between *G. californica* ($n = 12$) and *G. bracteata* ($n = 8$), was very slow growing and abnormal in appearance. The plant was sterile and the meiotic analysis revealed that division of PMC's was arrested at metaphase I and consequently no pollen was formed.

The only other successful cross was one between members of two populations of *G. sarothrae* from Nevada and Colorado, respectively. The population from Nevada belongs to the more robust and erect form, while that from Colorado is a rather dwarfed form of slow growth. Several plants were obtained from this cross and the hybrids were vigorous and of normal appearance. Unfortunately, the plants were accidentally lost before meiosis could be studied.

The planning of hybridization experiments conducted during 1956 and 1957 was hindered at the time by a poor knowledge of relationships in the genus. It is now realized that the significance of these crosses is less than might have been anticipated because of two main reasons: (1) the crosses attempted were not always those which might have shed the most light on an understanding of the evolution of the group; and (2) the work is incomplete and more experiments are needed. Technical difficulties also taxed heavily the success of this approach. Nevertheless, one conclusion of taxonomic and evolutionary significance can perhaps be drawn. That is the experimental confirmation of the theoretical assumption that in *Gutierrezia,* polyploidy presents an effective barrier to genetic interchange. Occasional hybrids between plants with different chromosome numbers can be obtained in the experimental garden and are found in nature (see next subsection), but if an occasional exchange of genes between different polyploid levels occurs, it must be rather exceptional and of little evolutionary significance. A mechanism for an interchange of genes between different levels of ploidy, as discovered by Zohary and Nur (1959) in *Dactylis,* is not likely.

CYTOLOGY

TECHNIQUE. Studies were made of mitosis in root tips and of meiosis in dividing pollen mother cells.

Root tips were obtained both from germinating seeds and from growing seedlings and fixed in Carnoy's fixative, or in any one of several modifications. The root tips were then macerated in the usual way with 1 N HCl or a mixture of concentrated HCl and 95% ethyl alcohol and then placed in a drop of aceto-carmine or aceto-orcein on a slide and squashed under a cover glass. Some root tips were processed according to the Feulgen technique.

Most floral buds used for the study of meiosis were fixed in the field; others were obtained from plants grown in the greenhouse or the Botanical Garden. Buds were fixed in 3 parts absolute alcohol and 1 part glacial acetic acid for 24 hours and then washed twice and stored in 70% ethyl alcohol in the refrigerator at near 0° C. until they were processed. Propionic acid was used occasionally in place of glacial acetic acid. Drops of a saturated solution of $Fe(OH)_3$ in absolute alcohol, which acts as a mordant, were usually added to improve staining. Meiotic slides were prepared by teasing the flowers apart in a drop of aceto-carmine, heating slightly, and squashing under a cover slip. Permanent slides were made whenever possible.

RESULTS. Because of the small size of the chromosomes, studies of chromosomal morphology did not reveal any structural details. Pretreatment with paradichlorobenzene was equally unsuccessful for the same reason. The cytological investigation was therefore restricted to the determination of chromosome number and to the discovery of possible meiotic irregularities.

Gutierrezia texana and *G. glutinosa,* the only annual species of the genus, revealed a haploid chromosome number of four in all the plants investigated (Table 1). No irregularities in meiosis were noted.

Gutierrezia sarothrae and *G. serotina* (Table 1) both have four pairs of chromosomes. Meiosis was regular in all plants investigated. Four of the populations of *G. sarothrae* studied have eight pairs of chromosomes. Meiosis in these plants, as far as it has been possible to detect, is perfectly normal and no multivalents have been found.

Eight or twelve pairs were found in populations belonging to the *Gutierrezia bracteata* complex. Meiosis was usually normal, but some irregularities were discovered in several instances. Anaphase bridges were common, but no fragments could be detected, which indicates that the bridges were of the "sticky" type. Two plants belonging to different populations are remarkable enough to merit more detailed description.

TABLE 1. CHROMOSOME NUMBERS IN SPECIES OF GUTIERREZIA

Species	Locality	Collector		n	2n
G. sarothrae	12.6 mi. E. of Ash Fork, Arizona	Solbrig	2801	4	
	0.8 mi. E. of Hyde Park, Arizona	"	2805	4	
	12 3 mi. W. of Aguanga, California	"	2760	4	
	9.9 mi. S. of Santa Ysabel, California	"	2763	4	
	2 mi. W. of Temecula, California	"	2758	4	
	9.8 mi. S. of Santa Ysabel, California	"	2765	4	
	1.6 mi. W. of Rancho Sta. Fe, California	"	2769	4	
	8.5 mi. E. of Chula Vista, California	"	2766	4	
	6.2 mi. E. of Chula Vista, California	"	2768	4	
	11.1 mi. E. of Idyllwild, California	"	2773	4	
	Fort Collins, Colorado	A. Weber		4	
	Virginia City, Nevada	R. H. Miller		4	8
	Mt. Rose, Nevada	"		4	
	Field Creek, Oregon	R. Ornduff		4	
	Wasatch Mts., Utah	R. K. Vickery Jr.		4	
	Wasatch Mts., Utah	"		4	
	5 miles N. of Payson, Arizona	Solbrig	2794	8	
	9.8 mi. W. of Seligman, Arizona	"	2802	8	
	19.8 mi. N. of Roosevelt Dam, Arizona	"	2792	8	
	Jct. Payson-Phoenix and Hwy. 488, Arizona	"	2793	8	
G. serotina	17 mi. E. of Tucson, Arizona	"	2777	4	
G microcephala	Silver Canyon, White Mts., California	Rancho Santa Ana Bot. Gard.	9389	8	
	Morongo, San Bernardino Co., California	"	8382	8	
	10 mi. E. of Roswell, New Mexico	G. W. Thomas		8	
	5 mi. W. of Bronco, Texas	"		8	
	Hondo, New Mexico	"		8	
	Douglas, Arizona	Solbrig	2789	16	
G. bracteata	Cuyama Valley, California	"	2166	12	
	Padres Nat. Forest, California	"	2167	12	
	22.5 mi. E. of Idyllwild, California	"	2774	12	
	1.4 mi. N. of Jct. Hidden Valley & Parkfield roads, California	"	2830	12	24
	Kern & S. Luis Obispo Co. line, California	"	2753	12	
	Tahquitz Canyon, California	"	2775	12	
	Corral Hollow, California	"	2159	8	16
	Cache Creek, Yolo Co., California	Rancho Santa Ana Bot. Gard.	8	16	
	La Panza, California	Solbrig	2751	8	
	7.2 mi. W. of Patterson, California	"	2743	8	
G. californica	Oakland Hills, California	"	2154	12	
G texana	Red River St., Austin, Texas	B. C. Tharp		4	
	Austin Chalk, Austin, Texas	B. C. Tharp		4	
	Dallas, Texas	L. Shinners		4	
G. glutinosa	Matehuala, San Luis Potosí, Mexico	Solbrig & Ornduff	4590	4	
	San Luis Potosí, San Luis Potosí, Mexico	"		4	

The first is from a population in San Luis Obispo County, California. Most of the cells have eight pairs. Nevertheless we find a small number of multivalents (2%) and also univalents (8%). Supernumeraries, easily distinguishable by their size and disposition at meiosis, were also present. We are possibly in the presence of a small translocation here, but there may be also some homologies between non-sister chromosomes.

The other plant is from near Coalinga, Fresno County, California. In this area both eight- and twelve-chromosome populations occur, sometimes in the same locality. In this plant, most cells showed nine pairs of chromosomes, although it varied from nine to eleven. Univalents and multivalents were also present. The most plausible explanation is that this plant might be a hybrid between eight- and twelve-chromosome *Gutierrezia bracteata*, as the presence of 10 pairs in some cells would indicate, the tenth chromosome having been lost in a pre-meiotic division. The existence of cells with eight pairs and even eleven indicates the possibility of irregular division prior to meiosis. This does not rule out the origin of this plant through a back-cross, but this possibility seems to me to be remote.

Gutierrezia californica has 12 pairs of chromosomes in all the plants studied, and meiosis was regular.

The picture presented by the *Gutierrezia microcephala* complex is a very different one. The first plants investigated came from seed received from the Rancho Santa Ana Botanical Garden, and proved to have eight pairs of chromosomes at metaphase. It was observed at the time that there were very few PMC's undergoing meiosis in each preparation. This was attributed at the time to the fact that there are only one or two flowers per head with pollen. In the fall of 1958 buds were gathered from several populations in California and Arizona. These plants showed very irregular meiosis with little or no fertile pollen. Most cells which could be counted showed eight pairs of chromosomes, but some had 16 or even 32 chromosomes. One population of *Gutierrezia microcephala* showed 16 pairs of chromosomes and a regular meiosis.

As a result of these studies we may conclude that: (1) *Gutierrezia* is a polyploid complex with a base number of x = 4; and (2) different levels of ploidy are genetically isolated.

DISTRIBUTION AND ECOLOGY

Gutierrezia sarothrae is the most widely distributed of all North American species of the genus. It is found throughout the region extending from northern Mexico to southern British Columbia and Alberta in Canada, between the Sierra Madre Occidental and Sierra Nevada-Cascades in the west and the Great Plains on the east. It grows also in southern California and in Baja California, Mexico (fig. 2). *Gutierrezia californica* is restricted to the area of San Francisco Bay, California, while *G. bracteata* grows in the central and

FIG. 2. Distribution of *Gutierrezia sarothrae* (dotted area).

south Coast Ranges and from Inyo County to the Tehachapi Range and occasionally southward to about Baja California, Mexico (fig. 3). *Gutierrezia serotina* grows in an area

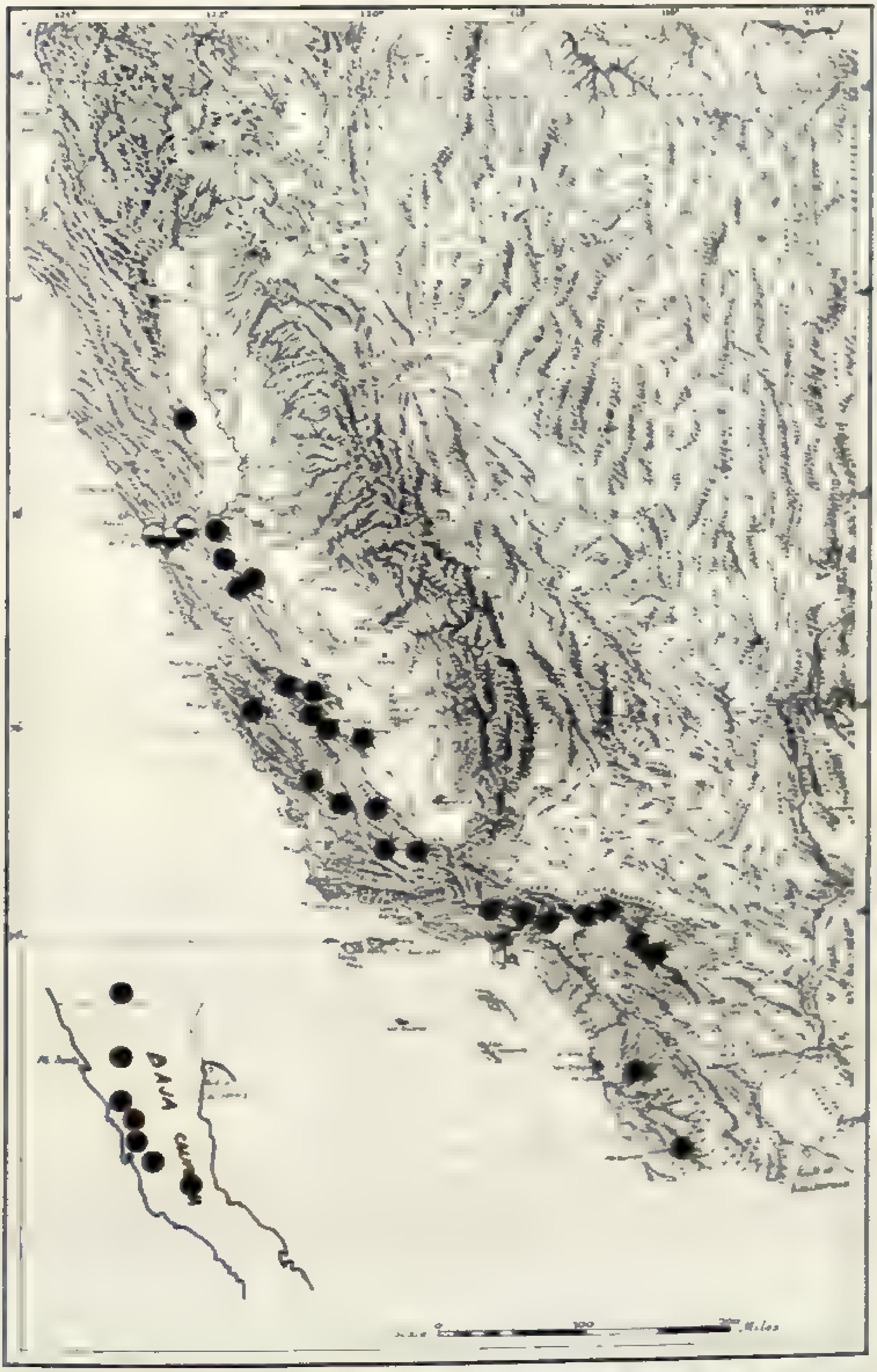


FIG. 3. Distribution of *Gutierrezia californica* (half-full dots) and *G. bracteata* (full dots). Physiographic map of California used by special permission of Ginn and Company. Copyright by Ginn and Co.

around Tucson, Arizona, and occasionally southward into Mexico. *Gutierrezia microcephala,* on the contrary, is more widely distributed, being found in a belt extending through southern California, Arizona, New Mexico, southwestern Texas, and northern Mexico(fig. 4). Finally, *Gutierrezia texana* ranges from northern Mexico to southern Oklahoma, and *G. glutinosa* from central Mexico to Texas, through northeastern Mexico and eastern New Mexico (fig. 5).

In order to discover whether or not environmental conditions determine this distributional pattern, it was necessary to investigate the ecology and distribution of the species of *Gutierrezia* in more detail. These studies consisted of careful observations of the type of distribution and growth, ecological preferences, and plant associates. Mechanical analyses were performed on 19 soil samples associated with six of the eight species, and several pH readings and some nitrate determinations of soils were made in the field.

SOIL STUDIES

Table 2 shows the results of mechanical analyses made on 19 soil samples from California, Arizona, Oregon and Idaho.

TABLE 2. MECHANICAL ANALYSIS OF 19 SOIL SAMPLES

Species	Coll. No.	Moisture[1]			Organic Matter			Coarse Sand		
		A	B	$\bar{x}$	A	B	$\bar{x}$	A	B	$\bar{x}$
G. sarothrae	2756	.060	.052	.056	.395	.401	.398	4.184	4.221	4.202
	2763	.224	.183	.203	.455	.432	.443	4.196	—	4.196
	2766	.242	.694	.468	.515	.394	.454	4.721	4.578	4.649
	2769	.326	.337	.331	.917	.806	.861	1.146	2.481	1.813
	2801	.556	.451	.503	.755	.707	.731	.390	.357	.373
	2905	.500	.360	.430	.647	.651	.649	1.664	2.257	3.417
	2912	.128	.118	.123	.739	.702	.720	2.579	—	2.579
	2792	.094	.090	.092	.312	.584	.448	2.970	2.750	2.860
	2794	.033	.051	.042	1.522	1.363	1.442	1.485	—	1.485
G. serotina	2777	.069	.063	.066	.284	.291	.287	5.452	5.394	5.423
G. microcephala	2807	.024	.009	.016	.123	.147	.135	6.793	6.981	6.887
	2789	.122	.107	.114	.657	.652	.654	2.773	2.839	2.806
G. bracteata	2722	.034	.034	.034	.450	.427	.438	3.475	3.552	3.513
	2604	.042	.074	.057	.304	.361	.332	2.487	2.940	2.713
	2755	.211	.147	.179	.575	.472	.523	1.638	1.942	1.790
	2723	.207	.173	.190	.511	.476	.493	4.646	4.799	4.722
	2748	.036	.010	.023	.164	.182	.173	6.462	5.786	6.124
	2743	.162	.142	.152	.625	.646	.635	1.986	—	1.986
G. californica	2428	.234	—	.234	1.605	—	1.605	3.420	3.297	3.358

[1] All measurements expressed in grams

TABLE 2 (cont.)

Fine Sand			Clay			Silt			Total		
A	B	$\bar{x}$	A	B	$\bar{x}$	A	B	$\bar{x}$	A	B	$\bar{x}$
4.132	4.766	4.449	.998	.506	.752	.100	.061	.080	9.869	10.007	9.937
4.319	—	4.319	.805	—	.805	.056	—	.056	10.055	—	10.022
3.089	3.564	3.326	.909	.863	.886	.103	.091	.097	9.579	12.114	10.846
3.541	3.328	3.434	3.305	2.952	3.128	.151	.146	.148	9.386	10.050	9.718
3.577	3.551	3.564	4.537	4.500	4.518	.105	.136	.120	9.921	9.702	9.809
3.225	3.321	3.273	1.938	3.280	2.609	.130	.158	.144	8.296	9.931	9.113
5.851		5.851	.294	—	.294	.152	—	.152	9.743	—	9.719
4.202	4.667	4.434	1.668	1.447	1.557	.053	.089	.071	9.299	9.627	9.463
4.921	4.549	4.735	1.159	.988	1.073	.056	.095	.075	9.179	—	8.852
3.021	3.233	3.127	.717	.691	.704	.058	.055	.056	9.601	9.727	9.664
2.708	2.547	2.627	.109	.076	.092	.100	.100	.100	9.854	9.860	9.857
4.195	4.173	4.184	1.696	1.509	1.552	.103	.071	.087	9.446	9.371	9.351
4.211	2.455	3.333	.774	.857	.815	.063	.054	.058	9.007	7.379	8.191
4.640	4.688	4.664	.685	.873	.779	.083	.070	.076	8.241	9.005	8.621
5.661	5.262	5.461	1.990	1.836	1.913	.256	.134	.195	10.331	9.793	10.061
2.580	2.634	2.607	1.413	1.520	1.466	.050	.060	.055	9.407	9.662	9.533
2.709	3.446	3.077	.373	.380	.376	.099	.099	.099	9.843	9.903	9.872
5.483	—	5.483	1.213	—	1.213	.113	—	.113	9.582	—	9.582
3.085	2.881	2.983	1.832	1.940	1.886	.095	.082	.088	10.271	—	10.154

TABLE 2 (cont.)

Species	Coll. no.	% Moisture	% Organic Matter	% Coarse Sand	% Fine Sand	% Clay	% Silt	Soil Type
G. sarothrae	2756	0.6	4.0	42.0	44.5	7.5	1.0	Sand
	2763	2.0	4.4	42.0	43.2	8.0	0.6	Sand
	2766	14.7	4.5	46.5	33.3	8.7	1.0	Sand
	2769	3.3	8.6	18.1	34.3	31.3	1.5	Sandy-Clay-Loam
	2801	5.0	7.3	3.7	35.6	45.2	1.2	Sandy-Clay
	2905	4.3	6.5	16.6	33.3	26.1	1.4	Sandy-Clay-Loam
	2912	1.2	7.2	24.2	59.0	3.0	1.5	Sand
	2792	0.9	4.5	28.6	44.3	15.6	0.7	Sandy-Loam
	2794	0.4	14.4	14.9	47.4	10.7	0.8	Sand
G. serotina	2777	0.7	2.9	54.2	31.3	7.0	0.6	Sand
G. microcephala	2807	0.2	1.4	68.9	26.3	0.9	1.0	Sand
	2789	1.1	6.5	28.1	41.8	15.5	0.9	Sand
G. bracteata	2722	0.3	4.4	35.1	33.3	8.2	0.6	Sand
	2604	0.6	3.3	27.1	46.0	7.8	0.8	Sand
	2755	1.8	5.2	17.9	54.6	19.1	2.0	Sandy-Loam
	2723	1.9	4.9	47.2	26.1	14.7	0.6	Sand
	2748	0.2	1.7	61.2	30.8	3.8	1.0	Sand
	2743	1.5	6.4	19.9	54.8	12.1	1.1	Sand
G. californica	2428	2.3	16.1	33.6	29.8	18.7	0.3	Sandy-Loam

The samples were taken in localities supporting a good growth of *Gutierrezia*. The soil surface was scraped clean of debris and vegetation, and the sample was taken from the upper layers where the bulk of the roots of the *Gutier-*

rezia plants were found. In every case only one horizon was involved.

The technique in the analysis of particle-size followed is the so called "Beaker method" as described by Piper (1942). The analyses were run on 10 grams of the soil sample after it had been passed through a 5-mm. screen and thoroughly mixed. Each analysis was repeated twice unless otherwise indicated.

The analysis was intended as a rough guide to detect possible gross requirements of the different species in relation to soil texture. As can be seen, the results are rather uniform, the variation in soil type is not great from sample to sample, and the differences cannot be correlated with the occurrence of any one of the species. This does not rule out variations in tolerance to different soil types by the species, especially to heavy soils, but this is still to be shown experimentally.

Table 3 indicates the results of pH readings performed in the field. A Beckmann portable pH meter was used in most cases, the readings being made directly from a soil solution extracted with distilled water. A few of the readings were obtained by a colorimetric method. The reason for making these readings was the same as that which led to the undertaking of soil analyses, and the results were similarly uniform. Table 4 shows the results of a few determinations of the content of nitrates in the soil. The nitrate was determined colorimetrically by the diphenylamine method from a soil solution extracted with a weak acid, with the aid of a commercial field soil kit known as the "La Motte Field Soil Kit". Since no significant differences were obtained, it was deemed unnecessary to perform more of these determinations.

TABLE 3. pH DETERMINATIONS MADE ON SOILS SUPPORTING GUTIERREZIA

Species	Locality	pH
G. bracteata	Corral Hollow, Alameda County, California	7.5
	Patterson, Santa Clara County, California	7.6
	La Panza, San Luis Obispo County, California	8.5
G. sarothrae	Idyllwild, Riverside County, California	6.4
	Temecula, San Diego County, California	6.2
	John Day, John Day County, Oregon	7.1
	Hansen, Twin Falls County, Idaho	9.2
	Ash Fork, Coconino County, Arizona	8.0
G. serotina	Tucson, Pima County, Arizona	8.0

Even though the analytical soil data failed to reveal any ecological differences between species, they provide some indication of the over-all requirements of the genus as a whole. The North American species of *Gutierrezia* seem to grow on loose, sandy, alkaline or neutral soils, and apparently those also with a low content of organic matter and nitrates.

A careful chemical analysis of the principal elements of the soil does not fall within the scope of this work. A chemical analysis *per se*, in the present state of our knowledge about the complex soil-plant relations, would not have been very significant in any case if it had not been complemented by experiments to determine the importance of trace elements, differential absorption of different soil constituents, etc. Nevertheless, it would be helpful if such data were to be available some day, especially in relation to *Gutierrezia californica sensu stricto* (see page 50). This species is of interest in this connection because of its restriction to the San Francisco Bay area and because it grows on serpentine soils.

TABLE 4. NITRATE NITROGEN DETERMINATIONS ON SOILS SUPPORTING GUTIERREZIA

Species	Locality	Nitrate p./million
G. bracteata	Patterson, Santa Clara County, California	1.5
	La Panza, San Luis Obispo County, California	1.5
G. sarothrae	Temecula, San Diego County, California	1.5

It is known that many species of plants cannot grow on serpentine, while others are restricted to it. Finally, a third group can grow either on or off serpentine (Kruckeberg, 1951, 1954, 1957). The reasons for this behaviour are not altogether clear; several authors have investigated this fascinating problem and various explanations have been suggested (Walker, 1954).

None of the species of *Gutierrezia* can be classed as a so-called "serpentine species" with the possible exception of *G. californica*. In northern California, where serpentine outcrops are rather common, the author knows of only four populations of *Gutierrezia* which grow unmistakably on serpentine: the Oakland Hills, Point Bonita, and Angel Island populations of *Gutierrezia californica* and the large serpentine outcrops of New Idria in the central Coast Ranges, where both eight- and twelve-chromosome populations of *G. bracteata* are found.

A few preliminary experiments were performed in order to determine tolerance to serpentine in different populations of *Gutierrezia californica* and *G. bracteata.* Seeds of the Oakland Hills population of *G. californica* and of the Corral Hollow and Cache Creek populations of *G. bracteata* (both of these last with eight pairs of chromosomes) were sown in two different pots, one with pure serpentine soil, and the other with a mixture of equal parts of sand and greenhouse top-soil. In each case both sets of seeds germinated normally and no difference could be detected relating to speed of ger-

FIG. 4. Distribution of *Gutierrezia glutinosa* (dotted area), *G. serotina* (half-shaded circles), and *G. grandis* (full shaded circles). Goode Base Map used by special permission, Dept. of Geography, Univ. of Chicago. Copyright by the University of Chicago.

mination or number of seedlings. The seedlings were later transplanted to individual pots and grown to maturity with the same type of soil as that in which they had been germinated. In all three cases the plants on soil grew slightly better than those on serpentine, notwithstanding the fact that one set of seeds (Oakland Hills) came from plants growing on serpentine in nature.

FIG. 5. Distribution of *Gutierrezia microcephala* (crosshatched area) and G. *texana* (black dots). Goode Base Map used by special permission, Dept. of Geography, Univ. of Chicago. **Copyright by the University of Chicago.**

This experiment, aside from showing that *Gutierrezia californica* can grow off serpentine under experimental conditions, also demonstrates that there is no element in serpentine deleterious by itself to the growth of those plants of *G. bracteata* which normally do not occur on serpentine.

In addition to the experiments just reported, plants from the Oakland Hills and Angel Island populations of *Gutierrezia californica* and from the New Idria population of *G. bracteata* (12-chromosome type) were grown in pots in the greenhouse and also in the Botanical Garden in common agricultural soil without any visible effect on them, aside from the production of larger and more vigorous specimens because of the greater care (mainly freedom from competition) and watering they enjoyed.

While performing these rough experiments the author observed that the pots which contained serpentine required more frequent watering in order to maintain in them the same moisture content as in pots containing non-serpentine soil. To verify this observation and its effect on the plants, a group of pots with plants of *Gutierrezia californica* (Oakland Hills population) and *G. bracteata* (Cache Creek population) grown in serpentine were watered with exactly the same frequency as plants of the same populations growing in non-serpentine soil. The plants in pots of serpentine soil died after some two months of this treatment, due to lack of a sufficient supply of water. This low water-retention capacity of serpentine soils is a known characteristic (Walker, 1954). In the author's opinion, serpentine soils are to be put in the same class with loose sand soils, which are also poor water retainers.

Since the plants of *Gutierrezia californica* have a shallow root system and grow in association with mesic grasses it may be, therefore, that their presence in the San Francisco Bay Area on serpentine is determined by this "loose" characteristic which gives the plants an advantage over other components of the vegetation, especially grasses, while on the heavier soils this situation would be reversed. In this case it may be that the low water-retention capacity of serpentine, rather than its mineral content, accounts for the growth of *Gutierrezia* on it.

FIELD OBSERVATIONS

The various species of *Gutierrezia* usually grow in company with perennial grasses and shrubs in the open broadleaf shrub communities. Munz and Keck (1949), in their study of California plant communities, characterize *Gutierrezia sarothrae* as a member of the Shad-Scale Scrub. Nevertheless, after visiting and studying populations of all the species from central Mexico to Idaho, it has been observed that the species of *Gutierrezia* are not restricted to defined communities. This is not to say that they are not characteristic in a certain area of a certain type of vegetation, or that their tolerances are so broad that they grow under almost any conditions. This is certainly not the case: limitations of soil and climate are as important to them as to any other plant species. But aside from certain broad physiographic and ecological characteristics, in the many localities visited, *Gutierrezia* was the only conspicuous element present in all.

Whenever possible, a list was made of the species growing in association with *Gutierrezia* (table 5). Unfortunately, when the genus blooms in late summer or fall, most of the herbaceous vegetation is dried up and not easily identifiable. The list of table 5 is therefore tentative and incomplete, and is presented only as a guide to the type of vegetation which may be expected to occur in association with *Gutierrezia*.

TABLE 5. PLANTS GROWING IN ASSOCIATION WITH VARIOUS SPECIES OF GUTIERREZIA

A. Gutierrezia sarothrae. — *Pinus ponderosa* Dougl. *P. cembroides* Zucc., *Juniperus communis* L., *Avena fatua* L., *Bromus tectorum* L., *B. brizaeformis* L., *B. japonicus* L., *Poa* sp., *Allium* sp., *Atriplex canescens* (Pursh) Nuttall, *Chenopodium* sp., *Salsola kali* L., *Polygonum aviculare* L., *Erigonum umbellatum* Torr., *Erigonum* sp., *Alyssum alyssoides* (L.) L., *Potentilla flabelliformis* Lindl., *Rosa woodsii* Lindl., *Melilotus officinalis* (L.) Lam., *Astragalus* sp., *Epilobium paniculatum* Nutt., *Lomatium* sp., *Phlox douglasii* Hook., *Penstemon pratensis* Greene, *Castilleja* sp., *Scutellaria antirrhinoides* Benth., *Helianthus annus* L., *Solidago* sp., *Cirsium vulgare* (Savi) Tenore, *C. undulatum* (Nutt.) Spreng., *Xanthium canadense* L., *Grindelia* sp., *Lactuca scariola* L., *Chrysothamnus nauseosus* (Pall.) Britt., *Artemisia tridentata* Nutt., *Senecio canus* Hook., *Achillea lanulosa* Nutt., *Blepharipappus scaber* Hook.

B. Gutierrezia californica. — *Pellaea andromedaefolia* Fée, *Polypodium scouleri* H. & G., *Koeleria cristata* (L.) Pers., *Chlorogalum pomeridianum* (Ker) Kunth, *Quercus agrifolia* Née, *Eriogonum nudum* Dougl., *Umbellularia californica* Nutt., *Rhamnus crocea* Nutt., *Rhus diversiloba* T. & G., *Silene gallica* L., *Eschscholtzia californica* Cham., *Arabis glabra* (L.) Bernh., *Dudleya* sp., *Lathyrus vestitus* Nutt., *Lupinus albifrons* Benth., *Sidalcea malvaeflora* Gray, *Sanicula bipinnatifida* Dougl., *Monardella villosa* Benth., *Achillea lanulosa* Nutt., *Artemisia californica* Less.

C. Gutierrezia bracteata. — *Pinus sabiniana* Dougl., *Juniperus communis* L., *Avena fatua* L., *A. sativa* L., *Festuca* sp., *Quercus douglasii* H. & A., *Q. lobata* Née, *Yucca whipplei* Torr., *Eriogonum* sp., *Grayia spinosa* (Hook.) Moq., *Adenostoma fasciculatum* H. & A., *Astragalus* sp., *Euphorbia peplus* L., *Eriodictyon californicum* (H. & A.) Greene, *Arctostaphylos* sp., *Monardella villosa* Benth., *Scutellaria* sp., *Grindelia* sp., *Madia* sp., *Trichostemma* sp., *Artemisia californica* Less., *Lepidospartum squamatum* Gray, *Chrysothamnus* sp.

D. Gutierrezia serotina. — *Eriogonum* sp., *Cercidium microphyllum* (Torr.) Rose & Johnston, *Prosopis juliflora* (Swartz) DC., *Carnegia gigantea* (Engelm.) Britt. & Rose.

OTHER OBSERVATIONS

Gutierrezia has a shallow root system which puts it in direct competition with shallow-rooted herbaceous plants, especially grasses. Since it blooms in the fall, it is in a vegetative state all through the summer, a season of very little or no rainfall throughout its range. Water relations therefore become critical and no doubt play an important role in the distribution of the species, both in determining the range and the localities within the range.

The author has observed that wherever one finds a population there is some kind of physical accident in the environment which presupposes a higher moisture content in the soil than in the surrounding area, such as a depression, a gulch, sometimes even a creek bed, or running water. Exposure also plays an important role and it is not uncommon to find plants growing only on north or northeast slopes. This is probably due to the north-facing slopes having less sun exposure, with less evaporation and less transpiration by the plants.

It has already been mentioned that *Gutierrezia* must compete with grasses, especially perennial ones. The competition here is believed to be mainly for the available water supply in the ground. Xerophytic grasses are better adapted morphologically and anatomically than *Gutierrezia* and apparently eventually crowd it out of better soils. In poorer soils, on the other hand, the situation appears to be reversed, and a possible explanation may be the requirement by grasses of more fertile soils (Tisdale, personal communication, and my own field observations).

This dynamic balance between grasses and *Gutierrezia* is expressed most clearly when the natural equilibrium is disturbed. One frequent cause of disturbance is over-grazing. Grasses are eaten avidly by both cattle and sheep while *Gutierrezia* is eaten very little. In such cases the latter plants spread rapidly, to the point that throughout their range both *Gutierrezia sarothrae* and *G. microcephala* are considered, wherever they grow abundantly in rangelands, to be indicators of over-grazing. A second frequent case of unbalance is produced when the soil is disturbed by road construction or some similar accident. *Gutierrezia* plants may frequently be seen growing in the barren slopes where the subsoil has been exposed, while the grasses rapidly take over the better spots.

The distribution of rainfall also plays an important role in determining the area of distribution. The concentration of species and abundance of individuals in the southwestern United States and northern Mexico seems to be directly correlated with late summer and fall rains. *Gutierrezia bracteata* is, of course, an exception to this, since, after the spring rains have ceased, it receives very little or no rain before September-October. It is interesting, therefore, to note that *Gutierrezia bracteata* is the latest bloomer, by about a month, of all the species of the genus.

These field observations are substantiated by those made on the cultures in the Botanical Garden at Berkeley. Plants of *Gutierrezia californica* (Oakland Hills and Angel Island, California, populations), *G. bracteata* (Yolo County, Corral Hollow, Temblor Range, and Cuyama Valley, California, populations), *G. sarothrae* (Fort Collins, and Grand Junction, Colorado; Wasatch, Nevada; and Lake Elsinore, California, populations), *G. microcephala* (Clark Mts., Nevada, population), *G. glutinosa* (San Luis Potosí, Mexico, population) and *G. texana* (Austin, Texas, population), were grown together. Water was provided in amounts sufficient so that it never became a limiting factor. All the plants attained much greater stature than they normally do in nature, but their flowering time was similar to that which had been observed in the field. The first to bloom were the Colorado populations of *G. sarothrae*, about mid-June. A month later all populations of *G. sarothrae* were in full bloom. In August, *G. microcephala* and *G. glutinosa* began blooming; toward the end of the month the Texas populations of *G. texana* and the populations of *G. bracteata* and *G. californica* were in anthesis. By October all but these last two species had passed their blooming period. Finally, in December *G. bracteata* and *G. californica*, especially the latter, were still blooming, while the Grand Junction population of *G. sarothrae* was flowering for a second time.

If we correlate these observations with rainfall, we see that the Colorado plants come from a region where the summer rains start first, and the California plants from the region which gets its rain latest. Undoubtedly, environmental conditions can hasten or retard flowering time but, as the experiments of Clausen, Keck, and Hiesey (1940, 1945, 1948) and Clausen and Hiesey (1958) have shown, flowering time seems to be determined genetically.

VARIATION STUDIES

Preliminary herbarium studies revealed among the perennial North American species the existence of an over-all morphological similarity; no clear-cut qualitative differences could be detected. In addition all those characters, which classically had been used to separate the species of *Gutierrezia*, showed some degree of variation. Field studies confirmed these observations and also showed a higher degree of inter-than intra-population variation. These preliminary observations were restricted mainly to such characters as size of heads and number of flowers, which have usually been employed to characterize the various species.

In order to evaluate the amount of variation and to find correlations, if any, with specific taxonomic units, it was decided to study and measure the largest possible number of characters. Another object of this investigation was to determine the validity of the morphological characterization of the species.

An approach different from the mere study of herbarium specimens was thought to be important since studies of this kind in the past had failed to produce satisfactory results in *Gutierrezia*. It was decided therefore to study the variation of populations in nature with the aid of simple standard statistical methods. This, it was hoped, would produce a better understanding of the population dynamics.

MATERIAL AND METHODS

Eleven characters were selected after some preliminary inquiry. These are the following: height of plant; height and width of involucre; length and width of achenes of both ligulate and tubular flowers; length of pappus of both ligulate and tubular flowers; and number of ligulate and tubular flowers per capitulum.

A total of 17 populations, belonging to five species, from the states of Oregon, Idaho, California, and Arizona was studied. These populations were chosen at random. Lack of time and transportation facilities precluded the study of populations in other states. A sample of 50 individuals was selected from each population. In order to randomize, each population was measured as to length and width and a rough outline of it was drawn on paper. A rectangle was then circumscribed around it and each side was divided into six equal parts, and a grid consisting of 36 equal divisions was constructed. The vertical columns and horizontal bars were then numbered from one to six, so that each square of the grid was identified by two numbers. Finally with the aid of two different colored dice, ten squares in the grid were selected. Taking a corner of the rectangle circumscribing the population as an origin, five plants of each of the selected squares nearest to the origin were then chosen. After the height of the plant had been measured, one head of each plant was collected and deposited in an envelope, for subsequent measurement and study in the laboratory. It is not therefore possible to establish any correlation between a single measurement of height of plant and any of the other characters, although it is possible to do so for any of the other characters.

This laborious sampling method has been followed in order to try to eliminate any kind of voluntary or involuntary bias, so as to obtain a true random sample from which meaningful statistical conclusions can be drawn. It is also hoped that randomization has largely changed systematic errors such as possible differences in soil, moisture, exposure, etc. within the population, into fluctuating errors, and that these have been subsequently made negligible by the use of the common standard statistical methods used in this study. If the sources of bias and systematic errors have been taken care of, and we may rather safely assume so, the samples are a true representation of the phenotypes of the populations studied.

Gutierrezia californica was not included in this study initially. By the time it had become apparent that data from this species would be of interest, its flowering season had passed. Consequently, the largest number of herbarium specimens of two populations well known to the author were gathered and one head from each available plant was removed and studied. This sample is less reliable than those obtained directly in the field, since it is very possible the collectors selected specimens for their vigour, size, or some other special characteristic. Another source of error is introduced by the fact that they were collected in different years and hence under different seasonal climatic conditions. Nevertheless, since both populations are small, the data may have comparative value and certain meaningful preliminary conclusions may perhaps be drawn from this material.

STATISTICAL METHOD. Hubbs and Perlmutter (1942) have provided a graphic method for the rapid comparison of representative samples of several populations. This method is a modification of that of Dice and Lleraas (1936) and consists in plotting in a graph the range and the mean of the sample and in addition one standard deviation and two standard errors on each side of the mean. If the ranges of the four-standard errors so plotted do not overlap or just barely touch, and provided that the ratio between them is no greater than two, the mean of the two samples can be assumed to be significant (P=0.01 to 0.005). If there is overlap, when it is no more than 33% of the length of the shorter of the two four-standard errors rectangles com-

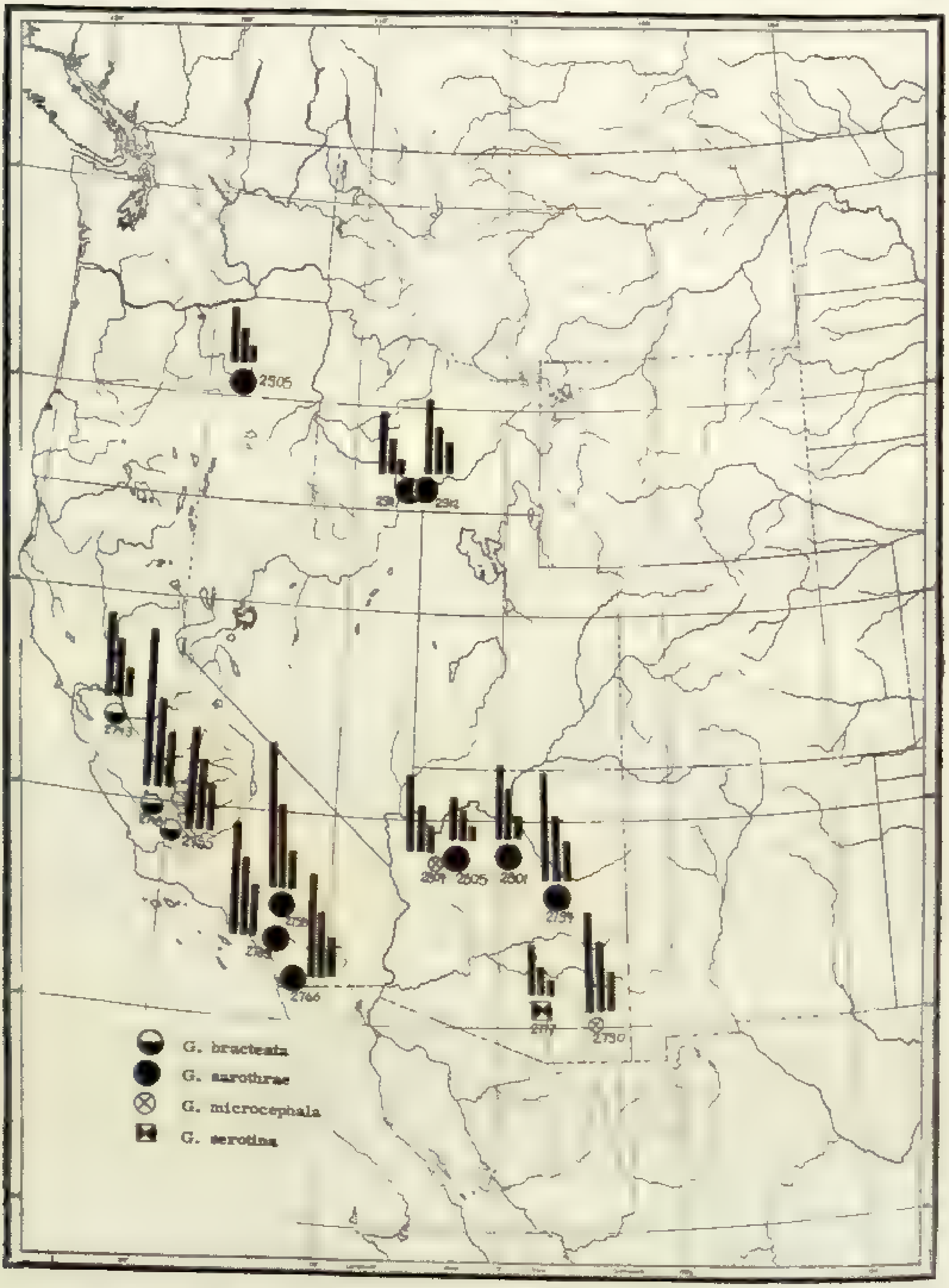


Fig. 6. Maximum (left bar), minimum (right bar), and mean (central bar) plant height measurements of fifteen populations of *Gutierrezia*.

pared, Hubbs and Perlmutter present tables (t values) which show that the mean still can be significant ($P = 0.05$). In cases where the larger four-standard errors rectangle is two to four times longer than the shorter, an overlap of 50% or even 75% still can be somewhat significant ($P = 0.072$ for 50% overlap and a ratio of 2/1; $P = 0.089$ for 75% overlap and a ratio of 4/1).

This method has been used in comparing the means of six characters: length and width of achene of tubular and ligulate flowers and length of pappus of tubular and ligulate flowers (fig. 9-14).

On the other hand, a frequency distribution was thought to be more meaningful for comparing the number of both ligulate and tubular flowers, since in this case actual number rather than mathematical mean is the important feature. Measurements of the involucre were combined in a pictorial diagram so that width, length and shape can be compared. Finally, size of plant was plotted on a map in relation to the geographical location of the population.

RESULTS

PLANT HEIGHT. Nine populations of *Gutierrezia sarothrae*, three of *G. bracteata*, two of *G. microcephala*, and one of *G. serotina* were investigated as to this character. Fifty plants were measured in every case with exception of a population of *G. sarothrae* from San Diego County, California (Solbrig 2769) which consisted of only 35 plants.

Measurements were taken in the field with the aid of a steel measuring tape. The height recorded is that between the base of the plant and the tip of the longest branch. All measurements of plant height are expressed in inches, since no tape marked in meters could be found, and converting inches to centimeters would have introduced a source of inaccuracy.

There was an appreciable difference in the size of the plants both between and within populations. The mean height of the populations also varied widely, as did the range and the standard deviation. No meaningful correlations could be detected between the variation of these parameters and any definite geographic or specific character.

The mean heights of the populations of *G. bracteata* and *G. microcephala* are situated in the upper range of the distribution; the only population of *G. serotina* investigated has the smallest mean height, while the populations of *G. sarothrae* range from values not significantly larger than those of *G. serotina* to some which fall well within the range of *G. bracteata.*

INVOLUCRE. Size and shape of involucre is an important character in the separation of genera in Astereae, and it also has been employed in the delimitation of species of *Gutierrezia.* It is important, therefore, to know to what extent this structure may provide reliable taxonomic characters.

TABLE 6. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF PLANT HEIGHT

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{n}$
G. sarothrae	Temecula, Calif.	2758	50	22.4	22	10	38	28	13.90	1.966
	Chula Vista, Calif.	2766	50	17.3	16	10	27	17	9.70	1.371
	Rancho Santa Fe, Calif.	2769	35	20.3	20	13	29	12	7.48	1.263
	Payson, Arizona	2794	50	17.3	17	10	28	18	5.74	.811
	Hyde Park, Arizona	2805	50	7.8	8	4	11	7	3.18	.450
	John Day, Oregon	2905	50	9.3	9	4	14	10	4.84	.684
	Hansen, Idaho	2911	50	9.1	11	4	16	12	4.92	.695
G. bracteata	Patterson, Calif.	2743	50	15.0	15	7	22	18	6.62	.936
	Pond Ranch, Calif.	2748	50	23.7	23	14	31	17	9.88	1.397
	Temblor Range, Calif.	2755	50	18.5	19	12	27	15	6.90	.975
G. microcephala	Saint David, Arizona	2790	50	17.8	17	10	26	16	6.74	.953
	Hyde Park, Arizona	2804	50	12.6	10	7	20	13	6.00	.848
G. serotina	Tucson, Arizona	2777	50	7.7	7	4	13	9	4.24	.599

All measurements expressed in inches.

Figure 7 shows the shape and the mean dimensions of the involucre in the populations of *Gutierrezia* studied for this structure. The range of dimensions is illustrated by means of two superimposed crosses, the larger being proportional to the maximal sizes and the smaller to the minimal ones; the range is the difference between the largest and the smallest cross. In both crosses the vertical bar represents height and the cross bar indicates width.

Two populations may be singled out easily from the rest: population No. 2777, representing *G. serotina,* and population No. 2804, which belongs to *G. microcephala.* The shape and also the proportion between length and width (almost as high as broad in *G. serotina* and several times longer than broad in *G. microcephala*) are so characteristic that the two species can be identified readily by these characters.

The involucre of *G. californica* is of approximately the same shape as that of *G. bracteata* and *G. sarothrae*. The mean dimensions of the former are larger than those of the latter species. In spite of a slight overlap in range with *G. bracteata* it is believed that this character is of some taxonomic value.

TABLE 7. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF HEIGHT OF INVOLUCRE

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	σ	$\sqrt{n}$
G. sarothrae	Temecula, Calif.	2758	50	43.6	45	49	35	14	5.64	.797
	Chula Vista, Calif.	2766	50	35.1	31	45	25	20	2.35	.332
	Rancho Santa Fe, Calif.	2769	50	34.3	35	39	27	12	6.00	.848
	Payson, Arizona	2794	50	56.5	55	65	45	20	8.52	1.205
	Ash Fork, Arizona	2801	50	37.3	39	43	27	16	1.61	.227
	Hyde Park, Arizona	2805	50	39.2	40	49	35	14	2.58	.364
	John Day, Oregon	2905	9	39.3	*	45	33	12	8.58	3.031
	Hansen, Idaho	2911	3	47.0	*	*	*	*	*	*
G. bracteata	Patterson, Calif.	2743	50	51.2	51	59	40	19	3.40	.480
	Pond Ranch, Calif.	2748	50	51.6	51	58	46	12	2.25	.318
	Temblor Range, Calif.	2755	50	55.7	59	63	49	14	8.60	1.216
G. microcephala	Hyde Park, Arizona	2804	50	35.9	35	41	17	24	8.38	1.185
G. serotina	Tucson, Arizona	2777	50	28.6	29	45	19	26	8.78	1.241
G. californica	Angel Island, Calif.	2428	10	57.0	*	*	*	*	*	*
	Oakland, Calif.	2154	19	52.1	*	*	*	*	*	*

* Data insufficient

All measurements expressed in mm. × 10.

TABLE 8. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF WIDTH OF INVOLUCRE

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	σ	$\sqrt{n}$
G. sarothrae	Temecula, Calif.	2758	50	24.8	25	19	29	10	2.68	.379
	Chula Vista, Calif.	2766	50	18.5	19	13	27	14	2.69	.380
	Rancho Santa Fe, Calif.	2769	50	21.5	19	15	25	10	4.12	.582
	Payson, Arizona	2794	50	21.2	20	18	28	10	2.48	.350
	Ash Fork, Arizona	2801	50	19.6	19	13	25	12	2.34	.330
	Hyde Park, Arizona	2805	50	16.7	17	11	27	16	2.52	.356
	John Day, Oregon	2905	9	30.1	*	25	35	10	7.16	2.530
	Hansen, Idaho	2911	3	31.3	*	*	*	*	*	*
G. bracteata	Patterson, Calif.	2743	50	33.9	32	29	42	13	3.56	.503
	Pond Ranch, Calif.	2748	50	33.0	32	26	48	22	3.25	.459
	Temblor Range, Calif.	2755	50	26.1	29	19	35	16	7.30	1.032
G. microcephala	Hyde Park, Arizona	2804	50	10.0	10	5	16	11	2.49	.352
G. serotina	Tucson, Arizona	2777	50	26.5	25	19	35	16	7.46	1.055
G. californica	Angel Island, Calif.	2428	10	42.0	*	*	*	*	*	*
	Oakland, Calif.	2154	19	37.7	*	*	*	*	*	*

* Data insufficient.

All measurements expressed in mm. × 10.

Gutierrezia sarothrae and *G. bracteata* cannot be separated on the basis of involucral characters alone, even though in the populations studied the involucres of *G. bracteata*

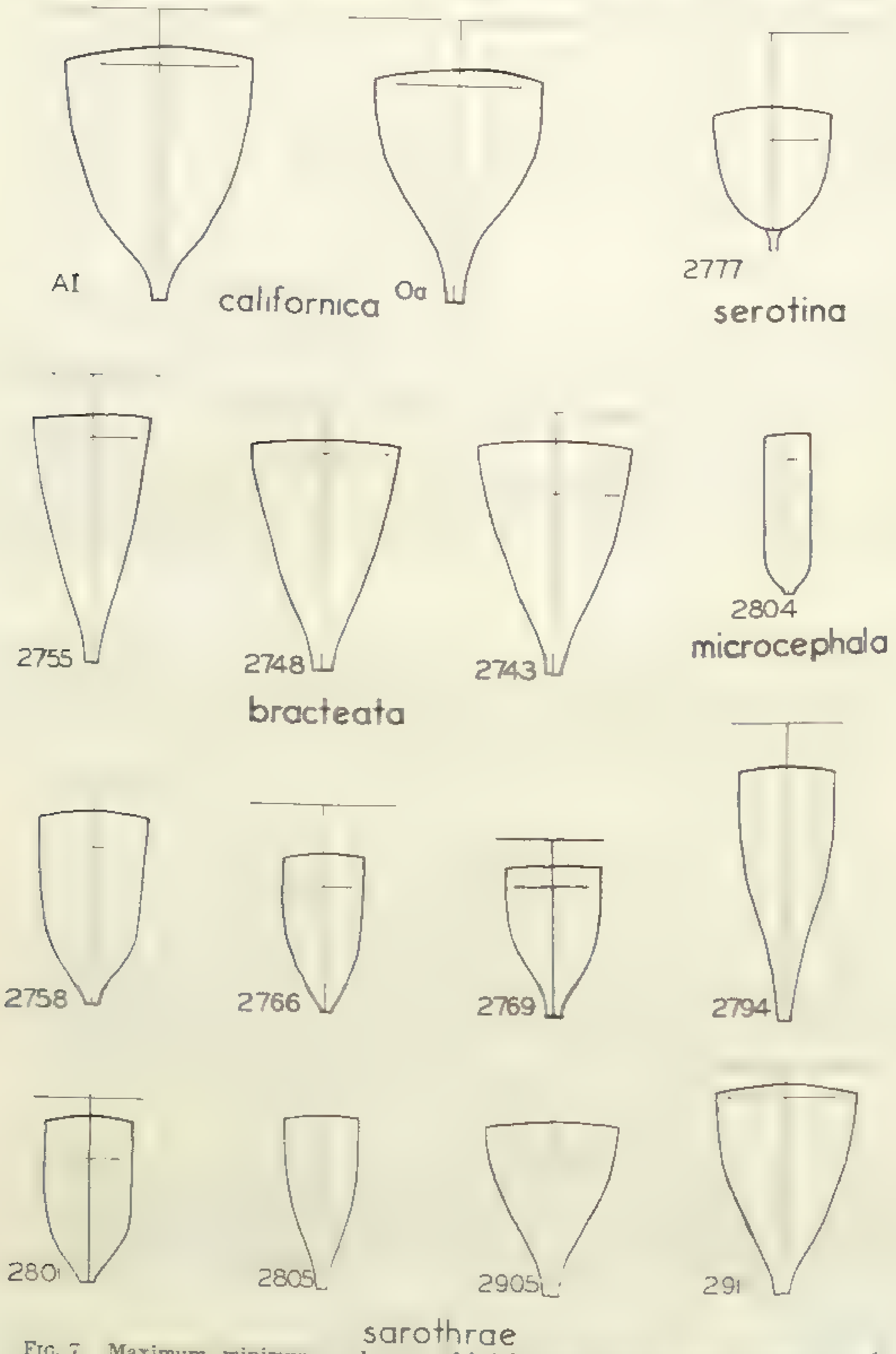


FIG. 7. Maximum, minimum, and mean of height and width of the involucre. Each outline drawing is proportional to the mean dimensions; the larger vertical and transversal bars represent the maximum dimensions; the smaller inner bars the minimum dimensions.

were slightly larger than those of *G. sarothrae*. The overlap is so large and consequently the chances of error so great that, even if we were to assume that size were a valid difference, the use of this character would lead to confusion rather than to clarification.

Nevertheless, certain trends can be pointed out: (1) the trend toward larger involucres in *G. bracteata* (see above); (2) the relatively narrower involucre of *G. sarothrae;* (3) the funnelform involucres of *G. bracteata* in contrast to the more turbinate ones of *G. sarothrae*. These slight differences in shape can be correlated with a tendency in the involucral bracts of *G. bracteata* to reflex slightly and consequently to loosen the involucres somewhat, while in *G. sarothrae* the involucral bracts are closely appressed at anthesis.

Aside from the differences noted above between populations belonging to different species, figure 7 shows also that populations of the same species differ from one another not only in the mean of the characters considered but also in the range. Population No. 2794 of *Gutierrezia sarothrae* is of interest in this respect. As may be seen in figure 7, the involucres are larger, although not broader, than in all the other populations studied of the same species. It is thought to be significant that this population is a polyploid with n = 8, while all the others are diploid with n = 4. It is also of interest that the mean length of the involucres of population No. 2794 approaches that of the 8-chromosome populations of *G. bracteata*.

NUMBER OF FLOWERS. This character is very important because it has been used extensively to separate species. In this case it is believed that frequency distribution and range are more meaningful than mean and standard deviation, and therefore the latter will not be considered (although it has been calculated and the interested reader is referred to tables 9 and 10).

Figure 8 shows the distribution of the frequencies of ligulate and tubular flowers of 14 populations of *Gutierrezia*. In most cases the mode class has a frequency of about 50%. An exception to this is the only population of *G. microcephala* studied, which shows a greater frequency for the modal class and far less variation than all the other populations investigated. Herbarium studies appear to confirm this observation.

A second feature which may be observed is that the range between the lowest and highest values observed is not great. The Oakland Hills population of *G. californica* might be an exception to this, but since the representativeness of the sample is questionable (see page 25) this cannot be confirmed.

Another characteristic is that different populations of the

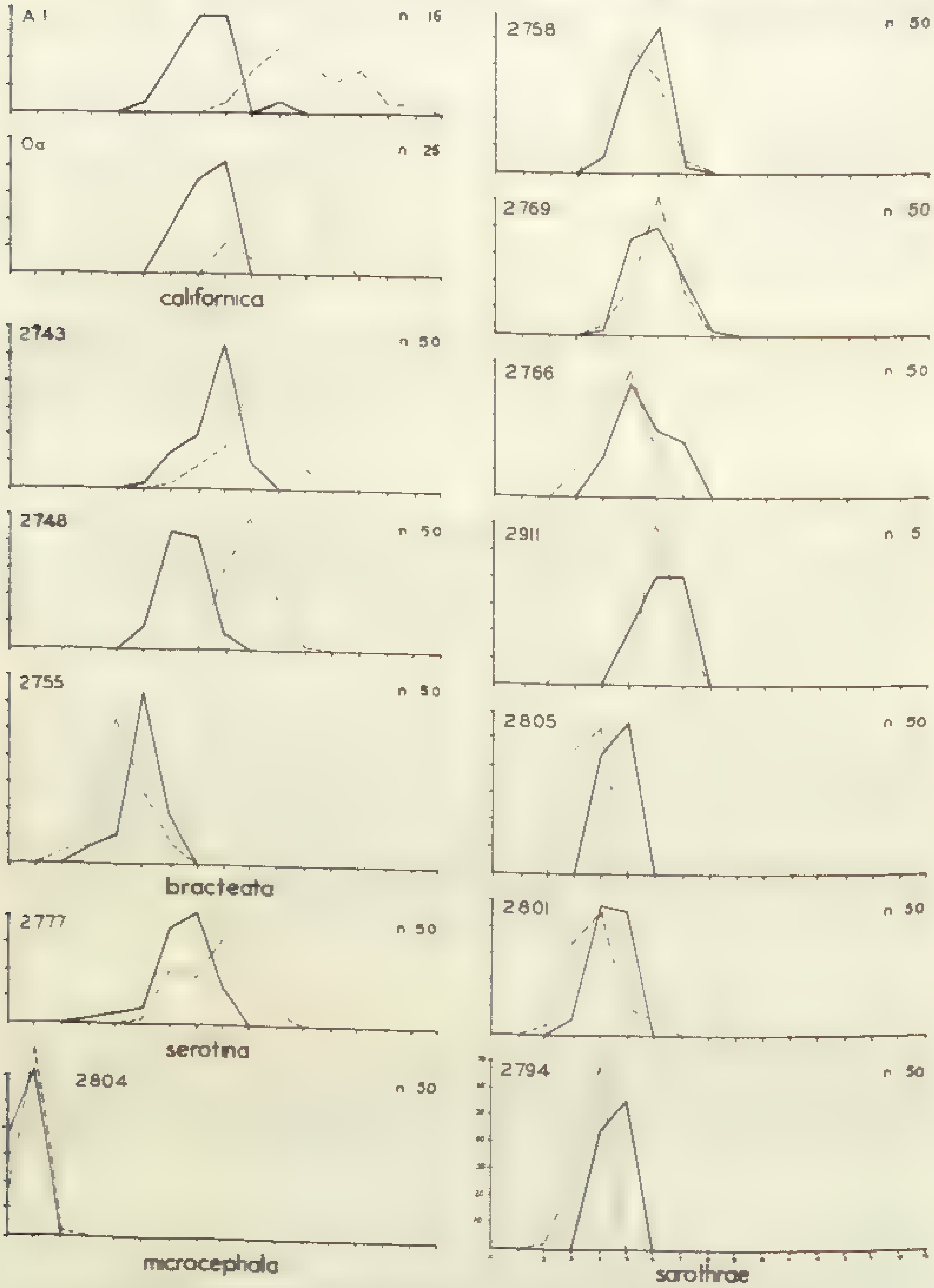


FIG. 8. Frequency distribution of number of ligulate (full line) and tubular flowers (broken line) in one head.

same species have different modal classes and also vary in the range. This finding is believed to be important because all the species considered have been characterized at one time or another by number of ligulate or tubular flowers or both.

TABLE 9. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF NUMBER OF TUBULAR FLOWERS IN ONE HEAD

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{n}$
G. sarothrae	Temecula, Calif.	2758	50	5.3	5	4	7	3	.77	.108
	Chula Vista, Calif.	2766	50	4.6	5	0	6	6	1.09	.154
	Rancho Santa Fe, Calif.	2769	50	5.9	6	4	7	3	.70	.099
	Payson, Arizona	2794	50	3.6	4	0	4	4	1.30	.183
	Ash Fork, Arizona[1]	2801	50	3.8	4	2	6	4	.90	.127
	Hyde Park, Arizona	2805	50	3.5	4	3	4	1	.50	.070
	Hansen, Idaho	2911	5	5.6	6	6	7	1	*	*
G. bracteata	Patterson, Calif.	2743	50	9.0	9	6	11	5	1.09	.154
	Pond Ranch, Calif.	2748	50	8.9	9	8	11	3	.75	.106
	Temblor Range, Calif.	2755	50	4.3	4	2	6	4	.86	.121
G. microcephala	Hyde Park, Arizona	2804	50	—	1	0	2	2	.42	.059
G. serotina	Tucson, Arizona	2777	50	7.7	8	5	10	5	1.25	.176
G. californica	Angel Island, Calif.	2428	16	10.2	10	8	12	4	*	*
	Oakland, Calif.	2154	25	11.1	10	8	15	7	5.71	1.142

* Data insufficient.

[1] Sample taken from two plants.

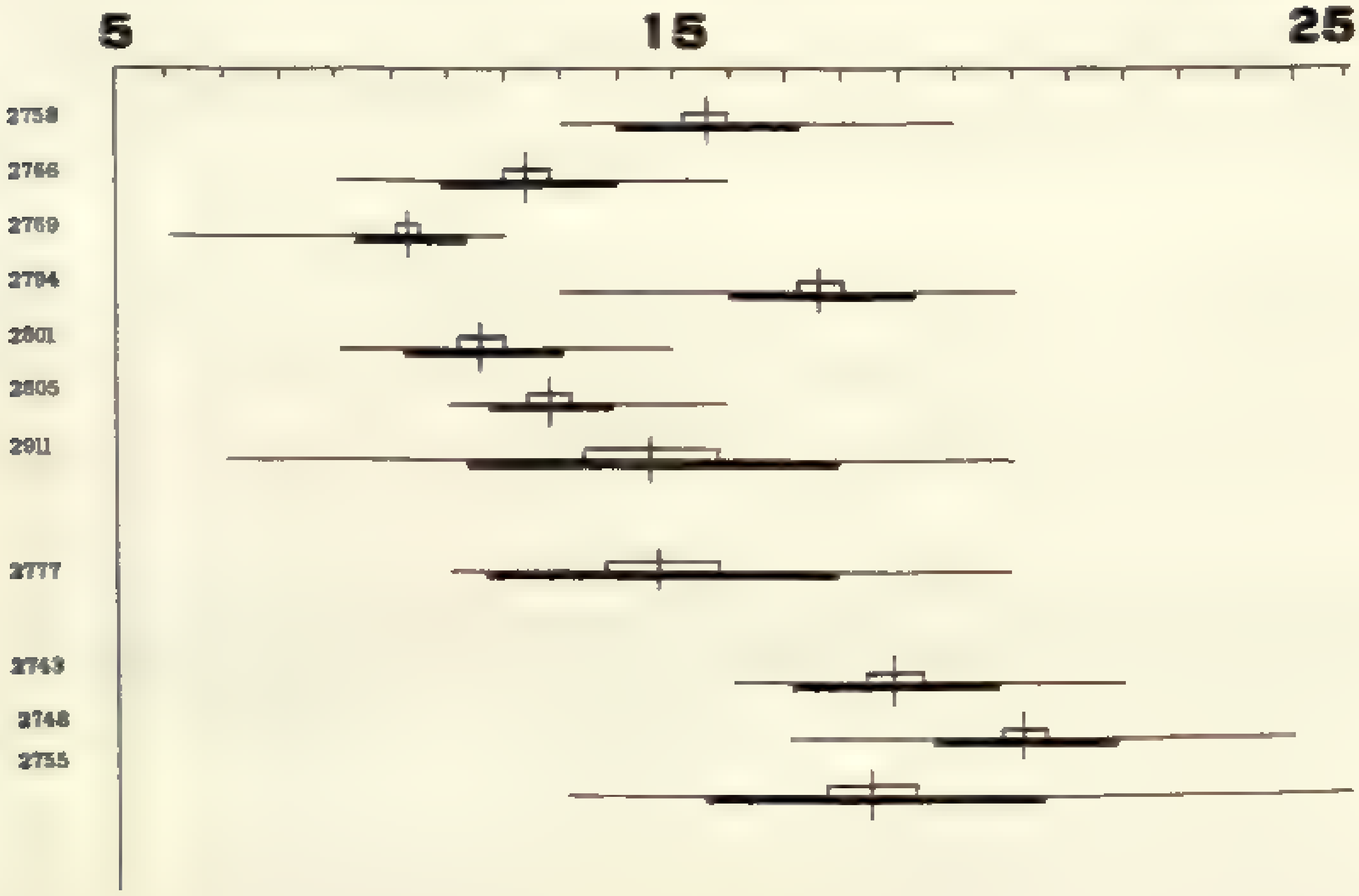
TABLE 10. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF NUMBER OF LIGULATE FLOWERS IN ONE HEAD

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{n}$
G. sarothrae	Temecula, Calif.	2758	50	5.5	5	4	7	3	.65	.091
	Chula Vista, Calif.	2766	50	5.5	5	4	7	3	1.47	.207
	Rancho Santa Fe, Calif.	2769	50	5.8	6	4	8	4	.84	.118
	Payson, Arizona	2794	50	4.6	5	4	5	1	.50	.070
	Ash Fork, Arizona[1]	2801	50	4.4	4	3	5	2	.60	.084
	Hyde Park, Arizona	2805	50	4.6	5	4	5	1	.50	.070
	Hansen, Idaho	2911	5	6.2	*	5	7	2	*	*
G. bracteata	Patterson, Calif.	2743	50	7.6	8	5	9	4	.93	.131
	Pond Ranch, Calif.	2748	50	6.5	6	5	8	3	.73	.103
	Temblor Range, Calif.	2755	50	4.9	5	3	6	3	.74	.104
G. microcephala	Hyde Park, Arizona	2804	50	—	1	0	1	1	.49	.069
G. serotina	Tucson, Arizona	2777	50	6.5	7	3	8	5	1.23	.173
G. californica	Angel Island, Calif.	2428	16	7.3	*	*	*	*	*	*
	Oakland, Calif.	2154	25	7.2	7	5	10	5	6.34	1.268

* Data insufficient.

[1] Sample taken from two plants.

Neither in range nor in mean is there any absolute difference between species. A general trend is nevertheless present. *Gutierrezia californica* has from 8 to 15 tubular flowers, with a mode of 10, which is more than in any other species. Ligulate flowers vary from 5 to 8 with modes of 7 and 8. The populations of *G. bracteata* have a range of from 6 to 11 tubular flowers, and 5 to 9 ligulate flowers in two popula-



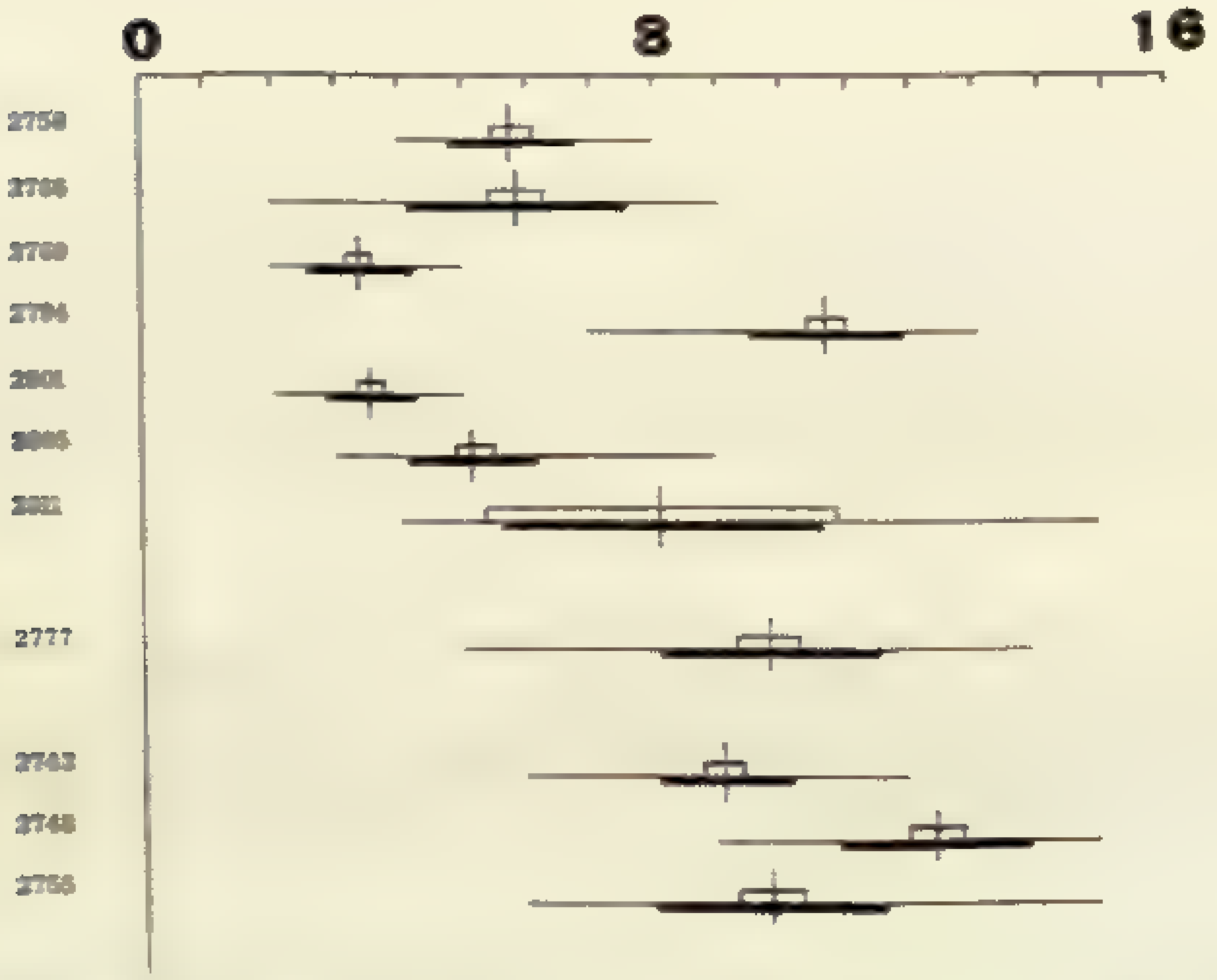


FIG. 9. Mean (vertical line), range (middle horizontal line), standard deviation (dark lower bar) and standard error (light upper bar) of length of pappus of tubular flowers. Fig. 10. Id. of pappus of ligulate flowers. For further explanations see text.

tions, with modal classes of 9-6 and 8, respectively. However, a third population (Solbrig 2755) has only 2 to 6 tubular and 3 to 6 ligulate flowers and modes of 4 and 5. This last population thus follows the pattern of *G. sarothrae* rather than that of *G. bracteata*. This feature shows up in other characteristics too, as will be seen. At this stage of our investigations, however, there is insufficient information to give an explanation for this behavior.

Gutierrezia serotina has 5 to 10 tubular and 3 to 8 ligulate flowers per capitulum in the population studied. The modal classes are 8 and 7, respectively.

TABLE 11. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF LENGTH OF PAPPUS OF TUBULAR FLOWERS

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
G. sarothrae	Temecula, Calif.	2758	50	14.6	15	12	19	7	1.60	.220
	Chula Vista, Calif.	2766	50	11.4	12	8	15	7	1.56	.220
	Rancho Santa Fe, Calif.	2769	50	9.3	10	5	11	6	1.04	.147
	Payson, Arizona	2794	50	16.6	16	12	20	8	1.57	.222
	Ash Fork, Arizona	2801	50	10.6	10	8	14	6	1.38	.195
	Hyde Park, Arizona	2805	50	11.8	12	10	15	5	1.05	.148
	Hansen, Idaho	2911	28	13 6	15	6	20	14	3.30	.634
G. bracteata	Patterson, Calif.	2743	50	17.9	19	15	22	7	1.77	.250
	Pond Ranch, Calif.	2748	50	20.2	20	16	25	9	1.55	.219
	Temblor Range, Calif.	2755	50	17 5	18	12	26	12	2.98	.421
G. serotina	Tucson, Arizona	2777	50	13.8	12	10	20	10	3.22	.455

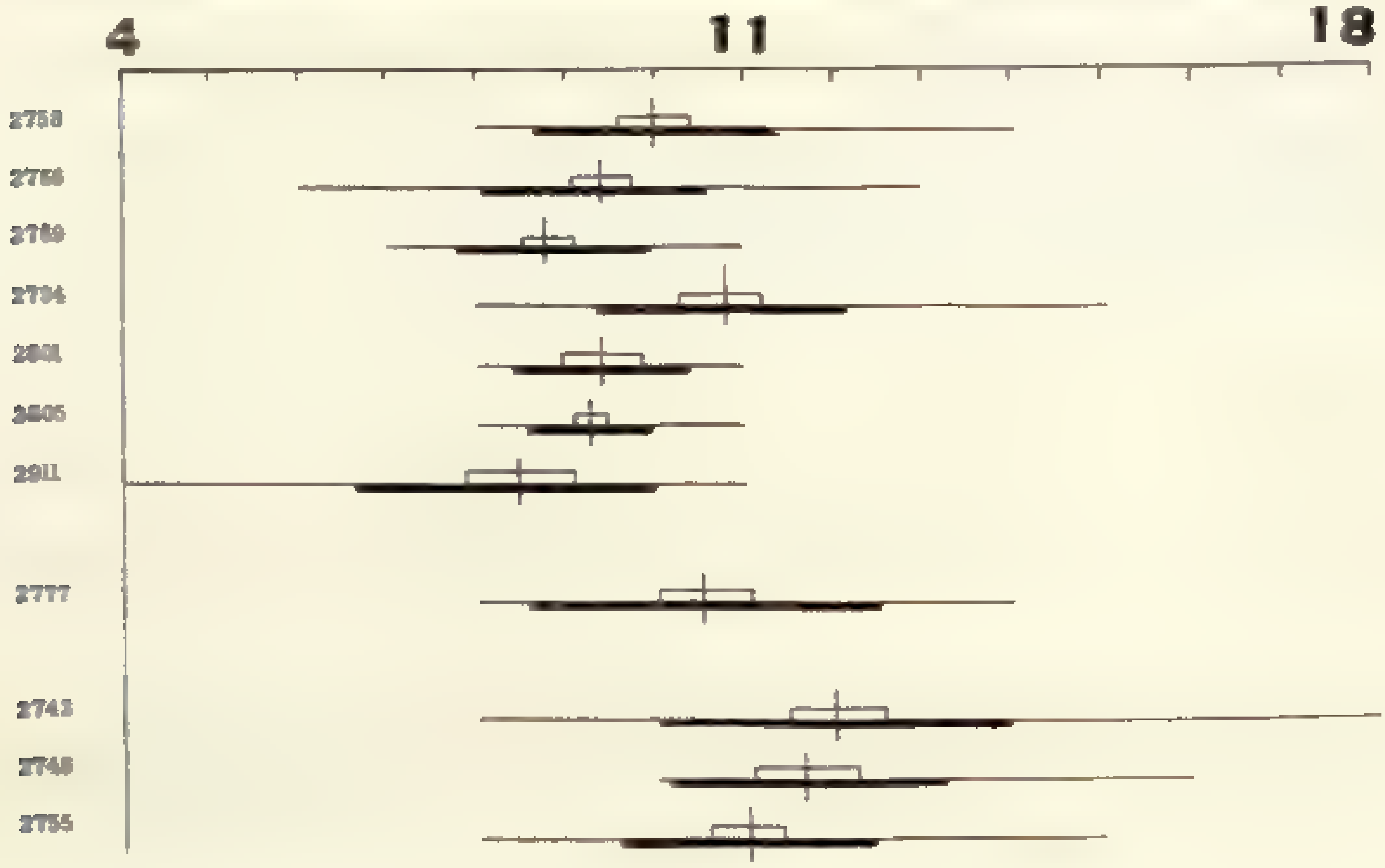
All measurements expressed in mm. × 10.

TABLE 12. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF LENGTH OF PAPPUS OF LIGULATE FLOWERS

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
G. sarothrae	Temecula, Calif.	2758	50	5.8	5-6	4	8	4	1.01	.142
	Chula Vista, Calif.	2766	50	5.9	5	2	9	7	1.67	.236
	Rancho Santa Fe, Calif.	2769	50	3.4	3	2	5	3	.76	.107
	Payson, Arizona	2794	50	10.7	10	7	13	6	1.17	.165
	Ash Fork, Arizona	2801	50	3.6	3	2	5	3	.67	.094
	Hyde Park, Arizona	2805	50	5.2	5	3	9	6	.95	.134
	Hansen, Idaho	2911	31	8 1	7	4	15	11	2 48	1.433
G. bracteata	Patterson, Calif.	2743	50	9 1	9	6	12	6	.99	.140
	Pond Ranch, Calif.	2748	50	12.4	12	9	15	6	1.46	.206
	Temblor Range, Calif.	2755	50	9.8	10-11	6	15	9	1.73	.244
G. serotina	Tucson, Arizona	2777	50	9.8	10	5	14	9	1.70	.240

All measurements expressed in mm. × 10.

The number of tubular flowers varies from 3 to 7 in *G. sarothrae* (one head had no tubular flowers) with modes of 4 or 5. The polyploid population No. 2769 had a mode of 6,



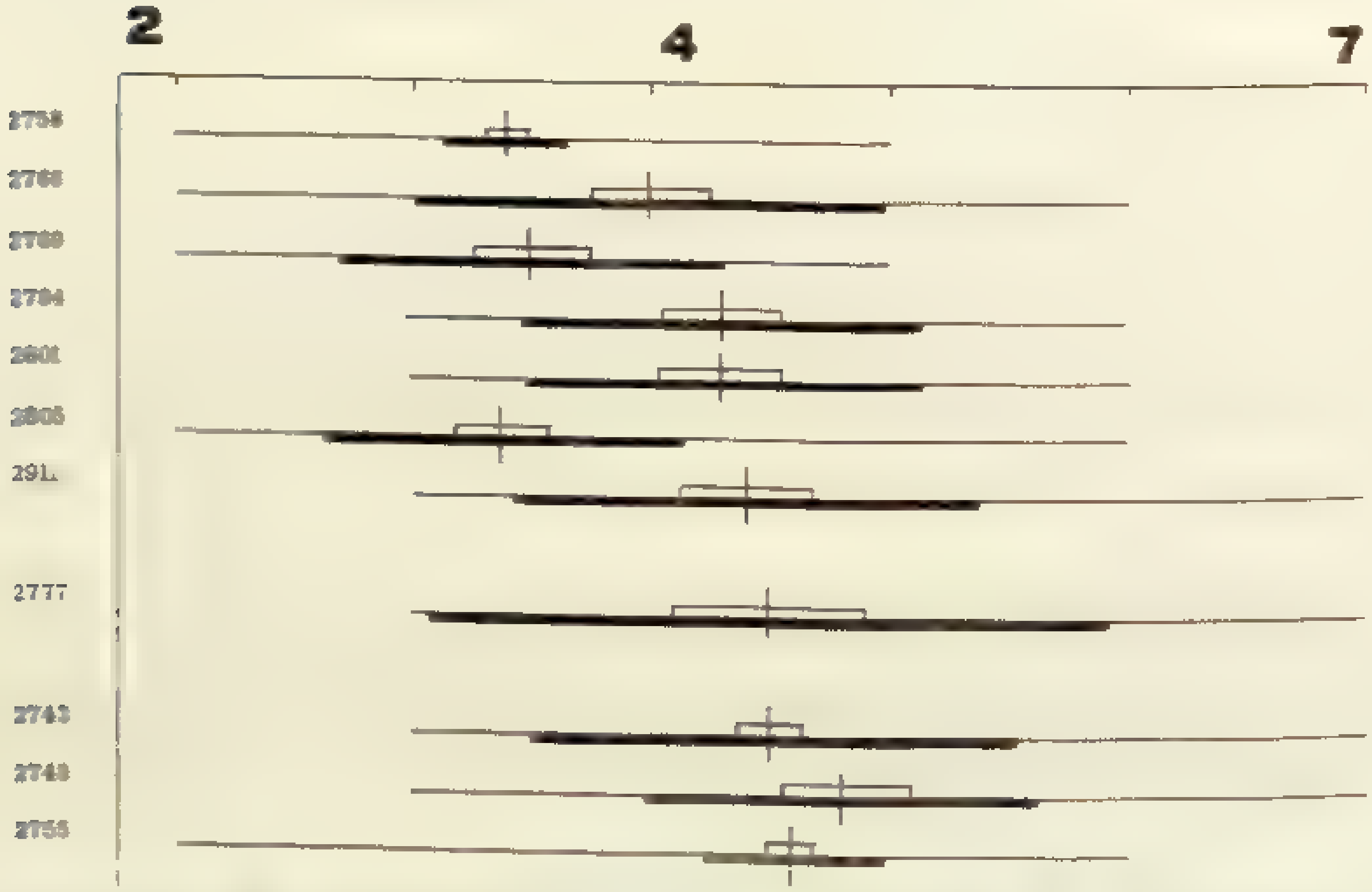


FIG. 11. Mean (vertical line), range (middle horizontal line), standard deviation (dark lower bar) and standard error (light upper bar) of length of achene of tubular flowers. Fig. 12. Id. of width of achene of tubular flowers. For further explanations see text.

as did population No. 2911. Only five heads could be counted in this last population so that these data cannot be taken into consideration. The number of ligulate flowers varied from 4 to 8, while the most frequent modal classes were 5 and 6 if we disregard population No. 2911.

Gutierrezia microcephala showed 0 to 1 tubular and ligulate flowers. One head had 2 tubular flowers, while 1 was the mode for both ligulate and tubular flowers.

TABLE 13. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF LENGTH OF ACHENE OF TUBULAR FLOWER

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\frac{s}{\sqrt{n}}$
G. sarothrae	Temecula, Calif.	2758	50	10.0	10	8	14	6	1.37	.193
	Chula Vista, Calif.	2766	50	9.3	9	6	13	7	1.27	.179
	Rancho Santa Fe, Calif.	2769	50	8.8	9	7	11	4	.94	.132
	Payson, Arizona	2794	50	10.8	10	8	15	7	1.43	.202
	Ash Fork, Arizona	2801	50	9.4	10	8	11	3	.97	.137
	Hyde Park, Arizona	2805	50	9.2	9	8	11	3	.65	.091
	Hansen, Idaho	2911	28	8.5	9	4	11	6	1.88	.360
G. bracteata	Patterson, Calif.	2743	50	12.0	11	8	18	8	1.93	.272
	Pond Ranch, Calif.	2748	50	11.7	11	10	16	6	1.61	.227
	Temblor Range, Calif.	2755	50	10.7	10	8	15	7	1.47	.207
G. serotina	Tucson, Arizona	2777	50	10.5	10	8	14	6	1.97	.278

All measurements expressed in mm. × 10.

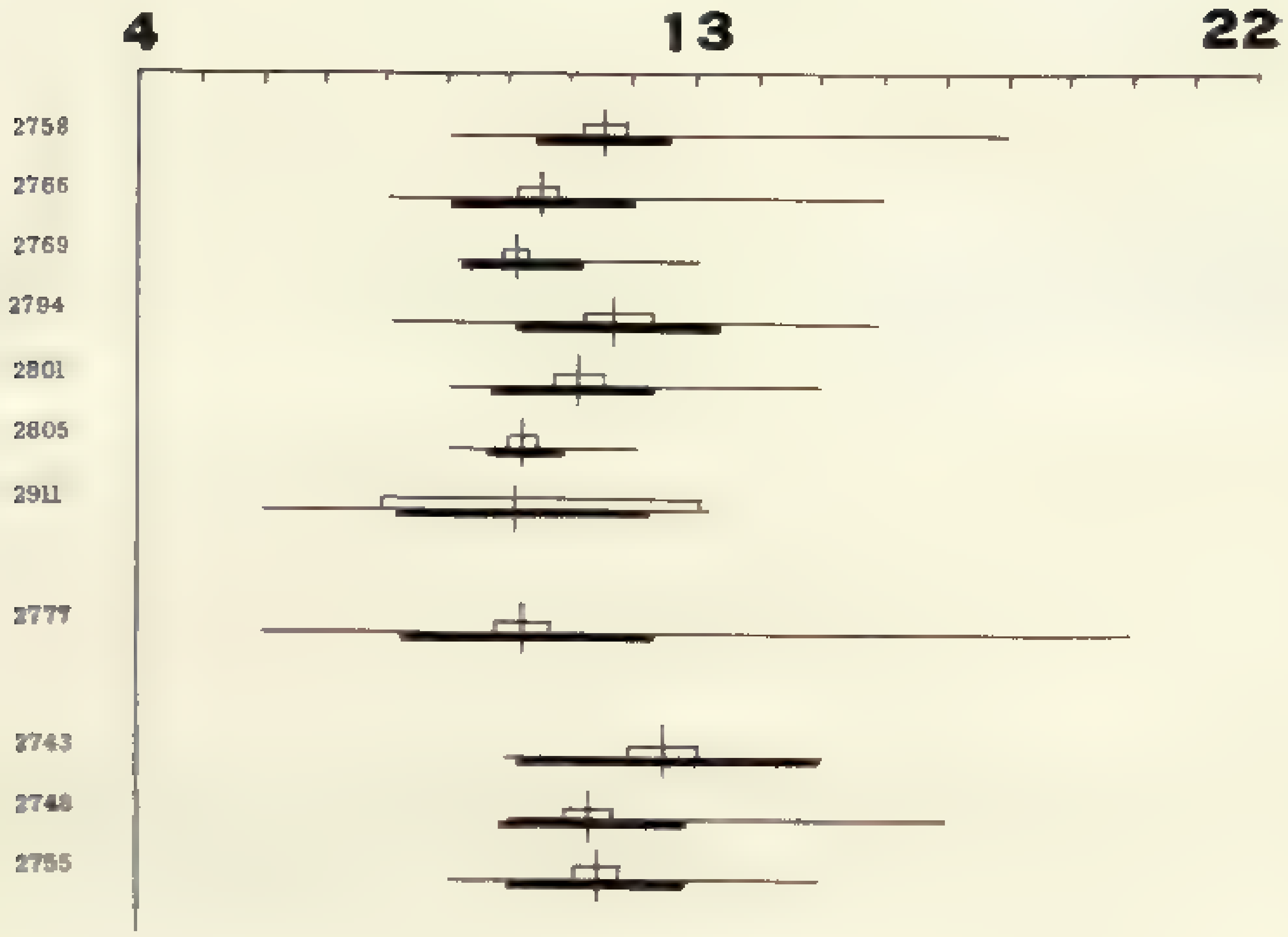
TABLE 14. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF WIDTH OF ACHENE OF TUBULAR FLOWER

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\frac{s}{\sqrt{n}}$
G. sarothrae	Temecula, Calif.	2758	50	3.4	3	2	5	3	.21	.029
	Chula Vista, Calif.	2766	50	4.0	4	2	6	4	.97	.137
	Rancho Santa Fe, Calif.	2769	50	3.5	3	2	5	3	.79	.111
	Payson, Arizona	2794	50	4.3	4	3	6	3	.82	.115
	Ash Fork, Arizona	2801	50	4.3	5	3	6	3	.83	.117
	Hyde Park, Arizona	2805	50	3.4	3	2	6	4	.75	.106
	Hansen, Idaho	2911	28	4.4	5	3	7	4	.96	.181
G. bracteata	Patterson, Calif.	2743	50	4.5	5	3	7	4	.99	.140
	Pond Ranch, Calif.	2748	50	4.8	5	3	7	4	.83	.117
	Temblor Range, Calif.	2755	50	4.6	5	3	6	3	.36	.050
G. serotina	Tucson, Arizona	2777	50	4.5	5	3	7	4	1.40	.198

All measurements expressed in mm. × 10.

The information presented above may be summed up in the following tabulation:

	californica		bracteata		serotina		sarothrae		microcephala	
	range	mode	range	mode	range	mode	range	mode	range	mode
ligulate	5-8	7-8	3-9	3-5	3-8	7	4-8	5-6	0-1	1
tubular	8-15	10	2-11	4-9	5-10	8	3-7	4-6	0-2	1
total	13-23	17-18	5-20	7-14	8-18	15	7-15	9-12	0-3	2



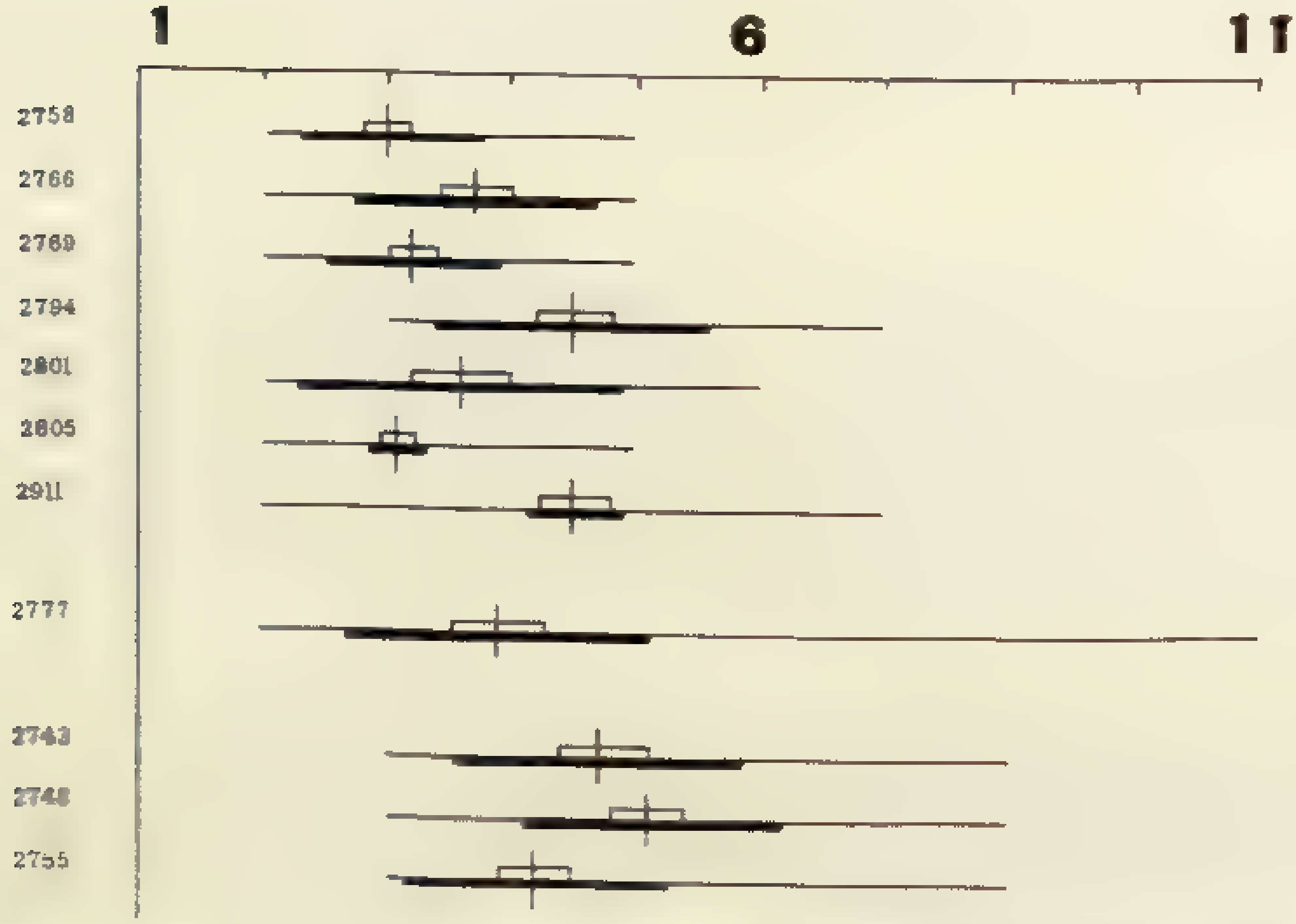


FIG. 13. Mean vertical line), range (middle horizontal line), standard deviation (dark lower bar) and standard error (light upper bar) of length of achene of ligulate flowers. Fig. 14. Id. of width of achene of ligulate flowers. For further explanations see text.

Thus, *G. microcephala,* and to a certain extent *G. californica,* may be characterized by the number of flowers in a head. The other species cannot be identified on this character alone. However, if the flowers of a sufficiently large number of heads are counted, some clue may be obtained as to their identity, and in some cases a preliminary determination can be made.

PAPPUS. The pappus of the ligulate flowers is shorter than that of the tubular ones. Nevertheless, there is considerable similarity in the relative distribution of the means. The mean of pappus length of *G. bracteata* is significantly larger than that of *G. sarothrae,* with the exception of the poly-

TABLE 15. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF LENGTH OF ACHENE OF LIGULATE FLOWER

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$s_{\bar{x}}$
G. sarothrae	Temecula, Calif.	2758	50	11.5	11	9	18	9	1.11	.157
	Chula Vista, Calif.	2766	50	10.5	10	8	16	8	1.46	.206
	Rancho Santa Fe, Calif.	2769	50	10.1	10	9	13	4	.67	.094
	Payson, Arizona	2794	50	11.7	11	8	16	8	1.59	.224
	Ash Fork, Arizona	2801	50	11.1	10	9	15	6	1.31	.185
	Hyde Park, Arizona	2805	50	10.2	10	9	12	3	.61	.086
	Hansen, Idaho	2911	31	10.1	10	6	15	9	1.986	1.444
G. bracteata	Patterson, Calif.	2743	50	12.5	12	10	22	12	2.38	.336
	Pond Ranch, Calif.	2758	50	11.3	11	10	17	7	1.52	.214
	Temblor Range, Calif.	2755	50	11.4	11	9	15	6	1.31	.185
G. serotina	Tucson, Arizona	2777	50	10.2	10	6	20	14	2.02	.285

All measurements expressed in mm. × 10.

TABLE 16. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF WIDTH OF ACHENE OF LIGULATE FLOWER

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$s_{\bar{x}}$
G. sarothrae	Temecula, Calif.	2758	50	3.0	3	2	5	3	.700	.099
	Chula Vista, Calif.	2766	50	3.7	3	2	5	3	.980	.139
	Rancho Santa Fe, Calif.	2769	50	3.2	3	2	5	3	.690	.097
	Payson, Arizona	2794	50	4.5	5	3	7	4	1.110	.157
	Ash Fork, Arizona	2801	50	3.6	3	2	6	4	1.310	.185
	Hyde Park, Arizona	2805	50	3.1	3	2	5	3	.130	.018
	Hansen, Idaho	2911	50	4.5	5	2	7	5	.330	.190
G. bracteata	Patterson, Calif.	2743	50	4.7	4	3	8	5	1.170	.165
	Pond Ranch, Calif.	2748	50	5.1	5	3	8	5	.930	.131
	Temblor Range, Calif.	2755	50	4.4	4	3	8	5	1.050	.148
G. serotina	Tucson, Arizona	2777	50	3.9	4	2	10	8	1.270	.179

All measurements expressed in mm. × 10.

ploid population of this last species (see page 31). The length of pappus of *G. serotina* is somewhat intermediate.

ACHENE. No significant differences in length or width of achene could be detected. *Gutierrezia bracteata* had the largest achenes and some populations of *G. sarothrae* the smallest; however, the differences are believed to have no taxonomic significance.

CONCLUSION. A certain amount of variability in the characters of the populations of an outbreeding species can be predicted on theoretical grounds. The variability encountered in species of *Gutierrezia* is therefore not surprising. Nevertheless, unbiased estimates of the amount of variability in higher plants are few and usually deal with woody plants (Critchfield, 1958). Statistical methods are of common use in genetics and related fields but are used only occasionally in taxonomic studies. The novelty in this study lies in the sampling method, which is a variation of the "completely randomized" method, applied to observational, rather than experimental studies.

As for the results themselves, "key" characters and their variability are expressed in terms of frequencies and ranges and can be dealt with in a more objective fashion as a consequence. The most important aspect is that in most cases we have a continuous range of variability for most characters throughout the range of the genus. Species therefore become meaningful only when they are expressed in terms of series of populations with "frequency peaks" for more than one character, rather than in terms of presence or absence of a fixed frequency of a character (such as an x number of flowers per capitulum).

EVOLUTION

GENERAL CONSIDERATIONS

Several groups of plants in which polyploidy has played an important role in speciation are known today (Goodspeed, 1954; Clausen, Keck and Hiesey, 1945, etc. For a review see Stebbins, 1950). In most cases polyploid species can be separated morphologically from their diploid ancestors and relatives. Nevertheless, some instances are known in which the polyploid plants cannot be separated from the diploids in any other way than by counting their chromosomes (Bell, 1954; Thompson, 1951; Cave and Constance, 1950; Heckard, 1960). Some of the species of *Gutierrezia* have polyploids which cannot be separated either morphologically or ecologically from plants with a lower level of ploidy. Tetraploids of *Gutierrezia sarothrae* with n = 8 are apparently insufficiently distinct from diploids with n — 4 to permit their identification on gross morphology. One tetraploid population from Payson, Arizona (Solbrig 2794) was studied in some detail: the mean of several but not all characters measured was slightly larger in the tetraploids than the mean of the same characters in the diploids. There nevertheless was an overlap in the range, which seems to justify not giving a separate designation to the polyploid in spite of the probable barrier that exists to crossing. Pollen grain and stomata diameter measurements did not reveal any significant differences. Neither could any substantial difference be detected betwen the diploids and the known polyploid plants of *G. microcephala* and *G. bracteata*.

Stebbins (1950), after surveying the corresponding literature, has indicated that the production of a "*gigas*" effect as a result of autopolyploidy is correlated with the existence of a strongly heterozygous diploid. Assuming that the polyploids encountered are autopolyploids, this might indicate that the diploids are rather homozygous. Nevertheless, it is the author's opinion that the polyploids are the result of segmental allopolyploidy (Stebbins, 1950). The author has no direct or indirect evidence to support this assumption other than the indirect evidence of work done with other plants (Goodspeed and Clausen, 1928; Sears, 1948; Schnack and Solbrig, 1952, etc.) and the more direct, but still insufficient, proof of the perfect or nearly perfect pairing at meiosis observed in all instances in the polyploids.

Most species of *Gutierrezia* grow in small to moderately large populations. Exceptions to this are, to a certain extent, the annual species, *G. texana* and *G. glutinosa*, the perennial *G. microcephala* and populations of *G. sarothrae* in the southwestern United States. All the other species observed grew in an over-dispersed fashion, the populations containing approximately 20 to 500 plants. The area occupied varied from a few hundred square meters to some hectares. Each population studied showed greater uniformity within than between populations. This pointed out that there was some kind of isolation mechanism which prevented the free flow of genes from one population to the other. Consequently an investigation of the breeding mechanism was undertaken which it was felt might shed some light on this problem.

As has been indicated before, the flowers are mechanically adapted for outbreeding, even though tests performed showed that there apparently is no genetical mechanism to prevent selfing. In outbreeding plants one usually expects a greater amount of heterozygosity than in self-pollinating plants; the Astereae, so far as known, are insect pollinated and *Gutierrezia* is no exception.

All plants of *Gutierrezia* observed are visited by insects; the amount of visitation varied from very heavy to light. These variations are somewhat correlated with time of day and the number of other plants in bloom in the surrounding vegetation. As a rule, in the months of August to October, when *Gutierrezia* blooms, there are few or no other plants flowering in the surrounding area with the exception of shrubby Compositae (usually Astereae!). The sporadic collections of insects made were not very meaningful, since no systematic studies and observations of pollinators were attempted. Nevertheless, some observations may be recorded. In several instances populations of *Gutierrezia bracteata* and *G. sarothrae* in California were heavily infested with beetles of the genus *Epicauta*. These beetles are gregarious, feed on pollen, and crawl over the plants in large numbers. Undoubtedly by doing so they achieve at least some pollination. But since, unlike bees, they tend to remain on one plant, visiting one flower after another until the food source is depleted and only then moving to another plant, they necessarily pollinate mostly flowers with pollen from the same plant.

Beetles of the genus *Crossidius* also were collected on *Gutierrezia sarothrae*. This genus of beetles is largely confined to arid regions of western North America. Its larvae are all root borers, chiefly in roots of *Chrysothamnus, Haplopappus, Artemisia* and *Gutierrezia* (Linsley, 1957). The adults feed on pollen of the same species and also use the heads as mating places; in doing so they contribute to the pollination of the flowers. They are better fliers than *Epicauta* and it is believed that they contribute to outbreeding. Several species have been recorded by Linsley (1957) on *Gutierrezia sarothrae, G. bracteata*, and *G. microcephala*.

In some cases species of *Crossidius* seem to be specific on *Gutierrezia.*

In addition to beetles, bees were also collected. Honeybees were observed in several instances gathering nectar and pollen. But since this species *(Apis mellifera)* is of relatively recent introduction in the United States, it is not considered to be as important as native bees which also were observed. It is of interest to note here that no large bees, aside from the domestic bee, were found, while some small ones were. In a recent monograph of *Perdita*, a genus of oligolectic bees (Timberlake, 1954, 1958), several species are indicated as feeding on *Gutierrezia bracteata*, *G. sarothae*, and *G. microcephala.* In some instances the *Perdita* species seem to be monolectic in relation to species of *Gutierrezia*, but the collections are far too few to allow an absolute statement. According to MacSwain (personal communication), it is most likely that other genera of oligolectic bees feed on *Gutierrezia.* Nothing is known about oligotropic and monotropic bees in relation to the genus.

The species of *Perdita* are small and their flights probably do not cover a large area. They would therefore contribute to cross pollination of plants within a single population, but they would not be very effective in carrying pollen between populations separated by as much as a few miles. It may be said that, in general, bees contribute to reinforce the geographical isolation of populations (Grant, 1949).

The preliminary picture that emerges from these observations is as follows: The species of *Gutierrezia* are mechanically adapted to outbreeding, although there seem to be no barriers to selfing (see section of Cytology and Genetics). The flowers are pollinated by insects, mainly beetles and small bees. These insects are generally poor fliers, which, due to their habits or constitution, tend to remain within a population and its surrounding area. They produce outbreeding between plants of the same population, hence the intrapopulation variability, but they contribute also to some extent to the selfing of plants. On the other hand, their limited range of movement reinforces the geographical barriers between populations.

Several papers dealing with evolutionary relationships of flowers and bees have appeared recently (Grant, 1950 b; Leppik, 1957, etc.). Others have investigated the relationships between oligolectic bees and flower constancy (Linsley, 1958; Linsley and MacSwain, 1957, 1958, etc.). Oligolectic bees can be defined "as those in which the individual members of the population, through its range and in the presence of other pollen sources, consistently and regularly collect pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only in the face of a local pollen shortage" (Linsley and MacSwain, 1957). The ability to recognize the pollen source is apparently transmitted to the larva when it is fed with pollen of the host plant and is most likely related to olfactory and gustatory characteristics in the pollen. Morphological and physiological adaptations exist in both the bee, to permit a better synchronization with the host, and in the plant, to attract the insect. In the presence of a shortage of the pollen source the oligolectic bee can change to other sources (Linsley and MacSwain, 1957, 1958). It is possible, therefore, that in each population of *Gutierrezia* pollinated by oligolectic bees, as for example *Perdita*, the insects are adapted to a certain pollen or flower type and favor it over other types. This could be in response to a mutation especially favorable to the bee (Grant, 1950a) or as a result of chance, as will be seen.

New populations of *Gutierrezia* are established when new favorable sites are open. As has seen (under Ecology and Distribution) this may be due to such causes as over grazing or soil disturbance. These new populations are probably initiated by a few seeds (and hence there is an advantage to the species of being capable of self-pollination), since the seeds are not especially adapted to dispersal. Under favorable conditions the population might in time expand to a few hundred plants. The genotypes of the first members of the colony will be determined strictly by chance between the genotypes present in the neighboring populations, provided not one genotype in the sum-total of those present in neighboring populations has a comparatively very high frequency. This process is part of what is known as random genetic drift (Wright, 1949; Dobzhansky, 1953). A combination of random genetic drift and selection by oligolectic bees could explain the uniformity within populations of *Gutierrezia* and the differences between populations (which often are statistically significant, see Variation Studies). This is to be viewed as a possible although not necessarily a probable explanation, and it does not necessarily rule out environmental or edaphic selection even if no such differences could be detected (see Ecology and Distribution).

SPECIATION

The basic chromosome number for *Gutierrezia* is x — 4. This number was found in *Gutierrezia texana*, *G. glutinosa*, *G. serotina*, and in the great majority of the populations of *G. sarothrae* investigated. The tetraploid populations of *G. sarothrae* and the diploid populations of *G. bracteata* and *G. microcephala* have n = 8. Twelve is found in several polyploid populations of *G. bracteata* and in *G. californica*. Finally, one population of *G. microcephala* had 16 pairs of chromosomes.

Four is a rather uncommon number in Compositae-Astereae, while nine seems to be the basic number of the tribe (Raven, Solbrig, Kyhos and Snow, 1960). Apparently a process of chromosomal reduction has taken place in those genera which show less than nine chromosomes (cf. also Stebbins, Jenkins and Walters, 1951). In *Gutierrezia* an increase in chromosome number through polyploidy has taken place secondarily.

Gutierrezia sarothrae is envisioned as the North American species most directly related to the basic stock. All other perennial species in North America are considered to be derived from it or from one of its direct ancestors, either by adaptive radiation or by polyploidy or both. This assumption is based on cytological, distributional and morphological data.

As has been stated, *Gutierrezia sarothrae* has four pairs of chromosomes in most of the populations investigated, which is considered to be the basic chromosome number in the genus. It is the most widely distributed of all the species and its range overlaps that of all the others. It also shows the widest ecological as well as morphological diversity. In short, it seems to have all the characteristics necessary to be considered the most primitive living North American species of the genus.

Polyploid populations of *G. sarothrae* show what might possibly have been the first stages in the speciation and differentiation of *G. bracteata* and *G. microcephala*. The polyploid populations of *G. sarothrae*, in addition to having a double number of chromosomes, show slight deviations in the mean of certain characters. Some of these same deviations are so pronounced in *G. bracteata* and *G. microcephala* that they can be identified readily, which is not true of the 8-chromosome population of *G. sarothrae*. The inconclusive evidence supporting the view that the polyploid populations arose as a result of hybridization between two populations of a lower chromosomal level has been stated above. The same process occurring between populations of *G. microcephala* and *G. bracteata* could account for the polyploids of those two species, or these might be the result of backcrossing with polyploid or diploid *G. sarothrae*. An attempt to investigate this possibility through the study of herbarium specimens of 12- and 8-chromosome *G. bracteata* and 4-chromosome *G. sarothrae* failed to yield any conclusive answer. Nevertheless, there were indications that the 12-chromosome *G. bracteata* might be an allopolyploid between 8-chromosome *G. bracteata* and 4-chromosome *G. sarothrae*. The morphological characters of the 12-chromosome *G. bracteata* seem to be intermediate between the characters of the two other groups. More work, especially of an experimental nature, is needed in this area.

Gutierrezia serotina seems to be an extreme morphological variant of *G. sarothrae*. It would be interesting to know whether it is also isolated from it genetically. Cytological information is lacking in the case of *G. grandis*, and no ideas as to its evolution can be advanced.

Gutierrezia californica seems to be related to *G. bracteata* and might have been derived from it. On the other hand, *G. californica* is very similar morphologically to the Chilean *G. paniculata*. The fact that *G. californica* grows in such a specialized habitat as serpentine would seem to speak against the idea that *G. californica* was derived directly from *G. paniculata* through long-range dispersal. Also, the fact that a hybrid between *G. californica* and *G. bracteata* was obtained seems to rule out this hypothesis. Nevertheless, more information is needed, especially with regard to *G. paniculata*.

No suggestions on their evolution can be advanced in respect to the annual species. The pappus of *G. glutinosa* is more like that of the other species of the genus, while *G. texana*, in spite of its reduced pappus, has an involucre more in accordance with the generic type. Xerophytic annuals seem to be specialized life forms within the tribe, which consists mostly of shrubs (Raven, Solbrig, Kyhos, and Snow, 1960). If this is so, it would reaffirm the advanced nature of the genus. It also suggests that section Hemiachyris has been derived from section Gutierrezia.

In concluding this discussion, it is appropriate to emphasize the importance that the type of distribution has played in the evolution of the genus. In a group like *Gutierrezia*, where we are dealing with a series of populations more or less isolated from each other, the role of the population as the recombination unit is greatly increased. If we consider also the fact that most species are distributed over a wide territory, in which profound environmental differences undoubtedly occur, we can easily understand the range of morphological diversity encountered.

In addition to the influential micro-environmental differences which might account for part of the differences between populations, random genetic drift is thought to be largely responsible for the morphological diversity between populations. This is inferred from the following circumstances: (1) We are dealing with a series of populations separated by relatively large distances. (2) The populations are generally small. (3) The seed-dispersal mechanism is rather inefficient for the family. (4) Once the populations are established, there seems to be little chance for interchange of genetic material. On the other hand, the populations are rather stable in the sense that being composed of perennial plants they do not show the yearly fluctuations in number characteristic of populations of annuals. Nevertheless, field observations indicate that they respond strongly to yearly environmental fluctuations, as measured by the number of seedlings found. Since the ability to produce offspring is in the last analysis the crucial point where selection pressures are expressed, these annual fluctuations in production of seedlings may be as vital to the species and perhaps of the same or a greater degree of importance for the operation of such a process as random genetic drift, as the more impressive fluctuations of populations of spring annuals in the California deserts (Epling, Lewis and Ball, 1960).

RELATIONSHIPS WITH OTHER GENERA

The phylogenetic relationship of *Gutierrezia* with other genera is still an open question. An exhaustive investigation of most genera of Astereae is needed before any conclusive answers can be given. However, it may be appropriate to record some suggestions that have occurred to the author in the course of the present investigation.

Gutierrezia was placed by Hoffmann (1897) in subtribe Solidagineae because of the homochromous character of the capitula, i.e., both tubular and ligulate flowers are of the same color, usually yellow. In the light of work done in other genera of Compositae (Babcock and Cave, 1938) it would seem that such a characteristic may not be of much importance. Nevertheless, the Solidagineae have been accepted by most authors, even though relationships with other subtribes, particularly the Asterineae are obvious.

The chromosome numbers for at least some species are known in about half of the genera of the subtribe. Nine is the most common number encountered in some of the large genera such as *Solidago*, and sections of *Haplopappus*, as well as in *Acamptopappus*, *Amphipappus*, *Chrysopsis*, and *Heterotheca* (Raven, Solbrig, Kyhos, and Snow, 1960, and literature in same; Solbrig, 1960).

The pappus characteristic of the tribe is one comprising well developed hairs, as in *Haplopappus*. *Gutierrezia* and a few other genera differ in having a scaly or reduced pappus; these genera are *Grindelia*, *Gymnosperma*, and *Xanthocephalum*. *Amphipappus* and *Amphiachyris* are somewhat intermediate, while *Hysterionica* has a pappus with a row of hairs and a row of minute scales. All but *Amphipappus*, *Hysterionica*, and *Grindelia* are closely related (Shinners, 1950; Solbrig, 1960). While *Amphipappus* and *Hysterionica* are not closely allied to the rest of the genera cited above, there are certain characteristics in *Grindelia* (such as chromosome number, type of pappus, and shape of involucre) which seem to indicate affinity with these genera. However, probably no linear relationship exists between any of them, and the striking similarities between some species belonging to different genera are probably due to convergent evolution.

Finally, the heterochromous genus *Greenella* should be mentioned. The morphological similarity of one of its species, *Greenella arizonica* A. Gray, to *Gutierrezia glutinosa* is unquestionable and some authors have doubted the distinctness of the genus (A. Gray, 1884; Shinners, 1950). The other two species of *Greenella*, *G. discoidea* and *G. ramulosa*, are sufficiently distinct to establish the validity of the genus. Until more information is available, it is believed that *Greenella arizonica* should be maintained in ts present status, since it has enough characters in addition to its heterochromous character to separate it from *Gutierrezia.*

TAXONOMIC TREATMENT

Gutierrezia Lag. Nov. Gen. et Spec. 30, 1816
Brachyris Nutt. Gen. 2: 163, 1818.
Brachyachyris Spreng. Syst. 3: 574, 1825.
Hemiachyris DC. Prodr. 5: 313, 1836.
Odontocarpha DC. Prodr. 5: 71, 1836.

Suffruticose, erect, glabrous to tomentose, perennials or stout annuals. Leaves petiolate, alternate, subcoriaceous, linear-lanceolate, entire, narrow. Heads in corymbose or paniculate inflorescences, in clusters or solitary at the end of branchlets or solitary in the axils of leaves, on long to very short peduncles. Heads turbinate to campanulate, the involucral bracts in two to many rows, imbricated, with green and swollen tips. Flowers yellow, the ligules not more than 1½ times the involucre; tubular flowers campanulate with very short tube and a narrow throat with 5 small triangular lobes; stamens 5; styles of tubular flowers with long branches very much exserted at maturity and long stigmatic hairs in the upper part and stigmatic papillae in the lower part of the stigmatic branches; styles of the ligulate flowers only papillate; pappus of short to medium-long squamellae, shorter or absent in the ligulate flowers; achenes turbinate, slightly flattened, tomentose, with hairs arranged in loose rows.

Type-species, *Gutierrezia linearifolia* Lag. (No specimens identified by Lagasca have been found)

KEY TO THE SPECIES

A. Plants perennial; involucre turbinate except in No. 1; flowers 20 or fewer per head .... Section *Gutierrezia.*
  B. Heads about 10 mm. long, solitary or in small clusters at ends of branches; leaves broad, 5-6 mm. wide .... 6. *G. grandis.*
  B. Heads less than 10 mm. long, or if longer the leaves not more than 3-4 mm. wide
    C. Involucre campanulate; heads numerous, 3-6 mm. high, 3-5 mm. broad, solitary at the ends of branchlets; plants not more than 50 cm. high .... 5. *G. serotina.*
    C. Involucre turbinate; heads in clusters at ends of branchlets or, if solitary, more than 6 mm. high.
      D. Heads with only 2 or 3 flowers; involucre very narrow; achenes of disk flowers aborted .... 4. *G. microcephala.*

D. Heads with more than 4 flowers; involucre turbinate; achenes of disk flowers fertile.
  E. Heads clustered at ends of branchlets; flowers 5 to 10; involucre narrow, less than 5 mm. wide .... 3. *G. sarothrae.*
  E. Heads mostly solitary at ends of branchlets; flowers usually more than 10; involucre more than 5 mm. wide.
    F. Inflorescence loosely corymbose; heads 6-10 mm. high, 4-6 mm. wide; open, little-branched shrub .... 1. *G. californica.*
    F. Inflorescence paniculate; heads 4-7 mm. high 2-5 mm. wide; globose, much-branched shrub .... 2. *G. bracteata.*

A. Plants annual; involucre turbinate campanulate to campanulate; flowers more than 20 per head .... Section Hemiachyris.
  G. Involucre turbinate-campanulate; heads long-pedunculate along length of branches; pappus of ligulate flowers absent or reduced; tubular flowers 10-20 .... 7. *G. texana.*
  G. Involucre campanulate; heads at ends of branches; pappus present in both ligulate and tubular flowers; tubular flowers 20-40 .... 8. *G. glutinosa.*

1. **Gutierrezia californica** (DC.) T. & G. Fl. N. Amer. 2: 193, 1842
Brachyris californica DC. Prodr. 5: 313, 1836.

Perennial shrubs or bushes. Stems semi-woody, glabrous or sparsely tomentulose, rugose or irregularly striate, mostly simple or few-branched, arising from a short, woody base. Leaves arranged singly along the branches, linear, 5 to 35 mm. long, 1-3 mm. broad, the surface punctate, hairy, entire with ciliate margins. Heads solitary or sometimes in groups of 2-3 at ends of branches, arranged in loose-corymbose inflorescences. Peduncles 5 mm. or more long. The involucre 6 to 10 mm. high, 4-6 mm. broad, turbinate to campanulate, the bracts ca. 20, arranged in three overlapping series, lanceolate to ovate, acute or obtuse, some somewhat carinate, the outer shorter and narrower than the inner, coriaceous or sub-coriaceous, usually with a green, somewhat swollen tip, the inner bracts with a membranaceous border, glabrous. Receptacle flat or somewhat convex, alveolate. Ligulate flowers about 9, the ligules narrowly lanceolate, 3-4 mm. long, ca. 1 mm. broad; tubular flowers about 11, 3-4 mm. high, glabrous, the throat oblong, slightly larger than the tube. Pappus of 6 to 10 narrow scales, as long as the achene in tubular flowers, only a third in the ligulate ones. Styles of tubular flowers with well developed stigmatic hairs and a short border of stigmatic papillae at the base of the stigmatic branch on each side; the ligulate flowers with only a border of stigmatic papillae along the whole stigmatic branch. Achenes terete, tapering at base, tomentulose, the hairs slightly larger in achenes of ligulate flowers.

TYPE-LOCALITY. "In California", *Douglas.*

DISTRIBUTION. Known only from three populations in the area of San Francisco Bay, California, growing on serpentine soil (fig. 3).

REPRESENTATIVE SPECIMENS. **California.** Angel Island, 1957, *Solbrig 2428* (UC); Oakland, Redwood Park, 1956 *Solbrig 2154* (UC); Marin County, Point Bonita, 19-VI-1892, *Michener and Bioletti 1096* (UC);

Alameda County, Oakland Hills, beyond Paroltas, 10-XI-1869, *A. Kellogg and W. G. W. Harford 387* (US, MO); Hills near Oakland, 1-VII-1889, *E. R. Drew* (UC); Alameda County, dry summit of Redwood Ridge, 21-IX-1931, *Constance 382* (UC); Oakland Hills, VII-1888, *E. L.*

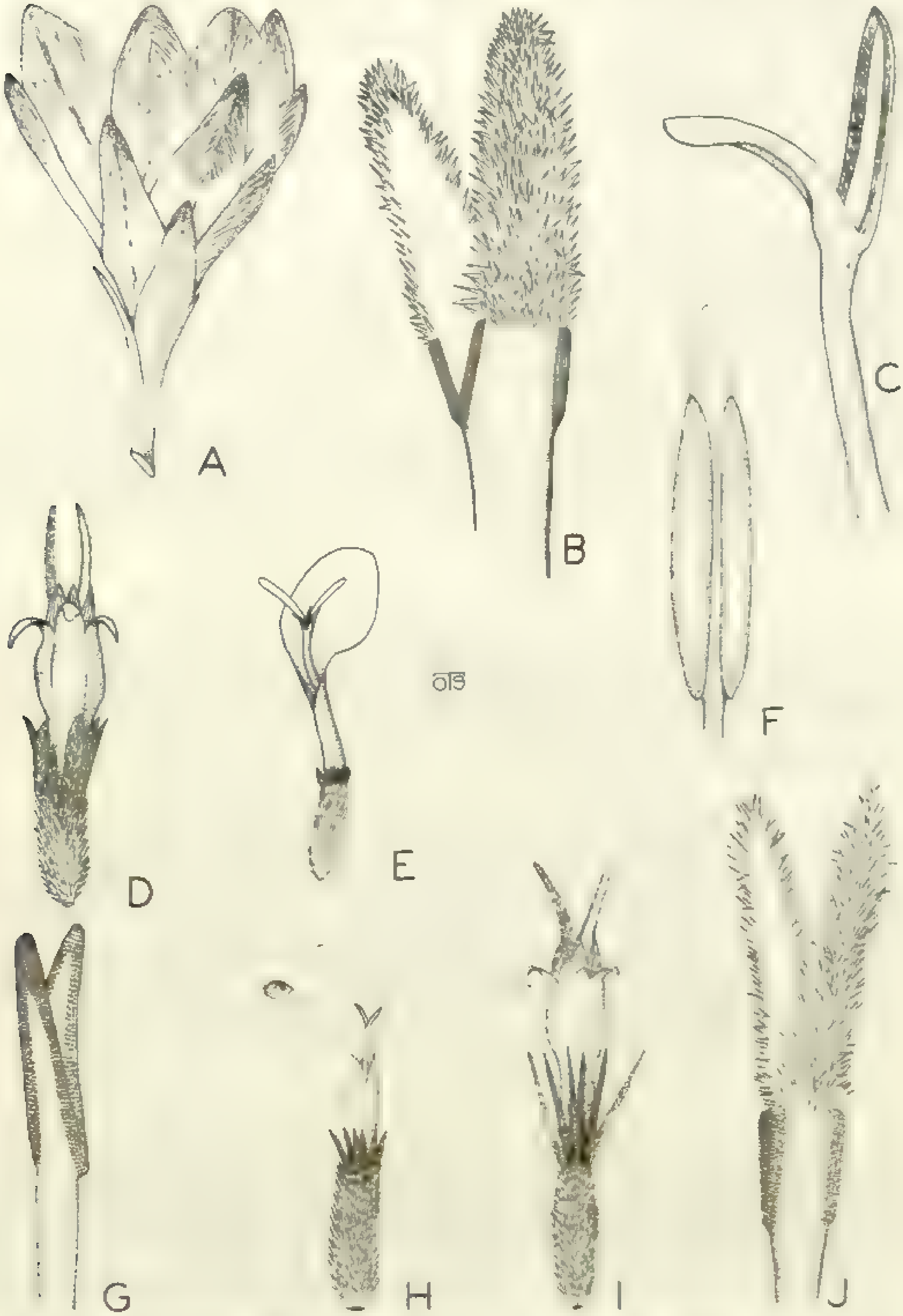


FIG. 15. *Gutierrezia californica* A. Involucre × 6 B. Style of tubular flower × 20: Style of ligulate flower × 20: D. Tubular flower × 6 E. Ligulate flower × 6· F. Stamen × 20. *Gutierrezia bracteata* G. Style of ligulate flower × 20; H. Ligulate flower × 6; I. Tubular flower × 10; J. Style of tubular flower × 20.

Greene (US); San Francisco, *Wilkes* (US); Near Oakland, *H. G. Bloomer* (NY).

2. **Gutierrezia bracteata** Abrams, Bull. Torr. Club 34: 265, 1907

Gutierrezia californica var. *bracteata* (Abrams) Hall, Univ. Calif. Publ. Bot. 3: 36, 1907.

Small suffrutescent shrub up to 50 cm. high, paniculately branched, the branches slender, flexible, the bark light to dark gray, the branchlets greenish, a root-crown present or lacking. Leaves arranged singly along the branches, somewhat clustered at the middle of the branches, filiform, 30-50 mm. long 1-2 mm. wide, the surface smooth, short-pubescent to glabrous, entire, smaller leaves ("bracts" in Abrams' original description) in the axils of branches. Heads in open-paniculate inflorescences, single or occasionally paired at ends of branchlets. Peduncles 5-50 mm. long. The involucre 5-6.5 mm. high, 2-3.5 mm. in diameter, conical to turbinate, involucral bracts arranged in approximately 3 rows, narrow and elongated, carinate or at least strongly convex with a green swollen tip, tightly appressed and imbricated, becoming loose at maturity, up to 4 mm. long and 2 mm. wide. Ligulate flowers usually 5 (3-6), 6-8 mm. long; tubular flowers usually 4 (2-6), 4-6 mm. long. Pappus of 10 to 12 scales, 1-2 mm. long in tubular flowers and 0.5-1.5 mm. in ligulate flowers. Achenes cylindrical, hairy, 1-2 mm. long, 0.5-1.0 mm. wide at anthesis.

TYPE LOCALITY. California, San Bernardino County, between Banning and Seven Palms, XI-1889, *C. R. Orcutt.*

DISTRIBUTION. Inner coastal ranges of California from Yolo County to Riverside County, occasional southward to about central Baja California, Mexico. (fig. 3)

REPRESENTATIVE SPECIMENS. **California.** Alameda County, Corral Hollow, 21-X-1956, *Solbrig 2159* (UC); Cuyama Valley, 54 miles E. of Hwy. 101, 22-XI-1956, *Solbrig 2166* (UC); Cache Creek, 5.8 miles N. W. of Rumsey, 19-X-1954, *Everett & Balls 20366* (UC, WTU, NY, RM); Los Angeles County, Azusa, 5-VI-1902, *Abrams 1577* (F, RM, UC, MO, POM, GH, NY); Waltham Creek, 5 miles W. of Alcalde, 14-XI-1936, *Belshaw 2735* (UC, WS, MO, GH); Upper end of Cuyama Valley, 18-XI-1932, *Wolf 4417* (A, WS, WTU, UC); Corral Hollow, 18-X-1861, *Brewer 848* (WS, US, UC, MO).

3. **Gutierrezia sarothrae** (Pursh) Britt. & Rusby, Trans. N. Y. Acad. Sci. 7: 10, 1887

Solidago sarothrae Pursh, Fl. Amer. Sept. 2: 540, 1814; *Xanthocephalum sarothrae* (Pursh) Shinners, Field and Lab. 18: 29, 1950.

Brachyris euthamiae Nutt. Gen. N. Amer. Pl. 2: 163, 1818; *Brachyachyris euthamiae* (Nutt.) Spreng. Syst. 3: 574, 1825; *Gutierrezia euthamiae* (Nutt.) T. & G. Fl. N. Amer. 2: 193, 1841-43. Based upon *Nuttall*, "On the arid plains of the Missouri from the Arikarees to the Mountains".

Brachyris divaricata Nutt. Trans. Amer. Phil. Soc. 7: 313, 1841; *Gutierrezia divaricata* (Nutt.) T. & G. Fl. N. Amer. 2: 194, 1841-43. Based upon *Nuttall*, "On the Platte near the Rocky Mountains".

Gutierrezia Haenkei Sch. Bip. Flora 38: 115, 1855. Based upon *Haenke*, "Mexico, Acapulco".

Gutierrezia juncea Greene, Pittonia 4: 56, 1899. Based upon *Skehan*, "near Gray, New Mexico", VIII-1898.

Gutierrezia diversifolia Greene, Pittonia 4: 53, 1899. Based upon *Watson 551*, "Laramie, Wyoming".

Gutierrezia divergens Greene, Pittonia 4: 58, 1899. Based upon *Parish*, "San Bernardino Mesas" [California].

Gutierrezia lepidota Greene, Pittonia 4: 57, 1899. Based upon *Greene*, "Plains about Grand Junction, Colorado", 27-VIII-1899.

Gutierrezia fasciculata Greene, Pittonia 4: 56, 1899. Based upon *Greene*, "Grand Junction, Colorado", 26-VIII-1896.

Gutierrezia filifolia Greene, Pittonia 4: 55, 1899. Based upon *E. O. Wooton*, "White Mts. of New Mexico", 24-VIII-1897.

Gutierrezia longifolia Greene, Pittonia 4: 54, 1899. Based upon *E. O. Wooton*, "White Mts. of New Mexico", VIII-1897.

Gutierrezia tenuis Greene, Pittonia 4: 55, 1899; *Xanthocephalum tenuis* (Greene) Shinners, Field & Lab. 18: 29, 1950. Based upon *Greene*, "Foothills of the mountains back of Silver City, New Mexico", 30-IX-1880.

Gutierrezia myriocephala A. Nels. Bot. Gaz. 37: 264, 1904. Based upon *A. Nelson 8645*, "near Badger, Laramie County, Wyoming", 3-IX-1901.

Gutierrezia scoparia Rydb. Bull. Torr. Club 31: 647, 1904. Based upon *Clements 16*, "Manitou, Colorado", 1901.

Gutierrezia linearis Rydb. Bull. Torr. Club 31: 647, 1904. Based upon *Earle 474*, "Gray, Lincoln County, New Mexico", 1900.

Gutierrezia laricina Greene, Rep. Sp. Nov. 7: 195, 1909. Based upon *C. R. Orcutt*, "Colorado Desert in California", X-1889.

Gutierrezia Goldmanii Greene, Rep. Sp. Nov. 7: 195, 1909. Based upon *E. A. Goldman*, "Florida Mts., in extreme southern New Mexico", 8-IX-1908.

Gutierrezia furfuracea Greene, Rep. Sp. Nov. 7: 195, 1909. Based upon *E. A. Goldman*, "Cactus flat, upper Rio Gila, southeastern New Mexico", 13-X-1908.

Gutierrezia fulva Lunell, Amer. Midl. Nat. 1: 235, 1910. Based upon *J. Lunell*, "Des Lacs, Ward County" [North Dakota].

Gutierrezia Greenei Lunell, Amer. Midl. Nat. 1: 233, 1910. Based upon *J. Lunell*, "Leeds, North Dakota".

Gutierrezia ionensis Lunell, Amer. Midl. Nat. 2: 194, 1911. Based upon *J. Lunell*, "east of Ione, Morrow County, Oregon", 16-VII-1903.

Gutierrezia sarothrae var. *pauciflora* Eastw. Proc. Calif. Acad. Sci. IV, 18: 480, 1929. Based upon *Mason 1971*, "Turtle Bay, Lower California, Mexico", 2-VI-1925.

Gutierrezia globosa A. Nels. Amer. Jour. Bot. 23: 265, 1936. Based upon *A. Nelson 11,739*, "Between San Ysidro and Bernalillo, New Mexico", 29-VIII-1931.

Gutierrezia corymbosa A. Nels. Amer. Jour. Bot. 23: 265, 1936. Based upon *A. Nelson*, "Ten miles east of Santa Fe, New Mexico", 30-VIII-1931.

Shrubs, 15-90 cm. high, profusely branched prevalently from the base, the secondary branching variable, usually slight and concentrated in the upper part, from shallow, fasciculate roots, or one central taproot Root-crown woody, up to 7.5 cm. thick. Leaves of two types, the primary scattered along the stems, 2-7 cm. long, up to 3 mm. wide, the secondary fascicled in axils of primary leaves or branchlets, up to 2 cm. long and 1-2 mm. wide, linear-lanceolate, entire, glabrous to tomentulose, often with regular amounts of resin on both surfaces. Heads in corymbose inflorescences, usually in fascicles of 3-10 at the ends of branchlets, sometimes single. Involucre 3-10 mm. long, 2-5 mm. wide, turbinate, involucral bracts narrow, acute, with a green and swollen tip, imbricated, usually appressed, forming a compact capitulum, in several rows and often covered with resin. Ligulate flowers usually 4 or 5 (3-7), 2-5 mm. long; tubular flowers 3 or 4 (2-6), 2-3 mm. long; pappus about as long as achene, of 8-10 scales, in ligulate flowers 1/2 - 1/3 shorter. Achenes terete, 1-2 mm. long, hairy.

TYPE-LOCALITY. "On the plains of the Missouri", *Lewis*.

DISTRIBUTION. Between the Cascades-Sierra Nevada and the Rocky Mountains from southern Canada to northern and central Mexico, eastern foothills of the Rocky Mountains and infrequent on the Great Plains. Also in southern California, and Baja California, Mexico (fig. 2).

REPRESENTATIVE SPECIMENS. **Canada.** Along Highway from Calgary to Waterton Lakes, near Pincho, 31-VIII-1938, *Nelson & Nelson 3122* (RM, MO, UC). **Mexico. Chihuahua.** Rocky hills near Chihuahua, 26-IX-1885, *Pringle 337* (PH, GH, US, WTU). **Baja California.** Between Ojos Negros and Neji Rancho, 16-IX-1929, *Wiggins & Gillespie 4155* (F, MO, NY, A, GH, US). **United States. Arizona.** 12.6 miles E. of Ash Fork, 26-VIII-1958, *Solbrig 2801* (UC). 5 miles N. of Payson, 26-VIII-1958, *Solbrig 2794* (UC). **California.** Dry Ridges, Bear Valley, 7-VIII-1902, *Abrams 2916* (LA, UC, NY, WTU, PH, US, F). Ramona, X-1903, *Brandegee* (GH, US, MO, RM, NY). 2 miles W. of Temecula, 18-VIII-1958, *Solbrig 2758* (UC). **Colorado.** Denver, 4-IX-1920, *Clokey 3880* (US, GH, NY, UC, WTU, MO, F, RM). Greenhorn, 2-IX-1921, *Clokey 4320* (WS, MO, WTU, RM, UC, US). Buena Vista, 1-2-VIII-1919, *Eggleston 15348* (GH, NY, MO, F). **Idaho.** Hansen, 23-VI-1958 *Solbrig 2911* (UC). McCammon, 4-VIII-1911, *Nelson & Macbride 1583* (US, RM, GH, NY, F, UC). **Kansas.** 2 miles E. Meade, 7-X-1936, *Horr 574* (SMU, UC, RM, US, WS). **Nevada.** Kyle Canyon, Charleston Mountains, 9-VIII-1937, *Clokey 7737* (MO, SMU, UC, NY, RM, WTU, WS). Kyle Canyon Fan, Charleston Mountains, 9-VIII-1938, *Clokey 8155* (MO, NY, F, UC, RM, WTU, WS). **New Mexico.** Sierra Blanca, 18-VIII-1904, *Metcalfe 1230* (UNM, MO, NY, UC). Pyramid Peak, 16-VIII-1930, *Fosberg S3775* (PH, MO, UC, US). **Oklahoma.** Altus, 24-X-1936, *Hopkins & Van Valkenburgh 695* (SMU, UC, US, RM, MO, WTU, WS). **Texas.** Randall County, Palo Duro State Park, 20-X-1945, *Cory 50407* (UC, SMU, US). Culberson County, north of Van Horn, 10-X-1944, *Waterfall 5780* (GH, MO, SMU). **Utah.** Western Bear's Ear, Elk Mountains, 2-VIII-1911, *Rydberg & Garrett 9370* (RM, US, UC, NY). **Washington.** Asotin County, north of Rogersburg, 7-IX-1936, *Constance 1813* (GH, MO, US, WTU, WS). **Wyoming.** Laramie, 12-IX-1899, *Nelson & Nelson 6858* (RM, NY, GH, MO).

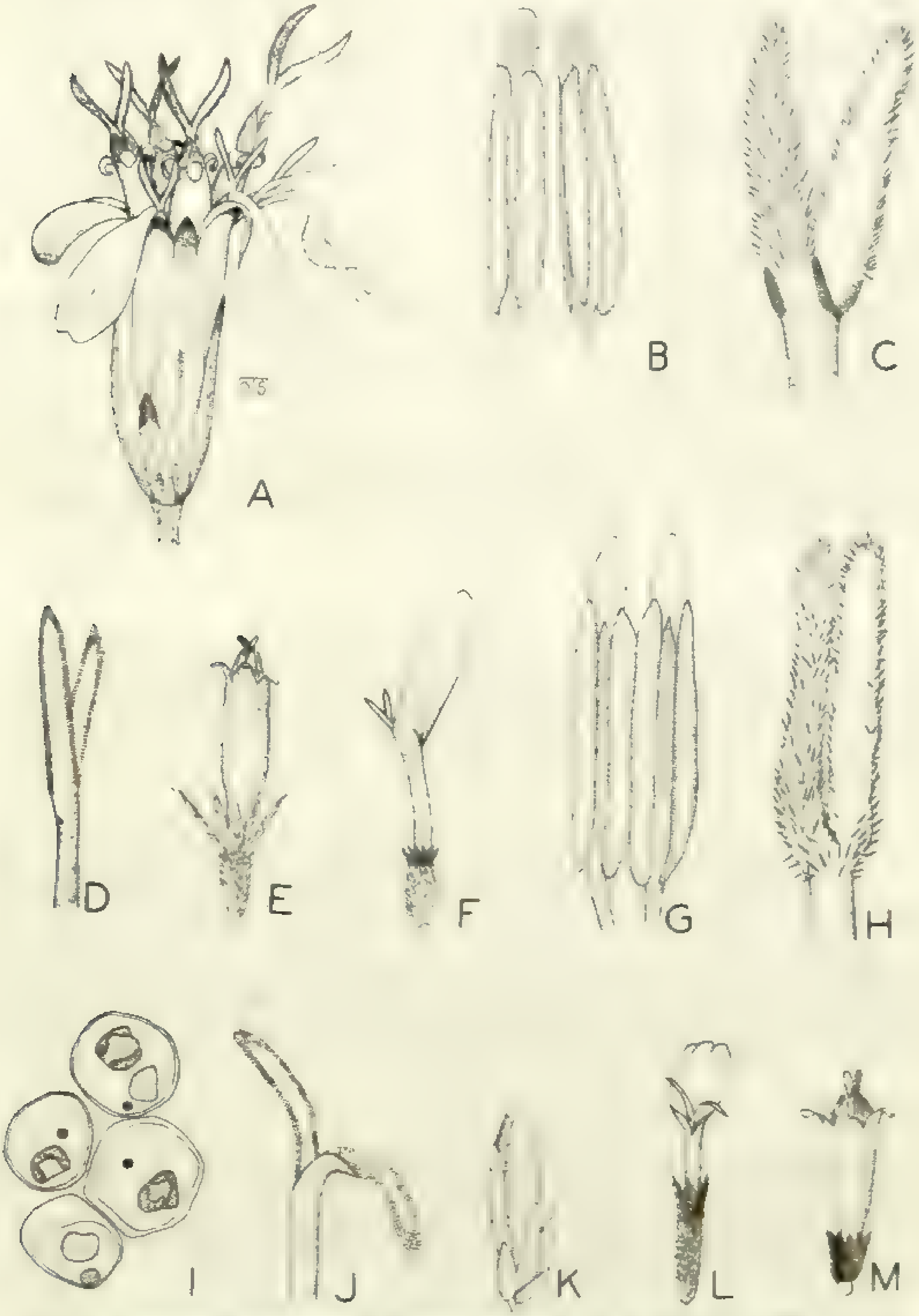


FIG. 16. *Gutierrezia sarothrae* A. Flowering head × 16. B. Stamens × 20. C. Style of tubular flower × 20. D Style of ligulate flower × 20 E. Tubular flower × 6; F Ligulate flower × 6: *Gutierrezia microcephala*. G. Stamens × 20. H. Style of tubular flower × 20: I. Aborted pollen grains × 1000. J. Style of ligulate flower × 20. K. Involucre × 10; L. Ligulate flower × 10; M. Tubular flower × 10.

This species is the most abundant, the most widespread, and the most variable. This variability, associated with a disjunct type of distribution, has led those botanists prone to emphasize small differences to describe a large number of taxa, as can be seen by the long list of synonyms. Nevertheless, when one considers the group in its totality, one realizes that these "species" represent only special combinations of characters, often not even representing one breeding population, but just a few isolated individuals. Nevertheless, some of the described taxa might be deserving of varietal rank. Although no subspecific taxa have been proposed since it is felt that more work is needed, certain regional types might be mentioned.

(1) Southern California and Baja California, Mexico. Some specimens from this region have the heads solitary and terminal, which causes them to resemble *G. bracteata.* Intensive study of some populations shows, nevertheless, that they belong to *G. sarothrae* on the basis of a large series of plants which show the typical characters. They also have the chromosome number of *G. sarothrae.*

(2) North of Utah-Colorado line. These are small, very globose plants, some 20 cm. tall. Specimens of this type were cultivated at the University of California Botanical Garden and maintained their morphological characteristics. They apparently hybridize freely with more typical forms and probably represent an ecotypic form. The type of the species comes from this area.

(3) Arizona, New Mexico, and Mexico. This common form has few flowers, a very narrow involucre and is reminiscent in aspect of *G. microcephala.* All kinds of intermediates to the typical form occur, however, and make an interpretation difficult. These plants have fertile tubular flowers and more involucral bracts than *G. microcephala,* and hence can be easily separated from that species.

(4) Uintah Mountains in northeastern Utah. A few specimens with large heads, very similar to those of *G. bracteata,* have been collected in this area. Not enough information is available on this material, and since there are also intermediates, a decision will have to be made when more is known about the Gutierrezias in this area.

4. **Gutierrezia microcephala** (DC.) A. Gray, Pl. Fendl. 74, footnote 18, 1849

Brachyris microcephala DC. Prodr. 5: 313, 1836; *Gutierrezia euthamiae* T. & G. var. *microcephala* (DC.) A. Gray, Syn. Fl. N. Amer. 1 (2): 115, 1884; *G. sarothrae* var. *microcephala* (DC.) Benson, Amer. Jour. Bot. **30**: 631, 1943; *Xanthocephalum microcephalum* (DC.) Shinners, Field & Lab. **18**: 29, 1950.

Xanthocephalum lucidum Greene, Pittonia **2**: 282, 1892; *Gutierrezia lucida* (Greene) Greene, Fl. Francis. pt. 4: 361, 1897. Based upon a specimen from "the region of the Mohave Desert and southward" [California], no collector indicated.

Gutierrezia linoides Greene, Leafl. Bot. Obs. **2**: 22, 1909. Based upon *J. C. Blumer*, "Limestone of the Chiricahui Mts." [Arizona], 1907.

Gutierrezia glomerella Greene, Pittonia **4**: 54, 1916. Based upon *Wooton 449* "Organ Mts., New Mexico".

Gutierrezia digyna Blake, Contr. U. S. Nat. Herb. **22**: 591, 1924; *Xanthocephalum digynum* (Blake) Shinners, Field & Lab. **18**: 29, 1950. Based upon *V. L. Cory 26,335*, "12 miles east of Marfa, Presidio County, Texas", 19-X-1937.

Globose shrub, 30-100 cm. high. Branches slender, grayish to yellowish-green, about 1 mm. in diameter, glabrous, slightly fistulate, arising from a well developed root-crown or short stem, up to 1-2 cm. in diameter, bark rugose, gray. Leaves narrow-lanceolate of two types, cauline 2-5 cm. long and 2-4 mm. wide, axillary leaves shorter and much narrower, often borne in fascicles, lanceolate, entire, often resinous, or either type absent, the axillary in young plants and the cauline in older specimens or under special environmental conditions. Heads in glomerules at the end of branches, sessile. Involucre 3-4 mm. long, 1-1.5 mm. wide, narrowly turbinate, involucral bracts less than 10, lanceolate, with a slightly thicker and greenish tip. Ligulate flowers usually 1 or 2 (up to 4), 3-4 mm. long; tubular flowers 1-3, 2-3 mm. long. Pappus of few scales up to 2 3 mm. long, shorter in the ligulate flowers. Styles of tubular flowers usually without stigmatic papillae but with well developed hairs, that of ligulate flowers only with stigmatic papillae. Achenes of tubular flowers aborted, those of the ligulate flowers fertile, 2-3 mm. long, hairy.

TYPE-LOCALITY. "In Mexico prope locum dictum Saltillo", *Berlandier*.

DISTRIBUTION. Southwestern United States from western Texas to California, and northern and central Mexico (fig. 5).

REPRESENTATIVE SPECIMENS. **Mexico. Coahuila.** Saltillo, 1898, *Palmer 143* (UC, F, MO). **United States. Arizona.** Douglas, 23-VIII-1958, *Solbrig 2789* (UC). 3.5 miles S. of St. David, 23 VIII 1958, *Solbrig 2790* (UC). Ft. Lowell, 20-X-1903, *Thornber 93* (US, UC). **California.** San Bernardino and Riverside County line, road from Yucca Valley to San Bernardino, 27-VIII-1958, *Solbrig 2807* (UC). Wyman Canyon, White Mountains, 29-VI-1931, *Duran 3151* (UC, F, MO, US, GH). **Colorado.** Naturita, 11-VIII 1914, *Payson 595* (GH, MO, WS, F). Deer Ann, 25-VIII-1901, *Baker 915* (MO, US, UC, GH). **Nevada.** Kyle Canyon, Charleston Mountains, 27-VI-1936, *Clokey 7413* (GH, UC, PH, SMU, US, MO, WS, WTU, F). **Texas.** Vicinity of El Paso, 8-X-1913, *Rose & Fitch 17847* (US, MO). **Utah.** Armstrong and White Canyons, near the Natural Bridges, 4-6-VIII-1911, *Rydberg & Garrett 9425* (US, UC, NY).

5. **Gutierrezia serotina** Greene, Pittonia 4: 57, 1899

Gutierrezia polyantha A. Nels. Amer. Jour. Bot. 25: 117, 1938. Based upon *Nelson & Nelson 1638*, "a few miles north of Tucson, Arizona", 26-IV-1935.

Small hemispheric shrub, 10-40 cm. high. Branches leafy to the top, green or lightly gray, slightly striate, glabrous or nearly so, with very few or no side branches, abundant from root-crown, 2-4 cm. in diameter. Root a slender taproot with abundant secondary roots. Leaves single along the branches or in fascicles at axils of single leaves in lower third of branches, linear, 1-2 cm. long and up to 1 mm. wide, glabrous. Heads solitary or in loose glomerules at the tip of branches, arranged in corymbose inflorescences, sessile or short-pedunculate. Involucre 2-4 mm. high, 2-3 mm. wide, hemispheric to turbinate-campanulate, involucral bracts broad, almost as wide as long, obtuse, glabrous, margin membranaceous, with a slightly thickened, greenish or brown tip, arranged in 2 or 3 loose series. Ligulate flowers about 7 (4-8), 4-5 mm. long; tubular flowers about 8 (5-10), 3-4 mm. long, salverform. Pappus of 10-12 lanceolate scales, 1.4 mm. (1-2) long in the tubular flowers, 1 mm. (0.5-1.5) long in the ligulate ones. Achenes of ligulate and tubular flowers approximately the same size, 1.5 mm. long; 0.5 mm. wide, hairy, with the trichomes arranged in parallel rows.

TYPE-LOCALITY. "Plains about Tucson in southern Arizona", 3-III-1892, *Toumey.*

DISTRIBUTION. Plains about Tucson, occasional southward into Mexico. (fig. 4)

REPRESENTATIVE SPECIMENS. **Arizona.** Tanque Verde Ranch, 17 miles E. of Tucson, 22-VIII-1958, *Solbrig 2777* (UC). 7.9 miles E. of Oracle Junction, 23-VIII-1958, *Solbrig 2791* (UC). Oracle, Spring 1941, *H. S. Gentry 6111* (UC). Martinez's Ranch, 16 miles E. of Tucson, 8-IV-1940, *L. J. Brass 14305* (GH, NY, UC). Redington Pass, Pima County, 28-IV-1938, *R. C. Foster 617* (GH,UC). Near Willcox, 25-V-1928, *R. H. Peebles 5436* (US). Pima County, Tucson to Redington, 27-V-1935, *R. H. Peebles 11315* (US). Mesas near Camp Lowell, 13-IV-1881, *C. G. Pringle* (F, PH).

6. **Gutierrezia grandis** Blake, Contr. U. S. Nat. Herb. 22:591, 1924

Xanthocephalum grande (Blake) Shinners, Field & Lab. 18: 28, 1950.

Large shrub, 30-60 cm. high. Branches few, not more than 2-4 mm. wide, greenish, striate, arising from a root-crown or stem a few cm. above ground, stem short, slender, grayish, glabrous. Root a strong taproot. Leaves linear-lanceolate, large and wide, 2-6 cm. long, 2-6 mm. wide, margin entire, surface smooth, glabrous or somewhat hairy, multinerved, the central nerve and to a certain extent the lateral ones prominent. Heads few, solitary at the ends of branchlets or in glomerules of 3-5, arranged in loose corymbose inflorescences, sessile or pedunculate, peduncle 1-10 mm. long. Involucre 5-6 mm. high, 3-4 mm.

wide, turbinate, appressed, involucral bracts elliptical, obtuse, in several series, with a thickened green tip and thicker median region. Ligulate flowers 5-9, 4-6 mm. long; tubular flowers 3-7, about 4-5 mm. high. Pappus of about 10 scales up to 1 mm. in length in the tubular flowers, somewhat shorter in the ligulate ones. Achenes about 1-2 mm. long, hairy.

TYPE-LOCALITY. "Head of Cañon de las Baretas, in the Sierra Madre, near Icamole, Nuevo León, Mexico", 3-II-1907, *W. E. Safford 1257.*

DISTRIBUTION. This species is known only from a few localities in central Mexico. (fig. 1).

REPRESENTATIVE SPECIMENS. **Mexico. Nuevo León.** Icamole, Head of Cañon de las Barretas, 3-II-1907, *W. E. Safford 1257* (US). **Coahuila.** Sierra de Parras, X-1910, *C. A. Purpus* (MO, NY, F, US, UC, GH). **San Luis Potosí.** Sierra de Catorce, no date, *F. Rodriguez* (F). Monts du Real de Catorce, 1827, *Berlandier 1360* (GH). Potrero, 8-IX-1939, *F. Shreve* (UC, GH).

7. **Gutierrezia texana** (DC.) T. & G. Fl. N. Amer. **2:** 194, 1842

Hemiachyris texana DC. Prodr. **5:** 314, 1836.

Robust annual, 20-80 cm. high. Stems one to several, subdivided or not, 2-4 mm. diameter, grayish-green, slightly ribbed, glabrous, branchlets grayish-green, fissured, glabrous or very slightly pubescent, not more than 1 mm. in thickness, arising from base. Root a slender taproot not more than 10 cm. long. Leaves lanceolate, up to 5 cm. long and 5 mm. wide, acute, glabrous, entire, surface rugose or smooth, multinerved with the middle vein prominent on both surfaces, the lateral longitudinal ones less so. Heads at the ends of branchlets and axils of leaves and branchlets. Peduncles 2-3 mm. long. Involucres 3-4 mm. high, 3-6 mm. broad, turbinate-campanulate, involucral bracts numerous, about 3 mm. long and 1.5-2 mm. wide, in about three irregular series, elliptical, margins membranaceous, tips green, midrib region darker-colored. Ligulate flowers 10-15, tube 1-2 mm. long and ligule 2-3 mm. long and 2 mm. wide; tubular flowers about 12-18, corolla campanulate, throat very short, about 0.5 mm. long, tube 1.5 mm. long. Pappus of about 10-12 scales, in the tubular flowers not longer than 1.2 mm., in the ligulate ones reduced to a crown of minute setae about 0.1 mm long. Styles elongated with well developed hairs and papillae, stigma branches long, up to 1 mm. in the tubular flowers, with papillae only and the stigma branches shorter in the ligulate flowers. Achenes of both ligulate and tubular flowers developed, 1 mm. long, 0.5 mm. wide at anthesis, growing to twice that size at maturity in some cases.

TYPE-LOCALITY. "Mexici prov. Texas", *Berlandier 1763, 1765.*

DISTRIBUTION. From southern Oklahoma to San Luis Potosí, Mexico, chiefly in central and western Texas (fig. 5).

REPRESENTATIVE SPECIMENS. **Illinois.** East St. Louis, 1897, *Letterman* (MO, PH, NY, US). **Texas.** Near Dallas, VII-VIII-, *Reverchon 1297* (NY, MO, US, F, GH). Comanche Springs, 1849-1851, *Lindheimer 921* (MO, F, US, UC). Dallas, 27-X-1900, *Bush 1624* (NY, GH). Fort Worth, 30-IX-1902, *Tracy 8159* (GH, F, NY, MO). Austin, 20-X-1937, *Tharp 283* (PH, WS, UC).

8. **Gutierrezia glutinosa** (Schauer) Sch. Bip. Flora **38:** 115, 1855

Hemiachyris glutinosa Schauer, Linnaea **19:** 724, 1847.

Gutierrezia sphaerocephala A. Gray, Pl. Fendl. 73, 1849; *Xanthocephalum sphaerocephalum* (A. Gray) Shinners, Field & Lab. **18:** 29, 1950. Based upon *Fendler 527*, "Low prairie, from the upper to the middle Spring of the Cimarron, VIII."

Gutierrezia eriocarpa A. Gray, Pl. Wright. **1:** 94, 1852; *Xanthocephalum sphaerocephalum* var. *eriocarpum* (A. Gray) Shinners, Field and Lab. **18:** 29, 1950. Based upon *Wright 280*, "Prairies along the Rio Grande, Texas".

Gutierrezia Coulteri Hemsl. Diagn. Pl. Nov. 33, 1879. Based upon *Coulter 315*, "Mexico, Zimapan".

Gutierrezia Berlandieri A. Gray, Proc. Amer. Acad. Arts & Sci. **15:** 31, 1880. Based upon *Berlandier 1298*, "Near San Luis Potosí" [Mexico].

Stout annual 2-60 cm. high. Stem branching from the base or at about 1 3 its height from the ground, gray or greenish-gray, 2-3 mm. in diameter, branchlets slender, light green, fistulose. Root a short taproot. Leaves lanceolate, 2-3 cm. long, 2-3 mm. wide, entire, surface smooth to rugose, glabrous. Heads at the end of branchlets, not numerous, sometimes less than 10, pedicellate. Involucre campanulate, 3-5 mm. high, 4-8 mm. wide, involucral bracts elliptical, arranged in 2 poorly defined series, acute, with membranaceous margins, tip and mid-rib section slightly darker and thicker. Ligulate flowers 10-20, corollas 3-4 mm. long; tubular flowers 20-40, corollas slightly campanulate 2-3 mm. long. Pappus variable in length, less than 1 2 mm. to as long as the achene, shorter in the ligulate flowers. Achenes about 1.5 mm. at anthesis, up to 2.5 mm. at maturity, turbinate, hairy, with the hairs in rows.

TYPE-LOCALTY. "Crescit in terris mexicanis", *Aschenbach 291*.

DISTRIBUTION. Central and northwestern Mexico to southwestern Texas and southern New Mexico (fig. 4).

REPRESENTATIVE SPECIMENS. **Mexico. Coahuila.** 2 miles NW of Frontera. 24-26-VIII-1938, *Johnston 7182* (GH, US). **Chihuahua.** Plains near Chihuahua, 11-X-1885, *Pringle 622* (WTU, F, NY). **United States. New Mexico.** 20 miles S. of Roswell, 8-IX-1900, *Earle & Earle 533* (NY). Near Las Cruces, 11-VI-1897, *Wooton 130* (NY, GH, MO). **Texas.** Ft. Quitman levee road, 18-VI-1943, *Waterfall 4596* (MO, GH). Chisos Mountains, 15-18-VII-1921, *Ferris & Duncan 2748* (NY).

LITERATURE CITED

BABCOCK, E. B., AND M. S. CAVE. 1938. A study of intra-and interspecific relations of *Crepis foetida*. Zeitschr. Abst. Vererb. **75:** 124-160.

BELL, R. 1954. The *Sanicula crassicaulis* complex (Umbelliferae). A study of variation and polyploidy. Univ. Calif. Publ. Bot. **27:** 133-230.

BENTHAM, G. 1873. Notes on the classification, history and geographic distribution of Compositae. Jour. Linn. Soc. Bot. **13:** 335-577.

———— & J. D. Hooker. 1873. Genera Plantarum, Vol **2**(1), 544 pp., London.

Cave, M. S., and L. Constance. 1950. Chromosome Numbers in the Hydrophyllaceae: IV. Univ. Calif. Publ. Bot. **23**: 363-382.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1940. Experimental studies on the nature of species; I. Effect of varied environments on western North American plants. Carnegie Inst. Publ. No. 520.

————————. 1945. Experimental studies on the nature of species; II. Plant evolution through amphiploidy and autoploidy, with examples from the Madineae. Carnegie Inst. Publ. No. 564.

————————. 1948. Experimental studies on the nature of species; III. Environmental responses of climatic races of *Achillea*. Carnegie Inst. Publ. No. 581.

Clausen, J., and W. M. Hiesey. 1958. Experimental studies on the nature of species; IV. Genetic structure of ecological races. Carnegie Inst. Publ. No. 615.

Cooper, W. S. 1922. The broad-sclerophyll vegetation of California. An ecological study of the chaparral and its related communities. Carnegie Inst. Publ. No. 319.

De Candolle, A. 1836. Prodromus systematis naturalis, Vol. 5, 706 pp. Paris.

Dice, L. R. and H. J. Lleraas. 1936. A graphic method of comparing several sets of measurements. Contr. Lab. Vert. Genetics No. 3, 3 pp., Univ. Mich.

Dobzhansky, T. 1953. Genetics and the Origin of Species. 3rd Ed., 364 pp. New York.

Epling, C., H. Lewis and F. M. Ball. 1960. The Breeding Group and Seed Storage: a Study of Population Dynamics. Evol. **14**: 238-255.

Goodspeed, T. H. and R. E. Clausen. 1928. Interspecific hybridization in Nicotiana; VIII. The *sylvestris-tomentosa-tabacum* hybrid triangle and its bearing on the origin of *tabacum*. Univ. Calif. Publ. Bot. **11**: 245-256.

—————. 1954. The genus *Nicotiana*. Chron. Bot. **16**: 1-536.

Grant, V. 1949. Pollination systems as isolating mechanisms in Angiosperms. Evol. **3**: 82-97.

———. 1950. a. The flower constancy of bees. Bot. Rev. **16**: 379-398.

———. 1950. b. The pollination of *Calycanthus occidentalis*. Amer. Jour. Bot. **37**: 294-297.

Gray, A. 1884. Synoptical flora of North America. Vol 1(2), 480 pp. New York.

Heckard, L. R. 1960. Taxonomic studies in the *Phacelia magellanica* polyploid complex. Univ. Calif. Publ. Bot. **32**: 1-126.

Hoffmann, O. 1897. Compositae. In Engler, A. and K. Prantl, Die Natürlichen Pflanzenfamilien, **4**(5): 87-394.

Hooker, W. J., and G. A. Arnott. 1835. Contributions toward a flora of South America and the Islands of the Pacific. Hooker, Companion to Bot. Mag. **2**: 41-53.

——————. 1841. The botany of Captain Beechey's voyage. 485 pp. and 49 tables, London.

Hubbs, C. L., and A. Perlmutter. 1942. Biometric comparisons of several samples, with particular reference to racial investigations. Amer. Nat. **76**: 582-592.

Kruckeberg, A. 1951. Intraspecific variability in response of certain native plant species to serpentine soil. Amer. Jour. Bot. **38**: 408-419.

——————. 1954. The ecology of serpentine soils: A symposium: III. Plant species in relation to serpentine soils. Evol. **35**: 267-274.

——————. 1957. Variation and fertility of hybrids between isolated populations of the serpentine species *Streptanthus glandulosus* Hook. Evol. **11**: 185-211.

Lagasca, M. 1816. Genera et species plantarum quae aut novae sunt. 35 pp., Madrid.

Leppik, E. E. 1957. Evolutionary relationships between entomophilous plants and anthophilous insects. Evol. **11**: 466-481.

Linsley, E. G. 1957. Host relationships in the genus *Crossidius* (Coleoptera, Cerambycideae). Jour. Kansas Ent. Soc. **30**: 81-89.

——————. 1958. The ecology of solitary bees. Hilgard. **27**: 543-599.

——————, and J. W. MacSwain. 1957. The nesting habits, flower relationships, and parasites of some North American species of *Diadasia* (Hymenoptera: Anthophoridae). Wasmann Jour. Biol. **15**: 199-235.

——————. 1958. The significance of floral constancy among bees of the genus *Diadasia*. Evol. **12**: 219-223.

Munz, P. A., and D. D. Keck. 1949. California Plant communities. Aliso **2**: 87-105.

Nuttall, T. 1818. The genera of North American plants and a catalogue of the species to the year 1817. Vol. **2**, 254 pp., Philadelphia.

——————. 1841. Descriptions of new species and genera of plants in the natural order of the Compositae. Trans. Amer. Phil. Soc. (n.s.) **7**: 283-453.

Piper, C. S. 1944. Plant and soil analysis. 368 pp., New York.

Pursh, F. 1814. Flora Americae septentrionalis. Vol. **2**: 751 pp., London.

Raven, P., O. T. Solbrig, D. Kyhos, and D. Snow. 1960. Chromosome numbers in Compositae: I. Astereae. Amer. Jour. Bot. **47**: 124-132.

Schnack, B. and O. T. Solbrig. 1953. El hibrido "Glandularia laciniata X G. peruviana" y su anfidiploide artificial. Rev. Fac. Agr. La Plata, III, **29**: 255-266.

Sears, E. R. 1948. The cytology and genetics of the wheats and their relatives. Advances in Genetics, **2**: 239-270.

Shinners, L. 1950. Notes on Texas Compositae IV. Field & Lab. **18**: 25-32.

Solbrig, O. T. 1960. The status of the genera *Amphipappus*, *Amphiachyris*, *Greenella*, *Gutierrezia*, *Gymnosperma* and *Xanthocephalum* (Compositae). Rhodora **62**: 43-54.

SPRENGEL, K. 1825. Systema vegetabilium. Vol. **3**(2), 933 pp., Halle.

STEBBINS, G. L. JR. 1950. Variation and evolution in plants. 645 pp., New York.

———————, J. A. JENKINS, AND M. S. WALTERS. 1953. Chromosomes and phylogeny in the Compositae, tribe Cichorieae. Univ. Calif. Publ. Bot., **26**: 401-430.

THOMPSON, H. J. 1951. The biosystematics of *Dodecatheon*. Contr. Dudley Herb. **4**: 73-154.

TIMBERLAKE, P. H. 1954. A revisional study of the bees of the genus *Perdita F. Smith*, with special reference to the fauna of the Pacific Coast (Hymenoptera, Apoidea) Part I. Univ. Calif. Publ. Ent. **9**: 345-432.

———————. 1958. A revisional study of the bees of the genus *Perdita F. Smith*, with special reference to the fauna of the Pacific Coast (Hymenoptera, Apoidea) Part III. Univ. Calif. Publ. Ent. **14**: 303-410.

TORREY, J. AND A. GRAY. 1841-43. Flora of North America. Vol **2**, 504 pp., New York.

WALKER, R. B. 1954. The ecology of serpentine soils: A symposium; II. Factors affecting plant growth on serpentine soils. Ecol. **35**: 259-266.

WRIGHT, S. 1949. Population structure in evolution. Proc. Amer. Philos. Soc. **93**: 471-478.

ZOHARY, D. AND U. NUR. 1959. Natural Triploids in the Orchard Grass, Dactylis glomerata L. Polyploid Complex and Their Significance for Gene Flow from Diploid to Triploid Levels. Evol. **13**: 311-317.

THE SOUTH AMERICAN SECTIONS OF ERIGERON AND THEIR RELATION TO CELMISIA[1]

In his studies on the family *Compositae*, M. Henri Cassini (1816-1830) laid the foundation for the modern treatment of this large and complex group. Fifty years after Cassini had begun his studies, George Bentham, using to a great extent the criteria elaborated by Cassini, attempted a world-wide study of generic boundaries within *Compositae* (Bentham, 1873; Bentham & Hooker, 1873). His work was so complete and of such fine quality that it has remained largely unchallenged up to our day, Hoffmann's (1893) later treatment for Engler's Pflanzenfamilien not differing appreciably.

Nevertheless, due to the discovery of many new and sometimes critical species and genera in the last hundred years, our understanding of *Compositae* has increased considerably. Also, with the completion of the main phase of plant exploration in many temperate areas, our knowledge of plant distribution has been greatly widened since the publication of Bentham and Hooker's Genera Plantarum. Furthermore, cytology, genetics, anatomy and embryology have added new dimensions to taxonomy and to our understanding of evolutionary processes. Geologists, although still disagreeing, can furnish more concrete ideas today than in Bentham's time about such topics as continental drift and land bridges; and, finally, our knowledge about climatic conditions in the Tertiary era, probably when most *Compositae* genera were differentiated, has also been augmented to a large extent. In the light of all these advances, it is not surprising that many of the generic boundaries established by Bentham are in need of revision.

The tribe *Astereae* is one especially suited for a careful analysis of generic boundaries. More or less detailed studies covering most or at least part of the tribe, have been completed on chromosome morphology (Huziwara, 1959), chromosome numbers (Raven, Solbrig, Kyhos & Snow, 1960, together with citations), embryology (Harling, 1951), and wood anatomy (Carlquist, in preparation). Several genera have been monographed recently and papers dealing with the redefinition of certain genera have been published. Also, in

---

[1] I am grateful to Dr. Rolla M. Tryon for reading the manuscript and making valuable suggestions.

a number of regional floras the problem of generic limits has been analyzed on a local basis. If a study of generic relationships is to reflect natural affinities and the correct evolutionary history of the tribe, undoubtedly it has to be world-wide in scope and has to involve as many different approaches as possible.

Erigeron is one of the larger genera of the tribe *Astereae*, both in number of species and in area of distribution. Although it is truly a genus of the northern hemisphere, with species native to both the Old and the New World, and with a probable center of origin in western North America, it is also found in South America, mainly along the Cordillera de los Andes. *Erigeron* is closely related to two other large genera, *Aster* and *Conyza*. The problem of delimiting these three genera has been dealt with on several occasions by Bentham & Hooker (1873), Bentham (1873), and Cronquist (1941, 1947), among others. Consequently, this problem is not discussed at length here, and the criteria enunciated by Cronquist for separating these three genera will be followed.

Bentham and Hooker (1873) divided *Erigeron* into six sections, based mainly on characters of the inflorescence, style, pappus, ligules and habit. Four of these sections, *Leptostelma, Erigeron (Euerigeron), Coenotus* and *Oritrophium* are represented in South America. Section *Coenotus* was transferred to the genus *Conyza* by Cronquist (1941). Section *Oritrophium*, as established by Bentham and Hooker, is composed of perennial herbs with monocephalous scapes, female flowers always ligulate and in one series, and the style linear and subulate. Habit in the typical species is like that of the New Zealand and Australian genus *Celmisia*. Section *Leptostelma* was also established by Bentham and Hooker and is based on the genus *Leptostelma* D. Don. It is composed of large herbs characterized by rather large heads and an alveolate receptacle. Section *Erigeron (Euerigeron)* is represented in South America by perennial herbs, small subshrubs, and a few shrubs. This is the largest and most variable of the North (Cronquist, 1947) and South American sections of the genus.

We see, therefore, that *Erigeron* is represented in South America by three relatively well distinguished groups. One, section *Erigeron*, composed of over 25 species, is closely related to the North American species. It shows great variation but in general this variability conforms to that of the genus as represented in the northern hemisphere. The other two groups, although apparently closely related to true *Erigeron*, show some characters that are absent in section *Erigeron.*

The object of this paper is to present some detailed observations on the morphology of species hitherto classified as belonging to sections *Oritrophium* and *Leptostelma* and to reevaluate the taxonomic position of the South American sections of *Erigeron.*

MATERIALS AND METHODS

All observations were made on herbarium material. In addition to studies of dried and boiled material, fragments of both leaves and heads were cleared with sodium hydroxide and stained according to Foster's technique, as explained elsewhere (Solbrig, 1960), and permanent mounts prepared.

Materials of the Arnold Arboretum (A) and Gray Herbarium (GH) of Harvard University; Museo de Ciencias Naturales, La Plata, Argentina (LP); Museo Botánico, Córdoba, Argentina (CORD); and Instituto Miguel Lillo, Tucumán, Argentina (LIL) were available for this study.[1]

OBSERVATIONS AND RESULTS

Studies were made of the general habit; shape, venation and pubescence of leaves; secondary inflorescences; shape, arrangement and pubescence of involucral bracts; corollas, styles, achenes and pappus of both ligulate and tubular flowers; anthers and pollen; and receptacle. In addition, a few general habitat preferences are recorded.

GENERAL HABIT

All species of South American *Erigeron* studied are perennial. *Erigeron maximus* and *E. Tweediei*, of section *Leptostelma*, are gigantic herbs, up to 4 m. high in the case of *E. maximus* and 1 to 1.50 m. in the case of *E. Tweediei.* The latter species has a basal rosette of large leaves, which is absent in *E. maximus.* Both species have profuse foliage, greenish stems, and heads arranged in loose cymose secondary inflorescences. The habit of species of section *Leptostelma* is very much in accordance with the humid, tropical environment in which the plants grow.

Members of the section *Oritrophium* on the other hand are very different. They have a crowded basal rosette, with stiff, more or less lanceolate leaves, and a monocephalous floral

---

[1] I am grateful to the directors and curators of the institutions mentioned for making available the material in their custody.

scape not more than 30 cm. high. Three of the species of this section, *E. pellitus, E. crocifolius* and *E. hieracioides,* are covered with a thick indumentum. A great variety of habits is found in section *Erigeron.* The most common type, which is found along the Andes, is somewhat similar to section *Oritrophium,* with a basal rosette of leaves and a monocephalous or polycephalous leafy scape. The development of hairs on the leaves and involucral bracts is variable. Other species in this section are subshrubs, with a woody base, with or without a basal rosette of leaves. In these species, the arrangement of the capitula is usually secondary compound. Finally, in the Juan Fernández and Galápagos Islands some truly shrubby species *(E. fruticosus, E. tenuifolius,* and *E. lancifolius)* are found, ranging from about a meter *(E. fruticosus)* to a meter and a half *(E. tenuifolius)* in height.

It may be noted that sections of *Oritrophium* and *Leptostelma* can be separated from section *Erigeron* on characters of habit alone. In spite of this, their external appearance is not radically different from what is found in section *Erigeron* but constitutes two extremes within the general variation found in South America *Erigeron.*

LEAVES

As already pointed out, there is a marked difference in the leaves of species belonging to each of the three sections. Those of section *Oritrophium* are stiff and coriaceous, linear to lanceolate in shape, with entire margins, varying in length but not longer than 25 cm. in the largest basal leaves. The cauline leaves are very reduced, usually only about half a centimeter long. Leaves of species of section *Erigeron* are broadly linear to lanceolate in shape, entire, or in a few species somewhat crenate-serrate, and less than 15 cm. long. In section *Leptostelma,* large leaves are found, often over 30 cm. in length and 10 cm. in width, variably lanceolate and with a cut or serrate margin.

As to the surface of the leaves, in section *Oritrophium* a shiny almost glabrous upper surface is present and the lower surface is covered with a thick mesh of interwoven hairs, which gives it a silvery aspect. In some cases the upper surface also is covered with hairs. This peculiar type of pubescence is not found in any of the other sections but instead is characteristic of the genus *Celmisia.* Leaves of species of sections *Leptostelma* and *Erigeron* have a dull surface, glabrous or pubescent. If they are pubescent they are usually equally so on both surfaces but never to the extent found in the lower leaf surfaces of species of section *Oritrophium.*

The venation of the leaves is reticulate, with the veinlets free at their termination. No appreciable difference could be found in any of the sections.

INFLORESCENCE[3]

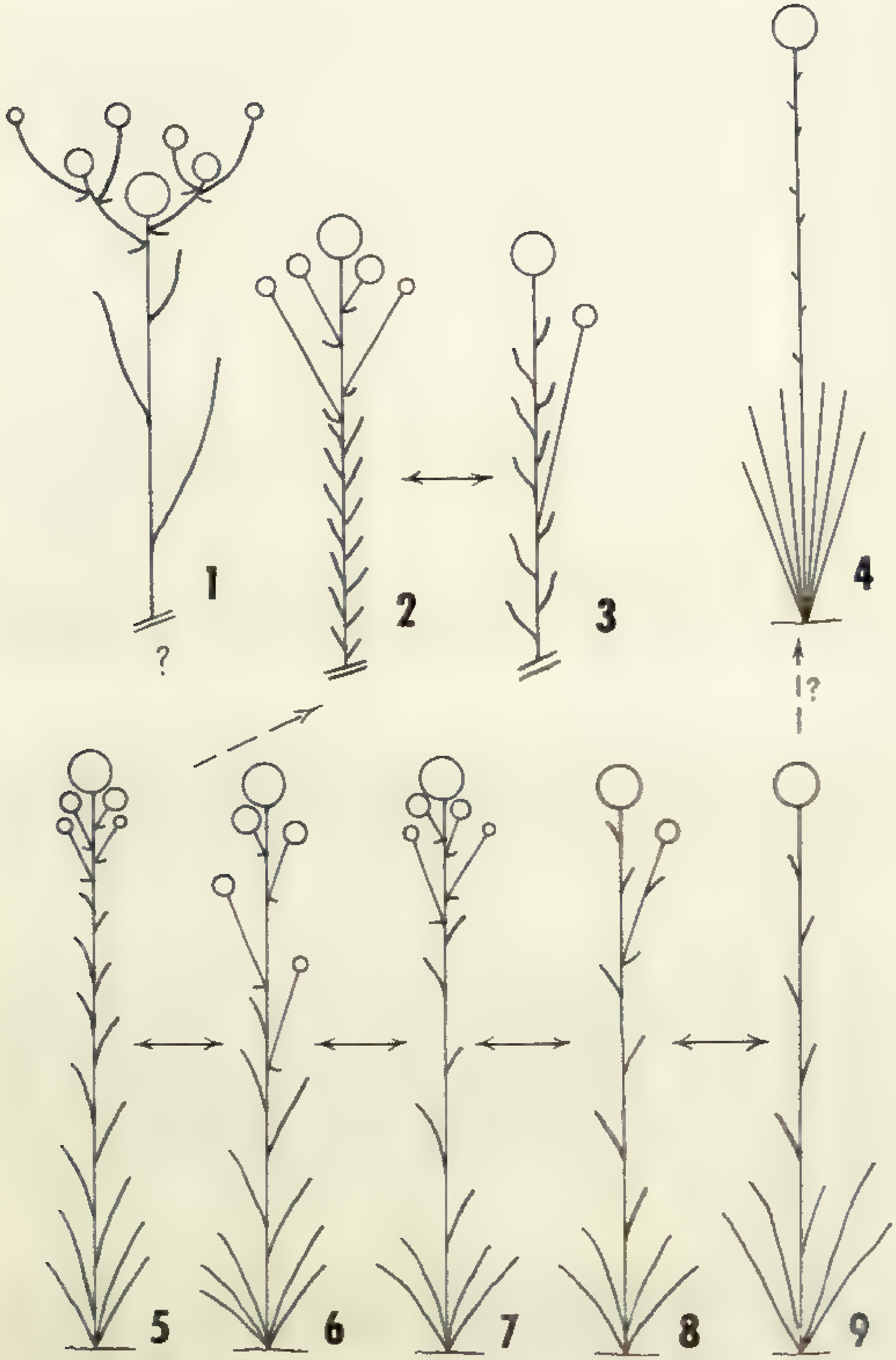
Differences in the inflorescence can sometimes be important in the taxonomy of the *Compositae.* In the present instance, this character can be used to some extent in separating sections *Oritrophium, Leptostelma* and *Erigeron.* While most species of *Erigeron* in South America have a polycephalous inflorescence, usually cymoid or racemose, members of the section *Oritrophium* have their capitula borne at the end of sparsely leafy scapes. On the other hand, some members of section *Erigeron,* such as *E. andicola,* also have their heads borne solitary at the end of slender scapose branches. The scapes of species of section *Oritrophium,* such as *E. pellitus,* are much more robust and rigid, while those of section *Erigeron* are relatively slender. An exception to this is *E. hieracioides* (section *Oritrophium),* which has scapes approximating those of *E. andicola.*

The inflorescence of *E. maximus* and *E. Tweediei* can be roughly characterized as an inverted compound cyme. After the terminal head has started to form and the growth of the branchlet has come to an end, one to three lateral branches develop from the axillary buds nearest to the head on the central axis. Eventually heads will develop at the ends of these branchlets but usually not until the tips of the lateral branchlets have grown past the end of the main one. This process may take place then in each of the lateral branchlets again, leading to double-compound inflorescence. The end result is that the last formed heads are at the top of the inflorescence, rather than at the lower part as in the cymose inflorescences of members of section *Erigeron.* In *E. maximus* this inflorescence type is quite distinct while in *E. Tweediei* it is more compact and there is some fluctuation between this type and a more typical cymose inflorescence.

If the pattern of inflorescence development is carefully

---

[3] Throughout this paper, inflorescence refers to the arrangement of the capitula, which are the real inflorescences, rather than the arrangement of the flowers. This use of the word inflorescence follows common usage in the *Compositae.*



FIGS. 1-9. Schematic representation of inflorescence types.
1. *Erigeron maximus.* 2. *E. Karwinskianus.* 3. *E. Bertenanus.* 4. *Celmisia pellita.* 5. *Erigeron pinnatus.* 6. *E. Poeppigii.* 7. *E. Gayanus.* 8. *E. andicola.* 9. *E. brevicaulis.*
For further explanation see text.

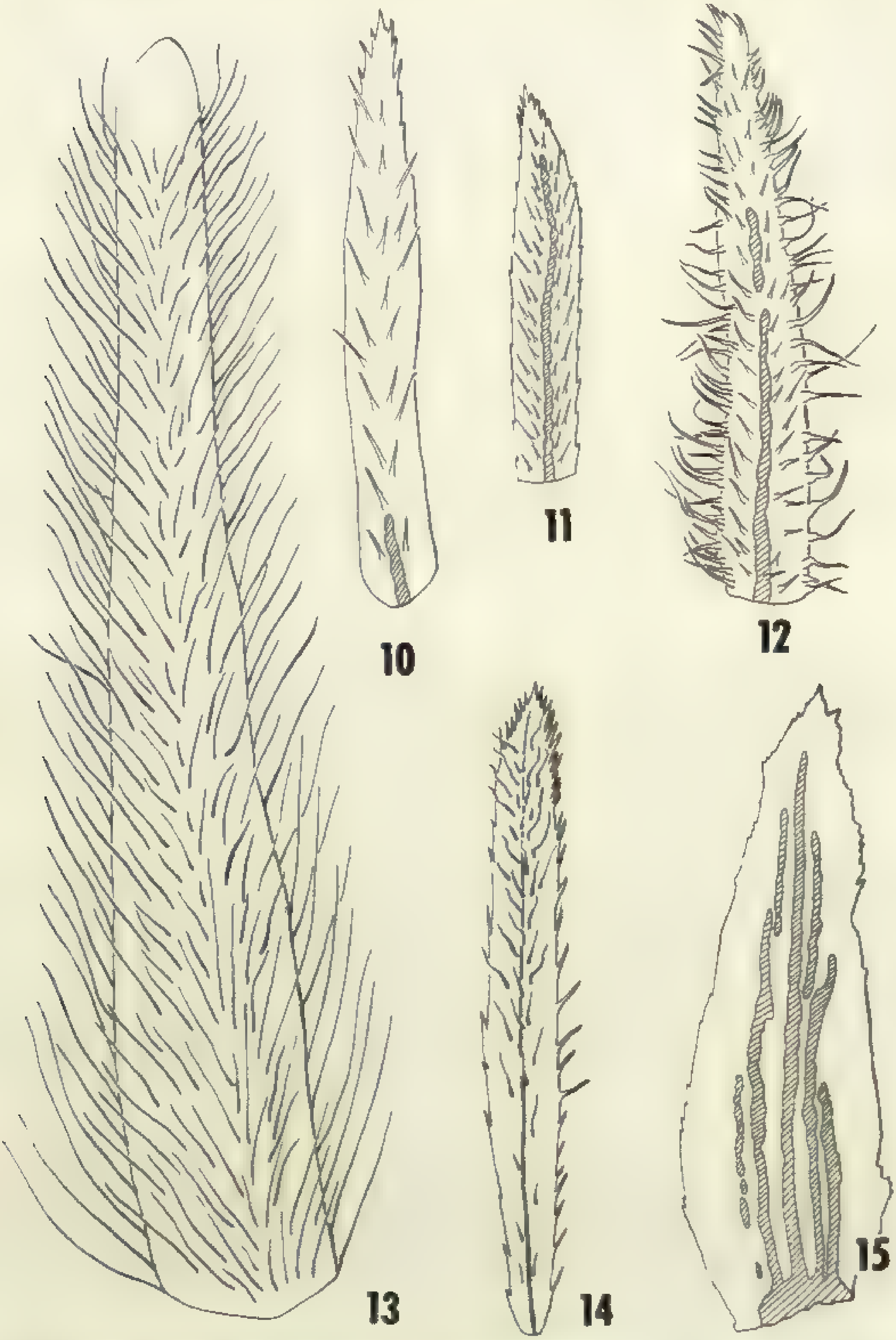
observed, an evolutionary series can be detected. If a simple cymose inflorescence, common in section *Erigeron* and such as is found in *E. Gayanus* (fig. 7) is first observed, it may be seen that one tendency is towards a reduction in the number of heads, correlated with a reduction in the size and number of the leaves of the scape. At the same time, the leaves of the scape become more distinct from those of the basal rosette (loss of petiole, shorter and narrower lamina, etc.), as exemplified by *E. andicola* (fig. 8). An extreme in this adaption is represented by *E. rosulatus* and *E. pulvinatus* where even the scape has disappeared, the terminal heads being borne singly at the ends of very short and leafy stems. Whether *E. pellitus* (fig. 4) and the other species of section *Oritrophium* constitute another specialization within this trend is difficult to decide but this possibility seems rather doubtful.

Another trend has been towards a type with less differentiation between basal and cauline leaves (e.g., *E. Poeppigii*, fig. 6) together with the formation of a tighter inflorescence. The suffruticose species, such as *E. Karwinskianus* (fig. 2), show a pattern essentially similar to *E. Poeppigii*, although obscured somewhat by the woody type of growth. The basal rosette has disappeared completely and all the cauline leaves are well developed. The inflorescences are borne toward the ends of the branches and are of the same cymose type as in *E. Poeppigii.* In some cases, as in *E. Berterianus* (fig. 3), we find a more reduced inflorescence. Whether the type of inflorescence found in members of section *Leptostelma* (fig. 1) is an elaboration of the one found in the shrubby species is hard to determine with any degree of certainty.

INVOLUCRAL BRACTS

In general, the involucral bracts are rather uniform within the *Astereae.* They are distinct structures, herbaceous or somewhat woody, usually imbricate in two or more rows. Sometimes, as in the genus *Grindelia*, they might take a more specialized aspect, but we do not find in *Astereae* large spines as in *Cirsium* or *Centaurea*, or any such other specializations in the bracts as are common in other tribes, e.g., *Mutisieae* or *Cynaroideae.* Small variations, therefore, become of taxonomic value, such as the arrangement of the bracts in the involucre, size, shape, pubescence, number of bracts, and degree of imbrication.

Characters of the involucre are important and have been used extensively to separate *Aster* from *Erigeron* (cf. Cronquist, 1947), but a certain degree of variation in involucral



FIGS. 10-15. Shape and pubescence of involucral bracts. 10. *Erigeron Philippii* (*Johnston 5911*, GH). 11. *E. brevicaulis* (*Johnston 5960*, GH). 12. *E. andicola* (*E. W. D. and Mary Holway, 1920*, GH). 13. *Celmisia pellita* (*Hitchcock 21997*, GH). 14. *C. gracilenta* (*Anderson 229*, GH). 15. *Erigeron Tweediei* (*Osten 1475 b*, GH).

characters is present from species to species within a genus and in some cases within a particular species, as is common in all biological material.

The species of *Erigeron* have herbaceous bracts which can sometimes be non-herbaceous at the base. They are of different sizes, with the outer ones shorter, loosely imbricate, and usually in two loose series. Pubescence varies greatly. Some species are glabrous and others are covered with a thick cap of hairs. The inner surface of the bracts is always glabrous. As to the shape, there is no appreciable difference, all species having loosely lanceolate bracts.

The involucral bracts of the South American species of *Erigeron* do not show any noticeable departure from this pattern, with the exception of section *Oritrophium.* In this group, the bracts are somewhat larger and less herbaceous and appear to be intermediate between typical *Erigeron* and *Aster* (fig. 13).

Pubescence of the involucral bracts is another character that has been used widely in *Erigeron*, especially in the separation of species (Cronquist, 1947). In the material studied, we found a great deal of variation in the amount of pubescence of the involucral bracts (fig. 10-15) which vary from completely glabrous to thickly pubescent. In addition, there is a qualitative character-difference in the trichomes of section *Oritrophium* and those of sections *Erigeron* and *Leptostelma.* The trichomes of the latter two sections are multicellular and uniseriate, as are those of section *Oritrophium*, but the trichomes in the involucral bracts of section *Oritrophium* are formed by a few elongated cells (sometimes branched), all of about the same width and length and tapering gradually towards the tip of the hair, whereas the trichomes of the involucral bracts of species of the other sections are formed by a few (3 to 6) short and wide cells at the base, followed by a series of cells several times longer and up to one half times narrower, forming a constriction. The trichomes of species of section *Oritrophium* (fig. 13) are generally larger than in section *Erigeron* but this is not always a very clear difference. In addition to the types of hairs described above, in species of both sections *Erigeron* and *Leptostelma*, we find a type of trichome formed by a few almost cubical cells. These hairs are rather short and are absent in species of *Oritrophium.*

FLOWERS

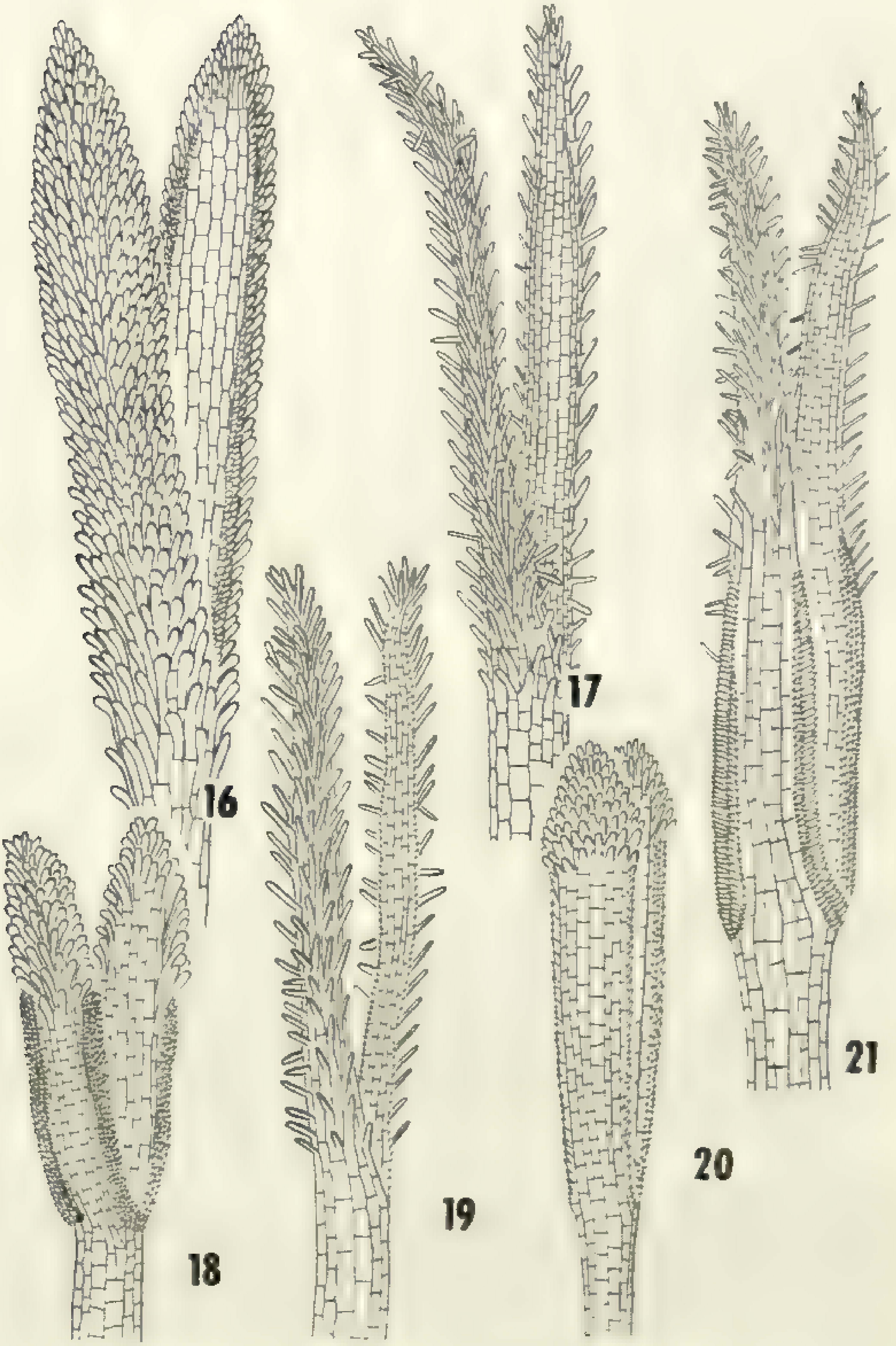
It is well known that species of *Erigeron* have two types of flowers in the capitulum: the ray flowers, which are pistillate and have a ligulate corolla; and the disk flowers, which are hermaphroditic and tubular. Flowers furnish some important characters helpful in the delimitation of species. In the present case, some substantial differences in flower-characters exist between section *Oritrophium* and the other South American species of *Erigeron*. Therefore, the pappus, corolla, anther, pollen, style, achene, venation of the flowers, and receptacle will be analyzed in some detail.

PAPPUS. The pappus is formed by a large number of bristles about the same length as the tubular corolla and arranged in one series. This holds true for all three sections.

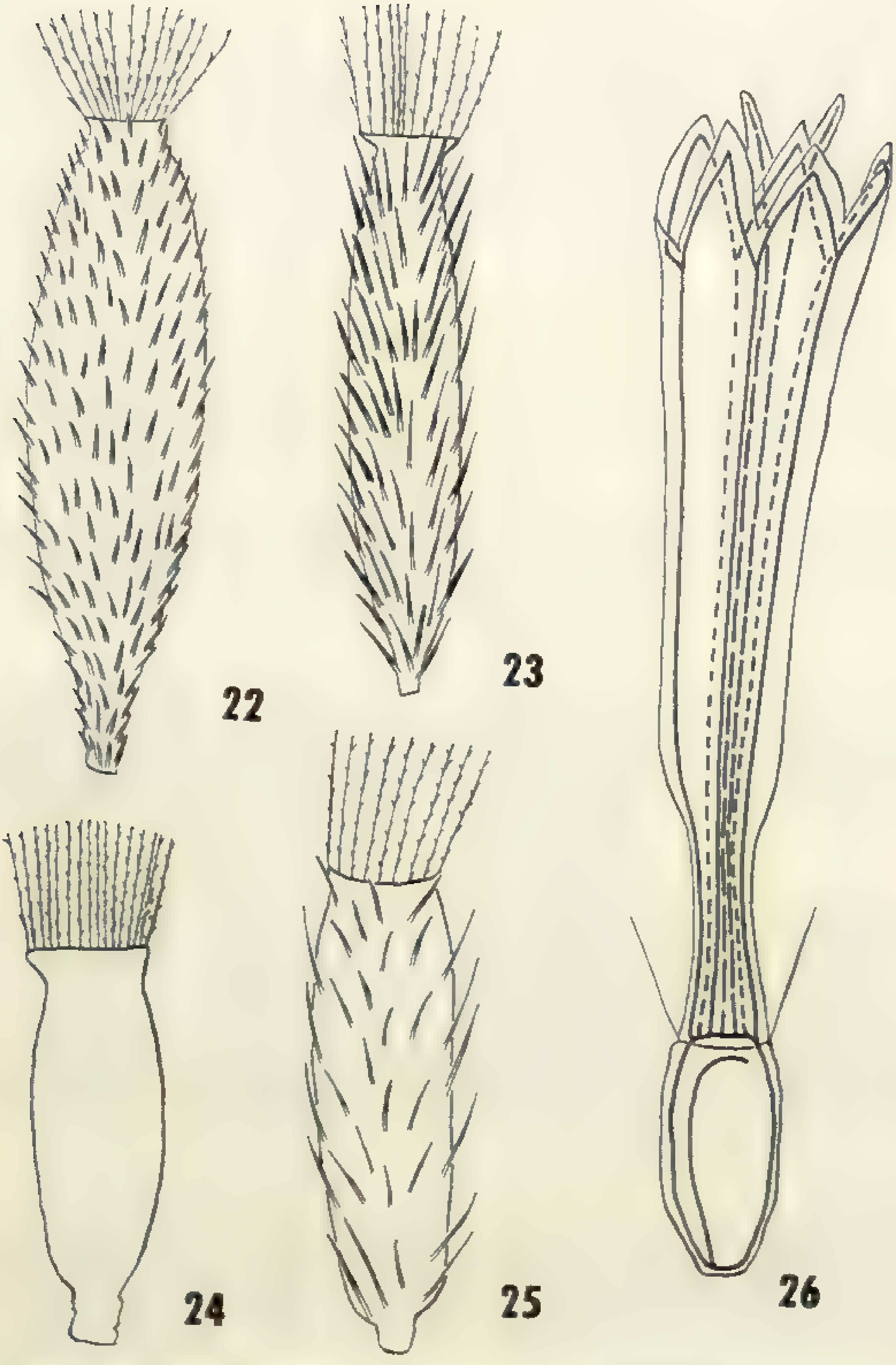
COROLLA. The only species-difference present in the ligulate corollas is the length of the ligule, which varies from about as long as the tube to about five times longer. Species of section *Oritrophium* have rather long ligules but it is in *Erigeron maximus* and *E. Tweediei* of section *Leptostelma* that the longest ligules in South American *Erigeron* are found. The width of the ligule varies somewhat but no pattern can be discerned, the variation being between the expected parameters for the genus. A similar uniform situation holds true in the tubular corollas, where the only difference is the presence of microscopic, uniseriate and multicellular hairs on the outer surface of the tubular corollas of species of section *Oritrophium*.

ANTHERS. The anthers are uniform and are of a typical asteraceous type with lanceolate upper appendages and no lower appendages. An exception is *Erigeron pellitus* of section *Oritrophium*, which has some very short appendages at the base, usually called "tails". Presence of "tails" on the anthers is the character used to separate the tribe *Inuleae* from the *Astereae* but it is also found in at least one genus of *Astereae*, the genus *Celmisia*.

POLLEN. Pollen of *E. andicola* (section *Erigeron*), *E. maximus* (section *Leptostelma*) and *E. crocifolius* (section *Oritrophium*) was investigated. No qualitative character of importance could be detected, aside from slightly larger spines on grains of *E. crocifolius*. Measurements based on samples of 25 grains are shown below:



FIGS. 16-21. Styles of tubular flowers. 16. *Erigeron rosulatus* (*Bang 912*, GH). 17. *Celmisia repens* (*Pennell and Hazen 9373*, GH). 18. *Erigeron maximus* (*Mexia 4341*, GH). 19. *Celmisia pellita* (*Hitchcock 21997*, GH). 20. *Erigeron andicola* (*E. W. D. and Mary Holway, 1920*, GH). 21. *Celmisia gracilenta* (*Anderson 229*, GH).



Figs. 22-26. Achenes of ligulate flowers. 22. *Celmisia hieracioides* (*Pennell 13875*, GH). 23. *C. pellita* (*Hitchcock 21997*, GH). 24. *Erigeron andicola* (*E. W. D. and Mary Holway, 1920*, GH). 25. *E. rosulatus* (*Bang 913*, GH). Fig. 26. Venation of tubular flower of *Erigeron maximus* (*Mexia 4341*, GH).

Species	Minimum	Maximum	Mean
E. andicola	25	29	26.84
E. crocifolius	28	33	30.32
E. maximus	24	31	27.32

Expressed in micrometer units for comparative purposes only

STYLES. The style has been, since Cassini, the most important single character used in the taxonomy of *Compositae.* Each tribe and many genera are supposed to have distinct and peculiar stylar appendages, so that the tribe and sometimes the genus to which a plant belongs can readily be determined by examining the style. Actually it is not as simple as this because a great deal of variation exists. A careful study of variation in stylar characters in all genera of *Compositae* is needed, but in order to be of value, any study of stylar characters must take into account the cellular details as well as the overall shape of the style, as has already been pointed out by Carlquist (1959).

The styles of the ligulate corollas are very similar in all the species under consideration and in most species of *Astereae.* They consist of two elongate, flattened branches, slightly pointed at the tip, with a border of stigmatic papillae all around the margin of the inner surface of the stigmatic branch.

The styles of the tubular flowers are of two types. In the first, in section *Oritrophium*, the stigmatic branches are narrow, elongate, and gradually attenuate towards the tip. Collecting hairs are more or less evenly scattered along the outer surface. The collecting hairs are formed by long narrow cells of even width and are rounded at the tip. The stigmatic papillae are small cells, usually pointed, which form a narrow strip along the inside border of the stigmatic branches (fig. 17). This type of style does not belong to the so called "*Erigeron* type", but is of a kind which is found in some Pacific Basin genera of *Astereae,* such as *Tetramolopium, Vittadinia, Podocoma,* etc.

The type of tubular flower style found in sections *Erigeron* and *Leptostelma* is as expected in the genus *Erigeron.* The stigmatic branches are broader than in styles of species of section *Oritrophium* and are of even width, terminating in a "triangular" tip, characteristic of *Erigeron.* The collecting hairs are appressed over the outer surface of this "triangular" tip and are short and somewhat rounded (figs. 18 & 20). The stigmatic papillae form two wide borders along both sides of the two stigmatic branches from the point of bifurcation to the start of the area of collecting hairs. Some variation can be observed in the downward extension of the collecting hairs but in general the styles are quite uniform. An extreme form of variation is found in *Erigeron pulvinatus* and *E. rosulatus*, where the collecting hairs extend down along the whole outer surface of the stigmatic branches and consequently restrict the papillae to the inner surface of the stylar branches (fig. 16). The type and density of the collecting hairs, as well as the shape of the stigmatic branches, indicate that *E. pulvinatus* and *E. rosulatus* are correctly classified in section *Erigeron*.

ACHENE. A difference exists between section *Oritrophium* and sections *Erigeron* and *Leptostelma* in the shape of the achene. Achenes of species of section *Oritrophium* are elongate and somewhat fusiform, tapering at both ends but particularly at the lower one (figs. 22 & 23). In contrast, the species of sections *Erigeron* and *Leptostelma* have shorter and more cylindrical achenes. All the species investigated had somewhat flattened, two-ribbed achenes, flatter in species of *Oritrophium* than in those belonging to other sections.

As far as pubescence of the achenes is concerned, we find a great amount of variation, ranging from species with glabrous achenes to species with densely pubescent ones. The trichomes are of three different types: (1) short, uniseriate, multicellular, formed by a few isodiametric cells; (2) long, uniseriate hairs with elongated cells; and (3) biseriate, multicellular hairs. In some cases hairs are found which are biseriate at the base, turning uniseriate toward the apex. No characteristic pattern can be discerned in any of the sections.

Another aspect to consider is the fertility of the achenes. In sections *Erigeron* and *Leptostelma*, the achenes of both the ligulate and tubular flowers are fertile, although shrunken and unfertilized achenes are found occasionally in both the ligulate and tubular flowers. In species of *Oritrophium*, the achenes of the tubular flowers are usually very shrunken and inviable while those of the ligulate flowers are fertile. Sometimes one can find tubular achenes which are full and apparently normal. In view of the great reduction of the stigmatic papillae in section *Oritrophium*, it can be speculated that only occasionally do pollen grains germinate and fertilize the ovules to produce a fertile achene. This would mean that section *Oritrophium* represents an intermediate stage between hermaphroditism and unisexuality in the tubular flowers, but it is also possible that the achenes are always sterile and that occasional development of the achene might be due to causes other than fertilization.

FLORAL VENATION. No appreciable difference exists in the venation of the tubular flowers of the species under study. The ray flowers, on the other hand, show a great amount of variability, even among flowers of the same head. Therefore, only the tubular flowers will be described.

There are usually two bundles in the achene (in a few cases three were observed) which pass into the corolla where they give rise to five corolla bundles, with adjacent pairs uniting at the tips of the corolla lobes, and to two stylar traces (fig. 26). In addition, a third trace can be seen in the achene, the ovular trace. No ovular trace can be detected in species of section *Oritrophium*, which enhances the suspicion that the achenes in this section might always be sterile.

RECEPTACLE. Section *Leptostelma* is supposed to have a "paleaceous" receptacle, while the other species of *Erigeron* are supposed to possess a naked receptacle. Close inspection shows that this difference is more apparent than real. All South American species of *Erigeron* have an alveolate receptacle, with the borders of the depressions extended into a thin microscopic membrane. In *E. maximus* and *E. Tweediei* this membrane is less than half a millimeter larger and cannot properly be called a "palea". All species investigated had a flat or slightly convex receptacle.

In conclusion, it is interesting to point out that many small differences exist in characteristics of the capitulum and flowers between *Oritrophium* and sections *Erigeron* and *Leptostelma*. Only in characters widespread in the tribe, such as the pappus and the corolla, is agreement found. In view of the uniformity and stability of flower characters in *Compositae*, these differences are considered to be significant.

GEOGRAPHIC DISTRIBUTION

Species of section *Oritrophium* grow in dry, almost barren high altitude plateaus in the northern Cordillera de los

Andes, locally known as the "páramos". Species of *Oritrophium* are found at altitudes of 3,000 to 4,000 m. in northwestern Bolivia, Perú, Ecuador, Colombia and western Venezuela. In Colombia is found the greatest development

FIG. 27. Geographical distribution of the South American sections of *Celmisia* and *Erigeron*.

in number of species and also the largest number of herbarium collections comes from that area. All species of section *Oritrophium* are typical high altitude plants and grow in the corresponding types of environmental niches. On the contrary, members of section *Leptostelma* are found in wet and marshy localities in southern and southeastern Brazil (states of Minas Gerais, São Paulo, Paraná and Rio Grande do Sul), northeastern Argentina (state of Misiones), Paraguay, in the lowlands of eastern Bolivia (Santa Cruz de la Sierra) and in the Departamento de San José in southern Uruguay. The plants are found at altitudes below 1,000 m.

The areas where members of sections *Oritrophium* and *Leptostelma* grow, the high Andes of northwestern South America and subtropical forests of eastern South America, have not been explored exhaustively and it is very likely that the range of species can be determined with greater accuracy than is depicted on the map of fig. 27 when botanical knowledge of those areas is more complete.

Section *Erigeron* is found in South America along the Andes from Ecuador to Tierra del Fuego, at altitudes ranging from sea level to about 5,000 m. Species belonging to this section are also found in the Sierras Pampeanas of Argentina, which are older geologically than the Andes, and also along the coast of Chile and southern Perú, extending northward to the area around Arequipa. Finally, a few species are found in the Juan Fernández and Galápagos Islands. In all of this region, species of section *Erigeron* are found in rather dry, rocky habitats, even though they sometimes spill over into more mesic environments.

Sections *Erigeron* and *Oritrophium* overlap somewhat in their ranges and ecological preferences in Bolivia, Perú and Ecuador, while section *Leptostelma* seems to be separated both geographically and ecologically. Cabrera (1957) described two species of *Erigeron* from eastern Brazil of which I have not seen any specimens. The description indicates that the plants are similar to the North American *Erigeron annuus* of section *Phalacroloma* and unlike any Brazilian species of *Erigeron*. The two Brazilian species described by Cabrera differ from *Erigeron annuus* in pappus details and have to be placed in section *Oligotrichium* (Cronquist, 1947). Neither section is represented in South America. It is always possible that a mutant of *E. annuus*, of relatively recent introduction, is the plant in question. *Erigeron annuus*, which has spread as a weed in both the United States and Europe, is a triploid ($2n = 27$) apomict. Some North American weedy *Compositae*, as for example *Heterotheca latifolia*, have been introduced into similar areas of Brazil (Wagenknecht, 1960).

DISSCUSSION

SECTION ORITROPHIUM. Morphologically, section *Oritrophium* is similar to *Celmisia*, a characteristic genus of the flora of New Zealand, found also in Tasmania and Australia. The similarities between *Celmisia* and section *Oritrophium* have been pointed out by Bentham, 1873; Bentham & Hooker, 1873; Gray, 1884; and Cronquist, 1948. Bentham (1873) comments as follows: "Around *Erigeron* may be grouped the following slightly divergent genera, designated as much by their geographical areas as by any structural characters, and yet natural enough to be readily recognized: 1. The Antarctic and Australian genera *Pleurophyllum* and *Celmisia*, closely connected with the Andine section Oritrophium of *Erigeron*, differ from it chiefly in the shape of the achene, which is more that of *Olearia* . . .". Gray (1884) says ". . . section Oritrophium (which must belong either to *Celmisia* or *Aster*) . . .". Hoffmann (1893) separates *Celmisia* from *Erigeron* (including section *Oritrophium*) on account of the tailed anthers.

TABLE 1. COMPARISON OF DIFFERENCES IN MORPHOLOGICAL CHARACTERS IN THE GROUPS UNDER STUDY

Character	*Celmisia* sect. *Celmisia*	*Celmisia* sect. *Oritrophium*	*Erigeron* sect. *Erigeron*	*Erigeron* sect. *Leptostelma*
General habit	Scapose with basal rosette	Scapose with basal rosette	Scapose with basal rosette, suffrutex or shrubby	Perennial herbs up to 4 m high with no basal rosette
Inflorescence	Monocephalous	Monocephalous	Mono- or Polycephalous	Polycephalous
Pubesc. Inv. bracts	Very thickly pubescent	Very thickly pubescent	Pubescent to glabrous	Thinly pubescent
Stylar append.	Subulate	Subulate	Triangular	Triangular
Achenes	Elongated	elongated	prismatic	prismatic
Anthers	usually with "tails"	occasionally with "tails"	never with "tails"	never with "tails"
Receptacle	naked	naked	naked	shortly "paleaceous"

As may be seen in table 1, neither the achenes nor the anthers of section *Oritrophium* differ from those of *Celmisia.* It is therefore proposed that section *Oritrophium* of *Erigeron* be transferred to the genus *Celmisia.*

SECTION LEPTOSTELMA. Species of section *Leptostelma* are easily separated from other species of *Erigeron* on the basis of vegetative characters. The floral characteristics do not differ appreciably. Consequently it is difficult to decide whether *Leptostelma* merits generic rank.

A chromosome count for *E. maximus* has recently been reported (Turner & Irwin, 1960). Unfortunately, the condition of the material did not permit an accurate determination and it was reported as 40 ± 4. The basic number for *Erigeron* is $x = 9$ (Raven, Solbrig, Kyhos and Snow, 1960; Montgomery and Yang, 1960). Polyploidy is known in North American species but, with the exception of the apomict *E. annuus* ($n = 13$; $2n = 26, 27$), all counts reported to date are multiples of 9 (Montgomery and Yang, 1960). No counts other than Turner's exist for South American species. Therefore, if the chromosome number of *E. maximus* is not 36, it might be an indication of a different generic stock.

Nevertheless, for the present, it is felt that, although on the basis of vegetative and distributional characters *Leptostelma* might be set up as an independent genus, it is better to wait until new information, especially cytological data, is available, before taking positive action.

PHYTOGEOGRAPHY. The inclusion of *Oritrophium* in *Celmisia* raises an interesting phytogeographical problem. *Celmisia* is an important element of the flora of both the North and South Islands of New Zealand, being one of the three largest genera and the largest genus of *Compositae.* The *Compositae* is the dominant family in New Zealand (Cockayne, 1928). That genera and even species are common to New Zealand and southern South America is a well known fact, but floristic connections between New Zealand and the high Andean areas of northwestern South America are not frequent. In this case, one could probably explain the distribution of *Celmisia,* section *Oritrophium,* by postulating a migration across Antarctica and along the Cordillera de los Andes, with an extinction of the genus in the areas where it is now absent. The asteraceous genus *Lagenophora* (subtribe *Bellidineae)* might be cited as providing a clue in the direction of the postulated explanation. *Lagenophora* is found in Australia, New Zealand, New Guinea, Hawaii and South America. In the latter, it has a disjunct distribution, with one species in the area of the subantarctic rain forest and a second species in the high mountains of Venezuela (Cabrera, 1954). Also, the fern family *Loxsomaceae* might be cited. This small family has only two genera, *Loxsoma*, with one species endemic in New Zealand, and *Loxsomopsis*, with three species, found along the Andes from Bolivia to Costa Rica (Copeland, 1947). As is evident, it covers largely the same territory as *Celmisia*.

The inclusion of section *Oritrophium* in *Celmisia* clarifies, to some extent, a picture of the relationships of *Erigeron* in the southern hemisphere. *Erigeron* is undoubtedly a genus of northern affinities, with a probable origin in western North America. It has expanded into the Old World and secondary centers of speciation can be postulated for Asia and Europe. It has also migrated into the southern hemisphere. There are two possible ways of explaining this latter migration. One, by postulating a migration along the Cordillera de los Andes; the second by long-range seed dispersal. Either hypothesis cannot be categorically proved or disproved and more data needs to be accumulated, pertaining to such things as breeding systems, before we can weigh both hypotheses in the light of our knowledge of Tertiary climate and conditions.

Erigeron is but one of a group of genera such as *Grindelia*, *Haplopappus* and *Solidago* in South America, which have migrated from western North America. Another group of South American *Astereae*, including *Vittadinia*, *Lagenophora*, *Podocoma* and *Celmisia*, is of Australasian origin. Finally, some genera, such as *Conyza*, seem to be pantropical in distribution. A better understanding of the origin of this distribution will aid greatly our knowledge of the phylogenetic relationships within the tribe *Astereae*.

SUMMARY

Erigeron L. section Erigeron.

Approximately 25 to 30 species in South America.

Selected specimens: *Erigeron andicola* DC., *Holway*, 1920 (GH); *E. brevicaulis* Phil., *Johnston 5960* (GH); *E. cinerascens* Sch. Bip., *Venturi 8633* (GH, LIL); *E. fruticosus* DC., *Bock 54* (GH); *E. Gayanus* Remy, *Banks and Solander s.n.* (GH); *E. Karwinskianus* DC., *Montero 2020* (GH); *E. Philippii* Sch. Bip., *Johnston 5911* (GH); *E. pulvinatus*

Wedd., *Bang 913* (GH); *Shepard 22* (GH); *E. tenuifolius* Hook. f., *Stewart 733* (GH).

Erigeron L. section **Leptostelma** (D. Don) Benth. & Hook., Gen. Pl. **2:** 280, 1873; *Leptostelma* D. Don ex Sweet, Brit. Fl. Gard., Ser. 2, t. 38.

Two species in eastern South America: *E. maximus* Link et Otto ex DC., Prodr. **5:** 284, 1836: *E. Tweediei* Hook. et Arn., Compan. Bot. Mag. **2:** 50, 1836.

Selected specimens: *E. maximus* Link et Otto, *Mexia 4341* (GH); *E. Tweediei* Hook et Arn., *Osten 1475 b* (GH).

Celmisia Cass. section **Celmisia.**

Some 50 species in New Zealand, Tasmania and Australia.

Selected specimens: *Celmisia bellidioides* Hook. f., *Hector s.n.* (GH); *C. discolor* Hook. f., *Cheeseman s.n.* (GH); *C. glandulosa* Hook. f., *Cheeseman s.n.* (GH); *C. gracilenta* Hook. f., *Hunnewell 13,781* (GH); *C. sessiliflora* Hook. f., *Hector s.n.* (GH); *C. Sinclairii* Hook. f., *Kirk s.n.* (GH); *C. spectabilis* Hook. f., *Hunnewell 13,780* (GH).

Celmisia Cass. section **Oritrophium** (HBK.) comb. nov.; *Aster* section *Oritrophium* HBK. (pro parte), Nov. Gen. et Sp. **4:** 89, 1820; *Erigeron* sect. *Oritrophium* (HBK). Benth & Hook., Gen. Pl. **2:** 280, 1873.

Four species in northwestern South America.

Celmisia crocifolia (HBK.) Sch. Bip. Bonplandia **4:** 50, 1856; *Aster crocifolius* HBK., Nov. Gen. et Sp. **4:** 89, 1820; *Erigeron crocifolius* (HBK.) Weddell, Chl. And. **1:** 191, 1857.

Celmisia hieracioides (Wedd.) comb. nov.; *Erigeron hieracioides* Weddell, Chl. And. **1:** 194, 1857.

Celmisia pellita (HBK.) Sch. Bip. Bonplandia **4:** 50, 1856; *Aster pellitus* HBK., Nov. Gen. et Sp. **4:** 91, 1820; *Erigeron pellitus* (HBK.) Weddell, Chl. And. **1:** 190, 1857.

Celmisia repens (HBK.) Sch. Bip. Bonplandia **4:** 50, 1856; *Aster repens* HBK., Nov. Gen. et Sp. **4:** 90, 1820; *Erigeron repens* (HBK.) Weddell, Chl. And. **1:** 191, 1857.

Selected specimens: *Celmisia crocifolia* (HBK.) Sch. Bip. *Hitchcock 21656* (GH); *C. hieracioides* (Wedd.) Solbrig, *Pennell 13875* (GH); *C. pellita* (HBK.) Sch. Bip. *Hitchcock 21997* (GH); *C. repens* (HBK.) Sch. Bip. *Weberbauer 6130* (GH); *Pennell & Hazen 9853* (GH).

LITERATURE CITED

BENTHAM, G. 1873. Notes on the Classification, History and Geographic Distribution of Compositae. Jour. Linn. Soc. Bot. **13:** 335-577.

————. and J. D. HOOKER, 1873. Genera Plantarum, Vol. **2**(1), 1279 pp., London.

CABRERA, A. L. 1954. Origen y Evolución de la Flora del Parque Nacional de Nahuel Huapí. Natura (Argentina) **1:** 43-58.

————. 1957. Compositae Brasilienses Novae. Arquivos do Jardim Botânico (Rio de Janeiro) **15:** 71-76.

CARLQUIST, S. 1959. Studies on Madinae: Anatomy, Cytology, and Evolutionary Relationships. Aliso **4:** 171-236.

CASSINI, H. 1816-1830. Dictionnaire des Sciences Naturelles. 70 vols. Paris.

COCKAYNE, L. 1928. The Vegetation of New Zealand. 456 pp. Leipzig.

COPELAND, E. B. 1947. Genera Filicum. 247 pp. Waltham, Mass.

CRONQUIST, A. 1943. The Separation of Erigeron from Conyza. Bull. Torr. Bot. Club **70**: 629-632.

———. 1947. Revision of the North American Species of Erigeron, North of Mexico. Brittonia **6**: 121-302.

GRAY, A. 1884. Synoptical Flora of North America. Vol. 1 (2), 480 pp. New York.

HARLING, G. 1951. Embryological Studies in the Compositae. Part III. Astereae. Acta Horti Bergiani **16**: 73-120.

HOFFMANN, O. 1897. Compositae. In Engler, A. und K. Prantl, Die Natürlichen Pflanzenfamilien, **4**(5): 87-394.

HUZIWARA, Y. 1959. Chromosomal Evolution in the Subtribe Asterinae. Evol. **13**: 188-193.

MONTGOMERY, F. H. AND S. YANG. 1960. Cytological Studies in the Genus Erigeron. Canad. Jour. Bot. **38**: 381-386.

RAVEN, P. H., O. T. SOLBRIG, D. W. KYHOS AND R. SNOW. 1960. Chromosome Numbers in Compositae. I. Astereae. Amer. Jour. Bot. **47**: 124-132.

SOLBRIG, O. T. 1960. Leaf Venation and Pubescence in the Genus Raoulia (Compositae). Jour. Arnold Arb. **41**: 259-269.

TURNER, B. L. AND H. S. IRWIN. 1960. Chromosome Numbers in the Compositae II. Meiotic Counts for Fourteen Species of Brazilian Compositae. Rhodora **62**: 122-126.

WAGENKNECHT, B. L. 1960. Revision of Heterotheca, section Heterotheca (Compositae). Rhodora **62**: 61-76, 97-107.

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXIX

Studies in the Guttiferae. I.
A Synopsis of Hypericum Section Myriandra

By

Preston Adams

Taxonomic Fern Notes. II.
Pityrogramma (including Trismeria) and Anogramma

By

Rolla Tryon

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

1962

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXIX

Studies in the Guttiferae. I.
A Synopsis of Hypericum Section Myriandra

By

Preston Adams

Taxonomic Fern Notes. II.
Pityrogramma (including Trismeria) and Anogramma

By

Rolla Tryon

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

Issued May 14, 1962

Manufactured

by

The Lexington Press, Inc., Lexington, Massachusetts

STUDIES IN THE GUTTIFERAE. I.

A SYNOPSIS OF HYPERICUM SECTION MYRIANDRA[1]

PRESTON ADAMS[2]

Hypericum L. is an easily recognized cosmopolitan genus with more than three hundred species classified among eighteen sections (Keller, 1925). One of these sections, Sect. *Myriandra* (Spach) Endl. (as delimited in the present work), is restricted to eastern North America. The thirty species of this group have never been studied as a sectional unit. Coulter (1886, 1897), in his treatments of the family, recognized many of the species involved but assigned them to the Linnaean genera *Ascyrum* and *Hypericum*. Subsequent studies have been regional and floristic (e.g. Fernald, 1950; Gleason, 1952; Small, 1933) or else they were concerned with special groups (Svenson, 1940; Adams, 1957). Nomenclatural notes on several species were contributed by Lott (1938).

A new approach to the systematics of *Hypericum* was initiated by Robson (1956) who surveyed the patterns of floral vascularization present in *Hypericum* and related genera. Information from his anatomical studies aided him in understanding the taxonomy of *Hypericum* in tropical and southern Africa (Robson, 1957). His work stimulated my interest in pursuing studies in the systematics of *Hypericum*, especially on the group of species here included within Sect. *Myriandra*. Through the kindness of Dr. Robson (now at Kew) and the Edinburgh University Library, I obtained a microfilm of his vascularization study which had been presented to that institution as a doctoral dissertation and is not yet published. Data from his manuscript supplemented by my morphological and cytological studies (Adams, 1959a) furnished the basis for a re-evaluation and re-assignment of *Ascyrum* L. and *Crookea* Small to the larger genus *Hypericum* (Adams & Robson, 1961).

Information derived from anatomy, morphology, cytology, and phytogeography has been used to construct this synopsis of the systematics of *Hypericum* Sect. *Myriandra*.

---

[1] Financial support of this study was provided by the following sources: the Fernald Fund for Field Study in Systematic Botany at Harvard University, established by Mr. F. W. Hunnewell of Wellesley, Mass.; a National Institute of Health grant-in-aid through the Department of Biology, Harvard University, and a research grant (RG-6305) to Dr. R. K. Godfrey of Florida State University from the Division of General Medical Studies, Public Health Service.

[2] Present address: Department of Botany and Bacteriology, DePauw University, Greencastle, Indiana.

A key to the species is accompanied by brief synonymy, citations of type and representative specimens, habitat information, statements of geographical ranges, and comments on interspecific relationships. Much more study of the group remains to be done although the main outlines of the taxonomy are clear. Detailed investigations of variation, both within and among species, and the anatomy of the leaves, sepals, and bark are in progress.

ACKNOWLEDGEMENTS

I am indebted to the following persons for their many helpful criticisms and suggestions: Reed C. Rollins, R. K. Godfrey, Robert C. Foster, Rolla Tryon, C. E. Wood, C. E. Kobuski, Lloyd H. Shinners, George Argus, Arthur S. Barclay, K. A. Wilson, and J. L. Thomas. The Latin descriptions were prepared by Richard Evans Schultes. Special collections of specimens were provided by Delzie Demaree, R. B. Channell, H. F. L. Rock, Wilbur H. Duncan, R. K. Godfrey, R. Kral, Charles B. Heiser, and Charles Schweinfurth. Mrs. Lazella Schwarten was most helpful in locating and obtaining bibliographic items. Laboratory space and equipment were made available by Jonathan J. Westfall at the University of Georgia during the summer of 1958.

Much helpful information was contributed by Norman K. B. Robson who has done intensive study of *Hypericum*. The loan of his unpublished manuscript from the Library of Edinburgh University is much appreciated.

Specimens from the following herbaria have been used in this study (abbreviations according to Lanjouw & Stafleu, 1959): Arnold Arboretum (A); Brooklyn Botanic Garden (BKL); Canadian Department of Agriculture (DAO); Charleston Museum (CHALR); Duke University (DUKE); Chicago Natural History Museum (F); University of Florida (FLAS); Florida State University (FSU); University of Georgia (GA); Gray Herbarium (GH); State University of Iowa (IA); Indiana University (IND); Louisiana State University (LSU); University of Michigan (MICH); Mississippi State College (MISSA); Missouri Botanical Garden (MO); Michigan State University (MSC); North Carolina State College (NCSC); University of North Carolina (NCU); New England Botanical Club (NEBC); Tulane University (NO); New York Botanical Garden (NY); University of Oklahoma (OKL); Oklahoma State University (OKLA); Ohio State University (OS); University of Pennsylvania (PENN); Academy of Natural Sciences (PH); Purdue University (PUR); Southern Methodist University (SMU); U. S. National Herbarium (US); University of Tennessee (TENN); University of Texas (TEX); University of Arkansas (UARK); Virginia Polytechnic Institute (VPI); University of Wisconsin (WIS); and West Virginia University (WVA).

THE COLLECTING OF HYPERICUM

The ultimate writing of a definitive monograph on *Hyperi-*

cum Sect. *Myriandra* will be greatly aided if collectors will pay close attention to the following suggestions. Probably the most important is that samples of the stem and bark (of the woody species) be included with the usual herbarium specimens. Bark features are of paramount importance in showing definitive characteristics of several species, especially the *H. fasciculatum* complex. Fruiting specimens are not available for *H. densiflorum* from the Coastal Plain of the Carolinas, apparently having been overlooked by collectors even though the species has been known from that region for at least one hundred years. Specimens of *H. apocynifolium* and *H. sphaerocarpum* in mature fruit are needed. Carefully prepared plants (with accompanying rhizomes) of *H. ellipticum* would be most useful; the majority of the herbarium specimens I have seen appear to have been yanked from the soil! Observations (with specimens) of the winter and early spring aspect of *H. ellipticum*, *H. sphaerocarpum*, and *H. dolabriforme* are greatly needed. Collections of the *Hypericum* species growing in Alabama and Mississippi would be most useful in compilation of accurate distribution maps. Specimens and observations on sympatric occurrences of the following pairs of species would be of utmost value. *H. frondosum* and *H. prolificum*, *H. lobocarpum* and *H. prolificum*, *H. lobocarpum* and *H. densiflorum*, *H. ellipticum* and *H. adpressum*, and *H. stragulum* (= *Ascyrum multicaule*) and *H. hypericoides.*

CHROMOSOME NUMBERS

Meiotic chromosome counts are available for twenty-four of the thirty species in *Hypericum* Sect. *Myriandra* (Nielsen, 1924; Hoar & Haertl, 1932; Adams, 1959a; H. L. Striplin, personal communication). All species studied possess a haploid number of nine. Haploid chromosome numbers of eight, twelve, and sixteen are known in other *Hypericum* species native in eastern North America (but not in members of Sect. *Myriandra*). The number nine is not confined to this section, being present in several extra-North American species also.

HYPERICUM L., Gen. Pl. ed. 5, 341. 1754

Sect. MYRIANDRA (Spach) Endl., Gen. Pl. 1033. 1840. Based on *Myriandra* Spach, Hist. Nat. Vég. 5:434. 1836, as a genus.

Shrubs and perennial herbs. Leaves with or without an articulation at base; lamina expanded, or much reduced and the leaves needlelike; translucent secretory glands present as dots or elongate sacs, black ones absent. Trichomes absent. Sepals 5 or 4 (rarely 3 or 6), persistent long after fruit maturity, or deciduous at capsule dehiscence, with or without an articulation at base. Petals 5 or 4 (rarely 3 or 6), yellow, deciduous soon after anthesis. Androecium of numerous stamens arranged in a ring or narrow band (i.e. not fasciculate), deciduous or persistent. Gynoecium of 5, 4, 3, or 2 fused carpels; placentation pseudo-axile to parietal; styles same number as carpels, closely appressed to each other their entire length at anthesis, afterwards often separating slightly; stigmas minute; ovules numerous to few. Seed coats finely to coarsely reticulate, occasionally obscurely striated, raphe inconspicuous, or forming a keel.

TYPE SPECIES (of section Myriandra): *H. prolificum* L.

The circumscription of Endlicher's Sect. *Myriandra* is enlarged here in accordance with information yielded by recent investigations. Robson (1956), from intensive studies of the floral vascularization, concluded that the species formerly classified within the genera *Ascyrum* L., *Crookea* Small, and the sections *Myriandra* (Spach) Endl. and *Brathydium* (Spach) Endl. of the genus *Hypericum* L. are closely related. This idea was strengthened by subsequent morphological, geographical, and cytological investigations (Adams, 1959a). Recently Adams & Robson (1961) transferred to *Hypericum* the species formerly placed in the genera *Ascyrum* and *Crookea*. Additional nomenclatural changes involving Endlicher's sections are proposed here.

Within *Hypericum* Sect. *Myriandra* there are two groups of species which are distinguished by the presence or absence of an articulation at the base of the leaves and sepals and, to a lesser extent, by the degree of persistence of the withered stamens after anthesis. The rank of subsection is used for each of these groupings. The species of each subsection are closely allied although several evolutionary lines are discernible within each.

The relationships of Sect. *Myriandra* are with Sect. *Webbia* (Canary Islands and Madeira) and Sect. *Campylosporus* (of northeastern and tropical Africa). Studies of floral anatomy (Robson, 1956) and comparative morphology (Robson, 1956; Adams, 1959a) support this idea. These three sections share some or all of the following characteristics: quadrangular or winged stems, translucent glands, articulated leaves, persistent sepals and stamens, and a shrubby habit. Sect. *Myriandra* is also related to the cosmopolitan Sect. *Brathys* although less closely (Robson, personal communication). Features common to both include presence of pale glands, lack of black glands, persistent sepals and stamens, androecium composed of a ring or narrow band of numerous stamens, and parietal placentation.

Plants belonging to species of *Hypericum* Sect. *Myriandra* can be recognized by a combination of the following characteristics: woody stems (except four species); styles which are closely appressed their entire length at anthesis; minute stigmas (i.e. not capitate); presence of translucent or pellucid-puncate secretory glands (dots and or elongate sacs) in the stems, leaves, sepals, and petals; and the absence of black glands. In addition, the leaves and sepals of the plants of sixteen species (Subsect. *Centrosperma*) possess a small groove or articulation at the base (see Fig. 1). Articulated leaves occur in other species of *Hypericum* but the combination of grooved leaves and sepals is known to me in only one of these, *H. styphelioides* A. Rich., a plant of Cuba and British Honduras.

KEY TO THE SPECIES

A. Leaves clasping.

B. Flowers with 5 sepals and 5 petals; inflorescence a compound dichasium; bark becoming corky, especially on older stems .... 15. *H. myrtifolium.*

B. Flowers with 4 sepals and 4 petals; flowers solitary; bark thin, not corky .... 27. *H. tetrapetalum.*

A. Leaves sessile, not clasping.

C. Perianth tetramerous (except in occasional flowers); flowers solitary.

D. Gynoecium 2-carpellate, 2-styled.

E. Pedicels elongate, reflexed soon after anthesis; subtending bractlets at the base of the pedicel .... 30. *H. suffruticosum.*

E. Pedicels short, erect even at fruit maturity; subtending bractlets approximate to the sepals.

F. Plants erect, usually with a single stem, freely branched well above the ground level, often becoming 1.0-1.5 m tall (Fig. 3) .... 28. *H. hypericoides.*

F. Plants decumbent, with several prostrate stems arising from a primary rootstock near ground level, each with numerous erect branchlets and forming low compact mats, rarely over 0.3 m tall (Fig. 3) .... 29. *H. stragulum.*

D. Gynoecium 3-carpellate, 3-styled (infrequently 2 or 4 carpels and styles, especially in *H. microsepalum*).

G. Outer pair of sepals only slightly larger than the inner; leaves linear to broadly oblong or oblanceolate, usually less than 1.2 cm long and 0.5 cm wide; margins of the leaf and sepal rounded, not hyaline .... 24. *H. microsepalum.*

G. Outer pair of sepals much larger than the inner; leaves elliptic-oblong or ovate-cordate, usually more than 1.0 cm long and 0.5 cm wide; margins of the leaf and sepal abruptly thin and hyaline, the edge thus like a honed knife.

H. Outer pair of sepals cordate and acuminate, 5-9 mm wide; stems usually much branched, producing a bushy aspect;

adventitious shoots from horizontal roots often present. (Glades, Highlands, and DeSoto counties, Florida) .... 26. *H. edisonianum.*

H. Outer pair of sepals broadly ovate or suborbicular, 10-15 mm wide; stems usually simple, or sparingly branched; adventitious shoots lacking. (Eastern Texas to Kentucky, Florida, and New Jersey) .... 25. *H. stans.*

C. Perianth pentamerous (except in occasional flowers); inflorescence a 3-many-flowered dichasium (except *H. frondosum* and *H. buckleyi* which often have solitary flowers).

I. Gynoecium 5-carpellate, 5-styled (often 3, 4, or 6 carpels and styles present also).

J. Capsules deeply lobed; inflorescence a many-flowered (usually 15 or more) terminal compound dichasium and with similar dichasia in upper 2-4 leaf axils, producing a panicle-like aspect. (Mississippi Embayment region, especially Arkansas, Louisiana, Mississippi, and Tennessee) ... 2. *H. lobocarpum.*

J. Capsules unlobed or only slightly so; inflorescence a few-flowered (3 or 7, rarely more) terminal, simple or compound dichasium, rarely with similar dichasia in upper 1 or 2 leaf axils. (Dune areas on the shores of the Great Lakes; inland occasionally, especially in central Wisconsin and the Ottawa River of Quebec) .... 1. *H. kalmianum.*

I. Gynoecium 3-carpellate, 3-styled (rarely 2, 4, or 5 present also).

K. Mature leaf with an expanded blade, not needlelike, usually over 2 mm wide; sepals usually broadened, i.e. linear-elliptic, oblong-ovate, or spathulate.

L. Flowers terminal and solitary, or occasionally in 3- flowered dichasia.

M. Leaves without an articulation at base (see Fig. 2), elliptic, elliptic-obovate, or obovate, usually less than 2.5 cm long and 1.2 cm wide; plants decumbent, stems prostrate, each with numerous erect branches, forming low compact mats. (Endemic to the Blue Ridge Mountains of North Carolina and Georgia) .... 18. *H. buckleyi.*

M. Leaves with an articulation or groove at base (see Fig. 1), oblong-elliptic or ovate-lanceolate, usually well over 3 cm long and 1 cm wide; plants erect, stems not prostrate. (Calcareous soils, especially in the cedar glades of central Tennessee and adjacent northern Alabama) .. .. 5. *H. frondosum.*

L. Flowers in 3-many-flowered terminal and/or subterminal dichasia.

N. Shrubs, stems often 1-2 m tall.

O. Leaves and sepals without a basal articulation or groove (see Fig. 2); inflorescence appearing naked due to the much reduced bracts.

P. Leaves linear-oblong or oblong-lanceolate, usually less than 1.0 cm wide; stamens fewer than 55, usually persistent long after fruit maturity; seeds less than 0.8 mm long; placentation parietal .... 19. *H. cistifolium.*

P. Leaves elliptic to ovate-lanceolate, usually well over 1.0 cm wide; stamens more than 75, usually deciduous before fruit maturity; seeds over 1.2 mm long; placentation pseudo-axile, i.e. the placentae project inwardly toward the ovary axis, especially in the lower half.

Q. Inflorescence a many-flowered (rarely 3) dichasium; mature capsules 3.5-7 mm long, 3-4.5 mm wide; raphe of seeds well-developed, forming a conspicuous keel .... 16. *H. nudiflorum.*

Q. Inflorescence a 3-flowered dichasium, occasionally with 6 flowers, or reduced to 1; mature capsules 6-14 mm long, 4.5-7 mm wide; raphe of seeds only slightly developed, forming a low ridge, but not a conspicuous keel .... 17. *H. apocynifolium.*

O. Leaves and sepals with a basal articulation or groove (see Fig. 1); inflorescence appearing leafy due to the foliaceous bracts.

R. Largest leaves 1.5-3.0 cm long (rarely over 3.2 cm); seeds 0.7-0.8 mm long; placentation parietal. (Coastal Plain, North Carolina to northern Florida, westward to southeastern Texas) .... 6. *H. galioides.*

R. Largest leaves 3.0-7.5 cm long (rarely as short as 2 cm); seeds 0.9-1.6 mm long; placentation pseudo-axile, i.e. the placentae project inwardly toward the ovary axis, touching in the center but not united except at ovary base.

S. Mature capsules less than 6 mm long and 3 mm wide, slender-conic; flowers in 7-many-flowered terminal and subterminal compound dichasia, the inflorescence presenting an obpyramidal aspect; seeds reddish-brown, 0.8-1.3 mm long and 0.27-0.35 mm wide .... 3. *H. densiflorum.*

S. Mature capsules exceeding 7 mm in length and 3.5 mm wide, lance-ovoid; flowers in 3-7- (rarely 1-) flowered terminal and 1-7-flowered subterminal dichasia, the inflorescence usually narrow and compactly thyrsoid; seeds dark brown or black, 1.0-1.7 mm long and 0.32-0.50 mm wide .... 4. *H. prolificum.*

N. Perennial herbs, usually less than 1 m tall.

T. Plants with prominent and definite rhizomes, the bases herbaceous; young stems nearly terete, the 2 primary wings poorly developed; placentae project inwardly slightly or to one-half the distance to the ovary axis; seeds less than 0.8 mm long; seed coat finely reticulate; raphe poorly developed, forming a low ridge.

U. Leaves oval, short-elliptic to broadly elliptic, or somewhat spathulate; larger leaves 1.5-3.5 cm long; plants short and slender, rarely becoming 0.5 m tall .... 23. *H. ellipticum.*

U. Leaves elliptic below, gradually becoming linear-oblong to linear-lanceolate above; larger leaves 3.5-7.5 cm long; plants tall and stout, commonly becoming 0.8 m tall .... 22. *H. adpressum.*

T. Plants without rhizomes, but often bearing adventitious shoots from horizontal roots, bases often woody; young stems obviously flattened, the 2 primary wings well-developed; placentation parietal; seeds over 1.5 mm long; seed coat coarsely reticulate; raphe well-developed, forming a conspicuous keel.

V. Sepals equal or nearly so; stamens 45-85; seeds 2.0-2.7 mm long; seed coat very coarsely reticulate, the transverse striae much more prominent than the longitudinal .... 20. *H. sphaerocarpum.*

V. Sepals very unequal, the exterior pair larger; stamens 120-200; seeds 1.5-1.8 mm long; seed coat moderately reticulate, the longitudinal striae much more prominent than the transverse .... 21. *H. dolabriforme.*

K. Mature leaves and sepals linear-subulate or needle-like.

W. Largest leaves usually less than 11 mm long; sepals 4.5 mm long or less (occasionally to 5.5 mm).

X. Mature capsules 5.7-9.5 mm long (rarely less than 5.5 mm); plants often with decumbent stems, producing a low matted form, usually less than 0.5 m tall; nodes of youngest stems with 4 vertically-aligned, auriculate structures, 1 on each side of leaf base, each tapering into a low ridge extending downward to next node below (stem 6-angled in cross section); seed coat coarsely reticulate, the alveolae square-hexagonal (100X magnification) and in longitudinal rows, the longitudinal ridges imparting an obscure striated appearance; fresh leaves usually dull green above, hardly glossy, if at all .... 12. *H. reductum.*

X. Mature capsules 3.5-5.5 mm long; plants almost invariably erect, often reaching 1.5 m in height; stem without auriculate structures at leaf base (stems 2-winged and flattened in cross-section); seed coat finely reticulate, the alveolae circular-hexagonal (100X), and irregularly arranged, ridges about equally developed; fresh leaves shiny-green above .... 11. *H. brachyphyllum.*

W. Largest leaves usually more than 13 mm long; sepals more than 4.5 mm long (occasionally only 4 mm).

Y. Bark smooth, metallic-silvery, exfoliating in large thin curled plates; leaves, sepals, and young stems heavily glaucous; seeds over 1 mm long; seed coat coarsely reticulate but the longitudinal striae much more prominent than the transverse, thus the surface appearing furrowed. (Bay and Washington counties, Florida) .... 7. *H. lissophloeus.*

Y. Bark variously roughened, usually exfoliating in irregular strips or flakes; leaves, sepals, and young stems scarcely or not at all glaucous; seeds less than 1 mm long; seed coat finely and evenly reticulate.

  Z. Plants with decumbent stems, often forming low mats (rarely over 0.5 m tall), or at least reclining and straggly. (Along the Fall Line, mostly in the Carolinas) .... 13. *H. lloydii.*

  Z. Plants definitely erect. (Coastal Plain, North Carolina to Florida and Mississippi).

    a. Bark soft and spongy-thickened, with conspicuous vertically-aligned, cord-like laticifers; youngest stems terete or nearly so, the primary wings poorly developed; flowers mostly in terminal and subterminal 3-flowered dichasia (or rarely with terminal and subterminal solitary flowers). (Wakulla Co., westward to Santa Rosa Co., Florida) .... 8. *H. chapmanii.*

    a. Bark usually not spongy-thickened, but if so, then the laticifers inconspicuous; youngest stems strongly flattened, the primary wings well-developed; flowers mostly in 7-32-flowered terminal dichasia, the nodes below not bearing flowers or more frequently with similar compound dichasia.

      b. Plants slender, less than 1 m tall, the stem rarely over 0.8 cm thick; apices of sepals and leaves long-acuminate; resin glands in leaves and sepals often darkening upon drying; flowering during May. (Bay, Gulf, Franklin, Liberty, and Washington counties, Florida) .... 14. *H. exile.*

      b. Plants stout, usually over 1 m tall (often to 4 m), the stem 1-5 cm thick; apices of sepals and leaves mucronate; resin glands in leaves and sepals usually remaining clear on drying; flowering throughout the summer, or all year in lower peninsular Florida.

        c. Bark spongy-thickened, exfoliating in grayish-reddish tissue-thin layers; leaves with a deep longitudinal groove below on each side of midrib, numerous whitish papillae present on the concave lower surface (best observed on living leaves); mature capsules elliptic-oval; terminal dichasium usually compactly cymose, subterminal solitary flowers or 3-flowered dichasia often present in upper 1 or 2 leaf axils; leaves of axillary branchlets usually crowded, presenting a fasciculate appearance .... 9. *H. fasciculatum.*

c. Bark thin, even on oldest stems, not spongy, exfoliating in flakes or narrow strips; leaves merely slightly concave below, not grooved, papillae inconspicuous, poorly developed; mature capsules oblong; terminal dichasium usually openly paniculate, subterminal many-flowered dichasia present in upper 3-7 leaf axils; leaves of axilary branchlets usually not crowded .... 10. *H. nitidum.*

Sect. MYRIANDRA, subsect. CENTROSPERMA Keller, in Engler & Prantl, Pflanzenfamilien 3 (6-6a) 214. 1895.

Shrubs. Leaves and sepals with an articulation or groove at the base (Fig. 1). Sepals 5 (rarely 4), deciduous after fruit dehiscence. Petals 5 (rarely 4). Withered stamens deciduous soon after anthesis.

TYPE SPECIES: *H. prolificum* L.

Fifteen species, nine of which are distributed on the Coastal Plain of the southeastern United States, Cuba, and British Honduras, and the remaining six in the central and eastern United States and adjacent Canada.

1. **Hypericum kalmianum** L., Sp. Pl. 2:783. 1753

Hypericum bartramium Miller, Gard. Dict. ed. 8, no. 10. 1768.

TYPE: LINN; photograph in A library; sketches and notes from type by H. K. Svenson, GH.

REPRESENTATIVE SPECIMENS: ONTARIO: Great Duke Island, *Grassl 5554* (MICH). ILLINOIS: Lake Co., Waukegan, *Gleason & Shobe 331* (DUKE). INDIANA: Starke Co., Bass Lake, *Deam 20133* (IND). MICHIGAN: Alpena Co., Alpena, *Fernald & Pease 3420* (GH). WISCONSIN: Jackson Co., shore of Black River, *Fassett 15716* (WIS).

Dunes and rocky shores about Lakes Michigan, Huron, and Erie; inland in central Wisconsin and the Ottawa River of Quebec. Flowering late June through early August.

This species is readily distinguishable from its closest relative, *Hypericum lobocarpum*, by various features, especially of the capsule and inflorescence (see that species). An interesting phytogeographical problem involving the origin of *H. kalmianum* and its distribution during the Pleistocene is discernible (McLaughlin, 1931; Hugh H. Iltis, personal communication).

2. **Hypericum lobocarpum** Gattinger, Bot. Gaz. 11:275. 1886

Hypericum oklahomense Palmer, Jour. Arn. Arb. 5:128. 1924.

TYPE: TENNESSEE: Carroll Co., Hollow Rock, *A. Gattinger* August 1867 (Lectotype, F, with dissections and sketches by Gattinger; isotype, GH).

REPRESENTATIVE SPECIMENS: ARKANSAS: Pulaski Co., Little Rock, *Demaree 8207* (A, BKL, GH, NY). KENTUCKY: Calloway Co., between Murray and New Concord, *Smith & Hodgdon 4083* (GH, US). LOUISIANA: Webster Parish, 4 miles west of Minden, *Correll & Correll 10310* (DUKE, F, GA, MO, NY, PH). OKLAHOMA: LeFlore Co., Page, *Palmer 22228* (GH, holotype of *H. oklahomense* Palmer; isotypes, A). TENNESSEE: Chester Co., *Sharp et al 9410* (TENN).

Creek and river bottoms, stream banks, moist pinelands, and ditches, Arkansas and southeastern Oklahoma, southward into eastern Texas, southern Louisiana, and southern Mississippi, northward into western Tennessee and Massac Co., Illinois (Mohlenbrock & Voigt, 1959). Flowering mid-June through early August, occasionally earlier (late May) or later (September and October).

This species is distinguished from its closest relatives, *Hypericum densiflorum* and *H. kalmianum,* by several characteristics, especially the morphology of the gynoecium. Carpel number, predominantly five in the first two species, readily separates *H. lobocarpum* from *H. densiflorum* (Table 1).

TABLE 1. Comparison of carpel numbers in the gynoecia of three species of ***Hypericum***

species	*number of collections studied*	*carpel number (in %)*					*gynoecia counted*
		2	***3***	***4***	***5***	***6***	
H. lobocarpum	23	0.0	1.7	19.2	79.1	0.0	2014
H. densiflorum	49	0.2	92.1	6.9	0.8	0.0	3197
H. kalmianum	25	0.0	1.0	22.1	76.2	0.7	389

Ovary lobing, best observed in the mature capsule, is pronounced in *H. lobocarpum*, present slightly in *H. densiflorum*, but virtually absent in *H. kalmianum.* The mature capsule dimensions overlap, but significantly different trends in proportion are discernible. The fruits of *H. lobocarpum*, often larger than those of H. densiflorum, never reach the relatively great size attained by *H. kalmianum.* Capsules 6-8 mm long and over 3 mm wide are produced by *H. lobocarpum* frequently but never occur in its eastern relative, *H. densiflorum.* Fruits of many individuals, otherwise definitely referable to *H. lobocarpum*, may be the same size as the smallest ones produced by *H. densiflorum*, a situation which has influenced the interpretation of the former as a variety of the latter (Svenson, 1940; Fernald, 1950; Gleason, 1952; Gillespie, 1959).

Nowhere does *Hypericum lobocarpum* overlap the range of *H. densiflorum*, the known stations of each being at least eighty miles apart (Winston Co., Mississippi and Tuscaloosa Co., Alabama, respectively). Further north in Tennessee the known populations of these two species are separated by some one hundred twenty miles (Carroll and Coffee counties).

3. **Hypericum densiflorum** Pursh, Fl. Am. Sept. 376. 1814

Hypericum foliosum Jacq., Hort. Schoenbrun. 3:299. 1797, not Aiton, Hort. Kew. ed. 1, 3:104. 1789.

Hypericum prolificum L. var. *densiflorum* (Pursh) Gray, Man. Bot. ed. 2, 50. 1856.

Hypericum glomeratum Small, Bull. N. Y. Bot. Gard. 1:281-283. 1899.

Hypericum interior Small, Bull. Torrey Club 28:359. 1901.

Hypericum revolutum Keller, Bot. Jahr. 58:194. 1923, not Vahl, Symb. Bot. 1:66. 1790.

TYPE: "On the dry ridges and savannahs of the Virginia mountains," but probably no longer extant (Svenson, 1940).

REPRESENTATIVE SPECIMENS: GEORGIA: Whitfield Co., *Harper 2032* (GH, NY, isotypes of *H. revolutum* Keller). NEW JERSEY: Cumberland Co., South Vineland, *Bassett & Long* 12 August 1923 (GH, PH). NORTH CAROLINA: Avery Co., *Adams 117* (DUKE, FSU, GH, NY, US); Grandfather Mt., *Huger* August 1896 (NY, type of *H. glomeratum* Small). SOUTH CAROLINA: Georgetown Co., *Adams 94* (FLAS, GA, K, MO, SMU). TENNESSEE: Jefferson Co., Dandridge, *Rugel* July 1842 (NY, type of *H. interior* Small). VIRGINIA: Grayson Co., *Adams 109* (NCU).

Abundant in wet meadows, lake margins, open stream banks, moist pinelands, bogs, and roadside ditches (especially on the Coastal Plain of the Carolinas); also on dry road embankments and rocky hillsides. The Coastal Plain of New Jersey, Delaware, and Maryland, southward (except southeastern Virginia) to eastern North Carolina and adjacent South Carolina; also in the Appalachian mountain region from extreme southwestern Pennsylvania southward to northern Georgia, eastern Tennessee, and central Alabama. Flowering late June through early September. Harper's report (1928) of *Hypericum galioides* from Jefferson, Tuscaloosa, and Bibb counties, Alabama, is probably based on plants of *H. densiflorum.* His comment that "some of the specimens [were] ten feet tall" is fairly conclusive, since plants of *H. galioides* rarely exceed 1.5 m in height. Specimens of *H. densiflorum* have been collected in Tuscaloosa County and in adjacent Jefferson County. *Hypericum galioides* does not grow in Alabama north of Geneva and Escambia counties, adjacent to the Florida border, according to Harper (1928).

Hypericum densiflorum, superficially similar to *H. galioides,* is closely related to *H. lobocarpum* (which see) and, to a lesser degree, *H. prolificum.* It may be distinguished from *H. prolificum* by narrower leaves and more floriferous inflorescences. Tricarpellate gynoecia are the rule in flowers of *H. densiflorum* plants but four, five, and even two carpels have been observed, even on the same individual. Mature seeds from the Carolina Coastal Plain populations of this species have not been available for study.

4. **Hypericum prolificum** L., Mant. Pl. 1:106. 1767

Myriandra spathulata Spach, Hist. Nat. Vég. 5:440. 1836.

Hypericum spathulatum (Spach) Steud., Nomencl. ed. 2, 789. 1840, not Keller, Bot. Jahr. 58:195. 1923.

TYPE: sheet number 943.20, selected by H. K. Svenson (1940), LINN; photograph, A library.

REPRESENTATIVE SPECIMENS: ARKANSAS: Drew Co., *Demaree 17648* (A, FSU, MO, NY, PH). NORTH CAROLINA: Union Co., 1.2 miles north of Sturtevant, *Fox & Whitford 3888* (NCSC, SMU, TENN). PENNSYLVANIA: Chester Co., Strafford, *Bartram 1390* (PH).

Rocky slopes, granite outcrops, dry rocky creek beds, roadside embankments, and abandoned fields. Widespread over central and eastern United States from Pennsylvania southward to northern Georgia, around the northern rim of the Mississippi Embayment to southeastern Oklahoma, northward to Iowa and Michigan. Abundant at the summit of Brasstown Bald, Union Co., Georgia, at an elevation of 4768 feet. Hardy around the Boston, Massachusetts area, having become well established at Wellesley and in Essex County. Flowering late June (southward) through early September.

This species is very variable but still retains a distinctive facies. The ovate to lance-ovate, relatively thin-walled capsules, while varying in size, cannot be mistaken for those of any other species (except *H. frondosum,* occasionally). *Hypericum prolificum* is distinguished from the related *H. lobocarpum* by a less floriferous inflorescence and unlobed capsules. However, the separation of this species from the closely related *H. frondosum* is more difficult. *Hypericum prolificum* usually has a smaller, thicker-walled capsule, smaller petals and seeds, and a more complex inflorescence. Plants of these two species may hybridize, at least in cultivation. A putative hybrid between them has been described as *H.* X *VanFleetii,* according to Rehder (1940). Specimens in the herbarium of the Arnold Arboretum which bear this epithet upon their labels are readily referable to *H. prolificum.* A highly variable population possibly originating from hybridization between cultivated plants of these species grows in a pasture on the Harbison farm at Highlands, Macon Co., North Carolina. Intensive study of this population and those of both species in the Central Basin of middle Tennessee is greatly needed.

After study of a "vast amount of herbarium-material" Fernald & Schubert (1948) were unable to identify plants of this species with the type of *H. prolificum* in the Linnaean Herbarium. Consequently, they revived the relatively unused epithet *H. spathulatum* (Spach) Steud. for this species. Other investigators (Svenson, 1940, 1952; Adams, 1959b) have amply demonstrated, however, that Fernald & Schubert's name changing was unnecessary, pointing out that the "aberrant" appearance of the type specimen (i.e. its "unusually revolute leaves") is due merely to wilting prior to collecting and to insufficient pressure during the drying process. The name *H. spathulatum,* used by Fernald (1950), is a later synonym of *H. prolificum.*

5. **Hypericum frondosum** Michx., Fl. Bor.-Am. 2:81. 1803

Hypericum aureum Bartram, Travels 383. 1791, not Loureiro, Fl. Cochinch. 2:472. 1790.

Hypericum amoenum Pursh, Fl. Am. Sept. 2:375. 1814.

Hypericum rugelianum Kunze, Linnaea 24:177. 1851.
Brathydium rugelianum (Kunze) C. Koch, Hort. Dendr. 66. 1853.
Brathydium aureum (Bartram) C. Koch, Hort. Dendr. 66. 1853.
Hypericum splendens Small, Bull. Torrey Club 29:291. 1901. 291. 1901.

TYPE: "Hab. in rupibus, ad flumen *Tennasee,*" *Michaux* (P; photograph, GH; sketches from type by H. K. Svenson, GH).

REPRESENTATIVE SPECIMENS: ALABAMA: Morgan Co., 2 miles south of Tennessee River, south of Huntsville, *Godfrey 57520* (FSU). GEORGIA: Dade Co., Cloudland Canyon, east of Trenton, *Cronquist 5293* (GA, GH, NY, SMU); DeKalb Co., Stone Mt., *Small* July 4, 1893 (NY, type of *H. splendens* Small). TENNESSEE: Wilson Co., 2 miles north of Lebanon, *Godfrey 59498* (FSU).

A showy plant in flower, *Hypericum frondosum* is abundant in the cedar glades of the Central Basin in middle Tennessee. It has also been collected at widely scattered localities, especially on river bluffs, in southern Kentucky, extreme eastern Tennessee, northern Alabama, and central and southwestern Georgia. Adventive plants have been collected in Connecticut, New York, and Massachusetts. Flowering late May through early July.

When best developed, plants of *Hypericum frondosum* are readily distinguishable from the related *H. prolificum* (which see). The separation becomes difficult with nonfruiting specimens and cultivated material.

The characteristics of the large-flowered *Hypericum* which grows on the slopes of Stone Mountain, DeKalb Co., Georgia, are within the *H. frondosum* variation pattern. Small, after several visits to that famous granite exposure, became so impressed with these plants that he described them as a new species, *H. splendens.* My studies of this population at various times during the growing season strongly suggest, however, that these plants represent merely a geographically isolated stand of *H. frondosum.*

6. **Hypericum galioides** Lam., Encyc. Méth. Bot. 4:161. 1797, not Freyn. & Sint., Bull. Herb. Boiss. 3: 103. 1895
Hypericum axillare Lam., Encyc. Méth. Bot. 4:160. 1797.

Hypericum fasciculatum Michx., Fl. Bor.-Am. 2:80. 1803, not Lam., Encyc. Méth. Bot. 4:160. 1791, not Tapeyr, Hist. Abr. Pl. Pyr. 450. 1813.

Hypericum michauxii Poir., Suppl. 3:696. 1813.

Hypericum ambiguum Elliott, Sketch. 2:30. 1821.

Myriandra michauxii (Poir.) Spach, Hist. Nat. Vég. 5:437. 1836.

Hypericum galioides, var. *pallidum* Mohr, Contrib. U. S. Nat. Herb. 6:621. 1901.

Hypericum spathulatum Keller, Bot. Jahr. 58:195. 1923, not Steud., Nomencl. ed. 2, 789. 1840.

TYPE: "Caroline," *Fraser*, P-LA; sketch and notes from type by H. K. Svenson, GH.

REPRESENTATIVE SPECIMENS: FLORIDA: Gadsden Co., 3.5 miles west of Greensboro, *Adams 362* (DUKE, FSU, GA, GH, NCSC, NY, TENN, US); Liberty Co., *Adams 370* (FLAS, MO, NCU, SMU). GEORGIA: *Harper 1155* (A, GH, NY, US, isotypes of *H. spathulatum* Keller). SOUTH CAROLINA: Berkeley Co., *Adams 89* (IND).

Abundant on open stream banks, seepage areas, swampy clearings, river bottoms, floodplains, hammocks, pond shores, moist roadside ditches, edges of borrow pits, and low pinelands on the Coastal Plain from North Carolina southward to northern Florida and westward to southeastern Texas (excepting the Delta region of Louisiana). Flowering late May through early August, occasionally to late October.

This species, equated by Lott (1938) and Svenson (1940) with the other members of the *Hypericum fasciculatum* complex, is distinguished by adult leaves with well-developed blades. The leaf margins may inroll on dried specimens, simulating the linear-subulate leaf on plants of the *H. fasciculatum* group. When best developed the lamina is 3-6 mm wide. Small (1933), Svenson (1940), and Gillespie (1959) confused *H. galioides* with the more northern *H. densiflorum*, especially with the populations of the latter in northwestern Georgia and eastern Tennessee. Superficially, the leaves are similar but the leaf length width ratio in the Georgia-Tennessee *H. densiflorum* is different, being more narrow in proportion to the length than those of *H. galioides*. Also, the parietal placentation and shorter seeds (with a finer seed coat reticulation) of *H. galioides* contrast with these features as present in *H. densiflorum*. Furthermore, the ranges of both species overlap on the outer Coastal Plain of the Carolinas but the two are readily identifiable, even from a moving automobile, and do not intergrade.

The reason for the usage of the name *Hypericum galioides* rather than *H. axillare* for this species (both published by Lamarck in his 1797 work) is as follows. Early American botanists, e.g. Pursh (1814) and Elliott (1824), were able to identify Lamarck's *H. galioides* fairly definitely but were unsure concerning *H. axillare.* For example, Pursh (1814) considered this name to be a synonym of *H. fasciculatum* Lam. Later authors, including Torrey & Gray (1838), Coulter (1886, 1897), Chapman (1897), Small (1903, 1913, 1933), and Svenson (1940), have employed the well-grounded *H. galioides.* I see no reason to change.

THE HYPERICUM FASCICULATUM COMPLEX

The following eight species are closely related. All have adult leaves which are linear-subulate or needle-like, the blade being poorly developed. The gynoecia are deeply lobed, 3-carpelled (rarely 2 or 4), and possess parietal placentation. With the exception of *Hypericum lissophloeus*, the seeds are remarkably similar, differing mainly in the seed coat markings. The asymmetrical, apiculate petals are also much alike in shape but differ somewhat in size. The capsules of each species exhibit a characteristic shape which is obviously related to the overall proportions of the fruit at maturity.

Taxonomic opinion regarding the *Hypericum fasciculatum* group has varied considerably. Coulter (1897), puzzled by the seeming "intergradation" of characters, recognized a single species, *H. fasciculatum* Lam. Chapman (1897), who possessed field experience with the complex, was able to distinguish two species, *H. fasciculatum* and a shorter-leaved plant which he called *H. aspalathoides* Willd. Small (1903, 1913, 1933) seems to have followed Chapman's treatment. Svenson (1940) considered these taxa as varieties of *H. galioides* Lam., a perfectly distinct although closely related species. Svenson's conception of *H. galioides* also included plants of *H. densiflorum* Pursh (Svenson, 1940, plate 587, figure 7). It is understandable, therefore, why he concluded that the plants represented by the names *H. fasciculatum* and

H. galioides "form an inseparable intergrading series." Insufficient properly prepared specimens of the *H. fasciculatum* group no doubt caused Svenson to conclude further that "some of these variations of *H. galioides* are of doubtful geographic significance and are probably not the equivalent of subspecies of zoological usage."

In recent years observant collectors in northern Florida, especially the Panhandle region, have been greatly puzzled by the *Hypericum fasciculatum* complex (R. K. Godfrey, R. Kral, and E. L. Tyson, personal communication). Their attempts to understand the group using the treatments of Small (1933) and Svenson (1940) have met with frustration; the reasons for this have now become clear (see below). I was introduced to the perplexities of *H. fasciculatum* and its relatives in June of 1958 while collecting in Florida with R. K. Godfrey. My field experience that summer combined with scrutiny of herbarium specimens led me to conclude that "the group is composed of at least four very striking variation patterns" and that "an inseparable intergrading series most probably does not exist" (Adams, 1959a). It was evident to me also that these "variation patterns" were most probably biological entities worthy of specific recognition.

Intensive field observation of the *Hypericum fasciculatum* complex by both R. K. Godfrey and myself, especially in northern Florida and southern Georgia, during the past two years, has revealed that the long-standing taxonomic confusion is due primarily to the presence of eight morphologically distinct taxa, each with a distinctive geographic range and specific habitat requirements. Close study, in the laboratory and in the field, has revealed no evidence of intergradation among these several taxa, despite their close association in the same habitats. Their flowering periods, while distinctive for each species, often overlap. Insects, chiefly bumblebees and honey bees, have been seen to visit the flowers of two or more species in succession. There is no evidence of polyploidy even though the chromosomes of only five taxa have been studied.

It is my considered opinion that each of the eight kinds of plants in the *Hypericum fasciculatum* complex represents a biological entity worthy of recognition as a species. Admittedly, they are closely related and may well be phylogenetically "young" species, compared to the other members of

Hypericum Sect. *Myriandra.* All evidence suggests that the eight species share a common ancestry and that they are related through *H. galioides* to the other members of Subsect. *Centrosperma.*

7. **Hypericum lissophloeus** P. Adams, sp. nov.

Arbuscula usque ad 4 m alta, trunco ad 4.5 cm in diametro. Rami juveniles, folia et sepala conspicue glauca. Cortex laevis (velut nitidus), statu juvenile castaneo-fuscus, statu adulta argenteo-metallicus, in plagulis magnis crispis decorticans. Folia basi articulata, lineari-subulata, lamina vix expansa, valde et carnoso-marginata, 9-17 mm longa, 0.5-0.75 mm lata, subtus minute papillata. Incrementa vegetativa indeterminata, cum floribus solitariis vel subinde dichasio tribus floribus. Sepala basi articulata, lineari-subulata, 7-8 mm longa 0.5-0.75 mm lata, ante capsulae dehiscentiam decidua. Petala flava, inaequalia, 10-12 mm longa, 5-6 mm lata. Stamina 170-221, 8-9 mm longa. Gynoecium 6-9 mm longum, 3- (vel raro 4-) carpellatum, placentatione parietale, cum 3 (vel raro 4) stylis. Capsula matura 6-7 mm longa, 2.5-3.5 mm lata. Semina fusca ad brunnea, carina aliquid humile, 1-1.6 mm longa, 0.5-0.6 mm in diametro, testa grossissime reticulata, striis longitudinalibus quam transversalibus prominentioribus, adspectu rugosa.

Shrub, to 4 m tall, with stem to 4.5 cm thick. Young stems, leaves, and sepals conspicuously glaucous. Bark smooth (as if polished), chestnut-brown when young, metallic-silvery on older stems, exfoliating in large thin curled plates. Leaves articulate at base, linear-subulate or needle-like, lamina poorly developed, edges thickened and turned abruptly downward (inrolled on drying), 9-17 mm long, 0.5-0.75 mm wide, minutely papillate beneath. Vegetative shoots often continuing growth throughout the season, producing solitary flowers (or occasionally 3-flowered dichasia) from the leaf axils. Sepals articulate at base, linear-subulate or needle-like, 7-8 mm long, 0.5-0.75 mm wide, deciduous before fruit maturity. Petals yellow, asymmetrical, 10-12 mm long, 5-6 mm wide. Stamens 170-221, 8-9 mm long. Gynoecium 6-9 mm long, carpels 3, rarely 4, placentation parietal, styles 3, rarely 4. Mature capsule 6-7 mm long, 2.5-3.5 mm wide. Seeds tan to dark brown, raphe developed into a moderately low keel, 1 0-1.6 mm long, 0.5-0.6 mm wide, seed coat very coarsely reticulate, longitudinal striae much more prominent than transverse ones, presenting a furrowed appearance. Specific epithet from the Greek meaning "smooth bark."

TYPE: FLORIDA: Bay Co., shores of Merial Lake, ca. 10 miles north of Panama City, *Godfrey & Triplett 59844* (Holotype, GH; isotypes, DUKE, F, FLAS, FSU, GA, IA, ILL, K, MSC, MO, MT, NCU, NCSC, NY, PAM, SMU, TENN, TEX, UC, US, USF, VDB, VPI, WIS).

REPRESENTATIVE SPECIMENS: FLORIDA: Bay Co., shores of Merial Lake (exact type locality), *Adams 685* (DUKE, FLAS, GA, K, MSC, NY, SMU, US); same locality, *Adams 734* (F, GH, ILL, K, MO, NCU, TEX); Washington Co., border of Long Pond north of Redhead, *Godfrey 60793* (FSU).

Known only from Bay and Washington counties, Florida. Abundant in sandy soil on the shores of sinkhole ponds and lakes. Frequently growing in water to 1.5 m deep. Flowering sporadically from late May until October.

Hypericum lissophloeus is distinguished from its closest relatives in the *H. fasciculatum* complex by many features, including a smooth, polished, metallic-appearing bark which exfoliates like birch (on older stems); the slender, wandlike, lax or drooping younger stems; a large seed size and a furrowed seed coat; and glaucous leaves, sepals, and young stems. It grows in company with one or both of two other species of the *H. fasciculatum* group. Plants of *H. reductum*, low, much-branched, and suffrutescent, grow about the bases of *H. lissophloeus* plants on the upper pond or lake shores out of the water. It is sometimes associated with *H. fasciculatum* either in the water or on upper drier shores, in the latter situations the three occurring together. Since the three grow together and are readily identifiable, no intergradation being apparent, this is taken as additional evidence of their specific nature.

8. **Hypericum chapmanii** P. Adams, nom nov.

Based on *Hypericum arborescens* Chapman, Fl. S. U. S., ed. 2, suppl. 2, 680. 1892, not Vahl, Symb. Bot. 2:86. 1791.

TYPE: FLORIDA: presumably around Apalachicola, *Chapman*, but not yet located. Bilt. Herb. no. 5735a, apparently collected in 1893, bears the name *Hypericum arborescens* and illustrates Chapman's conception of this taxon (A, NY).

REPRESENTATIVE SPECIMENS: FLORIDA: Bay Co., northeast of Vicksburg, *Adams 513* (FSU); Franklin Co., 8.6 miles west of Apalachicola, *Adams 508* (FLAS, FSU); Gulf Co., 3.6 miles of Wewahitchka, *Adams 340* (DUKE, GH, PAC, PUR, SMU, VDB); Liberty Co., 8 miles south of Hosford, *Adams 287* (FSU); Santa Rosa Co., *Tyson 485* (FLAS).

Abundant in flatwoods depressions, margins of cypress ponds, and borrow pits, from the Ochlocknee River (between Wakulla and Liberty counties, Florida) westward to Santa Rosa County, Florida. Not known to grow more than thirty-five miles inland from the Gulf of Mexico. Flowering early June through middle July.

Hypericum chapmanii stems are characterized by a soft bark with conspicuous, vertically-aligned, resin-filled laticifers occurring at discrete levels between layers of cork often 3 or 4 mm thick. Upon being torn apart, the layers of cork appear striated or fluted owing to the large size of the laticifers running through them. Within, the cork is reddish-brown to almost cinnamon-colored; on the surface it weathers to gray. The resin in the laticifers, clear and nearly colorless when fresh, gradually hardens, turning dark brown or almost black. As the stem grows in circumference the bark cracks externally and the cork layers disintegrate and fall away, leaving the more resistant strips of hardened, resinous laticifers, the whole presenting a stringy, ragged, unkempt appearance. Frequently the bark attains a thickness of 3 or 4 cm, especially near the bases of older stems. The soft spongy feature is evident even on young stems under 5 mm thick. The soft bark is sometimes used by mice to line their nests (E. L. Tyson, personal communication). These animals also build their nests in the branches of large plants of this species, according to Tyson.

When best developed, plants of *Hypericum chapmanii* usually have a single stem which produces a dwarf tree-like aspect, a feature which doubtless influenced Chapman in his choice of the name "arborescens." Individuals often attain a height of 3 or 4 m and a thickness of 10-15 cm, especially near the base. The strongly ascending, light green leaves have a deep channel or groove on their lower surface along each side of the midvein. Numerous tiny (but obvious under 10X magnification) white papillae cover the surface of these canalicula. The flowering season begins about June 1 and extends through late July. A second crop of flowers is never produced in the fall, at least not during the two years I have observed these plants.

The distributional area includes or overlaps those of the following related species: *H. fasciculatum*, *H. nitidum*, *H. exile*, *H. reductum*, *H. lissophloeus*, and *H. brachyphyllum*. However, observations in the field and on specimens of fresh and dried plants in the laboratory during the past two years have revealed no evidence of intergradation.

9. **Hypericum fasciculatum** Lam., Encyc. Méth. Bot. 4:160. 1797

Not Michx., Fl. Bor.-Am. 2:80. 1803, not Tapeyr., Hist. Abr. Pl. Pyr. 450. 1813.

Hypericum aspalathoides Willd., Sp. Pl. 3:1451. 1803, nom. superfl.

Myriandra brathydis Spach, Hist. Nat. Vég. 436. 1836, nom. superfl.

Hypericum galioides Lam. var. *aspalathoides* (Willd.) T. & G., Fl. N. Am. 1:672. 1840.

Hypericum galioides Lam. var. *fasciculatum* (Lam.) Svenson, Rhodora 42:12. 1940.

TYPE: "Caroline," *Fraser*, P-LA; photograph, GH; sketches and notes from type by H. K. Svenson, GH.

ILLUSTRATION: Svenson, 1940, plate 587, figure 1.

REPRESENTATIVE SPECIMENS: FLORIDA: Liberty Co., 7.7 miles east of Bristol, *Adams 357* (DUKE, FLAS, FSU, GH, NCSC, SMU, NCU, USF); Polk Co.,7 miles west of Frostproof, *Adams 393* (FLAS, FSU, USF); Wakulla Co., 1 mile north of Panacea bridge, *Adams 305* (FLAS, FSU, DUKE); Washington Co., Long Pond, north of Redhead, *Godfrey 60792* (FSU). GEORGIA: Echols Co., 8 miles west of Fargo, *Adams 820* (FSU, GA, GH); Lee Co., 3.5 miles south of Smithville, *Adams 3* (BH, GA, IA, IND, MSC, MT, NA, NCU, NY, SMU, US).

Common around the margins of cypress ponds and small lakes, in low pinelands and ditches, throughout Florida, southern Georgia, southeastern South Carolina, southern Alabama (Harper, 1928), and southern Mississippi. Flowering all year in southern Florida, beginning in late April-early May in northern Florida, sporadically through the summer and until November in northern Florida and Georgia.

Plants of *Hypericum fasciculatum* have a spongy-thickened bark which exfoliates in tissue-thin sheets. Vertically-aligned, resin-filled laticifers occur in definite layers between strata of cork. The resin in the laticifers is liquid and nearly colorless when fresh but gradually hardens to a reddish-brown color. As the stem grows in thickness the resinous layer cracks, exposing the cork which peels away in brown or cinnamon-colored tissue-like layers. The laticifers, being more resistant to weathering, remain longer but eventually exfoliate in elongate flakes or strips.

Both *Hypericum fasciculatum* and its relative, *H. chapmanii,* possess corky barks. However, each is distinctly different, being easily recognizable, even by touch. The bark of *H. fasciculatum* never attains the softness nor the thickness of *H. chapmanii.* Anatomically, the cork strata of the former species do not become as thick (i.e. have fewer cell layers) as do those of the latter. Since the laticifers of *H. fasciculatum* are relatively small and thread-like, the intervening layers of cork are smooth, in marked contrast to the conspicuously striated or fluted aspect produced by the large resin tubules in *H. chapmanii.*

Other characteristics of *Hypericum fasciculatum* which distinguish it from *H. chapmanii* include darker green, spreading to only slightly ascending leaves, a different inflorescence (see key), strongly flattened young stems, earlier initiation of flowering, development of a second crop of flowers in the fall (see below), smaller maximum height and thickness of stems, and much more extensive geographic range.

The distributional range of *Hypericum fasciculatum* overlaps or encompasses that of six related species. In the Bay-Gulf-Franklin-Liberty county region of Florida, plants of this species grow in close association with individuals of *H. lissophloeus, H. chapmanii, H. brachyphyllum, H. nitidum, H. exile,* and *H. reductum.* No evidence of intergradation among these species has been discovered.

At fruit maturity plants of *Hypericum fasciculatum* may produce a second increment of vegetative growth, the young shoots frequently bearing flowers at their tips. In the northern portion of the range this second crop of flowers rarely matures, usually being killed by frost in November.

The seedling leaves of plants of this species possess a strikingly different shape than the adult ones. These juvenile leaves are obovate, elliptic, or elliptic-oblong, with the blade well-developed, but gradually become modified in form and structure at successive nodes up the stem. Eventually, adult leaves with a linear-subulate or needle-like shape are formed. "Stump sprouts," originating when older stems are cut near the base (as along mowed highway right-of-way), show a similar leaf development. Occasionally, a mature plant will suddenly form juvenile leaves (see illustration in Svenson, 1940, plate 587, figure 2). Reversal to juvenility may occur also in greenhouse plants. This phenomenon has been responsible for some of the confusion concerning *H. fasciculatum* and the related *H. galioides*, the juvenile leaves of the former having been interpreted as evidence of intermediacy between these species.

10. **Hypericum nitidum** Lam., Encyc. Méth. Bot. 4:160. 1797

Myriandra nitida (Lam.) Spach, Hist. Nat. Vég. 5:436. 1836.

Hypericum cubense Turcz. [?], Bull. Soc. Nat. Mosc. 31:384. 1858, see discussion below. Type: *Linden 1696*, but not yet located.

Hypericum galioides Lam. var. *cubense* Griseb. [?], Cat. Pl. Cub. 39. 1866, see discussion below. Type: *Wright 2126* (GH, NY).

TYPE: P-JU; photograph, GH; fragment of type, GH.

REPRESENTATIVE SPECIMENS: FLORIDA: Bay Co., just east of Callaway, *Adams 350* (DUKE, F, FLAS, FSU, GA, GH, K, MO, NCSC, NY, SMU, US). GEORGIA: Colquitt Co., *Adams 33* (FSU, GA, GH, NA); Irwin Co., 11 miles southeast of Fitzgerald, *Adams 555* (FSU, GA); Brooks Co., 2.8 miles east of Barney, *Adams 376* (DUKE, FLAS, FSU, GH, IA, K, MO, MSC, NCSC, NCU, SMU, TEX); Thomas Co., 2 miles north of Pavo, *Adams 334* (DUKE, FSU, GA).

Moist soil along open stream banks and pond margins, low pinelands, highway fill excavations, and roadside ditches. Southern Georgia (excepting the coastal counties) nearly to the Fall Line and southward into the Panhandle of Florida from Liberty to Escambia counties. Also in Baldwin Co., Alabama, Lexington Co., South Carolina, and Brunswick Co., North Carolina. Flowering early June through early August, occasionally later.

Plants of *Hypericum nitidum* are usually very abundant locally, often forming dense thickets. In Bay, Gulf, and Liberty counties, Florida, these plants are often 2 m or more in height and frequently 3-4 cm in diameter near the base. The bark is thin, dark brown or reddish, and exfoliates in flakes or narrow strips. Plants of this species greatly resemble those of *H. brachyphyllum;* indeed, the two species seem to differ mainly quantitatively, the latter appearing to be a "miniature" of the former. However, they seem amply distinct morphologically, being easily distinguished even when growing in the same habitats. Plants of *H. nitidum*, besides having much longer and somewhat wider leaves, are typically much taller and the stems thicker in diameter. Furthermore, those of this species usually begin to flower at least two weeks earlier than those of *H. brachyphyllum*. In addition, each of these species possesses a distinctive geographic range, although their distributions overlap throughout the Panhandle of Florida and the lowermost portion of Georgia. *Hypericum nitidum* grows farther north toward the Fall Line in Georgia but does not occur in Florida southeast of Franklin County. Further intensive study is greatly needed to establish the exact morphological limits of each of these species.

The plants of the *Hypericum fasciculatum* complex which grow in Cuba and British Honduras seem to be closest to *H. nitidum*, with the exception of Grisebach's *H. limosum* (isotype, *Wright 2125*, GH) which greatly resembles *H. brachyphyllum*. The external morphology of the leaves of the Cuban specimens compares readily with that of the United States *H. nitidum*. However, stem samples with bark taken from near the base of the plants are needed before the Cuban material can be definitely classified. Interestingly enough, Asa Gray, upon his last visit to Paris in 1881, concluded that Grisebach's type of *H. galioides* var. *cubense (Wright 2126)* is "exactly *H. nitidum* Lam." (notes in Gray's handwriting, GH). An isotype of this taxon (GH) is comparable to many specimens of *H. nitidum* from Florida and Georgia.

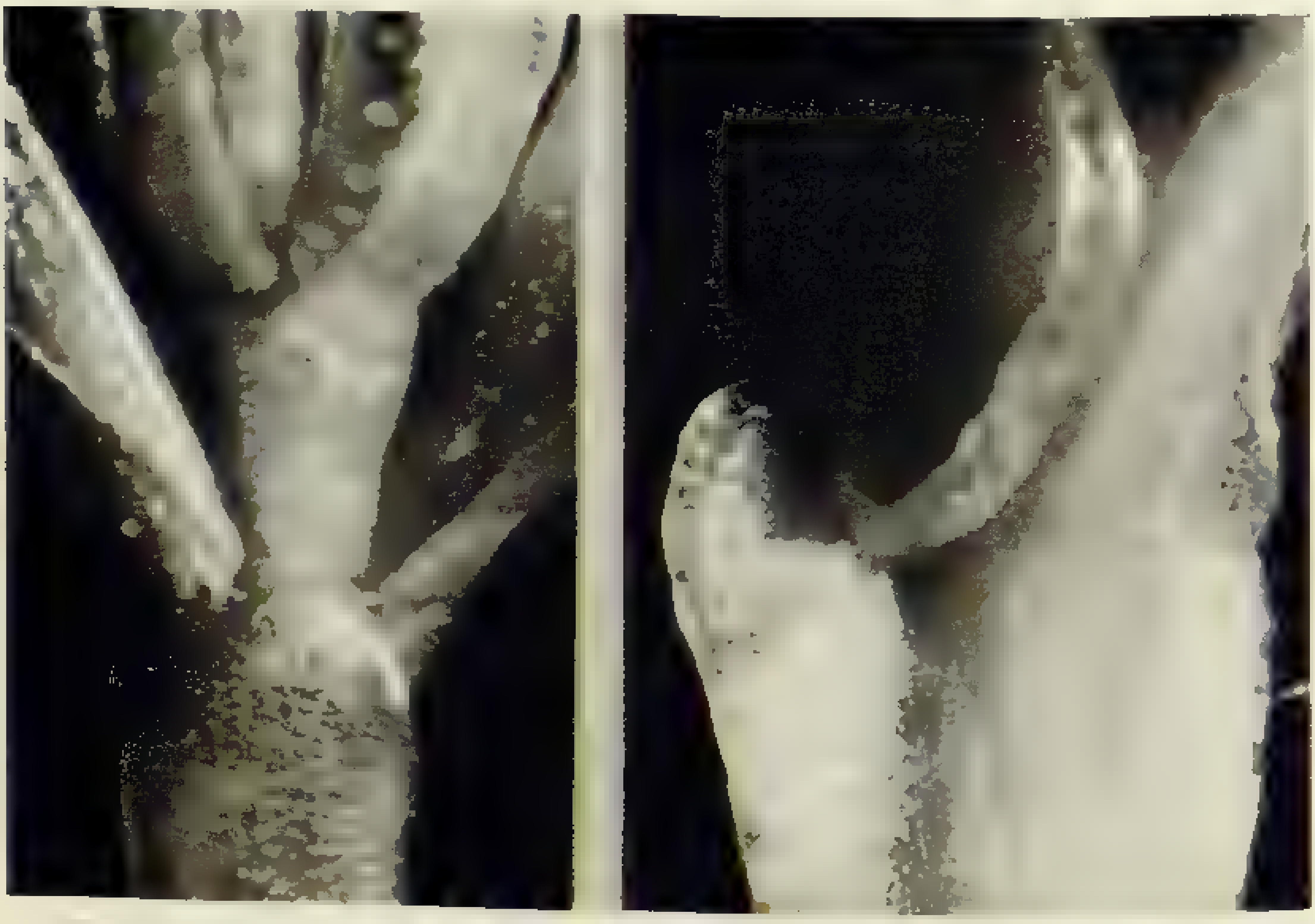
11. **Hypericum brachyphyllum** (Spach) Steud., Nomencl. 1:787. 1840

Based on *Myriandra brachyphylla* Spach, Hist. Nat. Vég. 5:435. 1836.

Hypericum limosum Grisebach [?], Cat. Pl. Cub. 39. 1866, see discussion below.

TYPE: FLORIDA, Apalachicola, *Drummond* (Isotypes, GH; K, two sheets, not seen).

REPRESENTATIVE SPECIMENS: ALABAMA: Covington Co., 7.4 miles south of Opp, *Shinners 27453* (FSU). FLORIDA: Calhoun Co., 2.5 miles south of Blountstown, *Godfrey 57582* (FSU); Franklin Co., west of Apalachicola, *Adams 309* (FSU); Levy Co., 14 miles south of Chiefland, *Adams 388* (FSU); Santa Rosa Co., 6 miles east of Munson, *Kral & Redfearn 2946* (FSU); Wakulla Co., 1 mile north of St. Marks, *Godfrey 57862* (FSU). GEORGIA: Coffee Co., 8 miles east of Douglas, *Adams 830* (FSU, GA); Early Co., 9 miles southeast of Blakeley, *Adams 791* (DUKE, FSU, GA, USF). MISSISSIPPI: Jackson Co., Ocean Springs, *Demaree 32846* (FSU).



FIGS. 1-2. Morphology of the leaf and sepal bases in *Hypericum* Sect. *Myriandra*. FIG. 1. Left. *Hypericum brachyphyllum* (Spach) Steud. *below*, bases of two opposite leaves, each with a conspicuous articulation or groove at the junction with the stem. *Above*, bases of the sepals (two visible), each with an articulation at the junction with the receptacle. FIG. 2. *Right*. *Hypericum nudiflorum* Michx., base of one leaf. Note the complete absence of an articulation. Magnification ca. 10X

Abundant in low pine flatwoods, pond margins, borrow pits, and roadside ditches, especially in the Florida Panhandle region and scattered stations along the Florida west coast to Collier County, westward into southern Mississippi, northward into lower Alabama and Georgia. Flowering late June through early September, occasionally sporadically to late November, or later in southern Florida.

Plants of *Hypericum brachyphyllum* characteristically possess a rounded bushy aspect due to the production and retention of numerous branches from the upper three-fourths or one-half of the stem. The height is usually about 0.5 to 1.0 m although occasional individuals may reach 1.5 m. Stem diameter near the base rarely exceeds 1.5 cm. The bark is relatively thin and tight, being composed of alternating strata of cork cells and thread-like laticifers, and exfoliates in small plates of strips, the whole presenting a dark reddish or brownish appearance.

Although plants of *Hypericum brachyphyllum* often grow in close association with individuals of *H. nitidum*, *H. exile*, *H. fasciculatum*, *H. chapmanii*, and *H. reductum*, no intergradation has been observed. Since it was described by Spach in 1836 few, if any, authors have recognized the biological distinctiveness of this species. Coulter (1897) included it within his concept of *H. fasciculatum*. Chapman (1897), who knew the species in the type region, referred it to *H. aspalathoides* Willd. I cannot be certain that Chapman also knew the related *H. reductum* which grows along the coast in the Apalachicola area. If so, then he did not distinguish between them. Small's treatments (1903, 1913, 1933) were essentially the same as that of Chapman. Svenson (1940) made no mention of the plants now referred to *H. brachyphyllum* but he did recognize *H. reductum* (as a variety of *H. galioides*, however). He demonstrated also that *H. aspalathoides* Willd. was merely a re-naming of *H. fasciculatum* Lam.

That the plants of *Hypericum brachyphyllum* are amply distinct from those of *H. reductum* has become evident to me from field observations extending over the past two years. In addition to the features listed in the key, each of these two species possesses different (although slightly overlapping) flowering periods, geographic ranges, and habitat preferences. Plants of *H. reductum* begin to flower earlier than do those of *H. brachyphyllum*. Flowers appear on plants of the former species in late April in southern peninsular Florida and early June in western Florida. However, those of the latter species do not begin to flower until the last week of June (except for sporadic individuals, especially in the southern portion of its range). Furthermore, the length of the flowering period is different in these two species. That of *H. reductum* is usually completed by the first of July whereas that of *H. brachyphyllum* extends through August. There is a tendency for plants of both species to produce a second crop of flowers during the fall but this phenomenon is much more pronounced in the latter.

Each of these species has different habitat preferences, the plants of *Hypericum reductum* being adapted to somewhat drier sites than those of *H. brachyphyllum*. Ecology, no doubt aided by past geological events, has influenced the creation of the distinctive distributional patterns which are discernible in these species. The geographic range of *H. reductum* appears to be composed of four isolated segments (see below). In each of these, there seems to be a relationship between the present distribution and the presence of recent or fossil sand dunes. The distributional pattern presented by plants of *H. brachyphyllum* is more or less continuous instead of being fragmented. The present distribution does not show any relationship with coastal physiography, the plants growing in low wet pinelands inland from the ocean.

Additional evidence supporting my interpretation of specific status for each of these two taxa has been obtained by observations on sympatric populations. During the course of my field studies I have encountered three widely separated stations where plants of both species were growing in close association. Two of these occurrences are in southeastern Georgia, one being three miles south of Pembroke in Bryan County, and the other about four miles west of Eulonia in McIntosh County. The third sympatric association is in Franklin Co., Florida, about five miles east of Eastport. At each of these places plants of each species were immediately and easily distinguishable, even though growing within a few feet of each other. The habitat differences were maintained at each site also, with *H. reductum* plants on the slightly drier and better drained soils. Further analysis of population samples made at these stations is in progress.

Grisebach's *Hypericum limosum*, type: *Wright 2125* (GH, NY), appears to be closest to *H. brachyphyllum*. However, better specimens must be available before a definitive interpretation can be made.

12. **Hypericum reductum** P. Adams, stat. & nom. nov.

Based on *Hypericum fasciculatum* Lam. var. *aspalathoides* T. & G., Fl. N. Am. 1:672. 1840, not *H. aspalathoides* Willd., Sp. Pl. 3:1451. 1803, nom. superfl.

Hypericum fasciculatum Lam. var. β T. & G., Fl. N. Am. 1:160. 1838.

Hypericum galioides Lam. var. *reductum* Svenson, Rhodora 42:14. 1940, nom. superfl. for var. *aspalathoides* T. & G.

TYPE: North Carolina, Wilmington, *Curtis* (Lectotype, GH; isotype, NY, fragment). Cited by Torrey & Gray (1838) under their description of *H. fasciculatum* var. β.

ILLUSTRATION: Svenson, 1940, plate 587, figure 5.

REPRESENTATIVE SPECIMENS: FLORIDA: Bay Co., Panama City Beach, *Godfrey & Triplett 59815* (FSU); Franklin Co., Alligator Point, *Adams 298* (DUKE, FSU, VDB); Highlands Co., Hicoria, *Adams 402* (DUKE, FLAS, FSU, GH, USF); Lake Co., 4 miles north of Altoona, *Adams 599* (F, FSU, GH, MO); Marion Co., 1 mile east of Lynne, *Adams 610* (FSU, GA, GH); Oklaloosa Co., 4 miles east of Ft. Walton, *Thorne & Davidson 17336* (FSU). GEORGIA: Bryan Co., 2.6 miles west of Pembroke, *Adams 540* (FSU); Bulloch Co., 17 miles southeast of Statesboro, *Adams 535* (FSU, GA, GH, NY); Evans Co., 5.2 miles west of Claxton, *Adams 544* (FSU); Tatnall Co., 3 miles northwest of Reidsville, *Cronquist 5342* (FLAS, GA, GH, NY, SMU, US). NORTH CAROLINA: New Hanover Co., Carolina Beach, *Godfrey 1260* (BKL, DUKE, FLAS, GA, GH, MO, NCU, NCSC, NY, SMU, TENN, US).

The range of *Hypericum reductum* appears to be composed of four allopatric segments. In the Wilmington region of southeastern North Carolina plants of this species grow among the dunes and dune hollows along the coast. Several stations are also known further inland in that area. It is very abundant over many acres of longleaf pine, scrub-oak sand ridge between Wilmington and Southport (R. K. Godfrey, personal commuication). A second segment occurs in the triangle formed by the towns of Swainsboro, Jesup, and Savannah, Georgia. Here the plants grow on the sands of fossil dunes (e.g. east side of the Canooche River, 8 miles east of Pembroke, Bryan Co.) and on the sandy soil of dry pinelands, roadside embankments, and borrow pits. The third population occurs in central peninsular Florida from Putnam County (east of Gainesville) southward to Highlands and Charlotte counties. The fourth portion of the range is along the coast of the Gulf of Mexico from Franklin Co., Florida, westward to Escambia County. In nothern Bay and southern Washington counties, Florida, *H. reductum* grows in the sandy soil on the shores of sinkhole ponds and lakes, its branches frequently touching the bases of *H. lissophloeus* plants. The former species also occurs in close association with plants of *H. fasciculatum*, *H. chapmanii*, and *H. brachyphyllum.* Flowering late April through late June in central and southern Florida, occasionally sporadically earlier in the spring or the fall; during June and occasionally July and November in western Florida; mid-June through late July in Georgia; and early June through mid-August in North Carolina.

Plants of *Hypericum reductum* possess a low, decumbent, matted aspect, especially when growing among the loose sands of dunes and dune hollows. In dense stands of grasses, palmetto, gallberry, and other plants an erect habit may be formed but a reclining and straggly tendency is still retained. Other features include the short leaves, four well-developed secondary wings on the young stems, and the straight-sided, elongated, mature capsules.

Svenson (1940), following Torrey & Gray (1838), cited *Hypericum tenuifolium* Pursh (Fl. Am. Sept. 2:377. 1814) as a synonym of *H. galioides* var. *reductum.* Pursh's description could be interpreted as fitting either *H. lloydii* or *H. reductum.* The specimen which he cited (collected "In Georgia" by Enslen) is not present in the Enslen Herbarium at Vienna (K. H. Rechinger, personal communication). A fragment of an Enslen collection of *Hypericum* is at Philadelphia but there is no indication on the sheet that it represents the same collection cited by Pursh. This specimen is definitely *H. reductum.*

✓ 13. **Hypericum lloydii** (Svenson) P. Adams comb. nov.

Based on Hypericum *galioides* Lam. var. *Lloydii* Svenson, Rhodora 54:207. 1952.

TYPE: SOUTH CAROLINA: Aiken Co., Graniteville, *Eggert* in 1898 (Holotype, NY; isotypes, MO, US).

ILLUSTRATION: Svenson, 1940, plate 587, figure 8.

REPRESENTATIVE SPECIMENS: ALABAMA: Tallapoosa Co., *Harper 3691* (GH, PH, US). GEORGIA: Richmond Co., August, *Cuthbert* July 17, 1899 (FLAS, NY). NORTH CAROLINA: Granville Co., Oxford, *Gillespie 394* (DUKE, FSU, NCSC). SOUTH CAROLINA: Lancaster Co., Elgin, *House 2568* (MO, NY, US).

Abundant on the sandy soil of scrub oak-longleaf pine sandhills, dry woods borders, granite outcrops, and roadside embankments along the Fall Line in the Carolinas; also Richmond and Heard counties of Georgia and Chilton (Harper, 1928) and Tallapoosa counties, Alabama. Flowering early June through mid-July, occasionally to late August.

A low rounded or straggly growth form, fairly long and narrow leaves, and short widened mature capsules with tapering sides mark *Hypericum lloydii*. This distinctive plant is related to the other members of the *H. fasciculatum* complex but it is not known to grow in association with any of them.

The range of this species is essentially isolated from other members of the *Hypericum fasciculatum* group. In North Carolina its range approaches that of *H. reductum* within a county or two but plants of the two species have not been discovered growing together. Nevertheless, I believe that the taxonomy of the group can be best understood by recognizing *H. lloydii* as a species. Morphologically it is as distinct as any of the other members of this complex.

14. **Hypericum exile** P. Adams, sp. nov.

Frutex exilis, pauci-ramosus, usque ad 1 m altus vel raro altior, usque ad 1 cm in diametro. Cortex tenuis, in laciniis vel segmentis parvis irregularibus decorticans. Folia basi articulata, patentia, lineari-subulata, lamina vix expansa, valde et carnoso-marginata, margine siccitate maxime involuta, (10-) 16-26 mm longa, 0.5-0.8 mm lata, apice longiacuminata, subtus obscure papillata, ramulis axillaribus haud conspicuis. Incrementa determinata, plerumque dichasis similibus in 3-6 nodis superioribus; inflorescentia compacta, paniculoidea. Sepala basi articulata, lineari-subulata, 6-7 mm longa, 0.5-0.8 mm lata, apice longiacuminata, ante capsulae dehiscentiam decidua. Petala flava, asymmetrica, 6-7 mm longa, 3-4 mm lata. Stamina 80-100, 5-7 mm longa. Gynoecium 4.5-7 mm longum, 3- (raro 2 vel

4) carpellatum, placentatione parietale, cum 3 (raro 2 vel 4) stylis. Capsula matura 6-7 mm longa, 1.5-2.5 mm lata. Semina rufo-brunnea, carina minuta, 0.4-0.6 mm longa, testa subtiliter reticulata.

Slender, sparingly-branched shrub, rarely over 1 m tall and usually less than 1 cm thick. Bark thin, exfoliating in small irregular flakes or strips. Leaves articulate at base, spreading, linear-subulate or needle-like, lamina poorly developed, edges thickened and turned abruptly downward (inrolled on drying), (10-) 16-26 mm long, 0.5-0.8 mm wide, apices long-acuminate, lower surface obscurely papillate, axillary branchlets poorly developed. Shoots terminating in a 3-7 flowered dichasium, usually with similar dichasia from upper 3-6 nodes, inflorescence compact, panicle-like. Sepals articulate at base, linear-subulate or needle-like, 6-7 mm long, 0.5-0.8 mm wide, apices long-acuminate, deciduous before fruit maturity. Petals yellow, asymmetrical, 6-7 mm long, 3-4 mm wide. Stamens 80-100, 5-7 mm long. Gynoecium 4.5-7 mm long, carpels 3, rarely 2 or 4, placentation parietal, styles 3, rarely 2 or 4. Mature capsules 6-7 mm long, 1.5-2.5 mm wide. Seeds reddish-brown, raphe poorly developed, keel minute, 0.4-0.6 mm long, 0.2-0.3 mm wide, seed coat finely reticulate. Specific epithet from Latin meaning "slender."

TYPE: FLORIDA: Gulf Co., 2.5 miles east of Port St. Joe, *Adams 456* (Holotype, GH; isotypes, DUKE, FLAS, FSU, GA, K, MO, NCSC, NCU, NY, SMU, US).

REPRESENTATIVE SPECIMENS: FLORIDA: Franklin Co., 10 miles west of Apalachicola, *Adams 473* (FSU); Gulf Co., 3 miles east of Jort St. Joe, *Adams 740* (FLAS, FSU, GA, GH, SMU); Liberty Co., 6 miles north of Wilma, *Adams 485* (FSU).

Known only in the sandy soil of open pinelands, Liberty, Franklin, Gulf, Bay, and Washington counties, Florida. Flowering throughout May.

Plants of *Hypericum exile*, as the epithet suggests, are slender, with a single stem which dichotomizes 25-40 cm above the ground. The inflorescence is relatively narrow and compact, with a panicle-like aspect. Leaf length, seemingly long for such a small slender plant, is strikingly reminiscent of *H. lloydii*. This hitherto undescribed species occurs in close association with *H. fasciculatum*, *H. chapmanii*, *H. brachyphyllum*, and *H. nitidum* but they do not intergrade.

15. **Hypericum myrtifolium** Lam., Encyc. Méth. Bot. 4:180. 1797. Not Spach, Hist. Nat. Vég. 5:399. 1836.

Hypericum rosmarinifolium Lam., Encyc. Méth. Bot. 4:159. 1797.

Hypericum glaucum Michx., Fl. Bor.-Am. 2:78. 1803.

Hypericum sessiliflorum Willd. ex Spreng. Syst. Veg. 3:346. 1826.

Myriandra glauca (Michx.) Spach, Hist. Nat. Vég. 5:442. 1836.

TYPE: P-LA; photograph, GH.

REPRESENTATIVE SPECIMENS: FLORIDA: Duval Co., near Jacksonville, *Curtiss 265* (BKL, F, GH, NY, PH, US); Lake Co., Eustis, *Nash 708* (A, MICH); Leon Co., 4 miles south of Tallahassee, *Adams 581* (FLAS, FSU). GEORGIA: 6 miles east of Adel, *Adams 47* (GA).

Sandy and peaty soil on the margins of evanescent ponds, in moist pine flatwoods, grass-sedge bogs, and low roadside ditches on the Coastal Plain of Georgia (nearly to the Fall Line), most of peninsular Florida, and westward to Jackson Co., Mississippi. Flowering mid-May through late July, occasionally also in October.

This is the only species of Subsect. *Centrosperma* in which the plants have clasping leaves. Other distinctive features include the glaucous sepals, leaves, and young stems, gnarled and woody caudex-like rootstock, moderate development of a corky bark, subcoriaceous, ovate, elliptic-ovate, or cordate-lanceolate leaves, and pyramidal-ovoid, strongly triquetrous, black, glossy-shiny mature capsules. It is superficially similar to *H. tetrapetalum* (Subsect. *Pseudobrathydium*), both having clasping leaves, and is often confused by the casual observer. Besides its articulated leaves and sepals, *H. myrtifolium* is readily distinguished from this species by a pentamerous perianth, spongy-thickened bark, and compound dichasial inflorescences.

Usage has firmly established the epithet *Hypericum myrtifolium* over *H. rosmarinifolium* (both published by Lamarck in his 1797 work).

Sect. MYRIANDRA, subsect. PSEUDOBRATHYDIUM Keller, in

Engler & Prantl, Pflanzenfamilien, 3 (6-6a) 214. 1895, excluding description.

Hypericum, Sect. *Myriandra*, Subsect. *Brathydium* (Spach) Keller, *l. c.*, based on *Brathydium* Spach, Hist. Nat. Vég. 5:442. 1836, as a genus.

Hypericum, Sect. *Myriandra*, Subsect. *Suturosperma* Keller, *l. c.*,

Hypericum, Sect. *Isophyllum* (Spach) Coulter, Bot. Gaz. 11:82. 1886, based on *Isophyllum* Spach, Hist. Nat. Vég. 5:432. 1836, as a genus.

Ascyrum L., Gen. Pl. ed 5. 342. 1754 (excluding *A. filicaule* Dyer), as a genus.

Hypericoides Adanson, Fam. Pl. 2:443. 1763, as a genus.

Crookea Small, Fl. Southeastern U. S. 786, 1335. 1903, as a genus.

Shrubs and perennial herbs. Leaves and sepals without an articulation or groove at the base (Fig. 2). Sepals 5 or 4, persistent long after fruit maturity (deciduous in *H. nudiflorum*). Petals 5 or 4. Withered stamens persistent long after anthesis (except in *H. nudiflorum* and *H. apocynifolium*).

TYPE SPECIES: *H. buckleyi* M. A. Curtis.

Fifteen species distributed mostly in the central and southern United States.

16. **Hypericum nudiflorum** Michx., Fl. Bor.-Am. 2:78. 1803

Hypericum mediflorum Darby, Man. Bot., part 2, 35. 1841.

TYPE: "Hab. in Carolina. Goose Creek, Berkeley Co., [South Carolina?]," P; photograph, GH.

REPRESENTATIVE SPECIMENS: ALABAMA: Etowah Co., Gadsden, *Vasey 385* (F, GH, NY, PH, US). FLORIDA: Wakulla Co., *Godfrey 57135* (FSU, GH). GEORGIA: Elbert Co., 11.9 miles west of Elberton, *Duncan 11699* (GA, NCSC). NORTH CAROLINA: Ware Co., 3 miles south of Raleigh, *Godfrey 4617* (DUKE, GH). TENNESSEE: Sequatchie Co., west of Dunlap, *Svenson 9554* (BKL, DUKE, MO, PH, TENN). VIRGINIA: Princess Anne Co., Macon's Corner, *Fernald & Long 4943* (A, NY, US).

Locally abundant on stream banks and in rich deciduous woods, southeastern Virginia, the inner Coastal Plain and outer Piedmont in the Carolinas, the Piedmont of Georgia, the Cumberland Plateau of Tennessee, the Panhandle of Florida, and westward to southern Mississippi. Flowering early June through late July, occasionally in late August.

Closely related to the following species.

17. **Hypericum apocynifolium** Small, Bull. Torrey Club 25:616. 1898

TYPE: TEXAS, Texarkana, *A. A. Heller* August 1897 (Lectotype, NY).

REPRESENTATIVE SPECIMENS: LOUISIANA: DeSoto Parish, 2 miles west of Hunter, *Correll & Correll* 10178 (DUKE, GH). ARKANSAS: Drew Co., Monticello, *Demaree 16231* (NY). GEORGIA: Decatur Co., Butler's Creek, *Thorne & Davidson 17211* (GA).

Stream banks and moist woods, widely scattered localities, southern Arkansas, western Louisiana, extreme northeastern Texas, the Flint River drainage in extreme southwestern Georgia, and the Apalachicola River bluffs in Gadsden Co., Florida. Flowering in June.

Vegetatively, plants of *Hypericum apocynifolium* cannot be distinguished from those of *H. nudiflorum*. The differences listed in the key, i.e. simpler inflorescence, larger fruit, and better-developed keel on the seed, are constant. Pending acquisition of additional specimens and further study, I think this taxon merits continued recognition as a species.

Svenson's conception of this species included several diverse elements (Svenson, 1940). One of the collections which he cited (*R. M. Harper 1755*, NY) is referable to *H. frondosum* Michx. A second collection (*R. M. Harper 1501*, NY, US) comprises plants of *H. myrtifolium* Lam. Finally, the Leavenworth specimens (NY) cited by Small in the original description of *H. apocynifolium* belong to that species and not to *H. lobocarpum* Gattinger, as Svenson believed.

18. **Hypericum buckleyi** M. A. Curtis, Am. Jour. Sci. 44:80. 1843 [as *Buckleii**]

TYPE: "In montibus Carolinae et Georgia," *S. B. Buckley*

---

*This species was named in honor of its discoverer, S. B. Buckley. Since classical Latin lacks the letter y, Curtis was correct in changing this letter to an . However, later authors, including Chapman, Small, and Svenson, used the spelling adopted here. As I interpret Art. 73 of the Code, both forms are correct (see the first and second paragraphs). Majority usage seems in favor of the spelling adopted in the present study.

(Lectotype, GH; isotype, NY, in less satisfactory condition).

REPRESENTATIVE SPECIMENS: GEORGIA: Rabun Co., Rabun Bald, *Pyron & McVaugh 895* (GA, US). NORTH CAROLINA: Haywood Co., Mt. Pisgah, Bilt. Herb. no. 1319 (A, GH, MO, NCU, US, WIS); Macon Co., Highlands, Bilt. Herb. no. 1319b (F, MICH, NCSC, NY, PH). SOUTH CAROLINA: Greenville Co., 1 mile from Caesar's Head, *Canby* June 15, 1881 (A, F, MO, NY, PH, US).

Endemic to the Blue Ridge Mountains of southwestern North Carolina and adjacent Georgia at high elevations (3,000 to 5,000 feet). Usually in seepage areas and moist crevices, sometimes along road embankments and ditches. Among the North Carolina stations are Cold Mt., Mt. Pisgah, Sassafrass Mt., Satulah Mt., Standing Indian Mt., Thomas Bald, Wayah Bald, and Whitesides Mt. The only known Georgia localities are Blood Mt., Brasstown Bald, Hightower Bald, and Rabun Bald. Also near Caesar's Head in Greenville Co., South Carolina. Flowering early June through mid-July.

Hypericum buckleyi superficially resembles *H. stragulum* in its decumbent growth form, elliptic to obovate leaves, and a tendency for its flowers to be solitary. The former species is readily distinguished by its pentamerous perianths, 3-carpelled gynoecia, and much larger fruit.

19. **Hypericum cistifolium** Lam., Encyc. Méth. Bot. 4:158. 1797

Hypericum opacum T. & G., Fl. N. Am. 1:163. 1838.
Hypericum punctulosum Bertol., Misc. Bot. 13:18. 1853.

TYPE: P-LA; photograph, GH.

REPRESENTATIVE SPECIMENS: FLORIDA: Duval Co., near Jacksonville, *Curtiss 253* (F, GH, MO, PH, US); Franklin Co., Lanark, *Gillespie G10-55-8* (DUKE, FSU, NCSC, SMU): Lee Co., Ft. Myers, *Hitchcock 12* (NY,US). GEORGIA: Miller Co., 1 mile west of Colquitt, *Thorne 5873* (GA, GH, US); Sumter Co., near Leslie, *Harper 441* (A, BKL, F). LOUISIANA: Tangipahoa Parish, 2 miles west of Robert, *Correll 10511* (F, GH, NY, PH). MISSISSIPPI: Harrison Co., Biloxi, *Pollard 1002* (F, GH, MO, NY, US). NORTH CAROLINA: Brunswick Co., *Godfrey 48428* (GA, SMU). SOUTH CAROLINA: Charleston Co., 5 miles northwest of McClellanville, *Godfrey & Tryon 1114* (DUKE, F, GH, MICH, MO, NY, PH, TENN).

Frequent in moist soil of pine flatwoods, seepage slopes, grass-sedge bogs, margins of swamps and marshes, ditches, and road embankments. Coastal Plain, North Carolina southward through peninsular Florida, and westward along the coast of the Gulf of Mexico to eastern Louisiana. Flowering early April, especially in southern Florida, through mid-September, occasionally to mid-October.

Perhaps the most distinctive feature of this species is the peculiarly lobed gynoecium. The carpel walls (between the margins) are greatly indented or depressed, nearly meeting in the center along the ovary axis to produce a trilocular appearance in cross-section. In contrast, the lobed gynoecia of other species in Sect. *Myriandra* are the result of indentation of the carpel margins (with their associated placentae) so that a multilocular aspect is produced.

20. **Hypericum sphaerocarpum** Michx., Fl. Bor.-Am. 2:78. 1803

Brathydium sphaerocarpum (Michx.) Spach, Hist. Nat. Vég. 5:444. 1836.

Brathydium chamaenerium Spach, Hist. Nat Vég. 4:445. 1836.

Brathydium hyssopifolium Spach, Hist. Nat. Vég. 4:445. 1836.

Hypericum chamaenerium (Spach) C. Koch, Hort. Dendr. 66. 1853.

Hypericum turgidum Small, Fl. Southeastern U. S. 788. 1903.

Hypericum sphaerocarpum, var. *turgidum* (Small) Svenson, Rhodora 42:17. 1940.

TYPE: "Hab. in Kentucky. Route de Louisville," *Michaux* (P; photograph, A; sketch from type by H. K. Svenson, GH).

REPRESENTATIVE SPECIMENS: ALABAMA: Morgan Co., Valhermoso Mt., *Harper 39* (A, GH, NY, US); Madison Co. *Canby 14* (NY, type of *H. turgidum* Small). ARKANSAS: Logan Co., *Iltis 5344* (MICH, SMU). INDIANA: Jasper Co., *Friesner 14557* (GA, MO). KANSAS: Osage Co., 3 miles south of Lyndon, *Horr & Franklin E323* (FLAS, IND, NCSC). MISSOURI: Oregon Co., near Thomasville, *Palmer & Steyermark 41694* (A, MO, NY). TENNESSEE: Bedford Co., 5 miles northwest of Shelbyville, *Adams 71* (DUKE, F, FSU, IA, IND, K, TEX, VPI).

Locally abundant on limestone outcrops, in cedar glades, rocky woods, prairie strips along railroads, and sandy stream banks, from southern Ohio southward to the Black Belt region of central Alabama, around the northern rim of the Mississippi Embayment to southwestern Arkansas and eastern Oklahoma, northward to central Iowa, southern Wisconsin, and northern Indiana. Flowering mid-June through mid-August.

Closely related to *Hypericum dolabriforme*, this species is readily distinguished by its nearly equal sepals, smaller number of stamens, and larger seeds. The seed coats are coarsely reticulate, with the transverse striae much better developed than the longitudinal ones. Fewer than eight seeds per capsule are produced by plants of *H. sphaerocarpum* as well as *H. dolabriforme*. All other members of the section have capsules in which numerous seeds are matured.

Much variation in the mature capsule is present in this species. Typically, the fruits are about as wide as long but in some plants the width is greater than the length, producing a depressed-globular form. In others, the capsules are longer than wide. This variation does not appear to be correlated with geography, judging from herbarium specimens. Further investigation is necessary.

21. **Hypericum dolabriforme** Vent., Hort. Cels. 45, t. 45. 1800

Hypericum procumbens Desf. ex Willd., Sp. Pl. 3:1450. 1803.
Hypericum procumbens Michx., Fl. Bor.-Am. 2:81. 1803.
Brathydium grandiflorum Spach, Hist. Nat. Vég. 5:443. 1836.
Hypericum Bissellii Robinson, Rhodora 4:135. 1902. Type: *Bissell 4025* (GH).

TYPE: "Trouvée par Michaux sur les collines très-arides du Kentucky," presumably the Delessert Herbarium, G.

RERESENTATIVE SPECIMENS: GEORGIA: Catoosa Co., 10 miles west of Ringgold, *Cronquist 5614* (GA, GH, IND, MO, NY, PH, SMU, US). TENNESSEE: Bledsoe Co., Pikeville, *Svenson 9354* (BKL, DUKE, PH); Knox Co., *Kearney* July 9, 1894 (F, NCU). KENTUCKY: Wayne Co., Monticello, *Smith & Hodgdon 4013* (F, GH, NY, US); Nelson Co., 12 miles south of Bardstown, *McFarland 50* (IND, MO, NY, PH, TENN, WIS).

Abundant on limestone outcrops, in cedar glades, and dry rocky beds of intermittent streams from north-central Kentucky southward through eastern Tennessee to northwestern Georgia. Flowering mid-June through mid-August, occasionally in early September.

Grossly unequal sepals, a large number of stamens, smaller seeds, and a finer seed coat reticulation are among the characteristics which distinguish *Hypericum dolabriforme* from *H. sphaerocarpum*, its closest relative. While these two species occupy similar habitats and their geographic ranges overlap, especially in Kentucky, they are not known to grow in close association.

22. **Hypericum adpressum** Barton, Comp. Fl. Phila. 2:15. 1818

Hypericum bonaparteae Barton, Fl. N. Am. 3:95. 1823.

Hypericum fastigiatum Elliott, Sketches 2:31. 1821, not HBK, Nov. Sp. & Gen. 5:195. 1821.

Hypericum adpressum, var. *fastigiatum* (Elliott) T. & G., Fl. N. Am. 1:673. 1840. Type: *Elliott* (CHARL).

Brathydium fastigiatum (Elliott) C. Koch, Hort. Dendr. 66. 1853.

Hypericum adpressum, var. *spongiosum* Robinson, Rhodora 4:135-137. 1902. Type: *Kennedy et al* 15 Sept. 1901 (GH).

Hypericum adpressum, forma *spongiosum* (Robinson) Fernald, Rhodora 51:112. 1949.

TYPE: Pennsylvania, "close to the Schuylkill, and not far above Breck's Island," *Barton* (PH).

REPRESENTATIVE SPECIMENS: GEORGIA: Dougherty Co., west of Pretoria, *Thorne 5709* (GA, IA). INDIANA: Jasper Co., 2.5 miles southeast of Tefft, *Deam 45934* (GH, IND). MASSACHUSETTS: Barnstable Co., Flax Pond, *Kennedy, Williams & Fernald 234* (BKL, F, MICH, NCSC, PH, TENN, US, WIS). NORTH CAROLINA: Northampton Co., near Margarettsville, *Heller 1155* (GH, NY, PH). SOUTH CAROLINA: Jasper Co., 1.7 miles south of Tillman, *Ahles 15675* (NCU). TENNESSEE: Coffee Co., south of Manchester, *Svenson 8783* (DUKE, PH, WIS). VIRGINIA: Sussex Co., Stony Creek, *Fernald & Long 10727* (BKL, DUKE, GH, MO, US).

Marshes, pond margins, and wet roadside ditches at widely scattered stations along the Atlantic coast from Cape Cod and Nantucket, Massachusetts, southward through

Long Island, New York, New Jersey, Delaware, southeastern Virginia, northeastern North Carolina, the outer Coastal Plain of South Carolina, Screven and Dougherty counties of Georgia, middle Tennessee, southeastern Missouri, northeastern Illinois, and northwestern Indiana. This distributional pattern is peculiar and unlike any other species of *Hypericum* in eastern North America. Flowering early July through early September.

Hypericum adpressum is closely related to *H. ellipticum* but differs in its much taller and more robust stems, stouter rhizomes, larger leaves, and different placentation (i.e. the placentae project inwardly much less). Spongy-thickened stems, especially in the lower portion, occur on plants growing in standing water. This condition is obviously due to the direct effects of the environment (Bicknell, 1913; Svenson, 1940).

23. **Hypericum ellipticum** Hooker, Fl. Bor.-Am. 1:110. 1830

Hypericum ellipticum, forma *submersum* Fassett, Rhodora 41:376. 1939.

Hypericum ellipticum, forma *foliosum* Marie-Victorin, Nat. Canad. 71:201. 1944.

TYPE: Canada, *Mr. Cleghorn* (Lectotype, K, not seen). The *Todd* and the *Richardson* specimens also cited by Hooker (1830) have not been located.

REPRESENTATIVE SPECIMENS: MARYLAND: Garrett Co., Mountain Lake Park, *Steele 56* (GH, US). MICHIGAN: Chippewa Co., Sugar Island, *McVaugh 8751* (MICH, NCSC). NEW HAMPSHIRE: Cheshire Co., Alstead, *Fernald 338* (F, GH, NY, PH, US). NEWFOUNDLAND: *Fernald & Wiegand 5843* (GH, NY). QUEBEC: Algoma District, *Taylor et al 1349* (GH). NOVA SCOTIA: Yarmouth Co., Kemptville, *Fernald & Linder 21857* (GH, MO, PH, US).

Abundant on pond and lake shores, stream banks, meadows, river flats and sand bars, and swamps, eastern Newfoundland, Nova Scotia, New England, southwestern Pennsylvania, West Virginia, northeastern Tennessee, the Lake Superior region of Wisconsin, Minnesota, and Michigan, and the Georgian Bay area of Ontario. Flowering late June through early September.

This species is closely related to *Hypericum adpressum*. Plants of both taxa have prominent rhizomes, a feature absent in all other members of Sect. *Myriandra.* Floral morphology and the size, color, and testa marking of the seeds are similar also. Each species is easily recognizable by leaf shape and size, placentation, and growth habit.

Tetramerous perianths, red or purplish petals, leaves, and stems, and peculiar submersed aquatic forms with simple stems and round to ovate "feather-veined" leaves (forma *submersum* Fassett; type: *Fassett 19172* WIS) are seen occasionally. Following fruit maturity the axillary branchlets may resume growth, even overtopping the infructescence (forma *foliosum* Marie-Victorin; type: *Marie-Victorin et al 56602,* MT, isotypes, F, GH, MO, PH).

24. **Hypericum microsepalum** (T. & G.) Gray ex S. Watson, Biblio. Index to N. Am. botany 1:456. 1878

Based on *Ascyrum microsepalum* T. & G., Fl. N. Am. 1:157. 1838.

Isophyllum drummondii Spach, Hist. Nat. Vég. 5:432. 1836. Not *H. drummondii* (Grev. & Hook.) T. & G., Fl. N. Am. 1:165. 1838, which is based upon *Sarothra drummondii* Grev. & Hook., Bot. Misc. 3:236. 1833.

Crookea microsepalum (T. & G.) Small, Fl. Southeastern U. S. 786, 1335. 1903.

TYPE: Florida, Apalachicola, *Drummond* (GH).

REPRESENTATIVE SPECIMENS: FLORIDA: Franklin Co., *Adams 125* (FSU); Jefferson Co., *Godfrey 60629* (FSU); Taylor Co., *Adams 807* (FLAS, FSU, GH, K, SMU). Without exact locality, *Dr. Alexander* (NY).

Abundant in low pine flatwoods of the Florida Panhandle from Taylor to Bay counties and northward into southern Georgia (Calhoun and Atkinson counties). Flowering late February through late April, often sporadically in May and November.

The features which mark this distinctive species include the following: a very early spring flowering time, four nearly equal sepals, four large showy petals, a 3-carpellate gynoecium, and parietal placentation. In addition, a tendency exists for some of the flowers on many plants to be pentamerous, with five nearly equal sepals and five petals. Not infrequently other flowers (on these same plants) will show tetramery in their calyces and pentamery in their corollas. The reverse situation is often encountered also.

This phenomenon is general throughout the range of the species and can be considered another distinguishing feature. This unstable floral situation could be interpreted as indicating that the species is undergoing evolutionary transition from the presumably primitive pentamerous condition to the more advanced 4-parted one.

25. **Hypericum stans** (Michx.) Adams & Robson, Rhodora 63:15. 1961

Based on *Ascyrum stans* Michx., Fl. Bor.-Am. 2:77. 1803. *Ascyrum cuneifolium* Chapman, Fl. Southeastern U. S. ed. 2, suppl. 2. 680. 1892. Type: *Chapman 1835* (NY).

TYPE: "Hab. in Va." (Presumably at P).

REPRESENTATIVE SPECIMENS: FLORIDA: Columbia Co., Lake City, *Nash 2489* (F, FLAS, GH, MICH, NCU, OS). GEORGIA: Douglas Co., 2 miles east of Villa Rica, *Cronquist 5559* (GA, NO, NY, PH, SMU, US). KENTUCKY: McCreary Co., *McFarland & James 48* (DUKE, IND, MO, PENN, TENN, WVA). MISSISSIPPI: Jackson Co., Ocean Springs, *Seymour 75* (NCU, SMU, TEX). VIRGINIA: Princess Anne Co., near Virginia Beach, *Heller 1268* (F, GH, NY, PENN, PH, US).

Dry to moist flatwoods, bogs, meadows, bottomlands, roadside ditches, and shores of ponds and lakes. Long Island, New York, southward through New Jersey, eastern Virginia, the Carolinas, to central Florida, westward to eastern Texas and central Arkansas. Also on the Cumberland Plateau through Tennessee into McCreary and Laurel counties of Kentucky (see Adams, 1957, for distribution map). Flowering late July through mid-October, occasionally in June and November.

This species is most closely related to *Hypericum edisonianum*, endemic in south peninsula Florida. The distinguishing features are those presented in the key and further discussed in the treatment of that species (which see).

26. **Hypericum edisonianum** (Small) Adams & Robson, Rhodora 63:15. 1961

Based on *Ascyrum edisonianum* Small, Man. Southeastern Fl 868. 1933.

TYPE: "21 miles east of Arcadia, Florida," *Hand 118* (NY).

REPRESENTATIVE SPECIMENS: FLORIDA: Highlands Co., 21 miles east of Arcadia, *Adams & Testasecca 100* (DUKE, F,

FLAS, FSU, GA, MICH, MO, NCSC, NY, PH); same locality, *Adams 140* (GH); Glades Co., Fisheating Creek, *Brass 14824* (GH).

Locally abundant on sandy soil of low open prairies, lake and pond shores, and roadside ditches, Highlands, Glades, and DeSoto counties, Florida. The known stations are in central and southern Highlands County from Lake Josephine southward to the Venus area and westward along the Arcadia highway (Fla. 70) to about the DeSoto County line. Also collected along Fisheating Creek in adjacent Glades County. Flowering probably throughout the year.

Closely related to *Hypericum stans*, this species may be easily recognized by the characteristics listed in the key. Other features include a much better developed laticifer system in the bark of *H. edisonianum* (especially noticeable on older stems) and the larger and more numerous resin dots in the leaves of *H. stans*.

Dense thickets, often 1.5 m in height, are commonly produced by plants of *Hypericum edisonianum*. A contributing factor is the tendency for numerous vegetative shoots to be produced at frequent intervals along horizontal roots of the plants. This form of reproduction, present in several other species of the section, is not known to occur in the closely related *H. stans*.

The range of *Hypericum edisonianum* appears to be essentially allopatric from that of its relative *H. stans*. The closest known stations of the latter species are at least thirty-five miles to the south (Immokalee in Collier County) and southwest (Ft. Myers in Lee County). Northward the nearest collection of *H. stans* was made at Haines City in Polk County, some sixty miles distance.

27. **Hypericum tetrapetalum** Lam., Encyc. Méth. Bot. 4:153. 1797

Ascyrum tetrapetalum (Lam.) Vail in Small, Fl. Southeastern U. S. 1:785. 1903.

TYPE: "Hab. in Florida." P-LA; photograph, GH.

REPRESENTATIVE SPECIMENS: FLORIDA: Clay Co., 2 miles north of Orange Park, *Moldenke 160* (DUKE, MO, NY, PENN, US); Dade Co., *Small, Mosier & Small 6703* (FLAS, GH, TENN, WVA); Duval Co., near Jacksonville, *Curtiss 245* (F, PH, US); Lake Co., Eustis, *Nash 1977* (DAO, MICH, NCU, PH). GEORGIA:

Irwin Co., 4 miles north of Ocilla, *Wilbur 3074* (FSU, NCSC, SMU); McIntosh Co., Sapelo Island, *Duncan 17970* (GA).

Sandy soil of pine flatwoods, peaty lake and pond margins, marshes, and wet roadside ditches, on the outer Coastal Plain of southeastern Georgia and peninsular Florida; Pinar del Rio, Cuba. Flowering late January (in southern Florida) through late April, occasionally sporadically in July, August, and September.

This species is distinguished from the related *Hypericum stans* by ovate-cordate, clasping leaves which are similar to the sepals and by the dichotomous branching pattern. From the superficially similar *H. myrtifolium* this species can be readily separated by its tetramerous perianth, terete capsules, solitary flowers, and thin, non-corky bark.

28. **Hypericum hypericoides** (L.) Crantz, Institut. rei herbariae 2:520. 1766

Based on *Ascyrum hypericoides* L., Sp. Pl. 2:788. 1753. See Adams (1957) for complete synonymy.

TYPE: "Hab. in Jamaica," *Patrick Browne* (LINN, specimen no. 944.2, designated neotype by Adams in 1957; photograph, GH).

REPRESENTATIVE SPECIMENS: ARKANSAS: Ashley Co., Parkdale, *Demaree 16398* (DAO, NY, OS, PENN, TENN, TEX). FLORIDA: Lake Co., Eustis, *Nash 1609* (F, GH, MICH, MO, NY, US); Manatee Co., *Tracy 7543* (SMU). MISSISSIPPI: Jackson Co., Ocean Springs, *Seymour 91914* (DUKE, NCU, TEX). SOUTH CAROLINA: Berkeley Co., Moncks Corners, *Godfrey & Tryon 8217* (DUKE, GH). BAHAMA ISLANDS: New Providence, *Britton & Brace 842* (F, NY, US). BERMUDA: Paget Marsh, *Brown, Britton & Seaver 1136* (F, GH, MO, PH, US). CUBA: Pinar del Rio, *Shafer & Leon 13616* (F, MO, NY, PH, US). JAMAICA: *Maxon & Killip 1721* (F, GH, US). PUERTO RICO: *Britton, Cowell & Brown 3847* (F, GH, NY, US). GUATEMALA: Dept. of Alta Verapaz, *Tuerckheim 88* (GH, NY, PH, US). MEXICO: Vera Cruz, *Pringle 8515* (F, GH, MO, NY, PH, US).

Abundant in dry sandy soil of open pine woods and sandhills. Also pine flatwoods, creek bottoms, pond, lake, and swamp margins, and hardwood slopes. New Jersey southward through peninsular Florida, westward to southeastern Missouri, eastern Oklahoma, and eastern Texas; the eastern escarpment in Mexico from Nuevo León and Tamaulipas

FIG. [illegible] Left, *Hypericum stragulum* Adams & Robson (*Ascyrum multicaule* Michx.), one plant, branches decumbent. Right, *Hypericum hypericoides* (L.) Crantz (*Ascyrum hypericoides* L.), a single plant with one main stem. Branching well above ground level. Hall. Co., Ga., ca. 8 miles west of Flowery Branch. (Photograph by courtesy of Dr. Wilbur H. Duncan.)

southward to Chiapas and the mountains of Guatemala and Honduras; Bermuda, the larger Bahamas, Cuba, Jamaica, Hispaniola, and Puerto Rico (see Adams, 1957, for distribution map). Flowering late June through late October (at least in the United States).

Geographically the most widespread and occupying the most diverse range of habitats, plants of *Hypericum hypericoides* nonetheless retain the facies characteristic of the species. Considerable variation is present in the leaf and sepal dimensions but this appears to be simply a response to habitat differences (Adams, 1957). An erect bushy growth form, two large outer sepals and two minute inner ones, four pale yellow, nearly symmetrical, early-falling petals, and a 2-carpelled gynoecium distinguish this species. Its closest relative is *H. stragulum* (*Ascyrum multicaule* Michx.), the erect growth form being the principal discernible difference (see Fig. 3).

29. **Hypericum stragulum** Adams & Robson, Rhodora 63:15. 1961

Based on *Ascyrum multicaule* Michx., Fl. Bor.-Am. 2:77. 1803, not *Hypericum multicaule* Lam., Encyc. Méth. Bot. 4:178. See Adams (1957) for complete synonymy.

TYPE: "Hab. in Va., Carolina." P; photograph, GH.

REPRESENTATIVE SPECIMENS: ARKANSAS: Cross Co., Crowley's Ridge, *Demaree 19579* (GH, MO, OKL, TENN). ILLINOIS: Pope Co., Golconda, *Palmer 16698* (NY, PH). KANSAS: Cherokee Co., *Hitchcock 1012* (MICH, US). MISSOURI: Ozark Co., Tecumseh, *Palmer 32882* (GH, MO). NORTH CAROLINA: Jackson Co., *Godfrey & O'Connell 51631* (DUKE, NCSC). TENNESSEE: Knox Co., Knoxville, *Ruth* July 1895 (F, GH, MO). TEXAS: Henderson Co., Eustace, *Lundell & Lundell 9574* (GH, MICH, NY, SMU). WEST VIRGINIA: Cabell Co., *Gilbert 548* (DUKE, F, PENN, PH, SMU, TENN, WVA).

Common on dry rocky slopes, road embankments, and moist rich woods, from Nantucket Island, Massachusetts, southward on the Coastal Plain to southeastern Virginia, the Piedmont of the Carolinas and Georgia, westward into Arkansas, northeastern Texas, Oklahoma, central Missouri, and the glacial boundary in Illinois, Indiana, and Ohio (see Adams, 1957, for distribution map). Flowering early July through early August.

A decumbent, low, matted, rounded growth form distinguishes *Hypericum stragulum* from the closely related *H. hypericoides.* The two species often grow in close association but each is readily identifiable (see Fig. 3). The decumbent habit appears in the seedlings of *H. stragulum.* The erect seedling soon loses its upright position and becomes nearly prostrate. One or more axillary branchlets, usually close to the base of the stem, begin growth and become almost prostrate. However, in young plants of *H. hypericoides* the stem remains erect, eventually producing an erect habit unlike that of *H. stragulum.* These two taxa require further extensive study.

30. **Hypericum suffruticosum** Adams & Robson, Rhodora 63:15. 1961

Based on *Ascyrum pumilum* Michx., Fl. Bor.-Am. 2:77. 1803, not *Hypericum pumillum* Sessé & Moc., Fl. Mexic. ed. 2, 177. 1894.

Ascyrum pauciflorum Nutt., Gen. 2:15. 1818. Not *Hypericum pauciflorum* HBK, Nov. Gen. 5:192. 1822.

TYPE: "Hab. in Georgia." Presumably at P.

REPRESENTATIVE SPECIMENS: FLORIDA: Columbia Co., Lake City, *Nash 2211* (GH, MICH, MO, NY, US); Duval Co., near Jacksonville, *Curtiss 246* (F, FLAS, PH). GEORGIA: Brooks Co., 3 miles northeast of Pavo, *Adams 37* (GA). MISSISSIPPI: Harrison Co., Biloxi, *Tracy 4489* (F, MICH, MO, NY, OS, US). SOUTH CAROLINA: Colleton Co., 11 miles northwest of Walterboro, *Adams 84* (FSU).

Dry sandy soil of pinelands on the Coastal Plain of southern Georgia, northern and western Florida, southern Alabama, and southern Mississippi. Also St. Tammany Parish, Louisiana, Bladen Co., North Carolina, and Berkeley and Beaufort counties of South Carolina (see Adams, 1957, for distribution map). Flowering mid-March through mid-June.

Morphologically, plants of this species exhibit more reduction than any other member of Sect. *Myriandra.* The low, inconspicuous habit, early-falling petals, obsolete or nearly absent inner pair of sepals, bicarpellate gynoecia, and relatively small leaves are all interpreted as evidences of extreme reduction. Although morphologically a well-isolated species, *Hypericum suffruticosum* is related to *H. stragulum (Ascyrum multicaule)* and, to a lesser degree, *H. hypericoides.*

The elongate pedicels which become reflexed soon after anthesis and the position of the bractlets at the pedicel base are among the features which serve to distinguish *H. suffruticosum* from these two species.

DUBIOUS AND REJECTED EPITHETS

Brathys prolifica Payer, Trait. Organog. Vég. Comp. Fl. 8, t. 1, 1857. This name may refer to *Hypericum prolificum* L. It was applied by Payer to a plant which he used in studies on the ontogeny of the *Hypericum* flower. It is doubtful if he intended to provide a formal taxonomic treatment of a new species or even a new combination.

Hypericum fulgidum Raf., Fl. Ludov. 88. 1817, description; Herb. Raf. 55. 1833, name. This epithet may refer to *H. fasciculatum* Lam. but the description is insufficient for a definite determination.

Hypericum rostratum Raf., Fl. Ludov. 88. 1817. Rafinesque furnished this name and a Latin description for a *Hypericum* which Robin (1807) had seen on his travels in Louisiana. These two descriptions suggest a plant similar to *H. lobocarpum* Gattinger. Since there is no type specimen and since Rafinesque received his information indirectly, the possibility of error in transcription must be considered. The best interests of nomenclatorial stability will be served by rejecting the Rafinesque name in favor of the well-grounded *H. lobocarpum* Gattinger.

Myriandra galioides (Lam.) Spach, Hist. Nat. Vég. 5:437. 1836. Torrey & Gray (1840) listed this name as a synonym of *H. galioides* Lam. The description is too vague for a definite determination.

Myriandra ledifolia Spach, Hist. Nat. Vég. 5:441. 1836. Cited by Coulter (1897) as a synonym of *Hypericum prolificum* L. but the original description is hardly sufficient to make an exact determination.

LITERATURE CITED

ADAMS, W. P. 1957. A revision of the genus *Ascyrum (Hypericaceae)*. Rhodora **59**:74-95.

————. 1959a. The taxonomy of *Hypericum* section *Myriandra (Hypericaceae)*. Unpub. Ph.D. Thesis, Harvard University.

————. 1959b. The status of *Hypericum prolificum*. Rhodora **61**:250-251.

ADAMS, W. P. AND N. K. B. ROBSON. 1961. A re-evaluation of the generic status of *Ascyrum* and *Crookea (Guttiferae)*. Rhodora **63**:10-16.

BICKNELL, E. P. 1913. The ferns and flowering plants of Nantucket. Bull. Torrey Club **40**:609.

CHAPMAN, A. W. 1897. *Hypericaceae*. Flora of the southern United States. Cambridge.

COULTER, J. M. 1886. Revision of the North American *Hypericaceae*. Bot. Gaz. **11**:78-88.

————. 1897. *Hypericaceae* in Gray, Synoptical Flora of North America. Vol. 1, part 1, 282-297.

ELLIOTT, S. A sketch of the Botany of South Carolina and Georgia. **2**:21-35. J. R. Schenck. Charleston.

FERNALD, M. L. 1950. *Guttiferae* in Gray's Manual of Botany. Ed. 8. American Book Co. 1008-1015. New York.

FERNALD, M. L. AND B. G. SCHUBERT. 1948. Studies of American types in British Herbaria. Part II. Some Linnaean Species. Rhodora **50**:167-168.

GILLESPIE, J. P. 1959. The *Hypericaceae* of Tennessee. Castanea **24**:24-32.

GLEASON, H. A. 1952. *Hypericaceae* in the New Britton and Brown Illustrated Flora. **2**:538-544. New York.

HARPER, R. M. 1928. *Hypericaceae*. Economic Botany of Alabama. II. Geological Survey of Alabama, Monograph 9. 270-273.

HOAR, C. S. AND E. J. HAERTL. 1932. Meiosis in the genus *Hypericum*. Bot. Gaz. **93**:197-204.

KELLER, ROBERT. 1925. *Ascyrum* and *Hypericum* in Engler and Prantl, Pflanzenfamilien 2 Aufl. **21**:154-234.

LANJOUW, J. & F. A. STAFLEU. 1959. Index Herbariorum, Part I. The Herbaria of the World. Ed. 4.

LOTT, H. J. 1938. Nomenclatural notes on *Hypericum*. Jour. Arnold Arb. **19**:149-152, 279-281.

MCLAUGHLIN, W. T. 1931. Preliminary reports on the flora of Wisconsin. XIV. *Hypericaceae*. Trans. Wisc. Acad. Sci., Arts, and Lett. **26**:281-288.

MOHLENBROCK, R. H. AND J. W. VOIGT. 1959. A flora of southern Illinois. Southern Illinois University Press. Carbondale.

NIELSON, N. 1924. Chromosome numbers in the genus *Hypericum*. Hereditas **5**:378-382.

PURSH, F. 1814. Flora Americae Septentrionalis. **2**:373-379. White, Cochrane and Co.

REHDER, A. 1940. *Hypericaceae*. Manual of Cultivated Trees and Shrubs. Ed. 2. New York.

ROBIN, C. C. 1807. Flore Louisianaise. Vog. Louis. **3**:88.

ROBSON, N. K. B. 1956. Studies in the genus *Hypericum*. Unpub. Ph.D. Thesis. Edinburgh University.

———————. 1957. The genus *Hypericum* in Africa south of the Sahara, Madagascar, and the Mascarenes. Kew Bull. No. 3, 433-446.

SMALL, J. K. 1903. *Hypericaceae*. Flora of the southeastern United States. 784-791. New York.

——————. 1913. *Hypericaceae*. Flora of the southeastern United States. 784-791. New York.

——————. 1933. *Hypericaceae*. Manual of the southeastern Flora. 866-875.

SVENSON, H. K. 1940. Plants of the southern United States. III. Woody species of *Hypericum*. Rhodora **42**:8-19.

———————. 1952. What is *Hypericum prolificum?* Rhodora **54**:205-207.

TORREY, J. AND ASA GRAY. 1838. *Hypericaceae*. Flora of North America. **1**:155-169.

TAXONOMIC FERN NOTES. II.

PITYROGRAMMA (INCLUDING TRISMERIA) AND ANOGRAMMA

ROLLA TRYON

During studies in *Pityrogramma*, *Trismeria* and *Anogramma*[1] in preparation of treatments of these genera as they may occur in Peru, various matters pertaining to other species, as well as the Peruvian ones, have been assembled. These seem better presented in a separate paper.

Pityrogramma, *Trismeria* and *Anogramma* are all closely related and have been usually maintained as distinct genera. Each of these is adequately separated from allied genera which are *Coniogramme*, *Gymnopteris*, *Bommeria*, *Hemionitis* and *Trachypteris* (Christensen[2]) and, in addition, *Saffordia*, *Paraceterach*, *Cerosora* and *Pleurosoriopsis* (Copeland[3]). My conclusions are to unite *Trismeria* with *Pityrogramma* but to maintain *Anogramma* as distinct from it.

Throughout this paper frequent reference is made to two publications by Karel Domin: "Generis *Pityrogramma* (Link) species ac sectiones in clavem analyticam dispositae", Publ. Fac. Sci. Univ. Charles, no. 88. 1928 and "The hybrids and garden forms of the genus *Pityrogramma* (Link)", Rozpr. II. Tr. Ceské Akad. 38^{4}. 1929. For the sake of brevity these will be referred to as Domin, 1928 and Domin, 1929 respectively.

I. THE GENUS PITYROGRAMMA

Pityrogramma proper consists of some 11 species and closely related to these are three species that evidently represent three isolated and specialized derivatives from it, or from a common ancestor. The species most "typical" of *Pityrogramma* are *P. chrysophylla*, *P. chrysoconia*, *P. dealbata*, *P.* "*Eggersii*", *P. sulphurea*, *P. tartarea* and *P. calomelanos*. These all have concolorous rhizome scales (or if darker and lighter areas are present there is no well defined central stripe); clustered petioles with a groove on their upper side and with two (or in large leaves more) roundish,

---

[1] Supported, in part, by a grant from the National Science Foundation (NSF-G1064).

[2] Christensen, in Verdoorn, Man. Pterid. 538. 1938.

[3] Copeland, Gen. Fil. 1947.

oval to C-shaped vascular bundles; fertile and sterile leaves that are monomorphic or nearly so; a more than 1-pinnate lamina; stalked pinnae; ceraceous indument on the lamina (some variants of *P. tartarea, P. calomelanos* and *P. "Eggersii"* are pubescent or glabrous) and sometimes also on the rhizome, especially at its apex; the veins of the ultimate segments arising from a single basal vascular branch; and distinctive spores (Fig. 2c) that are tetrahedral-globose (or somewhat flattened) and have the exospore with rather broad and dark ridges on a lighter background, the ridges forming prominent rings at the equator and mostly "hieroglyphs" or dots elsewhere (one variant of *P. calomelanos* has nearly smooth spores).

To these species must be added *P. argentea, P. Humbertii, P. ferruginea* and *P. schizophylla.* These are clearly closely related to the species of the "central group" although they differ in some ways from them. *P. argentea,* for example, has spores with the whole exospore dark and with fewer ridges and somewhat tuberculate. (I have seen no material of *P. Humbertii* but it is evidently closely related to *P. argentea*). *Pityrogramma schizophylla* has the lamina glabrous and bears proliferous buds, and *P. ferruginea* has the whole lamina densely and persistently lanate. The characters by which these species depart from those of the "central group" are not striking and together they all form a relatively uniform genus.

In contrast, there are the three specialized species previously mentioned. These also have ceraceous indument on the lamina and two vascular bundles (at least in large leaves) near the base of the petiole. They each depart, however, in several characters from the species of *Pityrogramma* previously mentioned.

Pityrogramma triangularis has the petiole terete, the pinnae are sessile or adnate and the spores are light colored, the exospore has a low, fine and sharply reticulate surface. The rhizome scales have marked light margins beyond the dark sclerotic central stripe.

Gymnogramma Lehmannii has the spores, grooved petiole and rachis and two vascular bundles typical of *Pityrogramma.* However, the lamina is only pinnatisect (Fig. 6a) and the ultimate segments (pinna-segments) are furnished with many veins arising from the costa (Fig. 6b), the petioles are spaced on the rhizome and the vascular bundles near the base of the petiole are elongate S-shaped.

Trismeria trifoliata has the two vascular bundles typical of *Pityrogramma;* they are, however, above the basal portion of the petiole (Fig. 3b), rather C-shaped but with the back of the C curved forward. The lamina architecture is somewhat different, the fertile and sterile leaves are subdimorphic and the spores are light colored with a nearly smooth exospore. These spores are quite similar to those present in one variety of *P. calomelanos* (var. *ochracea*). A relation of this species and *Pityrogramma* is shown by the 4 hybrids (discussed below) between them.

Comparing each of these three species, in their similarities and differences, with *Pityrogramma* it is evident that they represent close relatives of that genus. Two courses are possible for their classification: each may be placed in its own genus or they may all be placed in *Pityrogramma.* The former course would require the recognition of two new genera (one for *P. triangularis* and one for *Gymnogramma Lehmannii*) and this classification would emphasize the differences between them and *Pityrogramma.* However, the similarities must be considered equally and these are more than sufficient to place them all in *Pityrogramma.* Further, if this is done, the diversity of that genus is increased primarily in characters of the lamina architecture and venation, the attachment of the pinnae, and of the shape of the petiole and the vascular bundles. Such diversity can well be accommodated in a single genus, especially when the divergent characters are not correlated in a group of species. Accordingly, I am treating all of these species in *Pityrogramma.*

PITYROGRAMMA Link, Handb. Gewächse, 3:19. 1833

Type species: *P. chrysophylla* (Sw.) Link (*Acrostichum chrysophyllum* Sw.).

Ceropteris Link, Fil. Sp. Cult. 141. 1841, nom. superfl. illegit. Type species: the same as that of *Pityrogramma.*

Trismeria Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 164, t. 14, f. 1, 2. 1852. Type species: *Pityrogramma trifoliata* (L.) Tryon (*T. aurea* Fée, Op. Cit. 165, nom. superfl. illegit.

— *Acrostichum trifoliatum* L.). Copeland's choice[4] of *T. argentea* Fée as the type is surely not as suitable as that of *T. aurea by* Maxon[5], for the latter was not only more fully illustrated by Fée, but unequivocally represents the then well known *Acrostichum trifoliatum* L.

Gymnogramma section *Isgnogramme* Hieron. Engl. Bot. Jahrb. 34:474. 1904. Type species: *G. Lehmannii* Hieron.

AMERICAN SPECIES OF PITYROGRAMMA

From the key and notes which follow it will be evident that I take a very different view of the species of *Pityrogramma* than did Domin.[6] Specifically, I recognize, among the American species sufficiently studied, 10 species where Domin recognized 24. Some comments on the reasons for this treatment will be offered.

The species I recognize are based primarily on characters of the scales of the rhizome and petiole base, the color of the petiole and rachis, the relative development of the two sides of the pinna, the angle of the pinnules to the pinna rachis, the shape of the ultimate segments, the margin and relation of the veins ends to it and the spores. Other characters are the densely lanate lamina (in *P. ferruginea*) and the presence of proliferous buds on the lamina (in *P. schizophylla*). The complexity of the lamina is used as a supporting character in *P. dealbata*, as is the shape of the lamina in some species, and lack of indument in *P. schizophylla*. Indument color, although sometimes mentioned in the key where it may be useful, is not used to define the species. The use of these characters defines species which are consistent with our knowledge of the variability of these plants; and they have ranges (either contiguous or disjunct) which are of a pattern known in other species.

Domin used most of the kinds of characters previously mentioned (although not always the same ones) and also employed a considerable number of others, such as type of indument, color of the ceraceous indument, disposition of the pinnae and their shape, texture, size of segments and of the leaf, revolute or plane margin, spacing of pinnules,

---

[4] Gen. Fil. 76. 1947.

[5] Pterid. in Sci. Surv. Porto Rico & Virg. Isls. 6: 436. 1926.

[6] Domin, 1928.

toothing of segments, and relative length of petiole. Some of these are subject to variation in plants of different sizes, and others to variation under different environmental conditions, correlations which may be seen in large suites of specimens. Others, while evidently more stable, nevertheless do vary in some species to an extent that they can not be relied upon.

The type of indument on the undersurface of the lamina and its color, if ceraceous, has been so overemphasized that some additional discussion of this character is desirable.

The color of the ceraceous deposit on the under surface of the lamina may be of little or no taxonomic importance. It is true that some species such as *P. dealbata* and *P. sulphurea* are known in only one color form, but most others have two or more colors. That the color may easily vary is suggested by reports in the literature of a plant of one color giving rise, by spores, to plants with another color. These reports, however reasonable, must be subject to reservation because of the possibilities of contamination of a "culture" by spores of other kinds of *Pityrogramma.* There are some reports of two colors on a single plant. For example T. Smith[7] discusses a plant of *P. tartarea* with leaves with white wax and one leaf with golden wax. Hooker[8] reports a leaf of *P. calomelanos* with one pinna half white and half yellow. A specimen of *P. calomelanos* (Colombia, *Daniel 292*, US) has the indument on two leaves light yellow-orange and on one it is roseate.

Wax color forms are present but not recognized in the following species or varieties where the color is not correlated with any other character nor with geography: *P. calomelanos* var. *calomelanos* (white, lemon yellow, pale roseate), *P. tartarea* var. *tartarea* (white, cream yellow), *P. chrysoconia* (white, yellow), *P. chrysophylla* (white, bright yellow), *P. trifoliata* (white, yellow) and *P. "Eggersii"* (white, rose).

Some species that most commonly have ceraceous indument on the under surface of the lamina may be sometimes glabrous or pubescent. Species that have pubescent variants are *P. trifoliata*, *P. tartarea* and *P. calomelanos.* The latter rather rarely may be glabrous.

---

[7] Gard. Chron. n.s. 8: 599. 1877.

[8] Gard. Ferns, t. 50, f. 3. 1862.

That the presence and type of indument on the under surface of the lamina may be a "superficial" character is demonstrated by a plant of *P. calomelanos* from Peru.[9] This plant has 10 leaves with the following characters: the three oldest leaves are glabrous, the next one is sparsely ceraceous and the next two are white ceraceous, the following two are pubescent and the youngest two are white ceraceous.

The type and color of indument, nevertheless, are used as the sole characters for the varieties of *P. calomelanos* and of *P. tartarea.* In these species the strong correlation of the character with geography seems to provide it with an importance it would otherwise not have. Even so, with further knowledge, it may not be reasonable to maintain such a treatment.

The extent to which hybridization among the species occurs in nature is not known. Hybrids between *P. trifoliata* and *P. calomelanos* and *P. ferruginea* are proposed in this paper. It is perhaps significant that hybrids have been recognized only with *P. trifoliata* which is an especially distinctive species in its lamina architecture. It is quite possible that the difficulties of definition and identification that exist between *P. calomelanos* and *P. tartarea,* and some other species, may be due to hybridization. However, the rather few "intermediate" plants may as well be ecological or genetic variants of either species. Where two species grow together or in close proximity, the presence or absence of intermediate plants should be confirmed.

KEY TO THE SPECIES OF PITYROGRAMMA

(Four insufficiently known taxa, discussed at the end of the next section, have not been keyed out.)

a. Petiole terete; rhizome scales with a dark, sclerotic central stripe and narrow, thinner, pale margins. (Pinnae, except sometimes the basal pair, adnate to the rachis, the basal ones enlarged.) .... 9. *P. triangularis.*

a. Petiole grooved on the upper side; rhizome scales wholly sclerotic to subsclerotic, concolorous or often with a dark basal or central area. b.

  b. Lamina pinnatisect; pinna-segments entire, about as broad as long, broadly obtuse, with many veins arising from the costa of the lamina. .... 8. *P. Lehmannii.*

  b. Lamina 1-pinnate or more complex; pinnae elongate; veins of the ultimate segments arising from a single basal vascular branch. c.

---

[9] Tingo Maria, *Tryon & Tryon 5242* (GH).

c. Vascular bundles of the petiole (at about 1/3 the distance to the lamina) C-shaped with the back of the C curved forward. .... 7. *P. trifoliata* and hybrids of it.
The species has the pinnae entire, especially the apical ones, to commonly trifoliolate below, or a few to rarely many 5- (very rarely 7-) foliolate. The hybrids have the pinnae with many segments.

c. Vascular bundles of the petiole (at about 1/3rd the distance to the lamina) roundish, oval to C-shaped; pinnae with numerous, pinnately arranged lobes or segments. d.

d. Ultimate segments mostly shallowly (if at all) toothed, pinnately many veined (with a strong midvein), broadest at the base to lanceolate or elliptical; or rarely lacking a midvein (or with a poorly developed one) and obovate to oval. e.

e. Primary rachis and secondary rachises densely and persistently lanate, the petiole similar but sometimes deciduously lanate. .... 6. *P. ferruginea.*

e. Petiole, primary rachis and secondary rachises glabrous, ceraceous or thinly and irregularly pubescent. f.

f. Scales of the apex of the rhizome and the base of the petiole with a long portion one cell wide below the terminal cell. (Spores prominently ridged, the ridges with sharply defined margins). g.

g. Small leaves 1-pinnate-pinnatifid, or bipinnate-lobed only at the very base, large ones to tripinnate; ultimate segments oblong, deltoid, lanceolate, elliptical to long-triangular. h.

h. Pinnae equilateral; pinnules ascending, those on the basiscopic side more strongly so than those on the acroscopic side; scales of the apex of the rhizome and the base of the petiole with a long-conical terminal cell. (Fertile segments with a sterile costular area absent or substantially so, or if present, then a sterile marginal area present that is as broad or broader than the costular one.) .... 1. *P. calomelanos.*

h. Pinnae inequilateral; pinnules, on both sides of the pinna, at nearly right-angles to the pinna-rachis (or in large leaves the tertiary segments so disposed on the pinnule-rachis): scales of the apex of the rhizome and the base of the petiole with a spherical terminal cell. (Rachis and petiole reddish-brown to blackish, the ridges on the upper side of the rachis [or in larger leaves of the pinna-rachis] lighter in color than the rachis proper; absent from the Lesser Antilles). .... 2. *P. tartarea.*

g. Small leaves rather fully bipinnate-pinnatifid, many ultimate segments obovate or oval. (Mexico to Panama). .... 4. *P. dealbata.*

f. Scales of the apex of the rhizome and the base of the petiole with only a short portion one cell wide below the spherical terminal cell. i.

i. Rachis and the upper portion of the petiole (or all of it except the base) straw colored to light brown, the ridges on the upper side of the same color; spores prominently ridged, the ridges with sharply defined margins. .... 3. *P. chrysoconia.*

i. Rachis and petiole reddish-brown to blackish; spores heavily and closely ridged, the ridges with erose margins that give a granular appearance to the spore. (Fertile segments with a sterile costular area present, a sterile marginal area absent, or if present, then only half as broad as the costular one; Porto Rico and the Lesser Antilles). .... 5. *P. chrysophylla.*

d. Ultimate segments usually mostly toothed to deeply laciniate, dichotomously or subdichotomously few-veined (without a midvein), broadly to narrowly flabellate-cuneate. j.

j. Ultimate segments strongly laciniate into 1-veined lobes; indument lacking on the lamina. (Lamina usually bearing proliferous buds, narrowed at the base where the basal pinnae are more or less reduced. .... 12. *P. schizophylla.*

j. Ultimate segments entire and several-veined to deeply cleft into 2- several-veined lobes (these often strongly toothed); ceraceous indument usually present on the under surface of the lamina. l.

l. Basal pinnae reduced; apical pinnules usually strongly ascending; Greater Antilles. m.

m. Rhizome scales brown, firm but not thickened; indument yellow. .... 10. *P. sulphurea.*

m. Rhizome scales atropurpureous, thickened; indument white or rose. .... 11. *P. "Eggersii".*

l. Basal pinnae the largest or nearly so; apical pinnules usually spreading; Africa, Madagascar and Mascarenes. n.

n. Lamina lanceolate or deltoid-elongate with cuneate, emarginate lobes. .... 13. *P. argentea.*

n. Lamina broadly deltoid or pentagonal, segments rounded, not emarginate or cleft. ...... 14. *P Humbertii.*

NOTES ON THE SPECIES OF PITYROGRAMMA

In the following notes, the distribution of the American species and varieties has been taken from the material in the Harvard University Herbarium (A and GH) and in the United States National Herbarium (US).

In some matters of taxonomy, or nomenclature, this study is incomplete or inconclusive: a discussion of these matters is included in the appropriate places. I have tried to include all of the basionyms of species names that have been certainly or probably applied to native plants. Varietal names are given only where they are pertinent to the nomenclature. I have made no attempt to account for the names (in various categories) that have been applied to material of horticultural or presumed hybrid origin.[10]

1. **Pityrogramma calomelanos** (L.) Link, Handb. Gewächse 3:20. 1833

A discussion of the difference between *P. calomelanos* and *P. tartarea* is presented under the latter species.

1a. **P. calomelanos** var. **calomelanos**

Acrostichum calomelanos L. Sp. Pl. 1072. 1753. LINN sheet 1245.19, photo A, GH, is this species; maintained over *A. ebeneum* L. by Lam. Encycl. 1:38. 1783.

Acrostichum ebeneum L. Sp. Pl. 1071. 1753. Lectotype: Sloane, Hist. Jam. t. 53, f. 1. (Jenman, perhaps, made this choice in Jour. Bot. Brit. For. 24:38. 1886. The Sloane figure should stand as the type of *A. ebeneum* because the Linnaean specimen, LINN sheet 1245.14, photo A, GH, is a small plant of *Pityrogramma tartarea*).

Gymnogramma bidentata Presl, Rel. Haenk. 1:18, t. 2, f. 3. 1825, ex char. et icon.

Gymnogramma distans Link, Hort. Berol. 2:53. 1833. A presumably authentic specimen "Hort. Berol. Sept. 1842" det. Link is illustrated by Domin, 1929: t. 7. Link says "Hab. in Brasilia?" and this may be of horticultural origin rather than from a native source.

Gymnogramma calomelanos var. *denudata* Harr. Jour. Linn. Soc. Bot. 16:37. 1877. Isotype: Pebas, Peru, *Steere*, K!, photo GH.

Pityrogramma chamaesorbus Domin, 1928: 6. Type: British Guiana, *Schomburgk 390*, K!, photo GH.

Pityrogramma insularis Domin, 1928: 6. Syntypes: Princes Island, *Barter 1912*; Fernando Po, *Barter*, *Gustav Mann*. Tardieu-Blot, Flor. Madagasc. & Comores Fam. 5, 1: 117. 1958; and Alston, Ferns and Fern Allies W. Trop. Afr. (Fl. W. Trop. Afr., ed. 2, Suppl.), 38. 1959, both reduce this species to *P. calomelanos*.

Pityrogramma distans (Link) Domin, 1929: 49.

---

[10] See Domin, 1929.

Lamina ceraceous beneath, the wax white to pale (lemon) yellow or pale roseate; or rarely the lamina glabrous.

Southern Florida; Greater and Lesser Antilles; Mexico to Panama; French Guiana west to Colombia, Ecuador and Galápagos Islands south to Bolivia and Argentina; Paraguay and Brazil. Widely introduced in the Old World tropics.

1b. **P. calomelanos** var. **aureoflava** (Hook.) Weath. ex Bailey, Man. Cult. Pl. 64. 1926.

Gymnogramma calomelanos var. *aureoflava* Hook. Gard. Ferns t. 50 text. 1862. Of the several specimens cited by Hooker, I would take *Seemann 948* as the one that may best serve as a type but unfortunately I have not seen it. Other specimens may (or certainly do) represent either other species or else the pale yellow variant of *P. calomelanos* which I refer to var. *calomelanos*.

Pityrogramma austroamericana Domin, 1928: 7. (Also Kew Bull. 1929: 221.) Lectotype: Bolivia, *Mandon 1549 bis*, K!, photo GH; isotype, GH! (Five other collections were cited in 1928 and one additional one in 1929).

Pityrogramma calomelanos var. *austroamericana* (Domin) Farw. Am. Midl. Nat. **12**:280. 1931.

Bailey did not properly transfer Hooker's epithet to *P. calomelanos* but C. A. Weatherby, then Editor of the Gray Herbarium Index, accepted the name as cited above in the Index and this may be taken as a correction of Bailey's publication.

Lamina ceraceous beneath, the wax bright yellow to orange-yellow.

Costa Rica; Venezuela, Colombia, Ecuador and Galápagos Islands south to Bolivia and northwestern Argentina; Brazil. Introduced in the Hawaiian Islands, Java and Tahiti. Reported (as *P. austroamericana*) as introduced in Africa by Alston & Schelpe (Jour. So. Afr. Bot. 18:169. 1952).

1c. **Pityrogramma calomelanos** var. **ochracea** (Presl) Tryon, comb. nov. FIG. 1.

Acrostichum caudatum Cav. Descr. 242. 1802. Type: "Panama", *Née*, seen by C. Chr. at MA (Dansk Bot. Ark. 9^3: 10. 1937, where it is figured, in part, t. 2, f. 4-5.). I believe that this name belongs here (much less likely it is *P. tartarea* var. *Jamesonii*), and that it was obtained in Andean South America rather than in Panama.

Gymnogramma ochracea Presl, Rel. Haenk. **1**:17. 1825. Type: Peru, *Haenke*, PR (Herb. no. 24360), photo GH, US; probable isotypes, K, fragment NY!, B, fragment, NY!

Gymnogramma adiantoides Karst. ex Mett. Ann. Sci. Nat. V, 2:212. 1864. Syntypes: Colombia, Bogotá, *Karsten*, B!, photo GH, fragment NY!; Colombia, Caqueza, 1700 m., *Triana 606*, duplicate: BM, photo and fragments US!

Gymnogramma Hookeri J. Sm. ex Hook. & Bak. Syn. Fil. 381. 1868. Syntypes: Colombia, *Purdie*, fragment NY!; Colombia, *Schlim 609;* Bolivia, *Mandon 1547.*

Gymnogramma Ballivianii Rosenst. Fedde Repert. **6**:314. 1909. Type: Bolivia, *Buchtien 1038*, S-PA! fragment ex Rosenst. US! (*Steinbach 8507*, *Buchtien 35* and other specimens commonly so named are the same).

Ceropteris adiantoides var. *peruviana* Hieron. Hedwigia 48:221. 1909, ex char. & loc. Type: Peru, *Stübel 1096*, B. Not *P. calomelanos* var. *peruviana* (Desv.) Farw. (sub *P. tartarea*).

Ceropteris tartarea var. *ochracea* (Presl) Bonap. Notes Pterid. **2**:150. 1915.

Pityrogramma ochracea (Presl) Domin, 1928: 8.

Pityrogramma adiantoides (Mett.) Domin, 1928: 8.

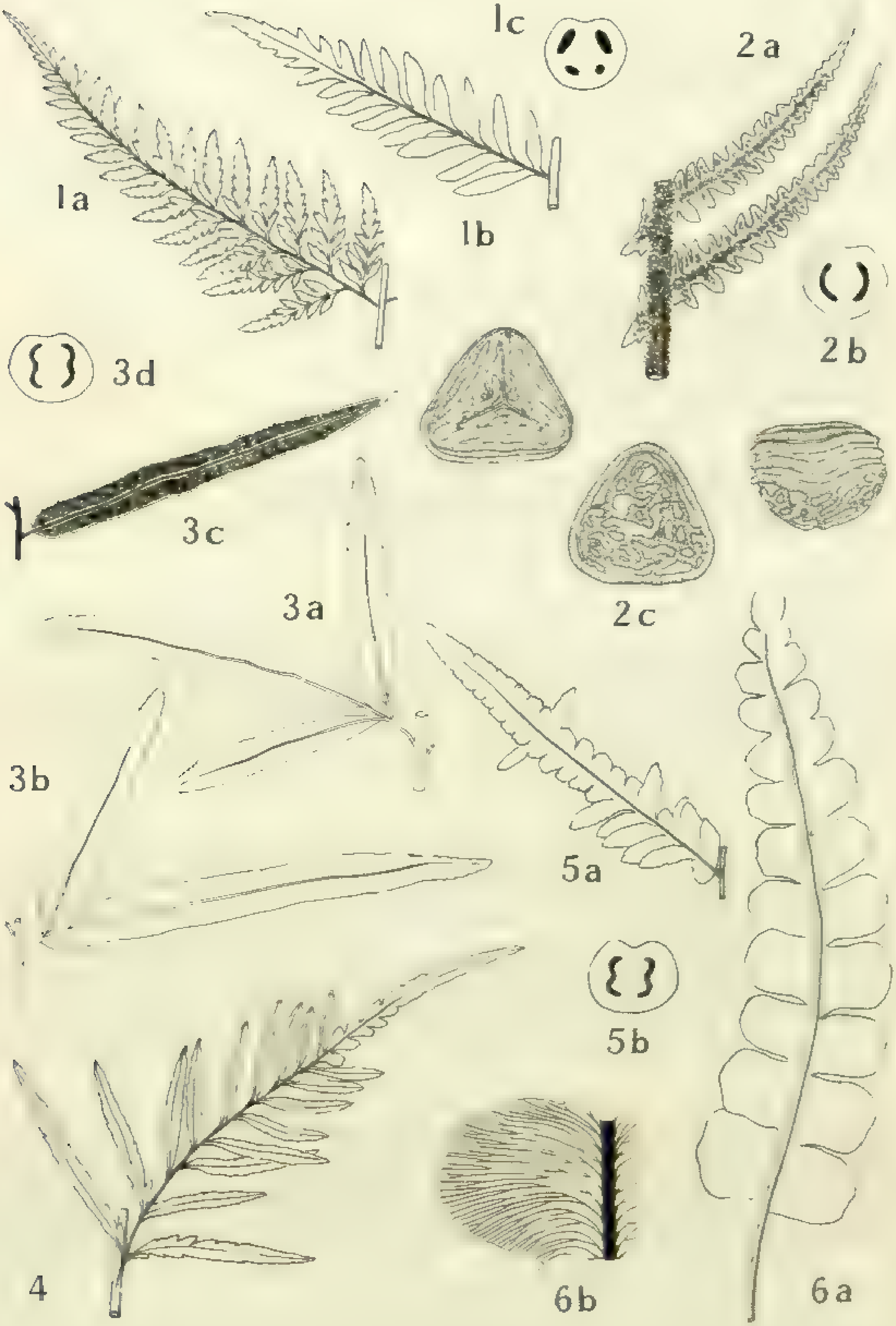
Pityrogramma Ballivianii (Rosenst.) Domin, 1928: 10.

Pityrogramma perelegans Domin, 1928: 8. Type: Tarapoto, Peru, *Spruce* in 1855-56, K!, photo GH.

Pityrogramma caudata (Cav.) C. Chr. Dansk Bot. Ark. 9^{3}:10. 1937.

The earliest varietal name, var. *peruviana* Hieron., cannot be transferred to *P. calomelanos* because of *P. calomelanos* var. *peruviana* (Desv.) Farwell. *Gymnogramma adiantoides* Mett. was ineffectively transferred to varietal status under *Ceropteris tartarea* by C. Chr. Ind. Fil 333. Other "combinations" have also been ineffective and I believe that *ochracea* is the earliest epithet in the varietal category.

FIG. 1. *Pityrogramma calomelanos* var. *ochracea:* 1a, pinna, × 1/2; 1b, pinna, × 1; 1c, vascular bundles in petiole, enlarged. FIG. 2. *P. ferruginea:* 2a, pinnae, × 1/2, 2b, vascular bundles in petiole, enlarged; 2c, spores, left to right — commissural face, distal face, lateral view, much enlarged. FIG. 3. *P. trifoliata:* 3a, sterile pinna, × 1/2; 3b, sterile pinna, × 1/2; 3c, fertile pinna, × 1/2; 3d, vascular bundles in petiole, enlarged. FIG. 4 *P. calomelanos* var *ochracea* × *trifoliata:* pinna, × 1/2, Peru, *Tryon & Tryon 5440.* FIG. 5. *P. ferruginea* × *trifoliata:* 5a, apical pinna, × 1/2; 5b, vascular bundles in petiole, enlarged; both from Peru, *Tryon & Tryon 5449.* FIG. 6 *P. Lehmannii:* 6a, lamina, × 1/2; 6b, venation of pinna-segment, × 1 1/2; both from Colombia, *Lehmann 8944.*


1a
1b
1c
2a
2b
2c
3d
3c
3a
3b
5a
5b
4
6b
6a

Presl's name has been often misapplied to forms of this species, or of *P. tartarea*, with yellow wax.

Lamina pubescent beneath, not ceraceous.

The spores of some specimens of var. *ochracea* are of the typical *Pityrogramma* type with well defined dark ridges. Other specimens have spores that are more spherical than the usual type, although somewhat flattened in three planes on the commissural face, and the tan exospore is smooth or only slightly roughened. It is exceptional to find such different spores in the same species (or variety) but I have been unable to find any character that correlates with the spore type and there is every indication that the unusual spores are mature.

Some specimens of var. *ochracea* with the "normal" spore type are the following (all from Peru): HUANUCO: *Macbride 4994* (US), *Allard 22022* (GH). AYACUCHO: *Killip & Smith 22667* (US). CUZCO: *Vargas 4023* (US), *Scolnik 881* (US), *Bües 1715* (US). Some specimens with the smoothish spores are: PERU: (all from CUZCO), *West 8013* (UC), *Cook & Gilbert 1715* (US), *Mexia 8089* (GH, US), *Herrera 1285* (US), *Tryon & Tryon 5366* (GH). BOLIVIA: *R. S. Williams 1373* (GH), *Krukoff 10094* (F, GH).

Honduras; Venezuela, Colombia, Ecuador, Peru and Bolivia.

2. **Pityrogramma tartarea** (Cav.) Maxon, Contrib. U. S. Nat. Herb. 17:173. 1913

More difficulty exists in the separation of this species from the previous one, *P. calomelanos*, than would be expected from an examination of the common forms of each. Some of this difficulty, it is true, is due to specimens that are single leaves, but the characters of each do vary toward the other. Both species are common, widely distributed, and grow in a variety of habitats and the extent to which their variation may be due to their own variability or to natural hybridization is not known. The following characters, in addition to those presented in the key, may be useful in the identification of material:

Lamina lanceolate to ovate-lanceolate, or in large leaves long-triangular, its apex often more or less acute or abruptly acuminate; apical pinnae strongly ascending; pinnules acute, serrate, or acutely pinnatifid; basal inferior pinnules more strongly ascending on the upper than on the lower pinnae. .... *P. calomelanos.*

Lamina long-triangular, to deltoid in large leaves, its apex evenly long-acuminate; apical pinnae nearly or quite at right angles to the rachis; pinnules obtusely lobed or pinnatifid; basal inferior pinnules at about the same angle to the pinna-rachis on all pinnae (or in large leaves the basal inferior tertiary segments so in relation to the pinnule-rachis). .... *P. tartarea.*

This species has a less extensive range than *P. calomelanos* and both the variety with yellow wax and the one with the lamina pubescent are also more restricted than their counterparts in *P. calomelanos.*

2a. **P. tartarea** var. **tartarea**

Acrostichum tartareum Cav. Descr. 242. 1802. Type: near Guamantanga, Peru, *Née,* seen by C. Chr. at MA (Dansk Bot. Ark. 9^3:10. 1937).

Hemionitis dealbata Willd. Sp. Pl. 5:131. 1810, nom. superfl., illegit. (=*Acrostichum tartareum* Cav.).

Gymnogramma peruviana Desv. Ges. Naturf. Freunde Berl. Mag. 5:329. 1811. Type: Peru, *Jos. de Jussieu* (Herb. Jussieu no. 1009) P!, photo GH.

Gymnogramma dealbata Link, Hort. Berol. 2:52. 1833, (epithet from *Hemionitis dealbata* Willd.), nom. superfl., illegit. (=*Acrostichum tartareum* Cav.), not Presl, 1825 (sub *P. dealbata*).

Ceropteris Stuebelii Hieron. Hedwigia 48:223, t. 10, f. 9. 1909. Type: Colombia, *Stübel 12,* B!, fragment US!; ex B, GH!

Pityrogramma peruviana (Desv.) Maxon, Contrib. U. S. Nat. Herb. 17:173. 1913.

Pityrogramma Stuebelii (Hieron.) Domin, 1928: 7.

Pityrogramma tripinnata Domin, 1928: 7. Type: Mexico, *Parry & Palmer 1004* in 1878, K!, photo GH; isotype, US!

Pityrogramma calomelanos var. *peruviana* (Desv.) Farw. Am. Midl. Nat. 12:280. 1931.

Lamina ceraceous beneath, the wax white to pale (cream) yellow, rarely very sparse and almost colorless; rarely partly ceraceous-pubescent.

Greater Antilles; Mexico to Panama; Venezuela, Colombia, Ecuador and Galápagos Islands south to Bolivia; Brazil (Rio Grande do Sul, Paraná and vicinity of Itatiaya).

2b. **Pityrogramma tartarea** var. **aurata** (Moore) Tryon, comb. nov.

Gymnogramma tartarea var. *aurata* Moore, Gard. Chron. 1870: 493. Type: Cultivated by Veitch from a collection by *Pearce* in Peru. (The specimen of *Pearce* 218 at K!, photo

GH, Domin, 1929: t. 1, may be the type as Domin says; it does clearly represent Moore's name).

Pityrogramma praestantissima Domin, 1928: 6. Type: Colombia, *Kalbreyer 1909*, K!, photo GH.

Pityrogramma Presliana Domin, 1928: 6. Type: Peru, *Matthews 1823*, K!, photo GH (although Domin also cited *Pearce 218*, he annotated that collection, K, as *P. Presliana* var. *aurata* (Moore) Domin and later[11] stated it to be the type of that variety).

Lamina ceraceous beneath, the wax bright yellow. Colombia, Ecuador and Galápagos Islands to Argentina.

2c. **Pityrogramma tartarea var. Jamesonii** (Baker) Tryon, comb. nov.

Gymnogramma Jamesonii Baker, Syn. Fil. 516. 1874. Type: Ecuador, "Pinchinchan" [Pichinchan] Andes, *Jameson*, K!, photo GH.

Gymnogramma xerophila Baker, Jour. Bot. Brit. For. 19: 206. 1881. Type: Colombia, *Kalbreyer 1563*, K!, photo GH.

Pityrogramma Jamesonii (Baker) Domin, 1928: 8.

Pityrogramma xerophila (Baker) Domin, 1928: 8.

Lamina pubescent beneath, not ceraceous. Colombia and Ecuador.

3. **Pityrogramma chrysoconia** (Desv.) Maxon ex Domin, 1928: 10

Acrostichum chrysoconium Desv. Mém. Soc. Linn. Paris 6:212. 1827. Type: Peru, evidently *Dombey*, P, photo GH; isotype, B!, photo GH, fragment US!

Gymnogramma guianensis Kl. Linnaea 20:413. 1847. Type: British Guiana, *Schomburgk 1154*, B!, photo GH, fragment NY!; isotype, K, fragment NY!

Gymnogramma Ornithopteris Kl. Linnaea 20:413. 1847. Type: Venezuela, *Moritz 288*, B!, photo GH, fragment US!; isotype, K!, photo GH.

Gymnogramma flexilis Kl. Linnaea 20:414. 1847. Type: Venezuela, Mérida, *Moritz 287*, B; isotype, K, fragment NY!

Ceropteris obtusa Fée, Mém. Fam. Foug. 8:80. 1857. Type: Colombia, *Schlim 873*; isotype, P!, photo GH.

Pityrogramma Ornithopteris (Kl.) Maxon ex Knuth, Fedde Rep. Beih. 43:95. 1926.

---

[11] Domin, 1929: t. 1.

Pityrogramma flexilis (Kl.) Domin, 1928: 5.

Pityrogramma obtusa (Fée) Domin, 1928: 10.

Pityrogramma subnivalis Domin, 1928: 5. (Also Kew Bull. 1929: 220). Type: Colombia, Santa Marta, *Purdie* in 1844, K!, photo GH.

Jamaica (Blue Mt. Peak); Costa Rica to Panama; British Guiana west to Colombia and south to Bolivia; principally or wholly at the higher elevations.

4. **Pityrogramma dealbata** (Presl) Tryon, comb. nov.

Gymnogramma dealbata Presl, Rel. Haenk. **1**:18, t. 3, f. 1. 1825. Lectotype: Panama *Haenke*, PR (sheet 24358a), photo GH (PR sheet 24358b, photo GH, is probably *P. calomelanos*).

Ceropteris Schaffneri Fée, Mém. Fam. Foug. 8:80. 1857, ex char. & loc. Syntypes: Mexico, Schaffner *165a, 165b*.

Pityrogramma Schaffneri (Fée) Weath. Contrib. Gray Herb. **114**:25. 1936.

The photograph of Presl's type is a very close match for some specimens of this species, for example, Costa Rica, *Scamman 7055* (GH) and Panama, *Allen 147* (GH). This species was long referred to as *Gymnogramma peruviana* Desv. (or *Pityrogramma* or *Ceropteris peruviana*) but in 1936 C. A. Weatherby pointed out that Desvaux's type was actually a specimen of *P. tartarea*.

Mexico to Panama.

5. **Pityrogramma chrysophylla** (Sw.) Link, Handb. Gewächse, 3:19. 1833

Acrostichum chrysophyllum Sw. Schrad. Jour. Bot. 1800²: 14. 1801. The specimen at S-PA (Herb. Swartz!), is this species.

Acrostichum aculeatum Desv. Ges. Naturf. Freunde Berl. Mag. **5**:310. 1811. See Weath. Contrib. Gray Herb. **114**:15. 1936. Not L. Syst. Nat. ed. 10, **2**:1320. 1759.

Ceropteris intermedia Fée, Mém. Fam. Foug. **11** (Hist. Foug. Antill.) :30. 1866. Type: Guadeloupe, *L'Herminier* in 1861, P, photo GH.

Gymnogramma Brackenridgei Carruthers in Seemann, Fl. Vit. 370. 1873, description from Brack. U. S. Expl. Exped. **16**:24 (sub *G. tartarea*), 1854. Type: near Pago-Pago, Island of Tutuila, Samoa, *Brackenridge*, US!

Pityrogramma Brackenridgei (Carr.) Maxon, Carnegie Instit. Wash. Publ. **341**:124. 1924.

Pityrogramma caribaea Domin, 1928: 6. Syntypes: Dominica, *Imray 71*, K!, photo GH; Dominica, *Bradford 395*, K!, photo GH.

The white and yellow color forms, although especially striking in this species, do not merit recognition.

The material I have seen from Samoa, which has consistently been recognized as an endemic (C. Chr. Pterid. Samoa, Bull. Bishop Mus. **177**:57-58. 1943), is surely this species. Porto Rico (rare); and the Lesser Antilles; introduced in Samoa.

6. **Pityrogramma ferruginea** (Kze.) Maxon, Contrib. U. S. Nat. Herb. **17**:173. 1913. FIG. 2

Gymnogramma ferruginea Kze. Linnaea **9**:34. 1834. Isotype: Quebrada de Chinchao, Peru, Jul. 1829, *Poeppig, Diar. 1160*, P!, photo GH.

Gymnogramma Bommeri Christ, Bull. Bot. Soc. Belg. **35**:237. 1896. Syntypes: Costa Rica, "*Biolley in Pittier 1066*"; Costa Rica, *Pittier 1169*. I have not seen either of these collections but am accepting *Wercklé*, Costa Rica, det. Christ, US! as an authentic representative of the name.

The material in Central America is more variable than that in Peru. The pinnae are often petiolulate there, while in Peru they are uniformly subsessile. Also the lamina may be long-triangular or deltoid in Central America while in Peru it is narrowly elliptic.

Guatemala to Panama; Peru.

7. **Pityrogramma trifoliata** (L.) Tryon, comb. nov. FIG. 3.

Acrostichum trifoliatum L. Sp. Pl. 1070. 1753. LINN sheet 1245.9, photo A, and Sloane, Hist. Jam. t. 45, f. 2, are both this species.

Trismeria argentea Fée, Mém. Fam. Foug. 5(Gen. Fil): 165, t. 14A, f. 1. 1852. Syntypes: Caracas, *Moritz;* Minas Geraes, *Pohl.*

Trismeria aurea Fée, Mém. Fam. Foug. 5(Gen. Fil):165. 1852, nom. superfl. illegit. (=*Acrostichum trifoliatum* L.).

Trismeria microphylla Fée, Mém. Fam. Foug. 5(Gen. Fil.):165. 1852, ex char. "Habitat in Peruvia".

Trismeria trifoliata (L.) Diels, Nat. Pflanz. 1^4:265. 1899.

Southern Florida; Greater Antilles; Mexico to Costa Rica (notably absent from Panama); Venezuela, Colombia south to Bolivia, Argentina and Chile (Arica); Paraguay, Uruguay and Brazil.

I am recognizing four putative hybrids of *Pityrogramma trifoliata*, one of them with *P. ferruginea* and the other three with the varieties of *P. calomelanos*. All of these have the long, narrow lamina of *P. trifoliata*, the strongly ascending-arching lower pinna-stalks and (at least in large leaves) the same type of vascular bundles. There is a strongly developed tendency in them toward long and entire segments. Characters of the pinnae and the vascular bundles of two of the putative hybrids, and their parents, are illustrated in Figs. 1-5. While these are of interest, I do not believe that a binomial is justified for any of them. The hybrids are all distinguished from *P. trifoliata* by their pinnae with numerous segments. In *P. trifoliata* the pinnae are entire to 3-, 5- or very rarely 7-foliolate.

The material has not been adequate to establish the degree of fertility of the hybrids. An examination of the fertile leaves available suggests that they may produce no viable spores or relatively few of them. The collections *Tryon & Tryon 5440* and *5449* were both single plants.

7a. **P. calomelanos** var. **calomelanos** × **trifoliata**

Gymnogramma longipes var. *concolor* Baker, Jour. Bot. Brit. For. **16**:301. 1878. Type: Paraguay, *Balansa 334*, K, is probably this hybrid.

Ceropteris longipes var. *argentea* Rosenst. ex Hassler, Trab. Instit. Bot. Farm. Buenos Aires 45:51. 1928. Type: Paraguay, *Hassler 3176*, is probably this hybrid.

Petiole and rachis glabrous or ceraceous, segments white ceraceous, or with nearly colorless wax, beneath.

ARGENTINA: Prov. Tucumán, July, 1912, *Castillon* (Inst. Lillo 41858) (GH, in part). PARAGUAY: April 25, 1946, *Rojas 13343* (GH), December, 1915, *Rojas 1117* (GH); *Pedersen 3158* (US). BRAZIL: Minas Geraes, 1948, *Macedo 1161* (US), 1950, *2220* (US).

7b. **P. calomelanos** var. **aureoflava** × **trifoliata**

Gymnogramma longipes Baker, Jour. Bot. Brit. For. **16**: 301. 1878. Type: Paraguay, *Balansa 333*, K!, photo GH.

Trismeria longipes (Baker) Diels, Nat. Pflanz. 1^4:265. 1899.

Trismeria trifoliata var. *subbipinnata* Hieron. Hedwigia 48:223. 1909. Type: Ecuador, *Stübel 733*, B, is probably this hybrid.

Petiole and rachis glabrous or ceraceous, segments with yellow wax beneath.

This is perhaps the same as 7a, the yellow wax being derived from a yellow form of *P. trifoliata* rather than from *P. calomelanos* var. *aureoflava.*

ECUADOR? ARGENTINA: Tucumán, *Venturi 9646* (US). PARAGUAY: December, 1902, *Fiebrig 610* (GH).

7c. **P. calomelanos** var. **ochracea** × **trifoliata** FIG. 4

Gymnogramma Herzogii Rosenst. Med. Rijks. Herb. **19**: 21. 1913. Type: Bolivia, *Herzog 2000;* isotype, US!

Petiole and rachis thinly pubescent to glabrous, segments pubescent beneath.

PERU: Dept. Junín, *Tryon & Tryon 5440* (GH); Dept. Cuzco, *Bües 1936* (US). BOLIVIA: *Herzog 2000* (US).

7d. **P. ferruginea** × **trifoliata** FIG. 5

Petiole and rachis closely and densely lanate, although deciduously so. The only collection has the pinnules markedly irregular in their length.

PERU: 10 km. sw. of San Ramón, Dept. Junín, Oct. 28, 1956, *Tryon & Tryon 5449* (GH).

8. **Pityrogramma Lehmannii** (Hieron.) Tryon, comb. nov. FIG. 6

Gymnogramma Lehmannii Hieron. Engl. Bot. Jahrb. 34: 474. 1904. Type: near Aquaclara, Popayan, Colombia, 1200-1400 m., *Lehmann 8944*, B!, photo GH; isotypes, GH! US!

The unusual characters of this distinctive species have been mentioned in the key and in the discussion of the genus. It is known only from the original collection.

Colombia.

9. **Pityrogramma triangularis** (Kaulf.) Maxon, Contrib. U. S. Nat. Herb. 17:173. 1913

The four varieties of this species were treated by Weatherby[12] and in spite of additional knowledge his taxa and their status are certainly still justified. The genetical and cytological study of Alt and Grant[13], for example, is an im-

---

[12] Rhodora **22**: 113-120. 1920.

[13] Alt K. S. and V. Grant, Cytotaxonomic observations on the goldback fern. Brittonia **12**: 153-170. 1960.

portant contribution to our understanding of this species but it does not furnish a basis for different taxonomic conclusions.

9a. **P. triangularis** var. **triangularis**

Gymnogramma triangularis Kaulf. Enum. Fil. 73. 1824. Type: San Francisco Bay, California, *Chamisso*, probably LE; isotypes, P, (*Chamisso 1875*) photo GH, B (fide Alt & Grant).

Baja California to sw. British Columbia, s. Nevada and sw. Utah.

9b. **P. triangularis** var. **viscosa** D. C. Eaton, Ferns N. Am. 2:16, t. 48, f. 5. 1879. Type: usually considered to be: San Diego, California, "Gymnogramme viscosa", *Nuttall*, PH; but other material cited, or especially that illustrated, by Eaton might be a better lectotype.

Pityrogramma viscosa (D. C. Eaton) Maxon, Contrib. U. S. Nat. Herb. 17:173. 1913.

Maritime: Baja California and s. California.

9c. **P. triangularis** var. **pallida** Weath. Rhodora 22:119. 1920. Type: California, *Heller 8141*, GH!

Pityrogramma pallida (Weath.) Alt & Grant, Brittonia 12:168. 1960.

Central California.

9d. **P. triangularis** var. **Maxonii** Weath. Rhodora 22:119. 1920. Type: Arizona, *Blumer 3271*, US; isotype, GH!

Baja California, s. California e. to Arizona.

10. **Pityrogramma sulphurea** (Sw.) Maxon, Contrib. U. S. Nat. Herb. 17:173. 1913

Acrostichum sulphureum Sw. Prod. Veg. Ind. Occ. 129. 1788. Type: Jamaica, *Swartz*, S-PA (Herb. Swartz)!, fragment US! (the Plumier, Fil. t. 44 cited by Swartz is *P. chrysophylla*).

Cuba, Jamaica, Hispaniola, Porto Rico.

11. **Pityrogramma "Eggersii"**

The commonly accepted name, *Pityrogramma Eggersii* (Christ) Maxon[14] can not be used for this species because the type specimen (Cuba, *Eggers*, comm. C. Rensch sub no. 4882a, Herb. Christ-P!) of *Gymnogramma Eggersii* Christ[15]

---

[14] Contrib. U. S. Nat. Herb. 24: 62. 1922.

[15] Bull. Soc. Bot. Belg. 33^2: 92. 1894.

is a species of *Asplenium* and has been so annotated by C. V. Morton. Although this species does not have a name, I am deferring to C. V. Morton's forthcoming work on the ferns of Cuba, where it will be described and named.

Cuba and Hispaniola.

Representative specimens: CUBA: *Howard 5017* (GH, NY, US); *Jack 7124*, (GH, NY, US). HISPANIOLA: *Ekman* (Haiti) *4824* (NY, US).

12. **Pityrogramma schizophylla** (Jenm.) Maxon, Contrib. U. S. Nat. Herb. 24:61. 1922

Gymnogramma schizophylla Jenm. Jour. Bot. Brit. For. 15:266. 1877. Type: Jamaica, *Jenman*, "No. 16, Hb. Kew, 1876", K!, photo GH; isotype, Jamaica, *Jenman*, NY!

Jamaica and Hispaniola.

13. **Pityrogramma argentea** (Willd.) Domin, 1928: 6

13a. **P. argentea var. argentea**

Hemionitis argentea Willd. Sp. Pl. 5:132. 1810.

Tropical and south Africa; Madagascar and Mascarene Islands.

13b. **P. argentea** var. **aurea** (Willd.) Domin, 1929: 20.

Hemionitis aurea Willd. Sp. Pl. 5:131. 1810.

Gymnogramma argentea var. *aurea* (Willd.) Mett. ex Kuhn, Fil. Afr. 59. 1868.

Pityrogramma aurea (Willd.) C. Chr. Cat. Pl. Madagas. Pterid. 46. 1932.

Madagascar and Mascarene Islands.

I have made no study of the African species and in this one and the next I have followed the treatment of Tardieu-Blot[16]. Christensen[17], however, treats var. *aurea* as a species.

14. **Pityrogramma Humbertii** C. Chr. Dansk Bot. Ark. 7:111, t. 43. 1932.

Madagascar (I do not know var. *elongata* C. Chr., op. cit. 112, from the Belgian Congo).

DUBIOUS TAXA AND NAMES

The four following names may represent valid taxa but the material I have seen has not been adequate to form a basis for definite conclusions:

Pityrogramma chrysophylla var. **euchrysa** Ekman ex C. Chr. Kungl.

---

[16] Fl. Madagas. & Comores, Fam. 5, 1: 118-120. 1958.

[17] loc. cit. and Dansk Bot. Ark. 7: 112, t. 43, f. 5. 1932.

Svensk. Vet. Akad. Handl. 16^2: 57, t. 14, f. 1-3. 1936. Type: Hispaniola, *Ekman 13881*, S; isotype, US!

This may be a variety of *P. chrysophylla*, as Christensen proposed, or perhaps a variety of *P. chrysoconia*; or it may represent an endemic species.

Pityrogramma Pearcei (Moore) Domin, 1928: 9.

Gymnogramma Pearcei Moore, Gard. Chron. 1864: 340. Type: Cultivated by Veitch from a collection by *Pearce* in "Chile". Two specimens at K!, photos GH, may be considered as authentic (I did not find a proper holotype): "Pinna of *Gymnogramma Pearcei*, n. sp. . . . . . ." and *Pearce 274*, ex Veitch 7/84. The original collection was undoubtedly not made in Chile. Illustration: Schneider, Choice Ferns **2**: f. 68.

Gymnogramma decomposita Baker, Gard. Chron. 1872: 1587. Type: "Andine side of South America, Hort. Kew ex Veitch"; this is probably the specimen at K!, photo GH, annotated by Baker as "*G. decomposita*" and with the original label "*Gymnogramma Pearcei*, H. Kew 10/71, from Veitch". Illustration: Garden **6**: f. on 495.

Gymnogramma fumarioides Rosenst. Mém. Soc. Neuchât. Sci. Nat. **5**: 45, 54, t. 6. f. 10. 1912. Type: Colombia, *E. Mayor 144*; isotype, US!, P! photo GH.

Pityrogramma decomposita (Baker) Domin, 1928: 7.

Pityrogramma fumarioides (Rosenst.) Maxon, Proc. Biol. Soc. Wash. **51**: 38. 1938.

The three basionyms listed above all represent plants with highly dissected leaves. I strongly suspect that this material represents a single species but it is not sufficient to enable me to present the synonomy with assurance nor to place the species among the others of the genus.

Pityrogramma pulchella (Moore) Domin, 1928: 9.

Gymnogramma pulchella Moore, Gard. Chron. 1856: 597, figure. Type: "Hort.", presumably ex Hort. Linden, ex Venezuela. I did not find a proper holotype at Kew; a specimen, K!, in Moore's herbarium, photo GH, "*G. pulchella*, Hort.", "Hort. Veitch, 1860", is probably another species.

I have associated the following material with this name on the basis of the small figure published by Moore. VENEZUELA: (probably Rancho Grande), *Tschudi 176* (VEN); Colonia Tovar, *Fendler 357* (YU, the specimen at K is figured in Domin, 1929: t. 6); ne. of Bergatín, Est. Anzoátegui, *Steyermark 61327* (F, VEN).

The principal characters of this taxon are the strongly dissected juvenile leaves, the inequilateral pinnae and the definitely to strongly toothed segments of the adult leaves. However, the material is insufficient to come to a conclusion concerning its status, or its relation with the equally uncertain *P. Pearcei* discussed above.

Pityrogramma triangulata (Jenm.) Maxon, Contrib. U. S. Nat. Herb. **17**: 173. 1913.

Gymnogramma triangulata Jenm., Bull. Bot. Dept. Jamaica n.s. **4**: 206. 1897. Type: Jamaica, *Jenman*, NY!, photo GH.

Most of the specimens that I have seen have a marked resemblance to *P. argentea* and I strongly suspect that species may have escaped from cultivation in Jamaica and probably hybridized to a degree with a native species there, most likely with *P. calomelanos*. *P. triangulata* has been collected only in St. Andrew Parish, Jamaica.

The deltoid to long-deltoid lamina, the rather triangular and inequilateral pinnae and the somewhat flabellate-cuneate ultimate segments of *P. triangulata* are all suggestive of *P. argentea*. Some specimens are rather intermediate between *P. argentea* and *P. calomelanos* in the relation of the vein to the margin. In *P. argentea* most of the veins end at the margin in a small sinus of an emarginate lobe, while in *P. calomelanos* they end well back of the margin in the center of a simple tooth. In *P. triangulata* they may end back of an often bifurcate tooth but there is a lighter colored extension of the vein to the margin. It should be mentioned, however, that the character of the veins and margin in *P. argentea* is not unique. It is sometimes similar in *P. "Eggersii"* and its development in *P. triangulata* may not show a relation to the African species.

The following names are probably synonyms of some of the American species but I have not been able to place them with certainty:

Ceropteris monosticha Fée, Mém. Fam. Foug. 7: 44, t. 22, f. 2. 1857. Type: Mexico, *Schaffner 155*. Perhaps = *P. tartarea* var. *tartarea*.

Ceropteris plicata Fée, Mém. Fam. Foug. 8: 80. 1857. Type: Mexico, *Schaffner 164*.

Ceropteris serrata Fée, Mém. Fam. Foug. 8: 81. 1857. Type: Mexico, *Schaffner 162*. Perhaps = *P. calomelanos* var. *calomelanos*.

Pityrogramma subflexuosa Domin, 1928: 7. Type: Montserrat, *Holme* in 1879, K!, photo GH. Probably = *P. chrysophylla*.

II. THE GENUS ANOGRAMMA

The genus *Anogramma* includes some five or six species which are clearly related to *Pityrogramma*, especially to *P. sulphurea* and others of spp. 10-13 (see above). The architecture of the lamina is similar to some of these, the axes are grooved in the same manner and the sorus is the same. The spores[18] which are identical or similar (the ridges are often closer and somewhat tuberculate) to those of typical *Pityrogramma* are perhaps the strongest evidence of affinity. In addition, there is in *Pityrogramma* an approach toward the annual habit of the sporophyte found in *Anogramma*. Some species of *Pityrogramma* show a strong tendency to grow in open soil and especially in *P. sulphurea* this is correlated with a reduction in the life-span of the sporophyte which apparently lives for only a few years.

The species of *Anogramma* grow on bare (or nearly bare) soil and the sporophyte evidently lives for only one growing

---

[18] Rather well figured by Lindman, Hedwigia 43: 310. 1904.

season. In the smallest species (*A. Lorentzii*) the sporophyte may consist of only a few small fertile leaves (to 1 cm. long), a minute stem and a few roots. A gametophyte is often found attached to herbarium specimens of the sporophyte. This prothallus is reported to be perennating, surviving the dry season and producing another sporophyte from specially developed lobes the next growing season[19]. This behavior of the prothallus, however, can not well be used as a generic character because it has been reported in only two of the species (*A. leptophylla* and *A. chaerophylla*) and because even in these it is not known to be of regular occurrence in nature. In other species the gametophyte may not behave in this way and its frequent occurrence on a sporophyte may be due to the fact that the growth of the sporophyte is so rapid that even when it is mature the gametophyte is still present.

This reduced and specialized evolutionary line can be recognized as a distinct genus, or as a group within *Pityrogramma* as Domin[20] did. Were there truly intermediate species, I would follow Domin's classification. However, there are none and the several species can be separated, among other less constant characters, on the basis of the rhizome (and usually the lamina) indument and the annual habit of the sporophyte.

Rhizome scales atropurpureous to light brown, rigid and sclerotic to firm and subsclerotic; sporophyte living for a few to many years, the stem correspondingly well developed; lamina glandular, strongly pubescent or most often ceraceous (rarely glabrous or slightly pubescent). .... *Pityrogramma*.

Rhizome scales thin, whitish, sometimes mixed with similar trichomes or only such trichomes present; sporophyte living only one growing season, the stem correspondingly poorly developed; lamina glabrous or rarely sparsely pubescent. .... *Anogramma*.

ANOGRAMMA Link, Fil. Sp. Cult. 137. 1841. Type: *A. leptophylla* (L.) Link (*Polypodium leptophyllum* L.)

The usually accepted species of *Anogramma* are the following:

1. **A. chaerophylla** (Desv.) Link (the largest species). Tropical America.
2. **A. guatemalensis** (Domin) C. Chr. may be a variant of *A. leptophylla*. Mexico to Costa Rica.
3. **A. leptophylla** (L.) Link. Tropical America, Africa and adjacent islands, southern Europe, and eastward to New Zealand.

---

[19] See, for example, Goebel, Bot. Zeit. 35: 671-711. 1877; Organographie, ed. 3, 1101, 1102. 1930. Bower, The Ferns 1: 276-278. 1923.

[20] Domin, 1928: 3, 9-10.

4. **A. ascensionis** (Hook.) Diels. Ascension Island.
5. **A. Osteniana** Dutra. Uruguay and Brazil (Rio Grande do Sul).
6. **A. Lorentzii** (Hieron.) Diels (the smallest species). Argentina, Uruguay, Brazil. *Gymnogramma Regnelliana* Lindm. 1903 (not Christ, 1900) may be a species distinct from *A. Lorentzii* rather than a variety of it (*Gymnogramma Lorentzii* var. *megaspora* Lindm. Hedwigia **43**: 309. 1904).

Other species that have been placed in *Anogramma* are referable to other genera (see C. Chr. Ind. Fil. and Suppls.). One, however, that has been maintained in *Anogramma* by Christensen (and others) clearly does not belong there. This is *A. microphylla* which Domin[21] treated in a separate section, *Pityrogramma* section *Monosorus*. He was certainly correct in removing it from his section *Anogramma*, but it is probably not closely related either to that genus or to *Pityrogramma*.

Anogramma microphylla (Hook.) Diels (*Gymnogramma microphylla* Hook.), of the eastern Himalayas, has a creeping rhizome with blackish, thickened trichomes, one U-shaped vascular bundle in the petiole, unusual somewhat elliptical segments, and tetrahedral-globose spores that are pale yellow and have a perispore with a few prominent wings and tubercules between them. The leaf, segments and sorus are well figured in the original publication[22]. This species may represent a monotypic genus; or perhaps it is a diminutive *Monachosorum*; or it may possibly be congeneric with or related to *Cerosora*. — GRAY HERBARIUM, HARVARD UNIVERSITY.

---

[21] Domin, 1928: 10.

[22] Hook. Ic. Pl. t. 916. 1854. (Cent. Ferns, t. 16, 1854).

CONTRIBUTIONS FROM THE GRAY HERBARIUM
OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CXC

PATTERNED GROUND AND VEGETATION ON SOUTHERN BYLOT ISLAND, NORTHWEST TERRITORIES, CANADA

By

WILLIAM H. DRURY, JR.

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

1962

PATTERNED GROUND AND VEGETATION
ON SOUTHERRN BYLOT ISLAND
NORTHWEST TERRITORIES, CANADA

CONTRIBUTIONS FROM THE GRAY HERBARIUM
OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CXC

PATTERNED GROUND AND VEGETATION ON SOUTHERN BYLOT ISLAND, NORTHWEST TERRITORIES, CANADA

By

William H. Drury, Jr.

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

Issued July 25, 1962

Manufactured

by

The Lexington Press, Inc., Lexington, Massachusetts

CONTENTS

INTRODUCTION

PATTERNED GROUND AND VEGETATION
ON SOUTHERRN BYLOT ISLAND
NORTHWEST TERRITORIES, CANADA

PATTERNED GROUND AND VEGETATION ON SOUTHERN BYLOT ISLAND, NORTHWEST TERRITORIES, CANADA

By William H. Drury, Jr.

INTRODUCTION

The study of frozen ground (*tjäle, dauerfrost, eisboden,* permafrost, *merzlota, pergelisol,* etc.) has always been closely associated with the study of patterns in the vegetation and in the ground. The features of patterned ground were recorded in the nineteenth century from arctic regions by geographical explorers (Adams, 1815; Von Baer, 1837/38; Beechey, 1831; Figurin, 1823; Lóven *in* Chydenius, 1869; and Von Middendorf, 1864-67), and by botanists (Kjellman, 1879; Martin, 1882). Then Högbom (1914) laid the foundation of the study which has recently become of broad international importance. Crampton (1912) and Thoroddsen (1913) recognized the importance and interrelation of microtopography and soil processes with vegetation. Frödin (1918) made a detailed study of the relation between earth movement and vegetation, and defined most of the ideas basic to understanding the effects of frost microtopography on vegetation. The study received a great stimulus with the excursion to Spitzbergen of the IXth International Geological Congress led by De Geer (1910) as shown by the flurry of publications which followed (Meinardus, 1912; Miethe, 1912; Penck, 1912; Sapper, 1912).

Meinardus (1930), Poser (1931, 1932, 1933), Steche (1933), and Cailleaux and Taylor (1954) published literature reviews and theoretical discussions of mechanisms producing what Nordenskjöld (1909) first named *Strukturboden.* I agree that this term is well translated (if necessary) as "patterned ground" (Washburn, 1950). Washburn's reviews (1950, 1956) define the problem, and his discussion of the mechanisms makes another review superfluous. Washburn did not deal with non-patterned ground including solifluction (Andersson, 1906), earth mounds, turf- and stone-banked terraces, and block streams. Steche (1933) reviewed and defined the terms (primarily German usage) for the various expression of frost action.

Troll's (1944) review included appreciation of the intimate mutual associtaion and influence of frost features with their vegetation, and established the climatic correlation of the major types.

Major frost patterns are not controlled by vegetation, although minor features may be in some places, such as in mid-latitude mountains (Denny, 1940). Péwé (1959) showed that fully-developed frost-crack polygons *(Spaltenboden)* are present around McMurdo Sound in the Antarctic in absence of vegetation. But vegetation cover and exposure may suppress solifluction (Frödin, 1918; Sigafoos and Hopkins, 1952) and strongly influence modification, once the major *Strukturboden* patterns are formed.

Antevs (1932) introduced the study of alpine frost features and their influence upon vegetation to the United States, and Polunin (1934) first used patterned ground to classify vegetation. The study of the geobotanical development of bogs in northern Europe has extended the knowledge of soil processes associated with frost action into the boreal regions (Cajander, 1913; Auer, 1920), although recent Scandinavian bog studies (Sjörs, 1948, 1950 a & b, 1959), and alpine vegetation studies (Dahl, 1951; Nordhagen, 1943, 1954; Gjaerevoll, 1950, 1956) have concentrated on biological phenomena — physiological requirements and effects of climate and other plants — rather than on soil features.

In America, Raup (1947, 1951) has led the study of the effects of soil movement on the growth of plants and vegetation patterns. His (1947) study of the McKenzie Mountains used soil forms to classify alpine vegetation, and similar work has been carried on in the New World chiefly by his students (see, however, Hanson, 1950; Billings & Mooney, 1959; Billings & Mark, 1961; Wiggins, 1951). Hopkins and Sigafoos (1950) studied the combined effects of frost action and plants in the wet or low tundra (Von Middendorf's term) region of Seward Peninsula, Alaska. Sigafoos (1951, 1952) discussed detailed effects of frost processes on microtopography and vegetation, emphasizing the dominance of local soil effects over climatic forces. Benninghoff (1952) described the expression of structural soils and solifluction in forested parts of Alaska and the importance of physical factors. Drury (1956) discussed the interaction of frost action, alluviation and vegetation on a bog-covered floodplain in interior Alaska. Denny (1951, 1956) and Goodlett (1954) applied these disciplines to the effects of periglacial climates on vegetation and to interpreting the climate from the frost effects still visible at the margin of the most recent ice in Potter County, Pennsylvania. Most American studies of periglacial geology have grown out of the influence of Kirk Bryan (1946, 1949) who, with his students (Denny, 1936, 1938, 1951; Horberg, 1949; Sharp, 1942 a and b; Schafer, 1949; Smith, 1949; Smith and Frazer, 1935), joined with students in central Europe in the study of ground conditions during the maximum Wisconsin-Würm ice advances (Büdel, 1944; Cailleaux, 1942; Dücker, 1933, 1951; Gripp, 1952; Högbom, 1923; Kessler, 1925; Poser, 1947; Schenk, 1955; Selzer, 1936; Soergel, 1921, 1939, 1940, 1943; Tavernier, 1944-45). Out of these studies, and the study of bog pollen and other fossils, they project climates of the period (Willett, 1953; Zeuner, 1937), and even map the vegetation (Büdel, 1949; Frenzel & Troll, 1952) and follow its post-glacial changes (Firbas, 1939; Aario, 1944). Elsewhere (Drury, 1956) I have discussed why I think most American periglacial geology studies do not give enough consideration to: (1) the climatic differences at the margins of the ice which existed between the Old World and the New; (2) the changes in precipitation and temperature which caused the ice to stop its advance; (3) what vegetation would be under climatic conditions which clearly do not occur anywhere today.

My studies on Bylot Island examine the interrelation of plants and soil structures in a high arctic region of dry tundra (Von Middendorf, 1864-67) where land surfaces are so recently exposed that all forces whose traces can be found in the soil must be active at present. Thus, we cannot postulate changing climate as an escape mechanism, when we are unable to explain land forms using only observable forces. My interpretations are based upon detailed study of many, repeated excavations in the thawed surface soil within a mile of our camp, and a limited survey of surface expressions within ten miles of camp. The study concentrates upon: (1) non-sorted circles (Washburn, 1956) (mud-boils, frost-boils, frost-scars); and (2) formation and modification of a four-sided pattern of frost-cracks.

Climatic Requirements.

Troll's (1944) review showed how very different are frost patterns in different climatic regimes. As he says, frost features are not restricted to perennially frozen ground, nor to humid climates, but only to regions where, periodically, there is strong and morphologically effective ground frost; thus patterned ground is not an arctic or a polar, but a subsnowline phenomenon. Large forms are characteristic of areas of perennially frozen ground, extreme cold, and *few* annual temperature changes which cross freezing; miniature forms are characteristic of high altitudes in low latitudes, snow-free for only a short period, and then subject to *many* shallow temperature fluctuations across freezing. Troll points out that sorted patterns and hummocks are characteristic of oceanic tundra regions and frost-crack polygons are typical of continental cold, dry regions.

Högbom (1914) emphasized that the frequency of freeze-thaw may not be the only feature of primary importance. If it were, the Lofoten Islands on the west coast of Norway should have maximally-developed frost features, as would most of the so-called temperate climates. He suggested that the following are important: (1) the number of degrees the temperature falls below freezing; (2) the number of months during which the temperature is below freezing; (3) the depth of frost penetration; (4) the presence of a sounding board (perennially frozen ground, ice, or bedrock); and (5) the presence of abundant moisture at the period of frost activity — whether spring or fall.

Statement of the Problems.

1. How do solifluction and depositional-slope processes modify raised surfaces? Are these actions expressed in changes visible in the course of a single season? Are frost forms sufficiently different on successively older surfaces to give a measure of the progress of their development?

2. Some force creates an upwelling of either fine- or coarse-grained soil, mud-boils, giving the impression of boiling up or *brodelerde* (Low, 1925; Gripp, 1926, 1929). Are cryostatic mechanisms suggested to produce both sorted patterns (Högbom, 1914; Huxley and Odell, 1924; Elton, 1927) and non-sorted patterns (Thoroddsen, 1913; Frödin, 1918;

Washburn, 1950, 1956; Hopkins and Sigafoos, 1950; Sigafoos, 1951) strong enough and active locally?

3. Many of the forces suggested for the development of patterned ground are concerned directly with sorting soil fines from coarses, but many of these forces must be questioned for adequacy of their strength. Furthermore, because the forms we found were all non-sorted, can these mechanisms be used, even with modifications, to explain the patterns we found?

4. (a) Can the mechanisms suggested for the wet climates of Spitzbergen, where the ground may be wet during autumn freeze-up, apply where the ground is dry to four feet by mid-July? (b) Do they act at the time of year (spring) in which we watched the frost features in action? (c) What relation does the cheese-like quality of the drying mud column and the swelling of the tacky surface have to the now generally discarded hypothesis (Steche, 1933) of colloidal activity? (d) What part do swelling or upwelling forces in water-saturated soils play in creating or modifying solifluction forms?

5. Some mammoth force is able to crack open the ground on Bylot's youngest surfaces, even under the pounding sea surf. Is the Von Bunge (1884, 1887, 1902)-Leffingwell (1915, 1919) hypothesis of frost-crack growth adequate to explain this large pattern? Taber's (1929, 1930) study of the segregation of ice into lenses and wedges in the ground made this tension-crack theory tenable and greatly advanced our understanding of the development of ground ice. But the frost-cracks at Bylot did not contain ice. They contained coarse sediments. On the other hand, is the theory of tension-cracks due to especially low temperatures adequate to explain the forces creating certain secondary modifications on the exposed uplands?

6. How are the original depositional surfaces modified and reworked by the combined agencies of frost action and plant growth so that in exposed areas they create frost ovals, in wet, sheltered areas they create peat ridges surrounding rectangular marshes or ponds, and on the broad uplands they create pentagonal, moss-colonized frost-cracks?

7. What forces (exposure, moisture, sun, sequence of snow-melt, soil instability) influence and control the distribution of plants? Are regional differences greater than microtopographic ones? How do other organisms respond to man-defined associations? What part does plant cover play in soil development and the modification of frost features?

8. Is the vegetation sufficiently different on successively older surfaces to suggest progression, development, or regional vegetation types?

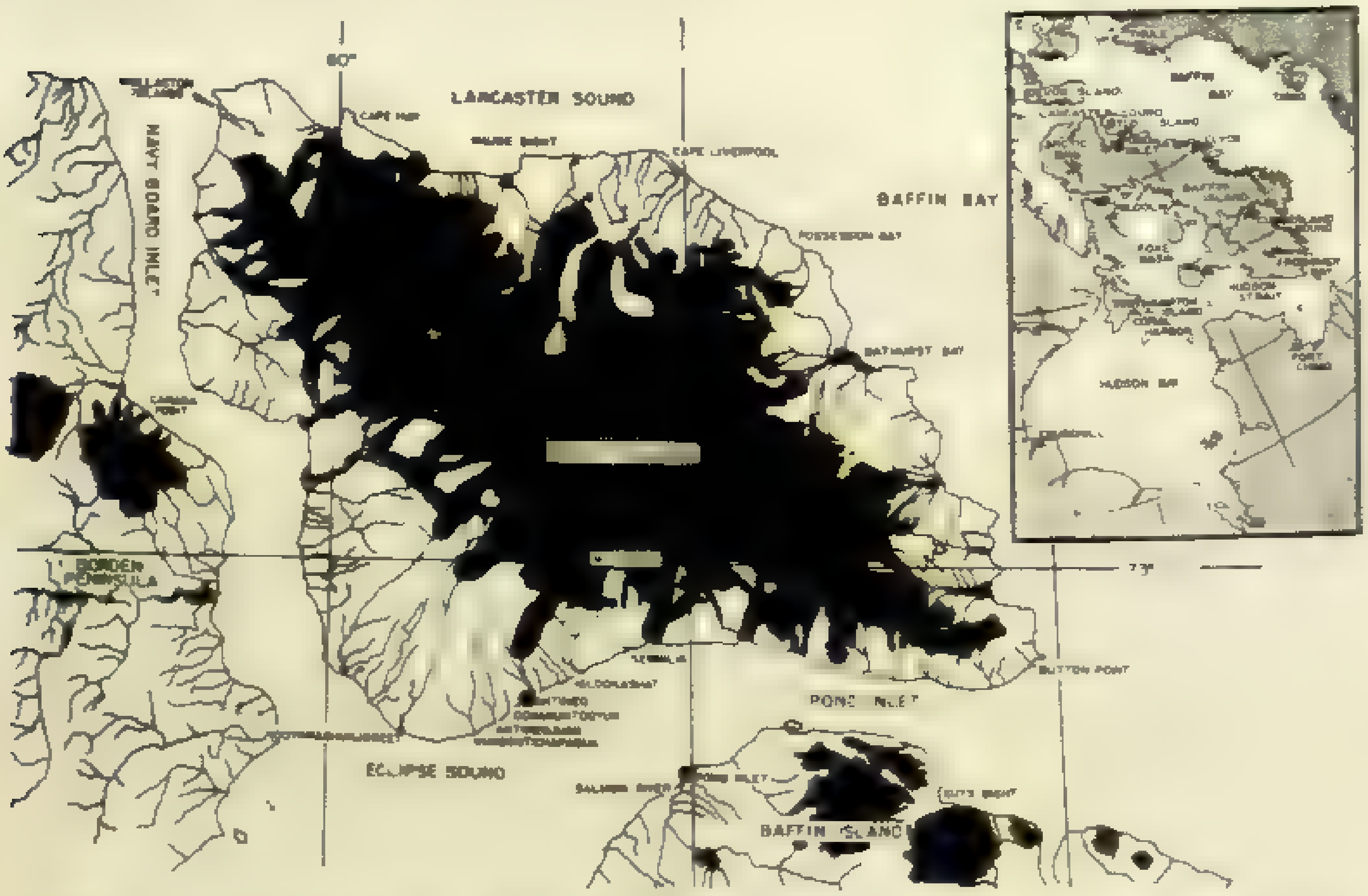
PART ONE

THE BYLOT ISLAND EXPEDITION

We made our studies between 12 June and 29 July 1954, on the south coast of Bylot Island at the mouth of the Aktineq River. Maps 1 and 2 show places mentioned. Scherman (1956) gives a delightful narrative of the expedition, emphasizing travel over Eclipse Sound and life with the community at Pond Inlet. The Drurys (1955) give a short account of the weeks at Main Camp. The expedition was paid for by a private grant with help from the New York Zoological Society. We made arrangements with Canadian officials through The Arctic Institute of North America.

Dr. Benjamin Ferris and Edward Ames gave unlimited help in the field. Ames dug many of the holes, and his unbiased, critical mind effectively deflated many hypotheses. Four papers on the biology of the breeding birds of Bylot Island have been published. The present paper, together with Miller (1955), Ferris (1958), and Van Tyne and Drury (1959), completes the reports.

Bylot Island is about 120 miles long and 60 miles across; the mountainous backbone of the island rises to a height of 600-700 feet, underlain by Paleozoic, igneous and metamorphic rocks (chiefly quartzites or granitic, with many dark minerals). This central mountain area is covered with a snowfield, from which about one hundred glaciers flow down to the lowlands on the northeast and southwest sides (Map 1). Our camp was seven miles from the Aktineq Glacier's snout, and on the east edge of the southwest



MAP 1. BYLOT ISLAND AND ECLIPSE SOUND. Snow fields are represented in black. Place names referred to in the text are shown.

plateau area underlain by poorly consolidated Tertiary sandstone containing some low-grade coal seams. These sediments dip gently north. The plateau extends about 50 miles west from camp to the shores of Navy Board Inlet; and it slopes from about 700 feet at the foot of the mountains to sea level, except near our camp where it ends at the top of 200-foot bluffs. Although frost disturbance and movement are evident in all soils, the major features of erosion are produced by a combination of cryoplanations and violent stream action during the spring thaw. This topography supports Peltier's (1950) concept of a cryoplanation-erosional scheme or cycle as an extension of the Davisian (1909) cycles of erosion. It agrees with Andersson's (1906) discussion of the relation of solifluction to the removal of detritus by running water, and the combination of the two as an especially effective erosion agent. The rolling plateau surface deeply cut by the shallow stream valleys, and the ankle-high vegetation make the topography resemble that of the high plains of the United States, and of the surfaces of most North American "uplifted and dissected peneplains." Many areas of the uplands show regular lines of vegetation alternating with barren soil (Figure 1). Many ponds are regular, both in outline and distribution, and occur on the tops of the hills (Figure 17); many slopes are deeply scarred with frost-cracks (Figure 8), or pitted with mud-boils (Figure 7) (Washburn 1950, 1956), but frost action on most of the uplands is inconspicuous, being expressed only as a polygonal pattern of shallow depressions where mosses thrive.

The Study Area.

Map 2 indicates the approximate topographic structure of the square-mile area studied in detail. We divided the topography into five parts: (1) the ridge running north and south of the west margin of the area — West Ridge; (2) the beach, sixteen feet above present high tide, at camp — 16-foot Beach; (3) the steep slope and rounded hill — Kungo Hill (from the Eskimo name for Snow Goose, *Anser coerulescens atlantica*); (4) the gently-sloping surface — Plover Plateau; and (5) the shallow mound — Tui-Tui Tabletop (from the onomatapoetic Eskimo name for Baird's Sandpiper, *Calidris bairdii*). Iceberg Lake is the northern margin of the study area; the Little River runs north of

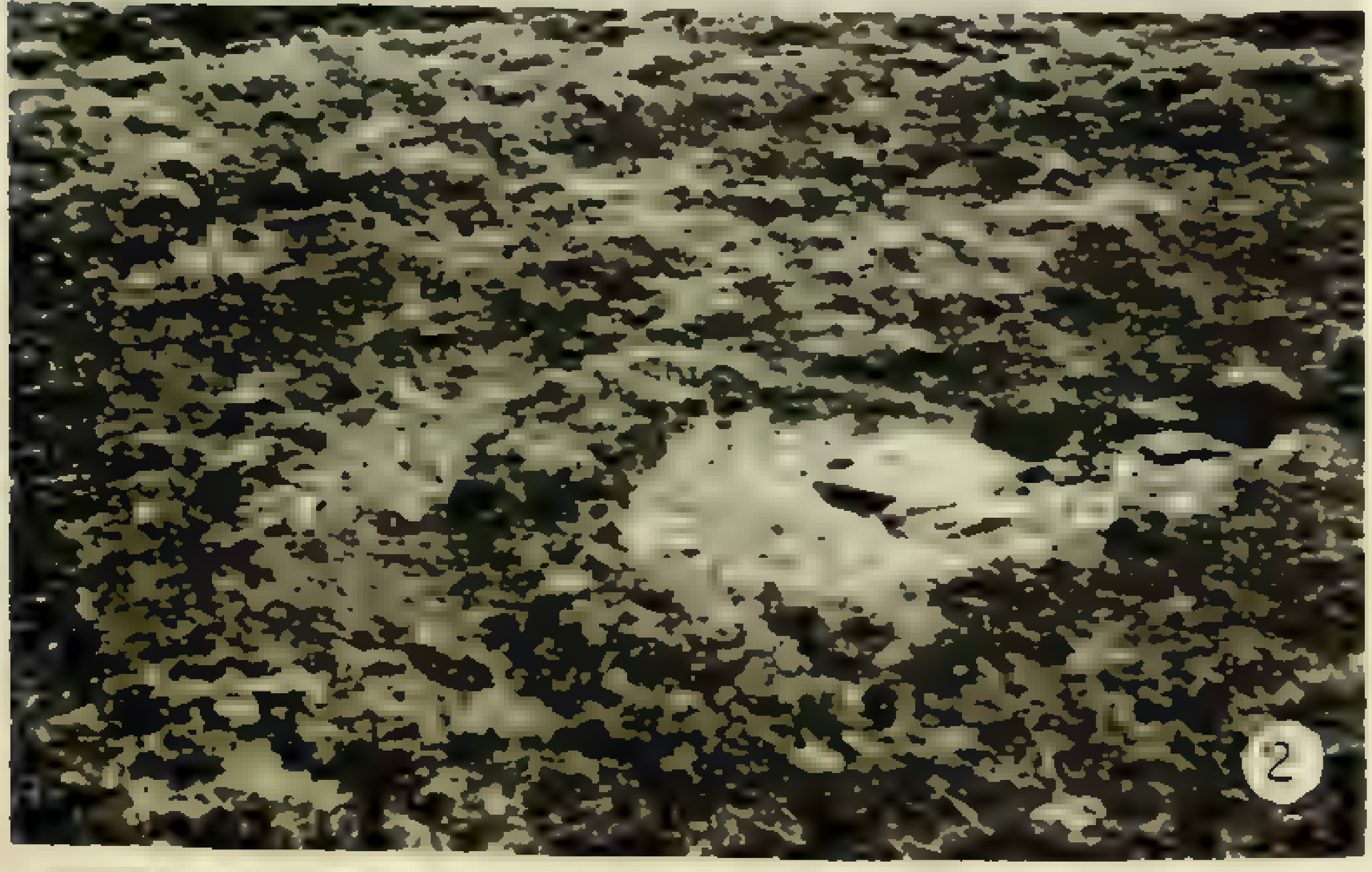


FIGURE 1. [illegible] EATION OF [illegible]. The pattern suggests that vegetation is confined to the lines of developing drainage. Vegetation stripes around the boulder in the right background are parallel. Vegetation is chiefly Avens and Arctic Willow. Scene is on the uplands east of Ooyarashukjooeet.

FIGURE 2. [illegible] OF MELT-WATER RILL. Silty sand deposits are in the shape of a solifluction lobe. Vegetation on the lip of the lobe is chiefly sedge and Arctic Willow. Excavations (Figure [illegible]) show that many lobes originate in this way. Photo taken on the south slope of Kungo Hill at about 70-foot elevation.

Plover Plateau, and Golden Plover Creek runs south of it, next to Kungo Hill. Both these creeks ran five to six feet deep, and moved rocks two feet across during the height of the thaw, but were completely dry by the end of July.

MAP 2. STUDY AREA AT AKTINEQ. Rivers and ponds are shown in black. Elevations were measured by hand-level transect; contour lines were drawn in the field and later compared to aerial photograph taken at 20,000 feet in 1948. Snow Bunting Creek drains the south side of Kungo Hill from the 135-foot level. Lark Gully drains the east side of West Ridge from the 150-foot level. Raised beaches are hatched. Areas of sand, damp at low water, are stippled.

Most of Tui-Tui Tabletop is scarred with frost-cracks (Figures 16, 17, and 18). The prevailing east wind keeps large areas of it barren of vegetation and the surface is so churned on the windward side that the major frost patterns are nearly lost (Figure 18). Plover Plateau is covered with a mat of mosses, Avens, Arctic Willow and Bell Heather.* At the upper end is a marsh, and at the lower end several ponds (Upper Phalarope Ponds) in another marsh. Kungo Hill is barren at the top and comparatively heavily vegetated on sheltered south slopes. Weedy vegetation covers disturbed soils ("frostings"), especially on the raised sea beaches on the south and east slopes of Kungo Hill and Plover Plateau. The 16-foot beach level at camp slopes gently up to a 35-foot beach, and is deeply scarred with frost-cracks modified by the growth of mosses into an orderly net of peat ridges, many of which act as dikes and hold in rectangular ponds or sedgy marshes resembling rice paddies or cranberry bogs (Figures 22 and 23). Loon Pond, the ponds on the west side of Tui-Tui Tabletop, and both groups of Phalarope Ponds are rectangular, resulting from thawing of the frozen ground below such places ("thaw sinks" — Muller, 1947; Wallace, 1948; Black and Barksdale, 1949; Hopkins, 1949).

The summer of 1954 was late; the sea ice never left Eclipse Sound. When we arrived on 12 June, eighty-five per cent of the land surface was still snow-covered (Figure 1 in Van Tyne & Drury, 1959), but already Opposite-leaved Saxifrage was in flower. The general thaw started 24 June; sheets of melt-water flooded the uplands 26 June, and most of the uplands were free of snow by 28 June. As soon as the snow left slightly sheltered areas, Bell Heather (conspicuous in such places) came into flower; most species bloomed in the last days of June and the first three weeks of July. Early flowering plants, such as the Cruciferae, had set fruit, but the sedges and grasses and most of the plants of the uplands were still in flower, or their flowers were just withering on the first of August when we left.

Intense frost churning was in progress in the thawing, water-saturated, snow-free areas when we arrived, but under the snow the soil was frozen and undisturbed. The most evident frost action occurred on exposed surfaces lying between snow patches, during the period 15-25 June. As the surface dried after the first of July, frost activity stopped.

---

*A taxonomic treatment follows the discussion of the vegetation, and in it scientific names are given for the plants whose common names are used in this part of the text.

PART TWO

GEOLOGICAL PROCESSES

It is convenient to divide frost action into three descriptive categories: (1) those affecting the rapid mechanical weathering of rocks — frost-riving; (2) those concerned with down-slope movement — solifluction; (3) those producing patterned ground or *Strukturboden.* The mechanisms involved grade into, combine with, and influence each other, as Högbom (1914), Elton (1927), Washburn (1956) and others have emphasized.

I. MECHANICAL WEATHERING

Frost-riven stones. We exhumed stones shattered into many pieces from many excavations, especially those on wet beaches. Either the sections were still in place or they were separated by a centimeter or more. (Fig. 18, Högbom, 1914, p. 317).

Wind-sculptured stones. Wind-cut stones are numerous on raised beaches, especially on the pavement of the beach east of the Aktineq River. These stones have been cut by sand driven by the prevailing east wind so that nearly flat upper side slopes down to the east and the anastomosing flutings point to the east. We found no *Drikante.* The polish on the cut surfaces of the stones (chiefly sandstone pebbles) is dark and shows little glisten.

Avalanche gullies in the sedimentary outcrops. Steep cuts in the bluffs west of camp have half-rounded, gutter-like bottoms, from which avalanche scouring has gouged coarse debris. The debris collects in tongues which often bury masses of ice at the foot of the gullies. These may develop when frost-riving products of several years are released in the spring by sun-melt, or early spring/late winter meltwater refreezes in the valleys, and gather snow to produce a glacier-like mass of ice and stones made unstable by later thawing.

Grenadiers. Högbom described frost action on mountain slopes creating stone towers *(Felsentürme).* (See Fig. 6 on p. 282 of his 1914 paper). Similar structures are characteristic of the ridges on the bluffs west of camp. The castellations — 3-25 feet tall — extend from the shore at sea level to the top of the bluffs at about 200 feet.

Block streams. We found block streams 30 yards across and 100 yards long on the depositional-slope-covered margins of shallow valleys seven miles inland on the west side of the Aktineq River. They are at the base of the bedrock outcrops and, because they are heavily lichen-covered, are presumably no longer active. Because they are at the same level as the solifluction products which fill these shallow valleys, I presume that they are of the same age. The creek draining the west side of West Ridge runs several feet below the surface rocks of a block stream.

II. SOLIFLUCTION

Down-slope movement of soil is everywhere conspicuous. It has rounded the hills of the plateau region and filled valley sides with debris so that there is little sharp topographic contrast. Motion down the valley sides has produced conspicuous lobes and low terraces. Does the entire soil mass move in the formation of slope features? Or is the motion the result of minor alluviation in which mud bursts out from under the vegetation mass and flows as a mud river? What are the effects of these two types of movement upon the vegetation cover?

Fisher (1866), Kerr (1881), and Davison (1888, 1889) commented on movement of soil on slopes associated with frost. Wood (1882) showed the importance of frozen ground as a water source to saturate the soil, and the importance of this in soil flow. Andersson (1906) first suggested that frost-riving together with what he named solifluction are especially effective erosion agents in arctic regions. Högbom (1914) separates *Fliesserde* from *ausfliessungen.* Frödin (1918) recognized the difference in these two movements. Beskow (1930) separated the slow movement *Erdfliessen* at the surface from rapid mud-flow *Erdrutsch,* especially at depth. Thus from the beginning, there is agreement that there are two major types of soil movement which we may call "creep" and "mud-flow."

The chief difference seems to be how much movement is related to the freeze-thaw cycles operating with a downslope component with each thaw which Taber (1943) thought especially important, and how much is related to the flow of waste saturated with water which Andersson (1906) first emphasized. Clearly, both are active and grade into each other. Frödin (1918) described accurately the surface expressions of these forces and the effects on vegetation in Swedish mountains. Sigafoos and Hopkins (1952) did the same for Seward Peninsula, Alaska.

Frost-Heaving.

Hamberg (1915) clarified that the thrust is straight upward unless the force resulting from frost-heaving is confined; and Taber (1929, 1930, 1943) showed that the mechanism is largely due to growth of ice crystals in the soil at right angles to the cooling surface. A ubiquitous expression of this action is the swelling of the topmost layers of the soil so that they pull away from large rocks (illustrated in Högbom, 1914). This is a common phenomenon in New England in late winter and spring, and was conspicuous on the muddy surfaces on the uplands of Bylot Island when a sharp freeze occurred during the thaw. As the thaw penetrates the top few inches of the soil, that soil becomes saturated with melt-water, and thus ready for maximum expression of frost-heaving by segregation of ice crystals on refreezing. Large stones seem to sink when the ground surface refreezes. It is not clear how this happens but it may be that: (a) on refreezing, the surface soil forms a stiff deck over the still unfrozen ground below, and this deck is pushed up and away from the stone. Being connected to the thawed layer below, the stone retains warmth during a short period of freezing, and thus is not frozen into the deck of soil and heaved up with it; or (b) a large stone extends down into the still frozen layer and is held there while the thawed surface layer heaves on refreezing. The association of these expressions with a sharp freeze during spring or mid-winter thaw is important because of the implications it suggests as to the conditions under which related solifluction features develop.

Solifluction Forms.

(a) As soon as solifluction lobes were visible, we put white flowerpot sticks into the lobes, perpendicular to the soil surface and in straight rows along and across them, to test for any motion. Displacement of just under an inch occurred between 25 June and 29 July, and amounted to a gradual sag in the fluid material at the center of a mud-boil which contributes a net displacement of the solifluction lobe. Washburn (1947) surveyed solifluction lobes on Queen Victoria Island and found movement of one and a half inches during June — the height of the thaw — and one-quarter inch during the following four months.

(b) Large boulders on the top of the uplands or terraces stand out on the surface as if they have either been frost-heaved or the upland has been moved away from them. On slopes, the soil overwhelms boulders from above, flows down the sides, and moves away from below.

(c) *Creep.* Excavations down the long axis of some solifluction tongues or lobes show organic material and vegetation mat turned under — the result of a slow movement of the whole soil-mass. Antevs (1932) and Sharp (1942a) suggested that the vegetation mat acts to slow up solifluction, hence to produce garlands or turf-banked terraces.

(d) *Mud-Flow.* In contrast, several excavations (Figure 19F) cutting longitudinally through solifluction lobes showed the old soil profile was not disturbed, but buried. In many places on the surface, fresh deposits show a small delta of mud built out over previous years' vegetation (Figure 2). These deposits also take the form of solifluction lobes. Saturated soil has burst out from under the vegetation mat and flowed over the surface as mud or "slud," and then when stopped by low slope, etc., has been subsequently colonized by vegetation. Frödin (1918) emphasized the force which pushes soil up through the vegetation mat and out over the surface to create the lobe and to keep it moving. Hopkins and Sigafoos (1950) discussed this when dealing with mud-boils and suggested, as did Frödin, that it is the result of forces which develop when wet soil freezes. Neither paper discussed the place of this upwelling in solifluction or the combined effects of freezing forces and mud-flow forces. I am convinced that the combination is very important on Bylot Island.

In small displacements, a general soil-sagging (creep) moves a large total mass of soil a short distance, but the usual conspicuous surface expression depends upon mud-flow out from below through the vegetation and over the surface. Evidence from our excavations supports Andersson (1906) and Högbom (1914) that the soil does not move along the surface of the perennially frozen ground as a slipping plane, as Beskow (1930), Steche (1933), and earlier authors such as De Geer (1910) believed. Instead, the motion depends upon viscous or fluid movement at all levels of the soil saturated by rapid snow-melt. Under these circumstances, runoff is contained above a still-frozen layer, such as annual frost or perennially frozen ground, which serves to conserve moisture.

Vegetation Effects. The effects of microtopography of a solifluction lobe on the vegetation vary according to its location on the lobe: (1) on the center of the lobe running down to the lip, is a relatively barren area scattered with blackened mosses and lichens; (2) most of the top of the lobe is covered with vegetation characteristic of dry uplands. Frödin (1918) took pains to show that this barrenness is not the result of wind exposure but of soil instability resulting from creep and mud-flow. Moisture held through midsummer in organic soil at the margins and in the shelter of the lobe encourages the growth of mat plants. In such places we found southern plants otherwise unusual in the uplands, such as Crowberry, Bilberry, Netleaved Willow, and Bell Heather.

Sapper (1913) believed that solifluction is more frequent in arctic regions because the thin vegetation does not restrain it; Högbom (1914), on the other hand, believed that the thinness of the vegetation is caused by disturbance of the soils associated with solifluction. Sernander (1905) and Frödin (1918) — and after them Seidenfaden (1931) and Sørensen (1935) — agree that the two work together.

Solifluction forms, and the forces which produce them, grade into the forms and forces discussed below under nonsorted stripes and circles.

Depositional Slopes.

Depositional slopes (Péwé, 1948, 1950) form gentle (2°-5°) slopes from one raised beach to the next. The slope from the 55-foot beach to the 35-foot beach is long and smooth, and almost completely covers the lower beach. We found peat ridges, mud-boils, small frost-cracks, well-developed soils, and rich vegetation on the surface of depositional slopes. The large frost-crack pattern discussed below is not expressed on the surface of depositional slopes, but during June and July 1954 the frost did not retreat deeply enough for us to dig through the depositional slope material to find out whether it lies buried underneath. Depositional slopes are continuous with the stream deltas near Golden Plover Creek, near Snow Bunting Creek, and the creeks east of Golden Plover Creek, formed when the beaches involved were at sea level. Streams have since cut sharp-sided valleys into these deltas and have re-deposited a delta on the present beach level.

Excavations through the depositional slope material into the sediments below will give important information (1) on dating the formation of frost-cracks and the development of depositional slopes, (2) on development of vegetation on progressively older surfaces, and (3) on processes of modification of the major frost-crack pattern with the passage of time.

The plateau surface and uplifted peneplains in temperate regions.

The concept of an uplifted, dissected peneplain has long been used to explain or to illustrate geographical history and development of land forms. Davis (1889, 1909) introduced this controversial conception in the Appalachian Mountains area. Denny (1956), however, presented cogent arguments against the existence of peneplains and concordance of summits in the Appalachian ridges in Pennsylvania where he studied. His re-creation of the "original" surface showed, in general, accord of summits with structure, and his evidence indicated effective erosion during several stages of the Pleistocene.

If studies of frost action and cryoplanation processes observed in the North (Andersson, 1906; Bryan, 1946; Peltier, 1950) apply validly to uplands in temperate regions during the periglacial climatic conditions, those uplands were exposed to the most powerful forces of cryoplanation. Troll (1944) points to the subsnowline position of intense frost action. If we combine these ideas, a reasonable explanation emerges for the rolling "peneplain" upland surfaces of periglacial regions such as the plateaus at the tops of the Green and White Mountains, Mount Katahdin, and the mountains of the Gaspé Peninsula, Cape Breton Island and Newfoundland. These upland surfaces are cut sharply by steep valleys of streams or valley glacier cirques (maps and photos in Antevs, 1932; MacClintock and Twenhofel, 1940). Tree line often occurs at the break in slope between the rolling plateau and the steep valleys. Raup (personal communication) suggests that this line reflects the lower limit of intense frost action and soil instability.

These mountain tops resemble lowlands of the Arctic created by cryoplanation, combining solifluction with massive erosion by snow-melt-water.

When mid-latitude uplands were above the main mass of an icecap or below a snowfield during an ice readvance, the uplands were subjected to vigorous arctic frost erosion, whose local base-level was the top of the surrounding ice sheet or the lower limit of deep frost penetration and snowline (Troll, 1944).

This process may be altiplanation (Eakin, 1916). It suggests that uplands at the tops of the Appalachians and eastern Canadian mountains may have developed *in situ* by rigorous high latitude or altitude erosion and do not require recourse to the intricacies of regional uplift (Matthes, 1959). The presence of tablelands, then, may indicate a period of rigorous ice-free climate in the schedule of the development of the landscape.

III. Strukturboden — The Development of Patterned Ground

Non-sorted stripes and non-sorted circles seem to be formed by similar mechanisms, but we found marked differences in the type of soils, depth of soils, and relation to other frost patterns.

Table I

Non-sorted Stripes — Vegetation or Soil Stripes	*Non-sorted Circles — Mud-Boils*
1. On gentle to steep slopes — dry by early July. Although saturated with water during the thaw, do not "sit" in it.	1. On gentle slopes or terracettes — wet late into season. Melt-water forms puddles and stands on the surface during the thaw.
2. Soil of angular sand and pebbles, with little cohesion.	2. Soil often dark, usually fine-grained, showing tilth; but sometimes centers are of sand.
3. Vegetation lines running down-slope, but not held in at	

Non-sorted Stripes — Vegetation or Soil Stripes	*Non-sorted Circles — Mud-Boils*
the lower end by vegetation or peat. In some places patterns resemble rill-work.	3. If elongated down-slope, lower border margined by peat ridge which merges into solifluction lobes.
4. Occur on rather exposed, high, rounded uplands in shallow soils; covered with snow until main thaw, or blown free of snow and therefore exposed to deep freezing.	4. Occur on south-facing sheltered terraced slopes or valley bottoms in deep soils; free of snow early in season and thus exposed to long freeze-thaw season.
5. Cracks appear parallel to the stripes. These cracks are wide, deep, and long, as if the result of a strong force.	5. Polygonal cracks appear on the surface as it dries; column pulls together as if by local cohesion.
6. Soil stripe has convex surface.	6. Earth column tends to bulge upward into convex top — tacky and cheese-like as it starts to dry.
7. a) Fines erupt in small patches which are elongated down-slope. Some fines are thrust up through cracks. b) Micropolygonal pattern of eruptions appears where stripes are subject to water seep, such as from a marsh.	7. On boils on south-sloping uplands, small eruptions appear in regular patterns.

A. Non-sorted stripes — vegetation or soil stripes

We found these only outside our study area. They consist of lines or patches of (1) bare, actively-disturbed tan soil, (2) less disturbed margins scattered with lichen thalli, tiny weedy mosses, Saxifrage and Draba, and (3) vegetation — chiefly Avens, mosses, Arctic Willow, Locoweed, and cushions of Opposite-leaved Saxifrage.

(1) Many soil stripes have eruptions of fine-grained soil of three types: (a) a foot across and two feet long (downslope) as if someone lifted out two or three shovelsful of soil during the thaw, and later the hole had nearly filled while the mounds had slumped, dried and cracked. These large eruptions are few and occur where surfaces are scattered with flat, angular stones, and disturbed areas are partly colonized by plants; (b) an inch across and three inches long, numerous where there is fine sand, silt and angular pebbles, and often associated with cracks running downslope; (c) one or two inches across, forming a small mesh in fine, sandy (often cheese-like) silts. These are covered

with tiny moss or lichen thalli and resemble miniature *Zellenboden* (Högbom, 1914, p. 320).

(2) Many vegetation-free soil stripes have cracks one to two inches wide and five to twenty yards long running down the center (Figure 11). In some places eruptions of damp, fine soil are thrust up through these cracks.

(3) Most vegetation lines are underlain by a shallow humus layer, but many have Locoweed whose deep taproot suggests deep soil stability.

(4) Some vegetation lines have a moss-filled depression or crack running down the center.

(5) Some vegetation lines converge where two gentle slopes come together, which suggests rill-work (Salomon, 1929). (Figure 1).

These observations suggest:

(1) that disturbance of the bare areas may be associated (a) with soil cracks, (b) with fluid upward flow of water-saturated soil (Frödin, 1918; Gripp, 1926, 1929; Steche, 1933);

(2) that the crack or depression (which may be of independent origin) now covered by vegetation is stable. Högbom (1914) suggested that solifluction is closely associated with the production of soil stripes, and so did Sigafoos (1952) who found vegetation stripes on obviously unstable soil. Rill-like patterns where vegetation lines converge support Huxley and Odell's (1924) hypothesis of water-flow through the coarse stones in sorted patterns first established by frost-heaving. Steche (1933) suggested the combination of the upwelling force with solifluction (see his diagram after Gripp, 1926). Most German authors recognize two separate processes and suggest that modification by solifluction must follow establishment of the sorted pattern.

Our observations suggest that (1) modification is contemporaneous; (2) shallowness of the soil prevents (a) formation of solifluction lobes, and (b) growth of vegetation which may obliterate the pattern on deep soils.

B. Non-sorted circles — mud-boils, frost-boils, or frost-scars (Cf. *Fleckentundra*, Troll, 1944).

As the snow melts, tufts of grass come through first, then the ground appears next to clumps of grass or Bell Heather; but the ground in such a place remains frozen to a depth

FIGURE 3. SUBSURFACE WATER-FLOW INTO MUD-BOIL EXCAVATION. Water flowing through the soil at least 3 inches below the surface has filled the 18-inch excavation. Continuing flow shows in the surface foam. Vegetation chiefly sedges and Arctic Willow with Hypnum moss ground cover. Site on the south slope of Kungo Hill at about 85-foot elevation. Field notebook gives size.

FIGURE 4. MUD-BOIL HUMMOCKS. Mud-boils, showing surface cracks, mineral soil core, and separated by moss-filled depressions are transitional between mud-boils and and hummocks. Vegetation chiefly Avens and sedges. Site on a gentle depositional slope above the 15-20-foot beach at Ooyarashukjooeet.

of 2-4 inches while some bare areas quickly thaw to 9-18 inches. These deeply-thawed spots are the nuclei of mud-boils. I found no way to forecast where they would appear, except that they are of uniform silts or sands and have few stones on the surface.

After several days of thaw, mud-boils have a slick, shiny surface when soaked with water, or a tacky, cheese-like surface when drying. They are still thawed deeper than the surrounding soil. How do these soft spots develop? What happens to the sediments inside from day to day and through the course of spring's saturation and summer's drying? Our observation showed the following:

(1) Some contain more fines than their surroundings, and on daily drying pull together into a cheese-like mass. Others contain coarser materials than the surrounding soil. Some consist of a column of fines topped by a half-inch layer of sand. Most boils have a concentration of small, angular stones near or at the surface, but very few stones within the earth column; angular, slab-sided stones, 1-5 inches long, may occur on edge in surface cracks (Figure 5).

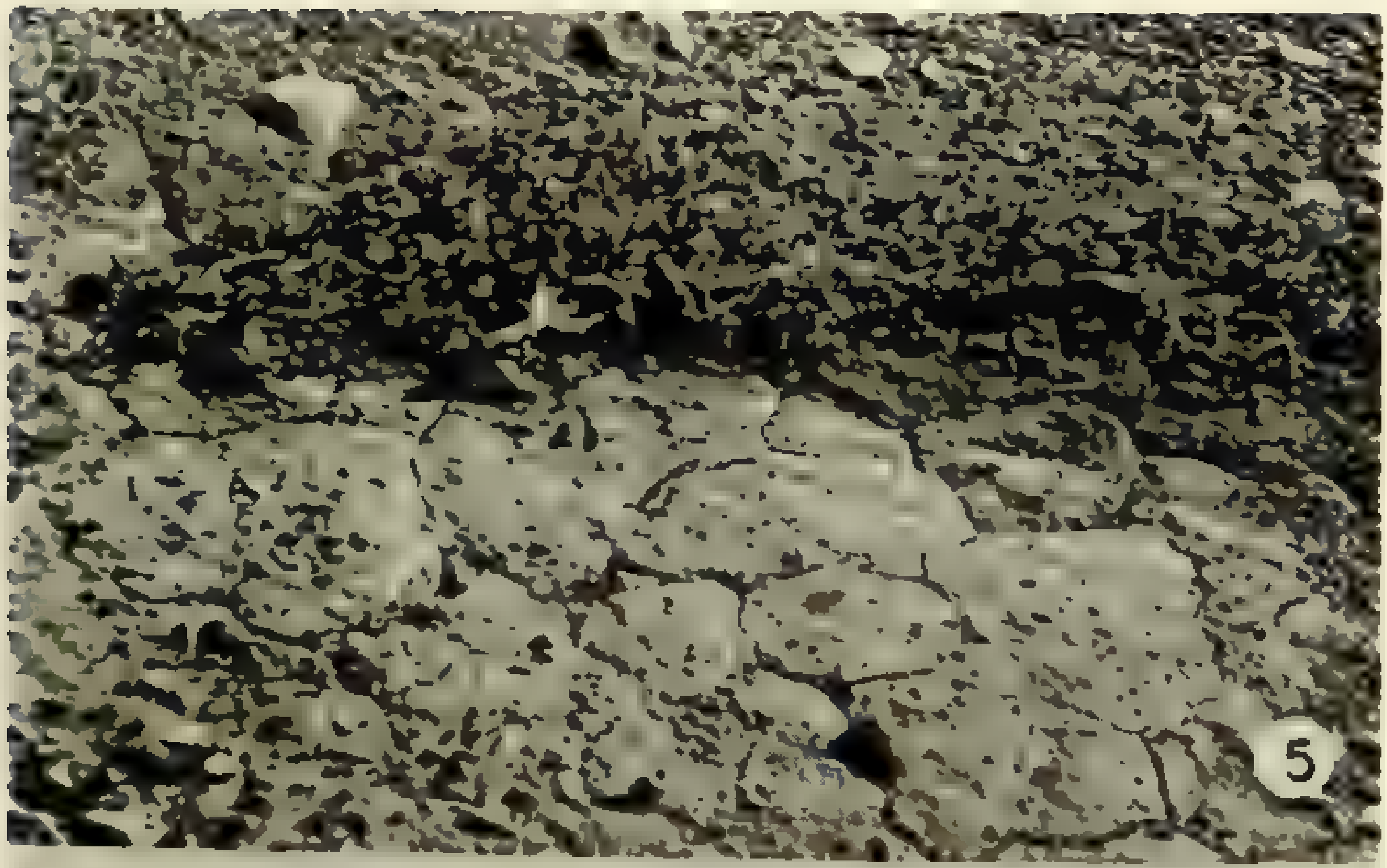
(2) Most, when dried out, show disturbance of horizontal strata on the edge of the column, and soil remnants (partly organic) turned on edge or floating in the column (Hopkins and Sigafoos, 1950).

(3) At the height of the thaw they are continuous with a subsurface flow of water (as Thoroddsen, 1914, observed), and quickly fill with water while being excavated — but no water flows out the top. In one case, clear water flowed into a trench from under the annual frozen layer (Figure 3).

(4) When wet and still active, recent footprints on their surface disappear, and a trench 8 inches deep is usually filled and obliterated overnight.

(5) While drying but still damp (water can be squeezed out), the surface soil draws together and cracks — first on the up-slope edges of the boil as if sagging, or around stones as if drawing away. As drying of the soil proceeds, while the surface is still damp, pentagonal cracks appear usually about 5 inches apart, extending into the soil 1-3 inches (Figures 4 and 5, and Rousseau, 1949). These cracks are damper than the meshes.

(6) During June, when the thaw has generally reached



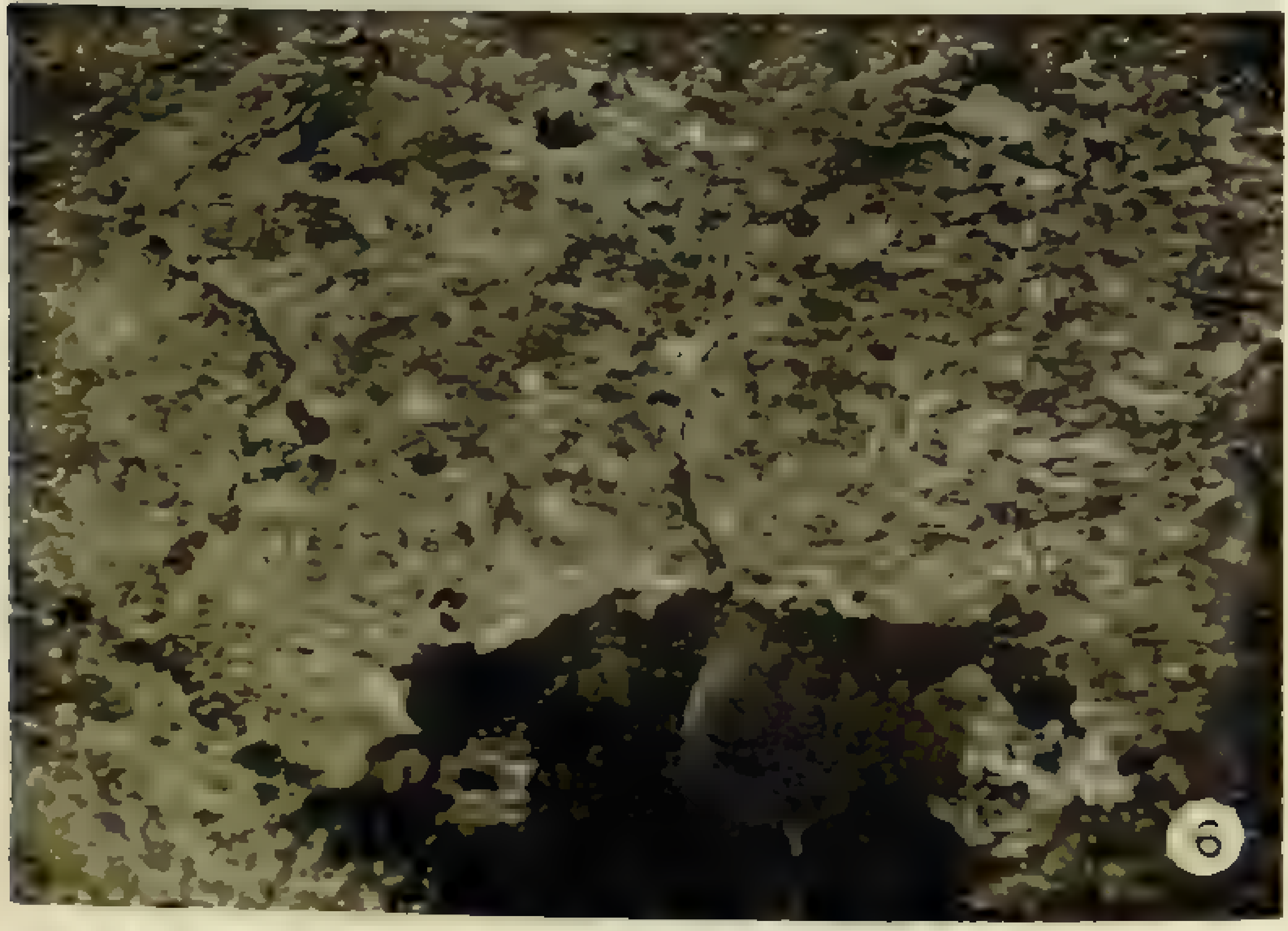


FIGURE 5. ARCTIC WILLOW AND MUD-BOIL [illegible]. Contraction crack polygons appear on the surface of mud-boil. Angular stone on edge in the crack suggests the presence of forces related to those which make sorted circles. Note Snow Goose tracks made in the soft surface. Note also the relative absence of stones where the soil is active. Arctic Willow grows in garlands, forming terracettes. Deflation and soil flow have exposed the stem and some roots. Photo taken on south slope of The Bluffs at about 100-foot elevation.

FIGURE 6. CONTRACTION CRACKS ON POND SHORE. Algal growth makes scum on mud

about 6 inches on sunny south slopes, the surface freezes on many nights, forming a crust 1/4-2 inches thick; short ice crystals form on muddy places. Repeated freezing, above a thawed and water-saturated soil layer, breaks up the soil tilth and creates a mobile mud. A daily cycle in which the mass is drawn together in the early morning, filled out and soaking wet by mid-morning, is repeated over the period of a week or ten days. Every day the same cracks come and go, and the soil changes from quicksand to a jelly. When the jelly forms and the columns swell, or when the surface freezes, the margins of the vegetation are thrust up, raising a ridge of black soil and vegetation (cf. Hopkins and Sigafoos, 1950). The movement of the mass down-slope pushes up a larger ridge on the down-slope side, upon which moss growth is lush.

(7) Bleached stems (occasionally roots) of living Arctic Willows cross the surface, and some roots cross the soil column two or three inches below the surface. The green photosynthesizing part of the plant lies beside the boil (Figure 5) as if the plant grows and produces leaves where there is less disturbance, while subsurface parts, once rooted, can persist even when a boil develops. Perhaps the age of such a plant can be used to measure the age of a boil.

(8) The flowerpot labels which we placed across mud-boils during the peak of activity, suggested down-slope movement at the center, but no indication of movement from the center toward the edge (Washburn, 1947).

(9) Step-like terracettes containing mud-boils show forms transitional to turf-banked terraces and solifluction lobes (Figure 5), and suggest functional relation of all of them via the upward and outward movement of saturated soil (Andersson, 1906; Högbom, 1914; Frödin, 1918, Beskow, 1930; Hopkins & Sigafoos, 1950; Hanson, 1950; Warren Wilson, 1952).

I agree with Washburn (1956) that frost-boils are frost-scars (Hopkins & Sigafoos, 1950), but I believe that upwelling of fines is necessary for their formation. Bergström

---

surface where scattered *Puccinellia* and *Phippsia*, *Stellaria humifusa*, and lichen thalli grow. The sinuous pattern of coarse sand in the crack suggests that the crack is formed by forces pulling the meshes apart, not pushing them apart. The present crack on one edge of the trace suggests that the site of the crack is perennial but that the exact location may vary two inches. The crack is in black organic fine sand with large areas of reddish stain, on temporary pond bottom on the 6 foot beach.

(1912) described mud-boils with loamy centers and the vegetation mat lifted at the margins. He suggested that saturated soil is thrust up in the center and bursts through the vegetation cover. Thoroddsen (1913), in explaining hummock formation in Iceland, suggested the segregation of crystaline ice into lenses just under the surface of bare or raised areas both updomes (swells) the surface (Figure 4) and draws up water from damp, unfrozen soil layers to allow further growth of the ice lenses. Thoroddsen observed that volcanic ash layers are bowed upward by the forces thrusting from below. This mechanism specifies Högbom's frost thrust, clarified by Hamberg (1915) as to the direction in which it acts, i.e., only perpendicular to the cooling surface. It further uses ideas later specified and supported experimentally by Taber (1929, etc.) relative to aggregation of ice lenses on crystalization, a process which will draw water from thawed soil. Thoroddsen (1913) also suggested that cryostatic forces are produced as frost penetrates the bare soil between vegetation hummocks and then into hummocks from the sides, creating closed cells (see Sharp, 1942b).

We observed that even when the ground surrounding the mud-boil is still frozen four inches below the surface, water and soil can pour through the bottom of a mud-boil and fill it with silt overnight. This suggests an artesian force. Our evidence is not sufficient to analyze artesian- or hydrostatic head-force hypotheses as opposed to differential direct inter-grain pressures (Terzagi, from Washburn, 1956), nor to analyze Steche's (1933) suggestion of a colloid sol-gel alternation.

Although our observation of the movement of the water-saturated soil indicates some form of upward thrust within the column of earth, I cannot see any support for a convection theory suggested by Nordenskjöld (1909) and later rejected by him (1911); then developed as the *Brodelboden* hypothesis (Low, 1925; Gripp, 1929; Gripp & Simon, 1933, 1934a & 1934b). If there were convections, there must be movement of soil and water down again — and we found no indication of this. Furthermore, as Washburn (1950, 1956) pointed out, the mechanisms do not seem to provide adequate engineering forces.

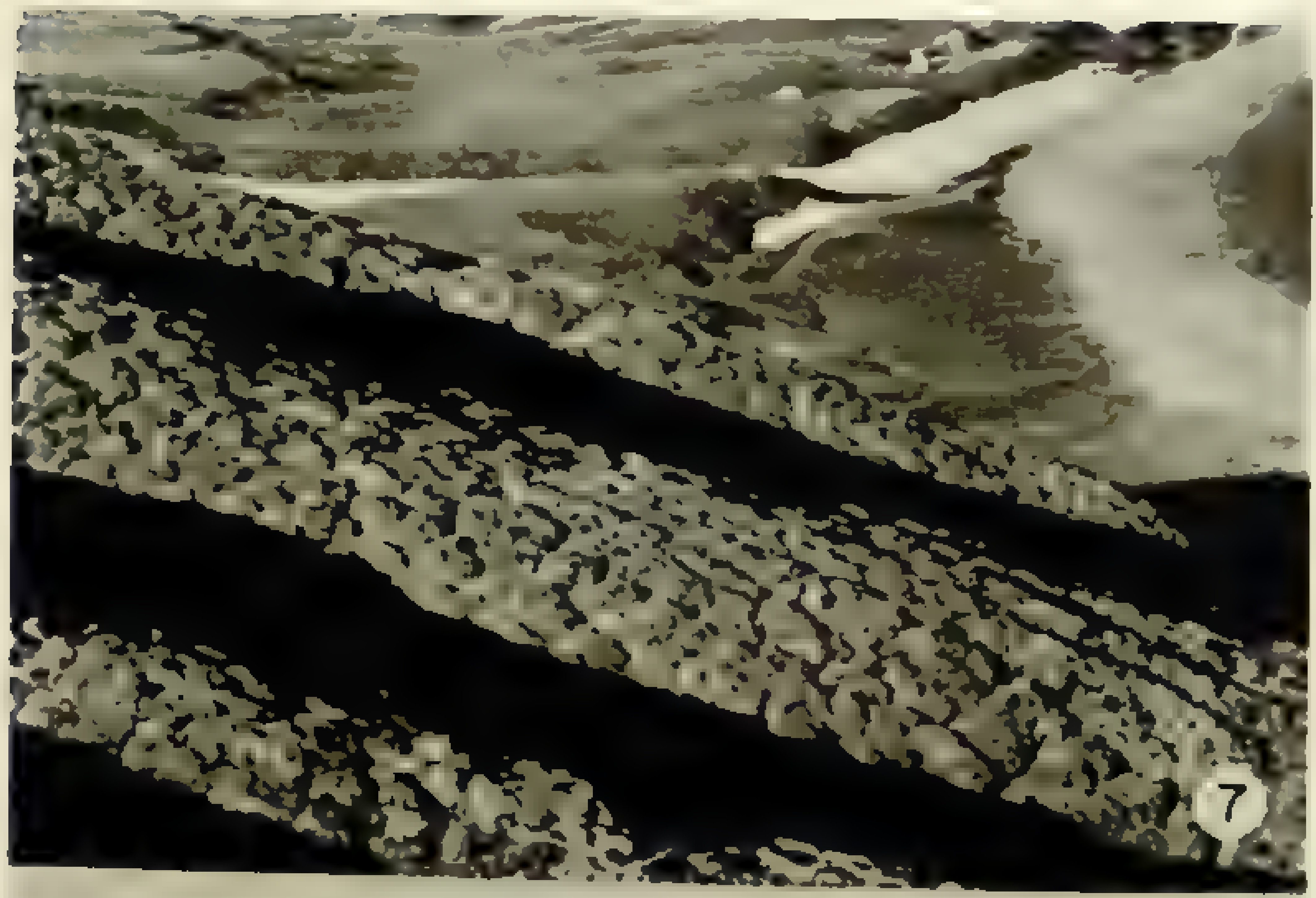
Because the action we observed was vigorous in the early part of the thaw, when daily frost penetrated an inch or less, it cannot depend upon horizontal thrusting from (a) cryostatic forces to disturb soil levels (Hopkins & Sigafoos, 1950; and Washburn, 1956), or (b) cellular containments within which frost thrust creates involutions (Sharp, 1942b). Both these require the pressure to be applied to unfrozen spots when most of the active layer is freezing onto the permafrost. If a long, intense freeze occurs following a week of thaw, suitable cryostatic forces may develop, but these did not develop in the summer of 1954.

When plants start to grow rapidly in the spring, the soil in mud-boils and stripes is deeply thawed. Movement in the fluid soil, and the results of freezing and thawing, create stresses in the growing root tips still partly frozen in. The process is self-stimulating because once the soil is bare, it is more subject to rapid and deep freezing and thawing than are the neighboring vegetation-insulated areas. Many authors, beginning with Frödin (1918), have recognized these effects.

Mud-boils and non-sorted polygons. On wet, flat places such as near sedge marshes, on slopes above the bluffs west of camp, and at Ooyarashukjooeet, we found mud-boils surrounded by a roll of peat (moss-sedge-willow) and separated by depressions resembling cracks (Figure 4). Transitional forms found at Ooyarashukjooeet suggest that when moss growth from the edge of the boil colonizes the bare, raised center, these boils merge into moss-covered hummocks which are regularly spaced so that the depression between hummocks resembles a crack. Some of these are raised mud-boil-hummocks; some are completely covered with vegetation and resemble moss or tussock hummocks (*Thufur* of Thoroddsen). On the other hand, mud-boils on upland, south-facing slopes merge into irregular net patterns on which lines of prostrate Arctic Willow surround bare earth meshes (Figure 5). The origin of patterns of hummocks separated by cracks is discussed below, after the development of contraction cracks.

C. Contraction cracks on the youngest alluvial surfaces

On the bare, muddy pond shores of the 6- and 16-foot beaches east of camp, there are cracks forming polygons 1-5



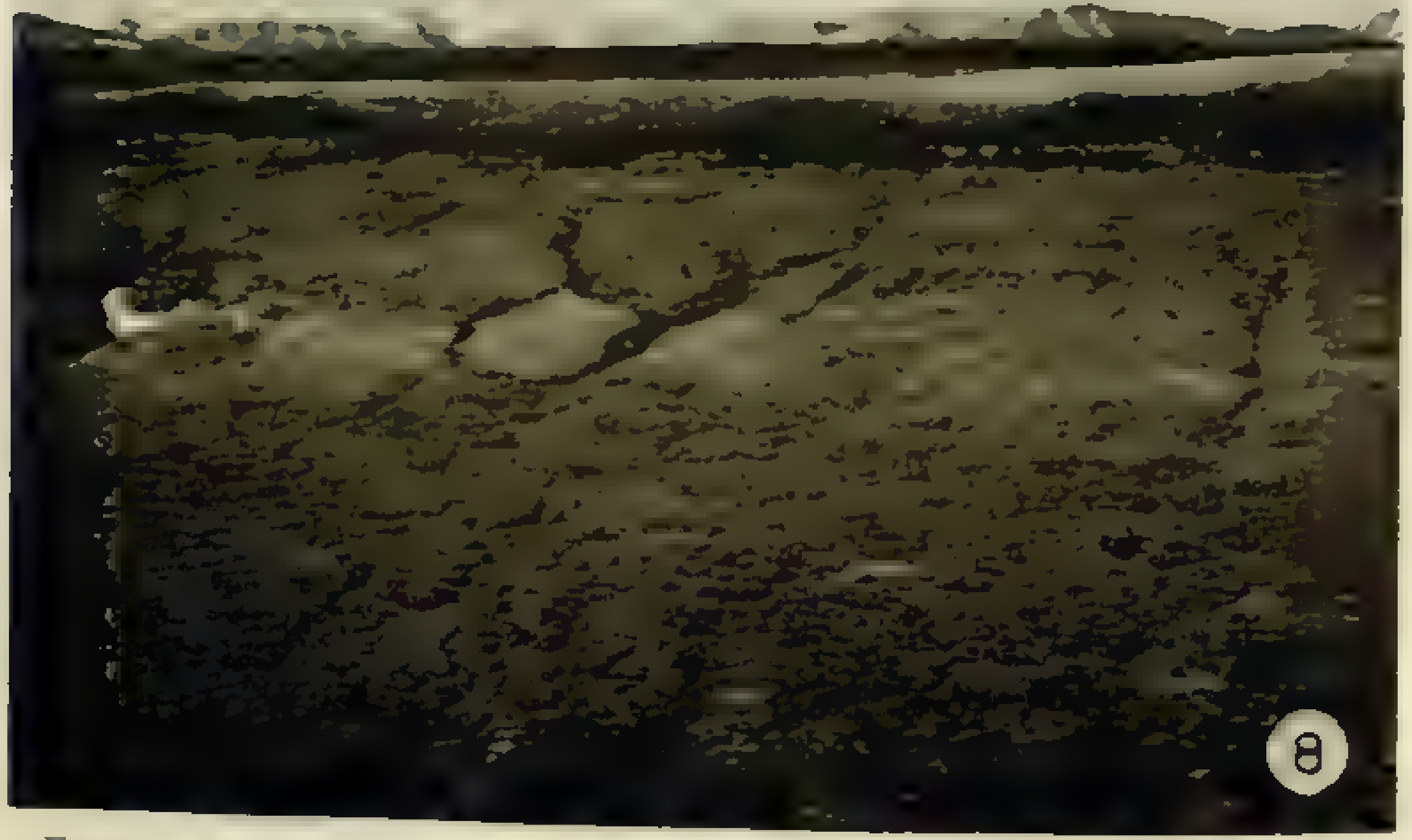


FIGURE 7. HUMMOCK POLYGONS ON SOUTH SLOPE. Hummocks of black, heavily organic soil overgrown chiefly with sedges and Arctic Willow are outlined by cracks. Neither ice cores nor ice wedges were found in excavations to the frost table. Site is south slope above The Bluffs

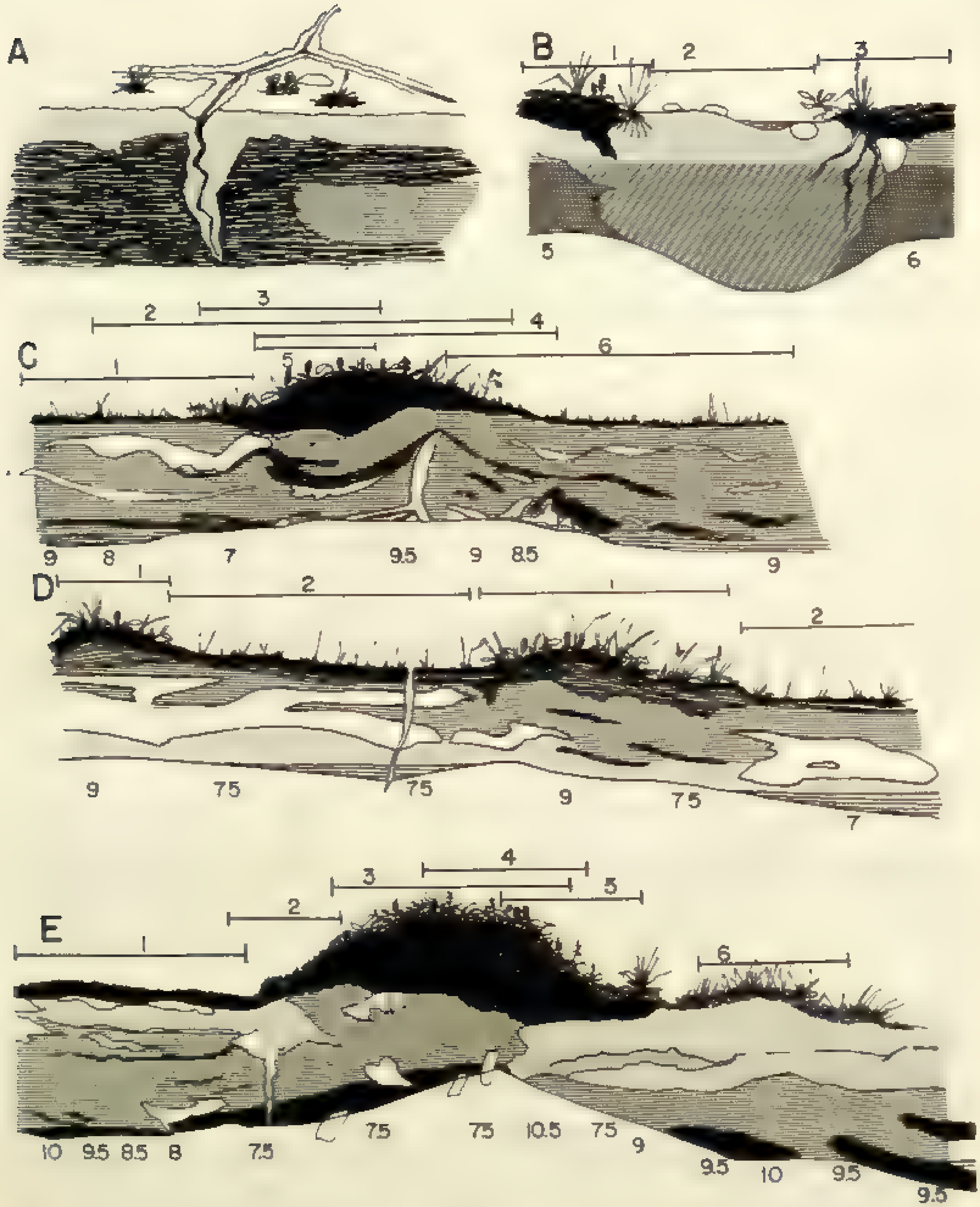
FIGURE 8. FROST-CRACK PENTAGONS UNDER LATE SNOWBANK. Photograph across steep valley side about five miles west of camp. Pattern of cracks is emphasized by thawing under a persistent snowbank whose extent is shown in the vegetation. Characteristic vegetation zonation is shown: (1) ridge-top barrens on top right: (2) Bell Heather zone: (3) Arctic Willow where snow persists: (4) tan area near deepest cracks is

feet in diameter. Excavations show that these cracks (1) are perennial, (2) contain coarse sediments and organic material, including leaves of previous years' vegetation (Figures 6 & 9A), and (3) often have a zone next to them where there is much less organic material than in most of the deposit (Figure 9A). As Washburn (1956) pointed out, these cracks grade horizontally into polygonal cracks marked in the vegetation on the low slopes. They also grade into hummock patterns.

As the snow first melts away from these surfaces, cracks appear in the bare soil which at that time is thawed only to a depth of a couple of inches. Cracks without regular pattern, as much as seven inches deep and several feet long, appear on open slopes (Figure 12), but in wet, muddy areas they tend to gather into pentagonal or hexagonal patterns (Figure 6). Excavations across them show no disturbance of the soil profile (Figures 9A, C, D and E). In time these cracks become filled with pebbles or organic material (Figures 10E, H, I, J, K, and 24 B). Our observations are that: (1) during the thaw they open every night when the surface freezes, and close during the day; (2) they may be open or closed as the snow lies on the ground (Högbom, 1914) and they close during the late stages of the thaw; (3) they open late in the season as the whole surface dries out; (4) their opening is not the result of thrust of materials that collect in the cracks, as is shown by these excavations (Figures 6, 9A and D, 10H, I, J and K, and 12). One force opens the crack when the ground is frozen, closing it at the first part of the thaw; and a second opens the crack as the soil changes from a saturated to a damp, tacky mass. Both freezing and drying draw free water out of the wet soil. Many authors have proposed hypotheses for formation of cracks without depending upon cold or dry contraction, but all involve sorting of soil particles. Högbom (1914) and Sapper (1912) agree that drying alone is not a sufficient mechanism to explain the formation of polygonal cracks *(Zellenboden, Spaltenboden)* for the following reasons: (a) drying cracks usually have an irregular pattern; (b) they do not cut so deeply into the soil as the observed cracks; (c) the tops of

---

where snow lay longest Arctic Willow and sedges. (5) Arctic Willow, Avens, Bell Heather mixed vegetation near the figure. Note the small polygons within the larger patterns.



9

FIGURE 9. EXCAVATIONS INTO CONTRACTION CRACKS, PEAT RIDGES, AND MUD-BOIL. Horizontal lines and numbers above diagrams refer to vegetation. Numbers below diagrams indicate depth to frost.

A. Pentagonal pattern of contraction cracks on bed of temporary pond.
Soil: Stippled is gray sand.
Horizontal shading is black organic sandy silt.
Horizontal hatching is red silt.
Note that the crack is marked by coarses and that crack zigzags down its depth and is not in its center. The crack must reappear in the same area, but not exactly the same, year after year.
The surface is a rough scum, with binding of algal growth.

B. Mud-boil on Raised Beach.
Excavation on 19 June. The edges of most boils are steep and uniform, without "floating" fragments of organic soil. Roots of living plants at the edges of the

boil suggest that the soil there is stable. There are several stones on the surface of the boil, and such stones are scarce through the soil. These stones usually have a crack around them when the surface dries out.

Soil: Black is organic.
Stippled is gray sand.
Horizontal hatching is gray-brown sandy silt.
Diagonal hatching is water level.

Vegetation: (1) Hypnaceae,, *Luzula confusa, Salix reticulata, Dryas intergrifolia.*
(2) Barren with scattered *Cladonia* thalli and dead Hypnaceae.
(3) Hypnaceae, *Luzula confusa, Salix arctica,* and *Dryas integrifolia.*

C. Isolated peat ridge across depositional slope on 16-foot beach.

Contrary to expectations, peat ridges thawed first on the lowland surfaces and the frost table was barely raised under them. Vertical trace of red soil suggests buried contraction crack and frost-heaving in soil layers associated with it.

Soil: Black is organic.
Horizontal shading is organic silt.
Horizontal hatching is gray-brown sandy silt
White is red ochre silt.

Vegetation: (1) *Campylium stellatum, Drepanocladus,* and *Carex aquatilis.*
(2) *Polytrichum piliferum* and *Tortella.*
(3) *Aulacomnium palustre.*
(4) *Tomenthypnum nitens, Carex aquatilis,* and *Saxifraga oppositifolia.*
(5) *Salix arctica* and *Pedicularis lanata.*
(6) *Drepanocladus* and *Carex aquatilis.*

D. Two parallel hummock ridges across depositional slope on 16-foot beach.

Contraction crack was open to a depth of at least 3 inches when the snow melted from this surface 25-28 June.

This, like other contraction cracks in frozen soils, was filled with dead leaves which must have gathered while the crack was open.

Soil: Black is organic.
Horizontal shading is peaty, sandy silt.
Horizontal hatching is gray-brown sandy silt.
Stippling is gray, sticky, sandy silt.
White is red ochre sandy silt.

Vegetation: (1) Tan *Drepanocladus, Tomenthypnum nitens, Tortella, Carex aquatilis,* and *Salix arctica.*
(2) Black *Drepanocladus, Campylium stellatum, Polytrichum piliferum,* and *Carex aquatilis.*

E. Tall, isolated peat ridge on 16-foot beach.

Vertical red silt trace suggests buried contraction crack. Angular stones on edge occur under the ridge and embedded in frost table. Note that depths to frost show less variation than surface features suggest.

Soil: Black is purely organic.
Horizontal hatching is dark chocolate, sandy silt.
Stippled is gray sandy silt.
White is red ochre sandy silt.

Vegetation: (1) *Drepanocladus.*
(2) *Tomenthypnum nitens.*
(3) *Salix arctica.*
(4) *Salix reticulata.*
(5) *Tomenthypnum nitens* and *Aulacomnium palustre.*
(6) *Carex aquatilis, Salix arctica,* and *Saxifraga oppositifolia.*

drying cracks are usually concave, not convex, with rounded edges; (d) the arctic forms appear when the earth is wet, and the cracks do not close even when covered with water; and (e) drying cracks occur in many regions, whereas the forms under consideration are restricted to the Arctic. European authors, following Högbom (1914) have in general rejected the idea of contraction due to drying (Andersson, 1906; De Geer, 1910; Meinardus, 1912) as a possible mechanism. Steche (1933) retained this hypothesis and Washburn (1950, 1956) has resurrected it.

My observations show that when the surface gradually dried in the late evening, the cracks remained damp longest. The water does not withdraw deeply because each morning the dry and frozen crust is only an inch or two deep. Below it there lies 10-12 inches of wet soil, still above the frozen ground. If hydrostatic pressure from water in the zone between two frozen layers led to the cracking upward of the frozen surface, water or silty material would flow up through the cracks thus created (viz., Frödin's 1918 excavations) and the cracks should form at the center of the stress and radiate outward. On the contrary, we found no indication of flow of water up through the cracks, and did find that the cracks form on the margins of the jelly-like mass, as if resulting from contraction.

The formation of cracks by differential segregation of fines which soak up moisture, gathering ice which thrusts upward and, when confined, outward, leading to the formation of cracks, is not shown in these soils in which there may be, in fact, segregation of coarse materials in a mud-boil. I have no evidence of thrust at the sides of the cracks, although I do have evidence of thrust at the side of the mud column. I agree with Washburn that there are probably several mechanisms involved in origin and several in subsequent modification.

D. Hummock polygons

On the steep slopes of the 16-foot beach, on areas covered late by persistent snowbanks, on the banks of small creeks or rivers, and on open slopes which are covered by shadows in the late evening (Figure 7), a regular pattern of polygons appears which is a combination of vegetation, hummocks, and cracks. In some places, contraction cracks draw an angular outline around small solifluction lobes (two feet across); on others the mesh is a luxuriant growth of mosses, Arctic Willow and often Bell Heather; in others the cracks are obscured by the growth of moss. Erosion may produce a slope covered with hemispherical knobs. I agree with Thoroddsen (1913), Frödin (1918) and Sharp (1942a) that these several expressions are related.

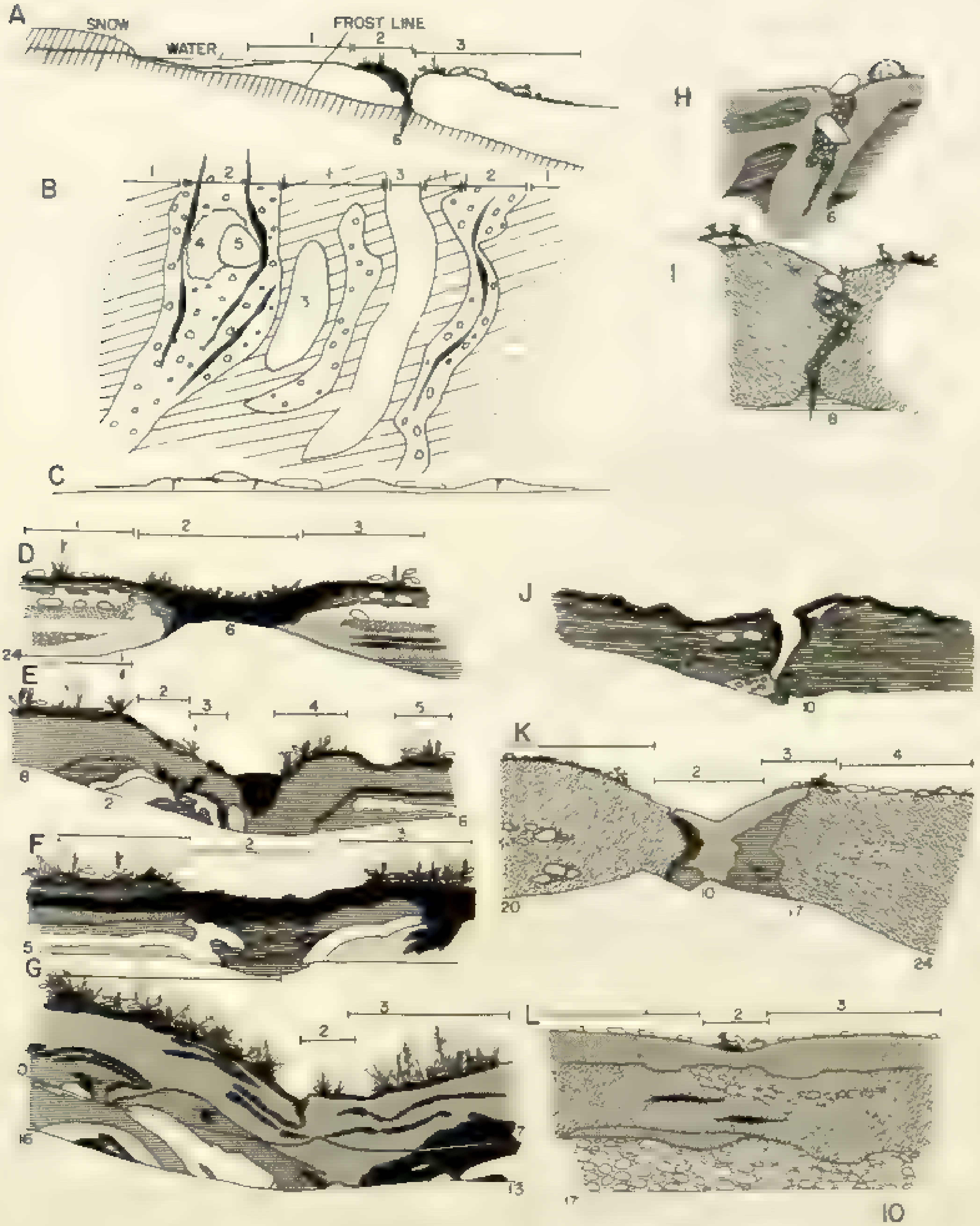


FIGURE 10. EXCAVATIONS INTO CONTRACTION AND DEFORMATION CRACKS. Horizontal lines and numbers above diagrams refer to vegetation. Numbers below diagram indicate depths to frost in inches.

A. Down-slope section showing snow patch, melt-water pool, frost-oval mound and mesh.

The crack is filled with dead leaves and has an ice wedge in the bottom. The soil is a coarse, sandy silt with pebbles and stones, and is soaking wet.

Vegetation: (1) Bare: Clumps of *Alectoria jubata*, *Stereocaulon alpinum*, *Stereocaulon paschale*, *Parmelias*, small *Hypnaceae*, and *Luzula confusa*.

(2) Peaty edge of crack: *Hypnaceae*, *Luzula confusa*, *Saxifraga oppositifolia*, *Cassiope tetragona*.

(3) Edge of mesh: *Alectoria jubata*, *Alectoria ochroleuca*, *Stereocaulon paschale*, *Thamnolia vermicularis*, four small *Hypnaceae*, *Salix arctica*, and *Saxifraga oppositifolia*.

B. Plan of mounds, meshes, and contraction cracks.

(1) Cross-hatching is *Stereocaulon paschale*, *Hypnaceae*, *Luzula confusa*, *Saxi-*

fraga oppositifolia, *Papaver radicatum*, and *Cassiope tetragona*.

(2) A mound: sandy silt with pebbles and some stones 5-12 inches long. Clumps of *Alectoria jubata*, *Stereocaulon alpinum*, *Stereocaulon paschale*, *Parmelias*, *Hypnaceae*, *Poa arctica*, *Luzula confusa*, and *Saxifraga oppositifolia*.

(3) Snowbank.

(4) *Poa arctica*, *Luzula confusa*, and *Salix arctica*.

(5) Rock.

Cracks are shown black; note their sinuous form. Soil of mounds is churned and damp with subsoil showing where it has been heaved up from below.

C. Diagramatic section across "B" to emphasize that contraction cracks occur on the high parts of mounds.

D. Deformation crack on vegetated, lower southeast-facing slope.

Crack is filled with organic silt and peat. The section shows lenses of sand and peat in the gray-brown coarse silt and a 4-inch layer of red stain on the right of the crack. This excavation runs parallel to the edge of a raised beach across a perpendicular crack. At 8-10 inches below the surface, most of the stones were cracked into many pieces and fell apart as they were lifted out.

Soil: Black is totally organic.

Horizontal shading is peaty silt.

Stippled is gray silt.

Coarse steppling is sand.

Diagonal hatching is red-brown sandy silt.

Vegetation: (1) *Stereocaulon alpinum*, *Stereocaulon paschale*, *Parmelias*, *Alectoria jubata*, *Luzula confusa*, *Saxifraga oppositifolia*, and *Cerastium alpinum*

(2) *Stereocaulon paschale*, *Thamnolia vermicularis*, *Cetraria nivalis*, *Luzula confusa*, *Salix arctica*, *Saxifraga oppositifolia*, and *Dryas integrifolia* in a dense mat of *Cassiope tetragona*.

(3) *Stereocaulon alpinum*, *Stereocaulon paschale*, *Parmelias*, *Alectoria jubata*, *Thamnolia vermicularis*, *Cladonia pyxidata*, *Hierachloe alpinum*, *Poa glauca*, *Luzula confusa*, *Silene acaulis*, *Cerastium alpinum*, *Saxifraga oppositifolia*, among big clumps of *Salix arctica*.

E. One of the pentagonal crack patterns on raised delta of Golden Plover Creek.

Soil at the edges of the crack shows soil-heaving. Heavy, gray-brown soil is associated with wet soil covered with mosses and sedges.

Horizontal hatching is gray-brown sandy silt.

Black is totally organic.

Horizontal shading is peaty, sandy silt.

Stippling is gray coarse silt.

White is red ochre, coarse silt.

Vegetation: Black V-shaped area to the left of center is fibrous organic material, chiefly roots.

(1) *Stereocaulon paschale*, Hypnaceae, *Carex*, *Luzula confusa* and *Salix arctica*.

(2) Bare, with clumps of blackened *Hypnaceae*.

(3) Bare, with clumps of Hypnaceae and *Luzula confusa*.

(4) *Stereocaulon paschale*, Hypnaceae, *Luzula confusa*, and *Salix arctica*.

(5) Bare, with *Stereocaulon alpinum* and *Salix arctica*.

F. Deformation crack parallel to edge of raised beach.

Edges of the crack show some heaving.

Soil: Black is entirely organic.

Horizontal lines, black-brown peat.

Vertical hatching is reddish, sandy silt.

Horizontal hatching is gray-brown, sandy silt.

Stippling is gray, sticky silt.

White is orange to yellow ochre, sticky silt.

Vegetation: (1) *Stereocaulon paschale* in thick moss cover, including *Aulacomnium palustre*, *Dicranum*, *Tortella*, and *Tomenthypnum nitens*, a complete cover of sedges and *Salix arctica*, and on higher places, scattered *Salix arctica*, *Saxifraga oppositifolia*, and *Cassiope tetragona*.

(2) Bare black soil with small Hypnaceae, scattered lichens, sedges, growing tips of willows, and scattered clumps of (1) and (3).

(3) The same as (1), with *Cetraria nivalis* and clumps of *Dryas integrifolia*.

G. Crack below raised beach and exposed plateau.

Note appearance of successive organic layers and what appears to be windblown fine sand from the exposed area. A fresh contraction crack appears in the characteristic place next to the steeper slope.

Soil: Black is organic material mixed with fine sand.

Diagonal hatching is reddish-tan, fine sand.

Horizontal hatching is chocolate-brown, silty sand.

Stippling is gray silty sand.

White is red ochre silty sand.

Depth to frost at 7-10 inch level is 22 June; at 13-16 inch level is 30 June.

Vegetation: (1) *Carex Bigelowii* and *Salix arctica* mats.

(2) Black, bare soil with clumps of *Carex Bigelowii* and *Luzula confusa.*

(3) *Carex Bigelowii, Carex aquatilis,* and *Salix arctica.*

H. Crack in frost-oval mound.

Crack is filled with pebbles up to 1 1/2 inches in diameter.

Diagonal hatching is tan fine sand.

Horizontal shading is red-brown to nearly black fine sand.

Vegetation: On edges of the crack is dense growth of *Stereocaulon alpinum;* in the crack are *Parmelias,* dead Hypnaceae, *Saxifraga oppositifolia,* some *Rhacomitrium lanuginosum* and *Polytrichum piliferum,* and cushions of *Saxifraga oppositifolia.*

I. Crack on frost-oval mound, Tui-Tui Tabletop.

Crack, filled with pebbles, is 8 feet long.

Soil: A mixture of coarse and fine sand; a vein of ice mixed with dirt and organic material follows the line of the crack, the trace of the crack showing in the frozen soil below the frost table.

Vegetation: The nearly bare soil of the mound has scattered clumps of *Saxifraga oppositifolia* and clumps of *Cerastium alpinum* and *Sagina intermedia* grow on the edges of the edges of the crack.

J. Fresh contraction crack on deformation crack on boggy slope.

Fresh crack is on the down-slope side of the major crack. Diagram is 3 feet across.

Soil is chiefly black-brown peat mixed with silty sand, in which are barely detectable patches of gray silty sand. A lens of pure ice rises an inch above the frost table and extends along the crack.

K. Crack on east slope of exposed plateau.

Soil is reddish-tan coarse and fine angular sand with lenses of coarse sand and gravel.

Horizontal hatching is brown fine sand.

Diagonal hatching is red-brown sandy silt.

Black is organic material.

Vegetation: (1) 2 1/2 feet, black crustose *Parmelias* on stones, *Stereocaulon paschale,* some *Rhacomitrium lanuginosum* and *Polytrichum piliferum* and cushions of *Saxifraga oppositifolia.*

(2) One foot, bare.

(3) 8 inches, black crustose *Parmelias, Stereocaulon alpinum, Saxifraga oppositifolia.*

(4) Barren with crustose *Parmelias* on stones, and *Stereocaulon paschale.*

L. Open gravelly surface of frost-ovals on east slope.

The surface layer of silt with a pavement of pebbles 1/4-1 inch in diameter is underlain by coarse sand with lenses of organic material and gravel overlying river-borne or beach sandy gravel.

The major polygons appear on the bare surface as lines of isolated *Stereocaulon alpinum,* black *Parmelias* on stones, *Luzula confusa, Salix arctica, Cerastium alpinum,* and *Saxifraga oppositifolia.*

Excavations such as this suggest that contraction cracks have worked the entire surface, churning the subsoil so that the soil pattern of deformation crack has been obliterated at least to the depth of the frost table in late June.

(1) The best development of mossy hummocks in our study area is on the 15°-20° slope between Snow Bunting Creek and Lark Gully (Figure 7). The slope is sheltered

from the east wind, faces south, and is early free of snow. In early July, a shadow from the bluffs covers this slope and the hummocks conform to the outline of the shadow at 1600. The hummocks are ill-developed where the shadow does not appear until after 1900. These forms resemble the features described by authors as *Bülten* (Tanttu, 1915), *Hügel* (Steche, 1933), and *Thufur* (Thoroddsen, 1913), but the hummocks I excavated did not contain an ice kernel and are too small for the *Palse* of continental tundra, called, *Pingos* by Porsild (1938). They consist of moss growth around an earth center, and stand 5-15 inches high, averaging 18-24 inches across. Mineral soil rises 1-10 inches in the base of the hummock and in some cases erupts through the top (cf. Figure 4). Above the mineral soil core, there is a 3-8 inch transition level of increasingly organic material, and the top of the hummock is usually capped by lichen growth except where mineral soil bursts through.

Because the south slopes are free of snow early in the spring, they are exposed to a long period during which the temperature rises above and falls below freezing; furthermore, the daily passing of the shadow over the slopes (a) increases the intensity and frequency of freezing and thawing, and (b) preserves moisture. The tops of the hummocks are dry (as shown by growth of lichens), and this may indicate both that the soil mechanisms are overextended and that the tops are exposed to the wind. The vegetation changes in these hummocks, reflecting differences in moisture and shelter, are the same as those on the edges of peat ridges or frost-cracks described below. Billings and Mooney (1959) discuss evidence that hummocks and soil polygons can form out of each other by action of the hummock-forming processes, or by drying out and degeneration accompanied by plant growth between hummocks.

(2) On other steep south- or west-facing depositional slopes, such as below terrace banks, there occur hummocks which form polygons 18-24 inches across, separated by cracks 3-10 inches deep. On the edges of persistent snowbanks these hummocks are especially high, and a turf may grow so that when the snowbank has melted away, its position is marked by a hollow. It must be, then, that a supply of water and the time of year when rapid growth

can take place are both important in the growth of these hummocks.

(3) Hummocks appear on the lower parts of unstable and nearly vegetation-free slopes, where the vegetation is first able to hold on; and as a better cover is formed, the hummocks grow taller and better integrated. These hummocks are of mineral soil below, with a humus layer, and are colonized chiefly by Arctic Willow. They are regularly spaced in a pattern such as is shown in Figure 7.

Origin of hummocks and hummock-polygons. The two forms are similar in origin, both dependent upon the formation of contraction cracks and differential growth of plants.

(1) The mechanism for the origin of mossy hummocks, first suggested by Thoroddsen (1913), does not depend upon a tussock of sedge or grass as do those described by Hopkins and Sigafoos (1950). They do not resemble the hummocks and ridges probably resulting from a combination of tussock growth, loess deposition and erosion in the New Zealand Mountains (Billings and Mark, 1961). I presume, however, that the moss hummock serves the same insulation function as the sedge or grass tussock to create discrete units of insulation and water-holding which tend to be isolated from the next unit by an area exposed to cold and wet. Tanttu (1915) suggested that moss hummocks in bogs freeze later in the autumn and are squeezed as the frost penetrates, and that they freeze deeper in the winter because they have a shallower snow cover so that ice persists in them in the spring.

(2) The origin of hummocks on drier surfaces is associated with the appearance of perennial contraction cracks, as the depositional slope builds up. Plants colonize the edges of small solifluction lobes, tending to retain moisture and hold the polygon together, as shown by transitional forms on the snout of talus slopes. The cracks form every year and plant growth thickens on the top and sides of the polygon. Then the hummock grows as above. On steep slopes, drainage may erode the cracks and in some places the hummocks grow together (Thoroddsen, 1913; Sharp, 1942a). This results in some hummocks being 18 inches across, with a crack or depression 9 inches across between them. The pattern still keeps an overall regularity (Figure 7).

The size, pattern and structure of these cracks and hummocks grade in type and space into the cracks formed on muddy, flat surfaces, as discussed above (Washburn, 1956).

E. Micropolygonal patterns — Zellenboden

The surface of many bare meshes is marked with hundreds of inch-long eruptions. These change the surface aspect and create an effect found frequently on the tops of New England mountains. In its fullest expression, each lump is surrounded by a polygon of small cracks, but in some places (with less slope and less exposure) the crack polygon surrounds every three to five eruptions, and the pattern is not as regular (Figure 11 bottom right corner). In other places, a net of the finest silt, or sand and small pebbles, surrounds a mesh of dark silt eruptions. These patterns penetrate barely an inch into the soil. They appear on south-facing gentle slopes, early free of snow, where there is a long period of shallow freeze and thaw. In this, the sites have climate similar to that of the temperate zone mountains. Having read Troll (1944), I looked for situations to mimic alpine conditions, and finding miniature forms in such places supports his thesis.

These micropolygons resemble those illustrated in Högbom (1914, p. 320). They appear to be the result of two forces — one which thrusts fine soil out through a more or less dried surface, and another the result of tension as the cheese-like surface layers draw together.

Once the eruptions and tension cracks are formed, the knobs dry; and in the early stages of stabilization, pioneer plants — lichen thalli and algae — colonize. Drying draws the lump together, aided by wetting and frost-thrust from needle ice. The alga-lichen crust holds the knob together when water runs in the cracks.

Some slopes, down which the overflow from upland ponds and sedge marshes drains, are covered with knobs three inches across, encrusted with tiny mosses and surrounded by one-inch deep cracks. Several knobs together may be surrounded by a deeper crack. These merge into soil stripes of higher, darker soil, alternating with depressions filled with thicker moss growth and having a sinuous crack down the center. Thus they are transitional forms in which micropolygons are superimposed upon a pattern of soil stripes.

F. Five- and six-sided polygons

A variety of polygonal patterns is expressed on the vegetated, dry uplands. These depend upon patterns of frost-cracks and are divisible into two types: the first are generally four-sided (*Taimyrpolygone* — Steche, 1933; Troll, 1944); the second are usually pentagons and hexagons *(Spaltenboden)*. Frost-cracks are one of the major expressions of frost action in polar regions and were described almost as early as sorted polygons. Washburn (1956) referred to Figurin (1823, p. 275-276) and Von Baer (1838, p. 403), both of whom reported frost-cracks and ice veins, as did Von Bunge (1884 and 1887) from Siberia. Their distribution, as far as I can discover, is correlated with alluvial deposits and intensely cold continental climates subject to occasional rapid and extreme temperature oscillations (cf. Troll, 1944). I will discuss the development of four-sided patterns in the next section.

We found three sizes of pentagonal or hexagonal polygons expressed in the vegetation: (1) a pattern 10-20 feet in diameter, within which was (2) a pattern 3-8 feet in diameter, and within this (3) a pattern 5-12 inches in diameter. If the major pattern is 25 feet across, the next is 10 feet across and within this is a pattern 3 feet across; or within a pattern 10 feet across is one 2 feet across, within which is one 5-8 inches across.

Are all these patterns the result of similar mechanisms? How do they develop and how are they modified? How do the combinations of cracks exist together?

Figure 8, taken across a steep valley, shows a large pattern in which the cracks are emphasized by thawing, presumably as a result of melt-water flow from a persistent snowbank whose area is evident in the vegetation. On most of the uplands these patterns appear only as changes in relative abundance of bare places, mosses and lichens among the mat plants. In some upland areas the meshes are completely barren or occupied by low hummocks; in other areas the whole surface is covered with vegetation — the meshes covered with Hypnaceae mosses, lichens, grasses and *Dryas*, while the patterns of "cracks" are marked by loose mosses and taller growths of Arctic Willow and Bell Heather. These variations are discussed below under "Vegetation."

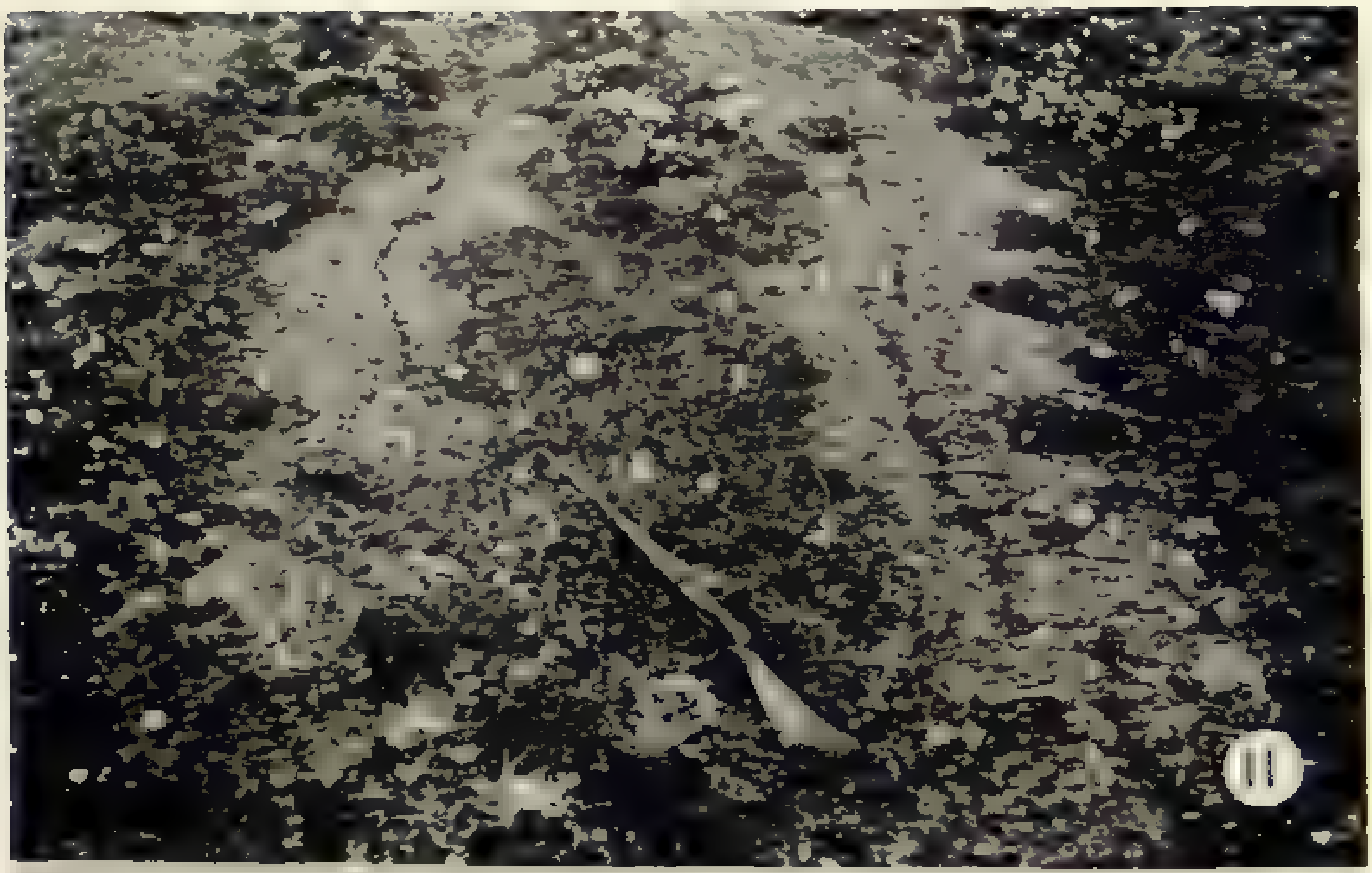


FIGURE 11. CONTRACTION CRACK IN NON-SORTED STRIPE. The soil is damp in the contraction crack just below the surface. A depression runs down the center of the vegetation stripes. Vegetation is chiefly sedges, Avens, Locoweed and Bell Heather on a heavy ground cover of Hypnum and clump mosses. Photo taken on a south slope near Oovarashukjooeet at about 300-foot elevation.

FIGURE 12. CONTRACTION CRACK AND PEAT RIDGE ON 16-FOOT BEACH. This crack is in depositional slope material from 35-foot beach (see diagram, Figure 9D). The soil is black, wet, and peaty and is pulled open, not in any way disturbed by the crack

Black (1952), discussing polygons on the arctic slopes of the Brooks Range in Alaska, suggested that the smaller crack-polygons form within the larger meshes as the surface becomes older. Most authors agree that the cracks are formed by the growth of frost wedges or ice wedges, as Von Bunge (1902), Leffingwell (1915, 1919), and Russian authors (see Muller, 1947) suggested — with modifications by Taber (1943). Non-sorted patterns and cracks of smaller dimension have been largely passed by, being of interest chiefly to botanists, while geologists have concentrated on sorted rings and nets.

My studies suggest that cracks on bare alluvial surfaces and the tops of mud-boils are caused by contraction as excess water present during the height of the thaw leaves the soil. They suggest that the large hexagonal and polygonal patterns widespread upon the uplands are the result of some other contraction force. The latter force may be intense cold and the formation of ice wedges. My studies did not examine their formation. Southern Bylot Island appears to be an ideal area for further excavations in this study.

IV. The Origin and Modification of Major Four-sided Patterns of Frost-cracks

Frost-cracks (or frost-gulls, see below) of the second major type — four-sided — are 1-4 feet across and extend an unknown depth into the ground; the meshes are 20-100 yards across and 30-500 yards long (Figures 13, 15, 16, 17 and 20). On level or gently-sloping surfaces, these cracks run parallel or at right angles to the shore (Figures 13, 15 and 20). Characteristically, a well-developed frost-crack runs just below the crest of a raised beach and intersects several cracks running at right angles to the beach. On the vegetated uplands, the traces of these cracks are in places so suppressed that they are visible only in details of the vegetation and in excavations. Cracks are most clearly expressed on south-facing slopes: (1) on flat, well-vegetated surfaces, the pattern is usually marked by peat ridges and rectangular ponds (Figures 21, 22 and 23); (2) on exposed surfaces, the pattern often appears only as a line of lichens or mat plants on an otherwise bare surface (Figure 18). In our camp area, the major crack-pattern extends from the hilltops across the 6-foot beach to the youngest areas of river gravels and the tidal beaches.

On the beach east of Aktineq, the broad, gently sloping surface from the mountains to the shore is marked by cracks that are essentially parallelograms (Figures 13, 15 and 20). In contrast, on the gently-domed top of Tui-Tui Tabletop, the cracks run radially from the center of the top and in concentric circles around the dome (Figures 16, 17 and 18). Elton (1927) described similar patterns on small hills in Spitzbergen. Washburn (1947) illustrated them from Victoria Island. In several places, long and especially deep cracks mark the edge of the floodplain and the upland, and run far inland for many hundreds of yards from the mouth of the river.

Frost-cracks are most vivid — often three feet across — on exposed beaches, where they may be bordered on each side by a ridge up to two feet high and four feet across (Figure 20). Cracks may be double and, although topped with sand, are usually filled with coarser material, up to middle-sized stones (Figures 19B and 20).

Péwé (1959) found similar structures in the vegetation-free areas of Antarctica, and his illustrations and discussions show that the cracks are held open "by themselves." I asked the local Eskimos whether they had seen any of these cracks open, or whether they had ever appeared different from the way they do at present. The answer was "No," but I am not sure we understood each other.

A. Geographic and climatic distribution

Troll (1944) pointed out that (1) frost-cracks occur on the arctic coast of Alaska, the arctic islands, and in north-central Siberia; (2) their distribution coincides with presence of continuous, perennially frozen ground. There seem to be two types of frost-crack patterns: (1) associated with a wet, cold climate; and (2) associated with a dry, cold climate. The type of cracks described by Von Bunge (1884) and Leffingwell (1919) seem to belong to the first, and those described by Von Middendorf (1864-1867) seem to belong to the second. Von Baer (1837/38) described both types. Troll's discussion (1944) suggested that the patterns tend to be quadrilateral in dry climates, and hexagonal or pentagonal in wet climates where there is more peat. This suggests that there may be two types of forces involved.

B. Origin of major frost-cracks

The following factors suggest that the origin of these cracks is directly related to solidly-frozen ground: (1) their formation does not disturb the parallel arrangement of sediments on the two sides of the cracks except at the very margin; (2) they occur in sediments (coarse sands) in which the finest material will not stand in a vertical wall (Figure 19B and 20); (3) they appear in a similarly-sized pattern in sediments of greatly different constitution — peat, silt, sand or cobbles.

1. *What force is strong enough?*

(a) *Contraction due to cold.* Washburn (1956) discussed the engineering forces and strains developed by super-cooling of the ground. It is a frequently observed phenomenon (Thoreau, 1854) that in the depth of winter in northern countries the ground cracks with an explosive sound. Zhukov (1944) had the most direct and specific description of this event: following a sharp drop in temperature, cracks filled with ice appeared to a depth of 2.5 meters, especially on surfaces not protected by snow. The area of study, Transbaikal, is like Bylot — little snow and temperature ranges of 25° C. In his study, he found that the cracks extended into the foundations of buildings.

Cracks of this major origin occur on Bylot (Figures 9D, 10A, B, H, I, J, 11 and 12), but I doubt that they are solely responsible for the large four-sided pattern. How can contraction be expressed in a pattern of cracks 50-100 yards apart and at right angles to each other (Figures 13, 15, 16, 17 and 20)? This requires that 5,000 square yards of surface act as a unit and that the tension and compression forces release only at the edges. Even without experimental evidence of the engineering forces necessary for such a cohesion, it seems to me unlikely that such a large unit of soil or ice should retain within itself forces of sufficient magnitude to create the cracks as expressed. A force resulting from super-cooling is released in lake ice by a number of small cracks 5-10 (not 100) yards apart — and they are not in a regular rectangular pattern, but rather scattered irregularly or radiating from centers. Washburn (1947) discussed the distance over

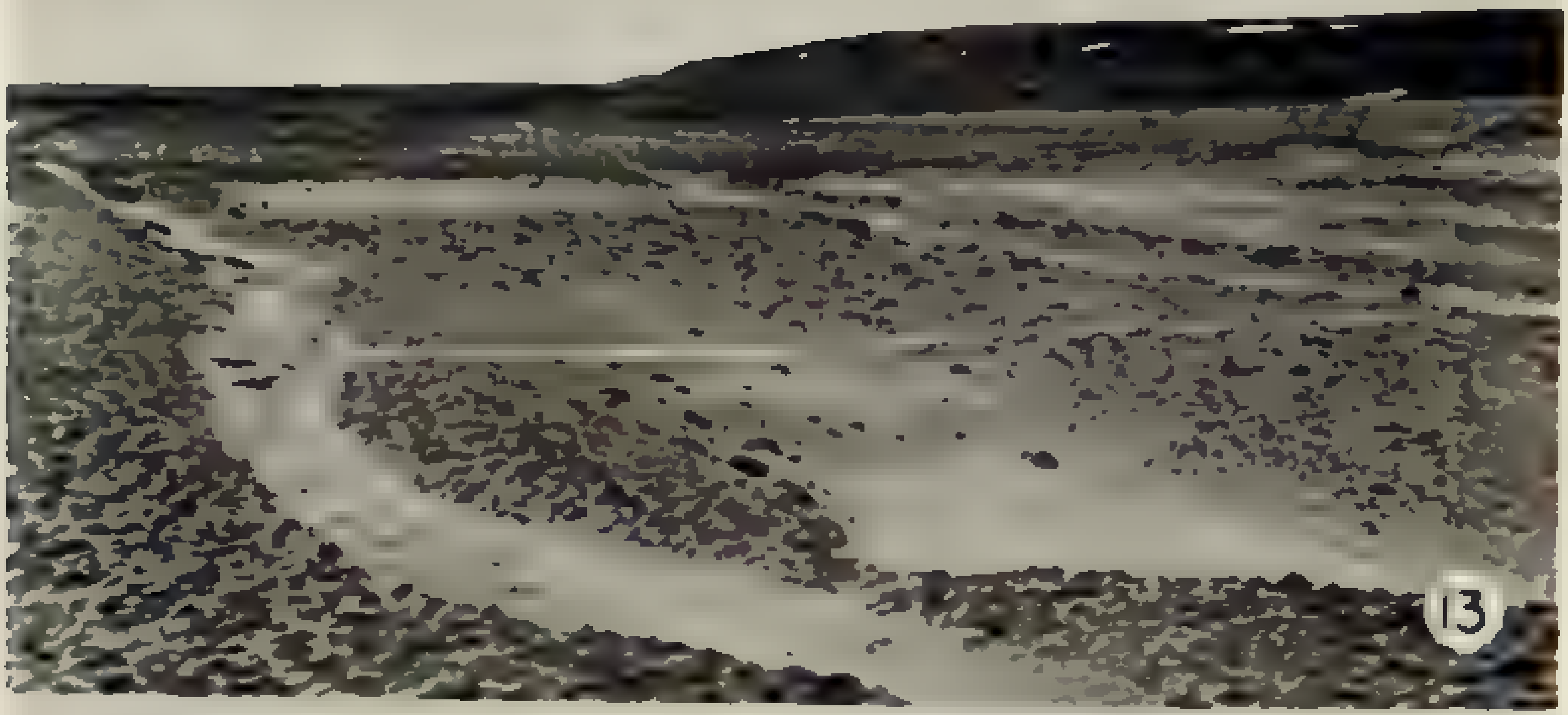


FIGURE 13. RECTANGULAR DEFORMATION CRACKS WITHOUT MOUNDS ON SEA BEACH. The shovel gives size. The cracks running away are parallel to the beach east of Aktineq, and are about [illegible] yards apart. The pavement stones are largely wind-cut and show that the wind almost always blows from the east toward the direction shown in the picture.

FIGURE 14. RECTANGULAR DEFORMATION CRACKS IN SEA ICE. Cracks about [illegible] yards and [illegible] yards apart on the sea ice along the south shore of Bylot Island east of Aktineq. These cracks form during the thaw, not in the cold of winter.

which the stress must extend (about 30 yards) to release a crack. The cracks which I discuss below (Figures 11 and 12) in the secondary modification of basic frost-crack patterns, seem to me to be of the magnitude and proper surface expression to be the result of the contraction forces suggested by Von Bunge and Leffingwell.

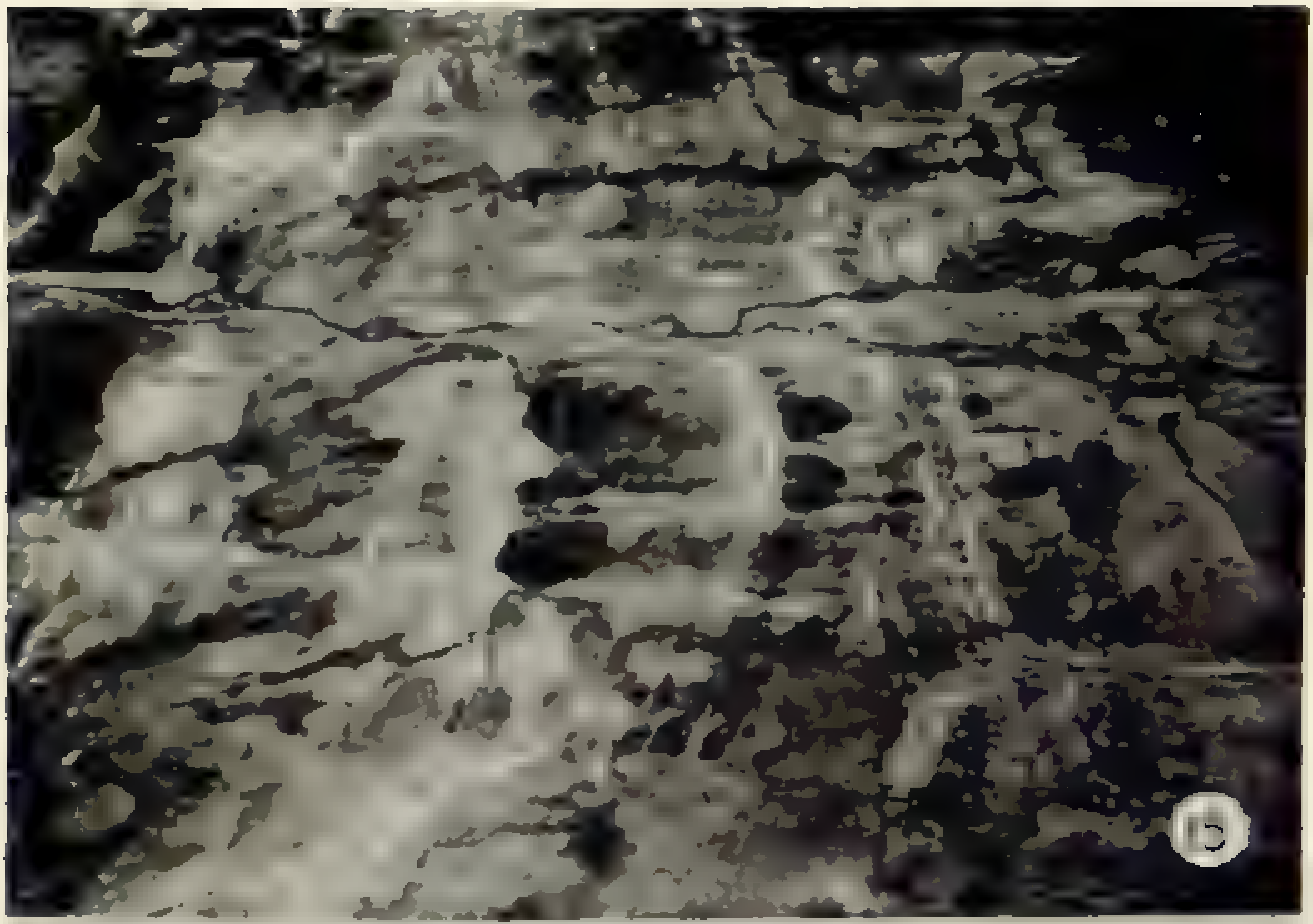
Washburn (1956) has outlined arguments against the simple application of rapid cooling contraction as an explanation for all frost-cracks. Black (1952) described the complexity and variability of polygonal patterns and their origins on the coastal plain of Alaska. He doubted any universal correlation with permafrost. Taber (1943) pointed out that there is no published evidence that contraction cracks will form regular polygons. He said: "Ice veins extend to a depth of 100 feet or more, at least three times as great as the depth of seasonal change in temperature." Taber (1943) and Beskow (1947) suggested that ice wedges (a) form by the crystallization of ice in ground fissures as moisture from the soil freezes, and (b) their growth wedges open the ground. If ice wedge growth forces open the ground, all cracks should have a mound on both sides. Some do (Figure 20); some don't (Figure 13). Dücker (1951) showed that (a) the adjacent beds are bent (see illustration in Péwé, 1957, and Figure 19B), not sheared as they would be by lateral pressure, and would result from heaving upward of areas between cracks; (b) the force due to ice formation should be perpendicular to the cooling surface. Dylik (1952) was not satisfied with Leffingwell's hypothesis and was convinced that Taber's ice formation better explains the involutions and other features related to his process—congelifluction — in Pleistocene deposits of central Poland. The excavations east of the Aktineq showed double cracks with a wedge of soil and narrow ridge between (Figures 19B and 20). For such a double crack to form by contraction or to cause a new crack to open beside the old one would halve the forces involved, and yet here the pattern size is the same — 50 yards between cracks. This crack is larger than its neighbors.

Various materials collect in the cracks: (a) ice — in cracks in the peat near Iceberg Lake; (b) organic material — in many cracks on the vegetation-covered beach levels west of the Aktineq (Figures 10E and G); (c) fine loam to coarse sand — in cracks on raised beaches near camp (Figures 6, 9A, 10H and I); and (d) pebbles and cobbles — in cracks east of the Aktnieq (Figures 19B, C, and D). In order for material to collect without dislocation of the adjacent sediments, as in these cases, the cracks must be held open by forces independent of their margins (note the slight deformation at the sides of the ice wedge illustrated in Péwé, 1957).

The presence of cobbles is, I believe, explained by a process similar to that of pavement formation on the beach surface (deflation). The sediments of the beach consist of layers one stone thick, alternating with strata of coarse sand (Figure 19B). The surface of the exposed beach is covered with a pavement (Figures 13 and 20). The layers of stones, some of which are wind-etched, suggest that the surface pavement has existed all through the period of deposition of the beach materials. Sand rests temporarily in the crack, is blown out again, and stones edge deeper while the crack remains open. Persistence and growth of the cracks, combined with the yearly effects of frost and deflation bringing stones to the surface, concentrate them and allow them to collect in the cracks. The sorting of cobbles and sand in the cracks must be an important clue to their history. The same sorting in nearly vertical wedges occurs in the upland frost-cracks of all sizes on all soils. They have been illustrated by Péwé (1959).

(b) *Deformation of frozen ground.* On a marsh-peat deposit northeast of Tui-Tui Tabletop, recently undermined at its margin by river erosion, we found large cracks lying open on 16 June. These cracks were parallel to, and perpendicular to the undercut margin and were filled with ice. Later in the season (mid-July), the cracks were filled with water, and superficial examination showed no disturbance of the peat layers at the edges of the cracks. I suggest that undermining of the edge of the peat deposits by the river has led to stresses within the frozen peat which are released by cracking. The cracks were the same dimensions and resembled those in the adjacent coarse sediments of Tui-Tui Tabletop, which is unlikely if forces dependent upon the sediments themselves are involved. The dimensions, then, must depend upon tensile strength of some factor common to both, which suggests ice in the perennially frozen ground.

On this basis, I have sought another force which would be



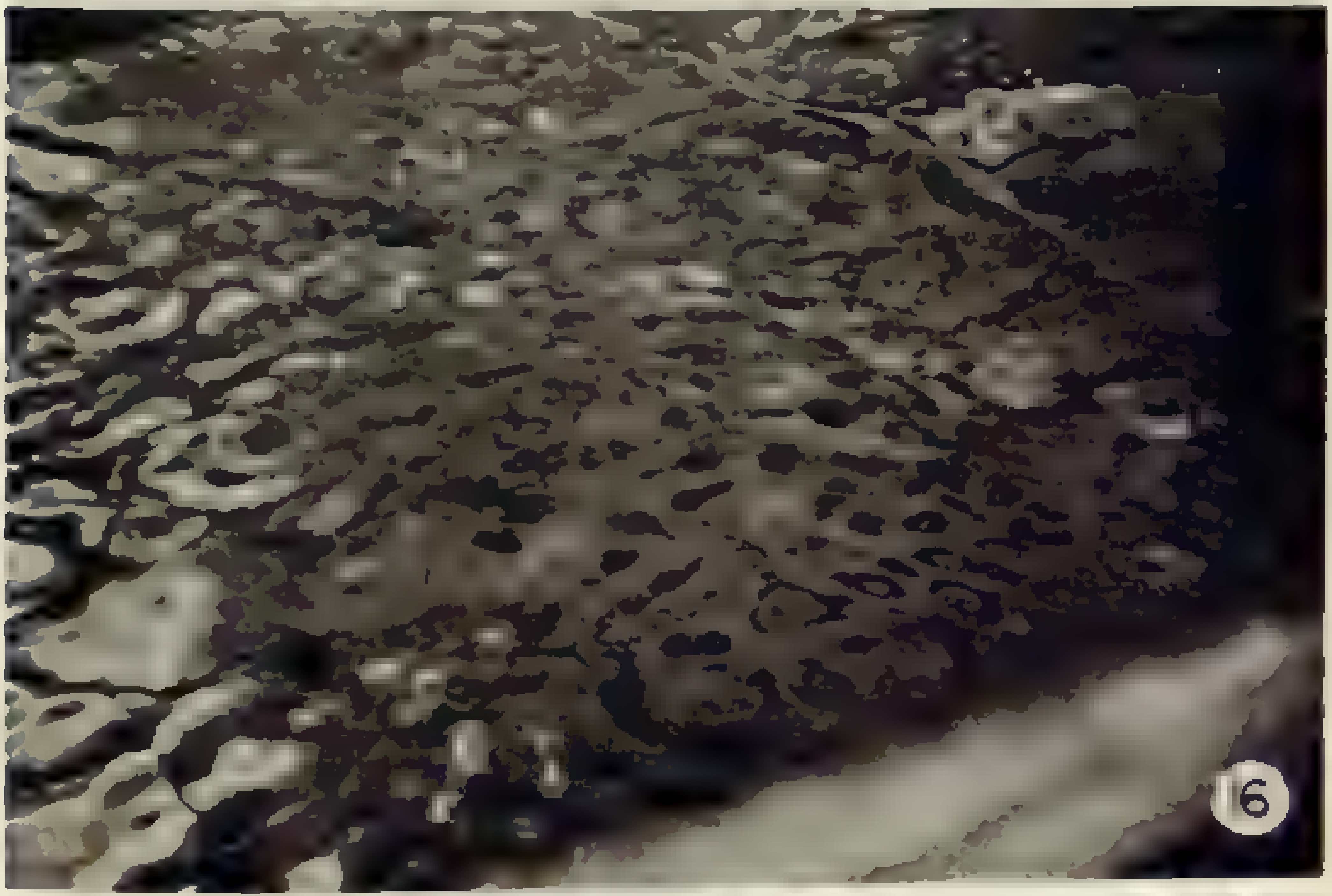


FIGURE 15. DEFORMATION CRACK RECTANGLES ON SEA BEACH FROM THE AIR. Low level aerial picture taken at about [illegible] feet above the beach east of Aktineq looking west. Incipient drainage runs from right to left and deformation cracks cross at right angles. Notice the multiplicity of the cracks in the right middle of the picture as if the surface were bending on around axis extending into the picture. [illegible] areas are ponds, muddy pond bottoms and patches of Bell Heather and Arctic Willow.

FIGURE 16. DEFORMATION CRACKS ON PLATEAU TOP FROM THE AIR. Low level aerial photo facing southeast. Notice the radiating and circular cracks on [illegible] Tabletop. Figure 17 was taken in the bottom right corner of this view. Figure 18 was taken on the lower left-hand edge.

active in a soil behaving like ice, of sufficient magnitude and acting in such a way as to create cracks of the dimension and pattern observed.

As the sea ice, approximately eight feet thick, started to break up in Eclipse Sound, it first broke clear of the shore and rode up and down daily with the rise and fall of the tide. With the passage of weeks and the continuation of the thaw, leads (cracks) formed and extended in a great sweep, first from the mouth of each river far out into the ice on Eclipse Sound; then the ice along the shore broke into rectangular pans because the cracks in the sea ice formed parallel to the shore and at right angles to it (Figure 14). We can presume that these cracks resulted from stresses, both of compression and tension, applied to the edge of the ice as a result of the rise and fall of the tide. The ice mass of Eclipse Sound released the stresses by cracking into rectangles of the same dimensions as the cracks on the neighboring beach (Figures 13 and 20). When the sea ice was let down on a boulder or bar under the water, it cracked in a radial and circumferential pattern of the same dimension and type as on the top of Tui-Tui Tabletop (Figure 16). A similar pattern can be found on frozen lakes when the water level drops the ice onto a boulder. My wife and I separately decided that these similar cracks result from deformation acting on similar materials.

Readjustment of sediments as the ice retreats — isostatic readjustment — will produce tension and compression forces in the unconsolidated sediments of Bylot Island's south shore (obviously a recently glaciated region), whose release in the solidly frozen ground should form patterns resembling those resulting from the forces exerted as the ice presses against the shore of Eclipse Sound. When sediments formed by the depositing river are covered with water or ice, they are protected from the development of perennially frozen ground; then as they are exposed, frozen ground will develop and thicken, and as the shoreline rises relative to the sea, stresses must develop between the unconsolidated sediments and bedrock, since isostatic readjustment indicates differential movement. These forces will be applied when the ground first emerges and while the depth of perennially frozen ground is still relatively shallow (less than fifty feet). This origin suggests similarity to the "gulls" described by Hollingsworth, Taylor and Kellaway (1944) and Judson (1947) when consolidated sediments are deformed. Judson suggested that ground ice wedges may be involved. Such forms should be called frost-gulls, to separate them from frost-cracks formed by contraction. The cracks on Tui-Tui Tabletop (Figures 16, 17 and 18) — a gently-mounded hill — suggest sediments let down on a bedrock core. The main bulk of materials in Tui-Tui Tabletop consists of river-borne sediments, as established by excavation, but we have no evidence of a bedrock core. Any collapse of the margins of Tui-Tui Tabletop relative to the center would create stresses and lead to radial and circumferential cracks.

2. *Are the cracks forming now?*

If the cracks are formed as perennially frozen ground thickens, and stresses are applied with the uplift of the ground, cracks should appear on the youngest surfaces in their fullest development. If, in contrast, cracks are developed gradually by annual increments of small cracks, according to the theory of contraction resulting from cooling (Von Bunge, 1887; and Leffingwell, 1919), or of ice crystalization (Taber, 1943; and Beskow, 1947), then cracks should reach their best development or complexity (Black, 1952) on the oldest surfaces.

Frost-cracks on Bylot reach their fullest expression on the lowest beaches; that is, the 6-foot and 16-foot beaches. In contrast, on the oldest surfaces the frost-crack pattern is extensively modified and, in many situations, obliterated. In fact, on the 16-foot beaches, many of these cracks have "already" been extensively modified. Frost-cracks are forming in the beach sediments below high tide and on the secondary channels of the Aktineq River. In other words, fully expressed cracks (6 inches to 2 feet across) are forming on surfaces still in the process of deposition, and are being modified as soon as they are formed.

C. Frost-cracks in other regions

The cracking of perennially frozen ground, resulting from isostatic readjustment, can be of general application in the origin of frost-cracks and polygonal ground on unconsolidated and poorly consolidated materials all across the North. Cracking is probably unlikely from this source where the bottom of the perennial frost is more than a few tens of feet below the surface, but it seems that this is a likely origin for cracks in those areas recently exposed and where the depth of the perennial frost is still shallow, i.e., alluvial and deltaic deposits, and in sediments overlain by peat — all of which are especially subject to readjustment. Presumably, contraction cracks will form within the pattern of cracks caused by the readjustment of sediments, so that this is not an "either-or" process. The windswept, snow-free surface of a beach or coastal plain is well suited for development of persistent frost, for especially effective results of sharp temperature drops, and for the formation of deeper and sharper cracks of both kinds. The deformation process can have widespread application and can influence the expression of cracks which result from rapid temperature drops.

D. Subsequent modification on windswept barrens

(1) On the most exposed areas of Tui-Tui Tabletop, the surface is a gently mounded, tan deposit of fines and angular pebbles, with the major frost-pattern indicated by thin lines of tufted lichens *(Stereocaulon)* and Saxifrage (Figure 18). (2) In areas where there is continuous thin vegetation, disturbed soil marks narrow rims next to the rectangular pattern of major cracks. (3) On the sheltered sides, densely vegetated areas show no bare soil, and here the major cracks appear as depressions or small creeks often widened by thawing and bordered by the moss-mat plant vegetation on a high mound. The center of the mesh is low and may be a marsh or a pond (Figure 17). This gradation in vegetation and exposure, shown from the air in Figure 16, gives comparative evidence on the processes concerned in the secondary modification of original patterns.

Figure 18 shows a shallow hollow on the northeast slope of Tui-Tui Tabletop, and Figures 19A, C and D show diagramatically the sediment structure. The wall of the trench shows (1) small fingers of organic soil extending down into the surface, parallel to each other and at an acute angle to the surface away from the major frost-crack; (2) indications of cobble-filled, modified wedges; and (3) undisturbed flat-lying strata. These concentrations of cobbles occur in patterns which are of the same size as the frost-cracks on the lower beaches.

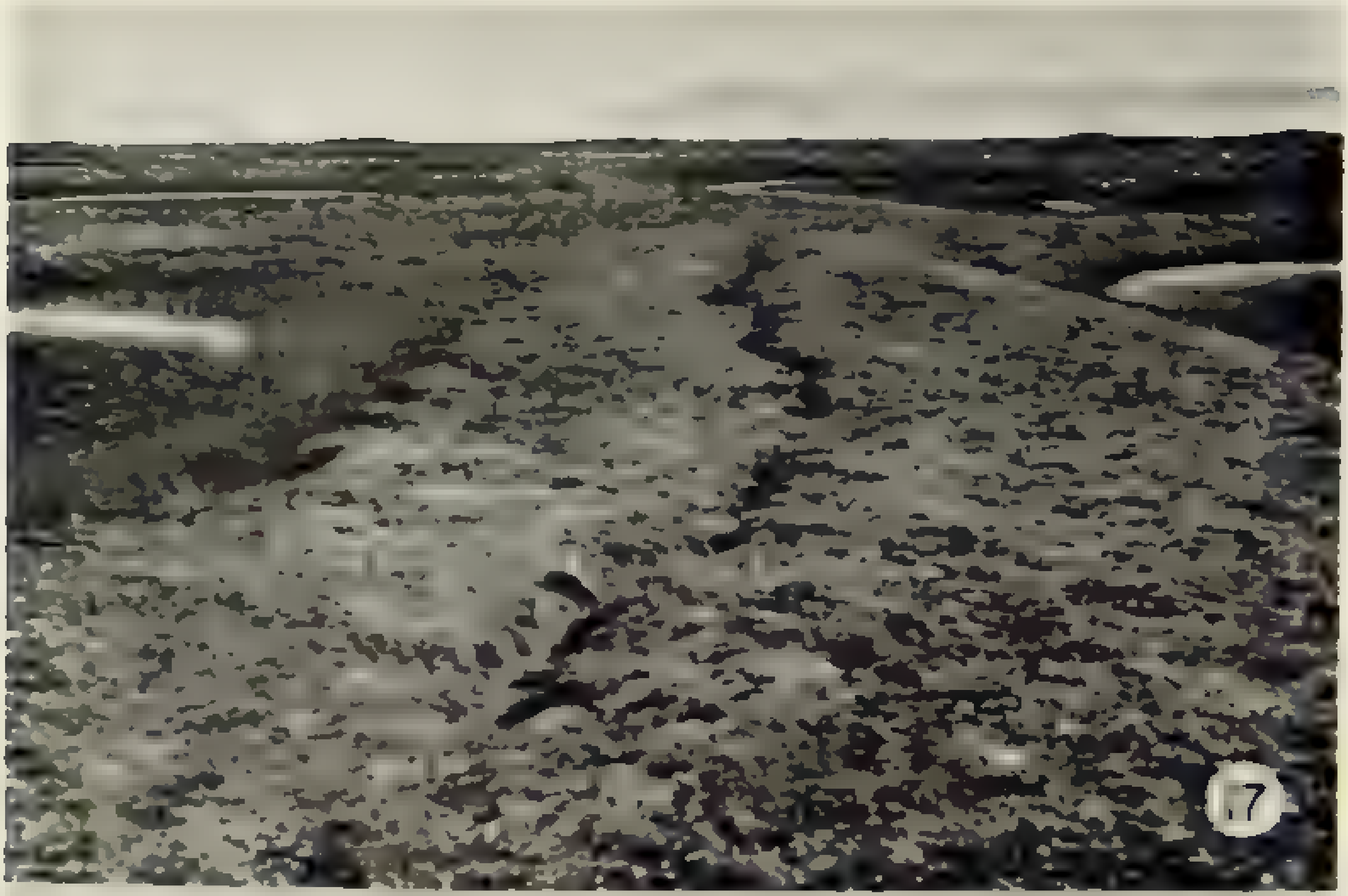


FIGURE 17. DEFORMATION CRACKS [illegible]unds with sedges, mosses and Arctic Willow and thaw ponds on both sides. Pond margin vegetation is *Eriophorum*. Note the regularity of the ponds and the curving of the crack toward the left.

FIGURE 18. FROST OVALS. An oval disturbed area in the mesh of polygons produced by deformation cracks. The steep disturbed margins of the frost mound are mostly bare but scattered clumps of Lichen, Saxifrage and Poppy persist. The vegetation in the meshes under the snow banks is Bell Heather. View looking northeast across exposed part of Tui-Tui Tabletop on [illegible] June.

During the thaw, while snow lines in the hollows (Figure 18), the rounded, barren surfaces are actively affected by the frost: (1) small cracks lie open and contain ice at their base (Figures 10A, B and I); (2) the surrounding soil is swollen and fines appear to break through the pavement of angular fragments in many places. No lichens or mosses grow on these disturbed places (Figure 18). The cracks become filled with leaves or blowing lichen fragments, and this material grades into organic stain, extending the trace of the crack into the soil 12-18 inches (Figure 10A, E, G and J).

An excavation made during the height of the thaw showed (a) that while snow persists in the mesh between cracks, water persists between the snowbank and the ridge; and (b) that on the ridge long, sinuous cracks occur scattered over the surface, but usually more or less parallel to the major crack (Figure 10B). The cracks are open and contain an ice wedge in the top of the frozen ground (Figure 10A and I). The excavation (Figure 10A) shows that the frost table drops gradually from the snowbank on the up-slope side of such a ridge, but drops steeply on the down-slope side. Frost activity is limited to ridges which are sodden, usually because they dam melt-water flow from the snowbank in the mesh. Excavations suggest (a) that these cracks are closed under the snow, (b) that they open and close daily in the course of the thaw while the soil is moist, working the crack deeper and deeper into the soil; and (c) that at the end of the thaw when the surface is dry, they are closed during the summer.

These cracks are characteristic of places where the snow will be blown away during the winter so that they are exposed to penetration of winter cold. They are probably produced by cold contraction forces and by ice wedges. In my experience, however, they do not form regular patterns Excavations show organic traces (identical to those produced by these cracks) crisscrossing the surface of frost-disturbed ridges (Figure 19A, C, D and E). This suggests that these cracks continue to form year after year on the edge of the disturbed areas, and disturb the soil progressively farther and farther away from the major crack region toward the center, because they form on the edge of the exposed surface next to the snow patch where soil is dampest. As the formation of cracks moves toward the center of the mesh, the sediments in the center are disturbed, churning up the soil and creating an oval of disturbed soil surrounding a more or less undisturbed central area (Figure 18). Figures 19A, C and D show excavations across the mounded border of a frost oval where this process is about one-third completed. The centers gradually become smaller and eventually are obliterated. When the entire area has been churned up by minor cracks (Figure 10L), the mounded area of tan, almost barren gravel is oval-shaped with the long axis pointed down-slope and with dimensions controlled by the original pattern of frost-cracks (Figure 18).

All transitional stages, from obliteration of the center to ponds in the mesh (Figure 17) occur on Tui-Tui Tabletop (Figure 16). Thus, the expression of the frost-crack pattern on the surface is not measured in time but according to degree of exposure, since all of Tui-Tui Tabletop can be considered the same geological age.

Effect of Vegetation. The survey of exposure, vegetation, and type of frost features on Tui-Tui Tabletop suggests that vegetation suppresses the opening of this secondary or annual crack, which in turn controls the modification of the soil next to the major crack patterns. Many authors agree on the relation of thin snow and thin vegetation mat to deep penetration of sudden temperature drops, and Zhukov (1944) relates it to the formation of cracks. Exposure, through its control of the vegetation cover, affects frost action which modifies the major frost-crack patterns.

Effect of Soil Character. Why do frost-ovals form on Tui-Tui Tabletop and not on the beaches? The cross-section and exposure of the major cracks are similar, but a marked difference in the size and nature of the sediments exists. The finest material east of the Aktineq was a coarse sand — stream- and wind-rounded — while much of the soil of Tui-Tui Tabletop was fine sand, perhaps coarse silt — angular, possibly from continued frost-riving. There are coarse pebbles and cobbles, many of them cracked by frost, in the sediments of the raised beach deposits, but few cobbles in the sediments on Tui-Tui Tabletop. The presence of finer material which (1) when wet, held together in clumps, (2) stood easily in a vertical wall in an excavation, and (3) produced eruptions in the sides of frost-cracks, allows the frozen soil to behave as described.

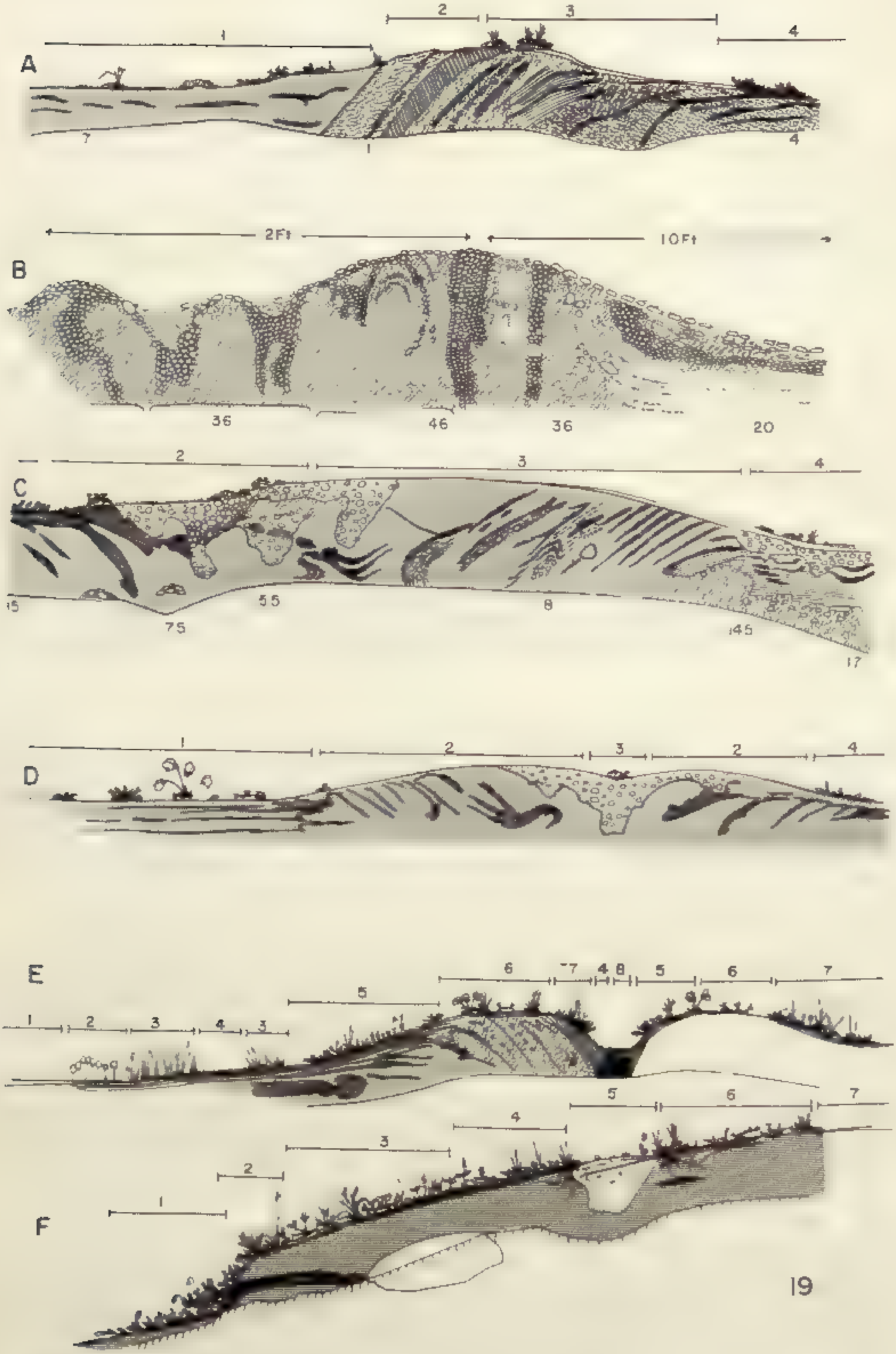


FIGURE 19. EXCAVATIONS INTO DEFORMATION CRACKS AND SOLIFLUCTION LOBE. Horizontal lines and numbers above diagrams refer to vegetation. Numbers below diagrams indicate depth to frost in inches.

A. Mound of Frost Oval.

This excavation is on the sparsely vegetated edge of the exposed top of Tui-Tui Tabletop (Figures 16 and 18). Excavation is 12 feet long.

Soil: Black is organic material. Note that these traces dip steeply into the soil where contraction cracks are to be expected on the mound.

Diagonally hatched is brown sandy silt.

Diagonally hatched and cross-hatched is a peat layer.

Splotched tone is coarse sand.

Vegetation: (1) *Isolated clumps of Stereocaulon paschale*, small Hypnaceae, *Polytrichum piliferum*, *Luzula confusa*, and *Salix arctica*.

(2) Bare sand.

(3) Chunks of peat blown out of open sandy soil, with clumps of *Luzula confusa*, *Cerastium alpinum*, and *Saxifraga oppositifolia*.

(4) Organic soil at the surface, protected from the wind and covered with *Stereocaulon paschale*, *Alectoria jubata*, *Alectoria ochroleuca*, and *Cassiope tetragona*.

B. Deformation Crack with Mounds.

Excavation across crack running up the beach east of Aktineq (Figures 15 and 20). Prevailing wind, east, is from the right. Finest material is a coarse sand and walls of excavation continually slumped. No vegetation.

Pebbles, stones and cobbles, 1-10 inches in diameter, are shown as circles. Irregular tone is coarse sand. Bedded material on the right alternates coarse sand with sand weathered into a poor soil profile. The duned sand on the right of the mound contained a large lens of wet sand.

Excavation is 22 feet long.

C. Rim of Frost Oval.

Excavation on Tui-Tui Tabletop (Figures 16 and 18).

Soil: Black shading is peaty, sandy silt.

Diagonal hatching is dark brown, sandy silt, grading into sand in many places This deposit was still damp on 17 June.

Splotched tone is sand.

Stippling with circles is gravel and cobbles in a matrix of sand.

Excavation is 20 feet long.

Note that organic streaks suggest lines of contraction cracks on both sides of the deformation crack which is marked by the deposit of sand and cobbles.

Vegetation: (1) Complete cover of mats of lichens, Hypnaceae, *Salix arctica* and *Cassiope tetragona*.

(2) Patchwork cover of *Stereocaulon paschale*, *Stereocaulon alpinum*, *Alectoria jubata*, *Cetraria nivalis*, *Cladonia* thalli, blackened Hypnaceae, *Polytrichum piliferum*, clumps of *Poa alpina*, *Luzula confusa*, *Saxifraga oppositifolia*, *Silene acaulis*, and *Cassiope tetragona*.

(3) Bare surface with patches of *Stereocaulon paschale*, *Stereocaulon alpinum*, and clumps of *Saxifraga oppositifolia*.

(4) *Stereocaulon paschale*, black *Parmelias*, blackened Hypnaceae, clumps of *Luzula confusa* and *Saxifraga oppositifolia*.

D. Frost Oval Mound.

Excavation on the exposed top of Tui-Tui Tabletop (Figures 16 and 18).

Soil: Black is organic material.

Diagonal hatching is damp, sandy silt.

Stippling and circles is gravel with sandy matrix.

Strata under the mesh are undisturbed. Under the mound their traces suggest heaving and contraction cracks. Gravel marks site of deformation crack.

Excavation is 25 feet long.

Vegetation: (1) Scattered clumps of *Stereocaulon paschale*, *Salix arctica*, *Papaver radicatum*, *Saxifraga oppositifolia*, and *Cassiope tetragona*.

(2) Barren.

(3) Clumps of *Stereocaulon alpinum* and *Saxifraga oppositifolia*.

(4) Mat of Hypnaceae, *Salix arctica*, and *Cassiope tetragona*.

E. Pond, Mound, and Crack.

Excavation on central Tui-Tui Tabletop (Figures 16 and 17).

Soil: Black is organic.

Black shading is peaty soil.

Diagonal hatching is brown, damp, sandy silt.

Splotched tone is reddish-tan fine sand.

Mound is underlain by traces of contraction cracks; mesh edge by horizontal strata.

Excavation is 15 feet long from pond margin to crack.

Vegetation: (1) *Drepanocladus, Pleuropogon Sabinei.*

(2) *Eriophorum Scheuchzeri.*

(3) *Tomenthypnum nitens, Aulacomnium palustre,* and *Carex aquatilis.*

(4) Hypnaceae, *Bryum,* and *Salix herbacea.*

(5) *Stereocaulon paschale,* Hypnaceae, *Salix arctica, Papaver radicatum,* and *Cassiope tetragona.*

(6) *Stereocaulon paschale,* dead Hypnaceae, *Luzula confusa, Papaver radicatum,* and *Saxifraga oppositifolia.*

(7) *Stereocaulon paschale,* Hypnaceae, *Carex aquatilis,* and *Cassiope tetragona.*

(8) *Calliergon, Drepanocladus.*

F. Longitudinal Section of Solifluction Lobe.

Excavation on the south slope of Kungo Hill.

Soil: Black is organic.

Horizontal hatching is brown, sandy silt.

Stippling is gray silt.

Vertical hatching is frost table.

Large oval at the frost line is a stone.

Excavation suggests that the lobe results from deposition over a soil profile. Soil profile and peat layer is not turned under.

Roots cluster at the border of the frost-boil and a root of *Salix arctica* is shown extending across it.

Vegetation: (1) Hypnaceae, *Salix reticulata, Vaccinium uliginosum, Cassiope tetragona.*

(2) *Stereocaulon paschale, Poa arctica, Papaver radicatum, Saxifraga oppositifolia.*

(3) Hypnaceae, *Carex Bigelowii, Luzula confusa, Salix arctica, Dryas integrifolia.*

(4) Hypnaceae, *Luzula confusa, Salix arctica.*

(5) Bare with *Carex misandra* and *Sagina intermedia.*

(6) Hypnaceae, *Arctagrostis latifolia, Salix arctica,* and *Saxifraga oppositifolia.*

(7) Blackened Hypnaceae, *Luzula confusa, Salix arctica.*

E. Subsequent modification in moss-vegetated areas

On the 16-foot beach there are a number of areas where single peat ridges, as orderly as if man-made, surround rectangular marshes or ponds (Figure 22). These patterns are especially well developed on the 1° to 3° slopes (by Brunton Compass), on the 55-foot beach, on Tui-Tui Tabletop, on Plover Plateau, and on the lower edge of the depositional slope, from the 35-foot beach to the 16-foot beach. Over most of the domed surface of Tui-Tui Tabletop, a peat or mineral soil ridge, covered with marsh or upland plants, appears on both sides of the frost-crack. The ridges may merge so that one broad ridge seems to have a crack running down its center (Figures 17 and 21). In sheltered places, during the height of the thaw, a creek runs down the crack (Figure 23), turning nearly at right angles as it meets the next crack, following an angular course between the peat ridges as if in a canal. The frost-crack is often deepened and widened by thawing and the places where two cracks meet perpendicularly is often widened into a pond with sloping banks.

Over most of the uplands the ridges are relatively dry and are occupied by dry upland vegetation so that a spectrum of vegetation, from the most barren to the richest, is found in a transect across one frost-pattern (Figures 17 and 19E). (See below under vegetation types). In the marshes, the ridges are marked chiefly by more healthy plant growth of the same species found in the meshes. In the wettest places, the vegetation on the ridges is of emergent mosses, marsh sedges, and Arctic Willow, in contrast to aquatic mosses and sedges of the centers. During the thaw these areas appear as a number of rectangular, ridge-bordered ponds (resembling rice paddies) which correspond in size and shape to permanent rectangular ponds two to four feet deep, such as (1) Loon Pond, (2) Phalarope Ponds, (3) Upper Phalarope Ponds, (4) ponds on the southeast corner of Tui-Tui Tabletop, and (5) ponds on the upland surfaces at Oonakuktooyuk and Ooyarashukjooeet. These forms have been described from other regions as early as Conway (1897) for Spitzbergen, Von Middendorf (1864-1867) for Siberia, and Kjellman (1879) for Siberia. In addition to these, there are many small isolated ridges and these grade into longer and longer ones, many running across the slope, but some running down the direction of the prevailing east wind. These peat ridges are probably the welts (Wülste) of Högbom (1914). Because the ridges accompany cracks on most surfaces and their pattern is identical to the major crack-patterns, I presume that they are secondary modifications associated with the crack.

Will differential frost-heaving and plant growth in vegetated areas explain these peat ridges? How can there be two ridges in some places and one in others? How are the ridges developed from cracks and how do they influence the development of bogs? How are the ponds formed? What is the origin of isolated, irregular peat ridges? Even superficial examination shows that these phenomena are confined to surfaces that are vegetated. What is the effect of vegetation upon soil formation, and what effects do vegetation cover and humus have upon the expression of frost-cracks and frost-heaving?

1. *The effects of vegetation on soil formation.* The most "mature" soils are found on the youngest beach surfaces on southern Bylot Island (the 6-foot beach), and many of the oldest upland surfaces where there is a little vegetation (the 55- and 85-foot beaches) have no soil-profile, but traces of organic soil are found in contraction cracks of previous years. Excavations show that the more luxuriant the present vegetation, the richer and deeper the soil-profile. In this region of the Arctic, soil-profile thus does not measure passage of time but the amount of vegetation present. Wind exposure seems to have an overriding influence because it governs the distribution of vegetation cover.

2. *Effect of the presence of organic material on frost activity.* Figures 10, 19 and 24 show sections across major frost-cracks. In those in Figure 19C and D, the regular sediments of the meshes are not disturbed at the sides of the crack, and there are coarse materials at the top of the crack, grading below into increased concentration of organic materials. Where the organic material increases, convolutions and churnings of organic soil are apparent. In other areas (Figures 24A, B and C) where the cracks are deeply filled with silt and organic soil, complex convolutions appear. It may be that we can see the effect of breakage and convolutions only where the organic material shows it, but certainly such activity, if present, would appear in excavations on Tui-Tui Tabletop. The appearance of convolutions only in the deformation cracks suggests either that the meshes are firm or that the cracks are subject to different forces. By digging across these ridges, and by tracing the patterns into areas of vegetation, I found transitions which show that the origin of the major peat-ridge pattern is the same, and that the difference between the ovals of the mounded regions of Tui-Tui Tabletop and the rectangular peat ridges on the bog surfaces must be explained in terms of modifications subsequent to the formation of the major frost-crack patterns.

3. *Occurrence of isolated contraction cracks in organic soils.* On depositional slopes and in low places, during the early part of the thaw, straight or sinuous cracks 1 inch across, 2-6 feet long and 1-7 inches deep appear with no overall pattern that I could find. They, like others, open with freezing at night, and close with the increase of moisture in the thaw

during the day. These minor cracks, as well as the large ones, are characteristically filled with fine- or coarse-grained material in exposed places, and with plant debris or organic soil in vegetated places. The small-scale cracks shown in Figure 12 occur without disturbing the soil-profile (Figure 9C). In many places these cracks run next to a sinuous peat ridge which also runs diagonally down-slope or without evident relation to soil or other frost patterns.

Where deep, wide, major cracks between peat ridges are not filled with water during the thaw, narrow cracks may appear in them, 2 inches across and 1-15 feet long, sinuous in form and asymmetrically placed in the major crack. Often these tiny cracks run diagonally across the bottom of the large crack which has collected a mixed organic and mineral soil (Figure 10G).

The smaller dimensions of the annual crack and its daily opening and closing show its relation to the annual cracks I have suggested to be operative in exposed places. Péwé (1959) illustrated this type of crack appearing in the major pattern of cracks in the Antarctic.

The difference in occurrence and expression of the two sizes of cracks, in this case as well as in the upland case, indicates that there are two forces involved, which I suggest are deformation and contraction.

4. *How do these two frost-crack types combine to form peat ridges?*

(a) Excavations to the frost table across isolated peat ridges consistently showed frost-heaving: (i) organic layers are disrupted upward and (ii) a ridge of frozen soil rises above the general soil-frost level underneath the peat ridges and is bordered by slight depressions in the frost table. Broken stones and fragments of stones occur on edge on the frozen ridges. The frozen ridge is consistently above the level of the water table.

(b) The cross-sections of frost-cracks east of the Aktineq, on Tui-Tui Tabletop, and on the vegetated surfaces, show that where organic material has filled the cracks, heaving and convolution of soil layers occur. A frost-crack offers shelter where plants, especially mosses, grow luxuriantly, producing an organic soil which holds moisture. Frost-heaving occurs and is more evident in the organic material than in the coarse soil next to it. This frost-heaving raises ridges on one or both sides of the crack according to local conditions (see below) but leaves the sediments in the meshes undisturbed (Figures 10E and 24C).

On the uplands, where dryness and wind limit plant growth, ridges are barren and secondary cracks form on them (Figures 18 and 10A). In transitional areas, where ridges have little vegetation the ridge stops growing because lack of vegetation means little humus (Figure 17). In sheltered, level areas where water-soaking inhibits plant growth, and when a ridge is raised by heaving, clump mosses, marsh sedges, and Arctic Willow grow more luxuriantly than in the wetter places (Figure 9C and E). Differential plant growth encourages humus collection and raises the ridge farther, thus encouraging additional plant growth. This disturbance is limited to the margins of the cracks (Figure 21).

Once a ridge is formed, it acts as a dike during the spring thaw (Figure 23) and holds moisture during the summer. Growth of aquatic mosses and sedges tends to fill the depression to water level, and this smooths out the irregularities inherent in sediment deposits, producing a peat bog, the mesh of which is flat, crossed by rectangularly-shaped peat ridges (Figure 22).

5. *Depths to frost across the peat ridges.* During the thaw, a series of temperature measurements and depths to frost across the bogs showed that the depth to frost below the vegetation of a ridge (Figure 9E) — 12 inches on 8 July — was greater than that below the vegetation between the ridges — 8 1/2 to 9 inches on 8 July. The frost level was deeper under the surface of the plants on the ridge because of the looser growth, in contrast to the stunted, dense plants in the centers. The more open growth allows better penetration of heat. Even so, the frost table was higher under the peat ridge because the plants on the ridge were much thicker and the frost table is higher under the ridge. This suggests that it is not actually the frost level that influences the luxuriance of growth, but that the plants on the ridge are raised during the thaw and can start to grow sooner.

In rice-paddy-like peat ridge areas, the frost is consistently deeper in the mesh on the up-slope side of the ridge (10

FIGURE 20. DEFORMATION CRACK WITH MOUNDS [illegible]. Figures give size of this four-sided pattern. Cracks are 6 feet across and filled with sand on the surface; mounds are 3 feet high. Deflation has produced a pavement of wind-cut stones. This is the site of the excavation in Figure 19B.

FIGURE 21. DEFORMATION CRACK CONTINUOUS WITH PEAT RIDGE. Crack on the 16-foot beach showing low mounds with hummocks of sedges in the foreground. In the background the course of the crack can be traced beside a well-developed peat ridge and between two parallel ridges. A crack in the near foreground runs at right angles to the conspicuous one. An ice ax gives size. Photo looking west across Loon Pond on the 16-foot beach.

inches extending 2 to 3 feet away from the ridge up-slope) and consistently shallower (8 inches within a foot of the ridge) below. This is related to the sun's heating the standing water held in by the ridge. The heated water stands on the up-slope side, then flows through or over the peat ridge, and is cooled by passage through the ridge. Auer (1920) pointed out this phenomenon in *Strangmoor* and discussed differential plant growth on peat ridges.

6. *How does one peat ridge develop from ridges on two sides of a frost-crack?* The crack excavated east of the Aktineq and a survey of the cracks on Tui-Tui Tabletop show that a crack may be simple, with a ridge on both sides; or compound, with a larger hillock on one side than on the other; or a hillock may form in the middle between two small cracks (Figure 20). Figure 21 shows a crack with low ridges on both sides which can be traced on the photograph into a single and then double peat ridge. On low slopes (1°-3°), water flow will emphasize one ridge at the expense of the other, since each ridge tends to act as a dam and the whole tends to form step-like terraces, such as on the slopes from the 55- and the 35-foot beaches.

7. *Rectangular, regularly spaced ponds.* Standing water in the low places hemmed in by the regular pattern of peat ridges is heated by the sun and this leads it to thaw the frozen ground below, producing a thaw sink, as described from western and northern Alaska by Wallace (1948), Black and Barksdale (1948), and Hopkins (1949).

8. *Peat ridges not associated with frost-cracks.*

(a) On depositional slopes, minor mud-flows burst out from under the vegetation and flow over the surface of the ground (Figure 2). A ridge of vegetation usually forms at the margin.

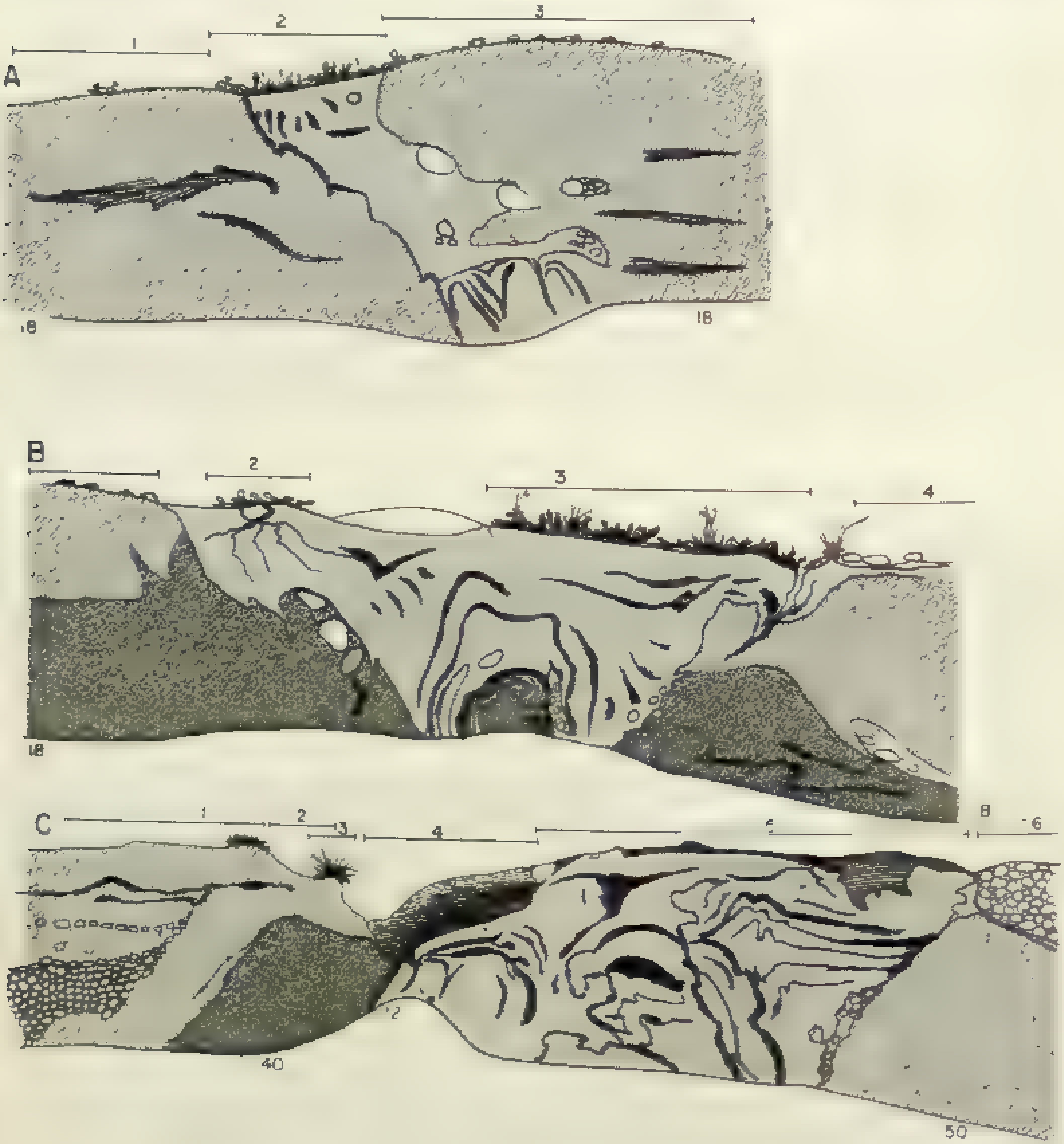
(b) On the edges of the delta of the ephemerous streams off Plover Plateau, peat ridges run circumferentially around the snout of the delta, tracing the margins of the garlands of soil deposited by daily melt-water floods.

(c) The water flows over these deltas as a sheet, within which riffles (tiny terraces about an inch high) appear in the same pattern as the lines of peat ridges. The sinuous form of these riffles, coinciding in size, form and pattern with the peat ridges, suggests that one is developed from the

FIGURE 22. [illegible] and asso-ciated with the mounds [illegible] cracks. Note the [illegible] ridge in the left foreground becoming a single ridge at the left edge of the picture, and compare with Figure 23. Most of the vegetation is tuft mosses, sedges, and Arctic Willow. In the smooth, boggy areas, mosses are *Calliergon* and *Drepanocladus* and the sedges Cotton Grass. Scene is on the [illegible]-foot beach from Kungo Hill.

FIGURE 23. PEAT RIDGE DIKES. Peat ridges, associated with deformation cracks and extending into the background toward camp on the [illegible]-foot beach, have jammed drainage from Golden Plover Creek. A transverse crack forms the drainage channel in the foreground. Ice ax gives size.

other. As the delta deposits thicken, and the surface is no longer flooded daily, these areas are raised slightly above their surroundings by the collection of silt or by drying out of the step, and vegetation of Arctic Willow and clump mosses grows more luxuriantly, producing peat ridges. Similar effects control the development of ridges on peat bogs farther south (the *Strangmoor*) (Drury, 1956). The



24

Figure 24. EXCAVATIONS SHOWING CRYOTURBATION IN DEFORMATION CRACKS. Horizontal lines and numbers above the diagrams refer to vegetation. Numbers below the diagrams indicate depth to frost in inches.

A. Frost-oval mound.

On the northeast slope of Plover Plateau toward the Little River (top right corner of Figure 16).

Soil: **Horizontal shading is peaty.**

Splotched tone is angular sand and pebbles.

Diagonal hatching is red-brown, partly organic, sandy silt: irregular ovals are stones.

Vertical and convoluted organic traces at the base show the beginnings of frost heaving. Excavation is 10 feet long.

Vegetation. (1) Bare, with clumps of *Festuca brachyphylla, Kobresia myosuroides, Salix arctica, Cerastium alpinum,* and *Saxifraga oppositifolia.*

(2) Closed mat of *Parmelias, Umbellicaria, Stereocaulon paschale, Stereocaulon alpinum, Festuca brachyphylla, Kobresia myosuroides. Salix arctica* mats and *Saxifraga oppositifolia* cushions grow on the two margins.

(3) Bare mound with pavement stones partly covered with crustose lichens.

B. Crack of rectangular pattern.

On southeast edge of Tui-Tui Tabletop on the south edge of the exposed plateau (Figure 16 at the top of the picture).

Excavated 22 and 30 June. Frost line of 30 June shown.

Soil: Black is organic matter.

Diagonal hatching is damp, red-brown, fine sand.

Splotched tone is ochre, coarse and fine sand containing angular pebbles.

Vertical hatching is moisture zone of sand.

Stippled with ovals is sand with gravel.

Vertical and convoluted organic layers show that frost heaving reaches nearly to the surface.

On the right southeast edge of the deformation crack is a contraction crack 1/2 inch across on 22 June which extended as a crack into the still-frozen subsoil. It was full of *Salix arctica* leaves. Note the diagonal organic trace extending into the sand below this crack. Clear oval on the surface near the center of the deformation crack is pale gray sand. At 18 inches in the center of the deformation crack were many stones shattered into plates parallel to the crack.

The excavation is 7 1/2 feet long.

Vegetation: (1) Bare surface with scattered black *Parmelias, Stereocaulon paschale, Stereocaulon alpinum,* and cushions of *Saxifraga oppositifolia.*

(2) Mat of *Salix arctica* with black *Parmelias* and *Stereocaulon paschale* in the shelter of its edges.

(3) Closed mat of *Cetraria nivalis, Luzula confusa,* and *Cassiope tetragona.*

(4) Bare, with pavement of stones, clumps of black *Parmelias, Stereocaulon paschale, Luzula confusa,* and *Saxifraga oppositifolia.*

C. Deformation crack on 6-foot beach.

Soil: Black is entirely organic.

Horizontal shading is peaty sand.

Diagonal hatching is dark brown fine sand.

Splotched tone is gray coarse and medium sand.

Ovals are gravel lenses.

Vertical hatching is wet sand.

The low place on the edge of the crack is filled with a rotting mass of *Salix arctica* leaves.

Convolutions suggest frost thrust up and to the right from the ridge in the frost table below the depression and up and to the left from the right edge of the deformation crack's finer sediments.

The excavation is 18 feet long.

Vegetation: (1) Blackened lichen thalli, *Stereocaulon paschale,* black Hypnaceae, mats of *Salix arctica,* and scattered plants or clumps of *Luzula confusa, Polygonum viviparum, Silene acaulis, Papaver radicatum, Saxifraga oppositifolia,* and *Pedicularis lanata.*

(2) Bare, with individuals of *Salix arctica, Silene acaulis, Papaver radicatum,* and *Saxifraga oppositifolia.*

(3) Margin of the crack a mat of *Luzula confusa, Salix arctica,* and *Saxifraga oppositifolia.*

(4) On the matted willow leaves grow *Poa arctica, Luzula confusa, Stellaria humifusa, Ranunculus nivalis,* and *Potentilla hyparctica. Salix arctica* branches extend into this from the next.

(5) Barren, with clumps of *Stereocaulon paschale, Luzula confusa, Salix arctica, Polygonum viviparum, Cerastium alpinum, Papaver radicatum,* and *Saxifraga oppositifolia.*

(6) On the gravel, *Stereocaulon paschale,* blackened Hypnaceae, *Salix arctica, Papaver radicatum,* and *Saxifraga oppositifolia.*

step-like riffles occur wherever water runs over a surface in a sheet. They are especially well expressed where daily melt-water floods cross frozen ground.

(d) In a number of places, minor frost-cracks appear on depositional slopes. Peat ridges, usually rather short but of the same height and width as other peat ridges, often accompany them. We found ridges of this sort 15-35 feet long and parallel to the prevailing wind. Perhaps Arctic Willow grows faster downwind in its own shelter and these ridges form by heaving of organic material collecting under the willows; then the cracks form later. Figures 9D and 12 show a crack, and the soil structure under such isolated peat ridges.

PART THREE

VEGETATION

INTRODUCTION

The small number of plant species which grow in the area limits the number of "plant associations," but the habitats of the tundra are highly varied and therefore the variations find expression as different combinations of these few plants. It is generally recognized, but often forgotten, that each plant species grows over a spectrum of conditions to which it is well-enough adapted to exclude others, and to prevent its own exclusion by competition (Darwin, 1859). Even in this extreme habitat, many species coincide or complement each other in their requirements and tolerances, and thus occur together. Mason and Langenheim (1959) have recently proposed the term "aggregates" to get away from the term "association," but why add a new word to the mess that already exists?

The early students of the relation of vegetation to patterns in the ground in the North were not concerned with the nature of the relations between the plants that grow together. Frödin (1918) simply described the plants that grew in certain sites and their relation to solifluction. Polunin (1934), and Seidenfaden and Sørensen (1937) included the European concept of characteristic or indicator species, and numerical abundance of a species in a site sample. Polunin (1934) was the first after Frödin to classify vegetation on the basis of site and habitat, and discussed why — coming to the conclusion that the surface is kept young by the extremes of climate and soil disturbance that the vegetation has not time to develop a humus layer and thus achieve any maturity which is necessary for the development of an organized vegetation type. Seidenfaden and Sørensen (1937) developed the site concept further for the botany of East Greenland. Raup (1942) has urged the inductive method to describe what is found and to associate what is found with the habitat conditions found. But we must choose which details to stress. Polunin's (1948) descriptions emphasized the recognisable, but only slightly different, associations which proliferate over the North, perhaps because of the homogeneity of the subsoil by cryoturbation (Raup, 1951) combined with many site differences created by microtopography. My field notes repeat these minutely separable differences and the main intent of a field study must be to bring some simplicity out of the evident complexity in nature. To do this, we may try to answer some questions:

A. Ecological amplitude and species success

Do plants occur together in a limited variety of associations, or do they occur in all combinations? Of the more than 100 species collected in southern Bylot, only 34 formed the vegetation of 85 per cent of the land surface; the rest were scattered plants in specialized parts of bogs or sunny, weedy sites — the "good collecting" places. The primary species (those that give the aspect of vegetation to the human observer) consisted of ten species of higher plants: *Hierochloë alpina*, *Arctagrostis latifolia*, *Eriophorum angustifolium*, *Carex aquatilis*, *Luzula confusa*, *Salix arctica*, *Papaver radicatum*, *Saxifraga oppositifolia*, *Dryas integrifolia*, *Cassiope tetragona;* and the following lower plants: *Stereocaulon paschale*, *Cetraria cucullata*, small *Hypnaceae*, *Aulacomnium palustre*, *Campylium stellatum*, *Drepanocladus* sp., *Tomenthypnum nitens*, *Polytrichum piliferum*.

Plants like *Salix arctica*, *Saxifraga oppositifolia*, the small, dense *Hypnum* mosses, and *Cetraria cucullata* occur essentially everywhere. These plants are of no use in indicating site. Others, such as *Dryas integrifolia* and *Luzula confusa*, occur widely in the open areas of the uplands, while *Cassiope tetragona* and *Salix reticulata*, *Cetraria islandica* and *Rhacomitrium lanuginosum* grow in sheltered spots and give indication of site character. Some species occur in dense stands over many habitats, such as *Salix arctica,* while others occur over a wide variation in habitat, but are everywhere rare, such as *Saxifraga cernua;* still others occur only as one specimen in one locality *(Androsace septentrionalis).* Certain species are restricted, although abundant where they occur, such as *Vaccinium uliginosum* in sheltered nooks below solifluction lobes; *Salix herbacea* in late snow patches; *Pleuropogon Sabinii* in the centers of boggy ponds; *Mertensia maritima* and *Arenaria peploides* on sea beaches. In some places there is profusion of weedy flowers, such as the screes below the bluffs: *Taraxacum lacerum, Arnica angustifolia, Erigeron uniflorus, E. compositus, Epilobium angustifolium, Draba, Papaver radicatum, Oxytropis Maydelliana,* and *Astragalus alpinus.*

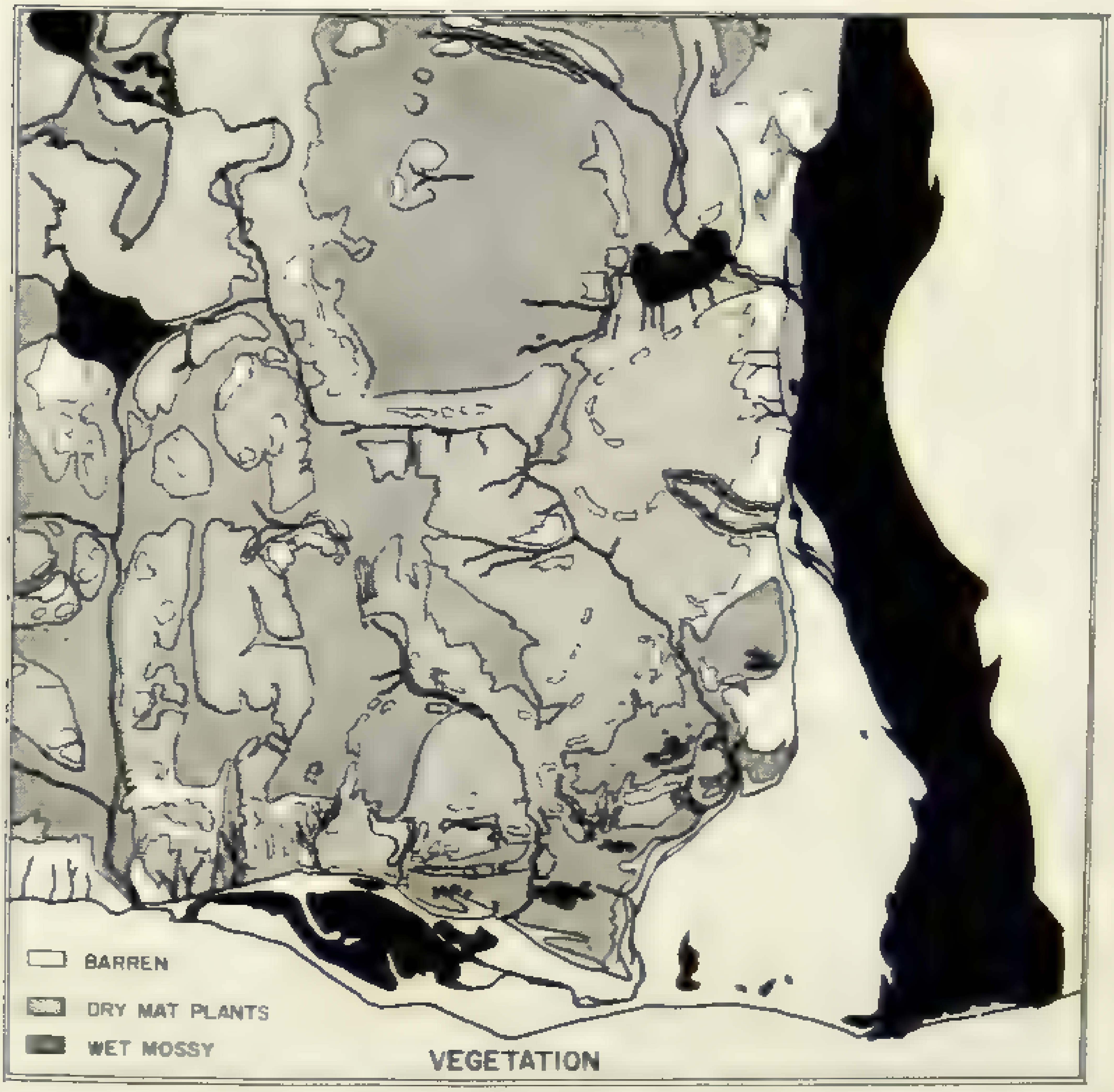
Thus certain species occur essentially everywhere, whether conspicuous or inconspicuous, rare or common; but other species also rare, common, conspicuous, or inconspicuous may be valuable as site indicators.

B. Regional and microtopographic differences

Do major regional vegetation types exist, or do local topographic differences create all the differences in vegetation that one may find? Are there hilltop vegetations, in contrast to valley-bottom vegetations?

The vegetation of the heavily frost-cracked area on the west side of Tui-Tui Tabletop shows, in a transect from the center of one polygon to the ridge next to the frost-crack (Figure 19E), the following types: (1) a pond in the center of the mesh with *Pleuropogon* and *Drepanocladus;* (2) a border of *Tomenthypnum, Aulacomnium* and *Carex aquatilis;* (3) a thick ground cover of *Hypnum* mosses and *Cassiope;* (4) an area of mixed *Dryas integrifolia, Luzula confusa* on the slope of the ridge, and (5) scattered clumps of *Luzula, Stereocaulon paschale,* and cushions of *Saxifraga oppositifolia* on the top of the ridge. *Salix arctica* grows in all but the wettest sites, and *Cassiope tetragona* grows in scattered clumps on the ridge and in mats on the sheltered places. These samples, in an area 20 feet across, include the extremes of vegetation found in all the non-mountainous parts of Bylot Island we visited, from the most exposed hilltops to the most sheltered valley bottoms (Map 3). Raup

(1947, 1951), showed that the physical features of the habitat are of over-riding influence. There are no special vegetation types that occur on slopes, or on hilltops, or on valley bottoms.



MAP 3. VEGETATION OF THE STUDY AREA. Rivers and ponds are shown in black; wet, mossy areas are primarily behind raised beaches, on plateau tops, or on gentle east slopes. Isolated barrens are usually raised beaches and ridgetops.

C. Primary factors controlling vegetation

All factors act together and two may be directly dependent upon each other, or both upon another governing force. For example (as above), the depth and clarity of the soil-profile are not correlated with the age of the surface, but with the exposure to the east wind, and moisture factors which control the growth of the vegetation mat. This in turn controls growth of organic material in the soil, affecting the subsequent frost action.

Raup (1951) and his students, Benninghoff (1952) and

Sigafoos (1951), at the same time as they point to the uniformity of the soil because of the homogenizing effects of cryoturbation, emphasize that the physical conditions of the environment, especially expressed in frost action, are more important than the age of the surface. Sigafoos (1952) with Hopkins, could not use vegetation as any measure of the age of a deposit, of its materials, or slope, because frost action has, by disturbance and by microrelief, superseded all. These interpretations may offer a dilemma but the observations are repeatable anywhere in the Arctic. In this area many factors are limiting, and microtopographic details change the specific limiting factor which applies and what plants grow there. Wiggins (1951) said that for the growth of plants, uniform soil conditions are generally lacking even within a few square meters (humus, muck and clay, sand and gravel, all occur within a meter.)

1. *Exposure and shelter.* (a) In the most exposed places are scattered tufts *(Luzula)*, cushions *(Saxifraga oppositifolia)*, or mat plants *(Salix arctica)*, clumps of lichens such as *Stereocaulon*, and large areas of blackened, dead mosses. Most of the surface is barren. One of the first signs of increasing shelter is the appearance of *Cassiope tetragona*, and mosses below its branches. With the appearance of *Cassiope* and then *Salix arctica*, there is a marked increase in the percentage of the ground covered. Areas more exposed to the wind contain more lichen cover; shallow hollows have a moss cover.

(b) Most of the uplands are covered with a patchwork of lichen-predominance and moss-predominance, over which a general net of *Dryas*, *Cassiope*, and *Salix arctica* (in which are scattered grasses, sedges and *Luzula confusa*), runs as if ignoring the ground cover.

(c) As moisture and shelter further increase in sheltered, deep slopes, such as those related to frost-cracks or solifluction lobes, *Cassiope* and *Salix reticulata* become abundant and, locally, with *Salix reticulata* appear *Vaccinium uliginosum* and *Empetrum nigrum*, and a complete moss undercover. This is the maximum expression of "matured" vegetation on drained sites.

Wiggins (1951) showed that the densest and most continuous vegetation occurs where snow lies deepest and most continuously during the winter, near Point Barrow, Alaska. Flat surfaces and standing water for part of the season are necessary for the next step in the thickness of the vegetation mat.

2. *Moisture availability.* The first effect of standing moisture is the sudden appearance of a thick growth of sedges, *Eriophorum angustifolium* and *Carex aquatilis*, and mosses, *Aulacomnium*, *Drepanocladus*, and *Tomenthypnum*. *Salix arctica* and *Saxifraga oppositifolia* are still abundant in these marshy places, especially on depositional slopes and behind raised beaches.

3. *Sequence of snow-melt.* (a) Areas exposed to the prevailing east wind which blows away the snow cover, are subject to bitter cold in winter and to deep freezing and thawing during a long spring thaw. The effect is to produce a barren, frost-churned surface. These areas cover about 10 per cent of the surface we studied.

(b) There are areas which are covered by thin snow in winter, and melt before the main thaw — about 15 per cent of the surface studied.

(c) Most of the uplands lie under a few inches of snow, which is probably seldom more than a foot deep during the winter, and this cover disappears during a week or ten days of rapid thaw. We put out several hundred flowerpot stakes on the broad slopes and the general uplands, marking the day-by-day change in the outline of snow during the main thaw — 20-30 June, 1954 — and found no correlation with vegetation patterns, except that sheltered and moist places are grown to *Cassiope* and mosses. These areas cover about 50 per cent of the surface studied.

(d) Areas on the shady side of hills or on the stream bottoms keep snow cover until two weeks after the general uplands have thawed. These places are occupied by thick patches of moss, verdant growth of sedges, and dense growth of *Salix arctica*. They show a characteristic lack of *Dryas* and *Cassiope*. Mosses form cushions or hummocks surrounded by a crack and topped by lichens. These sheltered, shady areas cover about 20 per cent of the surface studied.

(e) In some places snow lies in persistent drifts in valley bottoms and northwest slopes until the third week of July, and in these places the general ground cover is almost entirely *Salix herbacea*, a few tiny *Equisetum arvense*, *Juncus* and *Ranunculus*, and weedy *Bryum* mosses. This specialized habitat exists uniformly in site and vegetation across Siberia, North America, and in the mountains of Norway and Sweden. Gjaerevoll (1956) has discussed it in detail. These cover about 5 per cent of the surface studied.

4. *Effects of the full rays of the sun.* There was no vegetation shelter from the sun's rays except for mosses, but certain slopes were exposed to full sunshine for the maximum period of time during the heat of the day, while others sloping to the east, north, or northwest were in shadow most of the "heat" of the day. We found no general differences in vegetation between that of the gentle upland slopes and that on south-facing gentle slopes. On gentle northeast, north, and northwest slopes, there is an increase of *Cassiope*. On disturbed soils of south-facing frostings, scree, or alluvium in the ravines, weedy masses of flowers grow.

D. Time of flowering

When we arrived, the temperature was below freezing most of the time, and regularly went below freezing every night until after the first of July. Yet in this period *Saxifraga oppositifolia* reached its full bloom, and we found that several of the richly-flowering tufts had ice in their centers. *Draba nivalis*, *D. glabrata*, *Potentilla Vahliana*, *Cerastium alpinum*, *Salix arctica*, *Erysimum Pallasii*, and *Oxyria digyna* were all in flower.

After the first of July, when there was no regular occurrence of frost, the full flood of flowering appeared; and on 2 July the following plants were in flower: *Festuca brachyphylla*, *Kobresia myosuroides*, *Salix reticulata*, *Stellaria longipes*, *Papaver radicatum*, *Draba alpina*, *D. nivalis*, *Braya purpurascens*, *Lesquerella arctica*, *Saxifraga nivalis*, *S. cernua*, *Dryas integrifolia*, *Astragalus alpinus*, *Oxytropis Maydelliana*, *Pedicularis lanata*, *Antennaria Ekmaniana*, *Erigeron uniflorus*, and *Arnica alpina*. By the second week of July most of the plants were in full flower except the sedges which were just then coming into flower.

E. Variation in the richness of site

Our study area shows the familiar phenomenon of some sites being rich in species and others poor. Disturbed soil and fine-grained alluvium of steep, sandy slopes in the ravines west of camp — out of the wind and south-facing — were covered with a weedy growth of many species of limited distribution. Yet some of the species in these places (such as the *Drabas*, *Epilobium*, *Astragalus*, *Saxifraga oppositifolia*, *Salix arctica*, and *Oxytropis*) also grew on the uplands or on river gravels. In contrast, on "poor" sites such as the persistent snow patches in valley bottoms, only one or perhaps three species occurred together. There are all gradations imaginable between these two extremes, while the average site — 75 per cent of the land surface — supports the fifteen common species growing everywhere, mixed into which occur a variable number of less conspicuous, less common species.

Seidenfaden (1931) states one unanswered problem: "The difference in types of vegetation, therefore, can hardly be said to consist in a more abundant representation of species in the gneiss localities, for nearly all the species represented there may, with more or less success, be met within the areas of sediments. When, therefore, the difference is so pronounced as is practically the case, this is principally due to the luxuriance — a phenomenon which cannot easily be expressed numerically." He mentions, further, plants which grow as a few scattered plants nearly everywhere without anywhere becoming abundant.

I agree with Gjaerevoll (1956) in his discussion of the occurrence and vegetation "value" of *Salix herbacea*. He makes the point that acidophilous species of plants have a general adaptation and lack of specificity, while calciphiles are much more specific as indicators. The relative inhospitality of limestone prevents rich, closed societies from developing, and by the openness of the society, the poverty of limestone allows the plants which would otherwise be less able to compete, to hold on in small numbers (Polunin, 1934). On this basis only, acidic barrens should also be rich in species. I presume that isolation, which is to be expected by the geological nature of the limestone deposits, has encouraged formation of species by geographic isolation. The flora of southern Bylot is rich in calciphiles.

F. Vegetation types and habitat selection by birds

To test the validity of the vegetation types, I compared them with habitats selected by birds. Many experiments show that birds respond to the same sort of environmental stimuli as men. If they select the same vegetation types as we do, we can assume it is for a different purpose, and that our assay indicates something real, or expresses factors of general influence in the environment.

I found a large degree of coincidence; for example, Baird's Sandpiper *(Calidris bairdii)*, Snow Goose *(Anser coerulescens atlantica)*, Black-bellied Plover *(Pluvialis squatarola)*, and Horned Lark *(Eremophila alpestris hoytii)* nested on the exposed areas. I am convinced, however, that Baird's Sandpipers and Horned Larks selected the only surface areas free of snow when they "had" to nest — not necessarily because of the vegetation. Black-bellied Plovers and Snow Geese arrived later and, being wary, selected areas with a wide prospect — terrace margins or hilltops — and perhaps the barrenness is coincidental in the case of the Snow Goose; but in the case of the Black-bellied Plover, the nests are specifically placed in areas of nearly barren soil. These four species are characteristic of the High Arctic dry tundra. Other species of birds — White-rumped Sandpiper *(Heteropygia fuscicollis)*, Oldsquaw *(Clangula hyemalis)*, and Golden Plover *(Pluvialis dominica)* — selected areas of more or less complete vegetation cover. Their geographical distribution is more southern, coinciding with the wet tundra vegetation. Thus there is a general geographic coincidence in the distribution of vegetation and habitat selection in these species.

Lapland Longspurs *(Calcarius lapponicus)* nest in a recess under a hummock, usually a sedge tussock, over most of its range. On southern Bylot Island where there was little development of tussock growth, it nested on the edges of frost-cracks, under overhanging vegetation of *Salix arctica* and *Cassiope*, or in the edges of peat ridges (Drury, 1961). Each of these situations, most conspicuously *Cassiope*, supplies a recess with an overhang, and, I presume, the recess, not the plants, is selected.

Raunkiaer's (1934) system of form categories has been used by Böcher (1933a and b) in contributions to understanding the ecology of arctic plants in Greenland. Ornithologists studying habitat and nesting-site selection have come to the conclusion that there are many features to be considered: (1) form; (2) aggregation of the individual plants to create topography (relation of clumps to openings); (3) internal structure of the individual plants; and (4) details of the ground cover. For example, Dwarf Willows and Dwarf Birches and Alders fill the function by being bushes, but, having different internal branching, they are separated as nesting sites.

Further pursuit of this topic gets us into *Gestalt* or total impression psychology and the *Umwelt* or selective reactivity of non-human organisms. It is a treacherous morass. I conclude that birds respond to landscape and to the form of the vegetation cover, and that associations are important only as they supply required forms.

G. Indicators, Dominance, Succession and Frost Action

There are fundamentally different bases for the systems of classifying vegetation as developed in the United States and in Europe. One difference is the idea of succession and development described by Cowles (1899, 1901) and Clements (1916), and expanded by Tansley (1935, 1939) to include the concept of eco-systems. On the other hand, the initially more inductive Continental systems are divided into two parts: The Braun-Blanquet Montpelier school considers the concept of indicator species; and the Scandinavian system includes the idea of dominant species. Separate from these differences is the bifurcation between Clements' superorganismic concept and Gleason's (1917, 1926) individualistic concept of plant association.

A further dichotomy is between those who seek similar and uniform details of vegetation and follow the details over many sites where the similar vegetation appears; and those who seek similar sites and deal in summarizing and explaining variation in vegetation found on the sites. The concept of the indicator, or characteristic, species tends toward site characteristics. On the other hand, pure plant sociology discovers layers or units which repeat themselves regularly, while other species may come and go, independent of that layer. Bog students (Sjörs, 1948) have been working in detail on the physiology of "site" requirements. Goodlett (1960) discussed in detail the development of the concept of site and the tremendous importance that soil, microclimate, slope, and so on, have in forecasting stand development and productivity. This is the conviction of students of habitat, i.e., given similar site and flora, similar associations or communities appear. Stout (1952) illustrated studies of site in the deciduous forests by showing how deep soil structure directly affects the composition of a stand of trees.

One difficulty is extricating ourselves from the all-pervading Clementsian dogma; for example, Whittaker (1960), in his able discussion of Serpentine Vegetation, feels he must justify a permanent "successional" stage. If the vegetation retains characteristic elements, of what importance is it whether it fits into some overall climax scheme? Each species of plant is out for itself and where two or more grow together, it is the result of coincidence of requirements.

The differences in "systems of classification" lie not in the conclusions drawn from observable facts, but in the development of these ideas following deductive lines of logic beyond the facts.

Understanding will come from detailed studies of the biology of individual species and of geographical forces producing ground structures and soils. The plant association is useful to describe landscape and, to an esoteric few who are familiar with the plant species, habitat, but it is of little ecological importance *per se* to the plants concerned.

I use the association concept developed by Raup (1951), but include the subjective concept of site. This association may be equivalent to the alliance of the Zurich-Montpelier school. But within it, many detailed variants may appear, some of striking uniformity. These variants would conform to the Scandinavians' sociations. My descriptive categories, however (primary vs. secondary) are equivalent to the Hult-Sernander scale in that primary is equivalent to the value 5 in the case of mat plants, and to 4 in the case of plants growing in clumps. The other concept, secondary, includes 1, 2 and 3; that is, a cover equivalent from 1/4 to less than 1/16 of the total area. Primary species used here include a combination of frequency and degree of cover, without regard for dominance. The judgment which is involved in this weighs frequency more than degree of covering for certain species. Thus, a grass, sedge, or clump species *(Saxifraga oppositifolia)* is called primary, while according to the Braun-Blanquet system's degree of covering, its habitat form gives it 2 or less. Botanists are familiar with the observation that in a certain stand, using any classification, certain plants are much more conspicuous than the second-level plants. These are of frequency over 80 in Raunkiaer's (1934) system, or over 3 in the Braun-Blanquet system. The next level of frequency in Raunkiaer might well be 50 or 60, and Braun-Blanquet, less than 2. There are similarities of association between my studies and those in East Greenland (Seidenfaden and Sørensen, 1937), in the Canadian Arctic (Polunin, 1934, 1948) and in Scandinavia (Nordhagen, 1943). This shows that botanists choose similar patterns.

VEGETATION ASSOCIATIONS

1. Exposed Sites: MAP 3, Barren

Primary: Blackened and dead clumps of mosses (Polytrichum and Hypnaceae — including Dicranum), Stereocaulon paschale, Luzula confusa, Salix arctica, Papaver radicatum and Saxifraga oppositifolia.

Secondary: Cetraria nivalis, Stereocaulon alpinum, Poa arctica, Cerastium alpinum.

2. Uplands: (a) Exposed: MAP 3, Barren

Primary: Stereocaulon paschale, Cetraria cucullata, Parmelia saxatalis, Alectoria jubata, A. ochroleuca, Polytrichum piliferum and some Hypnaceae.

Secondary: Cetraria islandica, C. nivalis, Thamnolia vermicularis, Cladonia rangiferina, C. sylvatica, Stereocaulon alpinum, Hypnaceae (including Rhacomitrium lanuginosum), Hierochloë alpina, Poa arctica, P. glauca, Festuca brachyphylla, Arctagrostis latifolia, Kobresia myosuroides, Luzula confusa, Cerastium alpinum, Silene acaulis, Papaver radicatum, Draba nivalis, Saxifraga oppositifolia, Dryas integrifolia, Cassiope tetragona.

(b) Sheltered: MAP 3, Dry Mat Plants

Primary: Stereocaulon paschale, Dicranum sp., Polytrichum piliferum, Tortella sp., Didymodon sp., Rhacomitrium lanuginosum, Aulacomnium acuminatum, Poa glauca, Luzula confusa, Salix arctica, Dryas integrifolia, Cassiope tetragona.

Secondary: Alectoria ochroleuca, Cetraria cucullata, Equisetum arvense, Arctagrostis latifolia, Alopecurus alpinus, Hierochloë alpina, Salix arctica, Oxyria digyna, Polygonum viviparum, Salix herbacea, S. reticulata, Stellaria longipes, Silene acaulis, Papaver radicatum, Eutrema Edwardsii, Draba alpina, D. glabella, Saxifraga oppositifolia, Pedicularis lanata.

These two — (a) and (b) — alternate, merge and combine in Map 3, Dry Mat Plants. In places, streams of one run through a general cover of the other, or meshes of (a) are surrounded by lines of (b) in non-sorted polygons. Gentle north and east slopes are covered with (b) but with *Cassiope tetragona* forming almost a complete cover on their upper slopes and almost completely lacking on the lower slopes.

On many upland surfaces, polygons of several sizes are expressed in the vegetation. The pattern expressed in the meshes five feet across is typically: (a) the barren areas have scattered, blackened mosses, *Stereocaulon paschale, Luzula confusa, Salix arctica,* and *Saxifraga oppositifolia;* (b) the margins of the meshes have low Hypnaceae mosses, *Luzula confusa,* or *Carex Bigelowii, Salix arctica* and *Dryas integrifolia;* (c) growing out onto these margins from the cracks which form the polygons are *Aulacomnium palustre* and *Tomenthypnum nitens.* These mosses fill the cracks and in them grow *Arctagrostis latifolia, Alopecurus alpinus, Eriophorum angustifolium,* and *Cassiope tetragona.*

On more exposed sites the cracks have only Hypnum mosses; the marsh mosses and the marsh grass and sedge do not appear. The patterns are built of relatively exposed sites alternating with relatively sheltered sites, rather than of any specific and regular vegetation differences. On all sites, the impression is that the plants from the cracks are constantly advancing into the centers of the mesh and is prevented from colonization by disturbance of the soil. As soon as the disturbing forces diminish, the vegetation of both centers and cracks becomes "more mesophytic."

3. Damp Slopes: MAP 3, Wet, Mossy

Primary: Tomenthypnum nitens, Dicranum sp., Didymodon sp. and other Hypnaceae, Carex aquatilis, Luzula confusa, Salix arctica.

Secondary: Cetraria islandica, C. cucullata, Cladonia rangiferina, Arctagrostis latifolia, Carex misandra, Salix reticulata, S. herbacea, Oxyria digyna, Cerastium alpinum, Ranunculus nivalis, Eutrema Edwardsii, Saxifraga oppositifolia, S. cernua, S. nivalis, Potentilla hyparctica, Dryas integrifolia, Cassiope tetragona, Pedicularis lanata, P. hirsuta.

4. Late Snow Areas:

Primary: Bryum sp., Tortella sp., Salix herbacea.

Secondary: Cetraria islandica, Stereocaulon paschale, Alopecurus alpinus, Carex aquatilis, Luzula confusa, Juncus biglumis, Salix arctica, Oxyria digyna, Polygonum viviparum, Ranunculus nivalis, Saxifraga oppositifolia, S. cernua.

5. Sunny South Slopes: MAP 3, Dry Mat Plants

(a) Fine-grained slump:

Primary: Stereocaulon paschale, Cetraria cucullata, Poa glauca, Trisetum spicatum, Hierochloë alpina, Kobresia myosuroides, Luzula confusa, Salix arctica, S. reticulata, Dryas integrifolia.

Secondary: Thamnolia vermicularis, Alectoria ochroleuca, A. jubata, Equisetum arvense, Poa arctica, Festuca brachyphylla, Alopecurus alpinus, Oxyria digyna, Polygonum viviparum, Cerastium alpinum, Silene acaulis, Papaver radicatum, Draba nivalis, Saxifraga oppositifolia, S. nivalis, Potentilla hyparctica, Astragalus alpinus, Oxytropis Maydelliana, Vaccinium uliginosum, Antennaria Ekmaniana.

(b) Sandy alluvial fan:

Primary: Poa glauca, Hierochloë alpina, Salix arctica, S. reticulata, Oxytropis Maydelliana, Arnica alpina, Taraxacum lacerum. *Conspicuous flowers:* Cerastium alpinum, Papaver radicatum, Erysimum Pallasii, Astragalus alpinus, Epilobium latifolium.

Secondary: Poa arctica, Festuca brachyphylla, Trisetum spicatum, Elymus arenarius, Kobresia myosuroides, Carex maritima, Oxyria digyna, Polygonum viviparum, Lesquerella arctica, Draba subcapitata, D. lactea, D. nivalis, D. glabella, D cinerea, Arabis arenicola, Braya purpurascens, Saxifraga oppositifolia, S. nivalis, S. hieracifolia, Potentilla hyparctica, P. rubricaulis, P. Vahliana, Pedicularis hirsuta, Erigeron uniflorus, E. compositus.

(c) Stable raised beaches or ridges, lemming fertilized:

Primary: Poa arctica, Poa glauca, Trisetum spicatum, Hierochloë alpina, Luzula confusa.

Secondary: Equisetum arvense, Festuca brachyphylla, Stellaria longipes, Papaver radicatum, Saxifraga oppositifolia, S. cernua, S. nivalis, S. hieraciifolia, Potentilla hyparctica.

6. Marshes: MAP 3, Wet, Mossy.

(a) Raised ridges and margins:

Primary: Hypnaceae, Aulacomnium palustre, Tomenthypnum nitens, Carex aquatilis, Salix arctica.

Secondary: Poa arctica, Arctagrostis latifolia, Eriophorum angustifolium, Salix reticulata, Stellaria longipes, Silene acaulis, Ranunculus nivalis, Saxifraga oppositifolia.

(b) Wet centers:

Primary: Drepanocladus sp., Tomenthypnum nitens, Campylium stellatum, Arctagrostis latifolia, Hierochloë pauciflora, Eriophorum angustifolium, E. Scheuchzeri, Carex aquatilis.

Secondary: Stereocaulon paschale, Salix arctica, S. reticulata, S. herbacea, Cerastium alpinum, Silene acaulis, Potentilla hyparctica, Pedicularis lanata, P. Langsdorfii.

(c) Ponds:

Primary: Drepanocladus sp., Pleuropogon Sabinei.

7. Drifting Sands and Raised Gravel Bars:

Clumps of Salix arctica, Oxyria digyna, Cerastium alpinum, Papaver radicatum, Saxifraga oppositifolia, Astragalus alpinus, Oxytropis Maydelliana, Epilobium latifolium.

8. Sea Beaches:

Phippsia algida, Puccinellia Langeana, Deschampsia pumila, Elymus arenarius, Sagina intermedia, Arenaria peploides, A. humifusa, Stellaria humifusa, Cochlearia officinalis, Arabis arenicola, Mertensia maritima.

To illustrate how these site types are built together into the vegetation which covers a certain slope, I include two samples:

A. Transect across a solifluction lobe on a south-facing slope: (Cf. Figure 19F)

(a) Top:

Primary: Blackened mosses, Arctagrostis latifolia, Luzula confusa, Salix arctica.

Secondary: Stereocaulon paschale, Cetraria cucullata, Alectoria ochroleuca, Poa arctica, Carex Bigelowii, Polygonum viviparum, Cerastium alpinum, Papaver radicatum, Saxifraga oppositifolia, Dryas integrifolia, Cassiope tetragona.

(b) Mud-boil — the center of the top:

Carex misandra, Luzula confusa, Polygonum viviparum, Sagina intermedia, Saxifraga oppositifolia.

Mud-boil — the edges:

Arctagrostis latifolia, Alopecurus alpinus, Luzula confusa, Salix arctica, Saxifraga oppositifolia, S. nivalis.

(c) Crescent-shaped, gentle slope forming most of the surface of the lobe:

Primary: Carex Bigelowii, Luzula confusa. Dryas integrifolia.

Secondary: Dead mosses, Stereocaulon paschale, Poa arctica, Hierochloë alpina, Oxyria digyna, Polybonum viviparum, Silene acaulis, Kobresia myosurcides, Oxytropis Maydelliana, Vaccinium uliginosum.

(d) Sheltered hollow below the lobe, and on the riser of the lobe.

Primary: Hypnaceae mosses, Cassiope tetragona.

Secondary: Stereocaulon paschale, Luzula confusa, Salix arctica, S. reticulata, Papaver radicatum, Dryas integrifolia, Vaccinium uliginosum.

B. Transect across frost-crack polygon: (Cf. Figure 19C and D)

(a) Exposed area:

1. Crack: clumps of Stereocaulon paschale, Cassiope tetragona.
2. Ridges: bare or clumps of Stereocaulon paschale.
3. Centers: Stone pavement, Stereocaulon paschale, Salix arctica, Papaver radicatum, Saxifraga oppositifolia, Cassiope tetragona.

(b) Out of the direct wind: (Cf. Figure 19E)

1. Crack: water, Calliergon sp., Drepanocladus sp.;
   Bank: Aulacomnium palustre, Salix herbacea;
   Sheltered slope of ridge, in crack: *Primary:* Hypnaceae, Stereocaulon paschale, Carex aquatilis, Cassiope tetragona; *Secondary:* Cetraria cucullata, Thamnolia vermicularis, Salix arctica, Stellaria longipes, Saxifraga oppositifolia, Pedicularis lanata.
2. Ridgetop:
   Primary: Blackened mosses, Lichen thalli, Stereocaulon paschale, Luzula confusa, Saxifraga oppositifolia, Cassiope tetragona.
   Secondary: Cetraria cucullata, Alectoria jubata, Thamnolia vermicularis, Polytrichum piliferum, Poa arctica, Salix arctica, Papaver radicatum.
3. Sheltered sides of the polygon center:
   Primary: Stereocaulon paschale, Cassiope tetragona.
   Secondary: Cetraria cucullata, Cladonia sylvatica, Alectoria jubata, Thamnolia vermicularis, Polytrichum piliferum, Poa arctica, Hierochloë alpina, Arctagrostis latifolia, Luzula confusa, Salix arctica.
4. Wet margins:
   Primary: Tomenthypnum nitens and Aulacomnium palus-

tre or Polytrichum piliferum, Carex aquatilis or Salix herbacea.

Secondary: Cetraria cucullata, Stereocaulon paschale, Hierochloë pauciflora, Arctagrostic latifolia, Eriophorum angustifolium, Luzula confusa, Salix arctica.

5. Pools:
    - Moss: Drepanocladus sp., Pleuropogon Sabinei.
    - Mud: Eriophorum Scheuchzeri.

The Altitudinal Limit of Vegetation on Mt. Thule:

Ferris and Ames reported that *Cetrarias, Alectoria ochroleuca, Stereocaulon paschale, Thamnolia vermicularis, Hierochloë alpina* and other grasses, *Luzula confusa, Salix arctica* and *Draba cinerea* grew in sheltered places up to 2,600 feet. At the highest level of vascular plants (3,000 feet) grew *Cerastium alpinum, Papaver radicatum,* and *Saxifraga oppositifolia.* Black *Umbellicaria,* crustose Parmelias and *Alectoria jubata* grew to 4,00 feet. Crustose Parmelias and unidentified mosses (collected) grew at 4,800 feet.

PART FOUR

PLANT LIST

In identifying my collections, I have used the Gray Herbarium and Arnold Arboretum collections, and chiefly the works of Polunin (1940, 1959), and Porsild (1957), as well as recent monographs. My conclusions follow closely those of Polunin even in preference to the work of recent specialists. My comments concentrate on species about which I differ or which I consider of especial interest. The short list of non-vascular plants includes those which I felt I could recognize in the field. I have not compared these collections with herbarium specimens.

All collections were made in 1954; all localities are at the mouth of the Aktineq River on southern Bylot Island, Northwest Territories, Canada, unless otherwise noted.

NON-VASCULAR PLANTS

Lichens	*Common Name*
Cladonia alpestris (L.) Rabenh.	Alpine Reindeer Lichen
Cladonia rangiferina (L.) Web.	Reindeer Lichen
Cladonia deformis (L.) Hoffm.	Scarlet Wand Lichen
Cladonia pyxidata (L.) Fr.	Goblet Lichen
Stereocaulon alpinum Laur.	——
Stereocaulon paschale (L.) Ach.	Gray Lichen

Lichens	*Common Name*
Stereocaulon denudatum Flk.	Smooth Gray Lichen
Parmelia sp.	Shield Lichen
Cetraria islandica (L.) Ach.	Iceland Moss Lichen
Cetraria nivalis (L.) Ach.	Snow Lichen
Cetraria cucullata (Bell.) Ach.	White Lichen
Alectoria nigricans (Ach.) Nyl.	Black Mane Lichen
Alectoria ochroleuca (Ehrh.) Nyl.	Roan Mane Lichen
Caloplaca sp.	Orange Star Lichen
Thamnolia vermicularis (Sw.) Ach.	Worm Lichen
Mosses	
Sphagnum sp.	Sphagnum
Mnium sp.	Leafy Moss
Dicranum sp.	Broom Moss
Tortella sp.	Twisted Moss
Didymodon sp.	——
Rhacomitrium lanuginosum (Hedw.) Brid.	Gray Moss
Bryum sp.	——
Aulacomnium palustre (Hedw.) Schwaegr.	Marsh Moss
Campylium sp.	Star Moss
Drepanocladus sp.	Curly Moss
Calliergon sp.	Golden Moss
Tomenthypnum nitens (Schreb.) Loeske	Shining Moss
Polytrichum sp.	Haircap Moss
Polytrichum piliferum Hedw.	Awned Haircap Moss

VASCULAR PLANTS

Conspicuous species are in boldface type. Species which are numerous but do not attain as great "importance" in the vegetation are marked with an asterisk.

Equisetum arvense L. (Horsetail) 54204 — 27 July — Muddy shore of the Little River.

Widespread but scattered; on sparsely vegetated, sheltered places, e.g., late snow patches.

Equisetum variegatum Schleich 54114 — 14 July — Mossy sedge-bog on the floodplain at Ooyarashukjooeet.

Hierochloë alpina (Sw.) R.&S. (Sweetgrass) 54201 — 27 July — Dry frost-heaved, raised beach on the south slope of Kungo Hill.

Widespread, and especially common on dry, sunny slopes.

Hierochloë pauciflora R.Br. (Marsh Sweetgrass) 54178 — 26 July — Mossy, wet marsh on the 16-foot beach.

The narrow heads contrast with the spreading awned heads of *H. alpina*. This grass was common in "rice-paddy" areas.

Alopecurus alpinus Sm. (Foxtail) 54134 — 13 July — Sandbank at Ooyarashukjooeet; 54156 — 20 July — Blackened moss area of non-active mud-boils on the 35-foot beach; 54218 — 26 July — Lower part of sandy scree below the bluffs one-half mile west of camp.

Scattered on disturbed soil of well-drained soils, usually on south slopes. It grows as scattered individuals.

Arctagrostis latifolia (R.Br.) Griseb. (Redtop) 54174 — 24 July — In sedgy, wet seep at the head of Golden Plover Creek.

Most upland habitats, but is commonest in closed vegetation on undisturbed soils, usually with a ground cover of mosses. It occurs in wet seeps and on solifluction lobes, but is uncommon in dry, exposed sites and in marshes covered with water.

Deschampsia pumila (Ledeb.) Ostenfeld. (Hairgrass) 54184 — 26 July — On mud and sand shore of temporary fresh-water pond behind the 6-foot beach ridge.

The inflorescences of these specimens were just starting to open.

Trisetum spicatum (L.) Richt.* (Spikegrass) 54195 — 26 July — In clumps on steep slope of sandy scree below the bluffs, one-half mile west of camp.

Abundant on steep, south-facing, well-drained slopes, on the edges of beaches, on solifluction lobes, and especially on lemming mounds; scattered in the upland vegetation. The spikes of the local population are dense, purplish and not interrupted.

Phippsia algida (Soland.) R.Br. 54182 — 26 July — On mud-sand shore of fresh-water pond behind the 6-foot beach.

Pleuropogon Sabinei R.Br.* (Pond Grass) 54120 — 14 July — On muddy shores of an oxbow at Ooyarashukjooeet; 54166 — 24 July — In standing water with *Drepanocladus* in the Upper Phalarope Ponds.

All ponds with a mossy bottom.

Poa abbreviata R.Br. 54110, 54112 — 14 July — In a sheltered frost-crack on the sandy seashore beach at Ooyarashukjooeet.

A low, dense tuft with dense, purple inflorescences. 54110 has just started to flower; 54112 is past full flowering.

Poa glauca M. Vahl* (Blue Grass) 54190, 54192, 54225, 54229 — 26 July — On well-drained, sandy scree, south-facing ravines in the bluffs west of camp.

Common on the uplands, but most conspicuous on disturbed soil and widespread on solifluction forms and frostings. It produces especially dense growth on lemming mounds.

This wiry plant is highly variable, it forms loose to dense tufts, and its inflorescences are from green to purplish-red. 54190 is a large, coarse, tufted plant with coarse inflorescence.

Poa alpina L. Not represented in my collection. Recognized by its tuft growth and flat leaves, and recorded in field notes from barren areas on terrace and ridge-tops in our study area.

Poa Hartzii Gandoger, var. *vivipara* Polunin (Viviparous Bluegrass) 54211 — 25 July — With *Oxyria* on wind-swept low dune sand, northeast of the Little River.

Compared to Polunin's material, this has longer, more pointed ligules and whitish leaf-sheaths. It grows in tufts. It does not match well, but fits best here.

Poa arctica R.Br.* (Arctic Bluegrass) 54216 — 26 July — Bog in mesh of frost-crack pattern near the Upper Phalarope Ponds; 54219 — 26 July — On steep, sandy scree at the base of ravines in the bluffs west of camp.

Varied habitats: well-drained sandy scree, frost-churned raised beaches, barren ridge-tops, dry upland slopes, and low places with peaty, sandy soil; widespread but nowhere in dense stands.

var. *vivipara* Hook. 54213 — 25 July — In peaty, sandy soil in hollows in low dune area northeast of the Little River.

My specimens have rather broad, angularly divergent leaves. The other grass at this site was viviparous, too.

Fernald used *Poa rigens* Hartm. which Porsild and Polunin list in synonymy.

Dupontia Fisheri R.Br., var. *aristata* Malte ex Polunin (Marsh Grass) 54168 — 24 July — On wet margins of the Upper Phalarope Ponds; 54217 — 25 July — On muddy shore of pond in frost-crack polygon mesh on Tui-Tui Tabletop.

This material is hard to key out, because as Polunin says "The genus lacks an awn." The lemmas in my material have long awns.

Puccinellia Langeana (Berl.) Sørensen
(syn. *P. paupercula* (Holm) Fernald). (Goose Grass) 54183 — 26 July — On muddy, sandy shore of temporary pond on the 6-foot beach.

The tiny, dense tufts are less than 5 cm. tall, panicle is more than one-half the length of the culm, branches are not scabrous, glumes are very unequal and entire, lemmas are sparsely hairy, 1.2-1.5 mm., paleas are glabrous, anthers are 0.8 mm. long. Sørensen's key in Porsild (1957) is unsatisfactory and Swallen's key in Hitchcock (1950) does not work either. My material fits well with Polunin's (1940) discussion, in which he calls this material *P. paupercula.* In Polunin (1959), he treats it as *P. Langeana*, and my material matches his description.

Festuca brachyphylla Schultes (Fescue Grass) 54111 — 14 July — In a frost-crack on the sandy beach at Ooyarashukjooeet; 54230, 54231 — 26 July — On the sandy shore of a fresh-water pond behind the 6-foot beach. This material grew around a muddy heap, a previous year's nest of Red-throated Loon *(Gavia stellata)*, the site being covered by water until mid-July. Plants low and dense; inflorescences are small and narrow.

Festuca baffinensis Polunin (Fescue Grass) 54194, 54222, 54223 — 26 July — On steep, sandy scree at the foot of ravine in the bluffs west of camp.

Habitat different from that of *F. brachyphylla*, but in the field I considered all *Festuca* material to be the same.

Taller than 10 cm., has a longer, broader inflorescence than brachyphylla and the upper half of the culm has a short, dense tomentum.

Elymus arenarius L., var. *villosissimus* (Scribner) Polunin (Strand Wheat) 54224 — 26 July — On a sandbank at high limit of ice-shove at the foot of the bluffs west of camp.

On sandbanks and dunes along most of the shore, common in dune areas on the uplands, and at all three Eskimo camps which we visited.

Culms of this material are about 25 cm. tall; glumes and lemmas are soft villous.

Eriophorum Scheuchzeri Hoppe (Mud Cotton-grass) 54121 — 14 July; 54135 — 13 July. On mud shores of low wet areas and old stream channels at Ooyarashukjooeet; 54164 — 24 July — Old stream channel at Aktineqjuak; 54177 — 24 July — Sandy delta of temporary stream at the head of Golden Plover Creek.

Common on muddy sand bottoms of shallow ponds. Its spherical heads are less than 2.5 cm. tall; anthers 1 mm. long, but, as Polunin points out, many scales are more or less attenuate and pale-margined.

Eriophorum vaginatum L. (Tussock Cotton-grass) 54122 — 14 July — In wet swamps, on river flats, low slopes and hilltops at Ooyarashukjooeet.

Locally distributed: near Upper Phalarope Ponds and in stony sedge marshes on the West Ridge. Tussocks 10-15 cm. from the roots to the tops of the heads.

My study of *E. vaginatum* in Alaska convinced me that *spissum* is a geographical variety of it. My eastern Arctic material indicates the same, and Polunin (1959) now includes *E. spissum* Fernald in *vaginatum*, reversing his earlier treatment (1940).

Eriophorum angustifolium Roth (Cotton-grass) 54173 — 24 July — In muddy delta of temporary stream at the head of Golden Plover Creek.

Widespread and conspicuous in nearly all places where *Tomenthypnum* and *Aulacomnium* grow in marshes. It had just started to flower in the last week of July.

The Eskimos recognize this species as separate from *Scheuchzeri* and *vaginatum*, and call it *pualnungwak*. They use the heads for the wicks of their seal-oil lamps (*kudlik*).

Kobresia myosuroides (Vill.) Fiori & Paol.*
(syn. *K. Bellardi* (All.) Degland apud Loisel.) (Spike Sedge) 54160 — 21 July — In mosses in a frost-crack on barren top of West Ridge; 54193 — 26 July — On open, sandy place in vegetated area on top of the bluffs west of camp.

Kobresia is not conspicuous because of its size, but it is widespread on unstable soils, exposed places, and dry upland vegetation.

My material has linear heads, blunt scales and fruit elongate-ovate, slightly cordiform at the base, i.e., pyriform.

Carex maritima Gunn 54221 — 26 July — On steep, vegetated, sandy scree below the bluffs west of camp.

To all appearances, the heads are single, until dissected, which makes keys to *Carex* (Fernald, 1950) misleading.

Carex misandra R.Br.* (Brown Sedge) 54125 — 14 July — In moss on uplands at Ooyarashukjooeet; 54159 — 21 July — In thin moss on a barren place on the 100-foot beach on Kungo Hill.

Common where there is a thin cover of Hypnaceae, on margins or stable areas in disturbed soil on the dry uplands.

Carex Bigelowii Torrey ex Schwein.* 54203 — 27 July — In wet moss on depositional slope on the 35-foot beach.

Much of my material appears to be transitional between this species and the next; but my field notes show that the *Bigelowii*-type was associated with solifluction areas and *Cassiope*, rather than with wet, mossy marshes.

Carex aquatilis Wahleng., var. **stans** (Drej.) Boott (Water Sedge) 54167 — 24 July — Sterile on pool margins, fruiting on moss ridges in the Upper Phalarope Ponds; 54172 — 24 July — In sedgy seep at the head of Golden Plover Creek; 54208 — 25 July — On wet meadow on the 35-foot beach; 54215 — 25 July — Bog ridges in the Upper Phalarope Ponds.

A most conspicuous and widespread species. It grows in damp places everywhere, in wet seeps on steep slopes, on sheltered, mossy slopes; and is the main vegetation of mossy marshes and river flats. It is an important element in the diet of Snow Geese.

I agree with Polunin (1940) that much of this material is not readily assigned either to *aquatilis* or to *Bigelowii*, viz., numbers 54208 and 54215. My material is low; the stems tend to aggregate; most of the leaves are below the middle of the culm; they are glaucous and not scabrous; the lowest bract equals the inflorescence; the terminal spike is 1 cm. long. The problem of intergradation between these two is conspicuous in the eastern Arctic, but I have found no confusion between the two in Alaska and the Yukon Territory.

Carex membranacea Hook 54124 — 14 July — In a wet marsh on a hilltop at Ooyarashukjooeet; 54163 — 24 July — In dry part of swamp with *Salix arctica* and *Stereocaulon* near Upper Phalarope Ponds; 54171 — 24 July — In sedgy seep at the head of Golden Plover Creek; 54199 — 26 July — On frost hummocks above the 55-foot beach.

Luzula confusa Lindeb. (Grass Rush) 5453 — 5 July — On dry slopes above the 135-foot beach on Kungo Hill.

A most widespread and conspicuous plant having a wide range of tolerance; on frost-churned barrens, raised beaches, undisturbed dry uplands, and numerous on gentle mossy slopes, especially on slight rises such as solifluction lobes.

Luzula nivalis (Laest.) Beurl. Not represented in my collections, but occurs widely scattered on the edges of mud-boils, raised beaches, frostings, and barren ridges; identified by its flat leaves and solitary head.

Juncus biglumis L. 54206 — 27 July — On muddy shores of the Little River, late snow patches, and mud-boils on the 35-foot beach and Tui-Tui Tabletop.

Juncus castaneus Smith Not represented in my collections, but recorded on wet mud behind raised beaches and on an abandoned river channel.

Toffieldia coccinea Richardson Not represented in my collections, but seen several times in barren areas such as terrace edge above Little River.

Salix reticulata L.* (Net-leaved Willow) 5467 (male) and 5468 (female) — 11 July — Under solifluction lobe on the 35-foot beach at camp.

Especially important on south slopes, sites with more shelter and moisture than pure *Cassiope* areas, also on mossy ridges in marshes.

The Eskimos call the leaves of this plant *Okouyuk*, the same as those of *S. arctica*, but they do not eat them.

Salix herbacea L. (Herb Willow) 5487 (male) and 5488 (female) — 11 July — On west-facing slope in Lark Gully — a late snow patch.

Characteristic of late snow patches, where it forms a golf-green-like carpet. Occurs also on shady, *Hypnum*-covered, shallow frost-cracks, between hummocks of *Cassiope*, or under solifluction lobes.

Salix arctica Pall. (Arctic Willow) 5405 (male), 5408 (female) — 17 June — Prostrate mats on low, sandy, well-vegetated, sunny slope west of camp; 5422 (male), 5423 (female) – 25 June — On gravelly, open soil on top of the beach at camp; 5461 (female) — 5 July — On slide rock at 2600 feet, Mt. Thule; 54101 (female) — 14 July — On gravel bar at Ooyarashukjooeet; 54180 (female) — 25 July On peat ridges at the mouth of Golden Plover Creek; 54227 (female) — 26 July — on sandy scree below bluffs west of camp.

Grows in all places from the most exposed ridges to mossy swamps. It is primary on the uplands and forms much of the total vegetation; one of the plants growing on newly-stabilized, drifting sands, and mossy ridges in bogs, thereby contributing to their further stabilization and growth; appears as mats in the minimum shelter of low hollows on ridge-tops and by its own cover protects soil from the most violent frost disturbance, thus contributing in an important way to the expression of patterned ground. Its old roots are able to hold on in stable areas while young growth repeatedly sends out shoots to cover open soil.

My material includes specimens which could be assigned to *Salix arctophila* Cockerell on the basis of catkin scales or leaves, but seldom both. My #54180 matches many herbarium sheets of *S. arctophila* and agrees with descriptions of several authors. The leaves of all my material are glabrate and vary from soft hairy gray-green to bright shining dark green and glabrous according to site and exposure. Some specimens have leaves with denticulate margins.

Because I can find no characters in the discussions in Schneider (1918, 1921), Fernald (1950), Hultén (1943), Porsild (1957), and Polunin (1940, 1959) that are not *inter alia* contradicted, and because I cannot find material I felt belonged to a population separate from *arctica* either in Alaska or the eastern Arctic, I am convinced that *S. arctophila* is not distinguishable in the areas where I have worked. The collections I have which might be included in *S. arctophila* are parts of populations continuous with *S. arctica;* they appear as ecotypes both in the field and when compared with herbarium specimens.

None of this material is referable to var. *kophophylla* (Schneider) Polunin, although 5423 has broad-based, glabrate leaves. Further, I hesitate to suggest that two geographical races occur in the same area.

Idlouk, one of our Eskimo companions (Drurys, 1955), called the young leaves of *S. arctica* Okowyuk and said that the local people eat them in the spring. He called the stems *Ookpiyuk* and said that people make baskets out of them, but I could not establish whether he meant his people or other people. He called willow cotton *Shuput* and said they use it for wicks in their seal-oil lamps. Occasionally they eat the roots, which they call *Eyerok.*

Salix Richardsonii Hook., var. *McKeandii* Polunin* (Shrub Willow) 54132 — 13 July — With *S. arctica* on wet hummocks on the floodplain and on mossy polygonal ground with *Eriophorum angustifolium* on the sheltered uplands at Ooyarashukjooeet; on low marshes east of the Aktineq, and in the most sheltered places at Aktinekjuak, Oonakuktooyuk, and Ooyarashukjooeet.

My material has short, hairy capsule pedicels as Polunin (1940) pointed out. Porsild (1957) says that the eastern Arctic material is "incorrectly said to have shorter and hairy-pedicelled capsules."

Oxyria digyna (L.)Hill (Mountain Sorrel) 5421 — 25 June — Sunny, sandy, steep bank at the foot of the bluffs west of camp, growing in silty places; 54212 — 25 July — Wind-swept area of low dunes northeast of the Little River.

Abundant on bare, fine sand or silt on steep unstable ravine slopes, frostings, raised beaches, and frost-heaves.

The plants are a rich purple and the Eskimos, who call it *Kungalik*, eat it in the spring as a salad, savoring the acid taste. They also use it as emergency food.

Polygonum viviparum L. (Alpine Knotweed) 54145 — 13 July — On vegetated lower scree, below slate outcrop two miles from the mouth of the river at Ooyarashukjooeet.

Disturbed soil in ravines, frostings, raised beaches, sunny, grassy slopes, and in open spots above and below solifluction lobes.

Silene acaulis (L.) L., var., *excapa* (All.) DC.* (Moss Pink) 5478 — 11 July — On stabilized, sandy landslide below the ravines in the bluffs west of camp.

Widespread but scarce on sunny, well-drained sites such as frost-churned soils of raised beaches and tops of solifluction lobes.

Lychnis affinis Fries (syn. *furcata* Raf.) 54109 — 14 July — On edge of frost-crack on the lowest sea beach at Ooyarashukjooeet; on stabilized, sandy scree and depositional fans below the bluffs west of camp; and on terrace edges.

Stems are thin and glabrous; leaves mostly basal, and flowers nodding.

Cerastium alpinum L.* (Mouse-ear Chickweed) 5406 — 17 June — On sandy, sunny, well-vegetated slopes west of camp; 5459 — 5 July — On slide rock at 2600 feet on Mt. Thule; 54100 — 11 July — On slaty alluvial fan at the foot of ravines west of camp; 54197 — 26 July — On sandy scree, in open vegetation at the foot of the bluffs west of camp.

Characteristic in sandy soil (well-vegetated or nearly barren) of sunny alluvial fans; common on barren river-wash gravels, frostings on raised beaches, disturbed soil on solifluction lobes, and polygonal ground.

It is densely tangled hairy on all surfaces.

Stellaria longipes Goldie* (Star Flower) 5480 — 11 July — In open place on vegetated steep slope below the bluffs west of camp; 54103 — 14 July — In a frost-crack on the lowest beach at Ooyarashukjooeet.

Inconspicuous but widespread in open and closed vegetation on sunny, dry, grassy slopes, and especially common on lush, grassy tufts of lemming mounds; scarce on dry ridges in marshes.

Stellaria humifusa Rottb. 54226 — 26 July — On muddy sand by temporary fresh-water pond on the 6-foot beach; scattered but locally common on shores of temporary ponds.

Arenaria humifusa Wahlenb. 54103a — 14 July — In frost-crack on the lowest beach at Ooyarashukjooeet.

Scattered but locally common; prostrate on damp, sandy beaches.

Arenaria peploides L. (Sea Beach Sandwort) 5475 — 11 July — On a sandy beach at the mouth of Lark Gully.

Scattered on the sea beaches just above high tide.

Arenaria rubella (Wahlenb.) Sm. 54105a — 14 July — In a frost-crack on the lowest beach at Ooyarashukjooeet.

Sagina intermedia Fenzl.* 5401 — 17 June — (previous year's fruit)

— Sandy beach on the delta of stream out of Lark Gully; 54105 — 14 July — In a frost-crack on the lowest beach at Ooyarashukjooeet; 54210 — 25 July — On low sand dunes in wind-swept place northeast of the Little River.

A tiny wiry plant in damp sand, the edges of mud-boils and on old river deposits.

Ranunculus hyperboreus Rottb. (Water Buttercup) 54232 — 26 July — On sandy mud on the edge of a temporary fresh-water pond on the 6-foot beach; on many sand- or mud-bottomed shallow ponds.

Ranunculus nivalis L. (Snow Buttercup) 5435 — 22 June — On peat ridges beside frost-cracks on the 16-foot beach; on depositional slope below the 35-foot beach; and in frost-cracks in the 16-foot beach crest; 54113 — 14 July — In *Drepanocladus-Tomenthypnum* bog in an abandoned river channel at Ooyarashukjooeet; 54115 — 14 July — On moss and mud in late snow area next to creek draining into the river at Ooyarashukjooeet; 54176 — 24 July — In sedgy, wet seep at the head of Golden Plover Creek; 54181 — 25 July — On lower slope, beside Golden Plover Creek.

Common in wet, mossy places where snow persists after the main thaw, on peat ridges, in frost cracks and in moss hummock areas.

Numbers 54115 and 54181, both of which grew in creek banks, are small and delicate; they match specimens of *R. Sabinei* in the Gray Herbarium, except that they have brown curly hairs on the sepals instead of pale brown-tan sparse hairs of *R. Sabinei.*

Ranunculus sulphureus Solander apud Phipps 54131 — 13 July — In wet hummocks area, with *Salix arctica*, on the floodplain of the river at Ooyarashukjooeet; 54175 — 24 July — In sedgy seep at the head of Golden Plover Creek.

Papaver radicatum Rottb. (Poppy) 5414 — 25 June — Sunny, sandy scree on the edge of the bluffs; 5452 — 5 July — On dry slope below the 135-foot beach on Kungo Hill; 5460 — 5 July — On slide rock at 2600 feet on Mt. Thule; 5494 — 11 July — Slaty scree at the foot of the bluffs west of camp; 54145 — 13 July — On vegetated sandy scree fan below slate rocks along the river at Ooyarashukjooeet.

Common and widespread on (1) disturbed soils of frostings, alluvial fans, sandy slopes below the bluffs, and frost-churned soil next to frost-cracks, (2) exposed areas: raised beaches and ridge-tops, and (3) scattered in dry *Dryas, Salix arctica-Cassiope* areas of the uplands.

In a dozen places we found clumps with white flowers, e.g., 5452a, var. *albiflorum* Lange. This is certainly not equivalent to a geographical variety and Polunin's quotation from Abbe describes the genetic activity of a sport at best.

The peak of flowering was about July 10. Flowers were past and young fruit developing by July 22.

Cochlearia officinalis L., var. *groenlandica* (L.) Gelert apud Andersson and Hesselman 5404 — 17 June — On sand in a rubble pile below the bluffs west of camp; 5465 — 2 July — On sand and cobbles in front of an Eskimo house at Sermilik; 54106 — 14 July — In a frost-crack on the lowest beach at Ooyarashukjooeet.

Damp soil of raised beaches or alluvial fans; often associated with Eskimo settlements.

The siliques are ovate and acute at the tips; plants depressed rosettes with the siliques barely raised above the tuft.

Eutrema Edwardsii R.Br.* 54148 — 13 July — In mossy ridges between mud-boils on hilltops about three miles inland at Ooyarashukjooeet.

Widely scattered as individuals, on mossy or muddy places on uplands.

Cardamine bellidifolia L. 54214 — 25 July — On mossy ridges in a bog northeast of the Little River.

Lesquerella arctica (Wormskj.) S. Watson 5451 — 29 June — and 5493 — 11 July — both on sandy alluvial fans below slaty sediments in the ravines in the bluffs west of camp; conspicuous among the weedy flowers.

Draba alpina L., var. *nana* Hook.* (Yellow Mountain Mustard) 5446 — 29 June — Almost buried in other plants (*Salix arctica, Potentilla hyparctica*) on sunny slopes of alluvial slope below the bluffs west of camp; 5497 — 11 July — Slaty scree at the foot of the bluffs west of camp; 54144a — 13 July — In mossy tussocks on the open uplands and around rock remnants on the hill-tops three miles inland at Ooyarashukjooeet.

Widespread but everywhere scarce; on sunny slopes on disturbed soil of fine-grained scree, mud-boils, or soil stripes.

All have yellow flowers, except 54144a which has cream-colored; all material is uniform in stems, leaves and fruit.

Idlouk called this, and all little yellow flowers, *Iutuk nyukoonyah.*

Draba subcapitata Simmons (Mountain Mustard) 54107 — 14 July — In sand in a frost-crack on the lowest beach at Ooyarashukjooeet.

A large series — all typical.

Draba lactea Adams (Mountain Mustard) 54123 — 14 July — In *Eriophorum angustifolium* and *Salix arctica* on a hilltop east of the river at Ooyarashukjooeet; 54162 — 21 July — In mossy areas, especially frost-cracks, on the uplands of Plover Plateau; 54170 — 24 July — On moss ridges at Upper Phalarope Ponds.

Scattered in mossy upland vegetation.

Polunin (1940) includes this in *D. fladnizensis* Wulfen, but I am not following his fine treatment because my material matches the *D. lactea* material in the Gray Herbarium and not *D. fladnizensis.* Fernald (1950) treats this as *D. fladnizensis,* var. *heterotricha.*

Draba nivalis Liljebl.* (Common Mountain Mustard) 5413 and 5416 — 25 June — (opening flowers fixed) 5445 and 5449 — 29 June — (opening flowers fixed) 5479, 5481 and 5482 — 11 July; 54185 — 26 July. All these numbers are from the sunny, south-facing slopes of fine to coarse sand alluvial fans and screes at the base of the bluffs west of camp; from nearly closed grassy *Salix arctica* vegetation to bare places with isolated plants, on all but the most open and active soil. 54108 — 14 July — In frost-cracks on the lowest beach at Ooyarashukjooeet.

This is one of the two really common Drabas and is readily recognized in the field. It prefers bare patches.

Draba glabella Pursh, var. *brachycarpa* (Rupr.) Fernald (Mountain Mustard) 54144 — 13 July — In tussocks and around rock remnants on hilltops three miles inland at Ooyarashukjooeet.

Resembles *D. cinerea* closely, but habitat is distinct.

Draba cinerea Adams (Ashy Mountain Mustard) 5403 and 5407 — 17 June; 5415 — 25 June (opening flowers fixed); 5447 and 5448 — 29 June (opening flowers fixed); 5484 and 5498 — 11 July; 54186 — 26 July — All on sandy screes and alluvial fans below slaty sediments in bluffs west of camp; 5459a — 5 July — On slide rock at 2600 feet on Mt. Thule; 54142, 54143 and 54151 — 13 July — On vegetated, sandy alluvial fan below slaty rocks on the river bank above Ooyarshukjooeet.

A large *Draba*, common in vegetated alluvial or scree fans. It grows in among the *Salix arctica* and other mat plants more than *D. nivalis* and avoids the open sandy patches.

The flowers vary from rich cream as they open to white in some several days later. The siliques are hairy. Porsild's (1957) key, which otherwise works well, does not include the cream flower color; the scapose infloresence which he uses to separate *cinerea* from *groenlandica* is not useable in my material.

Arabis arenicola (Richardson) Gelert, var. *pubescens* (Wats.) Gelert 5491 — 11 July — On sandy alluvial fan below a ravine cut into slaty rocks on the bluffs west of camp.

On fine-grained, unstable soils, but not on frost-churned soils.

Sparsely hairy, the younger leaves being much more hairy than the older.

Erysimum Pallasii (Pursh) Fernald 5409 — 17 June, and 5496 — 11 July — Both on open, unstable alluvial fans at the foot of slaty bluffs west of camp.

The deep tap root is well-adapted to the shifting sands of the slides, where it is numerous.

The flowers are magenta and siliques radiate from the rosette of leaves. The magenta flowers raise a question of how they are pollinated (*Epilobium* and *Pedicularis* as well), because insects are said not to see this color. Presumably they respond to the blue, but if so, why the red at all?

Braya purpurascens (R.Br.) Bunge apud Ledeb. 5450 — 29 June (flowers fixed); 5486 — 11 July — Both on mud, sand and angular pebbles of scree and alluvial fan at the base of ravines in the bluffs west of camp; scarce.

Flowers and fruits are weakly erect, 5 cm. above the rosettes; the siliques are long compared to the material in the Gray Herbarium, and they taper to their tips.

Saxifraga rivularis L. 54102 — 14 July — On sand in a frost-crack on the lowest beach at Ooyarashukjooeet; 54119 — 14 July — In a late snow patch on the bank of a creek tributary to the river above Ooyarashukjooeet; 54228 — 26 July — In damp, muddy sand by loon's nest on the temporary fresh-water pond on the 6-foot beach.

Sites are muddy, cold, and wet late in the season.

Saxifraga cernua L.* (Nodding Saxifrage) 5456 — 5 July — On west slopes with seasonally advanced vegetation above the 56-foot beach on Kungo Hill; 54104 — 14 July — In a frost-crack on the lowest beach at Ooyarashukjooeet; 54149 — 13 July — On the edges of mud-boils, among hummocks, on hill-tops two miles inland from Ooyarashukjooeet; 54187 — 26 July — Steep vegetated scree below the bluffs west of camp.

Scattered individuals in grassy, closed vegetation or damp, fine-grained open soils.

5456a — 5 July, and 54205 — 27 July — Muddy shores of the Little River are slender, short, glabrate, and late-flowering. They match var. *exilioides* Polunin. and differ from the typical population but grow mixed in with typical plants. Their growth may be affected by local conditions, their genetic basis simple, or there may be apomixis.

Saxifraga caespitosa L. 5490 — 11 July — Low, wet place in front of alluvial fan below Lark Gully; 54136 — 13 July — On *Dryas*-sandy area at the 10-foot beach at Ooyarashukjooeet; 54188 — 26 July — Sunny, vegetated scree below the bluffs west of camp.

All material is low and has one or rarely two flowers: forma *uniflora* (R.Br.) Engler & Irmsch.

Saxifraga stellaris L., var. *comosa* Retzius* (Star Saxifrage) 54116 — 14 July — In *Tomenthypnum* sedge bog on the floodplain above Ooyarashukjooeet; 54161 — 21 July — On a mossy area on the edge of a barren on the 100-foot beach on Kungo Hill; 54169 — 24 July — On moss ridges around the Upper Phalarope Ponds; 54207 — 27 July — On muddy shore of the Little River.

Matches *S. foliolosa* R.Br., because most of the flowering head is bulbils, which raises the question whether this population should be a species or a variety.

Saxifraga hieraciifolia Waldst. & Kit.* (Hawkweed Saxifrage) 5455 — 5 July — On sunny frosting above the 56-foot beach on Kungo Hill; 54117 — 14 July — In a late snow area on a creek bank above Ooyarashukjooeet; 54130a — 14 July — On dry *Dryas-Salix arctica-Saxifraga tricuspidata* raised beach at Ooyarashukjooeet.

54117 is young with clustered terminal inflorescence; its coarse stem and leaves indicate *hieraciifolia*, but the specimens are hard to separate from *Saxifraga nivalis*.

Saxifraga nivalis L.* (Snow Saxifrage) 5417 — 25 June — Sunny, vegetated slump below bluffs just west of camp; 5454 — 5 July — On dry slope of Kungo Hill at about the 135-foot beach; 54118 — 14 July — In a late snow patch on creek bank above Ooyarashukjooeet; 54130 — 14 July — On a dry raised beach with *Dryas*, *Salix arctica* and *Saxifraga tricuspidata* at Ooyarashukjooeet; 54198 — 26 July — In vegetated scree below bluffs west of camp.

Widespread on sunny slopes soon free of snow and soon dry.

54198 is large and coarse, also old; the rest of the material is slender and low, but I cannot separate out any population such as var. *tenuis* Wahlenb.

Saxifraga tricuspidata Rottb. (Spiny Saxifrage) 5473 — 11 July — On sunny scree below the bluffs; 54138 — 13 July — On dry raised beach about 25 feet above sea level at Ooyarashukjooeet; 54202 — 27 July — On dry frosting on the side of Kungo Hill.

Scattered but abundant where it appears on dry, sunny, sandy soil.

54202 has the lateral teeth and spines on the leaves almost completely lacking: f. *subintegrifolia* (Abrom.) Polunin.

The Eskimos make a brew out of the whole plant, and call it *kakilangnakotee*. Kakil refers specifically to this species. Idlouk allowed that the brew is pretty grim.

Saxifraga flagellaris Willd. 54150 — 13 July — On edges of mud-boils in a hummocky area on the hilltops two miles north of Ooyarashukjooeet.

Widely-scattered individual plants.

Saxifraga Hirculus L., var. *propinqua* (R.Br.) Simmons 54137 — 13 July — In wet sedge area on the floodplain at Ooyarashukjooeet.

Saxifraga oppositifolia L. 5412 — 17 June — On sandy scree with angular fragments below the bluffs west of camp; 5460 — 5 July — On slide rock at 2600 feet on Mt. Thule.

Grows in tiny clumps on almost wholly barren surfaces blasted by the east wind, as cushions (a) where there is a little shelter, (b) in the densely vegetated uplands, (c) on sunny slopes, (d) on unstable ravine screes, (e) on the drifting sands of floodplain washes, and (f) in wet *Tomenthypnum* ridges in the water-soaked bogs. It grows everywhere we found plants, other than the salt-tolerant strand plants, and is a conspicuous part of the vegetation almost everywhere it grows because of its cushions and purple flowers which continue to bloom through July. During June many clumps were in full bloom while the plant's base held snow and ice, and while the roots were embedded in frozen ground.

The Eskimos call it *Owbiletungwak* and eat the flowers and roots occasionally — calling the root *Eyerok.*

Chrysosplenium alternifolium L. 54127 — 14 July — In Mnium-mossy area on the floodplain of the river at Ooyarashukjooeet.

These specimens have 5 and 6 stamens, and cannot belong to var. *tetrandrum* Lund, which is the only form Polunin (1940) found in our area.

Potentilla hyparctica Malte* (Cinquefoil) 5402 — 17 June — On sandy, steep, sunny banks in clumps with *Salix arctica,* grasses and many flowers below the bluffs.

Scattered on steep upland slopes, on sheltered places next to barrens, and on the edges of lemming mounds.

Polunin (1940) calls this *P. emarginata* Pursh; Fernald (1950) and Polunin (1959) call it *hyparctica.*

Potentilla rubricaulis Lehm. (Cinquefoil) 5411 — 17 June — On sandy alluvial fan at the foot of ravines in the bluffs west of camp.

The denseness of tufts and number of flowers seem to be unreliable characters in *Potentilla,* but my material matches the specimens of this species in the Gray Herbarium, and it differs from other species.

Potentilla Vahliana Lehm. (Lemon Cinquefoil) 5477 — 11 July — In open areas on sandy, sunny slopes of ravines cut into the bluffs west of camp.

Its long hairs on all surfaces, and beards at the tips of the teeth on the leaves make it easy to recognize in the field. Found only at the bluffs.

Dryas integrifolia M. Vahl. (Avens) 5419 — 25 June — Open, sunny, vegetated slopes below the bluffs west of camp.

Primary on sunny, well-drained sites on gentle to steep vegetated slopes, and over most of the uplands. It forms the characteristic closed vegetation of many places between mud-boils, soil stripes, the tops of solifluction lobes, or the sheltered sides of ridges next to frost-cracks.

The peak of flowering was about 10 July, and the fruits were just appearing, still twisted, when we left.

Examination in the field and at the Gray Herbarium shows this material has entire or dentate leaves, and glabrous or tomentose leaves in one tuft. I can find no support for dividing the population into *intermedia, canescens* and *punctata.*

Astragalus alpinus L. (Vetch) 5420 — 25 June, and 5492a — 11 July

— Sunny, vegetated screes below the bluffs west of camp.

Abundant on sunny, sandy, well-drained slopes all over the area, on sandy alluvial fans at the mouth of ravines below the bluffs west of camp, on fine-grained, sandy soil on the river floodplains, and on sand dunes.

This is a conspicuous weed in disturbed, but not actively churned soils, and thus it is absent from the bare soil of frost patterns.

Its flowering peak was 20-25 July.

Oxytropis Maydelliana Trautv. (Locoweed) 5457 — 5 July — On edges of mud-boils and frostings on the 135-foot beach on Kungo Hill; 54196 — 26 July — On steep vegetated scree below the bluffs west of camp.

A conspicuous flower on sunny, well-drained slopes from the sides of Kungo Hill to vegetated screes in the ravines, and common with *Dryas* in vegetation stripes on the uplands. The flowering peak came 20-25 July.

The Eskimos call this *Eyerok* and dig and eat its thick root which, when fried, tastes like parsnip. The name probably means root because they call the root of *Salix arctica* and *Saxifraga oppositifolia* the same, and eat them also. They prefer this one.

Empetrum nigrum L., var. *hermaphroditum* (Lange) Sørensen (Crowberry) 54179 — 26 July — On dry *Cassiope* slope below the 55-foot beach on Kungo Hill.

This is the only station, but Leah (Idlouk's daughter) said that it is common at their main camp on the south shore of Eclipse Sound. They call it *paonga* and eat the berries.

Epilobium latifolium L. (Willow-herb) 5495 — 11 July — On slaty scree at the foot of the bluffs west of camp.

Abundant on sand and gravel alluvium at the mouth of creeks and ravines in the bluffs, on the abandoned channels and gravel bars of rivers, and on wet shores of fresh-water ponds behind raised beaches.

Epilobium arcticum Samuelss. 54140 — 13 July — On sedge-moss, wet area at the mouth of a tributary creek above Ooyarashukjooeet.

Polunin (1940, 1959) keeps this as a variety of *E. davuricum* Fischer ex Hornem.

Cassiope tetragona (L.) D. Don (Bell Heather) 5458 — 5 July — On edge of mud-boils and solifluction lobes on sunny slope near the 135-foot beach on Kungo Hill; 5459 — 5 July — On slide rock at 2600 feet on Mt. Thule.

Polunin's description of the habitat of this species is good. It grows in slightly moist, sheltered places over most of the uplands, but is replaced by grasses and flowers on dry, steep, sandy slopes, and by mosses and sedges in wet marshes; it is widespread in depressions and characteristic of frost-cracks, the vegetated pattern of soil stripes and mud-boils, polygon meshes, and the edges of solifluction lobes.

The complete lack of *Cassiope* is an outstanding feature of stream banks or places so sheltered from the sun that the snow lies until the first of July.

The flowering peak was 15-20 July.

The Eskimos call this a gutteral *chyuktak* and fill bags with it to make mattresses. They know the widespread use of its waxy branches to make an emergency fire.

Vaccinium uliginosum L., var. *alpinum* Bigel. (Bilberry) 5469 — 11 July — Under the slope of a solifiuction lobe on the side of the 35-foot beach at camp.

Scarce and restricted to sheltered hollows in the ravines in the bluffs, and the lips of raised beaches or solifluction lobes; rare in frost-cracks where most of its associates are common.

Androsace septentrionalis L. 54147 — 13 July — One plant in a steep alluvial fan below slaty outcrop above Ooyarashukjooeet.

Armeria labradorica Walbr. (Everlasting) 54165 — 24 July — At the bottom of a creek valley at Aktineqjuak; 54189 — 26 July — Below vegetated scree at the foot of the bluffs west of camp; 54209 — 25 July — On dry frosting above the 55-foot beach.

Polunin (1959) includes this in *A. maritima* (Miller) Willd. I did not look into the question.

Martensia maritima (L.)S.F. Gray, var., *tenella* Fries 5489 — 11 July — Sandy sea beach at Ooyarashukjooeet.

Characteristic of sea beaches above high tide.

Pedicularis sudetica Willd. (Fernweed) 54128 — 14 July — In sedgy area on the floodplain near Ooyarashukjooeet.

Most of the plants have leaves on their stems. Their flowers are pale purple with a magenta end on the long-toothed helmet and magenta spots on the lip.

Pedicularis lanata Cham. & Schl.* (Woolly Fernweed) 5437 — 22 June — On exposed, mossy *Luzula* area above the 135-foot beach.

Common and widespread, growing singly in the *Salix arctica-Drayas-Cassiope uplands.* It is one of the first plants to flower outside the sunny south slopes. Flowers wholly pink.

Pedicularis Langsdorfii Fisch., var. *arctica* (R.Br.) Polunin (Marsh Fernweed) 54155 — 20 July — In wet moss, sedges, and *Salix arctica* on top of the West Ridge.

Pedicularis hirsuta L. 54139 — 13 July — On *Dryas-Salix arctica* low alluvial fan slope below the terrace, one mile above Ooyarashukjooeet, in a weedy stand.

Flowers small, pale lavender with a paler lip and purple tip to the helmet. It is slender, with flowers sticking out to the sides through the silvery hairs.

Pedicularis capitata Adams* (Yellow Fernweed) 54133 — 13 July —

In *Dryas-Salix arctica* on wet, hummocky area on a depositional fan about a mile above Ooyarashukjooeet.

The only station for the species in flower, but it is widely scattered as individual very fern-like leaves in hummocky, mossy areas on the uplands. The silver spots on the leaves add to the resemblance to a fern because they suggest sporangia. If this were an animal, it surely would be credited with mimicry.

Its pale buff flowers have a pale purple tip to the helmet.

Erigeron uniflorus L., var. *eriocephalus* (J. Vahl) Abromeit (Fleabane) 5474 — 11 July, and 54189a — 26 July — On sunny screes and steep ravine sides in the bluffs west of camp; 54231a — 26 July — Mud-sand shore of temporary freshwater pond on the 6-foot beach.

The ray flowers are pale lavender; the young material (5474) has heads 1.5 cm. across and the older heads are 2-2.5 cm. across. Cronquist (1947) and Polunin (1959) include this in *E. uniflorus*.

Erigeron compositus Pursh. (Daisy) 5492 — 11 July — On sunny, sandy alluvial fans at the bottom of the ravines in the bluffs west of camp.

Antennaria Ekmaniana A.E. Porsild (Pussytoes) 5418 — 25 June, and 5472 — 11 July — On sunny, well-drained, sandy slopes above the depositional fans at the base of the bluffs west of camp; 54200 — 27 July — On dry frostings on raised beaches on the side of Kungo Hill.

5418 and 5472 match herbarium material; 54200 includes specimens with mostly two or three heads closely pressed together and many have single heads. They match sheets labeled *A. angustata* in the Gray Herbarium, but seem to me to belong with other specimens. Polunin (1959) includes *labradorica* (where he placed this in 1940) in *Ekmaniana*.

Arnica alpina (L.) Olin, var. **angustifolia** (Vahl) Fernald 5464 — 29 June, and 5476 — 11 July.

A conspicuous flower on the sunny, sandy slopes of the bluffs west of camp where the vegetation of grasses, *Salix arctica* and *Oxytropis* has stabilized the slopes.

Senecio congestus (R.Br.) DC., var. *palustris* (L.) Fernald 54129 — 14 July — In sedgy, mossy old stream channel near Ooyarashukjooeet.

Does not match Polunin's f. *polycricos*.

Taraxacum lacerum Greene (Dandelion) 5410 — 17 June, 5499 — 11 July, 54191 — 26 July, and 54220 — 26 July — All from unstable, open fans and vegetated ravine sides on sandy screes below slaty bluffs west of camp.

5499 and 54220 differ in that many plants lack the horns on the inner involucral bracts, but all belong to one variable population.

SUMMARY

Frost Features

Washburn (1956) has divided minor topographic features produced by frost action into solifluction forms and structural soils. On Bylot Island, solifluction forms (crescents, tongues, and transverse terraces) modify nearly all slopes below the bedrock mountains into microtopography to which the vegetation responds in detail. Soil creep and mud avalanches, covered by open nets or closed mats of plants, nearly obliterate some old raised beaches, while minor alluviation creates forms a foot across and an inch high. Frost-riving and solifluction have sculptured a gently-sloped plateau cut by steep stream valley sides on southwestern Bylot. These strongly resemble the so-called peneplain remnants of eastern parts of Canada and the United States, and suggest that cryoplanation whose base level is the lower altitudinal limit of periglacial arctic erosion processes may be the source of the raised surfaces, not a previous stream erosion cycle.

Patterned ground *(Strukturboden)* is expressed as non-sorted circles, polygons and stripes, or as frost-crack patterns. Circular, bare areas, usually of fine material, mud-boils, are active during spring thaw and may appear in aggregates as non-sorted polygons (bare patches alternating with mat vegetation, Arctic Willow, Avens, mosses, and a few scattered flowers). On gentle slopes, they become elongated into non-sorted stripes, tan angular fines and pebbles, alternating with stripes of vegetation. In some places these areas are hundreds of yards long and several square miles in area.

During the thaw the soil is saturated with water down to the top of persistent frost. Certain bare spots thaw rapidly to a depth many times that of the vegetation-covered surroundings, and islands of frozen ground may be underlain by thawed ground. Water flowing over, through, out of, and into the soil, or some related force, thrusts fines up from depths and creates mud-boils, solifluction lobes and mud avalanches which appear related in origin. The sediments in mud-boils (usually fines at the surface but often coarse at depths) draw together into a cheese-like surface and crack progressively from the margins and around stones —

thus suggesting colloidal action (Steche, 1933). Cracks on these surfaces *(Zellenboden)* are formed both by stresses and strains of alternating freeze-thaw and wet-dry. The instability which results prevents plant growth.

A master pattern of frost-cracks (ice-wedge polygons, *Spaltenboden, Taimyrpolygone*) exists on all surfaces of unconsolidated material, most clearly on the youngest beaches. They run down or across the slope and (a) meet at right angles on flat beaches, or (b) form concentric cracks following the contours crossed by cracks radiating from the center on hilltops.

(1) The close similarity of this pattern of frost-cracks to cracks formed when the sea ice yields to pressures and strains at the tidal zone, (2) the lack of deformation of sediments, and (3) the uniformity of cracks disregarding sediment sizes, suggest that the pattern results from the fracturing of perennially frozen ground under strains, such as differential isostatic readjustment. Expansion of ice in the cracks by addition of annual increments and yearly formation of new contraction cracks caused by violent drops in temperature raise a ridge beside the cracks of the master pattern.

Subsequent topographic modification on exposed hillslopes results from formation of secondary contraction cracks parallel to and on the edges of the ridges of the large patterns. Year by year these advance toward the center of the mesh where snow persists. As centers become smaller and are obliterated, the former master pattern persists as traces in lichens, or a new high-centerd polygon results, resembling those of northern Alaska (Black, 1952). In areas heavily grown to mossy and sedgy vegetation, modification results from peat formation associated with differential plant growth on the microtopographic features according to differences in moisture. Peat ridges form on the rectangular patterns beside frost-cracks and act as dams and create a rice-paddy effect. The ponds trapped this way lead to deeper thawing of the ground; and regularly spaced, rectangular thaw-ponds (Muller, 1947; Wallace, 1948) are produced.

Vegetation

The vegetation of southern Bylot Island is the result of responses of plants as species and individuals to gradations in wind and sun exposure, soil stability, moisture availability, and time of year when sites become free of snow. The variations in the vegetation from ridge-top to valley-bottom are often the same as that from the center to the mounds on the margins of the polygons formed by frost action. Sedge marshes occur around ponds on the tops of hills, and vegetation-free frostings are found where the east wind can blow through the bottom of a valley.

The minor elevations created by frost-heaving or slump lobes produce drainage and exposure effects which greatly influence the vegetation. On dry tops of such forms, dry sites are produced; the steep slopes are well supplied with moisture and are covered with a rich mat, usually of Bell Heather. Minor hollows collect moisture and hold it above the perennially frozen ground, allowing sedge and moss vegetation to colonize.

Most of the vegetation is made up of ten species; 85 per cent is made up of thirty-four. As is universally true, some species grow almost everywhere on Bylot, others are rare and local; some have site significance, others seem to have none; some sites are rich in species, most are poor. The flora of the area is rich in calciphiles.

Vegetation types selected by site and aspect agree with habitats selected by birds, and suggest that birds' selection is based on life form and the topography of the vegetation.

Cryoturbation makes a homogeneous subsoil but the resulting microtopography creates local physical conditions reflected in great variability between and within plant associations over a short distance. Dominance, site indication and frequency are all useful, but I find the concept of succession of little value in describing this vegetation.

We recorded 101 species of vascular plants.

Contribution No. 38 from the Hatheway School of Conservation Education, Massachusetts Audubon Society, South Lincoln, Massachusetts.

LITERATURE CITED

AARIO, L. 1944. Die spätglaziale Entwicklung der Vegetation und Klimas in Finnland. Geol. Rundschau, 34: 695-712.

ADAMS, M. F. 1815. De skeleto mammontes sibirico ad maris glacialis littora anno 1807 effossa. Acad. Sci. Pet. Mem., Vol. 5.

ANDERSSON, J. G. 1906. Solifluction, a component of subaerial denudation. Journ. Geol., 14: 91-112.

ANTEVS, E. 1932. Alpine zone of Mt. Washington Range. Publ. by the author. Auburn, Me. 118 pp.

AUER, V. 1920. Über die Entstehung der Stränge auf den Torfmoosen. Acta For. Fenn., **12:** 23-145.

BEECHEY, F. W. 1831. Narrative of voyage to Pacific and Bering's Strait. London.

BENNINGHOFF, W. S., JR. 1952. Interaction of vegetation and soil frost phenomena. Arctic, **5** (1) : 34-44.

BERGSTRÖM, E. 1912. En märklig form av rutmark från barrskogsregion i Lappland. Geol. för:s förh. Bd., **34** (3). (*In* Högbom).

BESKOW, G. 1930. Erdfliessen und Strukturboden der Hochgebirge im Lichte der Frosthebung. Geol. fören. i Stockholm förhandl., **52** (3) : 622-638.

————. 1947. Soil freezing and frost heaving with special reference to roads and railroads. Northwestern Univ. Tech. Inst. 145 pp.

BILLINGS, W. D. AND A. F. MARK. 1961. Interactions between alpine tundra vegetation and patterned ground in the mountains of southern New Zealand. Ecol., **42:** 18-31.

BILLINGS, W. D. AND H. A. MOONEY. 1959. An apparent frost hummock-sorted polygon cycle in the alpine tundra of Wyoming. Ecol., **40:** 16-20.

BLACK, R. F. 1952. Polygonal patterns and ground conditions from aerial photographs. Photogrammetric Engineering, **18:** 123-134.

BLACK, R. F. AND W. L. BARKSDALE. 1949. Oriented lakes of northern Alaska. Journ. Geol., **54:** 105-118.

BÖCHER, T. S. 1933a. Phytogeographical studies in the Greenland flora. Meddel. om Grønland, **104** (3) : 1-54.

————. 1933b. Studies on the vegetation of the east coast of Greenland. Meddel. om Grønland, **104** (4) : 1-132 + 6 pls.

BRYAN, K. 1946. Cryopedology — the study of frozen ground and intensive frost action, with suggestions on nomenclature. Am. Journ. Sci., **214:** 622-642.

————. 1949. The geologic implications of cryopedology. Journ. Geol., **57:** 101-104.

BÜDEL, J. 1944. Die morphologischen wirkungen des Eiszeit Klimas in Gletscherfrein Gebiet. Geol. Rundschau, **34:** 482-519.

————. 1949. Die Raumliche und Zeitliche Gliederung des Eiszeitklimas. Die Naturwissenschaften, **36:** 105-112; 133-140.

CAILLEAUX, A. 1942. Les actions éoliennes périglaciaires en Europe. Mem. Soc. Géol. France, **46:** 166 pp.

CAILLEAUX, A. AND G. TAYLOR. 1954. Cryopédologie, étude des sols gelés: Expeditions Polaires Française 4. Paris, Hermann & Cie. Actualités Scientifiques et Industrielles, **1203:** 218 pp.

CAJANDER, A. K. 1913. Studien über die Moore Finnlands. Acta For. Fenn., **2:** 208 pp.

CHYDENIUS, K. 1869. Svenska Expeditionen till Spitzbergen 1861. (Notes from the diary of S. Lovén for 1837 — in German by L. Passarge). Jena. 287 pp.

CLEMENTS, F. E. 1916. Plant succession. Carnegie Inst., Washington, Publ. 242.

COWLES, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gaz., **27**: 95-117; 167-202; 281-308; 361-391.

————. 1901. The physiographic ecology of Chicago and vicinity: a study of the origin and development of plant societies. Bot. Gaz., **31**: 73-108; 145-182.

CRAMPTON, C. B. 1912. The geological relations of stable and migratory plant formations. Scot. Bot. Rev., **1912** (1): 1-17.

CRONQUIST, A. 1947. Revision of the North American species of *Erigeron* north of Mexico. Brittonia, **6**: 121-300.

DAHL, E. 1951. On the relation between summer temperature and the distribution of alpine vascular plants in the lowlands of Fennoscandia. Oikos, **3** (1): 22-52.

DARWIN, C. 1859. The origin of species. London.

DAVIS, W. M. 1889. Rivers and valleys of Pennsylvania. Nat. Geogr. Mag., **1**: 183-253.

————. 1909. Geographical essays. Ginn and Co.

DAVISON, C. 1888. Note on the movement of scree material. Quart. Journ. Geol. Soc., **44**. (*In* Högbom).

————. 1889. On the creeping of the soilcap through the action of frost. Geol. Mag., dec. **3**: 255.

DE GEER, G. 1910. Guide de l'excursion au Spitzberg. IX Congr. Géol., Stockholm.

DENNY, C. S. 1936. Periglacial phenomena in southern Connecticut. Am. Journ. Sci., **32**: 322-342.

————. 1938. Glacial geology of the Black Rock Forest. The Black Rock Forest Bull., **8**: 70 pp. Cornwall-on-the-Hudson, New York.

————. 1940. Stone-rings on New Hampshire mountains. Amer. Journ. Sci., **238**: 432-438.

————. 1951. Pleistocene frost action near the border of the Wisconsin drift in Pennsylvania. Ohio Journ. Sci., 51 (3): 116-125.

————. 1956. Surficial geology and geomorphology of Potter County, Pennsylvania. Geol. Surv. Prof. Paper #288. v + 72 pp.

DRURY, W. H., JR. 1956.. Bog flats and physiographic processes in the Upper Kuskokwim River Region, Alaska. Contr. No. 178 from the Gray Herbarium of Harv. Univ., Cambridge, Mass. 130 pp.

————. 1961. Studies of the breeding biology of Horned Lark, Water Pipit, Snow Bunting, and Lapland Longspur on Bylot Island, Northwest Territories, Canada. Bird-Banding, **32** (1): 1-46.

DRURY, W. H., JR. AND M. C. DRURY. 1955. The Bylot Island Expedition. Bull. Mass. Aud. Soc., **39** (6): 259-265.

DÜCKER. A. 1933. Die wind Kante des Norddeutschen Diluvium in ihren Beziehungen zu periglacialen Erscheinungen und zu Decksand. Jahrb. ser Preuss. Geol. Landesanstalt., **54**: 457-530.

———————. 1951. Über die Enstehung von frostspalten. Naturwiss. Ver. Schleswig-Holstein Schr., Band **25**: 58-64.

DYLIK, J. 1952. Peryglacjalne struktury w plejstocenie srodkowej Polski. Panstwowy instytut geologiszhy, biuletyme **66**: 53-94. (English summary: 105-113).

EAKIN, H. M. 1916. The Yukon-Koyukuk region, Alaska. U. S. Geol. Surv. Bull. 631, 88 pp.

ELTON, C. S. 1927. The nature and origin of soil-polygons in Spitzbergen. Quart. Journ. Geol. Soc., London, **83**: 163-193 + 3 pls.

FERNALD, M. L. 1950. Gray's manual of botany, 8th Edition. lxiva 1632 pp. Amer. Book Co., New York.

FERRIS, B. G., JR. 1958. Arctic Interlude. Harv. Med. Alumni Bull., **1958**: 32-35.

FIGURIN, A. E. 1823. Izlechenie iz zapisok mediko-khirurgo Figurina, vednnjkh vo vremia opisi bereyov Severo-Vostochnôr Sibiri: Gosudarstu. Admiralt. Depart., Zapiski, **5**: 259-328.

FIRBAS, E. 1949. Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nordlich der Alpen. Allgemeine Waldgeschichte, G. Fischer, Jena Bd:1. 480 pp.

FISHER, O. 1866. On the warp. Quart. Journ. Geol. Soc., **22**. (*In* Högbom).

FRENZEL, B. AND C. TROLL. 1952. Die Vegetationszonen des Nordlichen Eurasiens wahrend der letzten Eiszeit. Eiszeitalter und Gegenwart, **2**: 154-167.

FRÖDIN, J. 1918. Über das Verhältnis zwischen Vegetation und Erdfliessen in den Alpinen Regionen des schwedischen Lappland. Lunds Universitetets Årsskrift, N.F., Afd. 2, Ed. 14, 2. Nr. **24**: 3-31 + iv pls.

GJAEREVOLL, O. 1950. The snow-bed vegetation in the surroundings of Lake Torneträsk, Swedish Lappland. Svensk Bot. Tidskrift, **44**: 387-440.

———————. 1956. The plant communities of the Scandinavian alpine snow-beds. Kgl. Norske Vidensk. Selsk. Skr., **1956**(1): 1-405.

GLEASON, H. A. 1917. The structure and development of the plant association. Bull. Torrey Bot. Club, **44**: 463-481.

———————. 1926. The individualistic concept of the plant association. Contr. New York Bot. Garden #279. Bull. Torrey Bot. Club, **53**: 7-26.

GOODLETT, J. C. 1954. Vegetation adjacent to the border of the Wisconsin drift in Potter County, Pennsylvania. Harv. Forest Bull., **25**: 1-93.

———————. 1960. The development of site concepts at the Harvard Forest and their impacts upon management policy. Harv. Forest Bull., **28**: 1-128.

GRIPP, K. 1926. Über frost und Strukturboden in Spitzbergen. Zeitsch. Geo. Erdk., Berlin, **1926**: 351-354.

———————. 1929. Glaziologische und geologische Ergebnisse der Hamburger Spitzbergen Expedition, 1927. Abt. Naturw. Ver. Hamburg, **22.**

———. 1952. Zwei Beiträge zur frage des periglacialen Vorgänge. Geol. Inst. Univ. Kiel, Meyniana, **1:** 112-118.

Gripp, K. and W. G. Simon. 1933. Experimente zum Brodelbodenproblem. Centralb. Mineral., Geol., Palaontol. Abt. **B.:** 433-440.

———. 1934a. Nochmals zum Problem des Brodelbodens. Centralb. Mineral., Geol., Paläontol. Abt. **B.:** 283-286.

———. 1934b. Die experimentelle Darstellung des Brodelbodens. Neues Jahrb. Mineral., Geol., Paläontol., Ref. II, p. 601.

Hamberg, A. 1915. Zur Kenntnis der Vorgänge im Erdboden beim Gefrieren und Auftauen. Geol. Fören. Stockh. Förh., **37:** 583-619.

Hanson, H. C. 1950. Vegetation and soil profiles in some solifluction and mound areas in Alaska. Ecol., **31:** 606-630.

Hitchcock, A. S. 1950. A manual of grasses. Second Edition, revised by Agnes Chase, Washington, D. C. 1051 pp.

Högbom, B. 1914. Über die geologische Bedeutung des Frostes. Bull. Geol. Inst. Upsala, **XII:** 257-389.

———. 1923. Ancient inland dunes in northern and middle Europe. Geogr. Annaler, **5:** 113-243.

Hollingsworth, S. E., J. H. Taylor, and G. A. Kellaway. 1944. Large-scale superficial structures in the Northern Ironstone Field. Quart. Journ. Geol. Soc., London, **C(1944):** 1-44.

Hopkins, D. M. 1949. Thaw lakes and thaw sinks in the Imuruk Lake area, Seward Peninsula, Alaska. Journ. Geol., **57:** 119-131.

Hopkins, D. M. and R. S. Sigafoos. 1950. Frost action and vegetation patterns on Seward Peninsula, Alaska. Geol. Surv. Bull., **974-C:** 50-100.

Horberg, L. 1949. A possible fossil ice wedge in Bureau County, Illinois. Journ. Geol., **57:** 132-136.

Hulten, E. 1941-1950. Flora of Alaska and Yukon. Lunds Univ. Arssk. N.F. Avd. 2, Vol. 37(1)-46(1). Vol. III, 1943, 39(1): 415-567.

Huxley, J. S. and N. E. Odell. 1924. Notes on surface markings in Spitzbergen. Geogr. Journ., **63:** 207-229.

Judson, S. 1947. Large-scale superficial structures — a discussion. Journ. Geol., **55:** 168-175.

Kerr, W. C. 1881. On the action of frost in the arrangement of superficial earthy material. Amer. Journ. Sci., Ser. 3, **21.** (*In* Högbom).

Kessler, P. 1925. Das eiszeitliche Klima und seine geologischen Wirkungen in nichtvereisten Gebiet. Stuttgart, 1925.

Kjellman, F. R. 1879. Om vaxtligheten på sibiriens Nordkust — Ofversickt Kungl. Sv. Vetensk. Akad. Forhandl., **36.** (*In* Högbom).

Leffingwell, E. de K. 1915. Ground-ice wedges. The dominant form of ground-ice on the north coast of Alaska. Journ. Geol., **23.**

———. 1919. The Canning River region, northern Alaska. U. S. Geol. Surv. Prof. Paper, 109. 251 pp.

LOW, A. R. 1925. Instability of viscous fluid motion. Nature, **115:** 299-300.

MACCLINTOCK, P., AND W. H. TWENHOFEL. 1940. Wisconsin glaciation of Newfoundland. Geol. Soc. Amer. Bull. **51:** 1729-1756.

MARTIN, A. R. 1882. Dagbok hållen vid resa till Norrpolen eller Spitsbergen. Ymer 1881. Stockholm.

MASON, H. L. AND J. H. LANGENHEIM. 1959. Language analysis and the concept environment. Ecol., **38:** 325-340.

MATTHES, F. E. 1959. The Incomparable Valley: A geologic interpretation of Yosemite. Univ. Calif. Press. 173 pp.

MEINARDUS, W. 1912. Über einige charakteristische Bodenformen auf Spitzbergen. Sitzungsberichte Naturhist. Vereins preuss. Rheinland Westfalens Erste Halfte, C. — Bonn, **26:** 1-42.

————————. 1930. Arktische Böden. In Handbuch der Bödenlehre, B. Blanck, Ed., Band **3:** 27-96. Berlin, J. Springer. 550 pp.

MIETHE, A. 1912. Über Karreeboden auf Spitzbergen. Zeitschr. Ges. für Erdkunde zu Berlin, 1912, #4.

MILLER, R. S. 1955. A survey of the mammals of Bylot Island, Northwest Territories. Arctic, **8**(3): 166-176.

MULLER, S. W. 1947. Permafrost or permanently frozen ground and related engineering problems. J. W. Edwards, Inc., Ann Arbor. 231 pp.

NORDENSKJÖLD, O. 1909. Die Polarwelt. Leipzig and Berlin. 220 pp.

NORDHAGEN, R. 1943. Sikilsdalen og norges fjellbeiter. (The Valley Sikilsdal and the mountain pastures of Norway). Bergens Museums Skrifter 22.

————————. 1954. Vegetation units in the mountain areas of Scandinavia. Veröff. des Geobot. Inst. Rübel in Zurich, No. 29.

PELTIER, L. C. 1950. The geographic cycle in periglacial regions as it is related to climatic geomorphology. Annals Ass'n. Amer. Geographers, **40:** 214-236.

PENCK, A. 1912. Über Polygonboden in Spitzbergen. Gesell. Erdkunde Berlin Zeitschr., **1912:** 244-248.

PÉWÉ, T. L. 1948. Terrain and permafrost of the Fairbanks area, Alaska. (Abstract). Geol. Soc. Amer. Bull., **59:** 1379.

————————. 1950. Origin of the upland silt in the Fairbanks area, Alaska. Geol. Soc. Amer. Bull., **61:** 1942.

————————. 1957. Permafrost and its effect on life in the North. 18th Biology Colloq. Proc., Oregon State College, 12-25.

————————. 1959. Sand-wedge polygons (Tesselations) in the McMurdo Sound Region, Antarctica — a progress report. Am. Journ. Sci., **257:** 545-552.

POLUNIN, N. 1934. The vegation of Akpatok Island. Journ. Ecol., **22:** 337-395.

————————. 1940. Botany of the Canadian Eastern Arctic. Part I: Pteridophyta and Spermatophyta. Bull. 92, National Museum of Canada. vi + 408 pp.

————————. 1948. Botany of the Canadian Eastern Arctic. Part III:

Vegetation and Ecology. Bull. 104, National Museum of Canada. vii + 304 pp.

————. 1959. Circumpolar arctic flora. Oxford. xxviii + 514 pp.

PORSILD, A. E. 1938. Earth mounds in unglaciated northwestern America. Geogr. Rev., **28**: 46-55.

————. 1957. Illustrated flora of the Canadian Arctic Archipelago. Bull. 146, National Museum of Canada. iii + 209 pp.

POSER, H. 1931. Beiträge zur Kenntnis der Arktischen Bodenformen. Geol. Rundschau, **22**: 200-231.

————. 1932. Einige Untersuchungen zur Morphologie Ostgrönlands. Meddel. om Grønland, **94**(5): 5-55.

————. 1933. Das Problem des Strukturbodens. Geol. Rundschau, **24**: 105-121.

————. 1947. Auftautiefe und frostzerrung im Boden Mitteleuropa während der Würm-Eiszeit. Die Naturwiss., **34**: 232-238; 262-267.

RAUNKIAER, C. 1934. The life forms of plants and statistical plant geography, being the collected papers of C. Raunkiaer. Oxford. 632 pp.

RAUP, H. M. 1942. Trends in the development of geographic botany. Ann. Ass'n. Amer. Geographers, **32**(4): 319-354.

————. 1947. The botany of southwestern Mackenzie. Sargentia, **VI**: 1-262, xii, photos, & 25 distribution maps.

————. 1951. Vegetation and cryoplanation. Ohio Journ. Sci., **51**: (3): 105-116.

ROUSSEAU, J. 1949. Modifications de la surface de la toundra sous l'action d'agents climatique. Rev. Canadienne Géographie, **3**: 43-51.

SALOMON, W. 1929. Arktische Bodenformen in den Alpen. Sitz.-Ber. Heidelberger Akad. Wiss., Math.-nat., Kl: 5.

SAPPER, K. 1912. Über fliesserde und Strukturboden auf Spitzbergen. Zeitschr. Ges. Erdkunde zu Berlin, 1912, #4.

————. 1913. Erdfliessen und Strukturboden in polaren und subpolaren Gebieten. Geol. Rundschau, **4**: 103-115.

SCHAFER, J. P. 1949. Some periglacial features in central Montana. Journ. Geol., **57**: 154-174.

SCHENK, E. 1955. Die Mechanik der periglazialen Strukturböden. Hess. Landesamtes für Bodenforschung, **13**: 1-92.

SCHERMAN, K. 1956. Spring on an arctic island. Little, Brown and Co., Boston. xvii + 331 pp.

SCHNEIDER, C. 1918. Notes on American Willows. I The species related to *Salix arctica* Pall. Bot. Gaz. **66**: 117-142.

————. 1921. Notes on American Willows. XII (incl. analytical keys). 111 Journ. Arn. Arboretum **3**: 61-125.

SEIDENFADEN, G. 1931. Moving soil and vegetation in East Greenland. Meddel. om Grønland, **87**: 2.

SEIDENFADEN, G. AND T. SORENSEN. 1937. The vascular plants of Northeast Greenland from 74°30′ to 79°00′ N. Lat. Meddel. om Grønland, **101**(4): 1-215 + 2 pls.

SELZER, G. 1936. Diluviale Loesskeile und Loesskeilnetze aus der Umgebung Goettingens. Geol. Rundschau, **27**: 275-293.

SERNANDER, R. 1905. Flytjord i svenska fjälltrakter. Geol. för. förh. Bd. 27, h. 2

SHARP, R. P. 1942a. Soil structures in the St. Elias Range, Yukon Territory. Journ. Geomorph., **5**(4): 274-301.

————. 1942b. Periglacial involutions in northeastern Illinois. Journ. Geol., **50**: 113-133.

SIGAFOOS, R. S. 1951. Soil instability in tundra vegetation. Ohio Journ. Sci., **51**(6): 281-298.

————. 1952. Frost action as a primary physical factor in tundra plant communities. Ecol., **33**(4): 480-487.

SIGAFOOS, R. S. AND D. M. HOPKINS. 1952. Soil instability on slopes in regions of perennially frozen ground. Frost action in soils: a symposium. Highway Research Board Special Report No. 2.

SJÖRS, H. 1948. Myrvegetation i Bergslagen. (English summary). Acta Phytogeogr. Suecica, 21. 340 pp.

————. 1950a. On the relation between vegetation and electrolytes in North Swedish mire waters. Oikos, **2**: 241-258.

————. 1950b. Regional studies in North Swedish mire vegetation. Bot. Not., **1950**: 175-222.

————. 1959. Bogs and fens in the Hudson Bay lowlands. Arctic **12**(1): 2-19, illus.

SMITH, H. T. U. 1949. Physical effects of Pleistocene climate changes in non-glaciated areas: eolian phenomena, frost action, and stream terracing. Bull. Geol. Soc. Amer., **60**(9): 1485-1516.

SMITH, H. T. U. AND H. J. FRAZER. 1935. Loess in the vicinity of Boston, Massachusetts. Amer. Journ. Sci., **30**: 16-32.

SOERGEL, W. 1921. Die Ursachen der diluvialen Aufschotterung und Erosion. Berlin, 1921.

————. 1939. Das diluviale System. Berlin.

————. 1940. Zur biologischen Beurteilung diluvialer Säugetierfaunen. Sitz.-Ber. Heidelberg. Akad. Wiss.

————. 1943. Der Klimacharakter der als nordisch Geltendend, 1941, 1943. Säugetiere des Eiszeitalters. Sitz.-Ber. Heidelberg. Akad. Wiss.

SØRENSEN, T. 1935. Bodenformen und Pflanzendecke in Nordostgrönland. Meddel. om Grønland, **93**(4): 69 pp.

STECHE, H. 1933. Beiträge zur Frage der Strukturboden. Ber, über die Verhandl. Sächsischen Akad. Wiss. Leipzig Math. Phys. Kl. **83**: 193-272.

STOUT, B. B. 1952. Species distribution and soils in the Harvard Forest. Harv. Forest Bull. No. **24**: 29 pp.

TABER, S. 1929. Frost heaving. Journ. Geol., **37**: 428-461.

————. 1930. The mechanics of frost heaving. Journ. Geol., **38**: 303-317.

————. 1943. Perennially frozen ground in Alaska: its origin and extent. Bull. Geol. Soc. Amer., **54**: 1433-1548, & 22 pls.

TANSLEY, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecol., **16**: 284-307.

———. 1939. The British Islands and their vegetation. Camb. Univ. Press. London. xxxviii + 930 pp.

TANTTU, A. 1915. Über die Entstehung der Bülten und Strange am Moore. Acta For. Fenn., IV.

TAVERNIER, R. 1944-45. Phenomènes periglaciaires en Belgique. Soc. Belge d'Etudes Geographique, **14**(2): 112-133.

TERZAGI, K. AND R. B. PECK. 1948. Soil mechanics in engineering practice. John Wiley & Son, Inc. New York. 566 pp.

THOREAU, H. D. 1854. Walden, or life in the woods. Ticknor & Fields, Boston.

THORODDSEN, T. 1913. Polygonboden und "Thufur" auf Island. Peterm. Mitt. 59.2. Gotha.

———. 1914. An account of the physical geography of Iceland, with special reference to the plant life. *In* Kolderup-Rosenvinge, L., and E. Warming, 1912-1918, The Botany of Iceland, Vol. 1. London. 675 pp.

TROLL, C. 1944. Strukturböden, Solifluktion und Frostklimate der Erde. Geol. Rundschau, **34**: 545-694.

VAN TYNE, J. AND W. H. DRURY, JR. 1959. The birds of southern Bylot Island, 1954. Occas. Papers Mus. Zool., Univ. Mich., No. 615. 37 pp. & 3 pls.

VON BAER, K. 1837-38. Expédition en Novaia Zemlia et en Lapponie. Bull. Scient. Acad. Impér. Sci. St. Pétersb., **2**(8-12): T3, p. 174.

VON BUNGE, A. 1884. Naturhistorische Beobachtungen und Fahrten im Lena Delta. Acad. Scient. St. Petersb. Bull. **29**: 422-476.

———. 1887. Bericht über den ferneren Gang der Expedition. Reise nach den Neusibirischen Inseln. Aufenhalt auf der Grossen Ljachof-Insel: Beiträge zur Kentniss des russischen Reiches und der angrenzenden Länder Asiens, Dritte Folge, Band **3**, St. Petersburg: 231-284.

———. 1902. Einige Worte zur Bodeneisfrage. Russ. k. mineral. gesell. Verh. 2d. Ser., Band **40**: 205-209.

VON MIDDENDORF, A. T. 1864-67. Reise in den aussersten Norden und Osten Sibiriens. St. Petersburg.

WALLACE, R. E. 1948. Cave-in lakes in the Nabesna, Chisana, and Tanana River Valleys, eastern Alaska. Journ. Geol., **56**: 171-181.

WARREN WILSON, J. 1952. Vegetation patterns associated with soil movement on Jan Mayen Island. Journ. Ecol., **40**: 249-264.

WASHBURN, A. L. 1947. Reconnaissance geology of portions of Victoria Island and adjacent regions, Arctic Canada. Geol. Soc. Amer., Mem. 22, 142 pp.

———. 1950. Patterned ground. Revue Canadienne de Géographie, **IV**: 5-54.

———. 1956. Classification of patterned ground and a review of suggested origins. Bull. Geol. Soc. Amer., **67**: 823-865, 4 figs., 7 pls.

WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol., **30**: 279-338.

WIGGINS, I. L. 1951. The distribution of vascular plants on polygonal ground near Point Barrow, Alaska. Dudley Herb. Contr., 4(3): 41-52.

Willett, H. C. 1953. Atmospheric and oceanic circulation as factors in glacial-interglacial changes in climate. *In* Climatic changes, H. Shapley, Ed. Harv. Univ. Press, pp. 51-71.

Wood, S. W. 1882. On the newer Pliocene Period in England. Quart. Journ. Geol. Soc., 38. (*In* Högbom).

Zeuner, F. E. 1937. The climate of the countries adjoining the ice sheet of the Pleistocene. Geol. Assn. Proc., 48: 379-395.

Zhukov, V. F. 1944. Morozoboinyye treschchiny v rayonakh Vechnoy Mersloty. (Fissures caused by frost cracking in the permafrost region). Trudy Instituta merslotovedeniya im. V. A. Obrucheva Acad. Nauk SSSR, Tom. 4: 226-230.

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by
Reed C. Rollins and Robert C. Foster

NO. CXCI

THE SOUTH AMERICAN SPECIES OF ERIGERON

By
Otto T. Solbrig

THE GENUS ERIOSORUS IN COSTA RICA

By
Edith Scamman

TAXONOMIC FERN NOTES. III

By
Rolla Tryon

A MONOGRAPH OF THE FERN GENUS JAMESONIA

By
Alice F. Tryon

Published by
THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.
1962

CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY

Edited by

Reed C. Rollins and Robert C. Foster

NO. CXCI

THE SOUTH AMERICAN SPECIES OF ERIGERON
BY
OTTO T. SOLBRIG

THE GENUS ERIOSORUS IN COSTA RICA
BY
EDITH SCAMMAN

TAXONOMIC FERN NOTES. III
BY
ROLLA TRYON

A MONOGRAPH OF THE FERN GENUS JAMESONIA
BY
ALICE F. TRYON

Published by

THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U. S. A.

Issued November 23rd, 1962

Manufactured
by
The Lexington Press, Inc., Lexington, Massachusetts

THE SOUTH AMERICAN SPECIES OF ERIGERON

OTTO T. SOLBRIG

The genus *Erigeron* is one of the largest and taxonomically most difficult genera of the tribe Astereae of the family Compositae. Primarily a montane group, it is common in eastern and western North America, Central and South America, Europe and Asia.

In spite of its abundance and widespread distribution (or possibly because of it) the generic boundaries are hard to define. Technically, *Erigeron* is usually characterized by its triangular-tipped stigmas with their surfaces covered by short and stubby collecting-hairs; by the possession of stout imbricated involucral bracts, arranged in approximately two series; and by its heterochromous heads, that is with the ligulate flowers of a different color from the tubular ones. If these criteria were applied rigorously, many species hitherto referred to *Erigeron* would have to be excluded. Such a procedure would lead to the creation of a series of small, often monotypic, genera, not adding to our knowledge of the evolution and phylogeny of the group, but probably increasing the taxonomic confusion. It is therefore best to maintain the genus as now established, until more and better information relating to these species is available.

Erigeron is very closely related to two other large genera, *Aster* and *Conyza*, and the separation of these three genera is not always an easy task. On the basis of characters of the style and the involucral bracts it is usually possible to decide if a species belongs to *Aster* or *Erigeron:* the styles being elongate or subulate and the involucral bracts more rigid in *Aster*. The separation between *Erigeron* and *Conyza* is more difficult. Classically, these two genera were separated according to the presence or absence of ligules in their ray flowers. Although this is apparently a qualitative difference, careful observation revealed the existence of minute ligules in the ray flowers of species usually considered as *Conyza*, and in some cases the presence or absence of ligules can be only determined after careful microscopic study. The absolute presence or absence of a ligule is not correlated with any other character of the genus. This led Cronquist (1943) to redefine the generic boundary between *Erigeron* and *Conyza*, according to the criteria of Bentham and Hooker

(1873). Rather than by the absolute presence of a ligule, *Erigeron* is characterized by the possession of ray flowers with ligules larger than the tubular flowers, usually arranged in one series. This new arrangement includes in *Conyza*, all the species previously treated as belonging to section Caenotus of *Erigeron*, including such well known weedy species as *Conyza(Erigeron)canadensis* and *C. bonariensis*. This new arrangement seems to be a more natural one, although reports of hybrids between *Erigeron acris* (sect. Trimorphaea) and *Conyza canadensis* (sect. Caenotus) cast a certain shadow of doubt on the "naturalness" of this new generic boundary.

In any case, it is clear that more study, especially of an experimental nature, is needed to solve this problem. The generic boundaries in the whole tribe (in the whole family unfortunately, with notable exceptions) are in need of much study, and the problem will not be solved from morphology alone. Cronquist's arrangement so far seems the most practical division of these two very closely related genera. This arrangement tends to separate the plants into two ecologically different groups: the montane, largely perennial *Erigeron*, and the more tropical, largely annual or biennial *Conyza*.

Erigeron has its center of distribution in western North America (Cronquist, 1947). The South American species occupy a similar habitat with the exception of those belonging to section Leptostelma *(E. maximum, E. tweediei, E. meyeri, E. tucumanensis* and *E. camposportoi)*. This section has diverged into a completely new habitat, the humid, often swampy, openings of the tropical and subtropical South American forest. Nevertheless it is not found in the Amazonian basin, but only from Goiás in Brazil south to Uruguay and west to the eastern part of Bolivia, usually on higher elevations (around 1000 m.). The new ecological requirement has produced taller plants (up to 4 m.) with large leaves, while the floral characteristics have changed relatively little. Nevertheless, certain doubts as to the systematic position of Leptostelma have been raised (see Solbrig, 1960).

Another niche occupied by *Erigeron* in South America is in the oceanic islands: Galápagos with one species, Juan Fernandez with four and, in the Atlantic, Falkland (Malvinas) with one species. The morphological uniqueness of some of the species indicates that we are dealing with ancient invasions. Especially remarkable is *E. tenuifolius* of the Galápagos Islands, a small tree, with stiff lanceolate leaves, unlike any other species found in the genus; also *E. fernandezianus* of Juan Fernandez, another shrub or small tree, sometimes considered a link between *Erigeron* and *Tetramolopium* of Hawaii (Bentham, 1873).

Finally it should be mentioned that *Erigeron* successfully occupied the Patagonian territories after the last Quaternary glaciation. The taxonomic confusion reigning in those species might reflect an early stage in the evolution of the group (see under *E. andicola complex*).

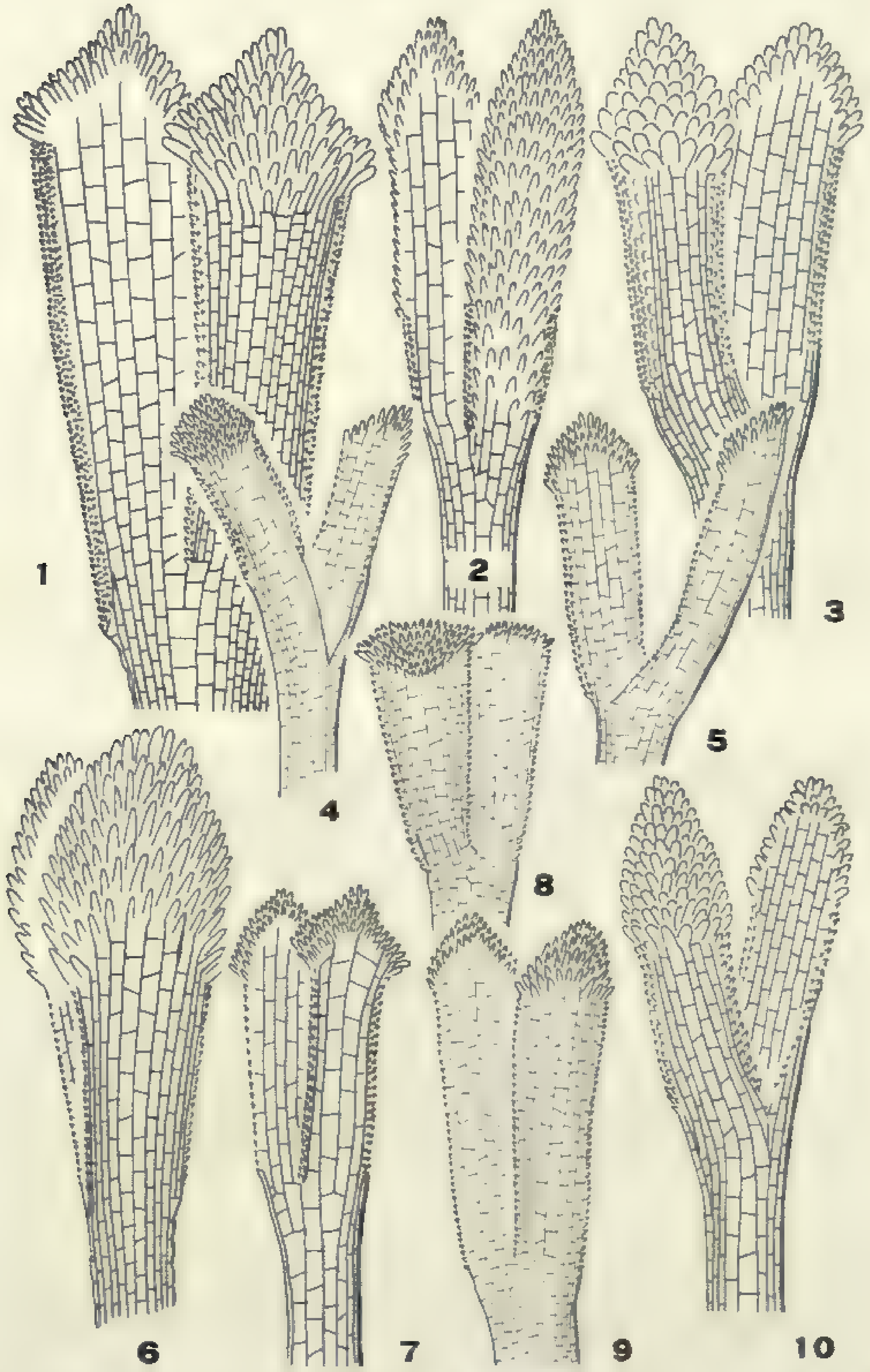
Considering the number of species and wide distribution of the genus *Erigeron*, relatively little is known concerning its cytology. This is rather surprising, since the available information indicates a high incidence of interesting and anomalous situations.

Montgomery and Yang (1960) have recently reviewed the literature and found only 35 species for which chromosome numbers are known. A few additional species have been counted by Turner (1959), Raven *et al.* (1960), Turner & Irwin (1960), Turner and Ellison (1960) and Turner *et al.* (1961). The basic chromosome number for the genus is $x = 9$, and most of the species counted are diploid, although tetraploids are also known. A surprising feature is that nine of the 40 odd species so far counted are triploids, while one species, *E. compositus*, appears to be a hexaploid. If the species so far counted are a random sample of the genus, the proportion of triploids is over 20%, a remarkably high percentage of species which, unless they possess a special mechanism, must produce a high percentage of sterile pollen and ovules. When investigated, some of these species proved to be at least partially apomictic, a mechanism which can successfully circumvent meiotic sterility.

No South American material has been investigated cytologically with the exception of *E. maximus* (Turner & Irwin, 1960), for which an inconclusive count of 40 ± 4 was reported, and of *E. karwinskianus*, which is a common weed of Mexican origin in many tropical and temperate areas. This has been counted from Europe by Larsen (1954), who reports a tetraploid count of 2n = 36 for the variety *mucronatus* (sometimes considered a distinct species), and by Turner *et al.* (1961) who reported a triploid plant with 27 univalents at meiosis and a diploid plant with n = 9 II, both from Mexico. Turner *et al.* indicate that the triploid plant is probably apomictic, which has also been reported for European material. It might be interesting to know if two fertile chromosome lines, a diploid and a tetraploid, exist in *E. karwinskianus*, the triploid being the result of hybridization. However, in such an event a higher degree of pairing at meiosis would be expected. Apomixis in the European *E. karwinskianus* var. *mucronatus* has been reported by Carano (1919) and Fagerlind (1948), although Gustafsson (1947), feels that reëxamination is necessary.

Our knowledge of the embryology of *Erigeron* is relatively satisfactory, due in great part to Harling's (1951) careful studies. Nevertheless, so far only some 25 species have been investigated in detail, no South American species among them, and certainly more work is necessary in order to confirm some of the interesting data obtained.

All genera of Astereae so far investigated, with the exception of *Erigeron,* possess a normal, monosporic type of embryo sac (Harling 1951, 1954). Among the species of *Erigeron* studied, *E. philadelphicus* is unique in possessing an exclusively monosporic, normal type of embryo sac (McDonald, 1927). All other species have either a tetrasporic (the most common situation) or bisporic embryo sac; or possess an unstable condition with monosporic, bisporic and tetrasporic embryo sacs present in different plants of the same species or sometimes even in the same plant (Harling, 1951). It is of interest to note that the species considered advanced by Cronquist (1947), in his revision of the North American species of *Erigeron*, are exclusively or predominantly tetrasporic, while the species regarded as primitive by that author have a bisporic or a mixed monosporic and bisporic condition. Cronquist considered *Erigeron* derived from the genus *Aster* and embryological data seem to back this assumption, or at least do not disprove it. *Aster peregrinus* (considered by Cronquist as an *Erigeron* on the basis of its affinities) which is related closely to both *Erigeron* and *Aster* has a monosporic type of embryo sac (Harling, 1951), as have all other species of *Aster*.



FIGS. 1-10. Styles of tubular flowers. 1. *Erigeron meyeri* (*Meyer 2125*, LP). 2. *E. lanceolatus* Wedd. (*Steinbach 5920*, DARW). 3. *E. incaicus* (*Ferreyra 8532*, GH). 4. *E. luxurians* (*Worth & Morrison 16431*, GH). 5. *E. tenuifolius* (*Stewart 737*, GH). 6. *E. lanceolatus* Wedd. (*Lorentz 627*, DARW). 7. *E. leptorhizon* (*Wilkes s.n.* GH). 8. *E. karwinskianus* (*Garavento 941*, GH). 9. *E. pratensis* (*Hicken, S.I. 20798*, DARW). 10. *E. ecuadoriensis* (*Andre s.n.*, GH).

Another very interesting result pertains to the relationships between *Erigeron* and *Conyza*. *Conyza bonariensis* and *C. canadensis*, the two species of *Conyza* section Caenotus (formerly ascribed to the genus *Erigeron*) so far studied, have monosporic, normal embryo sacs, and agree in this respect with the only other species of *Conyza* investigated. If these results were to be confirmed for more species, it would provide additional evidence for the inclusion of section Caenotus in *Conyza*.

From the results so far obtained it is evident that *Erigeron* presents a unique and highly interesting type of embryo sac development, and further study along these lines should be very rewarding for the embryologist and the taxonomist.

Five species of *Erigeron* have been reported to be apomictic: *Erigeron annuus* (Tahara 1915, 1921; McDonald 1927; Fagerlind 1948); *E. karwinskianus* var. *mucronatus* (Carano 1919, 1920, 1921, 1924; Fagerlind 1944, 1948); *E. strigosus* (Holmgren 1919; McDonald 1927); *E. divergens* (Harling 1951); and *E. compositus* (Beaman, unpublished). Of these, only the last species has been studied in relation to the taxonomic implication of apomixis. No South American species has been investigated so far, but the data obtained in this study (see under *E. andicola* complex) point to the possible presence of apomixis, at least in some degree. Embryological study should be very rewarding in this group.

The South American species of *Erigeron* have never been monographed. Over one hundred species have been described, largely by R. A. Philippi from Chile. The present investigation was started in 1953 as a revision of the Argentine species of the genus. However, it was soon apparent that in order to understand the group, all of the South American species would have to be included. Even so, the difficulties encountered have been very great, especially in trying to understand the patterns of variation, and the author is not sure that he has achieved a true comprehension of the problems and their solution. Apomixis and hybridization are suspected in certain groups, but the confirmation or disproof of these assumptions will have to await embryological and genetical studies. Lack of adequate material was also a big handicap. However, it is felt that this monograph, incomplete as it is in these respects, might serve the useful purpose of pointing out avenues of research, and of indicating some of the problems to be solved. Not more than 20 per cent of the herbarium material studied in the course of this investigation had been identified as to species, dramatically pointing out the need of a revision of the South American representatives of the genus.

This work was initiated while I was associated with the Museo de Ciencias Naturales of La Plata, Argentina, at the suggestion and under the guidance of Dr. Angel L. Cabrera, to whom I want to express my thanks for his help and encouragement. I was fortunate in being able to study the material of the following herbaria, to whose directors and curators I want to express my appreciation: Arnold Arboretum (A) and Gray Herbarium of Harvard University (GH); British Museum, Natural History (BM); Instituto Botánico Darwinion, Argentina (DARW); Chicago Natural History Museum (F); Jardim Botânico, Rio de Janeiro (RB); Royal Botanic Gardens, Kew (K); Instituto Miguel Lillo, Tucumán (LIL); Museo Botánico, Córdoba (CORD); Museo Javier Prado, Lima (USM); Museo de Ciencias Naturales, La Plata (LP); Museo Nacional, Santiago (SGO); Museo Nacional, Rio de Janeiro (R); Missouri Botanical Garden (MO); New York Botanical Garden (NY); U. S. National Herbarium (US); and Botanisches Museum der Universität, Wien (WU).

ERIGERON L. Sp. Pl. : 863. 1753[1]

Annual, biennial or perennial herbs, subshrubs or shrubs, rarely small trees up to 3 m. tall. Leaves alternate or rosulate, entire or lobed, rarely all basal or all cauline, the basal rosette leaves often quite different from the cauline ones. Heads borne on peduncles, solitary or in groups of less than ten, rarely in large numbers. Involucre hemispheric or campanulate; involucral bracts narrow, [varying from] herbaceous and subequal [to scarcely herbaceous] and imbricate; [loss of herbaceousness either uniform throughout or more prominent towards the tip]; receptacle flat or slightly convex, naked or with very short projections in section Leptostelma; ray flowers ligulate, pistillate, usually in one series, ligules narrow of variable length but always larger than the tubular flowers [or rarely absent], generally white, pink, [blue] or yellow; disk flowers yellow, tubular, numerous, [some species with eligulate pistillate flowers between the hermaphrodite flowers and the ligulate pistillate flowers], tube with five triangular lobes; style appendages varying from lanceolate and acute to broadly triangular

---

[1] Generic synonyms, now rarely used, are omitted. Parts of the description in brackets do not apply to South American material.

and obtuse, [rarely obsolete]; pappus of a few to rather numerous capillary and often very fragile bristles, [commonly but not always with at least a few outer short setae or squamellae, or rarely the pistillate flowers without bristles and bearing only short squamellae], in one or two series; achenes terete, often compressed, commonly 2-nerved [sometimes as much as 14-nerved].

KEY TO THE SPECIES

A. Large, non-woody herbs with hollow stems; plants 30 cm. or more in height.
- B. Ligules 10-15 mm. long; inflorescences open; heads long-pedunculate.
  - C. Leaves, at least the basal ones, petiolate, 1-10 cm. wide; plants 0.7-4 m. high. .... 1. *E. maximus.*
  - C. Leaves all sessile, 1-2 cm. wide; plants 30-50 cm. high. .... 2. *E. tucumanensis.*
- B. Ligules 2-5 mm. long; inflorescences tight, heads sessile or short-pedunculate. .... 3. *E. tweediei.*

A. Plants woody, at least at the base, with solid stems; if herbaceous, then usually less than 30 cm. high.
- D. Plants pulvinate; leaves rosulate. .... 19. *E. rosulatum.*
- D. Plants not pulvinate, with alternate leaves; if pulvinate, then never with rosulate leaves.
  - E. Small woody tree, 1.50 m. or more in height. .... 15. *E. tenuifolius.*
  - E. Herbs, subshrubs or shrubs not more than 1 m. tall.
    - F. Basal rosette not present.
      - G. Annual herb; leaves pubescent, lobed. .... 17. *E. leptorhizon.*
      - G. Shrubs, subshrubs or perennial herbs with at least a woody base.
        - H. Leaves, at least some, divided or lobed.
          - I. Ligules less than 3 mm. long. ...... 13. *E. ecuadoriensis.*
          - I. Ligules more than 5 mm. long.
            - J. Leaves glabrous or with occasional hairs; ligules 5-7 mm. long. .... 9. *E. fernandezianus.*
            - J. Leaves always pubescent; ligules 8-12 mm. long. .... 16. *E. karwinskianus.*
        - H. Leaves not divided.
          - K. Plants 70 cm. high; inflorescence an open panicle with many heads, leafy throughout. .... 5. *E. camposportoi.*
          - K. Plants less than 30 cm. in height; inflorescence a panicle of few heads, or a single-headed scape, naked or with very few leaves.
            - L. Ligules less than 3 mm. long, in 2-3 series.
              - M. Leaves 10-15 mm. wide, margins slightly toothed or lobed. .... 14. *E. incaicus.*

M. Leaves 1-4 mm. wide, margins entire. .... 12. *E. pazensis.*

L. Ligules more than 5 mm. long, in one series.

N. Prostrate shrubs, 5-25 cm. high; heads solitary at the end of the branches. .... 8. *E. othonnaefolius.*

N. Erect shrubs, 30-70 cm. high; heads borne in panicles at the end of the branches or occasionally solitary.

O. Involucre 10-18 mm. wide, plants densely pubescent. .... 7. *E. luxurians.*

O. Involucre 5-12 mm. wide; plants glabrous or slightly pubescent. .... 6. *E. fasciculatus.*

F. Basal rosette present.

P. Leaves at least 15 cm. long. .... 4. *E. meyeri.*

P. Leaves less than 10 cm. long.

Q. Leaves spathulate, at least in part. ...... 18. *E. rupicola.*

Q. Leaves not spathulate, acute.

R. Leaves stiff, often glutinous.

S. Leaf margin entire. ....20. *E. lanceolatus.*

S. Leaf margin toothed or serrate.

T. Leaves and achenes pubescent, plants 10-30 cm. high. .... 10. *E. ingae.*

T. Leaves and achenes glabrous, plants 25-35 cm. high. .... 11. *E. luteoviridis.*

R. Leaves neither stiff nor heavily glutinous.

U. Ligules 5-12 mm. long. .... 21. *E. pratensis.*

U. Ligules less than 3 mm. long.

V. Leaves with a clearly marked petiole, 15-30 mm. long, 5-10 mm. wide, obovate. ...... 22. *E. incertus.*

V. Leaves without a clearly marked petiole, more than 40 mm. long, if shorter, less than 5 mm. wide and not obovate. .... 23. *E. andicola complex.*

1. **Erigeron maximus** (D. Don) DC., Prodr. 5: 284. 1836
(Fig. 11)

Leptostelma maximum D. Don, in Sweet, Brit. Flow. Gard. II, 1: 38. 1831; D. Don, Sweet, Hort. Brit. edit. 2: 299, 1830, *nomen nudum; Aster maximum* Less., Syn. 182. 1832.

Erigeron sulcatum DC., Prodr. 5: 284. 1836; based on *Lund* "in Brasiliae . . . prov. Sancti-Pauli" (not seen).

Erigeron alpestre Gardner, Journ. Bot. London, 4: 123. 1845, based on *Gardner 5787* "moist places on the Organ Mts. . . . 6000′" (Holotype BM!, Isotype K! GH!)

Erigeron palustre Gardner, Journ. Bot. London, 4: 123. 1845; *Erigeron maximus* var. *palustris* (Gard.) Baker, in Martius, Fl. Bras. 6(3): 28. 1882; based on *Gardner 507* "In marshes, common in the Organ Mts., . . . 3000′" (Holotype BM!, Isotype BM!, GH!, K!)

Erigeron scaberrimum Gardner, Journ. Bot. London, 7: 80. 1848, based on *Gardner 4923*, "in marshy campos near Villa do Principe, Province of Minas Gerais, Aug. 1840" (Holotype BM! Isotype K!).

Erigeron schuchtii var. *minor* Baker, in Martius, Fl. Bras. 6(3): 28. 1882, based on "prope Villa do Principe, *Gardner 4923*" (BM!)

Erigeron catarinensis Cabrera, Arq. Jard. Bot. Rio de Janeiro 15: 75. 1957, based on *Reitz 2341* "Santa Catarina, Campo dos Padres, Bom Retiro, 2000 m.s.m. 15-II-1948" (LP!)

Giant herb, (0.5)0.7-4 m. tall. Root fibrous, slightly woody, sometimes tuber-like. Stems herbaceous, slightly woody at the base, especially in tall plants, 0.5-5 cm. in diameter, sulcate-striate, glabrous or slightly to heavily pubescent, often scabrous, hollow, green, green-gray or brown, leafy throughout and branching towards the top. Leaves large, lanceolate, oblong-lanceolate to oval, 5-90 cm. long and 1-10 cm. broad, margins entire, toothed or more commonly variously and irregularly lobed or serrate, acuminate, petiolate, sessile or more often clasping (especially in smaller and upper leaves), glabrous or pubescent, especially along the veins, scabrous, midvein protruding on lower surface, petiole, when present, up to 10 cm. long, often somewhat winged. Heads numerous, cymosely arranged at the end of the branches, peduncles 2-15 cm. long, glabrous, or more often pubescent. Involucres large, 10-20 mm. wide and 5-15 mm. high; involucral bracts triangular-lanceolate, 5-10 mm. long, arranged in one loose series, borders entire or somewhat toothed towards the apex, glabrous or pubescent, often resinous-punctate, center portion when dry usually of darker color than the borders; ligulate flowers numerous, in two series, white, showy, tube 1-3 mm. long, ligule 10-15 mm. long, 1-2 mm. wide; tubular flowers numerous, yellow, 4-6 mm. long; pappus copious, white, bristles ca. 5 mm. long; achenes terete, 1-2 mm. long.

TYPE: "A native of Mexico, a plant which was obtained by Mr. Hunnemann in the Autumn of 1827 from the Berlin Botanic Gardens" (not seen). The reference to Mexico is incorrect, and the specimen may not be now in existence.

COMMON NAME: "Margarida da banhado" (Brazil).

SELECTED SPECIMENS: **Brazil.** Minas Gerais, Ouro Preto, Saramemba, *Macedo e Barroso 2793* (MO, NY); Distrito Carangola, Summit of Serra da Gramma, 1700 m., *Mexia 4273* (MO, NY, US); Viçosa, Agricultural College lands, 670 m., *Mexia 4341* (MO, NY); Bello Horizonte, Serra do Jaguaril, *Barreto 3937* (MO); Viçosa, *A. Chase 9436* (MO); Santa Catarina, Campo Alegre, *Smith & Klein 10527* (NY, US). **Paraguay.** In viciniis Caaguazú, *Hassler 8950* (BM, DARW, GH, F, LIL, MO, RB, US).

This is a very common species of south and central Brazil, extending from the state of Minas Gerais along the coastal mountain chain to Santa Catarina and Rio Grande do Sul. One collection is from Caaguazú in Paraguay (fig. 12).

Erigeron maximus is most frequent in low marshy areas and on wet slopes, but is also found in open "campos" above timberline at altitudes of over 1700 m., and it has adapted itself to disturbed conditions where sufficient moisture is present. Specimens from the higher altitudes are usually

Fig. 11. *Erigeron maximus*, general aspect, × ½ (*Mexia 4341*, GH). Drawing by Ruth Hsu.

smaller and more pubescent. The leaves vary greatly in size and shape. A true basal rosette, such as that found in *E. tweediei*, is usually absent, although many plants, especially large ones, have larger, petiolate leaves toward the base of the plant (which can be up to 90 cm. long), while the upper leaves tend to be smaller and basally clasping. Equally variable is the foliar surface, which in a few plants is smooth and glabrous, in others scabrous-pubescent and in still others (especially those from the State of Minas Gerais) remarkably scabrous, the scabrousness being produced by a large number of minute crystalline projections. A certain amount of variation is also found within the same plant: young leaves as well as first leaves are much less scabrous than old and later leaves. Although most plants have sessile leaves, some specimens from Santa Catarina (described as *E. catarinensis* by Cabrera) show basal leaves which are petiolate and somewhat sagittate or auriculate at the base. Some intermediate conditions are also found.

A collection from the state of Espírito Santo should also be mentioned. This material has much smaller and narrower leaves, the plants are smaller and very reminiscent of *E. tucumanensis* from Argentina. It is the only collection made in that state.

Although some of the variations mentioned, especially those which seem to have a geographical or ecological association might deserve subspecific recognition, it is felt that in view of the tremendous variation present (which becomes obvious when one studies the plants in the field) and the constancy of the floral characters, no segregation on the basis of vegetative characters is warranted with our present knowledge.

2. **Erigeron tucumanensis** Cabrera, Notas Mus. La Plata Bot. **19:** 196. 1959

(Fig. 13)

Perennial, short-rhizomatous herb, 30-50 cm. high. Shoots one to several from the base, 2-3 mm. in diameter, hollow, grooved, slightly pubescent, unbranched or slightly branched towards the top. Basal leaves short-lived, not different from the cauline; cauline leaves sessile, auriculate, elongate-lanceolate, 10-15 cm. long, 1-2 cm. wide, margins widely toothed, surface short-pubescent to slightly scabrous. Capitula borne singly at the end of long pedicels, 2-5 at the end of each shoot. Involucre hemispheric 0.9-1.2 cm. wide, 0.6-0.8 cm. high; involucral bracts apparently in one row, triangular-elongate, punctate or short-

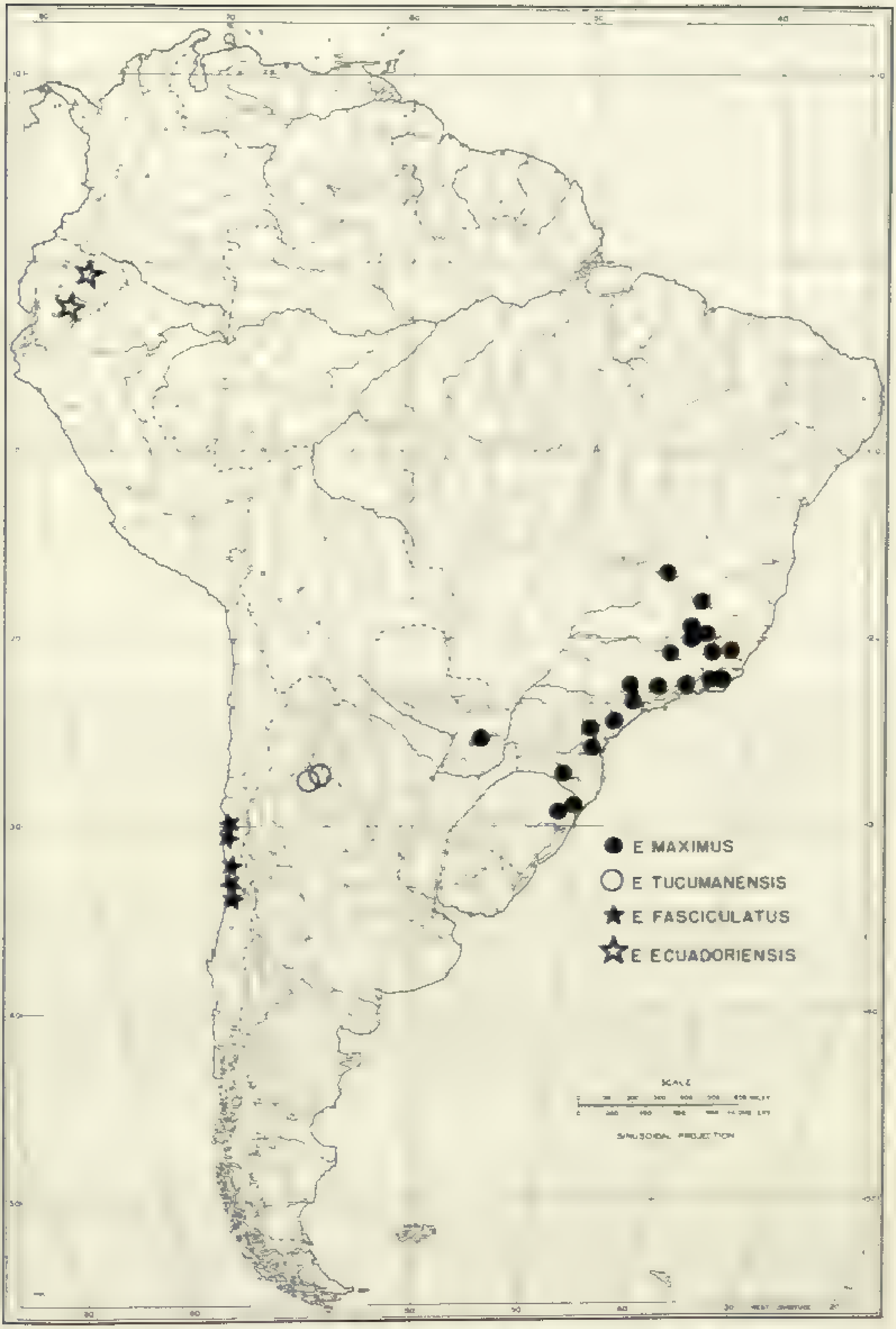


FIG. 12. Distribution of *Erigeron maximus*, *E. tucumanensis*, *E. fasciculatus* and *E. ecuadoriensis*. Goode base map, copyright by the University of Chicago.

pubescent, with dark-brown or slightly reddish midrib portion; ligulate flowers numerous, in one series, yellow, tube-portion 2-3 mm. long, ligule 6-8 mm. long; tubular flowers numerous, yellow, 3-4 mm. long; achenes terete, red-ochraceous in color, 1-2 mm. long, glabrous.

TYPE: **Argentina,** *Venturi 4745* "Tucumán, Dept. Chicligasta, Las Pavas, 2500 m" (Holotype LP!, Isotypes GH!, LIL!, US!)

MATERIAL STUDIED: **Argentina.** Catamarca, dept. Andalgalá (*sic;* Tucumán, dept. Chicligasta), Rio Cochuna, *Jorgensen 1514* (GH, MO, US).

This rare species from Tucumán in Argentina (fig. 12) is closely related to *E. maximus.* It differs by its smaller heads, borne singly or in groups of not more than five, the yellow ligules, the slender stems, the narrow leaves and the small size. It is also completely geographically isolated from that species.

3. **Erigeron tweediei** Hook. et Arn., Comp. Bot. Mag. 2: 50. 1836

(Fig. 14)

Erigeron seneciiformis Blake, Proc. Biol. Soc. Wash. **36:** 51. 1923, based on: Bolivia, "*White 1206*, Hacienda Rosario, near Reyes," 11-IV-1921 (US!)

Large herbs, 50-100 cm. tall. Roots fibrous arising from a short and stout rhizome, 2-5 mm. in diameter. Shoots few, slightly woody, hollow, 2-5 mm. in diameter, striate, glabrous or more commonly slightly pubescent, green to greenish-brown in color, leafy, unbranched or branched only at the top. Basal leaves forming a conspicuous rosette, 10-30 cm. long, 5-30 mm. wide, lanceolate, entire, acute, margins entire or dentate, surface smooth, glabrous or somewhat pubescent, especially along the midvein and margins; petiole elongate, 1-5 cm. long, expanding gradually into the lamina, 0.5-3 mm. in diameter, the dry bases of the petiole remaining after the leaves have fallen; cauline leaves triangular-lanceolate, acuminate, sessile, somewhat clasping, 1-10 cm. long. Heads numerous, arranged in cymes or panicles at the end of the shoot, usually rather tight; pedicels 2-50 mm. long, pubescent. Involucres large, 10-15 mm. wide, 5-10 mm. high. Involucral bracts triangular, acute, 3-5 mm. long, 1-3 mm. wide, borders entire or slightly dentate, surface glabrous or more commonly pubescent, borders often of lighter color; ligulate flowers yellow, in one outer series, tube 2-3 mm. long, ligule 2-5 mm. long; tubular flowers yellow, 3-5 mm. high; pappus white-yellowish; achenes terete 1-3 mm. long.

TYPE LOCALITY: **Uruguay,** *Tweedie 1058* "Maldonado in boggy ground" (not seen).

SELECTED SPECIMENS: **Argentina.** Corrientes, estero Batel, *Pedersen 3101* (US); Entre Rios, Concordia, *Burkart 1065* (DARW); Misiones, San José, *Bertini 2732* (F); Jujuy, Toldos bei Bermejo, *Fiebrig 2378* (GH, K). **Bolivia.** Santa Cruz, Sara, lomas de Buenavista, *Steinbach 6712* (MO, BM, GH), *2684* (DARW, LIL), *5293* (GH), *3166* (LIL). **Brazil.**

FIG. 13. *Erigeron tucumanensis*, general aspect × ½ (*Venturi 4745*, LIL).

Goias, *Gardner 4332* (K); Minas Gerais, Caldas, *Henschen 203* (US); Serra da Matuca, *Williams 5314* (GH); Paraná, Curytiba, *Hatschbach 609* (LIL); Rio de Janeiro, Rio, *Glaziou 11052* (K); Rio Grande do Sul, Lagoa Vermelha, *Bornmüller 704* (GH); Santa Catarina, Lages, *Rambo 49587* (LIL). **Paraguay.** Carapeguá, esteros Calistro, *Rojas 3297* (DARW, LIL); Caaguazú, Colonia Sommerfeld, *Sparre & Vervorst 2260* (LIL). **Uruguay.** Montevideo, *Arechavaleta 4182* (K); San José, Barra de Santa Lucia, *Herter 1540* (GH, LIL).

This species occupies the largest geographical area of all the South American species of *Erigeron,* growing in swamps and wet places, in the states of Goiás, Minas Gerais, Rio de Janeiro, Paraná and Rio Grande do Sul in Brazil, in Uruguay, in eastern Argentina, in Paraguay and in the lowlands of eastern Bolivia (fig. 20). In spite of its great range it does not seem to be too common (being much less frequent than the partly sympatric *E. maximus*), although one should remember that the area is in general poorly explored and collected. The species is quite distinct and certain doubts as to its status in *Erigeron* have been raised (see Solbrig, 1960). It is related to *Erigeron maximus,* from which it can be separated easily by the short yellow ligulate flowers and the tight inflorescences. The heads are also smaller than in that species.

4. **Erigeron meyeri** Cabrera, Notas Mus. La Plata Bot. **19**: 198. 1959
(Figs. 1, 15-18)

Perennial herb from a short stout rhizome, 40-60 cm. tall. Shoots several from the base, slightly grooved, brown to greenish brown. Basal rosette of leaves lax; leaves sword-shaped, 15-25 cm. long, 8-15 mm. wide, acute, margins entire, minutely dentate-pubescent, surface glabrous, petiole short, expanding gradually into the lamina; cauline leaves shorter and narrower than the basal, sessile. Capitula several per shoot in an open panicle, pedicels 5-15 cm, long, slightly pubescent. Involucre 8-12 mm. wide, 5-7 mm. high; involucral bracts in 1-2 undefined series, 0.5-1 mm. wide, 2-4 m. long, acuminate, dorsally pubescent, stiff; ligulate flowers in one series, tube 2-3 mm. long, ligule 3-4 mm. long, 1 mm. wide; tubular flowers numerous, 3-4 mm. long; styles of tubular flowers with triangular tips copiously covered with collecting hairs externally and with two rows of stigmatic papillae on each side of the stylar branches; achenes terete, 1-2 mm. long, pubescent.

TYPE: **Argentina**, Prov. Chaco, *Meyer 2234* (Holotype LP!, Isotype LIL!).

MATERIAL STUDIED: **Argentina**, Prov. Chaco, Fontana, *Meyer 2125* (LP, LIL).

FIG. 14. *Erigeron tweediei*, general aspect × ½ (*Dusen 14493*, GH). Drawing by Ruth Hsu.

This species, known from only two collections from one locality (fig. 19), is very distinct, and can be easily recognized by the basal leaves. Its affinities are unclear, but it is likely that it might be related to *Erigeron tucumanensis* or *Erigeron maximus*, the first one in particular having certain similarities in leaf shape and aspect of the capitula, although it lacks a basal rosette. Its distribution is restricted to a small area in the western part of the province of Chaco in Argentina, where it apparently is abundant (Meyer, personal communication).

5. **Erigeron camposportoi** Cabrera, Arq. Jard. Bot. Rio de Janeiro 15: 75. 1957

Perennial erect herb, 70 cm. high. Stem grooved, solid, with white, soft pith, brownish to brownish-green in color. Leaves 5-10 cm. long, 1.5-2.5 cm. wide, lanceolate, dentate, glabrous on both surfaces, short-petiolate; upper leaves smaller, entire, sessile. Heads borne at the tip of the branches in open panicles with many heads. Involucre hemispheric, 7-9 mm. wide, 4-5 mm. high; involucral bracts numerous, linear, in one to three series, 2-4 mm. long, 0.5-1 mm. wide, glabrous or very short pubescent, with short-ciliate margins; ligulate flowers numerous, white, in two series, tube 2-4 mm. long, ligule 3-4 mm. long, 0.5-1 mm. wide; tubular flowers yellow, 3-4 mm. long; styles triangular tipped; achenes dorsally compressed, turbinate, 1-2 mm. long, slightly pubescent.

TYPE: **Brazil**, estado do Rio de Janeiro, *Cabrera 12294* "Serra dos Orgaos, selva, 1800 m.s.m." (LP!)

MATERIAL STUDIED: **Brazil**, estado do Rio de Janeiro, Serra do Itatiaia, 900 m. s. m., *Malme 312* (B).

A rare species known only from two collections (fig. 42), it is very distinct from any other South American species. It grows in an area relatively well collected, and it is strange that it has not been found at any other time.

6. **Erigeron fasciculatus** Colla, Mem. Acad. Torino 38: 27. 1834

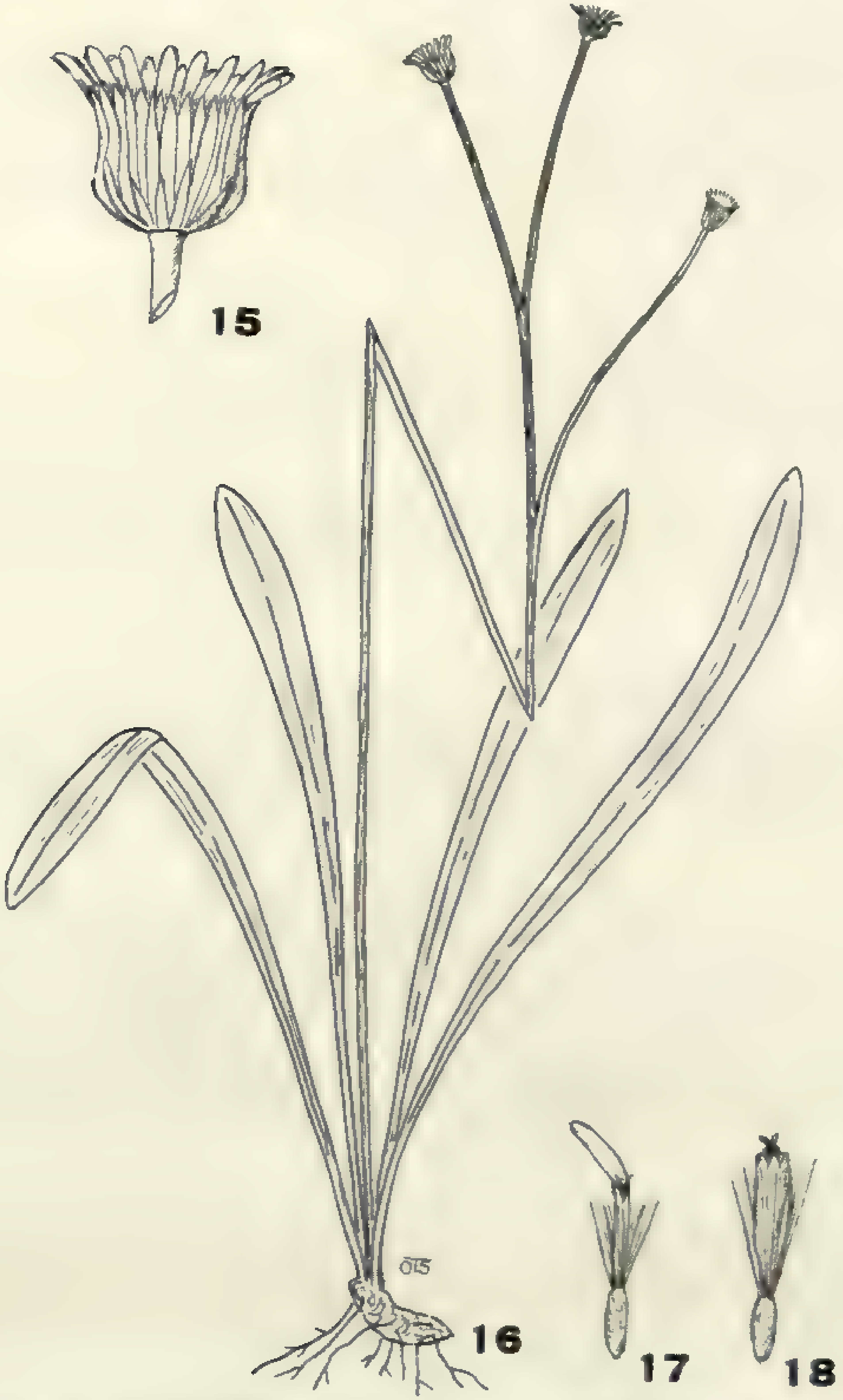
(Fig. 20)

Erigeron berterianus DC., Prodr. 5: 286. 1836, based on *Bertero s.n.* "lollium [sic] prope Valparaiso Chilensium" (suspected isotype BM!)

Erigeron spiculosus Hook. & Arn. var. α (var. "liguli longiori" Herb.) Comp. Bot. Mag. 2: 49. 1836, based on *Cuming 407* "Valparaiso" (BM!)

Haplopappus hispidulus DC., Prodr. 5: 348. 1836, based on "in Chile prope Coquimbo legit cl. *Gaudichaud 87*" (Isotype GH!)

Erigeron subandinus Phil., Linnaea 28: 723. 1858, based on *Gay 761* "in subandinis Sta. Barbara, prov. Concepción, Jan. 1839" (SGO!)



FIGS. 15-18. *Erigeron meyeri*. 15. Capitulum × 2. 16. General aspect × ½. 17. Ligulate flower × 4. 18. Tubular flower × 4 (All from *Meyer 2125*, LP).

FIG. 19. Distribution of *Erigeron meyeri, E. luxurians, E. pazensis* and *E. karwinskianus.* Goode base map, copyright by the University of Chicago.

Aster breviflorus Phil., Linnaea **33:** 131. 1864, based on *Volkmann s.n.* "Prov. Coquimbo, aestate 1860/61" (SGO!)

Aster litoralis Phil., Anal. Univ. Chile **43:** 486. 1873; *Erigeron litoralis* (Phil.) Skottsb., Acta Horti Gothob. **18:** 158. 1950; based on *Philippi s.n.* "in scopulis maritimis Guayacán, Nov. 1864" (SGO!)

Subshrub, 20-70 cm. high. Root woody; stems, especially near the base, woody and with brown-black, often corky bark. Shoots several from the base, or one or two, with few, sparse hairs or glabrous. Leaves spirally arranged, borne singly on shoots, or in fascicles in the axils of branchlets or older leaves, linear-lanceolate to spathulate, margins entire, or slightly and irregularly serrate or dentate, grayish-green in color, covered with short multicellular, uniseriate hairs on both surfaces, or glabrous, hairs usually dense but varying from collection to collection, leaves 5-30 mm. long, 1-5 mm. broad; petiole short, gradually expanding into the lamina, 1-2 mm. broad, 1-5 mm. long, pubescent or glabrous. Heads arranged in panicles at the end of the branchlets or occasionally solitary; peduncles up to 10 cm. long, glabrous to pubescent, covered with a few bracts or short leaves, 10 mm. long, up to 3 mm. broad, sessile, pubescent; involucre 5-12 mm. wide, 4-8 mm. high, involucral bracts triangular-lanceolate, 2-10 mm. long, 0.5-2.0 mm. wide, imbricate, arranged in two loose series, covered with medium to long, unicellular or more commonly multicellular hairs, sometimes dense, giving a white-woolly appearance, or occasionally glabrous; ligulate corolla white or yellow, 10-15 mm. long, 0.5-1.0 mm. wide, glabrous, tips of ligules sometimes slightly notched; tubular corolla 3-5 mm. long, whitish or yellowish; style of tubular flower with triangular tips covered with collecting hairs, pappus white-yellowish in herbarium material, 2.5-4.5 mm. long; achenes terete, pubescent, 1-2 mm. long.

TYPE: *Bertero* "in Chili locis sylvaticis collium Valparaiso" (not seen).

MATERIAL STUDIED: **Chile**, Prov. Coquimbo, Coquimbo, *Gaudichaud 87* (GH), *Harvey s.n.* (DARW, GH), *Ball s.n.* (GH, K), *Coppinger s.n.* (K), *Phillippi s.n.* (SGO), *Geisse s.n.* (SGO), *Hastings 596* (US), *Hicken 8689* (DARW), *Joseph 5422* (US), *Jaffuel 1207* (GH), *Montero 1890* (GH), *Werdermann 109* (BM, DARW, F, GH, LIL, MO); La Serena, *Joseph 5483* (US), Dept. Ovalle, Zorrila, *Jiles P. 1948* (LP), Tulahwen, *Geisse* (SGO); *Los Vilos* s.c. (SGO); prov. Aconcagua, Zapallar, *Betin* (F); playa Papudo, *Looser 2470* (LP); Prov. Valparaiso, Valparaiso, quebrada del Lúcumo, *Looser 3761* (LP), Quintero, *Albert s.n.* (SGO); Valparaiso, *Cuming 407* (BM), *406* (BM), *Wilkes s.n. Joseph 1587* (US), *Phillippi s.n.* (SGO); collium loco dicto Rennaca, *Bertero 819* (BM, GH); Cerro Campana, *Morrison & Wagenknecht 17153* (DARW, GH, K), *Looser 586* (GH), *Garaventa 1875* (GH).

Erigeron fasciculatus grows along the Chilean coast from Valparaiso to Coquimbo, on hills near the coast, or on the beach (fig. 12).

Since we are dealing with a shrubby species, the specimens available are still less satisfactory than the average

Fig. 20. *Erigeron fasciculatus*, general aspect × ½ (*Werdermann 109*, GH).

herbarium specimen. It is evident that at least in some cases they are misrepresentative of the species. The basal leaves (which are wider) are often missing, giving an entirely different aspect to the specimen. Also data as to habit, size of plant, color of flowers, etc. are almost entirely missing.

The collections from Cerro Campana near Valparaiso are quite interesting. Although the species has in general slightly to heavily pubescent leaves and stems, the specimens from Cerro Campana are almost completely glabrous. In addition the leaves are spathulate, at least the basal ones, and not in fascicles. Nevertheless, in view of the scarcity of material, it is thought best not to ascribe taxonomic status to this material for the present.

Skottsberg (1950) has expressed certain doubts that *E. berterianus* (which he considers conspecific with *E. litoralis*) and *E. fasciculatus* are synonymous, notwithstanding the fact that De Candolle in the original description of *E. berterianus* cites a specimen of Bertero from the same locality that Colla cites for his Bertero specimen, and especially in view of De Candolle's later (Prodr. 7: 274. 1838) statement that the two species are conspecific. Colla in the original description of *E. fasciculatus* indicates ". . . foliis . . . utrinque glabris margine denticulato-ciliato . . ." while De Candolle states ". . . foliisque setis minutissimis adpressis . . .", this being the only basic discrepancy between the two descriptions. I have seen a sheet from the British Museum and another from the Gray Herbarium, labelled exactly like the original De Candolle sheet in Geneva *(Bertero 819)*. These, I suspect, are isotypes, and I find that the pubescence character is variable. Therefore, I think there is no reason to maintain *berterianus* as a separate species.

Under *Erigeron spiculosus*, Hooker & Arnott described what is apparently a *Conyza* ("the ligule of the ray is sometimes short, about one-sixth the length of the tube"), since the ligules, according to their description, are less than ½ mm. long. Nevertheless, they describe a variety with long ligules, of which I have seen a specimen, cited in their original description (*Cuming 407*, BM), which should be placed under *E. fasciculatus* without any doubt.

Haplopappus hispidulus DC. was already referred by Hall (1928, p. 365) to *Erigeron*. The material of Gaudichaud at the Gray Herbarium, the picture of the type of De Candolle, as well as the description and locality, leave no doubt that it is a synonym of *E. fasciculatus.*

7. **Erigeron luxurians** (Skottsb.) Solbrig, stat. & comb. nov. (Figs. 4, 21)

Erigeron litoralis (Phil.) Skottsb. var. *luxurians* Skottsb. Acta Hort. Gothob. 18: 164. 1950.

Subshrub up to 50 cm. high. Shoots several from the base, up to 1.5 cm. in diameter, woody, bark dark, deeply grooved in age, leaf scars clearly present, leaves crowded towards the tip of the branches, lanceolate, 1-3 cm. long, 1-4 mm. wide, acute, margins entire, surface pubescent to very pubescent giving the leaves a white-grayish aspect in herbarium; sessile or with a short, not well defined petiole. Heads borne solitary at the end of long protruding pedicels up to 10 cm. long, white-pubescent, leafless or with a few bracts not more than 5 mm. long. Involucres hemispheric, 10-18 mm. wide, 6-10 mm. high; involucral bracts in 2-3 rows, 4-7 mm. long, white-pubescent, hairs multicellular, uniseriate; ligulate flowers numerous, white, turning lavender in age, 10-15 mm. long, pubescent in the throat, ligules 1-2 mm. wide; tubular flowers 4-5 mm. long; pappus white-yellow; achenes terete, pubescent, reddish, 1.5-2.5 mm. long at maturity.

TYPE: **Chile,** Carl o Inga *Skottsberg 822* "Prov. Coquimbo, Loma Frai Jorge" (Isotype LP!)

MATERIAL STUDIED: **Chile.** Prov. Coquimbo, Herradura, *Carl o Inga Skottsberg 709* (LP); Loma Frai Jorge, *Carl o Inga Skottsberg 822* (LP), *Werdermann 925* (BM, DARW, F, GH, LIL, MO, US), *C. Muñoz P-156* (GH, SGO), *Muñoz & Coronel 1341* (SGO), *Granjet 452* (SGO), *Worth & Morrison 16431* (DARW, GH, MO), *Schwabe 226* (SGO), *Fuentes s.n* (SGO), *Jiles 2732* (LP), *724* (SGO); Cerro Talinay, *Cabrera 12569* (LP), *Kausel 3805* (F, LP), *3356* (F), *Muñoz & Coronel 1281* (SGO).

This species is endemic to the area of the Frai Jorge forest in Coquimbo (fig. 19). It is very closely related to *E. othonnaefolius*, but although of similar habit (which separates it from *E. fasciculatus*, another allied species), it has larger heads and the plants are larger and not so compressed. Muñoz & Pisano (1948) determined material of this species as *E. berterianus* but, as Skottsberg (1950) already has pointed out, the two species are distinct. On the other hand, the name *E. litoralis* (Phil.) Skottsb., used by Skottsberg cannot be used because it is a synonym of *E. fasciculatus*, a conclusion I reached after seeing the type of *Aster litoralis* Phil. in the herbarium of the Museo Nacional in Santiago. Rather than coining a new name I have raised the appropriately named var. *luxurians* of Skottsberg to specific status.

FIG. 21. *Erigeron luxurians*, general aspect × ½ (*Werdermann 927*, GH).

FIG. 22. *Erigeron othonnaefolius*, general aspect × ½ (*Cabrera 3586*, LP).

8. **Erigeron othonnaefolius** Hook. et Arn., Comp. Bot. Mag. 2: 50. 1836
(Fig. 22)

Erigeron vidali Phil., Anal. Univ. Chile 87: 410. 1894; based on *Francisco Vidal G.* "inter Constitución & Duao." (SGO!)

Aster prostratus Phil., Anal Univ. Chile 87: 407. 1894; based on *Luis Landbeck s.n.* "Algarrobo [Chile], Febr. 1867" (SGO!)

Subshrub 5-25 cm. high, forming a low, dense, mat. Shoots stout, short, woody, up to 8 mm. in diameter with gray or grayish brown bark, several from the base. Leaves crowded around the shoot, lanceolate, 5-35 mm. long, 3-10 mm. wide, margins entire, color of leaves grayish-green due to a thick layer of hairs on both surfaces, hairs short, multicellular and uniseriate, petiole 3-12 mm. long, often persistent on the stems in old decayed leaves. Heads borne solitary at the end of short, leafless (or with a few short bracts) peduncles. Involucres 5-10 mm. high, 8-18 mm. wide; involucral bracts triangular-lanceolate, up to 10 mm. long, pubescent on the dorsal side, reflexed at maturity; ligulate corolla white, turning lavender or yellowish in age, 10-15 mm. long, 0.5-1.0 mm. wide, glabrous, tips of ligules some-

Fig. 23. Distribution of *Erigeron tweediei*, *E. othonnaefolius*, *E. incaicus*, and *E. rosulatus*. Goode base map, copyright by the University of Chicago.

times slightly notched; tubular corolla 3-5 mm. long, whitish or yellowish; style of tubular corolla with triangular tips covered with collecting hairs; pappus white-yellowish in herbarium material, 2.5-4.5 mm. long; achenes terete, pubescent, 1-2 mm. long.

TYPE: "Maule Province" *Cuming 831* (not seen).

MATERIAL STUDIED: **Chile.** Prov. Concepción, Hualpén, playa blanca, *Pfister 7569* (LP); Ramulcho, *Barros 7421* (LP), *1996* (LP). Prov. Maule, Constitución, *Grandjot 58c* (LP), *Philippi s.n.* (BM), *Cabrera 3586* (F, LP), *Azo-Cart. s.n.* (SGO).

A species closely related to *E. luxurians*, from which it can be easily separated by its stouter and wider leaves which are crowded, its more prostrate habit, and its larger heads borne on scapes which protrude from the plant. This species has been collected along the coast from Concepción to Constitución in only three localities, growing on or near the coastal sand (fig. 23). As in *E. fasciculatus*, the gaps in distribution are very likely collecting gaps.

9. **Erigeron fernandezianus** (Colla) Solbrig, nov. comb. (Fig. 24)

Terranea fernandeziana Colla, Mem. Acad. Torino 38: 8. 1835.

Erigeron fruticosum DC., Prodr. 5: 283. 1836, based on *Larrain* Herb. *Bertero 337* "insula Juan Fernandez" (Isotype BM!, GH!).

Shrub, or small tree up to 1 m. tall; small trunk which attains a height of a few feet sometimes present (cfr. Skottsberg, Nat. Hist. Juan Fernandez etc. 2: 183. 1921). Branches woody, up to 1 cm. in diameter, grayish-brown, leaf scars present. Leaves large, lanceolate to lance-pinnatifid, 2-10 cm. long, 2-10 mm. wide, acute, margins entire, serrate or dentate, surface glabrous or with occasional hairs, petiole up to 20 mm. long, expanding very gradually into the lamina, or leaves sessile. Capitula disposed in loose to semi-loose panicles along the branches; peduncles hairy. Involucre 4-8 mm. wide, 4-6 mm. high; involucral bracts in 2-3 series, 3-5 mm. long, glabrous to pubescent; ligulate flowers in one series, 5-7 mm. long, 1-2 mm. wide, white or white-yellowish; tubular flowers 4-5 mm. high, yellow; style of tubular flowers with triangular tips with a cover of collecting hairs on the outer surface and stigmatic papillae along the sides; achenes flat, reddish, glabrous or short-pubescent, 1-2 mm. long.

TYPE: **Chile,** *Bertero* "sylvaticis saxosis montium insulae Juan Fernandez" (not seen).

MATERIAL STUDIED: **Chile.** Juan Fernandez Islands. Masatierra, *Moseley s.n.* (BM); Cordon Salsipuedes, *Carl o Inga Skottsberg 73* (BM); Portezuelo de Villagra, *Carl o Inga Skottsberg 9* (US); Plazuela del Yunque, *Bock 54* (GH, US). Masafuera, *Seybold s.n.* (SGO). Juan Fernandez, *Philippi s.n.* (SGO, LP), *Reed s.n.* (SGO).

This is an endemic species of the Juan Fernandez Islands: Masatierra and Masafuera. A low, globose and well-

FIG. 24. *Erigeron fernandezianus*, general aspect × ½ (*Skottsberg 9*, GH).

branched shrub, with white-yellow flowers, blooming from November to February, it is a fairly common plant on the islands in spite of the few collections which have been made. It grows abundantly in sunny places above the forest, especially on rocky walls and slopes (Kunkel, 1957).

Erigeron fernandezianus has been considered closely allied to the genus *Tetramolopium* by Bentham (1873). Although the habit of *E. fernandezianus* is similar to that of *Tetramolopium*, this last has a subulate style and an elongated and pointed achene, characters not found in *Erigeron*. Furthermore, *T. humile* has been found to have 7 II chromosomes (Carlquist, 1956)[1], while all species of *Erigeron* counted to date have 9 II. Cytological information on *E. fernandezianus* should therefore be of considerable interest. On the basis of technical characters, such as style, involucre, pappus, etc., *E. fernandezianus* can be placed easily in *Erigeron*, even though it differs from other South American species of the genus. The similarity in habit to *Tetramolopium* is most likely due to convergent evolution, and in this connection it should be remembered that both are insular forms.

This species was first described by Colla in 1834 as *Terranea fernandeziana*. A year later, De Candolle, unaware of Colla's description, redescribed it as *Erigeron fruticosus* in vol. 5 of the Prodromus. He later realized the true identity of this species and stated its identity with *Terranea fernandeziana* in an appendix to vol. 7 of the Prodromus (7: 274. 1838). The plate published by Colla in his original description corresponds to the specimens of the type collection of *Erigeron fruticosus* which I saw. De Candolle's statement notwithstanding, his name, *E. fruticosus* has been used exclusively until the present.

10. **Erigeron ingae** Skottsb., Nat. Hist. J. Fernandez & Easter Isls. 2: 184. 1921
(Fig. 25)

Erigeron ingae var. *innocentium* Skottsb., loc. cit.: 184. 1921, based on *Skottsberg 557* "Juan Fernandez, Masafuera, Los Inocentes" (not seen).

Erigeron turricola Skottsb., loc. cit.: 185. 1921, based on *C. & Inga Skottsberg 483* "Masafuera, fell-fields near Las Torres" (Isotype BM!; US!)

---

[1] Since this article went to press, I have counted a plant of *Tetramolopium humile* with 9 II of chromosomes.

Subshrub, 10-30 cm. tall, from a woody base. Shoots one or several, grayish-brown 2-5 mm. in diameter, woody, covered with the bases of old leaves. Leaves elliptic-lanceolate, 20-50 mm. long, 3-6 mm. wide, acute, entire, lower leaves with coarsely serrate margins, upper leaves with entire margins, pubescent, hairs long, multicellular, uniseriate, lower leaves petiolate, upper sessile, petiole not more than 15 mm. long. Floriferous shoots one or more, leafy, pubescent, longitudinally grooved; heads in panicles or solitary. Involucre 8-12 mm. wide, 5-8 mm. tall; involucral bracts in two series, 6-8 mm. long, 2-3 mm. wide, pubescent; ligulate flowers in one series, 6-8 mm. long, 1-2 mm. wide, yellow; tubular flowers 4-5 mm. long; pappus in one series; achenes hairy, especially on the borders, 2 mm. long at maturity.

TYPE: **Chile,** *Carl o Inga Skottsberg 391* "Juan Fernandez, Masafuera, Las Torres, steep rocks" (Isotype BM!)

MATERIAL STUDIED: **Chile,** Juan Fernandez Islands, Masafuera, Las Torres *Carl o Inga Skottsberg 391* (BM); *483* (BM; US).

Erigeron ingae is very closely related to *E. fernandezianus.* This last species grows in mesic conditions, while *E. ingae* is an alpine species, and shows the expected differences: smaller size, leaves thicker and more compact, increased pubescence, and entire or slightly serrate leaves. It is easily distinguishable from *E. fernandezianus* by these characters, and also by the slightly larger heads.

As in the case of *E. luteoviridis,* I have been hampered by the lack of specimens and the impossibility of studying the species in the field. In his descriptions Skottsberg does not indicate the differences between *E. ingae* and *E. turricola.* The only difference I could find in studying sheets of both species from Skottsberg's collections was one of size, which I do not consider sufficient for maintaining these entities as different species.

It is interesting to note the adaptive radiation of *Erigeron* in the Juan Fernandez Islands, where one species, *E. ingae,* is adapted to alpine conditions and another, *E. fernandezianus* very closely related to more mesic, forest environment, with a third species, *E. luteoviridis,* apparently adapted to the drier subalpine regions. The fourth species of *Erigeron* in Juan Fernandez, *E. rupicola,* represents apparently an independent invasion, and grows at lower altitudes.

11. **Erigeron luteoviridis** Skottsb., Nat. Hist. J. Fernandez & Easter Isl. 2: 183, 1921

(Fig. 26)

Perennial herb from a woody base, 25-30 cm. high. Shoots several from the base, brownish-yellow, striate, glabrous; no true basal

FIG. 25. *Erigeron ingae*, general aspect × ½ (*Skottsberg 391*, GH).

rosette present. Basal leaves lanceolate, 4-6 cm. long, 4-6 mm. wide, acute, margins serrate, surface very glabrous, petioles up to 10 mm. long, expanding gradually into the lamina; cauline leaves lanceolate, 1-2 cm. long, 2-4 mm. wide, with entire margins, transition between basal and cauline leaves very gradual. Heads in a terminal panicle, peduncles 10-25 mm. long. Involucres hemispheric, 6-8 mm. wide, 4-6 mm. high; involucral bracts in 2-3 series, 2-5 mm. long, surface glabrous, borders ciliate; ligulate flowers in one series, 5-6 mm. long; tubular flowers 3-4 mm. long; pappus white; achenes glabrous, 1-2 mm. long at maturity.

TYPE LOCALITY: **Chile.** Juan Fernandez, Masafuera "Cordon atravesado, alpines" *Carl o Inga Skottsberg 500* (Isotype BM!)

Erigeron luteoviridis is undoubtedly very closely related to *E. fernandezianus* and might even be conspecific. I have had only a sheet of the type collection to study, which although very similar can be clearly separated from *E. fernandezianus.* I have followed Skottsberg's criterion in maintaining it as a separate species, since he has had the opportunity to study both species in the field. I reproduce Skottsberg's (1921) comments: "near *E. fruticosus* [*E. fernandezianus*] but undoubtedly quite distinct. The light color and the thick leaves characterize the new species; *E. fruticosus* is pure green, much more villous, and has much thinner leaves, generally also a distinct trunk, which attains the height of a few feet".

12. **Erigeron pazensis** Sch. Bip. ex Rusby, Mem. Torrey Bot. Club 3: 54. 1893. Sch. Bip., Bull. Soc. Bot. France 12:80. 1865 (nomen)

(Figs. 27-28)

Tall suffrutescent herb, 25-50 cm. high, with several branches from a woody or semi-woody base, leafy throughout but without a basal rosette, branched above; branches gray, gray-green or light green, striate, hairy, particularly in the younger portions. Leaves numerous, oblong, sessile, strongly ascending, up to 5 cm. long, 1-4 mm. wide, acute or slightly obtuse, borders entire, surfaces slightly scabrous, pubescent throughout with a strong central midrib prominent below. Heads borne singly at the end of leafy branches. Involucre hemispherical, 10-14 mm. wide, 5-8 mm. high; involucral bracts numerous, 5-8 mm. long, arranged in 1-2 loose series, stiff, grayish green, often with midrib or tips reddish, pubescent, the inner ones with glabrous membranous borders; ligulate flowers white (?), numerous, arranged in 2-4 series, tube of the corolla 3-4 mm. long, ligule 1.5-2.5 mm. long, 1 mm. broad, with a bifid tip; tubular flowers yellow, about twice the number of ligulate flowers, corolla 4-4.5 mm. long; style with a well developed triangular tip covered with collecting hairs and two lines of stigmatic papillae along the sides of both stylar branches; achenes 2-3

FIG. 26. *Erigeron luteoviridis*, general aspect × ½ (*Skottsberg 500*, GH).

mm. long, pubescent, the ligulate ones with two ribs, the tubular ones with three. Receptacle flat or slightly convex, slightly to medium papillate.

TYPE: Vicinity of La Paz, Bolivia, 10,000′ alt., *Bang 14* (NY!, Isotype BM!, GH!, LIL!, MO!, WU!)

MATERIAL STUDIED: **Bolivia.** Vic. La Paz, *Bang 67* (BM, GH, MO, US), *Buchtien 569* (BM, DARW, GH, LIL, MO, US), *3045* (US), *90* (US), *440* (US), *8595* (US), *4763* (US); *Pearce s.n.* (K); *Mandon 141* (BM); *Rusby 1663* (BM, GH, MO, US), *1662* (GH, NY, US); *Williams 2353* (BM); Cochabamba, *B. Julio II 170* (US); Bolivia without loc., *Bang 2874* (GH, NY, LIL, MO, US). **Peru.** Dept. Puno, Moho-Huancané, *Aguilar 437* (USM).

A common species in the vicinity of La Paz, Bolivia (fig. 19), where it has been collected on several occasions, it can be distinguished by the numerous pubescent shoots with only one head, the ligulate flowers in more than one row and the extremely short ligules. A species morphologically similar to *Conyza*, it is undoubtedly an *Erigeron* due to the preponderance of tubular over ligulate flowers, and the ligules, which are clearly larger than the tubes.

13. **Erigeron ecuadoriensis** Hier., Bot. Jahrb. **21**: 336. 1895 (Figs. 29-31)

Erigeron spathulatum Wedd. Chloris Andina **1**: 197. 1857 (not Vahl nor Schum. et Thonn.), based on Ecuador, *Jameson 273* "in graminis montes Pichincha, alt. 13000 pedes" (Isotype BM!)

Perennial herb, 12-30 cm. high, from a fibrous root. Stems several from the base, 2-3 mm. in diameter, pilose to white-woolly, grayish-brown in color. No true basal rosette present, although basal leaves are larger and more crowded than the cauline; basal leaves lanceolate to lanceolate-spathulate, 3-6 cm. long, 5-10 mm. wide, pubescent on both surfaces, margins irregularly toothed or lobed, lamina attenuating into a petiole up to 2 cm. long. Heads several on each branch, forming a short pseudo-spike or short-peduncled raceme, the upper heads maturing first and the peduncles elongating, the inflorescence thus ultimately somewhat panicle-like. Involucre campanulate, 12-15 mm. in diameter and 6-10 mm. high when fully mature; involucral bracts in two obscure rows, 6-8 mm. long and 1-2 mm. wide, with reddish tips and borders and with dense, white trichomes on the dorsal side; ligulate flowers white-purple in two rows, tube 3-4 mm. long, ligule 2-3 mm. long; tubular flowers 4-5 mm. long; style with triangular tips relatively elongate; achenes terete, pubescent, 2-3 mm. long.

TYPE: **Ecuador,** *Stübel 85* "Panecillo, . . ., inter Esperanza et Quito, 3600 m." (not seen).

MATERIAL STUDIED: **Colombia.** Páramo de Barbillas, between Guachicano and Almaguer, 3000-3400 m., *Lehmann 6175* (K). **Ecuador.** Coroyon, 3200 m., *Andre s.n.* (GH); Chimborazo, 4000 m., *Andre K. 294*

FIG. 27-28. *Erigeron pazensis.* 27. General aspect × ½. 28. Detail of root crown × ½ (*Buchtien 569*, GH).

(K); Urbina, Chimborazo, 11400 feet, *Anthony 378 & Tate* (US); Pife, 2700 m., *Mille 414* (GH, MO).

A little-collected plant characterized by its crenate-dentate leaves, and the many-headed scapes with their special type of growth, which nevertheless is not apparent unless one can study several specimens at different stages of growth. The plant is restricted in its distribution to high altitudes (over 2500 m.) in Ecuador and Colombia (fig. 12).

Cuatrecasas (1935) has placed *E. ecuadoriensis* Hier. as a synonym of *E. weddellianus* Hier., this last species having been erected by Hieronymus (Bot. Jahrb. 19: 49. 1894) as a segregate of *Erigeron (Celmisia) pellitus* (HBK) Wedd. *Erigeron ecuadoriensis* and *E. pellitus* are very different plants (belonging to different genera now, and are considered by Weddell as in different sections of *Erigeron*) and it is therefore improbable that Weddell would include both species under his concept of *E. pellitus*, especially since he described *E. spathulatus (= E. ecuadoriensis)* in the same work a few pages later.

14. **Erigeron incaicus** Solbrig, sp. nov.
(Figs. 32-34)

Herba perennis, erecta, ca. 55 cm. alta; caulibus parce ramosis, laxe hirsutis. Folia inferiora herbacea, alterna, sessilia, pubescentia, obovato-lanceolata, apice acuta, margine parce et minute dentata, 6-8 cm. longa, 10-12 mm. lata; folia caulina alterna, sessilia, lanceolata, margine integerrima, pubescente. Capitula ad apicem ramulorum solitaria, longissime pendunculata. Involucrum hemisphaericum, 8-10 mm. altum, 9-11 mm. crassum; bracteis multis, biseriatis, subaequilongis, linearibus, acutis, dorso dense pubescentibus; flores marginales biseriati, purpurelli, feminei, ligulati, tubulo 3-4 mm. longo, ligula 2-3 mm. longa, 1 mm. lata; flores disci numerosi, lutei, hermaphroditi, corolla tubulosa 3-4 mm. longa, pentidentata; styli ramuli breves, ad apicem deltoidei pubescentes; pappus luteus uniseriatus, setis aequilongis; achaenia leviter compressa, marginata, pubescentia, 2-4 mm. longa.

Perennial herb 55 cm. tall. Shoot one, dichotomizing two or three times, solid, grooved, somewhat woody, pubescent, gray-brown to green in color, about 3 mm. in diameter. Leaves all cauline, the lower ones obovate-lanceolate to obovate, 6-8 cm. long, 10-12 mm. wide, entire, sessile, acute, margins slightly toothed, surface scabrous, pubescent, lamina narrowing into a pseudopetiole: upper cauline leaves entire, sessile, lanceolate, surface scabrous, pubescent, margins entire, 2-5 cm. long, 5-10 mm. wide. Capitula borne singly at the end of the branches in a cyme-like disposition, peduncles long, pubescent. Involucre hemispheric, 9-11 mm. in diameter, 8-10 mm. high; involucral bracts numerous, imbricate, in two obscure rows, linear to linear-lanceolate, acute, 4-10 mm. long, 1-2 mm. wide, pubescent on the exterior, green to purple

FIGS. 29-31. *Erigeron ecuadoriensis.* 29. Ligulate flower × 4. 30. General aspect × ½. 31. Tubular flower × 4 (*Jameson 273*, BM).

in color, with dark purple tips; ligulate flowers purple, in two rows, female, ligulate, tube 3-4 mm. long, ligule 2-3 mm. long and 1 mm. wide; disk flowers yellow, numerous, hermaphroditic, corolla tubular 3-4 mm. long; styles with long triangular tips, externally covered with collecting hairs; pappus of bristles, yellowish, in one series; achenes terete, 2-4 mm. long, 1 mm. wide, slightly flattened, surface smooth, pubescent, light tan in color, borders brown-purplish, darker.

TYPE: **Perú,** Cajamarca, *Ferreyra 8532* "La Tahona, entre Bambamarca y Hualgayre, 2900-3000 m." (Holotype GH!; Isotype USM!)

A species related to *E. ecuadoriensis* and *E. pazensis*, combining characters of both. From *E. ecuadoriensis* it is easily separated by the heads borne singly at the end of the branches, the sessile leaves with entire or only toothed margins, and by its larger size. From *E. pazensis* it is distinguished by longer ligules, and wider leaves which are not as crowded as in *E. pazensis*. *Erigeron incaicus* grows completely separated from both these species, some 600 miles south of the nearest known locality of *E. ecuadoriensis* and some 1200 miles north of the known localities of *E. pazensis* (fig.23). So far, it is known only from the type.

15. **Erigeron tenuifolius** Hook., Trans. Linn. Soc. **20:** 207. 1847

Shrub 75-200 cm. high. Secondary branches with gray-brown bark up to 5 mm. in diameter in the specimens examined, with prominent leaf scars. Leaves clustered at the end of the branches, linear-lanceolate, 4-10 cm. long, 1-8 mm. wide, margins entire or slightly dentate, surface pubescent, especially on the lower side, midrib prominent below, petiole very short, less than 2 mm. long. Heads arranged in cymose inflorescences at the end of branchlets. Involucres cylindrical, 3-5 mm. in diameter; involucral bracts triangular-lanceolate, 1-4 mm. long, up to 1 mm. broad, arranged in several irregular series, borders entire, surface glabrous or with occasional hairs, midrib region of a darker brown than the borders; ligulate flowers white, tube 1-2 mm., ligule 1-3 mm. long; tubular flowers 3-4 mm. long, fragrant; style of tubular flower triangular tipped; pappus white, 2-3 mm. long; achene terete, about 1 mm. long, glabrous.

15a. **Erigeron tenuifolius** ssp. **tenuifolius**
(Fig. 36)

A subspecies based on the very narrow leaves, 1-2 cm. wide. It is found on Isabella (Albermarle) and islands to the east of it in the Galápagos Islands (fig. 37).

TYPE: **Ecuador.** Galápagos Islands. *Charles Darwin* Esq. "Charles and James Islands" (not seen).

MATERIAL STUDIED: **Ecuador.** Galápagos Islands. Indefatigable, *Svenson 119* (GH), *Stewart 737* (GH, US), *736* (GH, US); Charles,

FIGS. 32-34. *Erigeron incaicus.* 32. Ligulate flower × 4. 33. General aspect × ½. 34. Tubular flower × 4 (*Ferreyra 8582*, GH).

FIG. 35. *Erigeron tenuifolius* ssp. *lancifolius*, general aspect × ½ (*Stewart 724*, GH). Fig. 36. *Erigeron tenuifolius* ssp. *tenuifolius*, detail of flowering branch × ½ (*Stewart 738*, GH). Drawing by Ruth Hsu.

Stewart 733 (GH), *Baur 123* (GH), *Anderson s.n.* (GH); Albemarle, *Snodgrass & Heller 295* (GH); Abingdon, *Snodgrass & Heller 841* (GH); Duncan, *Stewart 735* (US); James, *Stewart 741* (US), *739* (GH, US), *740* (GH), *Snodgrass & Heller 370* (GH).

15b. **Erigeron tenuifolius** ssp. **lancifolius** (Hook.) Solbrig comb. & stat. nov.
(Fig. 35)

Erigeron lancifolius Hook., Trans. Linn. Soc. Bot. **20:** 208. 1847.

Erigeron lancifolius Hook. var. *glabriusculus* Stewart, Proc. Calif. Acad. IV, **1:** 151. 1911, based on *Stewart 724*, "Villamil Isl., Galápagos" (Isotype GH!)

A subspecies based on the wider and stiffer leaves, 2-8 mm. wide. It is restricted in distribution to the two western Islands of the Galápagos group, Isabella (Albemarle) and Fernandina (Narborough) (fig. 37).

TYPE: **Ecuador,** Galápagos, *Darwin 155* "Albemarle Island" (not seen).

MATERIAL STUDIED: Albemarle, *Baur 121* (GH); *Penny 452* (BM); *Blair 446* (BM); *Snodgrass & Heller 237* (GH, US), *278* (GH, US), *889* (GH, US), *930* (GH), *909* (GH), *253* (GH), *Stewart 732* (GH, US), *731* (GH, US), *723* (GH, US), *724* (GH, US); South Narborough, *Snodgrass & Heller 328* (GH), *344* (GH).

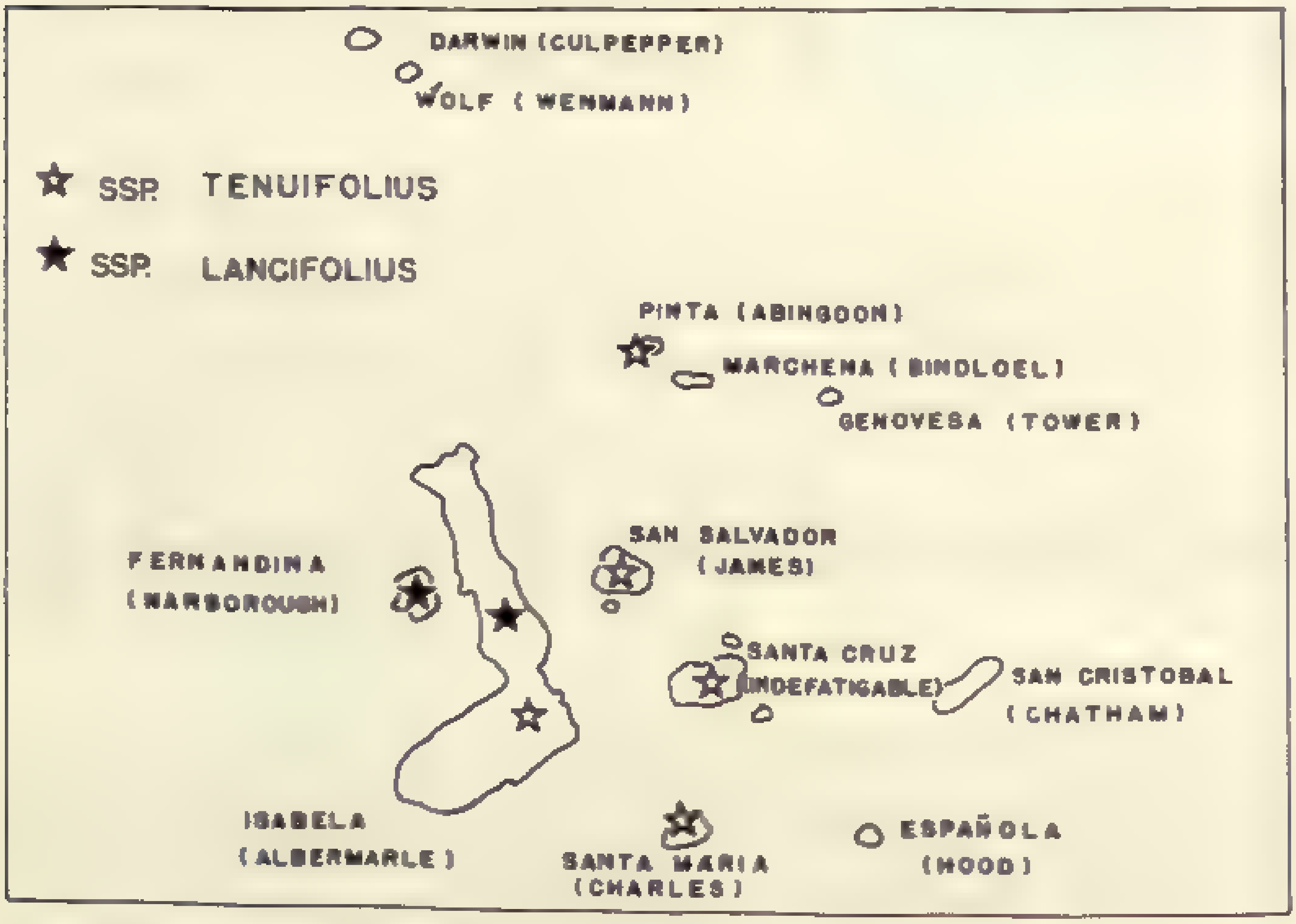


FIG. 37. Distribution of *Erigeron tenuifolius* ssp. *tenuifolius* and ssp. *lancifolius*.

This is a very peculiar species for an *Erigeron*. A woody tree, it is not close to any of the South or North American species of the genus. A close examination of the characters of the head, however, shows all the characters expected from an *Erigeron*. Although on vegetative characters alone it could be argued for the convenience of erecting a new genus, I prefer to leave this species here until more data, especially those of cytology and embryology, are available.

16. **Erigeron karwinskianus** DC., Prodr. 5: 285
(Figs. 8, 38)

Erigeron mucronatus DC., Prodr. 5: 285. 1836; *Erigeron karwinskianus* var. *mucronatus* Hieron., Bot. Jahrb. 28: 585. 1901, based on *Karwinski* "in Mexico" (not seen).

Erigeron trilobus Sonder, Hamb. Gart. and Blumenzeit. **12**: 78. 1856. excl. synon. (type unknown).

Slender herbs, 30-75 cm. high, from a thin rhizome or fibrous root. Stems several from base, 1-3 mm. in diameter, woody but flexible,

FIG. 38. *Erigeron karwinskianus*, general aspect × ½ (*Montero 2020*, GH). Drawing by Ruth Hsu.

grayish-brown to gray-green in color, bark slightly rugose especially in older stems, glabrous at the base, little to medium pubescent towards the tips; branches borne at about a 45° angle, 1-2 mm. in diameter, green-gray to green in color, bark smooth or rugose, often longitudinally grooved, low to medium pubescent. Leaves linear-lanceolate to lanceolate, 5-40 mm. long, 3-15 mm. wide, margins entire, or commonly finely toothed, or somewhat pinnatifid, acute, petiole 1-3 mm. long, expanding gradually into the lamina, surface smooth or rugose, pubescent especially along the midvein and the margins, hairs multicellular, uniseriate. Heads borne singly or in very lax panicles of 2-5 heads at the end of the branches. Involucre approximately campanulate, 5-10 mm. in diameter; involucral bracts numerous (more than 20), linear-lanceolate, 2-4 mm. long, 0.5-1 mm. wide, glabrous or slightly pubescent, with a long narrow tip and slightly toothed, often glandular-pubescent margins, surface smooth, often resinous; ray flowers numerous, showy, white or pinkish, seldom blue-pink, 8-12 mm. long, ligules up to 1 mm. wide; tubular flowers yellow, glabrous, 2-4 mm. high; stigmatic branches of styles of tubular flowers with obtuse triangular tips, almost blunt in appearance, covered with short stubby collecting hairs, a row of stigmatic papillae being present on each side of the branches; pappus white, 2-3 mm. long; achenes terete, 1-2 mm. long, slightly to medium pubescent.

TYPE: "in Mexico legit cl. Karvinski" (not seen).

SELECTED SPECIMENS: **Chile.** Cautin. Imperial. *Montero 2020* (GH); Valdivia, *Buchtien 11547* (US); Valparaiso. Limache, *Garaventa 941* (GH). **Colombia.** Santander, vicinity of California, *Killip & Smith 16762* (GH, US, NY), *17021* (GH, US, NY); Cundinamarca. Tequendama Falls near Bogotá, *Schiefer 482* (GH); *Killip 33988* (BM, GH); *Pennell 1963* (GH); *Juzepczuk 6775* (US); Cauca. La Manuelita near Palmira, *Pittier 850* (US); Boyacá. Soeta, *Cuatrecasas 1010* (US); Antioquia, Medellín, *Archer 438* (US); Norte de Santander. La Cabuya, *Cuatrecasas, Schultes & Smith 12188* (GH, US); Tolima. Rio Toche to Machin, *Killip & Hazen 9566* (GH). **Venezuela.** Menagas. Between Caripe & San Agustin, *Steyermark 61787* (F, GH, MO, NY). Mérida. San Rafael de Mucuchies, *Pittier 12901* (F, MO, NY, US). Lara. Between Buenos Aires to Canyon of El Callado, *Steyermark 55522* (F); Caracas, near Colonia Tovar, *Fendler 671* (GH, NY, MO).

Erigeron karwinskianus is a pantropical weed, originally native to Mexico and Central America. In South America it is rather common in Colombia and Venezuela, being found also in central Chile, probably as a garden escape, since the plant is sometimes cultivated. In synonymizing it with its variety *mucronatus* I am following Standley (1924).

Embryogenesis in this species has been studied by Carano (1921) Palm (1922; see Harling, 1954) and Fagerlind (1946). It was found that the species is largely apomictic, Fagerlind giving a frequency of 70% of unreduced embryosacs. There is disagreement as to the extent the reduced embryo-sacs are functional. Carano regards the species as only partially agamospermous, while Fagerlind on the basis of his studies feels that the reduced embryo-sacs "can scarcely produce to any great extent sporophytes capable of development" due to unbalanced chromosome numbers. Fagerlind notes that the lack of accord of his data with Carano's is possibly due to the fact that each worker had access to different biotypes of the species. Turner et al. (1961), working with Mexican material collected in the wild, report both sexual and presumed apomictic plants, with n = 9 II and n = 27 I respectively. Plants with n = 18 II have also been reported (Larsen, 1954. See introductory discussion). From these data it is clear that a careful embryological and cytological study of *E. karwinskianus* in the field should be very rewarding.

17. **Erigeron leptorhizon** DC., Prodr. 5: 288. 1836 (Figs. 7, 39-41)

Erigeron gaudichaudii DC., Prodr. 7: 274. 1836. Based on *Gaudichaud, 1836* (?) "in Peruvia" (F!, LP!)

Herbaceous annual from a slender rootstock. Several branches from the base, brownish-green, 1-2 mm. in diameter, hirsute, leafy. Leaves thin, simple, lanceolate-ovate, 1-6 cm. long and 5-15 mm. wide, margin crenate to entire, surface smooth, hairy. Heads on long peduncles arranged in loose cymose groups at the end of the branches, or axillary. Involucres 6-10 mm. wide and 5-8 mm. high; involucral bracts in one loose series, 2-4 mm. long and 0.1-0.8 mm. wide, lanceolate-triangular, borders entire, glabrous or short-haired, tips often purple, midrib region darker in color, dorsal suface glabrous or loosely pubescent; ligulate flowers numerous, white, tube 2-3 mm. long, ligules 1-3 mm. long; tubular flowers yellow, 2-4 mm. long with a narrow throat and open mouth; style with triangular tips and small, poorly marked stigmatic papillae; achenes terete, flattened, 1-2 mm. long, slightly pubescent.

TYPE: **Perú,** "in Amer. austr." *(Domb.)* (GH!). "Circa Limam" (Abadia) (not seen).

MATERIAL STUDIED: **Chile.** *Miers s.n.* (BM), possibly collected in what today is Perú. **Perú.** Dept. Lima, *Cuming 1083* (K); San Bartolo, *Sanchez s.n.* (USM); Amancaes, *Mathews s.n.* (K), *Ridoutt s.n.* (USM), *Ferreyra 4051* (USM); lomas de Atocongo, *Velarde Nuñez 587* (LP), *2230* (LP), *Maisch 43* (USM), *Ferreyra 1555* (US, USM), *2064* (USM), *178* (USM); Campoy, *Mexia 4033* (GH, MO); lomas de Caracoles, *Ferreyra 11876* (USM); lomas de Quilmaná, *Ferreyra 3998* (LIL, US, USM), *221* (USM), *Scolnick 971* (LIL); lomas de Asia, *Ridoutt s.n.* (USM); lomas de Lachay, *Cerrate 837* (USM), *Ridoutt s.n.* (USM), *Ferreyra 209* (USM); lomas de Chancay, *Ferreyra 8720* (USM); cerro San Jerónimo, *Soukup 3567* (LIL, MO), *1560* (US, USM); lomas de Pacha-

FIGS. 39-41. *Erigeron leptorhizon.* 39. General aspect × ½. 40. Tubular flower × 4. 41. Ligulate flower × 4 (*Weberbauer 5924*, GH). Drawing by Ruth Hsu.

camoc, *Cerrate 3554* (USM), Hacienda Villa, *Soukup 2154* (US, USM); Lurin, *Macbride 5945* (US), *Ferreyra 9539* (USM); Barranco, *Weberbauer 5712* (US); Insula San Lorenzo, *Wilkes s.n.* (GH, US), *Mathews s.n.* (K), *Esposto s.n.* (K), *Weberbauer 5924* (GH, US); Dept. Ancash, lomas de Lachay, *Stork, Horton & Vargas 9204* (GH, MO); Dept. La Libertad, Cerro Chiputur, *Lopez 377* (US, USM).

A species easily distinguished by its annual habit and crenate-dentate leaves, at least the basal ones. The small heads with white ligules are also characteristic.

This species is common in the dry hills (lomas) along the Peruvian coast, deriving the necessary humidity largely or entirely from the almost perennial fog and the infrequent light spring rains. It grows in loose, sandy soil.

18. **Erigeron rupicola** Phil., Bot. Zeit. **14**: 644. 1856 (Fig. 47)

Small, semiglobose, annual or short-lived perennial herb, 10-25 cm. high. Stems few from the base, slender, 1-3 mm. in diameter, bark brownish, rough. Leaves borne along the stems and at the end of the branches, 25-50 mm. long, 3-10 mm. wide, thin, spathulate, obtuse or acute, margins entire, surface glabrous, petiole 10-20 mm. long, expanding gradually into the lamina. Capitula borne solitary, peduncles 20-50 mm. long, leafless or with a few short bracts not more than 2 mm. long. Involucres hemispheric, 5-8 mm. in diameter, 3-5 mm. high; involucral bracts in 2-3 loose series, glabrous, with a darker midrib and a dark brown base; ligulate flowers in two series, ligules short, 4-6 mm. long, only 2 mm. longer than the tubes; tubular flowers 4 mm. long; pappus white; achenes hairy, 1-2 mm. long at maturity.

MATERIAL STUDIED: Chile, Juan Fernandez Islands, Masafuera, *Carl o Inga Skottsberg 417b* (BM), *514* (US); *Wagenknecht 18527* (GH, LIL, MO).

This is, according to Skottsberg (1921), a common species in many places on the coastal cliffs of the Island of Masafuera in the Juan Fernandez group. It is distinguished easily from the other Juan Fernandez species by the spathulate leaves with entire margins, and also by the annual or short-lived perennial habit.

19. **Erigeron rosulatus** Weddell, Chloris Andina **1**: 193. 1857 (Figs. 43-46)

Erigeron pulvinatum Wedd., Chloris Andina 1: 194. 1857, based on *Weddell 4334* "Bolivia: *punas,* aux environs de La Paz" (isotype F!)

Erigeron brittonianum Rusby, Mem. Torrey Club **3**: 54. 1893, based on *Bang 913*, "Songo, Nov. 1890" (Isotype BM!, GH!, K!, MO!, NY!, WU!)

Pulvinate perennial herb, 2-6 cm. high. Roots, root-crown and underground stems strong, woody, up to 1 cm. in diameter. The leaves are

FIG. 12. Distribution of *Erigeron camposportoi*, *E. leptorhizon*, *E. lanceolatus* and *E. pratensis*. Goode base map, copyright by the University of Chicago.

FIGS. 43-47. *Erigeron rosulatus.* 43. General aspect × ½ (*Mandon 224*, GH). 44. Capitulum × 4. 45. Tubular flower × 4. 46. Ligulate flower × 4 (*Bang 913*, GH). Fig. 47. *E. rupicola*, general aspect × ½ (*Skottsberg 717 b*, GH).

crowded in a very dense rosette around short, stubby shoots. Leaves linear-lanceolate, rosulate, 3-12 mm. long and 0.5-3 mm. wide, very densely covered with long, multicellular, uniseriate hairs on both surfaces, petiole 1-5 mm. long, expanding gradually into the lamina; the dried bases of the petioles covering the base of the shoots. Capitula borne singly at the apex of the branches, often surrounded by the upper leaves giving an aspect of being depressed, pedicels 0.5-5 cm. long. Involucre 4-7 mm. wide, 6-8 mm. high; involucral bracts lanceolate, borders entire, dorsal surface pubescent, border, midrib and tips often reddish; ligulate flowers white, ligule 3-6 mm. long, tube 3-4 mm. long; tubular flowers 4-5 mm. long; style with triangular tipped stigmatic branches, covered entirely by collecting hairs, pappus reddish-white to white; achenes pubescent, terete, 1-2 mm. long.

TYPE: *Weddell,* "Bolivie: punas, aux environs de La Paz" (not seen).

MATERIAL STUDIED: **Bolivia.** Prov. Larecaja, Combaya, *Mandon 224* (BM, GH, K). **Perú.** Puno, Pomata, *Shepard 22* (GH); La Raya, *Stafford 1001* (K); Cerro Caucapina, 4700 m. *Herzog 2356* (LP), *2359* (LP).

This rare little cushion plant has been collected only eight times, but it already has three names! It grows in the high Andean ranges around Lake Titicaca in Bolivia and Perú, at altitudes ranging from 3200 m. to over 4000 m.

Characteristics are the short rosulate leaves and the heads which look almost sunken into the branches. This last characteristic is not universal, a clearly visible pedicel being sometimes present.

20. **Erigeron lanceolatus** Wedd., Chloris Andina 1: 193. 1857 (Figs. 2, 6, 48-49)

Erigeron lanceolatus Wedd. var. *lorentzianus* Griseb., Plantae Lorentzianae: 123. 1874, based on *Lorentz 627* "Catamarca, in alpinis vayas altas pr. Belen alt. 9-11000'" (Isotype DARW!)

Erigeron lanceolatus Wedd. var. *subacaulis* Wedd., Chloris Andina 1: 193. 1857, based on *Weddell s.n.* "Bolivia, Cochabamba, Cordillère d'Ayopaya, 3800 m." (not seen).

Herbaceous perennial 5-25 cm. tall, rhizomatous. Root crown often woody, up to 3 cm. in diameter in old plants. Leaves numerous from a basal rosette, 1-10 cm. long, 1-10 mm. wide, lanceolate to linear-lanceolate, acute, margins entire or somewhat serrate, surface smooth, pubescent on both surfaces, trichomes uniseriate, multicellular, medium to very dense, petiole 2-10 mm. long, gradually merging into the lamina, pubescent, each scape with a few scale-like leaves, 1-15 mm. long, 1-3 mm. wide, acute, sessile. Heads borne singly at the end of scapes. Involucres 10-15 mm. wide, 6-10 mm. high; involucral bracts numerous in 1-2 not too well defined series, 4-8 mm. long, 1-2 mm. wide, dorsally pubescent, often with red tips and borders; ligulate flowers numerous in one outer series, white to white-rose, tube 3-4 mm. long, ligule 6-10 mm. long, 1-2 mm. wide; tubular flowers numerous, yellow, 4-6 mm.

FIGS. 48-49. *Erigeron lanceolatus.* 48. General aspect of a large plant × ½ (*Kalenborn 61*, GH). 49. General aspect of a small plant (*Cárdenas 3266*, GH). Figs. 50-51. *E. incertus*, general aspect × ½. 50. (*Sladen Fa 104 49*, BM). 51. (*Vallentin 2*, BM).

long; styles of tubular flowers with triangular tips covered externally by collecting hairs with two rows of stigmatic papillae on each side of the stylar branches; pappus yellowish; achenes terete, 1-3 mm. long, pubescent, brown-red.

TYPE LOCALITY: **Bolivia**, Cochabamba, *Weddell*, "Cordillère d'Ayopaya . . . a la hauteur de 3500 m." (not seen).

MATERIAL STUDIED: **Bolivia.** Cochabamba, Prov. Ayopava, Sailapata, *Cárdenas 3264* (US), *3266* (US), *3280* (US); Prov. Sacaba, Cerro San Benito, *Steinbach 5920* (DARW); Prov. Chapare, cerca de Aguirre, *Cárdenas 4331* (LIL); La Paz, Sorata, *Rusby 1661* (F, NY, LIL). **Argentina.** Tucumán, Chicligasta, Estancia Santa Rosa, *Venturi 9261* (US); Catamarca, sierra de Belen, *Lorentz 627* (DARW).

This rare species is easily distinguished by the very large white-rose rays, and the large heads borne singly at the end of a scape. There is quite a difference in size between specimens, which has led to the description of a variety *subacaulis* for the smaller forms. In view of the fact that in two collections both the large and dwarf forms were collected on the same spot, and, furthermore, considering that we are dealing with a plant of high altitude where microclimactic differences often have a tremendous effect on the vigor and development of the plant, I do not feel it warranted to recognize a sympatric variety based on size alone.

The species has been collected as far as I know only in six localities: three in Dept. Cochabamba and one in Dept. La Paz in Bolivia, and one each in the provinces of Tucumán and Catamarca in Argentina. Although there is a considerable gap between the Bolivian localities, the separation of 1000 km. between the Bolivian and Argentine localities is still more remarkable. One of the Argentine localities, sierra de Belen, is noted for the abundance of elements of northern and Bolivian distribution (A. Hunziker, personal communication). The general area where the plant grows is rather poorly collected, and if we remember that the plant is found in altitudes ranging between 3 and 1000 m., it is not too surprising that it has not been collected more often.

21. **Erigeron pratensis** Phil., Anal. Univ. Chile 87: 419. 1894 (Figs. 9, 52)

Aster gayanus DC., Prodr. 5: 227. 1836, based on Gay "in excelsis andibus chilensium" (not seen) [not *Erigeron Gayanus* Remy].

Aster alberti Phil. Anal. Univ. Chile 87: 406. 1894. Based on "Chile, Andibus prov. Colchagua et quidem in valle fluminis Tinguirrica, *F. Albert*" (SGO!)

Plants perennial, 20-60 cm. high, rhizomatous. Roots fibrous, strong.

Shoots several from the base (herbarium specimens often are formed by just one single shoot broken from the base!), somewhat woody beneath, herbaceous above, 1-3 mm. in diameter, pubescent, leafy throughout. Leaves much larger at the base, gradually becoming smaller towards the tips of the branches, often bract-like at the top. Leaves lanceolate, up to 10 cm. long and 1 cm. wide, margins slightly dentate, serrate or entire, usually with a line of tooth-like hairs along the border, surface smooth, pubescent or seldom almost glabrous; petiole well marked in the basal leaves, up to 4-5 cm. long, and 1-3 mm. wide; upper leaves sessile. Heads cymosely arranged in groups of 1-10 at the end of the branches, pedicels 5-50 mm. long, usually densely pubescent. Involucres 6-15 mm. wide and 5-15 mm. high; involucral bracts lanceolate, 3-7 mm. long, 1-3 mm. wide, acute, borders entire or finely toothed, dorsal side pubescent; ligulate flowers numerous, in one or two series, tube 3-7 mm. long, ligule 5-12 mm. long, up to 1.5 mm. wide; tubular flowers 3-5 mm. long; pappus white-yellowish, 3-4 mm. long; achenes terete, pubescent, often with two lines of hairs on each side.

TYPE: CHILE, *Philippi s.n.*, "In prato quodam montium Nahuelvuta in elevatione c. 1400 m." Holotype (SGO!), *Isotype* (LP!)

MATERIAL STUDIED: **Argentina.** Rio Negro. Cerro Tronador, *Maldonado 263* (LP), *Hicken 121* (DARW), *Scolnik 240* (LIL, LP), *Job 2432* (LP); Valle del rio Alerce, *Boelcke 2050* (LP), *Cabrera 5961* (LP); Cerro Belvedere, *Spegazzini 296* (LP); Cerro López, *Corte 208* (LP), *Guartino s.n.* (LIL); Cerro Catedral, *Cordini 247* (US); valle del arroyo Goye, *Hosseus 186* (CORD, LP); Neuquén. Cerro Colorado, *Diem 1125* (DARW), *53* (LP), *42* (LP). **Chile.** Curicó. El Planchón, *Barros 2114* (LP), Lomas Blancas, *Barros 2167* (LP); Colchagua. El flaco, *Barros 7426* (LP); Natales. Cerro Dorotea, *Barros 6125* (LP); Concepción, Volcan Villarica, *Hempel 7440* (LP); s. l., *Bridges 1164* (BM, K); *Gay s.n.* (GH).

An attractive plant found in the lake region of northern Patagonia both on the Chilean and Argentine side. It is related to the *Erigeron andicola* group, from which it is easily distinguishable by the large ligules.

22. **Erigeron incertus** (d'Urv.) Skottsberg, Sv. Vet.-akad. Handl. III, 50: 54. 1913

(Figs. 50-51)

Hieracium ? incertum d'Urv., Mém. Soc. Linn. Paris, 4: 608. 1826.

Erigeron sullivani Hook. f., Flora Antarctica **2**: 306. 1847, based on "Falkland Islands, moist cliffs near the sea, d'Urv. 54" (Holotype K!, Isotype BM!)

Small, caespitose, rhizomatous, perennial herb, 5-10 cm. high. Basal rosette of leaves tight, leaves obovate, 5-10 mm. wide, 15-30 mm. long, entire, densely pubescent, trichomes uniseriate and multicellular, particularly abundant on the margins and veins, margins entire, leaf apices blunt, petiole conspicuous, up to 5 mm. long, 1 mm. wide. Scapes one per plant, up to 10 cm. long, pubescent, leafy, cauline leaves linear,

FIG. 32. *Erigeron pratensis*, general aspect × $\frac{1}{2}$ (*Maldonado 263*, LP). Drawing by Ruth Hsu.

5-15 mm. long, 1-2 mm. wide, pubescent. Heads one per scape. Involucre campanulate, 10-15 mm. wide, 8-10 mm. high; involucral bracts numerous in 1-3 obscure series, 8-10 mm. long, 1-2 mm. wide, densely pubescent on the dorsal side, acute, red-purple in color; ligulate flowers rose-purple, numerous, tube 3-4 mm. long, ligule 5-6 mm. long, 0.5-1 mm. wide; tubular flowers numerous, yellow, 3-4 mm. long; pappus of yellowish bristles in one series; achenes flattened, highly pubescent.

TYPE: Falkland Islands "in litoralibus", *d'Urville* (not seen).

MATERIAL STUDIED: Falkland Islands, west Falklands, dry places, *Vallentin 3* (BM); *Sladen Fa 104/49* (BM).

This rare plant, endemic to the Falkland Islands, is undoubtedly closely related to the *E. andicola* complex and should possibly be included in it. Aside from distribution, it can be easily distinguished by the short and wide obovate leaves which have a clearly marked petiole, not present in any species of the *E. andicola* complex.

23. THE ERIGERON ANDICOLA COMPLEX

Along the Cordillera de los Andes from a latitude of about 30° S., corresponding to the cities of Serena and Coquimbo in Chile, and San Juan, in Argentina, down to the southernmost tip of Tierra del Fuego and adjacent areas, a complex of very closely related forms is found. They are characterized by a perennial habit, a basal rosette of leaves, a scape with one to six heads, these with one row of white-purple to purple short ligulate flowers, varying in height from not less than 5 cm. to a little over 35 cm. Thirty-seven species, based on such characters as pubescent *vs.* glabrous achenes, number of heads per scape, length of pedicels, presence and type of indument, shape of leaves, etc., have been described in this group. No attempt to date has been made to study the totality of the forms; Vierhapper's (1916) investigation of the material of the Swedish Antarctic Expedition is probably the nearest to a treatment of this group, but it is based on scant material; the same can be said of Macloskie's (1905) enumeration of the collections of the Princeton Expedition to Patagonia. Cabrera's (1939) treatment of *Erigeron* for the Compositae of the Nahuel Huapi National Park, is restricted to a very small area. Vierhapper considered in his treatment 7 species with 5 subspecies and 10 forms; Cabrera, basing his conclusions partly on Vierhapper's, recognized 5 species.

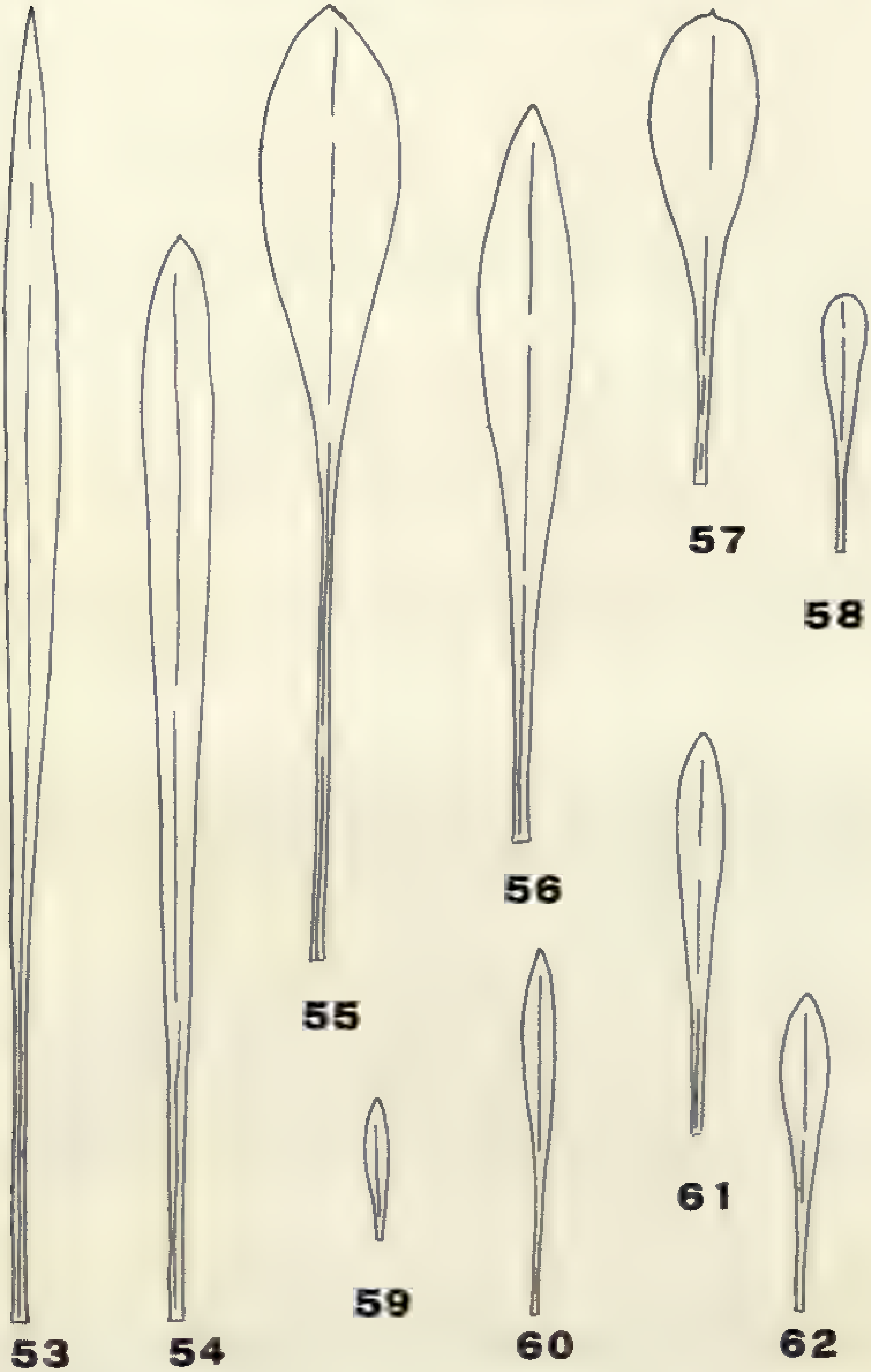
For the present study I have had at my disposal several hundred sheets encompassing the majority of the collected specimens. After studying these plants in detail for some time and trying to delimit the taxa in terms of the described species, it was evident to me that the plants are very variable, that most species had been based on one or, at the most, a few specimens, and, furthermore, that a large number were intermediate between the hitherto accepted taxa. Consequently I undertook a careful study of the variable characters in a manner that could lend itself to a quantitative analysis, since I felt it would be of great assistance. The results are summarized in Table 1 (fig. 63).

The characters investigated are the following: Size of plant, (tabulated in three categories: less than 10 cm., 10-25 cm., more than 25 cm.); number of heads per scape (1, 2-5, 6 or more); pubescence of the achene, involucre, stems and leaves (glabrous *vs.* pubescent). With these characters a total of 144 combinations can be formed, and of these 33 were found (Table 1). A total of 324 specimens were examined. Some correlations were found, mainly among pubescence *vs.* glabrousness of some organs, showing that all 14 characters investigated are not completely independent, but no constellation of tightly knit ones, as is expected of sexually reproducing species was found.

The most evident correlation is that of pubescence of leaves, scapes and involucre. No plant with a glabrous scape had pubescent involucre or leaves or both; only four plants of the total had all three structures glabrous; 27 plants had glabrous leaves and pubescent scapes and involucre; 2 had glabrous leaves and involucre and pubescent scapes; while 2 had a glabrous involucre and pubescent scapes and leaves; all other plants had all three structures pubescent.

A total of 182 plants had pubescent achenes, while 67 had glabrous ones, an almost perfect 3:1 distribution, which, in view of the fact that in other Compositae this character is determined by one gene, is suggestive of a similar situation here. No correlation could be found with other characters. Pubescence of the achene has been regarded as of primary importance in delimiting species in the past.

The larger the plant the greater the probability of having more than one head per scape. This "common sense" result could have been expected. The correlation is nevertheless far from absolute or linear (fig. 64). No correlation was found between number of heads per scape and the other



FIGS. 53-62. Variation in leaf shape in the *Erigeron andicola* complex. All drawings natural size. 53. *E. cinereus* (Chile, Andes antucenses, no coll., GH). 54. *E. myosotis* (*Eyerdam, Beetle & Grondona 24330*, GH). 55. *E. andicola* (*Malme 2918*, GH). 56. *E. cinereus* (*Buchtien 1370*, GH). 57. *E. andicola* (*Malme 2408*, GH). 58. *E. ciliaris* (*Furlong 135 d*, GH). 59. *E. leptopetalus* (*Morrison 16985*, GH). 60. *E. ciliaris* (*Eyerdam, Beetle & Grondona 24087*, GH). 61. *E. ciliaris* (*Eyerdam, Beetle & Grondona 23926*, GH). 62. *E. leptopetalus* (*Johnston 5911*, GH). In every case the drawing represents the largest basal leaf of the specimen.

characters investigated. The frequency of the classes was as follows: 110 plants had 1 head/scape, 122 had 2-5 and 17 had 6 or more. Although one head per scape is the most frequent single case (as opposed to 2, 3, etc. heads/scape), the probability is slightly more than 0.5 that a plant will have more than one head on a scape.

When plotted on a map (fig. 65), no definite correlation between the different types observed and geographical distribution can be found, except that the more southern plants tend to be larger in size. An interesting fact, is that the area occupied by this group is almost entirely within that covered by the Quaternary glaciations of Patagonia and the southern Andes (Auer, 1960).

No size group was represented more significantly than any other: 80 plants were less than 10 cm., 97 were 10-25 cm., and 72 more than 25 cm. tall. But if we consider that the first class has only a range of 5 cm. (no plant was less than 5 cm.) as opposed to intervals of 15 cm. for the other two classes, it can be safely said that there is a slight preponderance of plants between 5-10 cm.

In summary, it can be said as a result of this phase of the study that a large majority of the plants have pubescent leaves, scapes and involucres, although a few glabrous or almost glabrous plants were found; that plants with more than one head per scape are more frequent than those with only one, especially if they are more than 10 cm. tall; that about 2/5 of the plants are less than 10 cm. tall; that pubescence of the achene is a character completely independent from pubescence of the indumentum, size of plant or number of heads per scape, the plants with pubescent achenes being three times more frequent than those with glabrous achenes; that neither is a "constellation" of characters found, nor is there any special geographic distribution of any group of characters or of any single character, excepting size of plant, which tends to be larger the farther south the plants grow. Therefore the value of the characters investigated as "specific" or "key characters" in this complex is, at the most, doubtful, unless supporting evidence can be brought which shows them to be linked with other characteristics not investigated here.

In order to test this possibility other potentially important characters were investigated. Both style characters and

ERIGERON ANDICOLA COMPLEX			ACHENES												
			GLABROUS						PUBESCENT						
			INVOLUCRE						INVOLUCRE						
			GLABROUS			PUBESCENT			GLABROUS			PUBESCENT			
			HEIGHT			HEIGHT			HEIGHT			HEIGHT			
			-10	10-25	+25	-10	10-25	+25	-10	10-25	+25	-10	10-25	+25	TOTAL
LEAF GLABROUS	SCAPE GLABROUS	HEADS / SCAPE 1								1					1
		2-5			2						1		1		4
		6+											3		3
	SCAPE PUBESCENT	HEADS / SCAPE 1				1						5	3	1	10
		2-5						1		1	1	3	3	3	12
		6+										1	4	2	7
LEAF PUBESCENT	SCAPE GLABROUS	HEADS / SCAPE 1													0
		2-5													0
		6+													0
	SCAPE PUBESCENT	HEADS / SCAPE 1				15	16	3				40	19	6	99
		2-5				3	12	13			2	11	34	31	96
		6+					1							6	7
TOTAL			0	0	2	19	29	17	0	2	4	60	67	49	249

FIG. 63, TABLE 1. Analysis of six vegetative characters in the *Erigeron andicola* complex. Further explanations in the text.

anthers proved to be very uniform; length of ligules was variable within limits but not enough to distinguish size classes; habit was of some importance: some of the northern Chile plants were prostrate and somewhat cushion-like; the "andicola" type from Mendoza and Chile had usually glabrous achenes, many scapes per plant with usually one head each, although there were a number of exceptions; the Patagonia plants tended to be larger, with only one multiheaded scape, but all kinds of transitions towards smaller plants with only one head are present; leaf shape was investigated and a large array of types and shapes was found within the basic lanceolate pattern (figs. 53-62), but although no statistical analysis was made it was clear that again we were dealing with a highly variable and independent character, since no correlation with other characters was visible. Different types of trichomes can sometimes be discerned, but this is a concept hard to define and communicate when there are no anatomical differences (all trichomes are multicellular, one-layered, the differences being largely those of length and density). The investigation of the achenes was not of value since all plants have terete achenes of approximately the same size, but it led to the discovery that in some plants the achenes had not matured, but were shrunken and aborted, and that in some plants fully formed achenes are present at a very early stage of development. These two observations made the author suspect that a possible disturbance of fertility was present and led to an investigation of the pollen.

Anthers from unopened flowers were squashed under a coverslip in a drop of acetocarmine and/or a drop of cotton blue in lactophenol. Some pollen would stain very well, while pollen from other plants stained poorly or not at all, many degrees of intermediacy being observed. If staining is taken as a measure of the fertility of the pollen, it can be concluded that we have all degrees between complete fertility and almost complete sterility. It may be added that shrunken pollen, grains of very small or extremely large size, were common among non-staining grains. The situation is somewhat similar to that found by Beaman (1957) in *Townsendia*, another genus of Compositae-Astereae, where subsequent embryological work showed that nonstaining pollen was in effect sterile. Beaman also has unpublished data

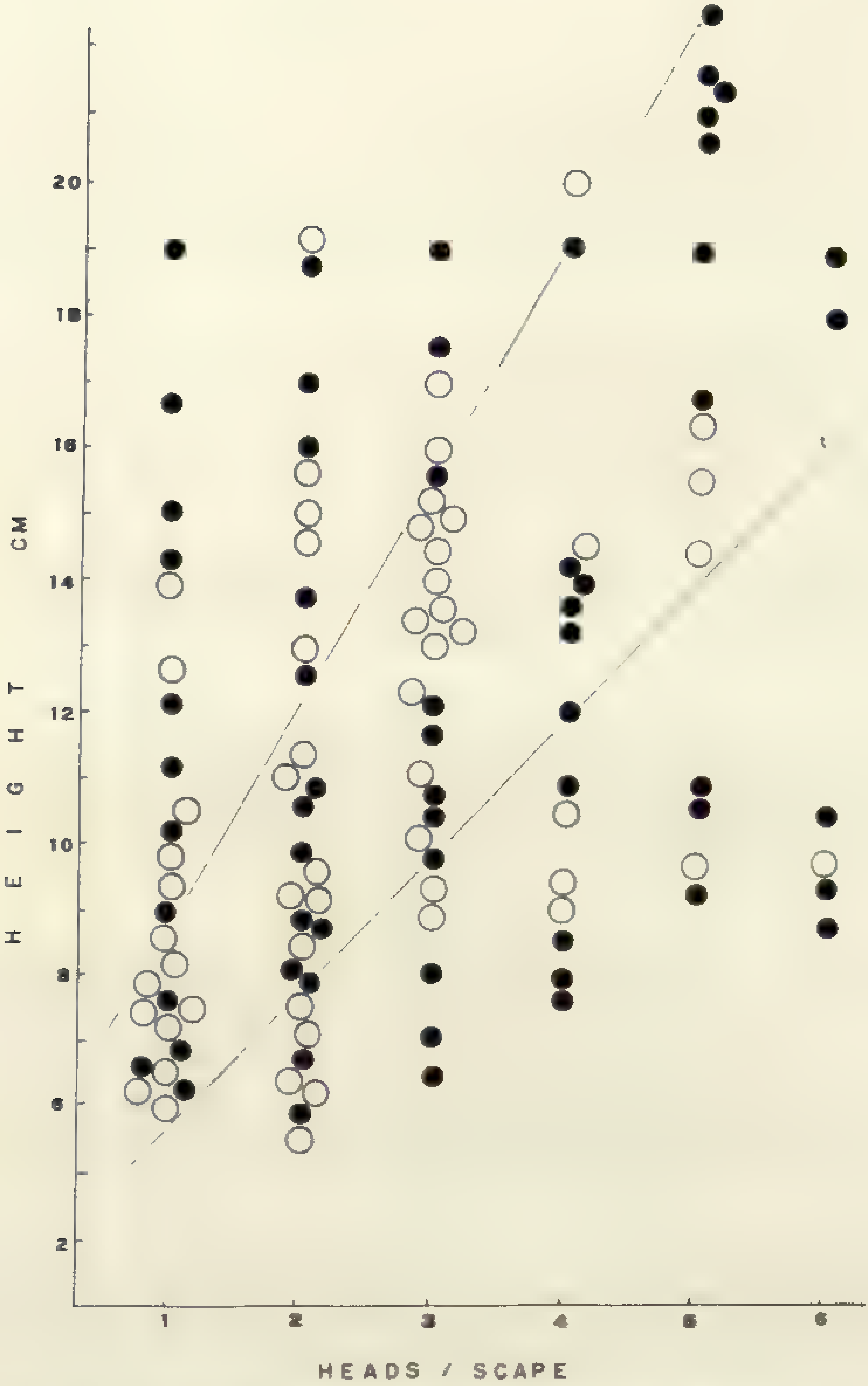


Fig. 64. Graph showing relation between number of heads per scape and height of plants in the *Erigeron andicola* complex. Open circles plants with glabrous achenes, black circles plants with pubescent achenes. There is no true correlation, although a tendency can be discovered for the taller plants to have more than one head per scape. Further explanation in the text.

showing a similar situation in the *Erigeron compositus* group of North America.

Although the evidence is very inconclusive and certainly solely circumstantial, the pattern of variation, the strange fertility pattern, and especially the pollen situation point to some kind of apomixis as a possible explanation. Since apomixis is not rare in *Erigeron*, this is not an unlikely possibility. But in order to confirm this, presently lacking cytological and embryological data are needed.

The detailed morphological analysis outlined above, unhappily did not solve the problem of the classification of this complex. With the type of variation present, a consistent classification based solely on morphological data would have to recognize a large number of taxa based solely on single characters, such as those already enumerated. Nevertheless, in view of the peculiar pollen situation, and especially of the present state of our knowledge of apomixis, hybridization, etc., I feel it might be more useful to postpone a final treatment and to present the following informal classification, rather than adding new names to a large list (of which I am not completely guiltless, see Solbrig 1953). It is hoped that it might be of some temporary use and especially that it might encourage a detailed study by somebody with more access than myself to living material.

The problem of classification in apomictic groups is very complex and will not be discussed here. The interested reader is referred to the discussions on the subject in Gustafsson's (1947) and Stebbins' (1950) works. It also should be kept in mind that, as stated above, there is so far no direct evidence of apomixis in this complex.

Three possible ways of classifying this group are: 1) To give formal recognition to each variant (involving a minimum of 33 taxa according to the morphological analysis stated above); 2) to "lump" all forms under one species; 3) to give formal recognition to the more commonly represented types and to a certain extent overlook the intermediate forms.

I have chosen the third of these approaches since evidently no classification of this group can be "natural" until the biological basis underlying the pattern of variability has been studied. I have recognized five major species within the complex, presenting a key and detailed description for each, followed by a critical list of closely related species which have been described.

KEY TO THE SPECIES OF E. ANDICOLA COMPLEX

A. Achenes glabrous.
  B. Plants 5-15 cm. tall, basal leaves lanceolate with clearly marked petiole, clearly demarcated from the cauline ones, which are small and bract-like. Scapes usually with only one head. .... 24. *E. andicola.*
  B. Plants 10-35 cm. tall, basal leaves few, not too well demarcated from the cauline ones. Scapes usually with more than one head. .... 25. *E. cinereus.*
A. Achenes pubescent.
  C. Plants pulvinate or nearly so, leaves narrow, pubescent, petiole not clearly demarcated. Scapes short with one head; plants from northern Chile and San Juan and Mendoza in Argentina. .... 26. *E. leptopetalus.*
  C. Plants small or large but not pulvinate, from Patagonia and southern Chile.
    D. Plants 5-15 cm. tall, white-hairy, usually with one head per scape. .... 27. *E. ciliaris.*
    D. Plants 10-35 cm. tall, usually pubescent, basal leaves few, not too well demarcated from the cauline ones. Scapes usually with more than one head. .... 28. *E. myosotis.*

24. **Erigeron andicola** DC., Prodr. 5: 287. 1836
(Fig. 66)

Caespitose perennial herb, 5-15 cm. high. Root woody, deep, robust. Root crown thickened, with a series of short, partly subterranean shoots. Rosette of leaves tight, leaves lanceolate, 6-8 cm. long, 7 mm. wide, acute, margins entire, surface smooth, pubescent, petiole 3-4 cm. long, gradually expanding into the lamina, pubescent to ciliate, bases of decayed leaves remaining attached to the rosette and protecting the younger ones. Floral scapes several, monocephalous, up to 15 cm. long, slightly grooved, pubescent and with a few leaves, these small, linear or lanceolate, acute, 1.5-2 cm. long, 1-2 mm. wide, sessile, margins entire, pubescent. Capitula 1.3-1.6 cm. wide and 0.8-1.2 cm. high; involucral bracts linear, in two or three series, pubescent on the dorsal surface, 0.4-0.8 mm. long; ligulate flowers purple-white, 1.2-1.5 cm. long; ligule 9 mm. long and 0.4 mm. wide; tubular flowers yellow, 7-8 mm. high; achenes glabrous, with two ribs, 4 mm. long.

TYPE: "in excelsis Andibus chilensium" *(Gay)* (G!)

DISTRIBUTION: Along the Cordillera from Patagonia to central Argentina and Chile, but most frequent in Mendoza (Argentina) and the area of Santiago in Chile.

SELECTED SPECIMENS: **Argentina.** Mendoza. Mala Dormida, *Carette 401* (DARW); Puente del Inca, *Malme 2954* (F), *2837a* (US), *2908* (GH,

FIG. 65. Distribution of the species of the *Erigeron andicola* complex and of *E. incertus*. Dark line shows eastern limit of glaciation, according to Auer, 1960.

MO), *King 704* (BM, LP); Las Cuevas, *Malme 2918* (GH), *King 163* (LP); San Carlos, Real de los 13, 2250 m.s.m., *Ruiz Leal 7150* (LIL); Laguna del Diamante, *Ruiz Leal 11738* (LP), *Hueck s.n.* (DARW). **Chile.** Braden Copper Mines, above Rancagua, *Holway & Holway s.n.* (GH); Rio Blanco, *Schwabe 2134* (LP); Talca, El Picazo, Alto de la Laguna, *Barros 614* (LP).

RELATED FORMS

E. cinereus β Hook. & Arn., Comp. Bot. Mag. **2**: 50. 1836, based on "San Pedro Nolasco, Andes of Chile, *Dr. Gillies*" (K!). A pubescent form with shorter leaves and only one scape per plant, although it should be remarked that the specimens are only scraps.

E. andinus Phil., Linnaea **28**: 722. 1858, based on "in Andibus prov. *Santiago* occurrit" (not seen). This form has smaller and narrower leaves, the plants are smaller and have a different hairiness on the involucral bracts than typical *E. andicola* DC.

FIG. 66. *Erigeron andicola*, natural size (*Malme 2908*, GH).

E. biflorus Phil., Anal. Univ. Chile **43**: 488. 1873, based on "*Volkmann* Lupulhue" (SGO!). Intermediate between *E. andicola* and *E. cinereus*.

E. araucanus Phil., Anal. Univ. Chile **87**: 412. 1894, based on "in Andibus Araucania, Trapatrapa, *Rahmer*, Feb. 1887" (SGO!). This species has narrower leaves than typical *E. andicola* and is also somewhat more glabrous.

E. orithales Phil., Anal. Univ. Chile **87**: 412. 1894, based on "*Philippi s.n.* Cordillera de Santiago, Martio 1883" (SGO!). A more glabrous form than *E. andicola.*

E. illapelinus Phil., Anal. Univ. Chile **87**: 411. 1894, based on "Cordillera de Illapel, La Polcura, Jan. 1888, *Philippi*" (SGO!). An interesting form, very similar to *E. andicola* in aspect but with pubescent achenes.

E. leiolepis Solbrig, Bol. Soc. Argent. Bot. **6**: 25. 1955, based on "Mendoza, Laguna del Diamante, *Boelcke 4118*, 3-II-1950" (BAB!). Characterized by being completely glabrous.

E. schnackii Solbrig, Bol. Soc. Argent. Bot. **6**: 26. 1955, based on "Neuquen, Termas de Copahue, *Cabrera 6160*, 17-II-1940" (LP!). Characterized by the obovate leaves and the dense pubescence.

25. **Erigeron cinereus** Hook. & Arn., Comp. Bot. Mag. 2: 50. 1836

(Figs. 68-69)

Perennial, caespitose plant, 25-35 cm. high, with a strong central root, somewhat rhizomatous. Basal leaves up to 10 cm. long in a loose rosette, oblong-spathulate to lanceolate, acute, margins and surface pubescent; petiole elongate, gradually broadening towards the lamina; cauline leaves lanceolate, sessile, entire, pubescent; the lower cauline leaves intermediate with the basal ones and no sharp demarcation possible. Floral scapes usually brown-green, pubescent, especially towards the top; heads borne in loose panicles of 2-6 heads per scape. Involucres about 1 cm. wide and 1.5 cm. high; involucral bracts in 1-3 series, 5-10 mm. long, 2-4 mm. wide, very pubescent dorsally; ligulate flowers white to pink, about 6 mm. long; tubular flowers 2-4 mm. long; achenes terete, glabrous.

TYPE: **Argentina,** "Los Palomares, Andes of Mendoza, *Gillies*" (K!)

DISTRIBUTION: Along the Cordillera from Patagonia to central Chile and Argentina.

SELECTED SPECIMENS: **Argentina.** Santa Cruz, Lago Argentino, *Prichard s.n.* (BM); Est. Cerro Fitzroy, *Sleumer 1266* (LP, LIL); Lago Viedma, *Witte 4* (DARW); Chubut, rio Corcovado, *Illin 161* (DARW); Rio Negro, cerro Utne, *Hosseus 494* (CORD); Bariloche, Cerro Otto, *Teague s.n.* (LIL); Cerro Gutierrez, *Buchtien 1320* (DARW, GH). **Chile.** Cordillera de Ñuble, Termas de Chillán, *Jaffuel 2726* (GH), *3810* (GH), *Delter 2103* (GH), cerro Pirigallo, 2400 m.s.m., *Cabrera 3657* (LP).

RELATED FORMS

E. poeppigii DC., Prodr. 5: 287. 1836, based on Chile, "Antuco, *Poeppig 21*" (Isotype BM!). Slightly larger than the type of *E. cinereus*, but essentially like it (*E. cinereus* has priority by less than a month!).

E. pulchrum Phil., Anal. Univ. Chile **43**: 487. 1873, based on "*Philip-*

pi, Valle del Iso, Jan. 1866" (SGO!). The achenes are possibly glabrous, although it is hard to say since they are immature. This species is characterized by the relatively large ligules and the two heads borne on large peduncles.

E. williamsi Phil., Anal. Univ. Chile 87: 413. 1894, based on "Cordillera de Talca, Feb. 1879, *Philippi s.n.*" (SGO!). No appreciable difference from *E. cinereus*.

E. dusenii Vierh., Bot. Not. for 1916: 242. 1916, based on "*Dusen 5659* Sta. Cruz, Lago Argentino, in der Steppe, 23-I-1905" (not seen). Characterized by the sparse indumentum with subrigid trichomes.

E. platylepis Vierh., Bot. Not. for 1916: 250. 1916, based on "Punta Arenas, Feb. 1896, *Dusen 68*" (not seen). Differs by the somewhat wider involucral bracts and the oblong, spathulate leaves.

E. imbricatus Vierh., Bot. Not. for 1916: 250. 1916, based on "Patagonia, Barranca Blanca, 3-I-1905, *Dusen 5517*" (not seen). Very close to *E. platylepis* Vierh., from which it differs by its smaller size and one-headed scapes.

26. **Erigeron leptopetalus** Phil., Linnaea 33: 136. 1864 (Fig. 67)

Perennial, caespitose herb, not more than 8 cm. tall. Basal leaves tightly appressed, leaves lanceolate, 0.5-2 cm. long, 1-3 mm. wide, surface and margins smooth, short and densely pubescent on both sides; petiole hardly distinguishable from the lamina. Floral scapes leafy, especially in their lower part, varying in length from a couple of cm. to 6-7 cm. in the more vigorous specimens, finely and densely pubescent. Heads borne singly at the end of the scapes. Involucre about 1 cm. wide and 1 cm. high; involucral bracts 4 mm. long and 1-2 mm. wide, arranged in two not too well-defined series, densely pubescent on their dorsal surfaces; ligulate flowers few, 5 mm. long; tubular flowers about 3.5 mm. long; achenes hairy, the pubescence varying from very little to abundant.

A characteristic of this species is the pulvinate type of growth and the heads at the end of scapes which in some specimens protrude several cm. and in others seem to be buried in the cushion.

TYPE: **Chile.** "Concepción, induliginosis andinum Sierra Velluda, Feb. 1839, *Germain*" (SGO!)

DISTRIBUTION: Found most commonly in the mountains north of Santiago in Chile, but also further south and in Argentina.

SELECTED SPECIMENS: **Chile.** Atacama, vicinity of Laguna Chica, *Johnston 5960* (GH, K, US); Vallenar, rio Laguna Grande, *Werdermann 240* (BM, DARW, F, GH, K, LP, MO); Coquimbo, La Vega Redonda, *Morrison 16984* (GH, K); east side of pass north of Cerro La Yerba Loca, *Morrison 16985* (GH). **Argentina.** San Juan, Quebrada Ortiga, *Johnston 6184* (F, GH, K, US).

RELATED FORMS

E. nubigenus Phil., Anal. Univ. Chile 87: 423. 1894, based on "Chile, laguna negra, inter 2700-4000 m., Martio 1873, *F. Vidal G.*" (SGO!). Somewhat intermediate between *E. leptopetalus* and *E. ciliaris*.

Figs. 67-69. 67. *Erigeron leptopetalus*, general aspect × ½ (*Johnston 5960*, GH). Figs. 68-69. *E. cinereus*. 68. General aspect × ½. 69. Detail of involucre × 4 (*Burkart 6409*, LP).

E. brevicaulis Phil., Anal. Univ. Chile **87**: 414. 1894, based on "Chile, Polcura, Andes de Illapel, estate 1888, *Herb. Philippi*" (SGO!). No appreciable difference from *E. leptopetalus.*

27. **Erigeron ciliaris** Phil., Linnaea 28: 722. 1858

Caespitose, perennial, rhizomatous herb, 5-15 cm. tall. Basal rosette of leaves present in varying density, from very dense (almost pulvinate) to rather loose. Leaves linear-lanceolate, 2-6 cm. long, 1-3 mm. wide, entire, glabrous or more often pubescent, petiole not distinct, expanding very gradually into the lamina; cauline leaves, when present, sessile and shorter; scapes one or many per plant, usually monocephalous but sometimes with up to 3 heads, pubescent. Capitula 6-8 mm. wide, 4-6 mm. high; involucral bracts linear-lanceolate, 4-5 mm. long, pubescent; ligulate flowers white-blue to pink, in one series, 4-6 mm. long, ligules 1-2 mm. long; tubular flowers numerous, 3-4 mm. long; achenes terete, pubescent, 1-2 mm. long.

TYPE: **Chile.** "Cordillera Linares, Enero 56, *P. Germain s.n.*" (Holotype SGO!, Isotypes BM?!, LP!)

DISTRIBUTION: Found in Patagonia, both on the Argentina and Chilean sides, south to Tierra del Fuego.

SELECTED SPECIMENS: **Argentina.** Santa Cruz. Isla Pavón, rio Santa Cruz, *Spegazzini 17219* (LPS, US); Lago Argentino, *Ameghino s.n.* (LPS); 40 km. north of Guer-Aiken, *Grondona 2063* (LP); lago Viedma, *Witte 30* (DARW); Rio Gallegos, estancia Stag River, *Tweedie 324* (K); Rio Gallegos, *Sleumer 781* (LIL, US); Cerro Friale, *James 425* (BM). Tierra del Fuego, *Reynolds s.n.* (BM).

RELATED FORMS

E. myosotis Remy ex Gay, Hist. Fis. Pol. Chile Bot. **4**: 25. 1849. Nomen nudum, later homonym.

E. coxi Phil., Linnaea **33**: 134. 1864; E. philippi Sch. Bip. ex Wedd. var. *coxi* (Phil.) Hosseus, Trab. Inst. Bot. Farmac. **33**: 83. 1915, based on "*Cox*, Volcan, pampa, probabile ex Andibus" Chile (SGO!). Characterized by the leaves "spathulato-linearibus".

E. cochlearifolius Phil., Anal. Univ. Chile **87**: 414. 1894, based on Chile "Andibus prov. Curicó, Baños, *Vidal G.*" (photo LP!). No appreciable difference from *E. ciliaris.*

E. patagonicus Phil., Anal. Univ. Chile **87**: 414. 1894, based on Chile "Punta Arenas, *Ibar s.n.*" (Isotype LP!). Distinguished by the wider leaves.

E. erianthus Spegazzini, Flora Patagonia Australis: 530. 1897. based on "Santa Cruz," no coll. (LPS!). A small, pulvinate form of *E. ciliaris.*

E. cabrerae Solbrig, Bol. Soc. Argent. Bot. **6**: 21. 1955, based on Argentina "Neuquen, Termas de Copahue, *Cabrera 6271*, 20-II-1940" (LP!). Very similar to *E. ciliaris* but larger and with stiffer leaves.

28. **Erigeron myosotis** Pers., Synop. Plant. 2: 431. 1807

Caespitose, perennial herb, up to 30 cm. tall. Root fasciculate, rhizomatous. Shoots one to several from the base, herbaceous, 1-3 mm.

in diameter, green-brown to reddish, striate, pubescent. Basal rosette of leaves when present not very prominent, leaves lanceolate, acute, entire, 3-10 cm. long, 1-6 mm. wide, usually pubescent on both sides, hairs often long, especially on the margins and petiole; lower leaves petiolate, cauline ones sessile. Heads one to several per scape; involucre 10-15 mm. wide, 8-10 mm. high in well developed capitula, sometimes small heads about half the size of the well developed ones are present; involucral bracts in two loose series, lanceolate, acute, 4-6 mm. long, pubescent; ligulate flowers numerous in one series, white-purple, 5-6 mm. long, ligule 2-3 mm. long; tubular flowers yellow, numerous, 4-5 mm. long; achenes, 1-3 mm. long, pubescent.

TYPE: "Hab. ad fretum magellanicum" (not seen).

DISTRIBUTION: Frequent in Patagonia and Tierra del Fuego, on both the Argentine and Chilean sides.

SELECTED SPECIMENS: **Argentina.** Neuquén. Isla Victoria, *Corte 152* (LP); Rio Negro. Cerro Otto, *Cabrera & Job 88* (LP, US); Paso de las Nubes, Valle del Alerce, *Cabrera 5960* (LP); Santa Cruz. Mesetas Altas, *Donat 202* (F, K); north bank of Lago Rico, *Eyerdam, Beetle & Grondona 24330* (DARW, GH, K); Tierra del Fuego. Ushuaia, *Alboff 571* (LP); 80 km. inland from Rio Grande, *Mexia 7921* (BM, F). **Chile.** Aisen. Region del Lago Buenos Aires: Valle Leon, *Rentzell 6238* (DARW, LP); Valle Coihaique, *Rentzell 6192* (DARW, LP, MO); Magallanes. Last Hope Inlet, *Mexia 7995* (MO); 50 km. southwest of Puerto Natales, *Eyerdam, Beetle & Grondona 24185* (DARW, F, GH, MO); 15 km. south of Punta Arenas, *Eyerdam, Beetle & Grondona 24119* (DARW, GH, MO).

RELATED FORMS

E. gayanus Remy ex Gay, Hist. Fis. y Pol. Chile Bot. **4**: 25. 1849, based on "*Gay*, Chile, Cordilleras centrales" (Photo type? GH!). Characterized by the inflorescence with six heads.

E. philippii Sch. Bip. ex Weddell, Chloris Andina **1**: 192. 1855, based on "Chile, sur le monte Pise [?], *Phillippi 51*" (Isotype LP!). Characterized by the larger size and monocephalous scapes.

E. remyanus Wedd., Chloris Andina 1: 195. 1857; *Guzmania chilensis* Remy ex Gay, Hist. Fis. Pol. Chile Bot. **4**: 13. 1849, based on "Chile, volcan Talcaregue, *Gay*" (not seen). According to the description the plants are large and with one or two heads.

E. polyphyllum Phil., Linnaea **33**: 135. 1864, based on "*Gay 754*, in uliginosis andium Antuco, Januario 1839" (Holotype SGO!, Isotype LP!). Possibly based on an isotype of *E. gayanus* Remy, with which it corresponds.

E. lacarensis Phil., Anal. Univ. Chile **87**: 424. 1894, based on "Andes San Ignacio de Pemehue, *Germain 1894*" (SGO!). It corresponds very closely with *E. myosotis*.

E. fernandezii Phil., Anal. Univ. Chile **87**: 418. 1894, based on *Otto Philippi* "Cordillera de Valdivia. Maipú, Febr. 1887" (SGO!). A very large (30 cm.) and pubescent plant.

E. angustifolius Phil., Anal. Univ. Chile **87**: 418. 1894, based on "in Araucania, Trapatrapa, *Rahmer* Jan. 1881" (not seen). Distinguished by its narrow leaves and large size (33 cm.).

E. ibari Phil., Anal. Univ. Chile **87**: 413. 1894, based on "aguas de Skyring, *Philippi*, Feb. 1879" (SGO!). No appreciable difference from typical *E. myosotis*.

EXCLUDED SPECIES[1]

Erigeron affinis Badillo, Bol. Soc. Venez. Ci. Nat. **10**: 308. 1946 (Venezuela) = **Oritrophium venezuelensis** (Steyermark) Cuatrecasas, Ciencia [Mexico] **21**: 26. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. australis Phil. Anal. Univ. Chile **43**: 488. 1873 (Chile), not *E. australis* Hornem. ex Spreng. Syst. **3**: 517. 1826. Later homonym. (The type of *E. australis* Phil. "*Mons Yate, 1871, Juliet*" (SGO!) = *Aster* **aff.** *vahlii* **(Gaud.) Hook. et Arn.).**

E. bilboanus (Remy) Cabrera, Revista Mus. La Plata Bot. **2**: 254. 1939 – **Conyza bilboana** Remy, ex Gay, Hist. Fis. y Pol. Chile, Bot. **4**: 75. 1849. Clearly a member of section Caenotus (see Cronquist, 1943, 1947).

E. blakei Cabrera, Revista Mus. La Plata Bot. **4**: 90. 1941 (Uruguay and Argentina) – **Conyza blakei** (Cabr.) Cabrera, Fl. Alred. Buenos Aires: 481. 1953.

E. blepharophyllus Blake Jour. Wash. Acad. **14**: 453. 1924 (Venezuela) = **Oritrophium blepharophyllum** (Blake) Cuatrecasas, Ciencia [Mexico] **21**: 25. 1961.

E. bonariensis L. Sp. Pl. 2: 863. 1753 – **Conyza bonariensis** (L.) Cronquist, Bull. Torrey Club **70**: 632. 1943.

E. cardaminaefolius (HBK) Wedd., Chloris Andina **1**: 198. 1857 (Ecuador) – **Conyza cardaminaefolius** HBK., Nov. Gen. et Sp. Pl. **4**: 71 1820. According to the description, it should be placed in section Caenotus.

E. chilensis (Spreng.) D. Don, ex Loudon, Hort. Brit.: 343. 1830 (Chile, Argentina, Brazil, etc.) – **Conyza chilensis** Spreng., Novi Proventus: 14. 1819. Clearly a member of section Caenotus.

E. chionophilum Wedd., Chloris Andina **1**: 191. 1857 (Colombia, Perú) – *Celmisia sp.* It is clear through Weddell's description that we are dealing with a species of section Oritrophium of *Celmisia* (Solbrig, 1960).

E. cinerascens Sch. Bip. ex Wedd., Chloris Andina **1**: 196. 1857; Sch. Bip Bonplandia **4**: 54. 1856 (Argentina, Perú) – **Conyza punensis** Cabrera, Revista Invest. Agr. Buenos Aires **11**: 403. 1958.

E. cocuyensis Cuatrecasas, Revista Acad. Colomb. **9**: 241. 1954 (Colombia) – **Oritrophium cocuyense** Cuatrecasas, Ciencia [México] **21**: 25. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. consanguineus (Phil.) Cabrera, Revista Chil. Hist. Nat. **40**: 227. 1937 (Chile) – **Conyza consanguinea** Phil., Linnaea **33**: 142. 1864.

E. colinensis Phil., Anal. Univ. Chile **87**: 420. 1894 (Chile) – *Conyza sp.* based on "*Phil. s.n., Colina, Dec. 1889* (SGO!)"

---

[1] This is not an exhaustive list of all *Erigeron* names used for South American plants. Only those used most frequently are included.

E. cordatus (O. Ktze.) Cabrera, Notas Mus. La Plata Bot. **2**: 177. 1937 = **Conyza cordata** O. Ktze., Rev. Gen. Plant. **3**: 142. 1898.

E. crocifolius (HBK) Wedd., Chloris Andina **1**: 191. 1857 (Perú) — **Celmisia crocifolia** (HBK) Sch. Bip., Bonplandia **4**: 50. 1856.

E. dianthifolius Gris., Abhandl. Königl. Gesell. Wissens. Göttingen 24: 174. 1879 (Argentina) — **Hysterionica dianthifolia** (Gris.) Cabrera, Notas Mus. La Plata Bot. **11**: 352. 1946.

E. domesticum Larrañaga, Escritos D. A. Larrañaga **2**: 254. 1923 (Uruguay) = nomen nudum.

E. depile Phil., Anal. Univ. Chile **87**: 417. 1894 (Chile) = *Aster sp.*, based on "*Chile, Mansel, Martio 1888,* SGO!"

E. ferrugineus Wedd., Chl. And. **1**: 195. 1857 (Bolivia) = **Oritrophium ferrugineum** (Wedd.) Cuatrecasas, Ciencia [Mexico] **21**: 26. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. flagellifolius Cabrera, Revista Chil. Hist. Nat. **40**: 229. 1937 (Chile) = *Conyza sp.*

E. frigidum Wedd., Chloris Andina **1**: 231. 1857 (Bolivia) — *Celmisia sp.* most possibly according to the description.

E. frutescens Phil., Linnaea 33: 134. 1864 (Chile) = *Aster sp.*, based on "*Volkmann 1858, Prov. Colchagua, in litoralibus,* SGO!"

E. gardneri Cabrera, Notas Mus. La Plata Bot. **2**: 177. 1937 (Argentina) = **Conyza rivularis** Gardn., Jour. Bot. Lond. **4**: 124. 1845.

E. glabrifolius DC., Prodr. **5**: 287. 1836 (Chile) = **Aster vahlii** (Gaud.) Hook. et Arn., Comp. Bot. Mag. 2: 49. 1836.

E. glaucifolium O. Ktze. Rev. Gen. Pl. **3**: 145. 1898 (Argentina) = **Hysterionica glaucifolia** (O. Ktze.) Solbrig, Bol. Soc. Argent. Bot. **6**: 29. 1955.

E. glaucum Ker, Bot. Reg. **1**: t. 10. 1824. Probably a North American species; the figure in Bot. Reg. doesn't correspond to any of the South American species known to me.

E. graminifolius Phil., Linnaea **28**: 723. 1858 (Chile) — **Aster vahlii** (Gaud.) Hook. et Arn., Comp. Bot. Mag. 2: 49. 1836, based on "*Philippi s.n., ad flumen Coiguero in prov. Valdivia, Febr. 1852,* SGO!"

E. hieracioides Wedd., Chloris Andina 1: 194. 1857 (Perú) = **Celmisia hieracioides** (Wedd.) Solbrig, Contr. Gray Herb. 188: 85. 1960.

E. hieracifolium Poir., in Lamarck, Encycl. Meth. 8: 491. 1808 (Argentina) = **Podocoma hieracifolia** (Poir.) Cassini, Dict. Scien. Nat. **42**: 60. 1826.

E. hirtellus DC., Prodr. **5**: 290. 1836 (Chile) = *Conyza.* According to the original description "*ligulis disco non superanti*".

E. hirtopilosus Hieron., Bot. Jahrb. **21**: 336. 1895 (Perú) = *Celmisia.*

E. hybridus Hieron., Bot. Jahrb. **21**: 334. 1895 (Colombia) = **Oritrophium peruvianum** (Lam.) Cuatrecasas, Ciencia [México] **21**: 22. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. involucratus Link ex Sweet, Hort. Brit. ed. 2: 294. 1830 = nomen nudum.

E. landbecki Phil., Linnaea **33**: 133. 1864 (Chile) = *Aster sp.*, based on "*Philippi s.n. Llico, Dec. 1861,* SGO!"

E. larrainianus (Remy) Cabrera, Revista Chil. Hist. Nat. **40**: 230.

1937 (Chile) = **Conyza larrainiana** Remy, ex Gay, Hist. Fis. y Pol. de Chile, Bot. 4: 71. 1849.

E. lehmannii Hier., Bot. Jahrb. **19:** 49. 1894 (Ecuador) = **Oritrophium peruvianum** (Lam.) Cuatrecasas, Ciencia [México] **21:** 22. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. limnophilum Sch. Bip., Bull. Soc. Bot. Fr. **12:** 81. 1865 (Bolivia) = **Oritrophium limnophilum** (Sch. Bip.) Cuatrecasas, Ciencia [México] **21:** 27. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. lorentzii (Gris.) Cabrera, Notas Mus. La Plata Bot. **2:** 177. 1937 (Argentina) = **Conyza lorentzii** Grisebach, Symbolae: 176. 1879.

E. loxensis Hier., Bot. Jahrb. **21:** 335. 1895 (Colombia) = **Oritrophium peruvianum** (Lam.) Cuatrecasas, Ciencia [México] **21:** 22. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. mendocinum E. L. Greene, Erythea **2:** 106. 1894 (Argentina) = **Hysterionica jasionoides** Willd., Mag. Ges. Nat. Fr. Berlin **1:** 140. 1807 (see Cabrera, A. L., Revista Mus. La Plata Bot. **4:** 62. 1941; also Notas Mus. La Plata Bot. **11:** 357. 1946).

E. microcephalum Sch. Bip., Linnaea **34:** 534. 1865-66 = Nomen nudum.

E. mölleri Phil., Anal. Univ. Chile **87:** 419. 1894 (Chile) = *Conyza sp.* I have only seen a picture of the type (no typical material is in Santiago).

E. monorchis Gris. Symbolae: 175. 1879 (Argentina) = **Conyza monorchis** (Gris.) Cabrera, Fl. Alred. Buenos Aires: 480. 1953.

E. montevidensis Spreng., Syst. **3:** 519. 1826 (Uruguay). According to Index Kewensis this plant = *Hysterionica montevidensis* Baker, ex Martius, Fl. Brasil. **6**(3): 13. 1882 (*Hysterionica villosa* (Hook. et Arn.) Cabrera), but according to Cabrera, Notas Mus. La Plata Bot. **11:** 351. 1946, the two plants are not the same. It most likely is *Conyza*, but this is not clear from the description. No true *Erigeron* is known from Uruguay.

E. montevidensis Baker, ex Martius, Fl. Bras. **6**(3): 30. 1882 (Uruguay) = **Conyza blakei** (Cabr.) Cabrera, Fl. Alred. Buenos Aires: 481. 1953 (see also Cabrera, Revista Mus. La Plata Bot. **4:** 90. 1941).

E. nevadense Wedd., Chl. And. **1:** 194. 1857 (Venezuela) = **Oritrophium nevadense** (Wedd.) Cuatrecasas, Ciencia [México] **21:** 25. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. pampeanus Parodi, Rev. Fac. Agr. Vet. Buenos Aires **7:** 252. 1930 (Argentina) **Conyza pampeana** (Parodi) Cabrera, Fl. Alred. Buenos Aires: 481. 1953.

E. papposanum Phil., Fl. Atacama: 29. 1860 (Chile) = *Conyza.* Based on "*Philippi s.n., Paposo,* SGO!"

E. paramensis Aristeguieta et Cuatrecasas, Bol. Soc. Venez. Ci. Nat. **22:** 5. 1961 (Venezuela) *Celmisia sp.* I have seen material of this species annotated by Aristeguieta which is clearly *Celmisia*, and the authors mention also in their description "close to *E. chionophilum* Wedd." which is a *Celmisia*.

E. pellitum (HBK.) Wedd., Chloris Andina **1:** 190. 1857 (Venezuela)

= **Oritrophium peruvianum** (Lam.) Cuatrecasas, Ciencia [México] **21:** 22. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. peruvianus (Lam.) Cabrera, Bol. Soc. Argent. Bot. **7:** 234. 1959 (Perú) = **Oritrophium peruvianum** (Lam.) Cuatrecasas, Ciencia [México] 21: 22. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. pinnatus Turcz., Bull. Mosk. Obshch. Isp. Pri. Biol. **24:** 173. 1851, non Linne. Later homonym. A *Conyza* (section Caenotus) most probably.

E. platense Spegazzini, Contrib. Flora Sierra Ventana: **33:** 1896 (Argentina) = *Conyza.* Evidently a member of section Caenotus, see Cabrera, Revista Mus. La Plata Bot. **4:** 81. 1941.

E. popayensis Hier., Bot. Jahrb. **28:** 586. 1901 (Colombia) = *Conyza.* Belongs to "sect. Caenotus . . . [*Conyza*] *bonariensis* affinis".

E. primulaefolium Juss. ex Cass., Dict. Sc. Nat. **42:** 61. 1826 = **Podocoma hieracifolia** (Poir.) Cass., Dict. Sc. Nat. **42:** 60. 1826 (see Cabrera, Revista Mus. La Plata Bot. **4:** 96. 1941).

E. pugae Phil., Anal. Univ. Chile **87:** 416. 1894 (Chile) = **Aster vahlii** var. **tenuifolius** (Phil.) Cabrera, Revista Mus. La Plata, Bot. **2:** 256. 1938. Based on "*Fred Pugae, Ad flumen Diguillin, Martio 1876,* SGO!"

E. repens (HBK.) Wedd., Chloris Andina **1:** 191. 1857 (Perú) = **Celmisia repens** (HBK) Sch. Bip., Bonplandia **4:** 50. 1856 (see Solbrig, 1960).

E. scorzoneraefolium Remy, ex Gay, Hist. Fis. y Pol. de Chile, Bot. **4:** 27. 1849 (Chile) = **Aster vahlii** (Gaud.) Hook. et Arn., Comp. Bot. Mag. 2: 49. 1836, based on "*Gay 270, Prov. Colchagua, Talcaregue, in herbidis uliginosis cerca nivem perpetuam, Febr. 1831,* SGO!"

E. senecioides Wedd., Chloris Andina **1:** 196. 1857 (Perú) = **Conyza senecioides** (Wedd.) Cabrera, Revista Invest. Agr. Buenos Aires **11:** 403. 1957.

E. sodiroi Hier., Bot. Jahrb. **29:** 20. 1900 (Ecuador) = **Oritrophium limnophilum** (Sch. Bip) Cuatrecasas, Ciencia [México] **21:** 27. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. sordidus Gill. ex H. & A., Comp. Bot. Mag. **2:** 254. 1836 = **Conyza bonariensis** (L.) Cronquist, Bull. Torrey Club **70:** 632. 1943.

E. spiciformis Gris., Plantae Lorentzianae: 171. 1874 (Argentina) = *Conyza sp.*, based on "*Lorentz 133, Tucumán: aus der Vegetation der Alpenweiden bei der Ciénaga, 25 31 III-1872,* Isotype CORD!"

E. spiculosus Hook. & Arn., Bot. Beech. Voy. **1:** 32. 1841 (Chile) — probably *Aster,* "*related to E. linifolium*" (= *Aster*).

E. stuebeli Hier., Bot. Jahrb. **21:** 335. 1895 (Colombia) = **Oritrophium peruvianum** (Lam.) Cuatrecasas, Ciencia [México] **21:** 22. 1961. In reality a *Celmisia* sect. Oritrophium (see Solbrig, 1960).

E. thermarum (Phil.) Cabrera, Revista Chil. Hist. Nat. **40:** 230. 1937 (Chile) = **Conyza thermarum** Phil., Anal Univ. Chile **21:** 381. 1862.

E. trifidum Larrañaga, Escritos D. A. Larrañaga **2:** 254. 1923 (Uruguay) = nomen nudum.

E. tripolioides Phil., Linnaea **33:** 135. 1864 (Chile) = **Aster vahlii** (Gaud.) Hook. et Arn., Comp. Bot. Mag. **2:** 49. 1836.

E. trihecatactis Blake, Jour. Wash. Acad. **27**: 380. 1937 (Colombia) = *Conyza. "a member of section Caenotus . ."*

E. tunariensis O. Ktze., Rev. Gen 3(2): 146. 1898 (Bolivia) = *Conyza. ". . related to E. bonariensis . ."* (of section Caenotus).

E. uniflorus L., Sp. Pl. **2**: 864. 1753 (Reg. boreal). A northern hemisphere species incorrectly cited for Patagonia and Tierra del Fuego.

SUMMARY

The South American species of *Erigeron* s. st. (Cronquist, 1943, 1947) are monographed. The genus comprises in South America 23 species and one species complex, which has been considered as being formed by five species. A detailed morphological analysis of the *E. andicola* complex is presented, and the reasons given why some form of apomixis, or hybridization and inbreeding is suspected.

LITERATURE CITED

AUER, V., 1960. The Quaternary history of Fuego-Patagonia. Proc. Roy. Soc. London B, 152 (949): 507-516.

BEAMAN, J. H., 1957. The Systematics and Evolution of Townsendia (Compositae). Contr. Gray Herb. 183: 1-151.

BENTHAM, G., 1873. Notes on the Classification, History and Geographic Distribution of Compositae. Jour. Linn. Soc. Bot. **13**: 335-577.

———— AND J. D. HOOKER, 1873. Genera Plantarum, 2(1): 1279 pp., London.

CABRERA, A. L., 1939. Las Compuestas del Parque Nacional del Nahuel Huapi. Revista Mus. La Plata Bot. **2**: 227-296.

CARANO, E., 1919. L'Erigeron Karwinskianus var. mucronatus e apogamo. Rend. Acc. Lincei Roma, Cl. Fis. Mat. Nat., V, **28**: 94.

————, 1920. Studio cito-embriologico sul genere Erigeron. Rend. Acc. Lincei Roma, Cl. Fis. Mat. Nat., V, **29**: 157.

————, 1921. Nuove ricerche sulla embriologia delle Asteraceae. Ann. Bot. Roma 15: 97-196.

————, 1924. Osservazioni sul meccanismo di divisione della cellula madre del sacco embrionale nelle piante apogame. Rend. Acc. Lincei Roma, Cl. Fis. Mat. Nat., V, **33**: 150-155.

CARLQUIST, S., 1956. Documented Chromosome Numbers of Plants. Madroño **13**: 206.

CRONQUIST, A., 1943 The separation of Erigeron from Conyza. Bull. Torrey Club **79**: 629-632.

————, 1947. Revision of the North American Species of Erigeron North of Mexico. Brittonia 6: 121-302.

CUATRECASAS, J., 1935 Plantae Isernianae I. Anal. Univ. Madrid IV: 206-265.

FAGERLIND, F., 1944. Der tetrasporische Angiospermenembryosack und dessen Bedeutung für das Verständnis der Entwicklungsmechanik und Phylogenie des Embryosacks. Ark. Bot. 31 A (11): 1-71.

————, 1948. Macrogametophyte formation in two agamospermous Erigeron species. Acta Horti Berg. **14**: 221-247.

Gustafsson, Å., 1947. Apomixis in higher plants III. Biotype and species formation. Lunds Univ. Arsskr. II. Sect. 2, **43**: 181-370.

Hall, H. M., 1928. The genus Haplopappus. A phylogenetic study in the Compositae. Carnegie Inst. Publ. 389: 1-391.

Harling, G., 1951. Embryological Studies in the Compositae. Part III. Asterae. Acta Horti Berg. **16**: 73-120.

————, 1954. The embryo-sac development of Vittadinia triloba (Gaud.) DC. Sv. Bot. Tidskr. **48**: 490-496.

Holmgren, J., 1919. Zytologische Studien über die Fortpflanzung bei den Gattungen Erigeron und Eupatorium. Sv. Vet.-akad. Handl. III. **59**: 1-118.

Kunkel, G., 1957. Uber einige endemische Kompositen der Flora fernandeziana. Ber. Schweiz. Bot. Ges. **67**: 428-457.

Larsen, K., 1954. Chromosome numbers of some European flowering plants. Bot. Tidsskr. **50**: 629-632.

Macloskie, G., 1905. Flora patagonica. Flowering Plants. Reports of the Princeton University Expedition to Patagonia 1896-1899, **8**: 595-810.

Mc Donald, C. C., 1927. A study of seed development in three species of Erigeron with special reference to apogamy. Bull. Torrey Club **54**: 479-497.

Montgomery, F. H. and S. Yang, 1960. Cytological Studies in the Genus Erigeron. Canad. Jour. Bot. **38**: 381-386.

Muñoz Pizarro, C., and E. Pisano Valdes, 1948. Estudio de la Vegetación y Flora de los Parques Nacionales de Fray Jorge y Talinay. Agr. Tec. **7**: 71.

Palm, B., 1922. The Embryo-sac of Vittadinia. Ann. Jard. Bot. Buitenzorg 32: 88-95.

Raven, P. H., O. T. Solbrig, D. W. Kyhos and R. Snow, 1960. Chromosome Numbers in Compositae. I. Astereae. Am. Jour. Bot. **47**: 124-132.

Skottsberg, C., 1921. Natural History of Juan Fernandez and Easter Islands, II, : 95-240, Uppsala.

————, 1950. Apuntes sobre la flora y vegetacion de Frai Jorge (Coquimbo, Chile). Acta Horto Goth. **18**: 91-184.

Solbrig, O., 1955. Notas sobre el género Erigeron (Compuestas). Bol. Soc. Argent. Bot. **6**: 21-29.

————, 1960. The South American sections of Erigeron and their relation to Celmisia. Contr. Gray Herb. 188: 65-86.

Standley, P., Trees and Shrubs of Mexico (Bignoniaceae-Asteraceae). Contr. U. S. Natl. Herb. **23**: 1313-1721.

Stebbins, G. L., 1950. Variation and Evolution in plants. 645 pp. New York.

Tahara, M., 1915. Parthenogenesis in Erigeron annuus Pers. Bot. Mag. Tokyo **29**: 245-259 (in Japanese).

———, 1921. Cytologische Untersuchungen an einigen Kompositen. Jour. Coll. Sci. Univ. Tokyo **43**: 1-53.

TURNER, B. L., 1959. Meiotic chromosome counts for 12 species of Texas Compositae. Brittonia **11**: 173-177.

———, AND H. S. IRWIN, 1960. Chromosome Numbers in Compositae II. Meiotic counts for fourteen species of Brazilian Compositae. Rhodora **62**: 122-126.

———, AND W. L. ELLISON, 1960. Chromosome Numbers in the Compositae. I. Meiotic chromosome counts for 25 species of Texas Compositae including six new generic reports. Tex. Jour. Sci. **13**: 148-151.

———, W. L. ELLISON AND R. M. KING, 1961. Chromosome numbers in the Compositae. IV. North American species, with phyletic interpretations. Am. Jour. Bot. **48**: 216-223.

VIERHAPPER, F., 1916. Analytische Ubersicht über einige patagonische und feuerlandische Erigeron-Formen. Bot. Not. f. 1916: 241-250.

THE GENUS ERIOSORUS IN COSTA RICA

EDITH SCAMMAN

This paper is the fourth of my studies of a genus of Costa Rican ferns, following *Adiantum*, *Pteris* and *Oleandra*.

Again I wish to thank Dr. Leslie R. Holdridge for his help in the field, and Dr. Rolla M. Tryon for his continued interest and advice in the preparation of these papers.

I am indebted to Dr. Alice Tryon for the use of photographs and notes taken while on a recent visit to European herbaria, and to Conrad V. Morton for the loan of all the specimens of this genus from Costa Rica in the U. S. National Herbarium, including Maxon's types.

The careful drawings of Mrs. Ruth Hsu Chen will help to illustrate the differences between the species.

ERIOSORUS Fée.

A genus of terrestrial ferns all found in tropical America except one species on Tristan d'Acunha. The rhizomes are suberect or wide-creeping, lacking scales, but with pluricellular usually castaneous hairs. Fronds are bipinnatifid to decompound, sometimes scandent and long-trailing; the rachis and pinna-rachises often flexuose, and the pinnules usually cuneate, forked or lobed, but varying in outline and in pubescence. Veins are free, with unprotected sporangia following the veins.

Gymnogramma Desv. included the type-species (*Pteris rufa* L.) of *Gymnopteris* Bernh. (earlier), and accordingly it is a superfluous and therefore an illegitimate name. The next available name is *Eriosorus* Fée.

The above description of the genus has been adapted from Copel. Ind. Fil. 58-59. 1947, and the key follows, in part, that given by Maxon under *Psilogramme*, Bull. Torrey Bot. Club **42**: 79-80. 1915.

KEY TO SPECIES

a. Fronds erect, narrow, the rachis and pinna-rachises straight or subflexuous; pinnae short, 3 to 8 cm. long .... *b.*
  b. Rhizome slender, wide-creeping, the fronds 1 to 2.5 cm. apart, stipe usually glabrous, but the rachises, veins and lower surface of the pinnae short-villous with lax hairs, upper surface smooth .... 1. ***E. Warscewiczii.***
  b. Rhizome thick, stout, ascending or decumbent; the fronds approximate or close, stipe, rachises and both upper and lower

surfaces of the pinnae densely long-villous with multicellular hairs .... 2. *E. congestus.*

a. Fronds much larger, scandent or recumbent, the rachis or pinna-rachises strongly flexuose; pinnae elongate, mostly 12 to 25 cm. long .... *c.*

  c. Secondary pinnae sharply retrorse, but at once curved upward, glabrous throughout .... 3. *E. glaberrimus.*

  c. Secondary pinnae retrorse only at a broad angle, or spreading, not recurved, variously pubescent .... *d.*

    d. Leaf-tissue scantily pubescent, lobes varying in size and shape, often widely divergent .... 4. *E. flexuosus.*

    d. Leaf-tissue densely short-villous beneath, less so above; lobes mostly short and closer together .... 5. *E. villosulus.*

1. **Eriosorus Warscewiczii** (Mett.) Copel. Ind. Fil. 59. 1947. Fig. 1

Gymnogramma Warscewiczii Mett. Ann. Sci. Nat. Bot. V, 2: 221. 1864. TYPE (chosen by Maxon): Cartago, Vulcan, 11000 ft., Costa Rica, *Warscewicz 20* (B, photo GH!).

Psilogramme Warscewiczii (Mett.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 17. 1882.

Psilogramme Jimenezii Maxon, Amer. Fern Journ. 18:3. 1928. TYPE: Crater del Volcán Poás, *Oton Jimenez 1034* (US!).

This fern is found only at high altitudes, as is true of most members of this genus in Costa Rica. Its fronds are borne singly an inch or more apart on a slender creeping rhizome; the stipes are stout with the pinnae lax, sessile or stalked; the lower ones distant. The rachis, pinna-rachises and lower surface of the pinnae are pubescent with lax, usually glandular hairs, which are mostly lacking on the upper surface. The texture is rigid and coriaceous with the veins deeply sunk in the tissue of the upper surface.

Costa Rica; Colombia.

On the upper slopes and near the summits of volcanoes and mountains from 2300 to 3450 m.

Specimens seen: ALAJUELA: Volcán Poás, *J. D. Smith 6930* (GH, US); *A. Alfaro 121* (US); Upper slopes of Volcán Poás, *Standley 34857, 34869* (US); Sommet du volcán de Poás, *Tonduz 10712* (US); Crater del Volcán Poás, *Jimenez 1034* (US); Poás Lake, *H. E. Stork 2353* (US). CARTAGO: Volcán de Turrialba, *Pittier 13256 (J. D. Smith 7488)* (GH, US); *R. Torres 14* (US); Southern slope of Volcán de Turrialba near the Finca, *Standley 35033* (US); Volcán Irazú, *P. H. Allen 701* (GH); *R. L. Rodríguez 319* (GH); Near top of Irazú, *Scamman 6070, 6071* (GH); *Williams & Molina 13907* (GH); *C. Weber 6020* (GH);

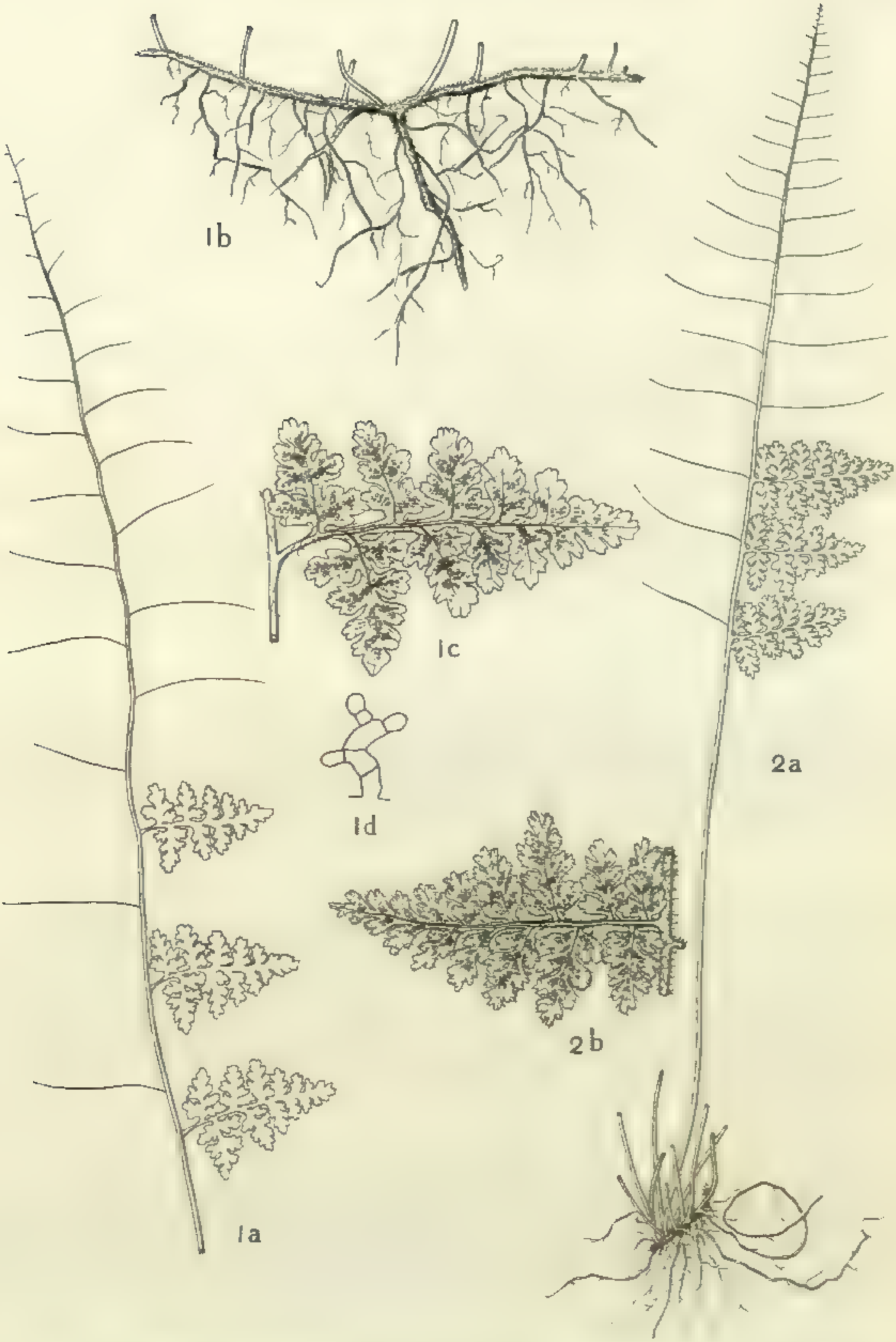


FIG. 1. *Eriosorus Warscewiczii:* 1a (from *Tonduz 10712*, Costa Rica, US), lamina, × 1; 1b (from *J. D. Smith 6930*, Costa Rica, US), rhizome, × 1; 1c (from *Tonduz 10712*, US), a fertile pinna, × 1; 1d (from *Jimenez 1034*, Costa Rica, US), uviform trichome from the lamina, enlarged (see text). FIG. 2. *E. congestus* (from *Scamman 6074*, Costa Rica, GH): 2a, leaf and rhizome, ×1; 2b, a fertile pinna, × 1.

Robert's, on road to Irazú, *Scamman 6073* (GH); Cerro de la Muerte, *J. B. Carpenter 288* (US), *Scamman 6072* (GH).

Maxon distinguished *P. Jimenezii* from *P. Warscewiczii* chiefly by the presence of "short uviform trichomes, with glandlike processes" and these can be seen in the type specimen (Fig. 1d). However, this characteristic was found by Jimenez on plants in the same locality — Volcán Poás — as several collections of typical *P. Warscewiczii*, and it seems to be a peculiar variation of it and not deserving specific rank.

Some specimens such as *Pittier 13256 (J. D. Smith 7488)* and *J. D. Smith 6930* have been misidentified as *Gymnogramma Biardii* (Fée) Baker.

2. **Eriosorus congestus** (Christ) Copel. Ind. Fil. 58. 1947. **Fig. 2**

Gymnogramma congesta Christ, Bull. Herb. Boiss. II, 4: 1098. 1904. TYPE (chosen by Maxon): La Palma, Costa Rica, 1459 m., Sept. 1898, *Tonduz 12575*, (P; isotype: US!).

Psilogramme congesta (Christ) Maxon, Bull. Torrey Bot. Club **42**:81. 1915.

The most common species of the genus in Costa Rica, it is easily distinguished from *E. Warscewiczii* by the short thick rhizome, the close arrangement of the pinnae and pinnules and the dense grayish multicellular pubescence on the stipe, rachises and both the upper and lower surface of the segments. Leaf-tissue is herbaceous and bright green.

This species seems to be endemic to Costa Rica (there is an uncertain record from Honduras) where it is common in thickets, on mossy banks and clearings at elevations usually from 1500 to 2500 m.

Specimens seen: 1901-1905 *Werklé* (US); Nov. 1886, *J. J. Cooper* (GH). HEREDIA: Vara Blanca between Poás and Barba, *Chrysler & Roever 5000* (US); *Maxon & Harvey 8380* (US); *Skutch 3518* (GH, US); *Scamman 7048* (GH); Cerros de Zurquí, northeast of San Isidro, *Standley & Valerio 50332* (US); Slope of Barba, *Scamman & Holdridge 7922* (GH); La Paz, a waterfall, *Scamman & Holdridge 7926* (GH). ALAJUELA: Upper slopes of Volcán Poás, *Standley 34634* (US); *Hunnewell 16508* (GH); Along road to Volcán Poás, *Scamman & Holdridge 7625* (GH); Region of Zarcero, *Austin Smith H.288* (US). SAN JOSE: Las Nubes, *Standley 38432* (US); *Scamman & Holdridge 7047, 7921* (GH); La Palma, Sept. 1898, *Tonduz 12575* (US); March 17, 1908, *Brade* (US); *Standley 32988* (US); La Palma on the road to La Hondura, *Maxon & Harvey 7916* (GH, US), *8086* (US); *Scamman 7623*, *7624* (GH); La Hondura, *Wercklé 16683* (GH, US); *Jimenez 594* (US); *Scamman & Holdridge 7924* (GH); Road to San Cristobal, *Scamman 6074* (GH); La Chonta, on Interamerican Highway, *Scamman & Holdridge 7923* (GH); El General, *Skutch 3048* (GH, US); Zurquí, *Standley & Valerio 48047, 48159, 48190* (US). CARTAGO: El Muñeco, *H. E. Stork 4710* (US); in clearing near El Copey, *Williams 16357* (US); La Congrejon, Cordillera de Talamanca, *Williams & Allen, 16464* (US); Santa Clara de Cartago, *Lankester 598* (US); *Maxon & Harvey 8159* (US).

3. **Eriosorus glaberrimus** (Maxon) Scamman, comb. nov. Fig. 3

Psilogramme glaberrima Maxon, Bull. Torrey Bot. Club 42:82-83. 1915. TYPE: La Palma, Costa Rica, 1459 m., Sept. 1898, *Tonduz 12531* (US!).

Gymnogramma glaberrima (Maxon) C. Chr. Ind. Fil. Suppl. Prélim. 19. 1917.

This rare fern was described by Maxon from collections in the forests of La Palma, *Tonduz 12531* (US) being the type specimen. It belongs to a section of the genus characterized by wide ample fronds 3- to 4-pinnate, scandent or recumbent instead of erect, stipe and rachises castaneous and lustrous and both primary and secondary rachises flexuose. The pinnules are mostly deltoid-oblong with wide rachises and the obtuse segments 1.5 to 2 mm. broad. The leaf-tissue is thin, membrano-papyraceous, grayish green, and entirely glabrous which, in addition to the habit of the secondary pinnae to curve upward, separates this from all the following species. The veins are solitary, brownish, extending to the narrow but deep sinus in the rounded apex of the lobe.

Costa Rica, and Nicaragua (collection by *Wright* at Omotepec, 1853-56, GH, US).

Wet forests and moist banks in the mountains from 1300 to 2300 m.

Specimens seen: HEREDIA: Vara Blanca, *A. W. Haupt 205* (US); slope of Volcán Barba, *Scamman & Holdridge 7927* (GH). SAN JOSE: Forêts de La Palma, *Tonduz 12531* (US); March 17, 1908, *Brade* (US); *Maxon & Harvey 7940* (US); Santa Maria, Cola de Gallo, *H. E. Stork 1952* (US). CARTAGO: La Estrella, *Standley 39424* (US); Santa Clara de Cartago, 1930, *Lankester* (US); Above San Isidro, *C. Weber 6014* (GH).

4. **Eriosorus flexuosus** (HBK) Copel. Ind. Fil. 58. 1947. Fig. 4

Grammitis flexuosa HBK. Nov. Gen. et Sp. 1:5. 1815.

TYPE: prope Caracas, Venezuela, *Bonpland*, P, photo GH!; isotype B, photo GH!

Gymnogramma flexuosa (HBK) Desv. Mém. Soc. Linn. Paris 6:215. 1827.

Gymnogramma refracta Kl. Linn. 20:410. 1847. TYPE: Sierra Nevada (Mérida), "Colombia", Venezuela, *Moritz 359;* isotype P, photo GH!, B, photo and fragment US!, photo GH!

Gymnogramma haematodes Christ, Bull. Herb. Boiss. II, 4:1097. 1904. TYPE: Sommet du volcán de Poás, Costa Rica, 2644 m., Oct. 1896, *Tonduz 10713,* (chosen by Maxon) P, photo GH!; isotype, US!

Psilogramme haematodes (Christ) Maxon, Bull. Torrey Bot. Club 42:84. 1915.

Psilogramme refracta (Kl.) Maxon, Bull. Torrey Bot. Club 42:85. 1915.

This species, named and described in the early years of the nineteenth century, is represented in herbaria by many specimens from the high, mountainous country of South America — Colombia, Venezuela to Peru and Bolivia, and also from Mexico, Guatemala, and Costa Rica, often near the summits of volcanoes.

The caudex is described as firmly rooting with coarse, wiry fibres, the stipes 6-18 inches long, chestnut-brown, glossy, flexuose; fronds scandent, tri-quadripinnate; rachis geniculate-flexuose or zigzag; pinnae reflexed, subdeltoid in general outline; segments more or less elongated, linear or oblong, obtuse, entire or forked. The texture is firm-herbaceous with slender, weak hairs scattered on both upper and lower surfaces.

Maxon in his treatment of *Psilogramme (Eriosorus)* does not include *E. flexuosus*, but refers the specimens with similar characteristics to two species: *P. haematodes* described from Costa Rica by Christ and *P. refracta* described from Venezuela by Klotzsch. According to Maxon's key the chief differences between them are in the size of the segments and distribution of hairs, small in *P. haematodes* with a few scattered hairs on both surfaces, and larger in *P. refracta* with a few hairs beneath among the sporangia. Both species are found on the slopes and near the crater of Poás.

Specimens of *E. flexuosus* from South America reveal a wide variation in the size of the pinnules and distribution of

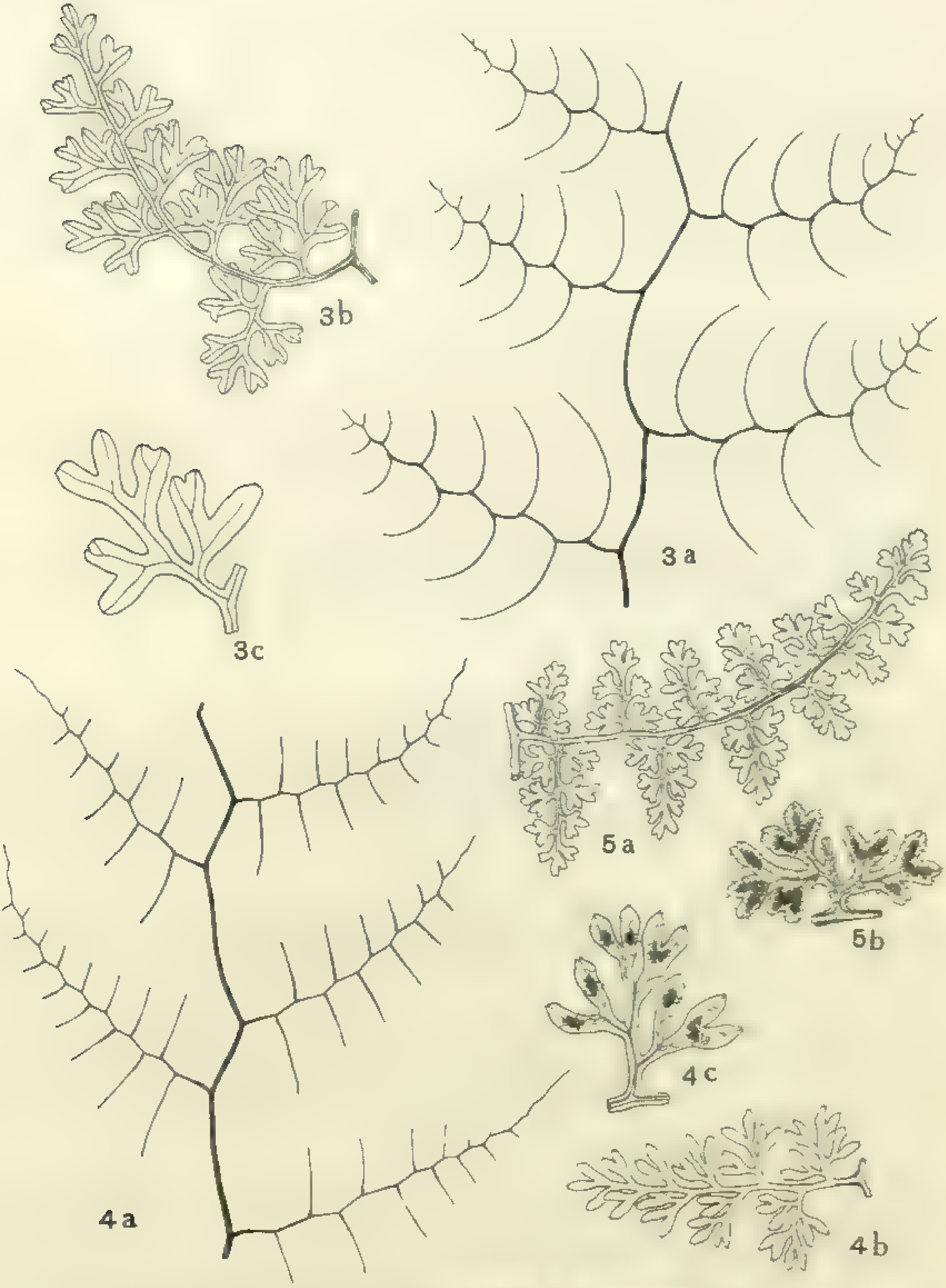


FIG. 3. *Eriosorus glaberrimus* (from *Scamman & Holdridge 7927*, Costa Rica, GH): 3a, diagram of pinna-rachises and a portion of the rachis, 3b, a secondary pinna, × 1; 3c, a tertiary segment, × 2. FIG. 4. *E. flexuosus* (from *Steyermark* [illegible], Guatemala, US): 4a, diagram of pinna-rachises and a portion of the rachis; 4b, a secondary pinna, × 1; 4c, a fertile segment, × 2½. FIG. 5. *E. villosulus* (from *Holm & Iltis 505*, Costa Rica, US): 5a, a secondary pinna, × 1; 5b, basal portion of a fertile segment, × 2.

hairs, sometimes in the same collection, as the fronds are often long and trailing and much divided. I am, therefore, referring to *E. flexuosus* all the specimens which resemble it, and which are from similar localities and altitudes.

Mexico, Guatemala, San Salvador, Costa Rica; Colombia, Venezuela to Peru and Bolivia.

On upper slopes of volcanoes and mountains from 2000 to 2800 m.

Specimens seen: HEREDIA: Forêts du Barba, *Pittier 1936* (US). ALAJUELA: Sommet du volcán de Poás, *Tonduz 10713* (US); *P. H. Allen 617* (GH, US); upper slopes of Volcán Poás between the Hotel and the crater, *Standley 34882* (US); near the top of Poás, *Scamman 7926* (GH); *G. Weber 6097* (GH); *J. D. Smith 6931* (GH, US); March 3, 1940, *W. N. Bangham* (US); Crater apogado del Poás, *Jimenez 1011* (US). (Maxon placed the three above-cited specimens under *P. refracta*). SAN JOSE: Las Nubes, *Standley 38637* (US); vicinty of Millsville, Interamerican Highway, *Scamman 6077* (GH); near La Chonta on Interamerican Highway, *Scamman & Holdridge 7925* (GH). CARTAGO: Volcán Turrialba, *R. Torres 4* (US); *A. Alfaro 52* (US); Southern slope of Volcán de Turrialba, *Standley 35024* (US); Volcán Irazú, *J. D. Smith 4999* (US); Cordillera de Talamanca, Panamerican Highway, *C. Weber 6060* (GH).

5. **Eriosorus villosulus** (Maxon) Scamman, comb. nov.

Fig. 5

Psilogramme villosula Maxon, Bull. Torrey Bot. Club. 42:83. 1915. TYPE: Cerro de las Vueltas, Costa Rica, 3000 m., Jan. 1897, *Pittier 10502* (US!).

Gymnogramma villosula (Maxon) C. Chr. Ind. Fil. Suppl. Prélim. 19. 1917.

According to Maxon "this is a very distinct species," characterized by short, yellowish, multicellular hairs on the stipe and rachises, and covering both surfaces of the delicately herbaceous leaf-tissue. The fronds are suberect, tripinnate to almost quadripinnate, with both the primary and secondary rachises subflexuose. The pinnules are rounded-triangular or narrowly subovate in outline with the obtuse lobes short and close together.

This may possibly be a variety of *E. flexuosus*, but none of the specimens of that species I have seen have been as abundantly villous. It has been collected at higher altitudes in Costa Rica than *E. flexuosus* and in the region of the "paramos." For these reasons I am maintaining it as a species.

Costa Rica only.

Semi-scandent and climbing over rocks in cloud forests and "paramos" at very high altitudes from 2700 to 3300 m.

Specimens seen: SAN JOSE: Cerro de las Vueltas, *Pittier 10502* (US), *Standley & Valerio 43563* (US); Cordillera de Talamanca, along Panamerican Highway, *C. Weber 6228* (GH); El Páramo, region du General, *Pittier 10452* (US). CARTAGO: Ojo de Agua Camp, near Panamerican Highway, *Wm. Dayton 3035* (US); vicinity of Millsville, Panamerican Highway, *Holm & Iltis 505* (US); near Cantina along Interamerican Highway, *Scamman 6075, 6076* (GH).

Other species described from Costa Rica are the following.

Gymnogramma amaurophylla Christ, Bull. Herb. Boiss. II, 4:1097. 1904. Costa Rica, 1903, *Wercklé*. Cited as a synonym of *Paesia anfractuosa* by C. Chr. Ind. Fil. 333. 1905. In his description Christ refers to the sori covered by the edges of the lobes, a characteristic of *Paesia*.

Gymnogramma Kupperi Losch, Mitteil. Bot. Staatss. München,**1**:21. 1950. Costa Rica, Chirripo grande, 3500 m., *Kupper 1223*. A photograph at the British Museum of a specimen in the herbarium at Munich was seen by Dr. Alice Tryon, who noted that "it resembled specimens of *G. elongata* or *G. Karstenii* in cutting and form of the leaf." Both these species with linear fronds are found in the mountains of South America, *G. elongata* in Ecuador, Peru and Bolivia, and *G. Karstenii* in Colombia. But no specimens of a similar nature have been seen in collections from Costa Rica. — GRAY HERBARIUM, HARVARD UNIVERSITY.

TAXONOMIC FERN NOTES. III.

ROLLA TRYON

The following notes include a new combination in Alsophila, a new species of Doryopteris and a new generic name for the ferns usually called Lonchitis. In addition to these new names, other matters are discussed, largely ones pertaining to my studies of Peruvian ferns. I am indebted to Mrs. Ruth Hsu Chen for her careful preparation of the illustrations.

1. ALSOPHILA MACARENENSIS (ALSTON) TRYON, COMB. NOV.

Dryopteris (Ctenitis) macarenensis Alston, Mutisia, 7:5. 1952. TYPE: Sierra de la Macarena, Colombia, *Philipson 2281* (BM), isotype: (COL!).

Alsophila scopulina Tryon, Rhodora 62:2, f. 2. 1960. TYPE: Cerro Isibukuri, Colombia, *Schultes & Cabrera 13411,* (GH).

The discovery that Alston's species is identical with the one I described eight years later requires the above new combination. It also considerably extends the range of the species and it may now be expected from others of the sandstone mesas of Amazonian Colombia. An additional collection from the Sierra de la Macarena is: *Idrobo & Pinto 2190* (COL).

2. A NEW SPECIES OF DORYOPTERIS AND AN OLD ONE

Doryopteris Allenae Tryon, spec. nov. Figs. 1-4

Rhizoma breviter repens paleis angustis curvatis ascendentibus medio obscuro semisclerotico vel sclerotico limbis dentatis pallidioribus (fuscis) cellulis longissimis quam latis, petiolus teres fasciculo vasculari uno, laminae steriles fertilesve monomorphae vel dimorphae, lamina sterilis oblongo-ovalis cordata vel 3-5 lobis latis venis areolatis areolis ad margem minoribus, venis marginalis plerumque connectentibus nonnullis liberis pagina superiore hydathodis nullis limbo membranaceo subalbulo vel subfusco, lamina fertilis oblongo-ovalis vel 3-7 lobis angustis, sporae perisporio brunneo modice inaequaliter papillato.

TYPUS: Gunong Idong, near Ipoh, Perak, Malaya, 450-500 ft., May 24, 1962, *B. Molesworth Allen 4763* (GH). Paratypi: Gunong Tempurong, Perak, Malaya, 1,400 ft., Jan. 12, 1959, *B. M. Allen 4103* (GH, US), Aug. 13, 1959, *B. M. Allen 4393* (GH).

On mossy banks and in crevices of limestone rocks in forest; leaves pale bluish green.

Doryopteris Allenae is most similar in its general appearance to *D. cordifolia* of Madagascar. However, this resemblance seems to be a superficial one for in its technical characters it is most closely related to *D. ludens*.

It differs from *Doryopteris cordifolia* in the following characters: it has a terete, rather than a sulcate petiole, no hydathodes on the upper surface of the sterile lamina, the sterile lamina has a whitish to brownish, membranaceous border, rather than a red-brown to black, sclerotic one, and the areolae are smaller toward the margin, rather than nearly the same size as those near the costa.

Doryopteris Allenae is similar to *D. ludens* in its rhizome scales (both their structure and position), its terete petiole and its spores with perispore. It especially differs from *D. ludens* in having the rhizome short-creeping, rather than slender and long-creeping, and in having the sterile lamina with the marginal veins mostly joined, rather than mostly free, and without hydathodes on the upper surface.

Mrs. Allen has sent notes that indicate this species also grows at Batu Caves, Selangor. The ample material I have designated as the type was received after the illustrations were prepared. It differs from the Gunong Tempurong material in being larger and in having some dimorphic fertile leaves.

This species is named in honor of Betty Molesworth Allen who has contributed to our knowledge of Malayan ferns by her collections and publications on them and who obtained, at considerable effort, the material I have studied.

Doryopteris papuana Copel. Phil. Jour. Sci. Bot. 6:86. 1911

In my revision of Doryopteris[1] I treated this name as a synonym of *Doryopteris ludens*. However, I have since then seen additional material from Papua and have come to the conclusion that, while *D. papuana* is a close relative of *D. ludens*, it is a valid species. It will key out to *D. ludens* in my revision but it may be separated as follows:

Rhizome scales somewhat spreading, curved-ascending to the upper side of the rhizome; dark sclerotic portion of the central costa extending well into the terminal lobe of the lamina .... 25. *D. ludens*.

Rhizome scales straight and closely appressed to the rhizome; dark sclerotic portion of the central costa not extending into the terminal lobe of the lamina .... 25A. *D. papuana*.

---

[1] Contrib. Gray Herb. 143. 1942.

In addition to the above characters, there are more lobes on the fertile and sterile lamina in *D. papuana* than in *D. ludens*. The sterile lamina has 14-27 lobes and the fertile one 21-35 lobes. Specimens of *D. ludens* from the Philippine Islands have the sterile lamina with 0, 3 or 5 lobes and the fertile one with (3-) usually 5-7 (-8) lobes; while those from India, Burma, Indochina, Malay Peninsula and Java have the sterile lamina with (5-) 7-9 (-11) lobes and the fertile with (5-) 8-12 (-14) lobes.

Doryopteris papuana is, like *D. ludens*, a calciphile. It is represented in the Herbarium of the Arnold Arboretum by the following collections: PAPUA: Milne Bay District, Cape Vogel Peninsula, *Brass 21623, 21853, Hoogland 4338.*

3. THE GENERA LONCHITIS AND BLOTIELLA

The genus *Lonchitis*, although maintained by most authors, has sometimes been united with *Pteris*, for example, by Kuhn[2] and recently by Copeland[3]. Some of the authors who maintained it included in it several areolate-veined species and one or two free-veined ones, for example, Diels[4] and Christensen[5]. Others have restricted it to the areolate-veined species and treated the free-veined ones in *Pteris*, for example, Hooker and Baker[6] and John Smith[7]. More recently the free-veined ones have been placed in a separate genus, *Anisosorus*, for example, Maxon[8] and Christensen[9].

Current treatments usually recognize *Pteris, Lonchitis* and *Anisosorus* as three related genera.

A study of the taxonomy has led me to this same conclusion, that the free-veined species and the areolate-veined species represent genera distinct from each other and from *Pteris*. However, the typification of *Lonchitis* has been confused and *Lonchitis* must be the name for the small genus of free-veined species *(Anisosorus)* while the larger genus of areolate-veined species requires a new name *(Blotiella)*. Also there seems to be good evidence that while the free-

---

[2] Fil. Afr. 73-90. 1868.

[3] Gen. Fil. 60. 1947.

[4] Nat. Pflanz. 1^4: 295. 1899.

[5] Ind. Fil. xliv. 1905.

[6] Syn. Fil. 128, 160. 1867.

[7] Hist. Fil. 292, 297. 1875.

[8] Pterid. in Sci. Surv. Porto Rico & V. I. 6: 429. 1926.

[9] Ind. Fil. Suppl. 3, 11. 1934 and Verdoorn, Man. Pterid. 536. 1938.

veined species are related to *Pteris*, as usually stated, that the areolate-veined ones are related to *Hypolepis*. This latter relationship was suggested by Christensen[10] but it has not been firmly proposed.

Both genera have trichomes on the rhizome and in this character differ sufficiently from *Pteris* which has a paleate stem. The trichomes are a single cell in width but sometimes they are rather large and very flat so they may be mistaken for narrow scales. This erroneous interpretation is especially possible for toward the base they may adhere to one another. I believe that the several reports of scales in *Lonchitis* and *Blotiella* were based on misinterpretation of the indument. The basic chromosome number in *Pteris* is n=29 in the considerable number of species counted[11] while it is n=ca. 50 in *Lonchitis* and n=38 in *Blotiella*.

Lonchitis L. Sp. Pl. 1078. 1753; Gen. Pl. ed. 5, 485. 1754. TYPE: ***Lonchitis hirsuta*** L.

Antiosorus Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetopt.), 347. 1882, nomen nudum.

Anisosorus Trev. Atti Istit. Veneto s. 2, **2**:166. 1851, nomen nudum; Maxon, Sci. Surv. Porto Rico & V. I. (Pterid.) **6**:429. 1926, nom. superfl., illegit. TYPE: the same as that of *Lonchitis*.

Stem creeping, thick and fleshy, bearing large flattened trichomes (one cell wide), leaves produced singly; petiole with 2 vascular bundles near the base, each bent twice (Figs. 9, 10); the lateral ridges of the rachis continuous beneath (not interrupted by) the pinna stalks; veins free or casually areolate; sorus borne between the sinus and the apex of a segment (it may closely approach the sinus but does not extend around it except in very minor sinuses), indusium arising from the inner edge of a marginal flange; spores tetrahedral-globose, trilete, hardly marked; chromosome number n=ca. 50[12].

The type species of *Lonchitis* has usually been considered to be *L. aurita* but since that name (see below) is not the name of a taxon, *L. hirsuta* must become the type. The only other species included in the genus by Linnaeus was *L. repens* and this was removed to *Hypolepis* by Presl where it still properly resides. Since the original diagnosis of *Lonchitis* applies better to *L. hirsuta* than it does to *L. repens*, there is no reason to question Presl's action.

---

[10] Verdoorn, Man. Pterid. 535 sub Hypolepis. 1938.

[11] Walker, T. G., Evolution **16**: 27-43. 1962.

[12] Manton, I. Jour. Linn. Soc. Lond. (Bot. **56**, Zool. **44**): 89. 1958 and in Alston, Fl. West Trop. Africa, ed. 2, Suppl. 78. 1959.

The relation of *Lonchitis* is evidently, as commonly considered, with the genus *Pteris.* The tetrahedral-globose spores of *Lonchitis* are similar to those of *Pteris,* the sorus is substantially the same, the marginal flange of the fertile segments is similar to that found in many species of *Pteris* and the enlarged basiscopic pinnule of each basal pinna (seen especially in the smaller leaves of *Lonchitis*) is suggestive of the branching in many *Pteris* species.

There are two species, one American and one African: —

1. **Lonchitis hirsuta** L. Sp. Pl. 1078. 1753. TYPE: Plumier, Fil. t. 20, from Martinique. The sori are not drawn accurately, but otherwise t. 20 is a good representation of the species. The Petiver, Pteri-graph. Amer. illustration (t. 4, f. 5), the only other element cited by Linnaeus is an almost exact but reversed copy of the Plumier plate; there is no specimen in the Linnaean herbarium.

Lonchitis aurita L. Sp. Pl. 1078. 1753, nomen illegit. (Art. 70). TYPE: Plumier, Fil. t. 17, from Martinique. The type is composed of two discordant elements (species) combined into one illustration. Although I am not sure that a name rejected under Art. 70 can be properly cited as a synonym, the only identifiable element is *L. hirsuta,* and it is convenient to place it here. The Petiver, Pteri-graph. Amer. illustration (t. 4, f. 4), the only other element cited by Linnaeus, is an exact but reversed copy of the Plumier plate; there is no specimen in the Linnaean herbarium.

Pteris laciniata Willd. Sp. Pl. 5:397. 1810. TYPE: Ind. Occ. ("India orientalis?"), *Flügge 104* (Herb. Willd. 20013!, photo GH).

Pteris lonchitoides Desv. Mém. Soc. Linn. Paris **6**:301. 1827. TYPE: "Peruvia". (See Weath. Contrib. Gray Herb. **114**:33. 1936).

Anisosorus hirsutus (L.) Maxon, Sci. Surv. Porto Rico & V. I. (Pterid.) **6**:429. 1926.

The identity of *Lonchitis aurita* has generally been uncertain and few authors have associated any plant material with the name. This is not surprising for the Plumier plate does not represent any known species. Jenman[12], however, probably considering only the areolate venation and the erect rhizome depicted in the plate, did use the name for

---

[12] Bull. Bot. Dept. Jamaica 40: 10. 1893 and Bull. Misc. Inf. Bot. Dept. Trinidad 21. Appendix, 112. 1899.

Jamaican material of the species referred to below as *Blotiella Lindeniana* (*Lonchitis* Hook.). The following characters shown in Plumier, t. 17 are definitely those of *Lonchitis hirsuta* and are ones which distinguish it from *Blotiella Lindeniana:* 1) The enlarged basiscopic pinnule at the base of each basal pinna (this character is seen especially in smaller leaves of *L. hirsuta*), 2) the basal pinnae broadest at the base, and 3) the pinnae, above the basal pair, have the basiscopic pinnule closest to the rachis and shorter than the acroscopic one. In addition, *L. hirsuta* grows in Martinique, while *Blotiella Lindeniana* does not occur in the Lesser Antilles.

The areolate venation and the erect rhizome shown by Plumier are not characters of *Lonchitis hirsuta* and must have come from some other species. They could hardly have been drawn in error. There are several species of *Pteris* in Martinique that could furnish such characters and I think it most probable that it was one of these that was the source of the discordant elements in the illustration. Other characters depicted in the Plumier plate are not sufficiently decisive to be of value in establishing the identity of his material.

All of the Greater Antilles, general in the Lesser Antilles; Mexico to Bolivia.

2. **Lonchitis occidentalis** Baker, Syn. Fil. 128. 1867.

Lonchitis Friesii Brause, in Fries, Wiss. Ergebn. Schwed. Rhodesia-Kongo Exped. 1911-1912, Bot. 1:6. 1914.

Anisosorus occidentalis (Baker) C. Chr., in Perrier, Cat. Fl. Madagas. (Pterid.) 54. 1932.

Tropical Africa and Madagascar.

Blotiella Tryon, nom. nov. generis

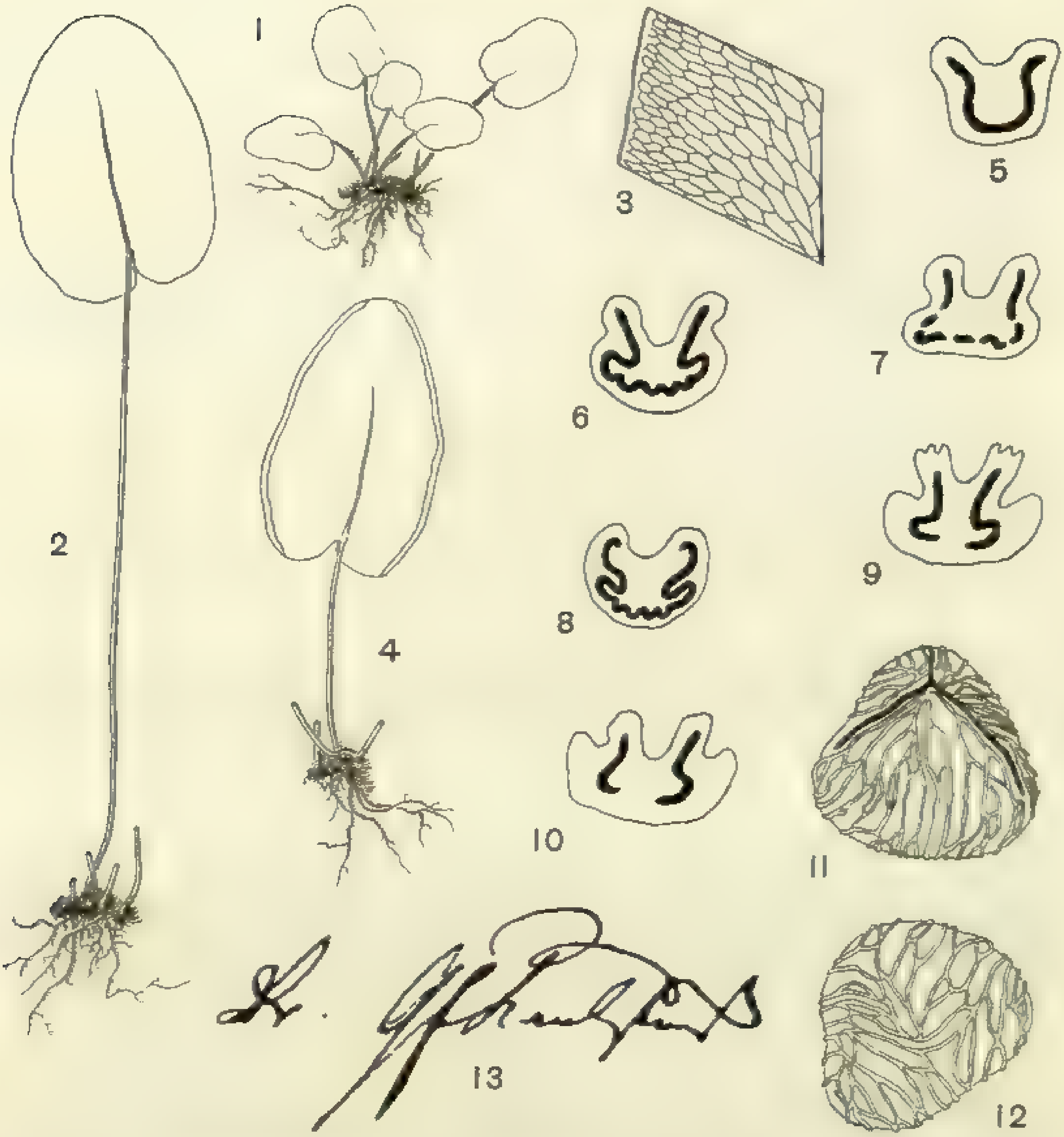
Based on *Lonchitis* sensu Kümmerle, Botanik. Köslem. **1915**:168-169, not L. TYPE: *Lonchitis glabra* Bory.

Compteris (Brazzaiana) Hort "ex Linden", Gard. Chron. s. 3, **29**: May, 25 Suppl.: 2. 1901; and Wein Illustr. Gart. Zeit. **26**:196. f. 20, May, 1901, nomen invalid. (Arts. 34, 42).

Stem erect[14] to decumbent, hard, bearing trichomes, leaves produced in a definite or irregular crown; petiole with one

---

[14] Johnston, H. H., Kilima-njaro Exped. f. 51 on p. 231. 1886, figures a species of *Lonchitis* (identified as *L. pubescens*) as a tree fern and Chiovanda, Rac. Bot. Miss. d. Cons. nel Kenya, 148. 1935, cites a collection (of the same species) with a trunk 4.5 m. tall.



FIGS. 1-4, *Doryopteris Allenae.* 1, sterile plant, × ½, *Allen 4103*, GH. 2, sterile leaf, × ½, *Allen 4393*, GH. 3, venation of sterile lamina, × 1, *Allen 4393*, GH. 4, fertile leaf, × ½, *Allen 4103*, GH.

FIGS. 5-10. Sections of petioles. 5, *Blotiella Lindeniana*, × 4, Jamaica, *Watt*, NY. 6, *B. Lindeniana*, × 2, Brazil, *Brade 9390*, NY. 7, *B. reducta*, × 2, Liberia, *Baldwin 6035*, GH. 8, *Hypolepis bogotensis*, × 2, Colombia, *Tryon & Tryon 6117*, GH. 9, *Lonchitis hirsuta*, × 2, Honduras, *Steeves & Ray 385*, GH. 10, *L. occidentalis*, × 2, Liberia, *Harley F158*, GH.

FIGS. 11-12. Spores of *Saccoloma elegans*, enlarged, Ecuador, *Mexia 8429*, GH. 11, apical view. 12, basal view.

FIG. 13. Signature of Dr. G. F. Kaulfuss.

vascular bundle (Fig. 5) which is much bent and contorted in large leaves (Fig. 6), or with several bundles forming, together, a similar pattern (Fig. 7); the lateral ridges of the rachis joining the pinna stalks; veins usually areolate; sorus continuous around the sinus (when present), either nearly confined to it or extending far on each side especially when the sinus is broad (rarely very long when no sinus is present); indusium a continuation of the margin; spores bilateral, reniform, monolete, usually papillose; chromosome number, n=38 or 76[15].

The new name for this genus recognizes the many contributions to Pteridology by Mme. Marie Tardieu-Blot.

The publication of the generic name *Compteris*, falls far short, I believe, of the requirements of Art. 42 for a *descript. generico-specifica* and also it seems to fall within the scope of Art. 34 (names that are mentioned incidentally). In neither of the publications cited is the genus or species proposed as a new taxon. Although there is an illustration in one of them, this is a poor photograph of the whole plant and portrays no technical characters. The name has been used, to my knowledge, only in the two publications mentioned and there seems to be no reason to accept it or to validate it now.

The relations of *Blotiella* are evidently closer to *Hypolepis* than to *Pteris*. The bilateral, reniform, monolete spores are similar in the two genera as is the continuation of the marginal leaf tissue into the indusium. The position of the sorus, also, is very similar in the two genera, if the more complex leaves of *Blotiella* are considered, and the petiole structure is identical in at least some species (compare fig. 6 of *Blotiella Lindeniana* and fig. 8 of *Hypolepis bogotensis*).

I believe that *Lonchitis* and *Blotiella* have been derived from different genera and that the similarities of the sori, which have been the principal reason for uniting them, are the result of convergent evolution.

In these ferns with usually large leaves it is interesting to observe that the mechanical support that might be derived from fluting of the supporting petiole has been achieved in different ways. In *Lonchitis*, large petioles (Fig. 9) are strongly fluted. There may be as many as eight ridges and seven grooves on the adaxial half of the petiole. The vascular bundles, on the other hand, are relatively simple in their form. In *Blotiella*, the situation is quite different. In a large leaf of *B. Lindeniana*, for example, (Fig. 6) the adaxial half of the petiole has but two ridges and one median groove, while the vascular bundle is greatly contorted, mostly in the abaxial half of the petiole.

---

[15] Manton, I., Jour. Linn. Soc. Lond. (Bot. 56, Zool. 44): 89. 1958 and in Alston, Fl. West Trop. Africa, ed. 2, Suppl. 78. 1959.

One American species and perhaps 12-15 in Africa, Madagascar and the Mascarenes. The following species seem to be sufficiently well established to transfer them to the new generic name:

1. **Blotiella Currori** (Hook.) Tryon, comb. nov.

Pteris Currori Hook, Sp. Fil. 2:232. 1858.

Lonchitis Currori (Hook.) Kuhn, v. Decken, Reisen Ost.-Afrika, 3^3: Bot. 10. 1879.

Pteris Mannii Baker, Syn. Fil. 168. 1867. (Ballard in Kew Bull. **1937**:348 considers this name to represent juvenile leaves of *L. Currori*).

Lonchitis Mannii (Baker) Alston, Bull. Soc. Brot. **30**:18. 1956.

2. **Blotiella glabra** (Bory) Tryon, comb. nov.

Lonchitis glabra Bory, Voy. **1**:321. 1804.

3. **Blotiella Lindeniana** (Hook.) Tryon, comb. nov.

Lonchitis Lindeniana Hook. Sp. Fil. 2:56, t. 89A. 1851. LECTOTYPE: Caracas, Venezuela, *Linden 543* (K, photo GH; isotype, US!). The specimen cited in Herb. J. Sm. (BM), "ex Jard. de Plantes" becomes a paratype.

Lonchitis Zahlbruckneri Kümm. Mag. Bot. Lapok. **13**:49, t. 2. 1914, ex char. TYPE: Brazil, *Warscewicz 30*, W.

I have made a considerable search to find a basis for distinguishing more than one American species but have failed to find any reliable characters. There is considerable variation in such characters as the density of pubescence, and its distribution, the color of the trichomes, the position in which they are borne and whether or not they are gland-tipped. I have not been able to establish correlations of characters with each other nor with geography. It must be admitted, however, that the available specimens are rather few and often incomplete, so that any conclusions based on such material must be tentative.

Costa Rica; Jamaica and Hispaniola; Venezuela to Colombia and south to Bolivia; Brazil.

4. **Blotiella madagascariensis** (Hook.) Tryon, comb. nov.

Lonchitis madagascariensis Hook. Sp. Fil. 2:58. 1851.

5. **Blotiella natalensis** (Hook.) Tryon, comb. nov.

Lonchitis natalensis Hook. Sp. Fil. 2:57. 1851.

6. **Blotiella pubescens** (Kaulf.) Tryon, comb. nov.

Lonchitis pubescens Kaulf. Enum. Fil. 195. 1824.

Bory (Voy. 1:321. 1804) applied the name *Lonchitis hirsuta* L., probably to this species, and the African fern has sometimes erroneously been called "*Lonchitis hirsuta* Bory."

7. **Blotiella reducta** (C. Chr.) Tryon, comb. nov.

Lonchitis reducta C. Chr. Fedde Rep. Spec. Nov. **9**:370. 1911.

Most of the following names have been recently proposed for species that should fall into *Blotiella* but I have not seen material of them. The others have been considered as synonyms, by some authors, or their identity is in some doubt. Accordingly I do not wish to formally transfer any of them to the new generic name.

LONCHITIS CRENATA Alston, Bol. Soc. Brot. **30**: 18. 1956.

LONCHITIS CORIACEA Tard. Mém. Inst. Sci. Madagas. ser. B, **6**: 228. 1955.

LONCHITIS COURSII Tard. Bull. Mus. Paris, s. 2, **29**: 293. 1957.

LONCHITIS GRACILIS Alston, in Exell, Cat. S. Tomé, Suppl. 7. 1956.

LONCHITIS × HIERONYMII Kümm. Botanik. Közlem. **1915**: 174. Proposed as a hybrid of *L. Currori* and *L. natalensis*.

LONCHITIS ISALOENSIS Tard. Bull. Mus. Paris, s. 2, **29**: 293. 1957.

LONCHITIS JAVANICA Desr. in Lam. Encycl. **3**: 594. 1789.

This is evidently an African species of *Blotiella* and represents the earliest name for one of them. Although reported from Java, the genus does not occur there. Posthumus[16] does not mention it but he does discuss how a number of African ferns, collected on early voyages, had been erroneously ascribed to Java.

LONCHITIS POLYPUS Baker, Jour. Linn. Soc. Lond. **15**: 414. 1876.

LONCHITIS SINUATA Alston, Bol. Soc. Brot. **30**: 19. 1956.

LONCHITIS STENOCHLAMYS Fée, Mém. Fam. Foug. **5**: (Gen. Fil.): 142. 1852.

LONCHITIS STIPITATA Alston, Bol. Soc. Brot. **30**: 19. 1956.

LONCHITIS TISSERANTII Alston & Tard. Mém. IFAN **28**: 85. 1953.

LONCHITIS TOMENTOSA Fée Mém. Fam. Foug. **5** (Gen. Fil.): 143. 1852.

4. THE GENUS SACCOLOMA KAULF.

The genus *Saccoloma*, originally including only the single species, *Saccoloma elegans*, was later variously enlarged to some 6 species[17] or 8[18].

---

[16] Verhand. Kon. Akad. Wet. Amsterdam (Tweede Sect.) 36^5. 1937.

[17] Diels, Nat. Pflanz. 1^4.

[18] Christensen, Ind. Fil.

Some of these, for example, *S. sorbifolium (= Cystodium)*, *S. Wercklei (= Dennstaedtia)* and *S. Imrayanum (= Ormoloma)* have properly been removed to other genera. The remainder of the species were segregated from *Saccoloma* by Copeland in 1929 into two genera, *Orthiopteris* and *Ithycaulon*, leaving the genus again containing only *S. elegans.* Since then some new species have been described under *Orthiopteris* or *Ithycaulon* and some old species have been transferred to one or the other. Later, in his Genera Filicum, Copeland reduced *Ithycaulon* to *Orthiopteris.* He recognized, then, the single segregate genus *Orthiopteris* and this treatment, *Saccoloma* with one species and *Orthiopteris* with perhaps 11, has been generally followed by subsequent authors.

The purpose of this note is to point out that the principal difference between *Orthiopteris* and *Saccoloma* is not a valid one; and that there are significant similarities between it and *Saccoloma.* The rhizome of *Saccoloma* has been considered to be prostrate and thus different from the erect rhizome of *Orthiopteris.* However, it is actually erect (at least apically) in both genera. The two genera are identical in the important characters of the spores and there are a number of other similarities.

Saccoloma Kaulf. Berl. Jahrb. Pharm. **1820**:51. TYPE: *S. elegans* Kaulf.

Orthiopteris Copel. Bishop Mus. Bull. **59**:14. 1929. TYPE: *Davallia ferulacea* Moore (*Davallia trichomanoides* Hook. Second Cent. Ferns, t. 64. 1861, not Blume, 1828).

Ithycaulon of authors, including Copel. Univ. Cal. Publ. Bot. **16**:79. 1929, as to the taxon, but not as to the type, *Davallia moluccana* Bl. which is *Tapeinidium moluccanum* (Bl.) C. Chr. Gard. Bull. Str. Settl. **4**:399. 1929.

In view of the obvious taxonomic and nomenclatural problems in some species, the following list of the species of *Saccoloma* is presented with reservation.

1. *S. elegans* Kaulf. (America), 2. *S. domingense* (Spreng.) C. Chr. (America), 3. *S. inaequale* (Kze.) Mett. (America), 4. *S. Henriettae* (Baker) C. Chr. (Madagascar), 5. *Orthiopteris Kingii* (Bedd.) Holtt. (*S. minus* (Hook.) C. Chr., *S. moluccana* of authors, not Blume) (Malaysia, Polynesia), 6. *Orthiopteris ferulacea* (Moore) Copel. (Fiji), 7. *Orthiopteris cicutarioides* (Baker) Copel.

(*Ithycaulon tenuisectum* C. Chr.) (New Guinea), 8. *Orthiopteris trichophylla* Copel. Univ. Cal. Publ. Bot. 18:217. 1942 (New Guinea), 9. *Ithycaulon acuminatum* (Rosenst.) Copel. (New Guinea), 10. *S. caudatum* Copel. (New Guinea) and 11. *S. firmum* (Kuhn) C. Chr. (New Caledonia and New Hebrides).

My conclusions are based on an adequate study of the first eight species in the above list. They all have the following important characters in common:

The stem is radially symmetrical with leaves arising on all sides. It is typically erect, although in *Saccoloma elegans* it may be decumbent in age with only the apex erect, and it bears numerous dark, sclerotic scales at its apex. Although the stem of *S. elegans* has been persistently reported as prostrate or creeping, adequate material shows it to be erect or decumbent. Specimens such as Panama, *Prescott & Caylor 4* (US), Ecuador, *Mexia 8429* (GH, US) and Bolivia, *Tate 421* (NY) show it to be quite erect and such collections as Peru, *Killip & Smith 24574* (GH), *26072* (GH) and Brazil, *Mexia 4964* (GH, US), with a small portion of the rhizome, are consistent with this interpretation. In Peru, *Killip & Smith 26072* (US) and Brazil, *Black 47-1736* (NY) the rhizome is decumbent.

The leaves are glabrous, or nearly so, throughout, the petiole, and sometimes the rachis, have two prominent lateral lines of pneumatic tissue, and the lamina (except in the 1-pinnate *S. elegans*) is acroscopically compound. The principal axes of the lamina are grooved on the adaxial side and the basiscopic ridge of a lesser axis is continuous with a ridge of the axis to which it is attached.

The sorus is davallioid to dennstaedtioid, terminal on a single vein, the outer lobe of leaf tissue being unmodified to definitely modified, the indusium is usually half-conical, to sometimes half cup-shaped, its outer margin is more or less even and entire to strongly rostrate.

The spores (figs. 11, 12) are tetrahedral-globose, light tan, translucent, the basal hemisphere is marked with long, low, narrow ridges that are sharply defined, well spaced, and anastomose irregularly, the commissural face is similar but less abundantly ridged and the ridges are somewhat parallel to one of the three commissural ridges.

The above characters combine to form a strong set of similarities that all of the species have in common. The principal generic characters are the radial stem, erect at least at the apex, with scales, the davallioid or dennstaedtioid sorus and the characteristically ridged spores. An examination of the spores of some species of the following genera showed them all to be different: *Culcita, Davallia, Dennstaedtia, Humata, Hypolepis, Leptolepia, Leucostegia, Microlepia, Odontosoria, Oenotrichia* and *Sphenomeris*. The type species, *S. elegans*, differs from the others only in less important characters: the lamina is 1-pinnate, imparipinnate, with large entire pinnae and the sori are close together and have a broad indusium. There is no reason not to treat *S. elegans* in the same genus as the species with compound leaves. It is quite comparable to such species as *Dennstaedtia Wercklei* and *Microlepia Hookeriana* which are also 1-pinnate species of otherwise compound-leaved genera. The different soral characters of *S. elegans* are similar to those of the above species and seem best interpreted in all three as an adjustment to a long entire margin.

A synopsis and some comments on the American species follow: — 1. **Saccoloma elegans** Kaulf. Berl. Jahrb. Pharm. 1820:51. TYPE: none mentioned, but in Enum. Fil. 224. t. 1. 1824, Kaulfuss cites Brazil, *Sello* and this may be accepted as the type. A specimen of this collection at B!, photo GH is undoubtedly an isotype.

Lamina, 1-pinnate, imparipinnate, the pinnae entire; sori on adjacent vein ends, indusium more or less broadly lunate, shorter than the rather modified, entire to crenate, margin.

Guatemala to Panama; Cuba, Jamaica and Hispaniola; Trinidad, French and British Guiana, Venezuela, Colombia to Boliva, Brazil.

2. **Saccoloma domingense** (Spreng.) C. Chr. Ind. Fil. 612. 1906 (not Prantl, Arb. Bot. Gard. Breslau 1:21. 1892, as cited).

Polypodium adiantoides Aubl. Pl. Guiane 2:962. 1775. TYPE: Plumier, Fil. t. 7. Not *Polypodium adianthoides* Burm. Fl. Ind. 234. 1768.

Davallia domingense Spreng. Einleit. Krypt. Gewächse, 3:149, t. 4, f. 33. 1804. TYPE: Santo Domingo, "Ich habe es durch einen Freund. . ." (The Plumier, Fil. t. 7, also cited, is this species).

Davallia adiantoides Sw. Syn. Fil. 131. 1806, nom. superfl. (= *Davallia domingense* Spreng.).

Dicksonia Plumieri Hook. Sp. Fil. 1:72. 1846, based on *Davallia domingense* Spreng., not *Dicksonia domingense* Desv. Mém. Soc. Linn. Paris 6:317. 1827.

Dicksonia Lindenii Hook. Sp. Fil. 1:72, t. 25B. 1846. TYPE: Caracas, Venezuela, *Linden 166* (K, fragment NY!, BR, photo GH).

Saccoloma adiantoides Mett. Ann. Sci. Nat. IV, 15:80. 1861, nom. superfl. (= *Davallia domingense* Spreng.), epithet from *Davallia adiantoides* Sw.; the same name was also published by Urban, Symb. Ant. 9:318. 1925, nom. superfl. (= *Davallia domingense* Spreng.), with its epithet from *Polypodium adiantoides* Aubl.

Ithycaulon domingense (Spreng.) C. Chr. Ind. Fil. Suppl. 3:116. 1934.

Orthiopteris domingense (Spreng.) Copel. Gen. Fil. 50. 1947.

Lamina bipinnate, or more complex, coarsely cut into mostly large, entire to shallowly toothed ultimate segments, apex gradually reduced, pinnatifid, as is the apex of the larger pinnae; sori mostly on adjacent vein ends, indusium broadly cuneate, nearly equal to the short, somewhat modified, indusiform, marginal lobule. The characters of the sori of this species and the next were well brought out by Maxon[19].

One basionym has syntypes that are certainly different species but I have not attempted to choose a lectotype since I do not have adequate information about one of the elements (the Raddi collection). If the Sloane table were chosen as lectotype, then the name would be a synonym of *Saccoloma domingense*. *Pteris Sloanei* Raddi, Pl. Bras. 1:49. 1825. Syntypes: Sloane, Hist. Jam. t. 47 (= *Saccoloma domingense*) and Raddi, t. 71 bis (or the original specimen) (= ?). *Davallia Sloanei* (Raddi) Jenm. Jour. Bot. 1886:37. A complete description is given of the specimen, Mount Diablo, Jamaica, *Sloane* in 1688 (BM, fragment NY!), from which Sloane, Hist. Jam. t. 47 was prepared. *Saccoloma Sloanei* (Raddi) C. Chr. Ind. Fil. 612. 1906.

All Greater Antilles; Dominica, Martinique and Guadeloupe; Venezuela, Colombia, Brazil.

Although most specimens of *Saccoloma domingense* and *S. inaequale* are very different in aspect, I have not been able to find reliable characters by which to separate them. Carl Christensen remarked that "The extreme forms of these two

---

[19] Sci. Surv. Porto Rico and V. I. (Pterid.) 6: 490. 1926.

species . . . look distinct enough, but several intermediate forms occur."[20] The characters of the complexity of the lamina, mentioned above, seem to be at least as reliable as those of the sorus brought out by Maxon. Usually the two sets of characters are closely correlated, but sometimes they are not, and the identification of an intermediate specimen may depend upon which character is principally employed.

It is difficult to interpret these intermediates as hybrids for they sometimes occur in areas well beyond the range of *Saccoloma domingense*. It is also difficult to consider that *S. domingense* might be a hybrid of *S. elegans* and *S. inaequale* for it occurs in the Lesser Antilles where *S. elegans* does not grow. I believe that *S. domingense* is a rather questionable species but I hesitate to suggest a change in its status without a better understanding of it.

3. **Saccoloma inaequale** (Kze.) Mett. Ann. Sci. Nat. IV, 15:80. 1861.

Davallia inaequalis Kze. Linnaea 9:87. 1834. Type: Yurimaguas, Maynas (now Alto Amazonas), Peru, Dec. 1830, Poeppig, Diar. 2113, probably at LZ, destroyed; isotype: GH!, B! photo GH.

Davallia nigrescens Kze. Bot. Zeit. 1850: 132. Syntypes: Brazil, *Blanchet 2507*, *Martius 379*, duplicate US!, *Godet*.

Saccoloma Guentheri Rosenst. Fedde Rep. Spec. Nov. 25: 58. 1928, ex char. Type: Bolivia, *Buchtien 16*.

Ithycaulon inaequale (Kze.) Copel. Univ. Cal. Publ. Bot. 16:80. 1929.

Ithycaulon Guentheri (Rosenst.) C. Chr. Ind. Fil. Suppl. 3, 116. 1934.

Orthiopteris inaequalis (Kze.) Copel. Gen. Fil. 50. 1947.

Lamina bipinnate or more complex, rather finely cut into mostly small, strongly toothed or lobed ultimate segments, apex gradually reduced, cut almost to the rachis, as is the apex of the larger pinnae; sori distant, indusium narrowly cuneate, shorter than the unmodified opposed margin.

I have not been able to establish the identity of *Dicksonia Eggersii* Prantl, Engl. Bot. Jahrb. 24:84. 1897, nomen nudum. The collection cited, Cuba, *Wright 897*, is represented by numerous specimens of both *Saccoloma inaequale* and *S. domingense*.

The following two names may belong to this species; an

---

[20] Kungl. Svensk. Vet.-Akad. Handl. 16^3: 44. 1936.

examination of the type, in each case, will be necessary to determine if it is a *Saccoloma*, a *Microlepia* or perhaps a *Dennstaedtia.* The first name, if it represents *S. inaequale,* would furnish the earliest epithet for this species.

Davallia distans Kaulf. Enum. Fil. 222. 1824. TYPE: Brazil, Herb. Mertens (the collection is probably at LE).

Microlepia brasiliensis Pr. Tent. Pterid. 125, t. 4, f. 23. 1836. Commonly referred to *Microlepia Speluncae. Saccoloma brasiliense* (Pr.) Mett. Ann. Sci. Nat. IV, 15:80. 1861.

Southern Mexico to Panama; all Greater Antilles; Dominica, Martinique and Guadeloupe; French Guiana west to Colombia, south to Bolivia; Brazil.

5. THE TYPE SPECIMENS OF KAULFUSS

Georg Friedrich Kaulfuss described many new species of pteridophytes, most of them in his Enumeratio Filicum of 1824. In this book he described the novelties collected by Chamisso, on his voyage around the world, as well as new species from material obtained from other sources. Kaulfuss' herbarium was acquired by Count von Roemer of Dresden and the Roemer herbarium, in turn, was acquired by the University of Leipzig.

The collection at Leipzig was destroyed during the last war so that, unless Kaulfuss returned material to a correspondent, all of the holotypes of his names may be assumed to be lost.

The purpose of this note is to call attention to the location of some of the collections that may serve to replace the lost holotypes.

The most important single collection described by Kaulfuss is that of Chamisso. The Index Herbariorum indicates that the original set of Pteridophyta is at Paris. However, an incomplete survey of the Chamisso collections at Paris and at Leningrad, that I made in 1960, indicated that the original set of Pteridophyta is at Leningrad with the other Chamisso material. The labels at Leningrad say "Herb. Chamisso" and, in comparing the same collection, the label and the specimen are both more ample there than at Paris. The specimens at Paris are all in Herb. Bory and, at least among the species I searched for, the set was not complete.

Other specimens that may replace Kaulfuss' types should be sought especially at B, C, LE, P and W. For example, an isotype of *Dicksonia rubiginosa* Kaulf. (Rio de Janeiro, Herb. Mertens) is at LE and one of *Saccoloma elegans* Kaulf. (Brazil, *Sello*) is at B. While these authentic specimens may be used to fix the application of the name, they should not receive any designation other than isotype until an adequate survey of other herbaria has established the specimen best qualified to serve as a neotype.

In this regard it is important to identify any annotations in Kaulfuss' hand and a specimen of his writing has kindly been furnished by Clive Jermy and J. A. Crabbe of the British Museum (Natural History). I have not been able to identify with certainty Kaulfuss' writing on any label. For the benefit of those who may have occasion to use it, I have reproduced Kaulfuss' signature in Fig. 13. — GRAY HERBARIUM, HARVARD UNIVERSITY.

A MONOGRAPH OF THE FERN GENUS JAMESONIA[1]

ALICE F. TRYON

Jamesonia is a well known genus, classically cited for the peculiar, indeterminate linear, habit of the leaves, but the species have been much neglected. Specimens have accumulated in herbaria for some two hundred years since Joseph de Jussieu collected a few leaves of it in Peru, sometime between 1747 and 1777. Many specimens were added during the European expeditions to South America by Karsten, Lehmann, Lindig, Née, and Schlim and they have increased more rapidly during the past thirty years through the collections of Asplund, Barclay, Cuatrecasas, Killip, Smith, and Schultes. Most of the botanists on the Cinchona Mission of the Foreign Economic Administration collected members of the genus and the South American botanists Bües, Cárdenas, Fernandez-Perez, Idrobo, Jahn, Vargas, Vareschi have added new records and collections of special interest. There is still need for complete specimens and distribution records from many areas but there has accumulated a sufficient number of collections to survey the species and to understand the relationship of the genus to others.

In this pursuit, I am indebted to many. In the search for type material in the herbaria of Europe, I was especially aided by Drs. J. Dandy, C. Jermy and by J. Crabbe at the British Museum; at Kew, Mr. F. Ballard facilitated the photographing of specimens; at Paris Drs. M. Tardieu-Blot and A. Lourteig were most helpful in locating type material; Dr. K. Kramer, at Utrecht has made suggestions on the geographic discussion; Prof. E. Asplund at Stockholm has generously shared duplicates of his collections and observations of these plants in Ecuador; at Berlin, Dr. D. Meyer was helpful in the study of the material arranged by Hieronymus; at Leningrad, Prof. B. Schischkin and A. Brobrov were most cooperative in locating and photographing the collections of Karsten.

It is with special pleasure that I recollect the many kindnesses received while collecting in Venezuela and Colombia. Drs. J. Steyermark and L. Aristeguieta expedited our trip to Mérida, Venezuela and at the University de los Andes

---

[1] Grant G18906 from the National Science Foundation has supported the field studies and collections in Venezuela and Colombia and the cost of the illustrations.

there, Drs. C. Liscano and L. Luna of the Facultad de Ciencias Forestales generously helped us with transportation. I was fortunate to meet at Mérida, Dr. F. Tamayo who has made many collections on the páramos.

The collections and data I obtained in Colombia are abundant and for these I am most indebted to Dr. A. Fernandez-Perez who made our trip there a successful and pleasant one. My special thanks are expressed to Maria T. Murillo whose cheerful company carried us through the bad weather of the páramos. The Padres G. Huertas and L. Camargo took us to and discussed the vegetation of the páramos they know especially well around Zipaquirá. In southern Colombia, in Popayán, we were fortunate to meet the Colombian ornithologist, F. C. Lehmann, who continues the interests of his famous grandfather, the botanical collector, in the natural history of this region.

I am grateful to the Curators of the herbaria cited for the loan of specimens for extended study. The abbreviations of the herbaria are from Index Herbariorum, The herbaria of the world, fourth edition, 1959, by J. Lanjouw and F. A. Stafleu.

I am especially appreciative of the help of Dr. Yu-Chen Ting, Research Fellow of the Bussey Institution, with the analysis of the chromosomes and the photograph of them; of Dr. Robert Foster for his considerable emendation of my Latin; and for his good company and council throughout the study I am indebted to my husband, Rolla Tryon.

HISTORY OF THE GENUS

The genus is named for William Jameson, born in Edinburgh in October, 1796. He was trained there in medicine and, soon after receiving his degree from the Royal College of Surgeons, became a surgeon on a whaler bound for Baffin's Bay. His first collections out of Scotland were made on Hare Island on that voyage, and he refers to his observations of arctic plants in his later work treating the alpine flora of the Andes. In 1820 he became surgeon on a ship bound for South America, landing first at Rio and then Callao. He left the ship to stay at Lima and later at Guayaquil and in 1826 he moved to the more salubrious climate of Quito. There he was appointed Professor of Chemistry and Botany at the University and later became Assayer of the

Mint and Director and Treasurer. In 1864 he was appointed by the Ecuadorian government to undertake botanical explorations and prepare a Flora of Ecuador. His three volumes, Synopsis Plantarum Aequatoriensium, printed in Quito, dated 1865, are notable as the first botanical work to be issued from the press in Quito, and the work was well reviewed by the Chilian botanist, Philippi. The Order Caballero of Spain was conferred upon him by Queen Isabella in 1867. He visited Edinburgh and London in 1872 and was entertained by J. D. Hooker and Bentham. He returned to South America early in 1873 and died, in Quito in June of that year, from fever contracted on the return voyage. His numerous collections were sent particularly to W. Hooker. This genus as well as many species of ferns and flowering plants commemorate his name and his contribution to our knowledge of the South American flora.

Hooker and Greville proposed the genus with one species, *Jamesonia pulchra*, in Icones Filicum (1830) from a collection sent by Jameson. In the addenda of the work they substituted for *Jamesonia pulchra*, a new combination *Jamesonia imbricata*, based on *Pteris imbricata* Swartz. They note that Kaulfuss called their attention to the earlier name although the description of this was not correct for their material. Indeed it was not, for *Pteris imbricata* is based on a collection of Joseph Jussieu from Peru and differs from Jameson's which is actually a mixture of two other species.

Gustav Kunze was the first to treat several species of *Jamesonia* with much thoroughness. In his sketch of the genus (1844) and in Die Farrnkraüter (1846) he described four new species including details of the stele, the orientation of the pinnae, the number of cells in the annulus and stomium and made comparisons between the species. Soon after, J. F. Klotzsch in his contributions to the flora of equatorial regions of the New World (1847), reduced *Jamesonia* to one of six sections under *Gymnogramma*. His sections are unsatisfactory in light of our present information but the classification of *Jamesonia* in a subgeneric rank was a progressive idea and set a precedent for subsequent work. The first botanist to study the plants in the field was H. Karsten. He described five new species in the Flora Columbiae (1862-65) from his collections in Venezuela and Colombia and made reference to the aspect of living plants.

His interest in the chemical composition of plant material is evident from the report of the glands, especially abundant on the young leaves, bearing stearoptene, soluble in alcohol. The excellent plates in this work, drawn by Düwel, are the finest done for the genus and have been reproduced in several later works.

In the fifth volume of Species Filicum (1864) by W. J. Hooker, *Jamesonia* was compressed into one species, *Jamesonia imbricata,* with four varieties. In his Reliquiae Mettenianae (1868) M. Kuhn recognized six species (under *Gymnogramma*) and in his studies of the *Chaetopterides* (1882) he treated these along with others in a new genus, *Psilogramme.*

Jamesonia was taken up again with eight species by L. Diels in his treatment of the *Polypodiaceae* (1899) in Die Natürlichen Pflanzenfamilien. Two new species were described by G. Hieronymus in his Plantae Lehmannianae (1904) in *Gymnogramma,* under section *Jamesonia* and although he published no more on them his organization and annotations of the specimens in the herbarium at Berlin illustrate an understanding of the group. In F. O. Bower's morphological studies on the *Polypodiaceae* (1928), the gymnogrammoid ferns were divided into four groups and the inclusion of *Jamesonia* in the first group of relatively primitive genera is based largely on the reports of J. M. Thompson (1918). Unfortunately these reports are erroneous in regard to the acrostichoid condition of the sporangia and the spore number 56-72 per sporangium.

C. Christensen in his classification of the Filicinae (1938) placed *Jamesonia* in its most natural alliance with *Gymnogramma* and *Pterozonium,* in the *Chaetopterides* in the tribe *Gymnogrammeae* of the *Polypodiaceae.* He remarked that *Jamesonia* is hardly different from *Gymnogramma.* In his review of the classification of Leptosporangiate ferns (1946), R. E. Holttum treated *Jamesonia* in *Adiantaceae* and followed Bower's classification of it in a group of primitive genera of the gymnogrammoid ferns, apart from *Gymnogramma.* In Genera Filicum (1947), E. B. Copeland places *Jamesonia* and *Pterozonium* after *Eriosorus,* the nomenclatorially correct name replacing *Gymnogramma,* in the *Pteridaceae,* along with 60 other genera.

Most recent studies of *Jamesonia* are represented by unpublished notes accompanying herbarium specimens in the United States National Herbarium, by W. R. Maxon (although he published two new species) and in the British Museum, by A. H. G. Alston. The ample collections of *Jamesonia* from Venezuela and Colombia made by Alston in 1939 are complete ones and illustrate some variants of special interest.

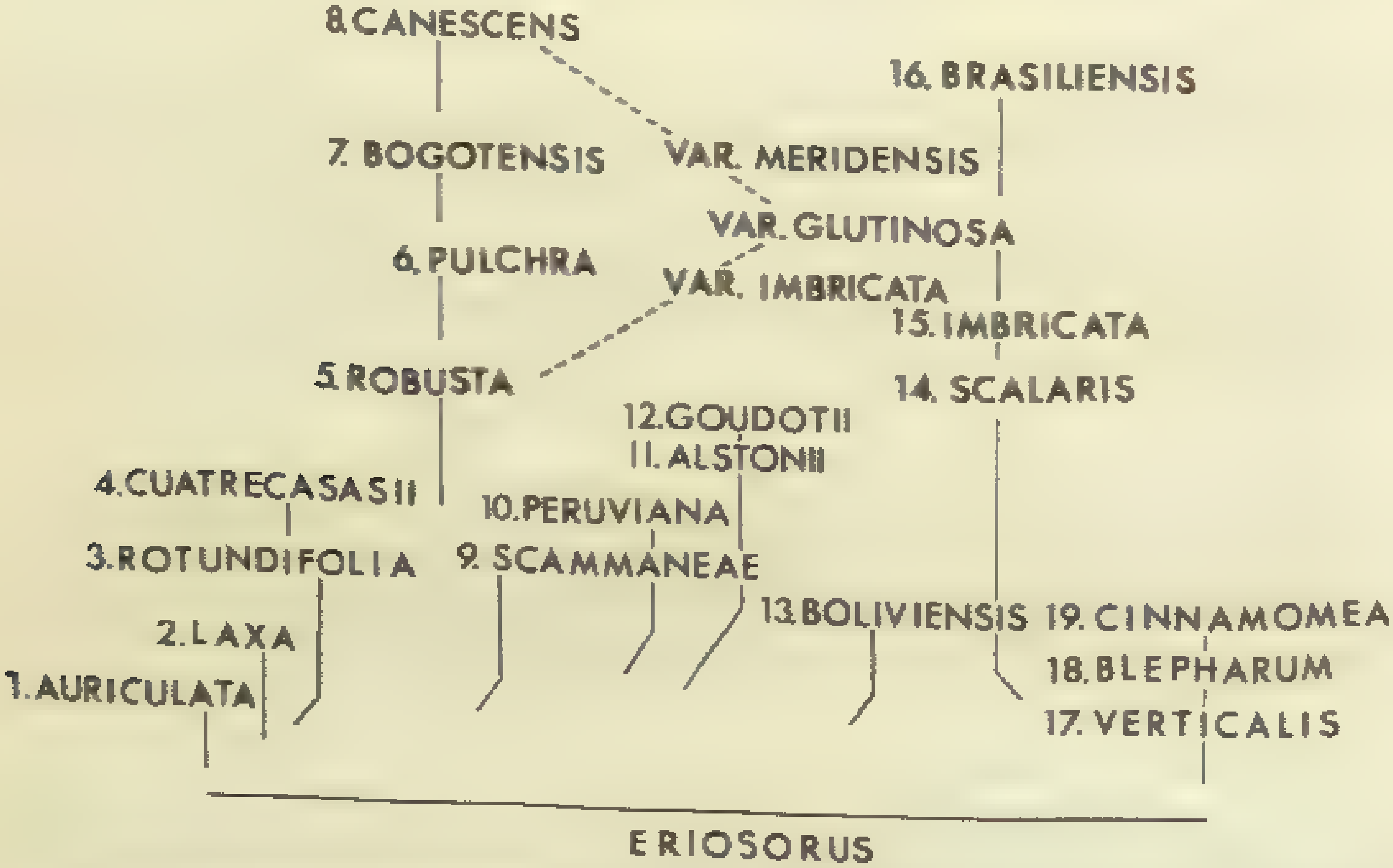
Comparative surveys of the species of *Jamesonia* virtually cease with the work of Karsten in 1865 and subsequent studies are either descriptions of a few new species or concern the generic classification with little new information that would contribute to a more satisfactory classification.

COMMENTS ON THE GENUS AND SPECIES

The Old World genera of gymnogrammoids, *Syngramma, Craspedodictyum* and also *Taenitis*, have been considered as a natural group by both Copeland and Holttum. These have bristle-like rhizome trichomes similar to those of *Jamesonia, Eriosorus* and *Pterozonium;* the spores are clear or white, with the proximal face round or sub-triangular in outline and smooth or nearly so (in *Taenitis blechnoides* there is a circumferential wing above the midplane on the proximal face); venation is predominately reticulate; sori extend along the veins or are variously interrupted on them in clusters or bands parallel to the margins; sporangia are in mixed stages of development throughout the sorus; and paraphyses are numerous. Manton (1958) reports a chromosome count of $n = 44$ in *Taenitis blechnoides* and $n = 116$ for *Syngramma quinata*, both from Malaya, and regards them as quite different cytologically. A detailed study of these Old World genera would be of much interest.

The American gymnogrammoids, *Eriosorus, Jamesonia* and *Pterozonium*, constitute a natural group distinct from the Old World genera in pattern of venation, soral arrangement, alignment of sporangia, indument of the lamina, and spores. Whether similarity of rhizome indument in the Old and New World genera is evidence of an ancient relationship or of parallel development of the character is not certain.

Jamesonia can be distinguished among the American genera by the linear leaves, usually indeterminate and once pinnate, often densely tomentose with pinnae usually entire and imbricate. There are at least two elements of the genus more closely related to species of *Eriosorus* than they are to each other. The phyletic chart will serve to illustrate these and to summarize the relations discussed in this and the following paragraphs. One of the elements comprised of *J. verticalis*, *J. blepharum* and *J. cinnamomea* differs from the other species in having the lamina apex often determinate, the rachis base sulcate, pinnae adnate or with short, broad stalks, rigid herbaceous or coriaceous, somewhat rectangular epidermal cells having walls scarcely undulate, pinna margins ciliate, and dark brown spores. There are resemblances in these characters to *Gymnogramma Mathewsii*, *G. longipetiolata*, *G. rufescens* and *G. setulosa* which have not been transferred to *Eriosorus*. The second element consists of largely diverse species some of which may be independently derived from *Eriosorus*. They are characterized by usually indeterminate leaves with the rachis terete or trigonus, pinnae with relatively long stalks, herbaceous with elongated or roundish epidermal cells having deeply undulate walls, pinnae usually with broad borders and tan or light brown spores. There are some resemblances to *Eriosorus elongatus* in these characters. *J. auriculata* is most closely related to *Eriosorus* and with two others, *J.*



Phyletic chart of *Jamesonia* showing two separate lines from *Eriosorus* at the right and left with related species placed as explained in the text. The broken lines connect taxa which have probably hybridized.

laxa and *J. rotundifolia*, form a relatively unspecialized group.

Four species *J. robusta, J. pulchra, J. bogotensis*, and *J. canescens* have broad, membranous, dentate borders and dense tomentum on the lower pinna surface and form a closely related series. On the basis of light colored spores and dense tomentum, *J. Scammanae* seems to belong with this group but it has nearly subsessile pinnae with the borders entire and of a firm texture. *J. Alstonii* and *J. Goudotii* are closely related species distinguished from the others by coriaceous pinnae with sparse tomentum, or none, on the under surface. *J. peruviana* and *J. boliviensis* are similar to these in having little or no indument on the lower pinna surface. The latter is distinct in the genus in having short, erect, one or few celled trichomes, similar to those in *Eriosorus elongatus* on all surfaces of the pinna and margin. *J. imbricata* var. *meridensis* and var. *imbricata* are considered as intermediates between var. *glutinosa* and other species. Although *J. brasiliensis* is distinguished in having thin, herbaceous pinnae with strongly enrolled margins, in the patelliform shape, truncate base and bent stalks of the pinnae, it is similar to *J. imbricata* var. *glutinosa.* On these characters the latter two and *J. scalaris* form a separate group somewhat intermediate to the *J. verticalis* and *J. auriculata* groups.

The rigorous páramo habitat has undoubtedly influenced the reduced leaf form in *Jamesonia.* Isolation is a conspicuous feature of the páramos although the wide geographic distribution of several species reflects more continuous ranges in the past. Interruption and reconvergence of ranges and populations in these highlands would likely fluctuate along with climatic changes accompanying Pleistocene glaciation. Adjustment to these changes in environment seems to have been through changes especially in the reduction of the leaves. This is illustrated in *J. Cuatrecasasii* in which the pinnae are drawn close together by short stalks fixed to the upper pinna surface. This is a unique adaptation in a largely isolated species which, in other characters, resembles more widely distributed ones.

Interspecific hybridization, perhaps brought about through adjustments of geographic ranges in response to the changing environment, has been another evolutionary mechanism. Intermediates occur in some areas where species grow together and there are also some intermediates with *Eriosorus*. The report of the hexaploid number n = 87 for *J. bogotensis* suggests that polyploidy and hybridization both have been operative in the genus.

The species of *Jamesonia* represent at least two and perhaps more distinct lines which seem to have come from *Eriosorus*. These reticulate relationships, as well as hybridization between the genera, support the idea that the species now treated as *Jamesonia* and *Eriosorus* belong in a single genus; the groups in *Jamesonia* representing some specialized elements of the larger unit. The combination of these genera necessitates no changes in nomenclature, for the species treated here, since *Jamesonia* is the earlier name. However, the transfer of species at present in both *Gymnogramma* and *Eriosorus* to *Jamesonia* is best delayed until a survey of these is completed.

The species concept that I have adopted is the evolutionary one given by Simpson (1961) as a lineage evolving separately from others with its unitary evolutionary role and tendencies. The lineages are surmised from the morphological similarities of the plants and the morphological discreteness of one group of similar plants from another and thus are consistent with the evolutionary definition.

Since polyploidy has evidently been operative in the group, the full clarification of relationships awaits further cytological evidence. The relationships as presented in the present paper are for the most part drawn from comparisons of the various kinds of similarities and differences observable among the taxa. The species are to some degree comparable although they are not equally distinctive. Most of them, such as *J. Cuatrecasasii*, *J. auriculata*, *J. Scammanae*, *J. scalaris*, *J. boliviensis*, *J. brasiliensis*, and *J. peruviana* are quite discrete. Species such as *J. robusta*, *J. bogotensis*, *J. canescens* and *J. pulchra* are closer to each other. The greatest similarities and fewest differences exist between *J. Alstonii* and *J. Goudotii* and between *J. verticalis*, *J. blepharum* and *J. cinnamomea*. Within these two groups the species are very close although the relationships are not the same. Between the latter three there are intermediate specimens which appear to form a continuous series although the extreme type of each is distinct and the intermediates are few. In *J. Alstonii* and *J. Goudotii* the differences are comparatively slight but there are no intermediates. It is possible that these might be better regarded as subspecies but I have treated them as species since they differ in several characters. Less distinctive taxa have been recognized as varieties under *J. imbricata* and hybridization involving them is presumed to be present. The taxonomic disposition of *J. imbricata* var. *imbricata* and var. *meridensis* rests upon morphological similarity with var. *glutinosa*. In regard to the taxonomic treatment of hybrids, I am in agreement with the remarks made by F. R. Fosberg (1961), ". . . hybridity is merely a matter of origin, or putative origin of the population, and its taxonomic disposition would not be determined by this, but by its morphology and behavior as a population just as with any other entity. It may well have characters which place it closer to one parent than the other".

ECOLOGY AND GEOGRAPHIC DISTRIBUTION

Jamesonia occurs from southern Mexico to central Bolivia and Brazil mainly on páramos or on cool, wet highlands at altitudes ranging from 1500-5000 meters (Map A).

The ecological data on collections of *Jamesonia* usually includes the term páramo which has not been precisely defined. It is generally applied to the Andean highlands south to Ecuador, between 3200 and 5000 m., above the forests and below the permanent snow, and includes the shrubby zone sometimes called páramillo or subparamo. The composite genus *Espeletia* characterizes the vegetation and its southern limit in Ecuador also delimits the páramo. *Jamesonia* is included among the genera distinguishing the páramo. The critical environmental factors to which the vegetation of the páramo is adapted are wind, strong insolation, high moisture in the soil and in the air in the form of clouds or fog, and cool temperatures ranging usually from 12° C. to -2° C. At the highest altitudes there are diurnal fluctuations in temperatures with freezing during the night. Dry seasons are mentioned for some páramos. In some species of *Jamesonia*, particularly *J. laxa*, there are growth zones on the leaves which evidently are the result of periodic growth.

There are several accounts of the vegetation of the Andean

PLATE 1. Páramo near Laguna de Anteojos, 4000 m., above Mérida, Venezuela. *J. imbricata* var. *meridensis* (lower right) at the base of a large rock, and rosettes of the Composite, *Espeletia*.

region which include portions on the páramo — the phytogeographic sketch of Latin America by A. C. Smith and I. M. Johnston (1945), a description of the large Páramo de Sumapaz, south of Bogotá by F. R. Fosberg (1944) and geobotanical observations of Colombia by J. Cuatrecasas (1934). In each of these there are excellent photographs of the páramo, and in the last, one of *Jamesonia* in fine detail.

Jamesonia is not restricted to the páramo or its subdivisions but I found it without exception and often in abundance on five páramos on which I collected in 1961 in the states of Mérida and Táchira, Venezuela and on ten of them in the departments of Caldas, Cauca, Cundinamarca and Huila, Colombia. On these it occurs frequently in soil at the base of rocks and boulders (plate 1) and sometimes in open grassy meadows growing with rhizomes deeply embedded in the grassy turf. In some cases the grassy areas are known to be burned and presumably the rhizomes are resistant to this. Several species grew in the open soil along road cuts which indicates the ability of these plants to establish themselves in newly available areas.

The páramos above Mérida are readily accessible by cable car covering 12.5 kilometers and 3125 meters altitude in a few minutes. The terrain is irregular here with several small glacial lakes and towering snow covered peaks, Espejo, Bolivar, Humboldt, and Bonpland. In mid-September there was heavy rain and fog in the afternoon and sometimes snow. *J. canescens* was abundant here in scattered colonies between 3400 and 4000 meters (plate 2). It was usually among rocks but also on grassy slopes where the leaves were more slender with delicate petioles and whiter tomentum. *J. imbricata* var. *meridensis* was less frequent but in large colonies growing near *J. canescens*. *Cystopteris fragilis* (L.) Bernh., *Polypodium peruvianum* Desv., *Blechnum loxense* (HBK.) Hieron., *Lycopodium contiguum* Kl. and species of *Elaphoglossum* and *Polystichum* also occurred there. *Compositae* were the most conspicuous of flowering plants with both the white and yellow flowered *Espeletia*, *Senecio*, *Baccharis* being common. Other families were represented by *Echeveria*, *Lobelia*, *Castilleja*, *Sisyrinchium* and *Gentiana*. The flora is a colorful one reminiscent of alpine regions of the North American Rockies. East of Mérida in the

Sierra de Santo Domingo the mountains are lower. The páramos are of similar rough aspect often surrounding glacial lakes but there may be shrubby vegetation in protected localities. Plants of *J. canescens* were widespread near the base of rocks and were conspicuously variable as to the size and indument of the pinnae. Some of them had many small, delicate, sterile leaves similar to those of *Eriosorus.* On the páramos and rocky ravines nearby there also occur *Woodsia montevidensis* (Spreng.) Hieron., *Pityrogramma chrysoconia* Desv., *Cheilanthes marginata* HBK. and species of *Dryopteris, Asplenium* and *Athyrium.* The largest colonies of *Jamesonia* observed were on the highest part of Páramo de la Negra in Táchira, Venezuela. There the plants form a carpet-like cover of white tomentose leaves in predominately grassy vegetation.

The floristically richest Colombian páramos were in the vicinity of Guasca and Páramo Palacio, north of Bogotá in Cundinamarca. *J. rotundifolia* and *J. imbricata* var. *glutinosa* were abundant in soil along the road cut and on the slopes above the road. There were also plants intermediate to these species and two species of *Eriosorus* growing among them. In patches of elfin-woods, the trees were covered with epiphytes including *Polypodium cultratum* Willd., *Polypodium radicale* Moritz, *Polypodium rigescens* Bory, and species of *Trichomanes* and *Elaphoglossum* and several small orchids. On the slopes above the road and in open soil along the road were *Lycopodium attenuatum* Spring, *Lycopodium firmum* Mett., *Lycopodium Jussiaei* Desv. and in high, flat areas *Lycopodium rufescens* Hook. occurred in *Sphagnum.* Several species of *Paepalanthus* were abundant and also *Gentiana* along with larger plants of *Puya, Berberis,* the ericaceous shrub *Macleania* and the arborescent *Blechnum Buchtienii* Rosenst. On a drier páramo, Patano Redondo, near Zipaquirá, which is known to be burned, we found *J. robusta* growing in a few large patches. It occurred also on an undisturbed hillside with outcropping sandstone to the east near Tausa, growing with *J. bogotensis.* In the Cordillera Central, on Páramo Ruiz, *J. robusta* also grew in drier, grassy areas and on the more moist road cuts there was *J. Scammanae.* On Ruiz there were some plants of *Espeletia* and *Lupinus alopecuroides* but the characteristic páramo vegetation has given way largely to grass through

PLATE 2. Above, a plant of *J. rotundifolia*, Páramo de Puracé, [illegible] m. Cauca, Colombia showing the densely tomentose, indeterminate apical buds of the leaves and stacked, sparsely indumented pinnae; below, leaves in a colony of *J. canescens*, Páramo near Laguna de Anteojos, 4000 m., above Merida, Venezuela.

burning and pasturing. The soil profile along the road there consisted of alternate bands of black and light brown soils. The black type formed the top layer, of the present páramo, and contained a large portion of humus presumably formed through slow deterioration. Humus was less evident in the lighter brown layers and this was formed, at least in part, from volcanic tuff. The banding showed repeated fluctuations which have interrupted the darker formation of páramo soils.

On Volcan Puracé, in Cauca, *J. Scammanae*, *J. imbricata* var. *glutinosa* and *J. rotundifolia* (plate 2) grew in scattered colonies along the road cut and adjacent slopes and on an open, grassy site there was a large colony of *J. pulchra*. The higher, wet areas of the volcano were rich in species of *Lycopodium*, *Begonia*, orchids and bromeliads, and the *Compositae*, except for *Espeletia*, were less conspicuous than in other páramos.

It is sometimes difficult to determine accurately the altitudes at which collections of *Jamesonia* have been made for they are reported as general ranges covering several hundred meters. Plants occur largely between 3000 and 4000 meters; the lowest record I have is at 1500 m. for *J. blepharum* in southern Peru and the highest at 5000 m. for *J. cinnamomea* in Ecuador. The three species with the widest geographic ranges also have the broadest altitudinal distribution with *J. Scammanae* having the greatest from 1830-4300 m. *J. brasiliensis* has the lowest altitudinal range, 2300-2600 m. and *J. cinnamomea* has the highest 3100-5000 m.

There is some correlation in the degree of specialization of species and the altitude at which they occur. *J. Cuatrecasasii* and *J. imbricata* var. *meridensis* are specialized forms and are reported from above 3500 m. In the closely related group of *J. verticalis*, *J. blepharum* and *J. cinnamomea*, the latter is most specialized and occurs at the highest altitude. In other species this correlation is not found for the relatively unspecialized species *J. rotundifolia* and the more specialized one, *J. canescens*, occur at nearly the same altitude.

The most restricted area in which all species occur (the least common area, Map A) is between Mérida, Venezuela and La Paz, Bolivia. The area of greatest species concentration, where eleven of the twenty-one taxa occur is between Bogotá, Colombia and Cuenca, Ecuador (Map A).

The geography of two groups in *Jamesonia*, distinguished on the basis of symmetry of the pinna and spore color, is considered separately. The first group of six taxa have symmetrical pinnae and dark spores. Among these *J. verticalis*, *J. blepharum* and *J. cinnamomea* form a distinct group. Each of these species occurs in the area of greatest species concentration, the first almost confined to it and the other two have widely disjunct stations extending south into Peru and Bolivia. Of the other three taxa, *J. imbricata* var. *glutinosa* occurs in the area of species concentration, *J. scalaris* and *J. brasiliensis* occur south of this in Peru and Bolivia. The last is the most notable member of the genus geographically because of its station on Mt. Itatiaia in Brazil. It was formerly considered to be endemic there but a few collections are now known from the highlands of central Bolivia. *Eriosorus* is also predominately Andean with a few species in Brazil. The latter are morphologically distinct from the Andean species except for *E. elongatus* which also occurs on Mt. Itatiaia and is widespread in Bolivia, Peru and Ecuador. The geographic history of this species seems to be similar to that of *J. brasiliensis*. A. C. Brade (1942) discussed the distribution of this along with other ferns having related species in the Andes. The disjunction between Brazil and Bolivia is noted in several fern genera by K. U. Kramer (1957) in his treatment of *Lindsaea* and he considers the possible connection through Matto Grosso and Minas Gerais. In a recent paper on the origin of the flora of southern Brazil, L. B. Smith (1962) takes up the Andean relationships in several genera of flowering plants. In *Tillandsia usneoides*, migration appears to have been from the Andes into southern Brazil and the same direction from the Andes into Brazil is evident in *J. brasiliensis*. There is, however, information from other groups that a westward migration has also occurred. This is discussed by R. Tryon (1944) in his study of the phytogeography of *Doryopteris* in which the species are concentrated in southeastern Brazil and migration is indicated westward into the Andes.

The species of *Jamesonia* having asymmetrical pinnae, and light brown or tan spores represent the largest group including the widest ranging as well as the most restricted members of the genus. *J. Alstonii* has the widest distribution from Central Bolivia to southern Mexico. *J. Scammanae* and *J. rotundifolia* also occur in both South and Central America and all three of these species occur on the volcanos of Costa Rica. They most probably migrated there from Colombia before the main orogeny of the Andes during the middle and late Tertiary. The land bridge connecting Colombia with Nicaragua was available for these species from late Miocene and Pliocene times. K. U. Kramer (1957) proposes a northward migration in *Lindsaea* from the Choco region of Colombia to the volcanos of Costa Rica on the basis of the close relationship of *Lindsaea Seemannii*, endemic to to the Choco, and the Costa Rican endemic, *L. pratensis*. In the distribution of species in *Eriosorus*, *Equisetum* and *Doryopteris* there is also evidence for a northward migration. In other groups, however, as *Pellaea* (Tryon & Britton, 1958) there are cytological data which show that a southward migration from Mexico into South America has occurred.

The species in *Jamesonia* having the most restricted distributions are *J. laxa*, *J. auriculata* and *J. canescens* in the State of Mérida, Venezuela and *J. Cuatrecasasii* and *J. imbricata* var. *meridensis* which also occur there and with second stations in the sierras of northern Colombia. The first two are relatively unspecialized forms and the latter three are specialized.

If the relatively restricted and isolated areas in which the species now occur are considered along with the relatively broad geographic ranges of some of the species, the idea that the conditions under which the plants now grow were at one time more widespread is supported. During Pleistocene glaciation when glaciers descended to an average of 4000 meters in the Andes, the cold, moist conditions under which these species grow would have reached lower altitudes resulting in a greater continuity of this type of habitat.

The present ranges of the species afford some evidence for past distributions. From the least common area between La Paz, Bolivia and Mérida, Venezuela, species such as *J. Alstonii*, *J. rotundifolia* and *J. Scammanae* probably migrated north into Mexico and the last also south of the area into central Bolivia. Eleven species occur in the area of concentration and it is possible that this may be a center of origin for some of them.

Some conclusions can also be drawn from the nine species which do not occur in the area of species concentration. Five of these are concentrated mainly in the Sierra Nevada de Mérida in Venezuela. Of these *J. auriculata* and *J. laxa* are most restricted and least specialized. They are species which have been either derived from an ancestor in *Eriosorus* in or near this region or perhaps represent isolated elements of once more widely ranging species. The others, *J. Cuatrecasasii*, *J. canescens* and *J. imbricata* var. *meridensis*, are more specialized taxa of Mérida which are related to species occurring southwest in Colombia. The three species that occur south of the area of species concentration, *J. boliviensis*, *J. scalaris* and *J. brasiliensis*, are morphologically distinct from the previous species and illustrate the development and migration of species in the southern and southeastern portion of the range.

MORPHOLOGY AND ANATOMY

RHIZOME. — The rhizome in *Jamesonia* is cylindrical, creeping, dichotomous and slender 0.5-5.0 mm., usually about 2 mm. in diameter (plate 3). Coarse roots, nearly equal to the petioles in diameter, arise in the stele and protrude from any surface. These are often dense and matted about the rhizome and are especially large adjacent to the petioles. There is a collar of epidermal tissue ensheathing the root where it emerges from the rhizome. The leaves are alternate and variously distant on the rhizome depending upon the compactness of the axis. A leaf gap occurs above the leaf trace, or if the internodes are shortened, the leaf gaps may overlap and the stele is correspondingly dissected. The rhizome is an amphiphloic siphonostele having dictyostelic stages. There is a central sclerotic pith and a neck of similar tissue connected to it where the stelar ring is interrupted by leaf gaps. The vascular tissues of the root are contiguous with those of the rhizome and with the exception of the endodermis are unbroken where these organs join.

The rhizome is composed of an epidermis, more or less covered by trichomes, cortex, and stele with a central pith which consists of thick walled cells. The epidermis consists of small, brown, thin walled cells which form a rather even

PLATE 3. Plants of *J. canescens* from Paramo de la Negra, 3000 m, Tachira, Venezuela showing the elongate creeping rhizome. Plants from this páramo have especially dense, whitish tomentum on the leaves. *Tryon & Tryon 5886* (GH).

surface. The trichomes arise from the epidermis and consist of larger, inflated cells and are usually darker colored. The cortex is composed largely of sclereids having thick, dark brown walls with slit-like pits and large lumina usually filled with spheroidal starch particles. The pith and cortex as well as the neck of tissue which connect these at the leaf gaps are of this same sclerotic tissue. There is an area of parenchyma tissue in the cortex adjacent to the outer endodermis which is unusual in fern rhizomes. This tissue completely surrounds the stelar ring or is adjacent to the outer layer of endodermis if the stele is dissected, and is also filled with starch particles. The stele has an internal and external layer of relatively small, brown-colored endodermal cells. There are thin walled cells, clear or scarcely colored, within the endodermal tissues which form the pericycle or possibly portions of the phloem. These are larger and less compressed than the adjacent angular cells of the phloem which are often crushed in transverse section. The xylem is composed of compact tracheids of various sizes having acute ends and scalariform to somewhat reticulate thickened cell walls. The amphiphloic stelar arrangement in *Jamesonia* occurs in several other genera with creeping rhizomes as *Adiantum* and *Dennstaedtia*. The dissected form of the stele, with overlapping leaf gaps resembles the form of some stages of the rhizome of *Anemia phyllitidis*. The rhizome of *Jamesonia* represents an intermediate type having both siphonostelic and dictyostelic stages and with fewer changes in form than rhizomes of *Anemia* or *Schizaea*.

The dermal appendages of the rhizome are concolorous, tan to lustrous black and range from 0.5-3.0 mm. long. For the whole or most of the length they are one cell wide although the basal cell may be larger and inflated and the attachment to the epidermis of the rhizome may be in the central rather than the basal portion of this cell. In several species there are two or more cells at or near the base and in the strict sense these appndages would not be trichomes but neither are they scales for they are thickened with clustered cells. The rhizomes in all species of *Jamesonia* have some trichomes only one cell wide and in some species only this kind occurs, thus I consider the more elaborate appendages, having more than one cell at the base, as modified or bristle-like trichomes. Light colored trichomes, only one cell wide, are usually lax and patent and darker ones, a few cells broad at the base, are usually rigid and appressed to the rhizome. The terminal cell of the trichome is usually acuminate as in *J. canescens* and *J. Scammanae* and similar to other cells of the trichome. In some species the terminal cell is bulbous, of a clear diaphanous material, and appears as if the outer portion of the cell wall has been cast off. In *J. Alstonii*, *J. verticalis* and *J. imbricata* var. *glutinosa* these occur on the older portions of the rhizome and the acuminate form nearer the apex. In *J. scalaris*, *J. brasiliensis* and *J. Goudotii* the rhizome trichomes are predominately of the bulbous form and in *J. blepharum* and *J. verticalis* an exudate is produced at the bulbous apex. In some species of *Jamesonia* the rhizome indument is relatively uniform, correlates with other characters and expresses relationships, but for the most part it is more plastic than other characters of the plants. In *Eriosorus* and *Pterozonium* the rhizome indument is of the same form, with the same variations as in *Jamesonia*, and may be useful in establishing natural lines between these genera. The rhizome indument is also similar in other gymnogrammoid genera *Syngramma*, *Craspedodictyum*, *Taenitis* and *Aspleniopsis* but if a relationship exists between these genera and *Jamesonia* it is more distant.

LEAVES AND PINNAE. — Most species of *Jamesonia* have leaves with indeterminate growth. This is evident in the continued development of the apical bud while the basal pinnae on the leaf have deteriorated or been lost. In *J. laxa* the pinnae are in marked growth zones. The leaf apex is usually fully expanded and determinate in *J. verticalis* and sometimes so in *J. cinnamomea*, *J. blepharum* and *J. imbricata* var. *glutinosa*. In seven of the species there are specimens in which the basal pinnae are thin textured, plane and with dentate margins and in these characters are distinct from the upper pinnae. There may be several small leaves wholly of this form and resembling those of *Eriosorus*. The leaf form in *Jamesonia*, although generally more reduced in most species, resembles that in *Eriosorus*, particularly *Eriosorus elongatus*. The leaves in this species may be bipinnate, pinnate-pinnatifid or once pinnate and slightly lobed. The generic separation between *Eriosorus* and *Jamesonia* on the division of the lamina breaks down with this material.

In *Eriosorus* diversity of leaf form is less notable than in larger genera as *Adiantum* or *Lindsaea* since its closest relatives have been segregated mainly on leaf division. The leaves in most species of *Eriosorus* are small — less than 30 cm. long, bi- or tripinnate and are broadest at the base. The most reduced form is *Gymnogramma longipetiolata* (this has not been transferred to *Eriosorus*) which has few, entire pinnae at the end of a long petiole. There is a group of species related to *Eriosorus flexuosus*, with scandent leaves which may be a few meters long and elaborately branched in several planes. In *Eriosorus* and related genera, generally, species with leaves more than once pinnate are treated in *Eriosorus*, those with entire, simple leaves are in *Pterozonium* — although in these the sori are also specialized — and those with once pinnate, linear leaves are included in *Jamesonia*. Generic separation of this kind based solely on leaf form is incongruous for in *Eriosorus elongatus*, *Pterozonium spectabile* as well as in *Jamesonia* the leaves are once pinnate and linear. The greatest diversity in leaf form occurs in *Eriosorus* and it is possible that the types found in related genera may have been derived from this source.

In *Jamesonia* there are specific differences in the form of the pinnae, the orientation of the stalk and especially in the elaboration of the margin. The contracted pinna form of most species is indicative of a reduced condition but in two species the pinnae are relatively elongate. In one of these, *J. auriculata*, the basal lobes of the pinnae are comparable in size and form to the whole pinnae in other species. In *J. canescens* the acroscopic lobe is bent or the whole pinna is twisted and in *J. bogotensis* one or both of the basal lobes project above the upper surface of the pinna. These species with bent or twisted pinnae are considered more specialized than *J. robusta* in which the pinnae are accommodated in one plane. Two closely related species *J. Alstonii* and *J. Goudotii* differ in pinna shape. In the former they are mostly orbicular or ovate and in *J. Goudotii*, which is more specialized in other characters, they are mostly reniform. The pinnae in *J. scalaris* are usually three lobed and they are sometimes irregularly lobed in *J. Scammanae*. *J. imbricata* var. *glutinosa* and *J. brasiliensis* have symmetrical pinnae with the bases incurved and truncate.

There are three types of modification of the pinnae stalks each of which seems to reflect an independent change toward the reduction of the lamina. In *J. verticalis* the pinnae stalks are broad or the pinnae adnate and *J. blepharum* and *J. cinnamomea* with shorter pinnae have longer pinna stalks. The stalks in *J. imbricata* var. *glutinosa*, *J. brasiliensis* and *J. pulchra* are strongly bent and in the latter they may be curved nearly 90° and overlay an enlarged pinna lobe. The stalks are attached to the upper pinna surface and easily articulate in *J. Cuatrecasasii*. They also freely articulate in *J. peruviana* and *J. scalaris*. They are sometimes glandular as in *J. bogotensis*. The stalk color is atropurpureus or brownish and is carried into the veins of the pinnae in *J. auriculata*, *J. laxa* and *J. rotundifolia*. In other species as *J. canescens* and *J. Goudotii* the dark color extends only part way into the stalk and the upper portion and the veins of the pinna are tan.

The form of the pinna margin is one of the most useful diagnostic characters although this must be examined at approximately 80 magnifications. There is usually a border of specialized cells several cells broad along the margin which differ in texture from the rest of the pinna. In some species, particularly *J. imbricata* var. *glutinosa*, there is much variation in the border but for the most part it is one of the most useful characters for identification of the species and for establishing their relationships.

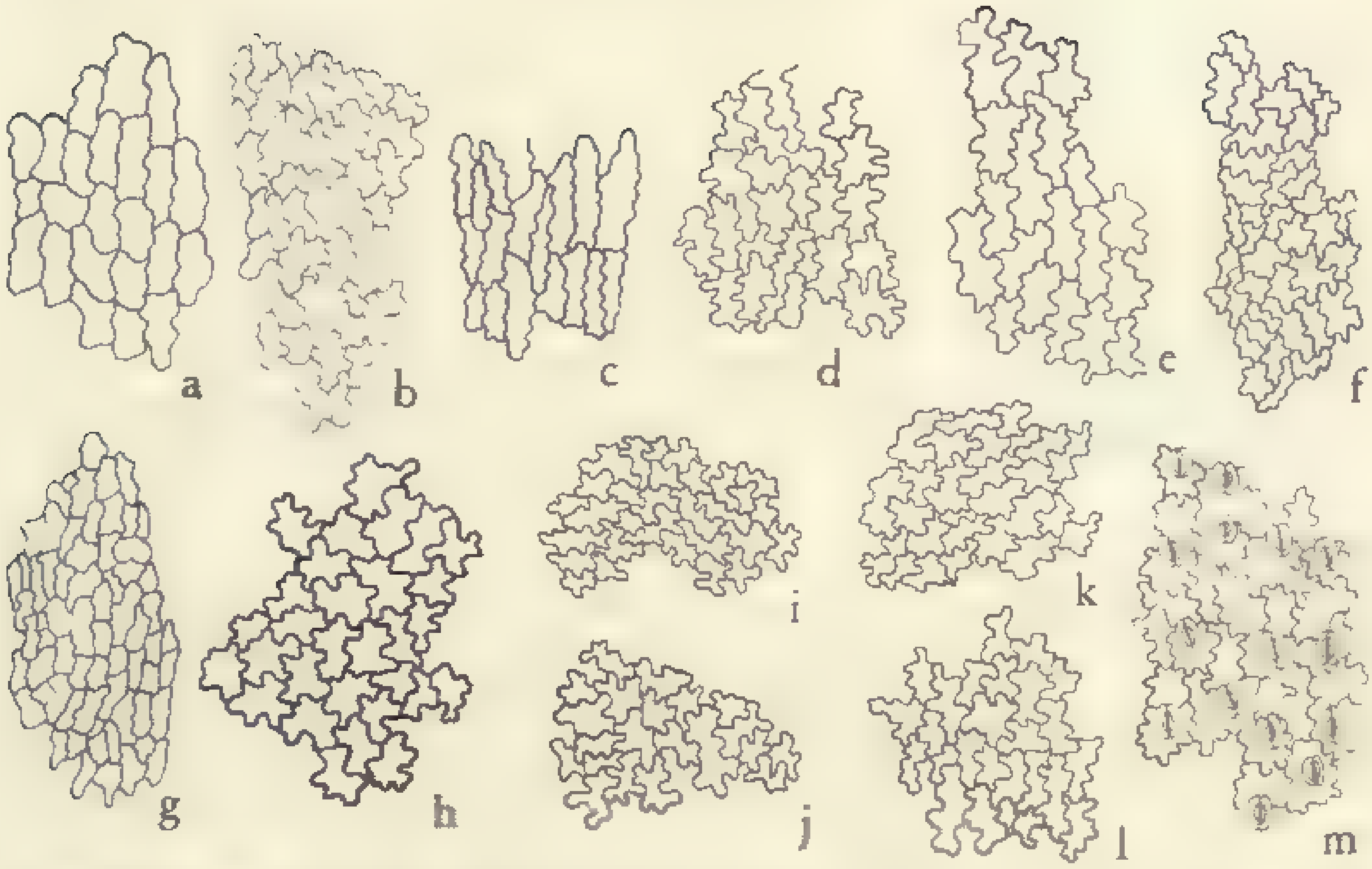
In the related species *J. auriculata*, *J. laxa* and *J. rotundifolia*, the margins are similar to those in many species of *Eriosorus* with few, irregular, protruding cells although in the latter a rather broad border may be developed. Other species close to these with tomentum on the lower surface have broad, membranous, dentate borders which may be indusioid. The less tomentose species related to *J. verticalis* have entire margins with cilia especially abundant at the vein ends.

Venation of the pinnae is open dichotomous. There may be characteristic patterns in groups of species but there is considerable variation depending upon size and shape of the pinnae. The position of the veins in the pinna tissues is usually near the upper surface or slightly sunken but in a few species they are raised. There are differences in the width and length of the veins, the angle at which the branches part and the shape of the ends. In *J. verticalis* and *J. blepharum* the vein angles are acute, the branches long and somewhat parallel and the ends broad and cuneate. The veins adjacent to the rachis are short and broad, the ultimate branches are long and equally dichotomous and there is usually no differentiated central member. They are also dichotomous with long ramifications in *J. rotundifolia*, *J. laxa* and *J. auriculata* but more slender and with wider angles than in the previous species. The venation is sympodial with a prominent central vein in *J. auriculata*. Most species particularly those with dense tomentum on the lower pinna surface have broad veins especially near the pinna stalk with wide angles and short to moderately long branches.

EPIDERMIS. — The cells of the upper epidermis have strongly undulate walls and are generally longer than broad. Near the veins they are rather rectangular and less undulate and near the pinna margin they are smaller with deeply undulate walls. In some species as *J. canescens* and *J. Alstonii* the epidermal cells are more uniform than in others. In *J. rotundifolia* and *J. canescens* the upper epidermal cells are about twice as long as they are in *J. Scammanae*, *J. imbricata* var. *glutinosa* and *J. scalaris*. The size of the cells is not correlated with the pinna size for a pinna of *J. scalaris*, about a third the size of one of *J. imbricata* var. *glutinosa*, may have epidermal cells as large as or larger than those of the latter.

The thick cell walls which occur in *J. Alstonii* and *J. Goudotii* are apparent in the dried condition. A distinct pattern of epidermal cells in *J. verticalis* and *J. auriculata* with nearly rectangular cells having slightly undulating walls is similar to that in species of *Eriosorus*.

The lower epidermis is distinguished from the upper by the stomata and smaller U-shaped cells with deeply undulate walls surrounding the guard cells. The pattern of the cell walls of the lower epidermis is relatively constant in all of the species although there are differences in the size of the guard cells. It would be of interest to survey larger samples to determine if these size differences might reflect different polyploid levels. The pattern of epidermal cells in most species of *Jamesonia* is illustrated by the series (d-f and h-l), and another form by (c and g) and also those of two



Epidermal cells from the mid-portion of the pinnae, equidistant from the veins: a-l upper epidermis, m. lower epidermis, all × 45. a, *Gymnogramma Mathewsii*, *Tryon & Tryon 5958* (GH); b, *Eriosorus elongatus*, *Killip & Smith 23249* (GH); c, *Jamesonia auriculata*, *Alston 7050* (GH); d, *J. rotundifolia*, *Cuatrecasas 20223* (GH); e, *J. canescens*, *Gabaldon*, in 1922 (US); f, *J. boliviensis*, *Vargas 1060a* (GH); g, *J. verticalis*, *Cuatrecasas 8793* (US), h, *J. Goudotii*, *Cuatrecasas 19110* (GH); i, *J. scalaris*, *Bues 2163* (US); j, *J. peruviana*, *Macbride & Featherstone 1883* (GH); k, *J. imbricata* var. *meridensis*, *Tryon & Tryon 5801* (GH); l, *J. imbricata* var. *glutinosa*, *Idrobo et al. 3150* (GH), m, *J. imbricata* var. *glutinosa*, lower epidermal cells and stomata, *Idrobo et al. 3150* (GH).

species of *Eriosorus* (a and b), illustrate the distinct patterns.

PETIOLE. — The petioles are castaneous to atropurpureous or sometimes blackish and usually strongly bent and appressed to the rhizome for a short distance before ascending. In most species they are shorter than the rachis but they may be up to four times longer in *J. verticalis*. The petiole thickness has in the past been reported in comparison to the thickness of the quills of various bird feathers. Both length and diameter of the petiole may vary in the species depending upon the habitat of the plant. Those from grassy or mossy sites where the rhizomes are deeply embedded in the vegetation have longer more delicate, filiform petioles than those growing higher among rocks. In species with filiform petioles they are thinnest just above the rhizome. The thickest petioles, about 3 mm. in diameter throughout, occur in *J. cinnamomea*. Petioles are terete, oval, or slightly flattened or channeled on the upper surface.

At 1 cm. above the rhizome the tissues are arranged similarly to those of the rachis. The epidermis is composed of dark brown cells and the cortex of thick walled, brown cells comprises the largest portion of the petiole. The cells of the cortical sclerenchyma are smaller adjacent to the epidermis and at the open side of the vascular arc. The endodermis surrounds the vascular tissues and as in the rhizome some parenchyma tissue occurs in the adjacent cortex. These cells and the adjacent sclerotic cells contain numerous, spherical starch particles. The vascular tissues form a central flattened U-shaped or C-shaped arc open at the upper surface of the petiole. The xylem consists mostly of large tracheids with smaller elements at the ends and sometimes at the center. The tracheid walls have scalariform or helical thickening. Adjacent to the xylem on the open side of the arc there are some angular and thin walled, homogeneous cells which may be phloem and possibly pericycle.

The indument on the petioles is less dense than on the rachis and is often lost with age but the form of the trichomes is similar to that of the rachis. The basal cell is often contracted into a foot-like portion as in the rachis trichomes.

RACHIS. — The rachis is generally the same color as the petiole or slightly lighter. The shape of the transverse section in the basal third of the lamina is terete to ellipsoidal or triangular with the lower surface convex and the upper surface of two planes converging in a broad angle or in a few species the rachis is channeled. The pinnae are decurrent on the rachis in *J. verticalis* and slightly so in some specimens of *J. Goudotii*. The pinna stalks in most species depart abruptly from the upper surface of the rachis nearly at right angles to it, and the pinnae are slightly imbricate to compactly stacked. In *J. brasiliensis*, *J. Scammanae*, *J. cinnamomea* and *J. imbricata* var. *glutinosa* the pinnae may overlay the upper surface of the rachis.

The rachis is composed of the outer epidermal tissue consisting of small dark brown walled cells from which project one to several trichomes. The cortical cells adjacent to the epidermis are smaller and thicker walled than those near the vascular tissue. The vascular trace is surrounded by a ring of brown-colored endodermal cells. In the central portion of the trace there is a V-shaped or U-shaped arc of xylem open toward the upper surface of the rachis with extended ends perpendicular to the main figure. The cells are mainly large metaxylem cells and smaller protoxylem at the bottom and ends of the figure. The pinna traces depart at the ends of the arc. There are homogeneous patches of thin, angular cells which appear to be phloem at the ends of the arc and also in the center. Between these and the endodermis there are thicker walled cells, somewhat longer than broad and often crushed, which appear to be pericycle.

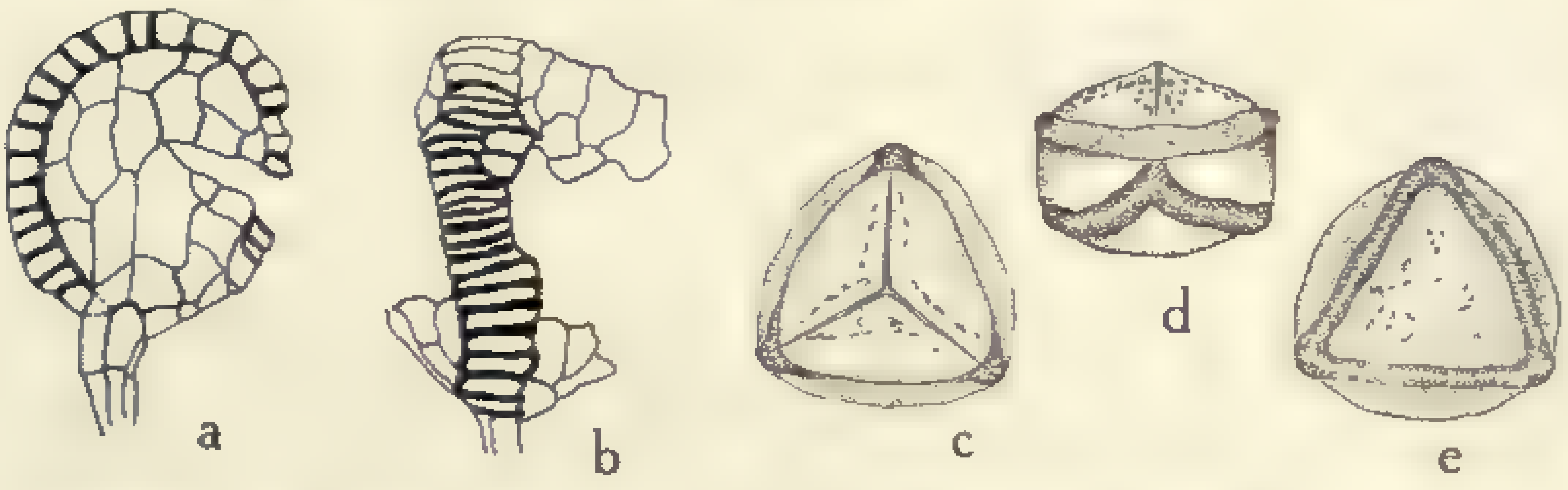
The rachis indument is similar to that of the petiole but denser and sometimes more elaborate. The trichomes are one rowed, multicellular with dark joints between cells. The cells are diaphanous, tan or ruddy brown and the upper ones sometimes darker. When dry the cells are twisted near the joints and alternately aligned in a catenate arrangement. The basal cell of the trichome is usually inflated and may have a constricted, foot-like portion attached to the epidermis. The apical cell of the trichome is long and acuminate or short and bulbous and one type is usually constant for the species although in some, both of these forms may occur on one leaf. In *J. Scammanae* and *J. imbricata* var. *glutinosa* there are glands on the rachis similar to those on the upper surface of the pinnae and these produce a crustose substance on the rachis.

SPORANGIA. — Sporangia may be borne along the veins from the pinna stalk to the distal portion of the veins but not terminally. In *J. laxa* and *J. brasiliensis* there are usually few sporangia located in the central portion of the pinna near the stalk. They are usually abundant in *J. Alstonii* and *J. Goudotii* and obscure the entire lower pinna surface and extend under the enrolled margins. The sporangia of *Jamesonia* have been described by Thompson and Bower as acrostichoid with some of them borne on the tissue adjacent to the veins. I have examined the species in which they report this condition, particularly *J. verticalis*, and have found that the sporangia are attached only on the veins although the capsules may cover the tissue between veins. In species with relatively large pinnae as *J. verticalis* and *J. auriculata* a progressive sequence can be seen in the maturity of the sporangia from the central portion of the pinnae toward the margins. In *Jamesonia* and also in *Eriosorus* sporangia develop in a acropetal sequence. In some material a few younger sporangia may be found among the mature ones. Trichomes occur among the sporangia in some species and these are similar to those on other parts of the pinnae. The position and sequence of maturity of the sporangia in *Jamesonia* and *Eriosorus* differ from those of other gymnogrammoid genera having rhizome trichomes. In *Syngramma*, *Taenitis*, *Craspedodictyum* and *Aspleniopsis* the sporangia are often on reticulate veins and are in mixed stages of development throughout the length of the vein or in sori variously interrupted along the veins. There are paraphyses, among the sporangia in these genera, of a specialized form, differing from other indument of the pinnae.

The sporangium shape in *Jamesonia* is generally pyriform, somewhat longer than broad or orbicular. The annulus is more or less oblique and interrupted by the stalk. The sporangium stalk is usually short, about one fourth the capsule length and usually of 2 or 3 tiers of cells. There are 3 cells adjacent to the capsule and there also appear to be 3 cells at the base. The stalk may be extended by the elongation of cells or increase in number by intercalary divisions. Cell division occurs in the lower portion of the stalk and may result in a cushion of cells subtending the capsule. The cushion is sometimes dark brown and with one or more trichomes.

The annulus is considered here as the uninterrupted series of indurated cells. The shape and position of the cells may be irregular or rarely the annulus is absent but it is usually a sequence of about 20, yellow or amber-colored cells approximately one fourth or one third the width of the capsule. The number of annular cells was considered by earlier workers to be characteristic of the species but variation seems to be greater than was realized. The greatest number, 33, is in *J. robusta* and the fewest, 12, is in *J. brasiliensis* but the number ranges between 15-25 in most species. The stomial region below the annulus consists of 2-4 small, thin walled cells followed by 2-5 indurated cells between which the sporangium usually opens. There are about 3-5 thin walled cells between the indurated ones of the stomium and the stalk. The capsule faces are unequal in size and can be distinguished by 2 rows of cells leading from the stalk to one face and a single row leading to the other face. The cells of the capsule face are generally angular and usually smaller and more numerous than those in the sporangia of *Polypodium* and *Vittaria* illustrated by Wilson (1959).

SPORES. — Spores were examined in the dried condition, in lactic acid preparations and in a few species material was prepared by acetolysis and mounted in glycerine. Observations of the spores were made under 125 and approximately 600 magnifications with apochromat objectives and compensating oculars. A spore identified as one of *Jamesonia imbricata* is included in the series of illustrations published by Erdtman (1957), and represents the general form for the genus. The spores of *Jamesonia* are similar to those of *Eriosorus* and *Pterozonium* and are of a form quite distinct from other gymnogrammoid ferns. In *Jamesonia*, spore color ranges from tan or straw to amber color or medium to dark, ruddy brown and is fairly constant within species. There are two fairly distinct groups based on spore color and symmetry of the pinnae. In *J. verticalis*, *J. blepharum*, *J. cinnamomea* and *J. scalaris*, *J. brasiliensis* and *J. imbricata* var. *glutinosa*, the pinnae are symmetrical and the spores are dark, ruddy brown (with the exception of a collection of *J. blepharum*, north of Bogotá). In the other species the pinnae are asymmetrical and the spores light colored from tan to medium brown (with the exception of *J. robusta* which usually has dark brown spores). Spore shape is tetrahedral, with three meridional planes which are contact planes in the tetrad, and a free convex surface which is greater than a half sphere. In polar view the three meridional or radial planes with the trilete dehiscence fissure is designated the proximal face and the rounded one the



Sporangia and spores. Sporangia: a, *J. cinnamomea*, lateral face, × 55, *Sodiro 9/900* (US); b, *J. canescens*, showing irregular cells in the annulus, × 55, *Tryon & Tryon 5832* (GH). Spores: *J. canescens*, c, proximal face showing the three angles darkened, not projecting beyond the equatorial wing in this species; d, lateral view, the darkest shading indicating a portion of the triangular ridge on the distal face; e, distal face with triangular ridge and slightly verrucose, *Tryon & Tryon 5826* (GH).

distal face. The spore outline in proximal view is sub-triangular with three convex sides and three more or less protruding angles. An equatorial ridge or wing, which may be lobed, divides the faces unequally. There is no perispore and the sculpture described is that of the exine. On the proximal face there is usually a lip or sculptured band parallel to the triradiate scars. The three planes are smooth, papillose to verrucose or slightly rugose. On the distal face there are three contiguous ridges forming a triangle. This serves as a base upon which the spore usually rests, thus the distal face is less often apparent. The angles of the triangle are usually connected by short ridges which join with and may project beyond the equatorial wing. The surface within the triangle on the distal face is smooth or more or less papillose to verrucose and may be more prominently sculptured than the proximal face.

The number of spores in an unopened sporangium is between 59 and 64 and the latter is considered a full complement. Thompson (1918) reports the number for *Jamesonia* to be 56-72 and considers this to be a basis for placing the genus between the gradate ferns and the simplices. I have not found more than 64 spores in a sporangium in any of the material I have examined and I have particularly surveyed the species *J. cinnamomea* and *J. verticalis* he mentions and the collection of *J. scalaris* that he cites from Peru. Irregularly developed spores are frequent in the material I have examined of *J. laxa* and *J. pulchra*. An unusual specimen of *J. Goudotii* from southern Colombia appears to be a hybrid and in this the spores are exceptionally large and irregular.

CHROMOSOME NUMBER. — A chromosome number for the genus was obtained in *J. bogotensis* from sporangia fixed in glacial acetic acid and alcohol. The spore mother cells were prepared by the aceto-carmine squash method. The collection is from Páramo de Chisaca, south of Bogotá, at 3400 m. made on October 27, 1961 (*Rolla M. and Alice Tryon 6178*, GH). Most of the cytological preparations of *Jamesonia*, fixed in three parts alcohol to one part glacial acetic acid were deteriorated a month after they were fixed and it was only the most recently collected material that yielded results. The report is a tentative one, based upon the analysis of two cells with n = 87, (plate 4). These were in polar view of

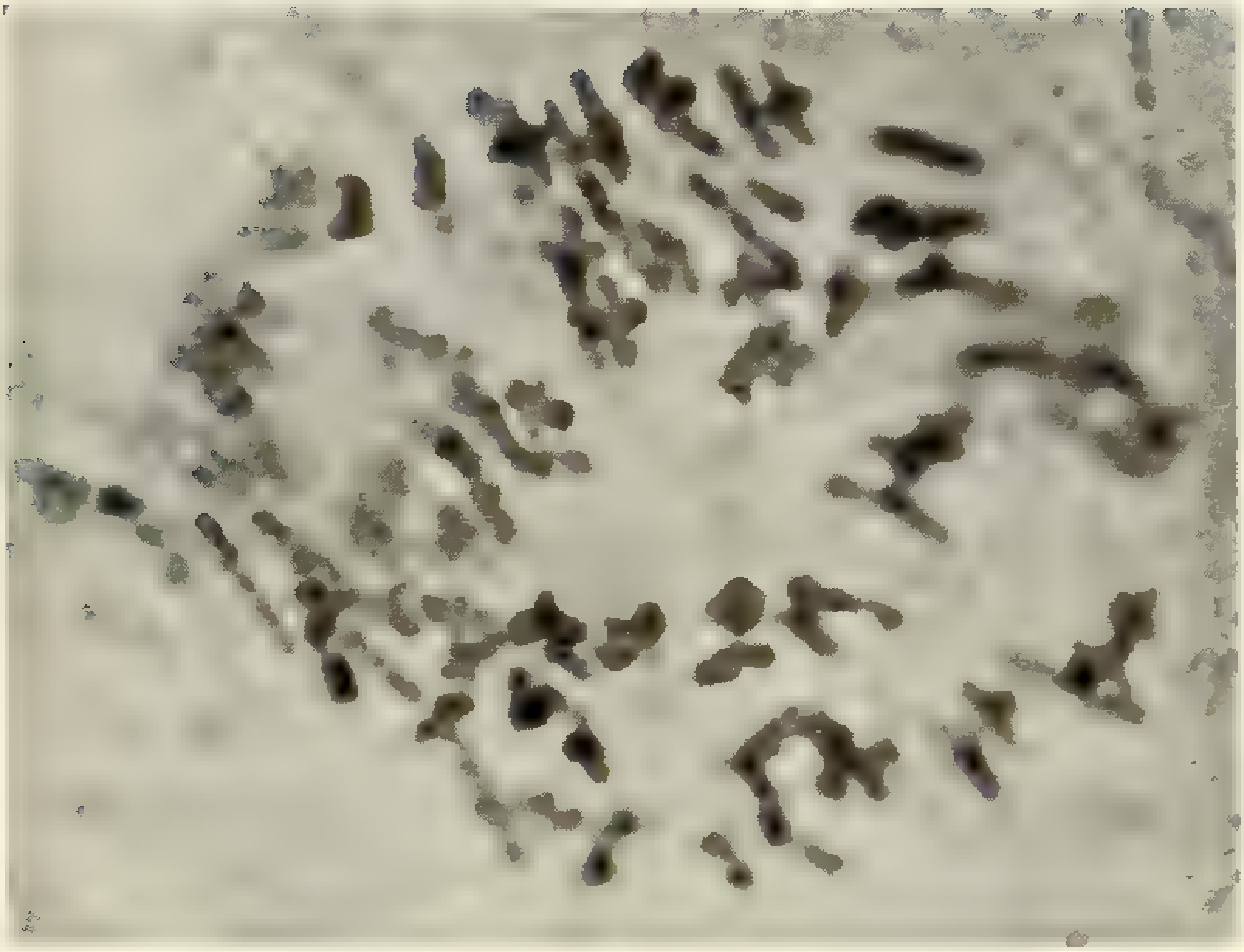
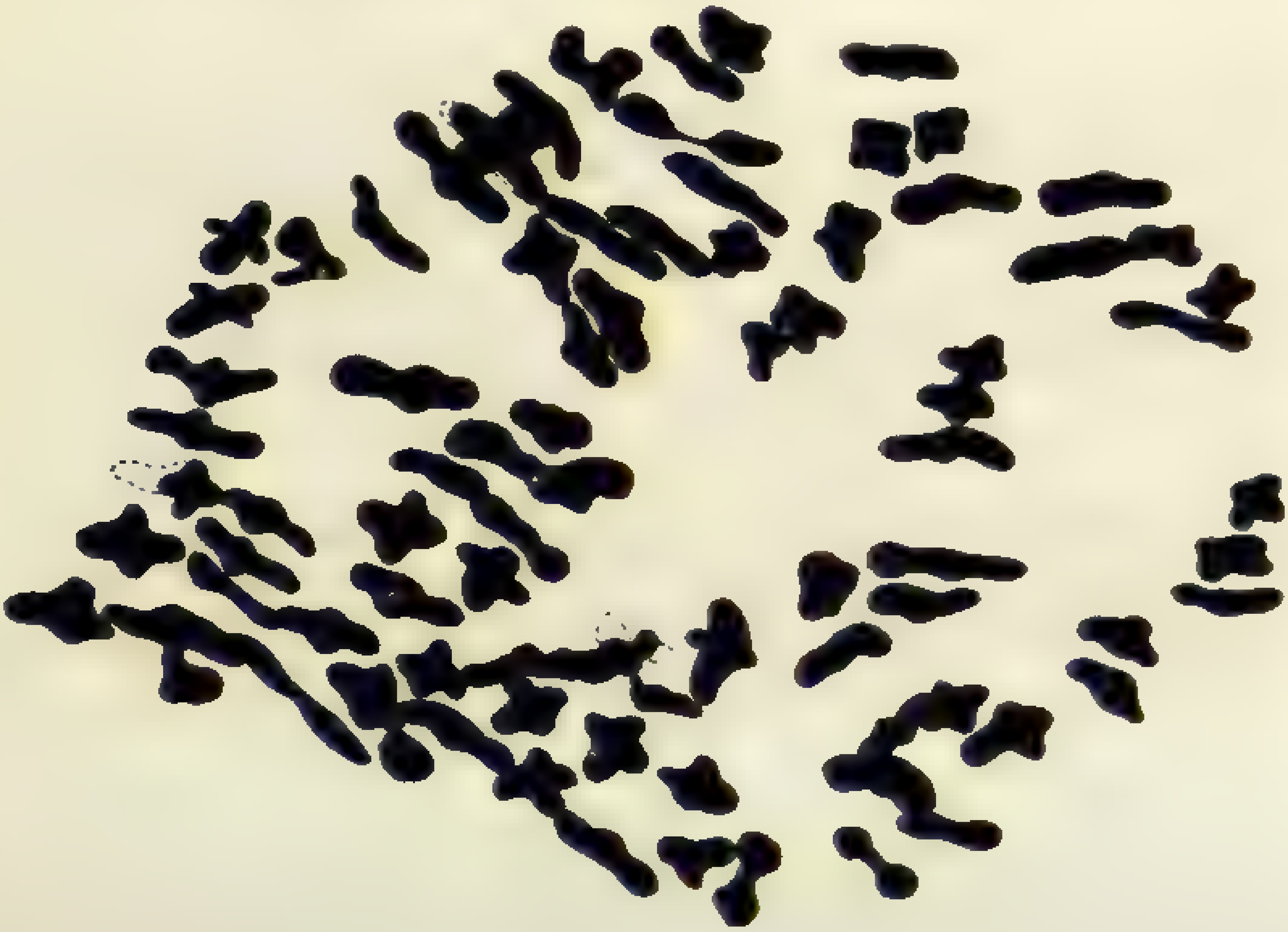


Plate 4. Above, chromosomes of *J. bogotensis*, polar view, late Metaphase I in meiotic division (n=87), about × 2000. *Tryon & Tryon 6178* (GH); below, explanatory diagram for photograph. The broken lines indicate three bivalents which are partly covered by overlaying ones.



late Metaphase I in meiotic division with nearly all of the chromosomes as bivalents and with no trivalents. Some of the chromosomes showed early Anaphase separation with a connecting strand of chromatic material. The number n = 87 is thought to be a hexaploid on the base of 29. Preliminary as this report may be, it is of particular interest, indicating that hybridization probably occurs in the genus and that morphological intermediates may be of hybrid origin. It also suggests the possibility that there exist, or have existed, other members at diploid, triploid and tetraploid levels from which the hexaploid might be derived. Some morphological intermediates occur where *J. bogotensis* and *J. imbricata* var. *glutinosa* grow together and should these be hybrids they would demonstrate further evolutionary potential from the hexaploid.

The report is also of interest in relation to the numbers reported by Manton (1958) for other gymnogrammoid genera — *Syngramma* n = 116 and *Taenitis* n = 44. In the correlation she draws between chromosome number and position of the genera in the *Pteridaceae* of Copeland, *Jamesonia* would be an exception of the same kind as *Syngramma* and out of place among the genera in Copeland's scheme.

On the basis of chromosome numbers in the series of 29, *Jamesonia* can be placed with genera as *Anogramma*, *Onychium*, *Pellaea*, *Cheilanthes* and *Pteris*. In these genera polyploidy is also a mechanism of evolutionary significance.

PREPARATIONS. — Descriptions and drawings of the pinnae were prepared from material cleared in sodium hydroxide. Measurements are from dried material with the exception of the trichomes which were made from preparations fixed in lactic acid. All of the outline drawings and those of cellular detail have been traced from specimens projected on a Bausch and Lomb Microprojector. I am most appreciative of the careful inking of these tracings by Mrs. Joyce Todd. The drawings of the spores were prepared by Mrs. Ruth Hsu Chen and I am grateful to her for the careful attention to detail and shading of these.

The maps of the distributions have been plotted on the Goode series of base maps, published by the University of Chicago Press.

SYSTEMATIC TREATMENT

Jamesonia Hook. & Grev. Icon. Fil. **2:** t. 178. 1830

Gymnogramma, Section *Jamesonia* (Hook. & Grev.) Kl. Linnaea **20:** 407. 1847.

Psilogramme, Section *Jamesonia* (Hook. & Grev.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 332. 1882.

Rhizome slender, long or moderately long creeping, siphonostelic with dictyostelic stages, densely clothed with tan to black, patent or appressed, bristle-like trichomes of 1-5 cells at or near the base. *Leaves* linear, usually 15-60 cm. long, seldom exceeding 90 cm. long, less than 5 cm. broad, indeterminate or sometimes determinate, once pinnate or rarely pinnatisect. *Petiole* and *rachis* channeled, terete or trigonous with the upper surface obtusely angled, tomentose, more densely so on the lower surface or glandular. *Pinnae* small, usually not exceeding 1 cm. in either length or breadth, mostly imbricate in 2 ranks laterally disposed or overlaying the rachis, more or less orbicular, ovate-cordate or long-ovate, seldom auriculate or lobed, herbaceous or coriaceous, more or less tomentose, especially the lower surface, or glandular, with margins incurved or enrolled having a membranous, entire, dentate and/or ciliate border. *Veins* free, dichotomous, the branches unequal. *Sporangia* on the veins in the basal portion of the pinna or crowded, extending to the distal portions and obscuring the lower surface of the pinna; sometimes immersed in tomentum on the lower pinna surface but without paraphyses, the stalks short to slightly longer than the capsule, 3 cells broad, often with intercalary cell divisions, the annulus interrupted by the stalk, of 12-33, usually 20 indurated cells. *Spores* tetrahedral-globose with trilete commissural ridges and 3 more or less projecting angles, with a prominent equatorial wing, the distal face with 3 ridges forming a triangle, exine smooth or more or less verrucose.

TYPE SPECIES: *Jamesonia pulchra* Hook. & Grev.

USE OF THE KEY

Macroscopic characters have been used in the key where possible but there are some rather critical characters which are obscure. Thus it is strongly recommended that the specimens be examined with up to 80 magnifications. This is especially important for observation of the pinna margin and indument. The latter is best observed on the younger pinnae near the lamina apex and with special care to distinguish between bulbous glands and the bases of broken trichomes. To observe the characters of the pinna, particularly the symmetry of the base, the stalk and the margin, it is usually necessary to make wet preparations of the material. Some specimens which are intermediates or peculiar variants may not agree with all of the characters under one heading. These are best identified on the totality of their characters rather than by any single one.

FACTITIOUS KEY TO THE SPECIES AND VARIETIES OF JAMESONIA

a. Apex of the petiole and base of rachis rounded or obtusely angled on the upper surface; pinnae in the central portion of the lamina with more or less terete, long to rarely short, stalks. ..... b

b. Pinna stalk attached on the upper surface of the pinna, above the sinus. ..... 4. *J. Cuatrecasasii.*

b. Pinna stalk attached in the sinus between the upper and lower surfaces of the pinna. c

c. Fertile pinna auriculate or lobed in the apical half of the lamina. ..... d

d. Pinnae coriaceous, cell walls of the upper epidermis thickened and raised (visible at 10 magnifications). ..... 12. *J. Goudotii.*

d. Pinnae herbaceous, cell walls of the upper epidermis not notably thickened or raised. ..... e

e. Central pinnae of the lamina 2 or more times longer than broad, up to 12 mm. long; upper surface of the pinnae pubescent. ..... 2. *J. auriculata.*

e. Central pinnae of the lamina about as long as broad, up to 4 mm. long; upper surface of the pinnae glandular. ..... f

f. Apical bud of the lamina vermiform, glutinose, with appressed trichomes; pinnae in the central portion of the lamina short stalked; pinna border entire or nearly so. ..... 9. *J. Scammanae.*

f. Apical bud of the lamina not vermiform or glutinose, with patent to slightly appressed trichomes; pinnae in the central portion of the lamina long stalked; pinna border ciliate ..... 14. *J. scalaris.*

c. Fertile pinnae entire in the apical half of the lamina, rarely lobed in species 5. ..... g

g. Pinnae inequilateral at the base; spores tan to light brown, or usually dark brown in species 5. ..... h

h. Lower surface of the pinnae densely pubescent to tomentose, with crispate or loosely curled trichomes. i

i. Pinnae glabrous to conspicuously pubescent on the upper surface. ..... j

j. Pinna margins plane to incurved, with narrow borders which are elaborated at the vein ends and not, or scarcely contiguous. ..... 2. *J. laxa.*

j. Pinna margins enrolled, sometimes tightly so, with usually broad borders which are contiguous, dentate, or entire. ..... k

k. Pinnae, especially the older ones, convex on the upper surface (patelliform); the borders often narrow, irregularly dentate. ..... 3. *J. rotundifolia.*

k. Pinnae plane or slightly concave on the upper surface; the borders broad, sometimes indusioid, entire or nearly so or regularly dentate. l

l. Pinnae stalks usually strongly bent and overlaying an enlarged basal lobe of the pinna; pinnae orbicular or ovate-cordate. ..... 6. *J. pulchra.*

l. Pinnae stalks straight; pinnae reniform (broader than long), rarely orbicular or lobed. ..... m

m. Rhizome trichomes lax, patent, tan or light brown, lighter than the rhizome surface; Ecuador and Colombia. ..... 5. *J. robusta.*

m. Rhizome trichomes rigid, appressed, dark brown or blackish, darker than the rhizome surface; Venezuela. .... 8. *J. canescens.*

i. Pinnae glandular on the upper surface rarely also with a few trichomes. .... n

n. Apical bud as broad as, or broader than, the expanded lamina, with patent trichomes; pinna stalks 1 mm. or more long. .... o

o. Rhizome trichomes lax, patent, tan or light brown, lighter than the rhizome surface; pinnae orbicular to ovate; Peru, Ecuador and Colombia. .... p

p. Upper surface of the pinnae with one or both basal lobes raised above the plane of the pinna, usually with numerous glands and sometimes also crustose or with a few trichomes; central and northern Colombia. .... 7. *J. bogotensis.*

p. Upper surface of the pinnae with both basal lobes in the same plane as the pinna, or directed downward from it, with few glands; Peru, Ecuador and southern Colombia. .... 15A. *J. imbricata* var. *imbricata.*

o. Rhizome trichomes rigid, appressed, dark brown to blackish, darker than the rhizome surface; pinnae ovate to usually long-ovate; Venezuela and Magdalena, Colombia. .... 15C. *J. imbricata* var. *meridensis.*

n. Apical bud smaller than the expanded lamina (vermiform), with appressed trichomes; pinna stalks less than 1 mm. long. .... 9. *J. Scammanae.*

h. Lower surface of the pinnae glabrous, or sparsely pubescent with short, rigid trichomes along the veins, usually with a tuft of trichomes on the pinna stalk and basal veins. .... q

q. Upper pinna surface, particularly the distal portion, with numerous, long, discrete trichomes, these appressed and bent near the base, usually enveloping several pinnae. .... 10. *J. peruviana.*

q. Upper pinna surface glabrous, glandular or with short, erect capitate trichomes or few longer ones. .... r

r. Lamina about the same breadth throughout, tomentum of the apex and rachis concolorous (specimens from Central America sometimes slightly bicolorous); pinnae in the apical half of the lamina usually slightly longer than broad. .... s

s. Upper surface of the pinnae with erect, capitate trichomes; tomentum of the lamina apex and rachis rust brown; vein ends protruding from the margin. .... 13. *J. boliviensis.*

s. Upper surface of the pinnae glabrous, or rarely with short, appressed glands or few trichomes; tomentum of the lamina apex and rachis yellow or tan; veins ending back of the margin. .... 11. *J. Alstonii.*

r. Lamina broader in the apical half than below (clavate), tomentum of the apex and rachis bicolorous, with a darker central streak; pinnae in the apical half of the lamina usually broader than long. .... 12. *J. Goudotii.*

g. Pinnae equilateral at the base; spores dark brown, or tan to amber in species 9 and 15. .... t

t. Pinnae glandular or crustose on the upper surface; Mexico to Bolivia. .... u

u. Central pinnae of the lamina with conspicuous stalks usually more than 1 mm. long, sometimes bent; spores dark brown, or rarely light brown. v

v. Pinna base truncate; lower pinna surface usually tomentose, to rarely glabrous, the border usually broad, dentate and or ciliate. .... 15B. *J. imbricata* var. *glutinosa.*

v. Pinna base cordate; lower pinna surface glandular or with a few, short trichomes, the border narrow, usually of a single row of cells, ciliate. .... 14. *J. scalaris.*

u. Central pinnae of the lamina with short, inconspicuous stalks less than 1 mm. long; spores tan or light amber color. .... 9. *J. Scammanae.*

t Pinnae glabrous to slightly pubescent on the upper surface; Bolivia and Brazil. .... 16. *J. brasiliensis.*

a. Apex of the petiole and base of the rachis sulcate, channeled or plane on the upper surface; pinnae in the central portion of the lamina broadly to narrowly adnate, or with short broad, somewhat flattened stalks. .... w

w. Central pinnae broadly to narrowly adnate; petioles usually stout, usually 2 mm. or more in diameter; pinnae long-ovate to oblong and usually auriculate or lobed, rarely orbicular and entire. .... 17. *J. verticalis.*

w. Central pinnae with short, broad stalks; pinnae orbicular, entire. x

x. Rhizome trichomes rigid, appressed, darker than the rhizome surface; rachis slender, 1 mm. or less, in diameter; apical bud smaller than a mature pinna; central pinnae approximate to distant. .... 18. *J. blepharum.*

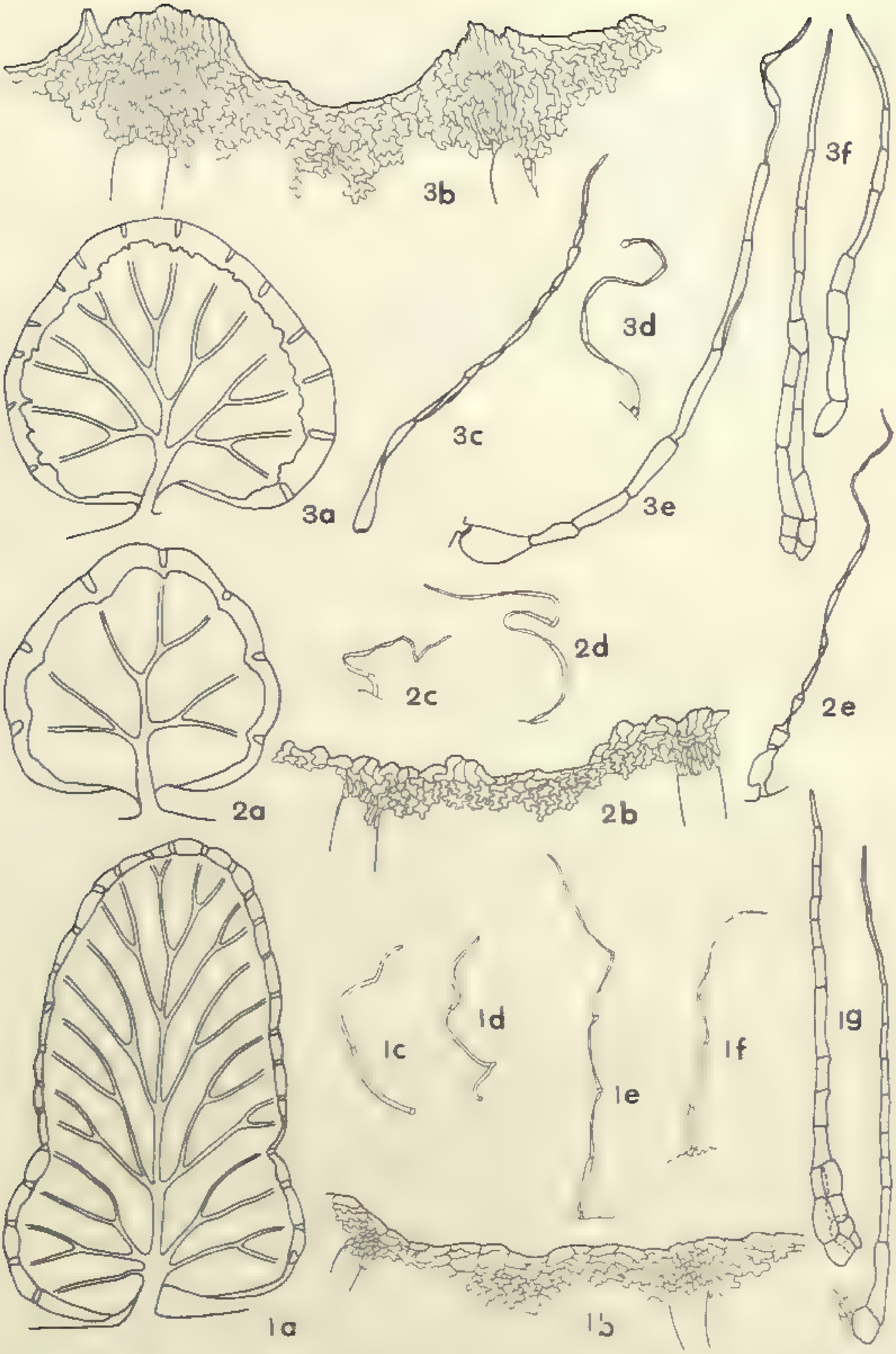
x. Rhizome trichomes lax, patent, lighter than the rhizome surface; rachis stout, 2-4 mm. in diameter; apical bud larger than a mature pinna; central pinnae imbricate. .... 19. *J. cinnamomea.*

1. **Jamesonia auriculata** A. F. Tryon, sp. nov. Fig. 1. Map 1

Trichomata rhizomatis patentia vel appressa castanea vel rufo-fusca, apex laminae indeterminatus gemmae tomento patente fulvo vel rufo-fusco, pinnae elongato-ovatae, plerumque auriculatae planae herbaceae ad 5-12 mm. longae 3-6 mm. latae, pinna adaxialiter pubescens, abaxialiter tomentosa trichomatibus fulvis crispatis, nervis latis prope petiolulum supra gracilioribus, dichotomis angulis modice latis, limbo angusto, brevilobato, latiore ad terminos nervorum, sporae fulvae vel pallide fuscae laeves.

TYPUS: Venezuela, State of Mérida, Páramo de la Negra, above La Canada, 2800 m. Feb. 14, 1939. *A. H. G. Alston 7050*, GH; isotypus, BM.

Rhizome long creeping, dichotomously branched, ca. 2-4 mm. in diameter with moderately dense, coarse roots, the internodes variable



FIGS. 1-3. FIG. 1. *J. auriculata:* a, pinna, × 5, b, pinna margin with two vein ends, × 35; c, trichome from upper pinna surface, × 30; d, trichome from lower pinna surface, × 30, e, rachis trichome, × 30; f, petiole trichome, × 30; all from *Alston 7050* (GH). g, rhizome trichomes, × 30, from *Steyermark 56291* (GH). FIG. 2. *J. laxa*. a, pinna, × 10, b, pinna margin with two vein ends, × 35; c, trichome from upper pinna surface, × 30, d, trichome from lower pinna surface, × 30; e, rachis trichome, × 30; all from *Funck & Schlim 1118* (LE). FIG. 3. *J. rotundifolia:* a, pinna, × 5, from *Cuatrecasas 20223* (GH); b, pinna margin with two vein ends, × 35, from *Scamman & Holdridge 7928* (GH) c, trichome from upper pinna surface, × 30; d, trichome from lower pinna surface, × 30; e, rachis trichome, × 30; the last three from *Alston 7232* (GH); f, rhizome trichomes, × 30, from *Alston 7419* (US).

in length, the trichomes rigid, appressed, castaneus or ruddy brown, slightly darker and more ruddy than the rhizome surface, 2.0-2.5 mm. long with usually 1 (-3) cells at the base, apex acuminate. *Petiole* strongly bent and somewhat appressed to the rhizome before ascending, 4.5-10.0 cm. long, 1/8-1/6 as long as the lamina, castaneus or atropurpureus, terete, ca. 1.0 mm. in diameter at the apex slightly more slender below, more or less pubescent, the trichomes similar to those of the rachis. *Lamina* once pinnate, 14-60 cm. long ca. 0.5-2.0 cm. wide, broadest in the central or upper portion (not at the apex) narrowed toward the base, with ca. 50-150 pinnae, indeterminate, the apical bud smaller than the mature pinnae, with trichomes matted or patent. *Rachis* atropurpureus usually the same color as the petiole or darker, terete, ellipsoidal, or trigonous and the upper surface with an obtuse angle, with dense matted pubescence, the trichomes not exceeding the length of the pinnae, somewhat longer on the lower surface adjacent to the pinnae, tan to rust colored, with the cells near the base sometimes clear, the apical cell acuminate. *Pinnae* alternate or subopposite in 2 ranks laterally disposed, imbricate or distant, (the basal ones usually smaller, distant, sterile, finally deciduous, sometimes flat and strongly dentate) long-ovate, usually auriculate, plane with the margin more or less enrolled, inequilateral at the base, 5-12 mm. long, 3-6 mm. wide, light green, herbaceous; *upper surface* pubescent with tan or gold colored trichomes, the epidermal cell walls unthickened; *lower surface* tomentose with tan, crispate trichomes of few long cells; *stalk* straight or oblique and slightly bent, ca. 0.5 to nearly 1.0 mm. long, the dark color of the stalk extending into the adjacent veins of the lower pinna surface. *Veins* broad, especially near the base, and more or less sunken, dichotomous, the angles wide, with moderately long branches, the ends clavate or flabellate, extending to the margin. *Border* narrow, shallowly lobed or slightly extended at the vein ends, clear or opaque white. *Sporangia* abundant near the pinna stalk, sometimes obscuring most of the lower pinna surface, the stalk short, of 2 tiers, sometimes elongate, the lower one with intercalary cell divisions and darker, the annulus of 18-23 indurated cells. *Spores* tan to light brown, smooth, with a moderately broad, equatorial wing, the 3 angles slightly projecting.

The species is endemic in the state of Mérida but has been collected on three different páramos. The pinnae are exceptionally long and the two lateral lobes at the base are comparable in size and form to the complete, orbicular pinnae in other species. The elongate form of the pinnae, is accompanied by an extended system of veins with a prominent central vein. In these characters and also in the pattern of elongate cells in the upper epidermis, *Jamesonia auriculata* appears to be closer to species in *Eriosorus* than to other species in *Jamesonia*. It occurs at relatively low altitudes for the genus.

Mérida, Venezuela, at 2600-2900 m. Additional specimens examined: VENEZUELA. MERIDA: Páramo del Molino, *Jahn 957* (B, BM, GH, US, VEN), *958* (GH, US, VEN); Páramo de Pozo Negro, *Steyermark 56291* (GH, K, US).

2. **Jamesonia laxa** (Mett. ex Kuhn) Diels, in Nat. Pflanz. 1^4: 260. 1899. Fig. 2. Map 2

Gymnogramma laxa Mett. ex Kuhn, Linnaea 36: 69. 1869. TYPE: *Engel 117*, Venezuela, Mérida B!, photos: COL, F, GH, NY, US; isotypes B! LE! US!.

Psilogramme laxa (Mett. ex Kuhn) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 333. 1882.

Rhizome not seen. *Petiole* estimated at 1/10 the length of the lamina, castaneus or atropurpureus, terete, ca. 0.5-1.0 mm. in diameter at the apex, more slender below, glabrous or with sparse, light brown trichomes similar to those of the rachis. *Lamina* once pinnate, ca. 26-66 cm. long, 0.3-1.0 cm. wide, the apex and base narrowed, with constricted zones of smaller pinnae in the central portion, with ca. 100-350 pinnae, indeterminate, the apical bud smaller than the mature pinnae with trichomes matted or slightly appressed. *Rachis* castaneus or atropurpureus, usually lighter colored than the petiole, terete or trigonous and the upper surface with an obtuse angle, usually sparsely pubescent, the trichomes not exceeding the length of the pinnae, ruddy brown the basal cells sometimes clear, the apical cell acuminate. *Pinnae* alternate or subopposite, 2 ranked laterally disposed, distant or approximate, imbricate near the apex, (the basal ones smaller, distant, sterile, finally deciduous, sometimes flat and broadly dentate) rotundate-cordate, plane the margin incurved or scarcely enrolled, inequillateral at the base, 2-5 mm. long, 2-7 mm. wide, bright green, delicate herbaceous; *upper surface* with sparse to dense tan trichomes, the epidermal cell walls unthickened; *lower surface* especially the central portion with dense, bright rust-brown, crispate trichomes of few cells, *stalk* oblique or slightly bent, 0.5 mm. long, the dark color of the stalk extending into the adjacent veins of the pinnae and apparent on both surfaces. *Veins* slender, in the plane of the upper surface, dichotomous with moderately wide angles, the branches long, the ends clavate to somewhat acute, extending to the margin. *Border* narrow, one or a few cells broad, irregularly dentate, whitish or lutescent. *Sporangia* few, mostly adjacent to the pinna stalk, sometimes filling most of the lower surface, the stalk short of 2 or 3 tiers with intercalary cell divisions, the annulus of 15-21 indurated cells. *Spores* light tan, verrucose, with a broad equatorial wing, the angles prominently projecting; sometimes shriveled.

The species is known from only three collections of leaves, taken about a hundred years ago in the Sierra Nevada de Mérida. The leaves are unusual in having pinnae of a more delicate texture than most of the Andean species of *Jamesonia* and they are nearly flat with scarcely enrolled margins. In the widely spaced position of the pinnae and their shape

MAPS A, 1, 2, 4. Map A, Distribution of *Jamesonia*, the outline enclosing the least common area of all species, the shaded area is the region of species concentration. Map 1, *J. auriculata*. Map 2, *J. laxa*. Map 4, *J. Cuatrecasasii*.

and margins, elaborated at the vein ends, there is a resemblance to species in *Eriosorus* and to *J. rotundifolia.* It is a relatively unspecialized species compared to *J. canescens* and more specialized than *J. auriculata,* both of which occur in the same area. It is difficult to assess the species on the fragmentary material available but I regard it as a more specialized one derived from *Eriosorus* or perhaps less specialized and related to *J. rotundifolia.*

Mérida, Venezuela, at 3050, 4270-4420 m. Additional specimens examined: VENEZUELA. MERIDA: *Funck & Schlim 1118* (B, BM, G, LE, P); *Karsten* (LE, W); *Linden 519* (B, BM, G, K, L, P).

3. **Jamesonia rotundifolia** Fée, Mém. Fam. Foug. 7: 41, t. 10. 1857.
Fig. 3. Map 3

TYPE: *Schlim 363,* Colombia, 8,000-10,000′ (3000 m.); isotypes: G! K! P!, photos: COL, F, GH, NY, US.

Gymnogramma rotundifolia (Fée) Mett. Ann. Sci. Nat. V,2: 209. 1864.

Psilogramme rotundifolia (Fée) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 334. 1882.

Rhizome somewhat creeping or especially on smaller plants compact, dichotomously branching, usually slender ca. 0.5-2.5 mm. in diameter with dense, sometimes long, compact roots, the internodes variable in length, the trichomes patent or appressed, castaneus or light brown, the same color or more ruddy than the rhizome surface, 1-3 mm. long, with usually 1 (-4) cells near the base, apex usually acuminate, sometimes bulbous. *Petiole* bent, often appressed to the rhizome for a short distance before ascending, 1.5-9.0 cm. long, 1 17-1 3 as long as the lamina, castaneus or atropurpureus, terete or oval, ca. 1.5-2.0 mm. in diameter at the apex, often more slender below, moderately pubescent, the trichomes similar to those of the rachis or darker brown. *Lamina* once pinnate, ca. 14-65 cm. long, 0.7-1.5 cm. wide about the same width throughout or somewhat narrowed at the base, with ca. 100-350 pinnae, indeterminate, the apical bud about the same size or smaller than the mature pinnae, with trichomes not or slightly appressed. *Rachis* castaneus, often lighter colored than the petiole, terete or trigonous with an obtuse angle on the upper surface, densely pubescent, the trichomes nearly as long as the pinnae, often matted on the lower surface, tan, ruddy or dark brown usually acuminate rarely bulbous. *Pinnae* alternate, usually laterally disposed in 2 ranks or slightly overlaying the rachis, distant, approximate, or sometimes imbricate, (the basal ones distant, sterile, often deteriorated) rotundate-cordate, patelliform, especially the older pinnae, the margin more or less enrolled and partly obscuring the border, inequilateral at the base, 2-6 mm. long, 1.5-9.0 mm. wide, light green, herbaceous; *upper surface* more or less pubescent, especially the distal portion with light brown, tan or sometimes gold colored trichomes, with epidermal cell walls unthickened; *lower surface* more or less pubescent with tan or clear, curled, 1 or few celled trichomes, or glabrous sometimes with a tuft of trichomes on the stalk or adjacent veins, *stalk* oblique or bent, ca. 0.5-1.0 mm. long, the dark color often extending into the larger veins of the pinnae especially evident on the lower pinna surface. *Veins* moderately broad, in the plane of the upper surface or sometimes sunken, dichotomous, the angles moderately wide to acute, the branches long, the ends acute, extending into the border. *Border* moderately broad, extended at the vein ends, irregularly dentate, whitish, clear or lutescent, sometimes little modified and similar to the texture of the pinna. *Sporangia* abundant adjacent to the pinna stalk sometimes crowded and obscuring the lower surface, the stalk usually short of 2 tiers each of 3 cells which are sometimes elongated and the lower darker, the annulus of 17-19 indurated cells. *Spores* light tan, verrucose, especially on the distal face, nearly smooth on the proximal face with a broad, sometimes lobed equatorial wing, the 3 angles not or slightly projecting.

Morphologically, *Jamesonia rotundifolia* is intermediate to a few less specialized species and to several which are more specialized. Compared to the less specialized ones, which are local in occurrence, it is geographically wide ranging from central Peru to Costa Rica. The characters are also generalized, rather than unique and on the basis of this and on the broad distribution, *J. rotundifolia* is regarded as a possible source from which one or more of the derived species might have originated.

On the ten páramos on which I collected in Colombia, *Jamesonia rotundifolia* occurred in abundance on six and where it occurred with *J. imbricata* var. *glutinosa* there were specimens intermediate between these two. Two collections, from Páramo de las Puentas, above La Baja, Santander, Colombia, *Killip & Smith 18191* and *18208*, are difficult to place. I am referring them to this species on similarities in the rhizome trichomes, the pinna form and orientation of the pinnae stalks although the specimens have exceptionally broad, membranous borders and dense tomentum on the lower surface of the pinnae for this species. *Jamesonia imbricata* var. *glutinosa*, *J. bogotensis* and *J. robusta* also occur in the region and it is possible that these specimens may be intermediate between *J. rotundifolia* and one of these, especially the last.

Costa Rica to Central Peru, at 2600-4200 m. Additional specimens examined: COSTA RICA. *H. Carson* in 1956 (GH). CARTAGO: Cerro de la Muerte, *Holm & Iltis 529* (B, BM, S-PA, US); Cerro du Buena Vista, *Pittier & Tonduz 3348* (P, US); Cerro de la Muerte, *Scamman 6079* (GH); *Scamman & Holdridge 7928* (GH). SAN JOSE: Cerro de las Vueltas, *Pittier 10504* (BM, GH, K, LE, P, US); Cerro de las Vueltas, *Standley & Valerio 43847* (GH, US). COLOMBIA. CAUCA: Páramo de Guancas, *Lehmann 5706* (B, F, K, P, US); *von Sneidern 2176* (GH, S); *Tryon & Tryon 5992* (GH), Páramo de Puracé, *5959* (BM, COL, GH, LE, US); *Yepes-Agredo 544* (COL). CUNDINAMARCA: Páramo de Guasca, *Alston 7455* (BM, GH, US), *7459* (BM, GH, US); *André 1534* (K); Páramo de Chipaque, *Apolinar-Maria 23* (US); *Bischler 1261* (COL); Guadalupe, *Cuatrecasas 5579* (US), Páramo de Guasca, *9494* (COL, US); Páramo de Guasca, *Fosberg & Valencia 21449* (GH, US); La Herrera, *Garcia-Barriga 10911* (COL), Páramo de Guasca, *11660* (COL, US); Alto de la Cruces, *Grant 9555* (US); Guadalupe, *Haught 5652* (COL, S-PA, US), *5653* (COL, US); *Holton* in 1854 (COL, G, GH); Páramo de Guasca, *Killip 34095* (COL, GH, K, US); *Lindig 83*, from San Fortunato (BM), from Choachi (B, K, P), from Fusagasuga (K); *Little & Little 7433* (COL, US), *7436* (COL, US); El Peñon, *Pennell 2657* (GH, US); Páramo de Guasca, *Tryon & Tryon 5915* (BM, COL, GH, LE, NY, P, US, VEN), Páramo de Palacio, *6040* (BM, GH, US), *6053* (GH), Alto de Aguila, *6071* (BM, GH), *6072* (BM, COL, GH), Páramo de Cruz Verde, *6081* (GH). NORTE DE SANTANDER: La Mesita, *Alston 7232* (BM, GH); Páramo de Romeral, *Killip & Smith 18658* (COL, GH, US), Páramo de Santurbán *19592* (GH, US); Páramo Almorzador, *Vareschi 4044* (VEN). SANTANDER: *Kalbreyer 726* (US); Páramo de las Vegas, *Killip & Smith 15695* (GH, US), Páramo Rico, *17752*, *17812* (GH, US), Páramo de las Puentes, *18191* (COL, GH, NY, US), *18203* (COL, GH, US), Páramo de Vetas, *21180* (GH, US). VALLE: Páramo de Bavaya, *Cuatrecasas 20223* (GH, US). ECUADOR. TUNGURAHUA: *Asplund 9882* (GH, S). PERU. HUANUCO: *Bryan 612* (F). PIURA: *Weberbauer 6076* (B, F, GH, US).

4. **Jamesonia Cuatrecasasii** A. F. Tryon, sp. nov. Fig. 4. Map 4

Trichomata rhizomatis rigida, appressa, obscuro-fusca vel atropurpurea, rachis tomento fulvo vel rufo-fusco, pinnae valde imbricatae et appressae, ovato-rotundatae, patelliformes herbaceae, 3.0-4.5 mm. longae, 3-5 mm latae, petioluli breves adaxialiter supra pinnas, pinna adaxialiter pubescens, abaxialiter glandulis capitatis vel trichomatibus sparsis, nervis latis, dichotomis, angulis latis, limbo angusto vel modice lato, dentato, sporae fulvae vel pallido-fuscae, papillatae.

TYPUS: Colombia, Dept. Magdalena, Sierra Nevada de Santa Marta, rocky and meadowy páramos around Laguna Naboba, Laguna Mamito and Laguna Mamo, 4200-4300 m. Oct. 3, 4, 5, 1959, *J. Cuatrecasas* and ***R. Romero Castaneda 24613***, **US**.

Rhizome creeping, ca. 3-4 mm. in diameter with few, coarse roots, the internodes short (in one specimen), the trichomes rigid, appressed, lustrous dark brown or atropurpureus, darker than the rhizome surface, 1.0-1.25 mm. long, with 3-6 cells near the base, apex acuminate. *Petiole* bent near the rhizome, 4.0-8.5 cm. long about 1 9 or 1 4 as long as the lamina, castaneus, terete, ca. 1-2 mm. in diameter at the apex, slightly more slender near the rhizome, more or less tomentose, the trichomes similar to those of the rachis but shorter and not as broad. *Lamina* once pinnate, 26, 35, 38 cm. long, 0.6-1.4 cm. wide, the lamina broadest at the apex narrowed toward the base with ca. 350-500 pinnae, indeterminate, the apical bud larger than the mature pinnae, with trichomes patent or slightly appressed. *Rachis* castaneus or tan, terete or ellipsoidal, tomentose, the trichomes exceeding the length of the pinnae 1 or 2 times, usually matted, tan or rust brown, with the basal cells usually clear, the apical cell acuminate or short bulbous. *Pinnae* subopposite, appressed in 2 ranks, and strongly imbricate, (the basal ones minute, distant, sterile) ovate-rotundate, the acroscopic lobe sometimes slightly elongate, patelliform, the margins enrolled, wholly or partly obscuring the border, inequilateral at the base, 3.0-4.5 mm. long, 3-5 mm. wide, light green, herbaceous; *upper surface* pubescent with tan, gold, or rust colored trichomes especially abundant on the distal part and also with shorter trichomes similar to those of the lower surface, with epidermal cell walls unthickened; *lower surface* with 2 or 3 celled capitate glands, sometimes also with sparse trichomes similar to but shorter than those of the upper surface, *stalk* straight, ca. 0.5 mm. long, castaneus, attached to the upper surface of the pinna, often articulating in the mid-portion. *Veins* broad, slightly sunken, dichotomous with wide angles, branches short to moderately long, the ends acute or clavate, extending to the border. *Border* narrow to moderately broad, membranous more or less dentate with sparse trichomes, tan. *Sporangia* sparsely distributed along the veins, the stalk short, of 2 tiers, sometimes elongate, the lower tier usually darker, the annulus of 19-21 indurated cells. *Spores* tan to medium brown, papillose, with a moderately broad equatorial wing, the 3 angles slightly projecting.

I am pleased to name this unique species from the Sierra Nevada de Santa Marta for Dr. José Cuatrecasas. His numerous collections of *Jamesonia* from Colombia and the completeness of his specimens have enabled me to know the species of *Jamesonia* and their distributions more fully.

The species is unusual in the genus in having the pinna stalks affixed to the upper surface of the pinnae. This condition appears to be an extreme expression of a trend toward the simplification of the lamina. The position of the pinna stalk in *Jamesonia Cuatrecasasii* actually appears to be the result of a combination of modified characters. The stalk has been shortened and the tissue at the base of the pinna adjacent to the stalk has coalesced about the lower surface of the stalk. In addition to these changes there has been a realignment of the pinnae in a closely compressed and imbricate or incubous arrangement especially in the apical portion of the leaves.

There is a record of this species from the Sierra Nevada de Mérida from the Jahn collection which is a mixture of this and *Jamesonia canescens*. There is a resemblance between these two species in the copious tomentum of the leaves but in *J. Cuatrecasasii* much of the indument which envelops the lower surface of the leaf is attached to the distal portion of the pinnae while in *J. canescens* it is largely the rachis tomentum which envelops the pinnae. In the patelliform and rotundate form of the pinnae and the light colored tomentum which envelops them there seems to be a greater resemblance between *J. rotundifolia* and *J. Cuatrecasasii* than between the latter and *J. canescens.*

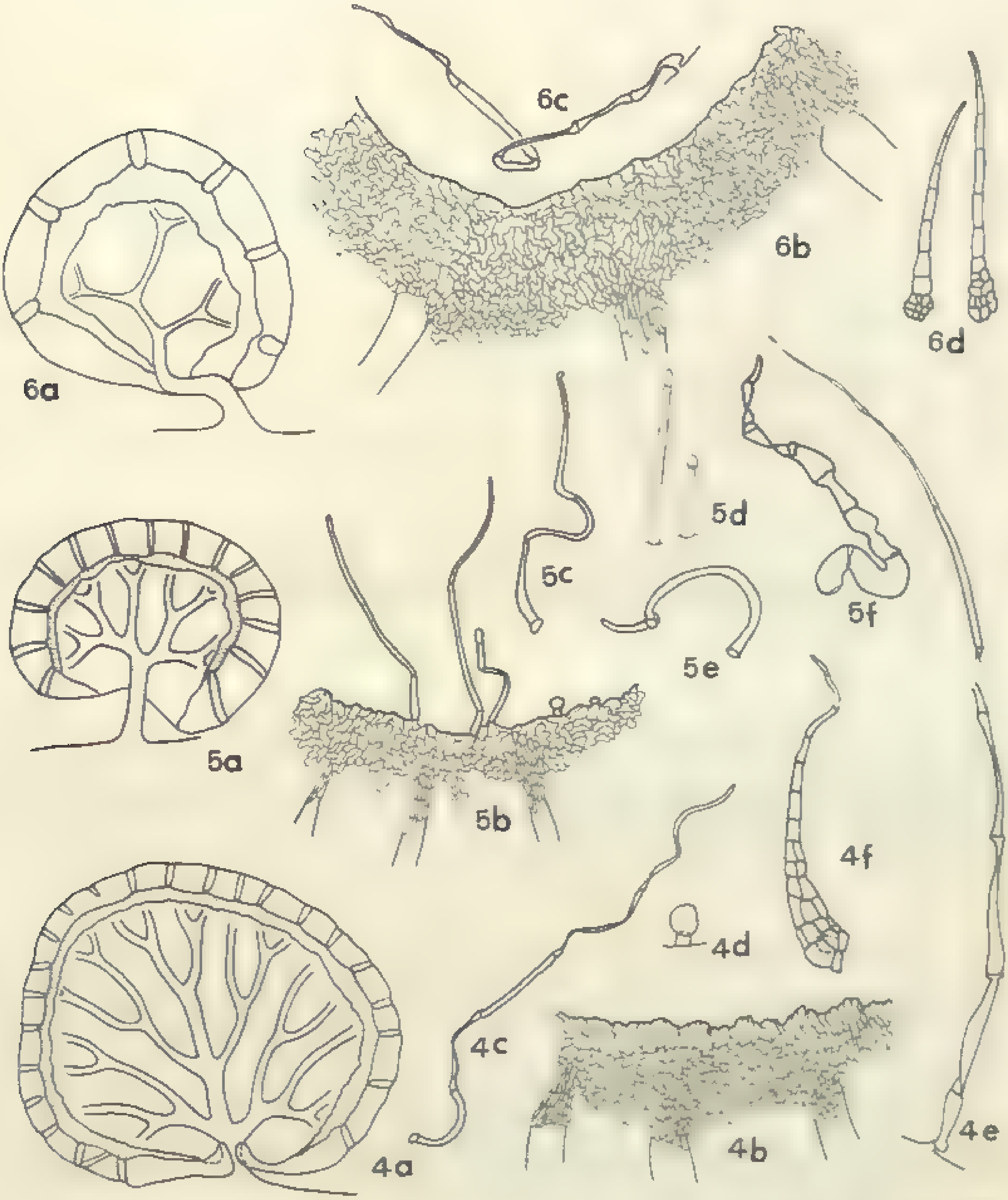
Colombia and Venezuela at 3500-4400 m. Additional specimens examined: COLOMBIA. MAGDALENA: *Barclay & Juajibioy 6560* (GH), Páramo de Macotama, *6933* (GH); *Cabot 27* (GH); *Schlim 850* (B, BM, G, K, L); *Seifriz 500* (US); *Wolleston 15* (K). VENEZUELA. MERIDA: *Jahn 137* (G, US).

5. **Jamesonia robusta** Karst. Fl. Columb. **2**: 29, t. 115. 1862.
Fig. 5. Map 5

TYPE: *H. Karsten,* Colombia, Bogotá, LE!, photo GH; isotype: W!, photo BM!, GH.

Gymnogramma robusta (Karst.) Hieron, Engl. Bot. Jahrb. **34**: 476. 1904.

Rhizome long creeping, dichotomously branching, often slender, ca. 0.5-2.0 mm. in diameter with many short, delicate roots, the internodes variable in length, the trichomes sparse, lax, patent, tan or light brown, lighter or the same color as the rhizome surface, 0.5-1.5 mm. long, usually with 1 cell, rarely 2 near the base, apex with a bulbous cell or acuminate. *Petiole* usually bent and appressed to the rhizome for a short distance before ascending, 4-10 cm. long, 1/5 to 1/3 as long as the lamina, castaneus to atropurpureus, terete or ellipsoidal, ca. 0.5 mm. in diameter at the apex usually more slender near the rhizome, with sparse, tan trichomes similar but shorter than those of the rachis. *Lamina* once pinnate, 24-36 cm. long, 0.3-0.7 cm. wide about the same width throughout or slightly broader at the apex with ca. 130-330 pinnae, indeterminate, the apical bud larger than the mature pinnae, with patent trichomes. *Rachis* castaneus or atropurpureus, terete or trigonous with an obtuse angle on the upper surface, pubescent, the trichomes equal to or usually up to two times longer than the pinnae, usually more densely tomentose on the lower surface, rust brown with the cells near the apex often grayed especially on older leaves, the apical cell acuminate. *Pinnae* alternate, subopposite in the apical portion of the lamina, 2 ranked, laterally disposed or slightly overlaying the rachis, imbricate, (basal pinnae smaller, distant, sterile, finally deciduous or often persistent) reniform, rarely with a slightly elongate central lobe, plane, margin enrolled, inequilateral at the base, 2-4 mm. long, 3-5 mm. wide, bright green, herbaceous; *upper surface* glabrous or slightly pubescent in the distal portion the trichomes tan or rust colored, with epidermal cell walls unthickened; *lower surface* with sparse to moderately dense rust brown, curled trichomes and shorter, capitate, glandular trichomes, *stalk* straight, ca. 0.5-1.0 mm. long, tan or light brown, not articulate. *Veins* broad, especially near the pinna



FIGS 4-6. FIG. 4. *J. Cuatrecasasii:* a, pinna, × 10; b, pinna margin with three vein ends, × 35; c, trichome from upper pinna surface, × 30; d, gland from lower pinna surface, enlarged; e, rachis trichome with four cells omitted from the mid-portion, × 30; f, rhizome trichome, × 30; all from *Cuatrecasas & Castaneda 24613* (US). FIG. 5. *J. robusta:* a, pinna, × 10; b, pinna margin with three vein ends, × 35; c, trichome from upper pinna surface, × 30; d, capitate trichomes from lower pinna surface, × 30; e, trichome from lower pinna surface, × 30; the last five from *Asplund 17827* (GH); f, rhizome trichome, × 30, from *Hitchcock 21638* (GH). FIG. 6. *J. pulchra:* a, pinna, × 10, from *Ewan 16100* (GH). b, pinna margin with three vein ends, the broken line indicating the limit of the border, × 35, from *Pennell & Hazen 10068* (GH); c, rachis trichome, × 30, from *Cuatrecasas 20124* (GH); d, rhizome trichomes, × 30, from *Pennell & Hazen 10068* (GH).

stalk, in the plane of the upper surface or slightly raised, dichotomous with wide angles, the branches moderately long, the ends acute or clavate extending to the border. *Border* broad, usually indusioid, more or less regularly dentate with few trichomes and glands, clear. *Sporangia* usually few near the pinna stalk, sometimes crowded obscuring the lower pinna surface, the stalk short with 2 or 3 tiers of cells, the lower one brownish and with intercalary cell divisions, the annulus of 24-27, or up to 33 indurated cells. *Spores* medium to dark brown, smooth or sparsely papillose, with a moderately broad equatorial wing, sometimes lobed, the angles not or slightly projecting.

The Karsten collection from the vicinity of Bogotá, upon which the name is based, is atypical in having pinnae with an elongated central lobe, and up to 33 indurated cells in the annulus of the sporangium. This is the greatest number of annular cells that I have observed in any of the species and most others have slightly more than half that number.

I found this species growing in large colonies in open fields, among rather dense clumps of grass at Patano Redondo, near Zipaquirá, Colombia. The rhizomes were deeply embedded among grass rhizomes and the leaves were easily broken at the delicate petioles. This páramo is known to be burned and plants having portions deeply embedded would have a better chance for survival in this circumstance. The species also occurs at Tausa, northeast of Zipaquirá where I found it growing among rocks with rather superficial rhizomes and the petioles less delicate. At this locality it occurs with, but is less abundant than, *Jamesonia bogotensis.*

In the reniform shape and broad indusioid borders of the pinnae, *J. robusta* resembles *J. canescens*, although it differs from that species in the relatively sparse, discrete trichomes on the lower pinna surface and the lax, light colored, rhizome trichomes. I consider *J. robusta* to be one of the intermediate species, more specialized than *J. rotundifolia* and less specialized than *J. canescens.*

Northern Colombia to southern Ecuador, at 2700-3570 m. Additional specimens examined: COLOMBIA. *Apollinaire-Maria 16* (US); *Ariste-Joseph A213* (US). BOYACA: Páramo de Rusia, *Langenheim 3442* (US). CUNDINAMARCA: Páramo de Choachi, *Apollinaire 12* (US); *Little & Little 9450* (COL, US); Mt. Aquila, *Pennell 2530* (GH, K, US); Patano Redondo, *Tryon & Tryon 6055* (BM, COL, GH, NY, P, US), Tausa, *6157A* (B, COL, GH, US). ECUADOR. AZUAY: *Asplund 17827* (GH, S); Páramos de Silván, *Barclay & Juajibioy 8372* (GH); *Hitchcock 21638* (GH, US); *Jameson* (K, US); Páramo Tinajillas, *Wiggins 10784* (US). CANAR: *Prieto P-143* (GH). PICHINCHA: *Jameson* (F, G, K).

6. **Jamesonia pulchra** Hook. and Grev. Icon. Fil. 2, t. 178. 1830. Fig. 6. Map 6

TYPE: *W. Jameson*, monte Cayambe, Ecuador, 12,000 ped., (cited as Peru) E!, photos: BM, GH, isotype: Herb Hook. K!.

Gymnogramma glabra Hieron. Hedwigia **48**: 215. 1909. TYPE: *Stübel 69*, Colombia, Tolima, Boca del Monte B!, photos: COL, F, GH, NY, US.

Jamesonia glabra (Hieron.) C. Chr. Ind. Fil. Suppl. 47. 1913.

Rhizome long creeping, dichotomously branched, slender ca. 1.0-2.5 mm. in diameter with numerous, coarse roots, the internodes variable in length, the trichomes rigid, appressed, lustrous, atropurpureus or dark brown, darker than the rhizome surface, 0.5-1.25 mm. long, with 1-4 cells near the base, apex acuminate. *Petiole* often bent or curled near the rhizome, sometimes appressed 4-16 cm. long, about 1/8 or 1/5 as long as the lamina, shining, castaneus, terete, ca. 0.5-1.0 mm. in diameter at the apex, sometimes more slender near the rhizome, with sparse tan or brown sometimes bicolorous trichomes having the basal cells clear, the apex acuminate. *Lamina* once pinnate, ca. 19-45 cm. long, 0.3-0.8 cm. wide, the central portion usually broader than the apex or base with ca. 140-350 pinnae, indeterminate, the apical bud about as large as the mature pinnae or up to twice as large, with trichomes patent or slightly appressed. *Rachis* similar in color to the petiole, ellipsoidal or trigonous and the upper surface with an obtuse angle and sparse indument, the trichomes shorter than the pinnae, similar to those of the petiole but usually longer and rust brown, the upper portion sometimes darker, the apical cell acuminate. *Pinnae* subopposite or alternate, usually laterally disposed in 2 ranks or slightly overlaying the rachis, imbricate, (the basal ones usually smaller, distant, sterile, usually gray or weathered, sometimes membranous, flat, with dentate margins) orbicular-cordate or ovate cordate with an oblique base, plane, the upper surface adjacent to the stalk not or sometimes concave, the margin enrolled sometimes partly obscuring the border, inequilateral at the base, the acroscopic lobe often prolonged, 1.5-4.0 mm. long, 1-4 mm. wide, yellowish or bright green, rigid herbaceous; *upper surface* usually glabrous or with few, tan trichomes, with epidermal cell walls unthickened; *lower surface* tomentose, the trichomes rust brown, crispate of 1 or few cells, *stalk* bent or strongly curved nearly 90° and often overlaying the acroscopic lobe of the pinna, ca. 1.0-1.5 mm. long, tan to castaneus. *Veins* moderately broad, in the plane of the upper surface or sometimes sunken, dichotomous with wide angles, the branches short or moderately long, the ends clavate extending to or shortly into the border. ***Border*** usually broad, often indusioid, delicate membranous, entire or somewhat dentate, ruddy tan or clear. *Sporangia* usually abundant, protruding above the tomentum, throughout the length of the veins, the stalk short of 3 tiers or moderately long with 4 tiers, the lowest a cluster of inflated cells, the annulus of 16-24 indurated cells. ***Spores*** light brown, smooth or with few broad ridges on the distal face, the equatorial wing moderately broad, the 3 angles not or slightly projecting; often shriveled.

MAPS 3, 5-9. Map 3, *J. rotundifolia*. Map 5, *J. robusta*. Map 6, *J. pulchra*. Map 7, *J. bogotensis*. Map 8, *J. canescens*. Map 9, *J. Scammanae*.

After Hooker and Greville described this species they retracted it in the addenda of their work with the following comment, "Tab. 178 *Jamesonia pulchra.* We are assured by Kaulfuss that this Fern is the *Pteris imbricata* of Swartz. The descriptions given of it, however we find to be incorrect. For *Jamesonia pulchra,* therefore, read J. imbricata". The Jameson collection upon which this name is based, in the Greville Herbarium at Edinburgh is mounted with a collection from Peru, *Mathews 979.* The Jameson collection from Cayambe, consists of two leaves, each representing a different species and neither of them *J. imbricata.* The larger leaf is from a plant of this species and the other is one from *J. robusta.* Both the description and figures of this material in the Icones Filicum are so generalized that it is not possible to positively identify either species as the predominant element of the treatment. The illustration of the straight pinna stalks applies better to *J. robusta,* but on the gross aspect of the larger apical bud, the more distantly spaced pinnae and the bent petioles there is a greater resemblance between the illustration and the larger leaf of the original collection. I am applying the name *J. pulchra* to this and the smaller leaf is now identified as *J. robusta.*

The strongly bent pinna stalks and prolonged basal lobe of the pinna in *J. pulchra* are rather distinctive, specialized characters. The tomentum on the lower surface of the pinnae and the broad indusioid borders show a similarity to *J. robusta* and the rigid, appressed rhizome trichomes are similar to those in *J. canescens.* It appears to be one of the species intermediate to these and with relatively specialized characters.

Cordillera Central of Colombia to northern Ecuador, at 3000-4270 m. Additional specimens examined: COLOMBIA. ANTIOQUIA: Páramo de Chaquiro, *Pennell 4270* (GH, US), *4282* (GH, K, US). CALDAS: *Cuatrecasas 23105* (GH, US); Páramo del Quindio, *Pennell & Hazen 9939* (GH, US), *10068* (GH, US); Páramo Ruiz, *Tryon & Tryon 6141* (COL, GH). CAUCA: *Cuatrecasas 18966* (GH, US), *19112* (GH, US); Páramo de Gabriel Lopéz, *Lehmann V.* in 1961 (GH); Páramo de Buena Vista, *Pittier 1136* (US); Páramo de Puracé, *Tryon & Tryon 5972* (B, BM, COL, GH, LE, NY, US). NARINO: Volcán de Chiles, *Ewan 16100* (GH, US), Volcán de El Galeras, *Ewan 16315* (GH, US). PUTUMAYO: Páramo de Bavaya, *Cuatrecasas 20124* (G, GH, US); Alta de Cruz, *Foster & Foster 2052* (COL); Páramo de San Antonio, *Schultes 3239* (GH, US). TOLIMA: Páramo Ruiz, *Pennell 3089* (GH, K, US). ECUADOR. CARCHI: *Holmgren 881* (B, BM, F, G, GH, K, S-PA, US).

7. **Jamesonia bogotensis** Karst. Fl. Columb. **2**: 29, t. 115. 1862. Fig. 7. Map 7

TYPE: *H. Karsten*, Colombia, Tausa LE! photo, GH, W; isotypes: LE!, W! photo BM!.

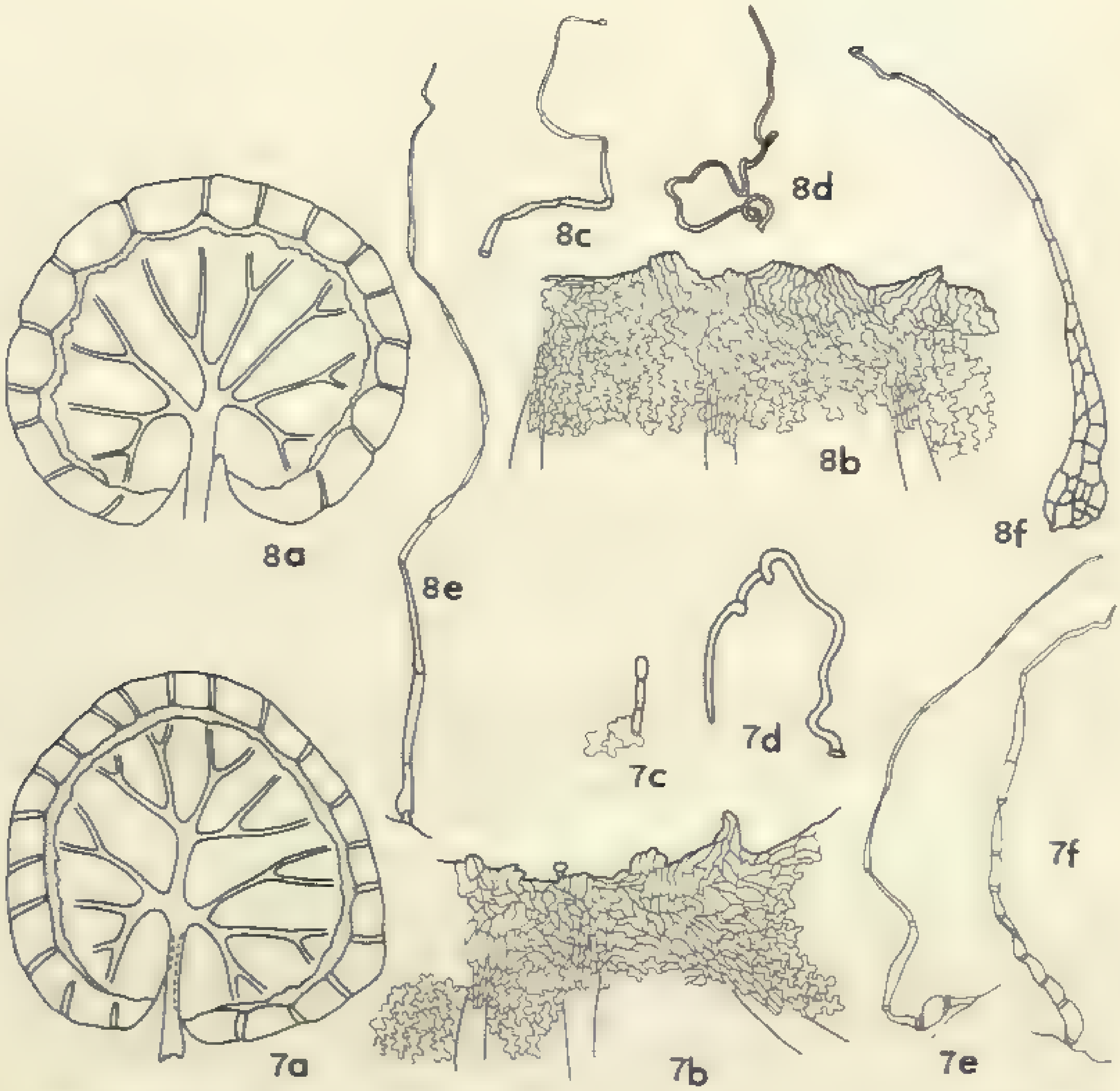
Gymnogramma bogotensis (Karst.) Hieron. Engl. Bot. Jahrb. **34**: 478. 1904.

Rhizome long creeping, dichotomously branching, ca. 1-4 mm. in diameter with numerous, coarse roots, the internodes variable in length, the trichomes lax, patent, lustrous, light amber color or light brown, usually lighter than or the same color as the rhizome surface, 1-2 mm. long with 1 cell at the base, apex acuminate. *Petiole* usually bent or curled and sometimes appressed to the rhizome for a short distance before ascending, 1-7 cm. long, 1/10-1/4 as long as the lamina, atropurpureus, terete or ellipsoidal, ca. 1.0-2.5 mm. in diameter at the apex, more slender near the rhizome with sparse tan trichomes similar to but often shorter than those of the rachis. *Lamina* once pinnate, ca. 10-35 cm. long, 0.3-0.6 cm. wide about the same size throughout or somewhat narrowed toward the base, with ca. 120-570 pinnae, indeterminate, the apical bud usually larger than the mature pinnae, with patent trichomes. *Rachis* castaneus, terete or trigonous with an obtuse angle on the upper surface, the upper surface pubescent, the lower surface tomentose, the trichomes equal to or slightly longer than the pinnae, not enveloping them except near the lamina apex, concolorous, tan or ruddy brown becoming gray above, the apical cell acuminate, rarely bulbous on the bud. *Pinnae* subopposite, laterally disposed, usually stacked in 2 ranks, imbricate, (the basal ones smaller, distant, sterile, persistent) ovate-cordate or orbicular-cordate, the basal lobes usually prolonged and protruding above the upper surface of the pinna, usually concave on the upper surface adjacent to the stalk, the margin enrolled partly or wholly obscuring the border, inequilateral at the base, 2-4 mm. long, 2-4 mm. wide medium or bright green, herbaceous; *upper surface* glandular, usually glutinose or crustose, also sometimes pubescent, the trichomes tan or clear, the epidermal cells unthickened; *lower surface* densely tomentose and matted, the trichomes crispate, 1 or few celled, also with short, capitate glands especially near the border, *stalk* straight, ca. 0.5-1.0 mm. long, tan or castaneus sometimes glandular, often articulating in the mid-portion. *Veins* broad, usually sunken especially the main veins near the stalk, sometimes slightly raised, dichotomous with wide angles, the branches short or moderately long, the ends clavate or acute, extending to the border. *Border* usually moderately broad, rarely broader, more or less regularly dentate, sometimes glandular, tan or rust brown. *Sporangia* usually abundant and enmeshed in the tomentum throughout the length of the veins, the stalk short, up to half as long as the capsule, with 2 or 3 tiers of cells these sometimes elongate, the annulus with 19-25 indurated cells. *Spores* tan to light brown, verrucose or irregularly papillose, with a moderately broad equatorial wing sometimes irregular, the angles not projecting.

Most specimens of this species are relatively easily identified but a few from northeastern Colombia on Páramo

Almorzadero and Nevado del Cocuy resemble *J. canescens* in having dense pubescence on the upper surface of the pinnae and few or no glands. Unfortunately these specimens are without rhizomes for the trichomes of these would be decisive in the determination. On some páramos in central Colombia, Cruz Verde and Chisaca, it occurs with *J. imbricata* var. *glutinosa* and there are some specimens which appear to be intermediate between them. The pinnae of *J. bogotensis* are unusual in having the basal lobes thrust above the upper surface of the pinna and the veins are relatively numerous and crowded for the size of the pinnae. It is possible that this species may have come from one of the species having larger, reniform pinnae, as *J. robusta* or *J. canescens* which occur within or adjacent to the range of *J. bogotensis*. The former is considered the better possibility as there are similarities in the rhizome trichomes. From the chromosome count of n = 87 *J. bogotensis* is thought to be a hexaploid and to be a derived and relatively complex species. It belongs to the group of species having dense tomentum on the under surface of the pinnae and broad, membranous borders although its relationship among these is not clear. It is distinguished from this group in having glands on the upper surface of the pinnae and in this character resembles *J. imbricata* var. *glutinosa* and *J. Scammanae.*

Central Colombia northeast to the Venezuelan border, at 2950-4400 m. Additional specimens examined: COLOMBIA. Páramo de Cachene, *Austin 25* (K); *Wercklé* in 1906 (GH). BOYACA: *Barclay & Juajibioy 7396* (GH); Chorreón de San Paulino, *Cuatrecasas & Garcia-Barriga 1328* (COL, US), *1421* (US). CALDAS: *Cuatrecasas 23225* (GH, US); Páramo del Quindio, *Pennell & Hazen 9931* (GH, US). CUNDINAMARCA: *Apollinaire*, in May 1905 (GH, P), in April 1906 (GH); Páramo de Zipaquirá, *Cuatrecasas 9540* (COL, US); *Fosberg 22022* (GH, US); *Goudot* (G); *Lindig 185* (K); *Little 9313* (US); *Mutis 3097* (US); *Pérez Arbeláez 1153* (COL, US), *1490* (US); Páramo de Chisaca, *Schultes 20172* (COL, GH, US); Páramo de Cruz Verde, *Tryon & Tryon 6080* (BM, COL, GH, P, US), Tausa, *6156* (GH), *6157* (B, COL, GH, LE, NY, P, US), Páramo de Chisacá, *6177* (B, BM, COL, F. GH, LE, NY, P, US), *6178* (GH). NORTE DE SANTANDER: *Funck & Schlim 1370* (BM, G, L, LE, P). SANTANDER: Páramo de Almorzaderos, *Alston 7386* (BM, GH); *Apolinar-Maria 20* (US); *Cuatrecasas 10032* (US), *13514* (COL, GH, US); Páramo de las Vegas, *Killip & Smith 15658* (COL, GH, S, US), Páramo de Vetas, *17412* (BM, COL, GH, US), Páramo de Santurbán, *17575* (B, GH, P, US), Páramo de Mogotocoro, *17647* (GH, US), Páramo Rico, *17725* (GH, US), Páramo de las Coloradas, *18446* (GH, K, LE, S-PA, US); Almorzador, *Vareschi 4040* (VEN), *4041* (VEN).



FIGS. 7 AND 8. FIG. 7. *J. bogotensis:* a, pinna. × 10; b, pinna margin with three vein ends, × 35; both from *Schultes 20172* (GH); c, glandular trichome from upper pinna surface with epidermal cells, enlarged, from *Cuatrecasas 13514* (GH); d, trichome from lower pinna surface, × 40, from *Killip & Smith 18446* (GH); e, rachis trichome, × 30, from *Cuatrecasas 13514* (GH); f, rhizome trichome, × 30, from *Killip & Smith 17647* (GH). FIG. 8. *J. canescens:* a, pinna, × 10; b, pinna margin with three vein ends, × 35; c, trichome from upper pinna surface, × 45; d, trichome from lower pinna surface, × 30; the last four from *Gabaldon,* in 1922 (US); e, rachis trichome, × 30, from *Alston 6601* (GH); f, rhizome trichome, × 30, from *Alston 6815* (GH).

8. **Jamesonia canescens** Kunze, Farrnkr. 1: 95. 1846.
Fig. 8 Map 8

TYPE: *Moritz 339,* Venezuela, Páramo de la Culata (cited as Colombia by Kunze) B!, photos COL, F, GH, NY, US; isotypes: BM! E! G! GH! K! P! US!.

Gymnogramma canescens (Kunze) Kl. Linnaea **20**: 407. 1847.

Jamesonia nivea Karst. Fl. Columb. **2**: 29, t. 115. 1862. TYPE: *H. Karsten,* Venezuela, Prov. Mérida, Jaji, LE! photos, GH, W; isotypes: LE! P! W!; photos BM, GH.

Jamesonia imbricata (Sw.) Hook. and Grev. var. *canescens* (Kunze) Hook. Sp. Fil. **5**: 106. 1864.

Psilogramme canescens (Kunze) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 333. 1882.

Psilogramme nivea (Karst.) Kuhn. op. cit. 333. 1882.

Jamesonia imbricata (Sw.) Hook. and Grev. var. *nivea* (Karst.) Sodiro, Crypt. Vasc. Quit. 387. 1893.

Rhizome long creeping, dichotomously branching ca. 1-3 mm. in diameter with sparse to numerous coarse roots, the internodes variable in length, the trichomes rigid, appressed, lustrous dark brown to black, darker than the rhizome surface, ca. 1.0-2.5 mm. long with 1-5 cells usually more than 1 near the base, apex acuminate. *Petiole* usually bent or curled and appressed to the rhizome for a short distance before ascending, 1.5-11.0 cm. long, 1/20-1/3 as long as the lamina, castaneus, terete or ellipsoidal, ca. 1.0-2.5 mm. in diameter at the apex, more slender near the rhizome, with sparse to moderately dense, tan or rust brown trichomes similar to those of the rachis. *Lamina* once pinnate, ca. 10-50 cm. long, 0.3-1.2 cm. wide, with the apical portion of the lamina broadest, narrowed toward the base, ca. 120-600 pinnae, indeterminate, the apical bud larger than the mature pinnae, with patent trichomes. *Rachis* castaneus, terete or trigonous with an obtuse angle on the upper surface, densely tomentose, the trichomes usually two or more times longer than the pinnae and usually enveloping them, rust-brown, tan or gray, concolorous, the apical cell long acuminate. *Pinnae* subopposite, laterally disposed, often stacked in 2 ranks, imbricate, (the basal ones smaller, distant, sterile, persistent, sometimes alternate, membranous, flat, with dentate margins) mostly reniform or orbicular, plane or sometimes with the acroscopic lobe prolonged and bent, the margins enrolled, sometimes partly obscuring the border, inequilateral at the base 2-4 mm. long, 1-5 mm. wide, medium green, rigid herbaceous; *upper surface* usually tomentose, the trichomes usually clear, tan or sometimes darker, the epidermal cell walls unthickened; *lower surface* with dense tan or rust colored, matted tomentum, the trichomes crispate, 1 or few celled, sometimes also with capitate glands, seldom glabrous, *stalk* straight (usually bent in intermediate specimens) ca. 0.5-1.0 mm. long, tan to castaneus, sometimes articulate in the mid-portion. *Veins* broad, especially the main ones adjacent to the stalk, sunken on the upper surface, dichotomously branching at wide angles, the branches moderately long, the ends acute or clavate, extending to the border. *Border* usually broad, sometimes indusioid, rather regularly dentate, clear or tan. *Sporangia* moderately dense, enmeshed in the tomentum, the stalk short, up to 1/2 as long as the capsule, with 2 or 3 tiers, the lower usually darker and with intercalary divisions, the annulus with 18-20 indurated cells. *Spores* tan to light brown, verrucose or irregularly papillose especially on the distal face, with a moderately broad equatorial wing, sometimes irregularly lobed, the angles not projecting.

There is some confusion as to the country of the type collection of Moritz for the description and most of the authentic specimens indicate Colombia. The specimen at the British Museum, appears to have the original ticket and has the following data, "Páramo de la Culata, Chalapa i via Mérida". Both Páramo de la Culata and Mérida are in

Venezuela and evidently an error was made, in copying the label, which was taken up by Kunze. There is also some doubt about which of the specimens represents the type for Kunze cites two specimens, one at Berlin and a second in the herbarium of Moritz which was later acquired by the British Museum. Neither of these specimens bears his annotation nor can they be positively identified with the figure in tab. 133 of his Farrnkräuter Supplement of 1851. I have cited the specimen at Berlin, which is more complete, as the type.

There are a few variations, particularly in the tomentum and size of the leaves of *J. canescens*, which do not merit taxonomic recognition, but should receive some attention. Field studies have been most helpful in the interpretation of some of these. In the Sierra de Santo Domingo around Laguna Negra there are plants on which the lower pinnae of the leaves, or all of them on small leaves, are nearly glabrous, flat and dentate. This appears to be a juvenile form which is retained for a longer period in some plants.

The color of the tomentum of the leaves in *Jamesonia canescens* varies from white to rust brown with most of the collections in the range between tan and rust colored. Those with grayish white tomentum have been recognized earlier as *J. nivea*. I have observed plants of this type at several stations in the Sierra Nevada de Mérida and find them to occur in the same habitat as those with darker tomentose leaves but in colonies discrete from them. They have generally more slender leaves and the pinnae are sometimes glabrous on the lower surface. I have included them in *J. canescens* since I do not find other morphological differences equivalent to those of other species.

The most heavily tomentose plants occurred in large colonies on Páramo de la Negra in Táchira. The leaves were covered with a felted, white tomentum and formed a dense carpet-like growth on the highest part of the páramo. These are quite distinctive plants and can be readily recognized as from this area.

There are several collections with green, sparsely tomentose leaves having small pinnae and usually bent pinnae stalks which occur within the range of *Jamesonia canescens*, particularly in the northern part of Mérida from páramos Timotes, Gavilan, Pico Aguila, Laguna Negra and Laguna Grande and on páramos Conejos and Quinora near the city of Mérida. These plants have some resemblance to *J. imbricata* var. *glutinosa* in having elongate pinnae with bent stalks which may be inserted at the pinnae base without a notch, the indument on the upper pinna surface is usually of coarse, short trichomes and on the lower surface it is usually of white or tan, crispate trichomes. There is also a similarity in these characters to *J. imbricata* var. *meridensis* although none of this material is glandular on the upper pinna surface as in that variety. The collections of this variation are cited apart from the others.

Except for collections on Páramo de Táma on the Colombian border all of the specimens are from Venezuela mostly from the Sierra Nevada de Mérida but extending northeast to Lara. It usually occurs above 3500 m. and up to 4400 but has been collected at 2600 m. on Páramo de Molino above Mérida. Additional specimens examined: VENEZUELA. LARA: *Steyermark 55493* (GH, K, US). MERIDA: Páramo de Timotes, *Alston 6594* (BM, GH), *6601* (BM, GH), Páramo de Mucuchies, *6638* (BM, GH), *6653* (BM, GH), *6815* (BM, GH), *6927* (BM, GH), Páramo de la Negra, *7000* (BM, GH), *7025* (BM, GH); Páramo de Mucubaji, *Barclay & Juajibioy 9557* (GH), *9636* (GH), Pico de Mucunuqui *9901* (GH); *Bellard 203* (US), *208* (US); *Boursey*, in Mar. 1901 (GH); *Chardon 305* (VEN); *Fortanier*, herb. no. 19938 (VEN); *Funck & Schlim 1097* (B, BM, E, G, L, LE, P); *Ewan 16966* (K, US, VEN); *Gabaldon*, in 1922 (US); *Gehriger 79* (G, VEN); *Gines 1728* (US); Páramo de Mucuchies, *Gutzwiller 13* (VEN), *26* (G); Páramo del Tambor, *Hanbury-Tracy 44* (K); Páramo de Timotes, *Jahn 138* (G, US), Páramo Quinora *726* (B, US, VEN), *855* (GH, US, VEN), Páramo del Molino, *956* (GH, P, US, VEN), Páramo de San José, *972* (GH, US, VEN), Páramo de Sto. Domingo *1103* (BM, US, VEN), *1308* (VEN); Páramo de Timotes, *Pittier 12724* (G, US, VEN); *Reed 74* (US); *Steyermark 55901* (GH, U, US, VEN); Páramo de El Gavilán, *Tamayo 38* (US, VEN), *39* (US, VEN), *40* (US, VEN), *41* (US, VEN), *42* (US, VEN), Páramo de *Mucuchies 3803* (VEN), *3804* (VEN); *Tryon & Tryon 5796* (BM, GH, US), *5798* (GH), *5800* (BM, COL, GH, NY, US), *5800* (GH), *5809* (B, GH, LE, P), *5812* (GH), *5819* (GH), *5824* (GH, NY), *5826* (GH, US), *5827* (F, GH), *5828* (GH), *5830* (GH), *5831* (GH, US), *5832* (GH), *5840* (GH, US), *5841* (GH), *5842* (GH), *5843* (GH), *5844* (COL, GH, P), *5845* (GH, F, US), *5846* (GH), *5848* (BM, GH), *5849* (GH), *5860* (GH), *5862* (GH, NY, P), *5863* (GH, LE), *5864* (GH), *5865* (B, GH), *5878* (GH); *Vareschi 6978b* (VEN); *Vareschi & Lasser 389* (VEN); *Vareschi & Pannier 941* (US, VEN), *1279* (VEN), *1430* (US, VEN), *1729* (VEN). TACHIRA: *Archer 3153* (US); Páramo de Tamá, *Cardona 306* (US, VEN); *Müller 1017* (VEN); Páramo de la Negra, *Tryon & Tryon 5884* (BM, COL, F, GH, US), *5886* (B, GH, P, NY). COLOMBIA. NORTE DE SANTANDER: Páramo de Tamá, *Cuatrecasas*, et al. *12606* (GH, US).

Variant with sparse tomentum, small pinnae and usually bent pinna stalks: VENEZUELA. MERIDA: Páramo de Timotes, *Alston 6600* (BM, GH), *6654* (BM, GH), Páramo de Mucuchies, *Barclay & Juajibioy 9702* (GH), Páramo de Mucubaji, *9812* (GH); *Gines 1744* (US); Páramo de Conejos, *Hanbury-Tracy 104* (K); *Jahn 162* (US), Páramo Quinora, *725* (US, VEN); *Mägdefrau 561* (GH, U); *Pittier 13184* (G, US, VEN), *13247* (US, VEN); *Tryon & Tryon 5829* (GH), *5834* (F, GH, US), *5847* (GH, US), *5850* (BM, GH, NY, US), *5851* (GH), *5853* (GH, US).

9. **Jamesonia Scammanae** A. F. Tryon, sp. nov. Fig. 9. Map 9

Trichomata rhizomatis plerumque appressa vel laxa, patentia, pallida usque obscuro-fusca, laminae angustae 2-6 mm. latae, gemma vermiformis, glutinosa, rachis glutinosa, crustosa, pinnae ovatae vel lobatae, subsessiles vel petiolulis ad 0.7 mm. longis, pinna adaxialiter vernicosa vel crustosa, abaxialiter tomentosa, trichomatibus crispatis, albidis vel fulvis, limbo modice lato, integro vel leviter undulato, sporae pallide succineae vel fulvae, laeves.

TYPUS: Costa Rica, Cerro de la Muerte, March 25, 1956, *Edith Scamman* and *L. R. Holdridge 7929* GH.

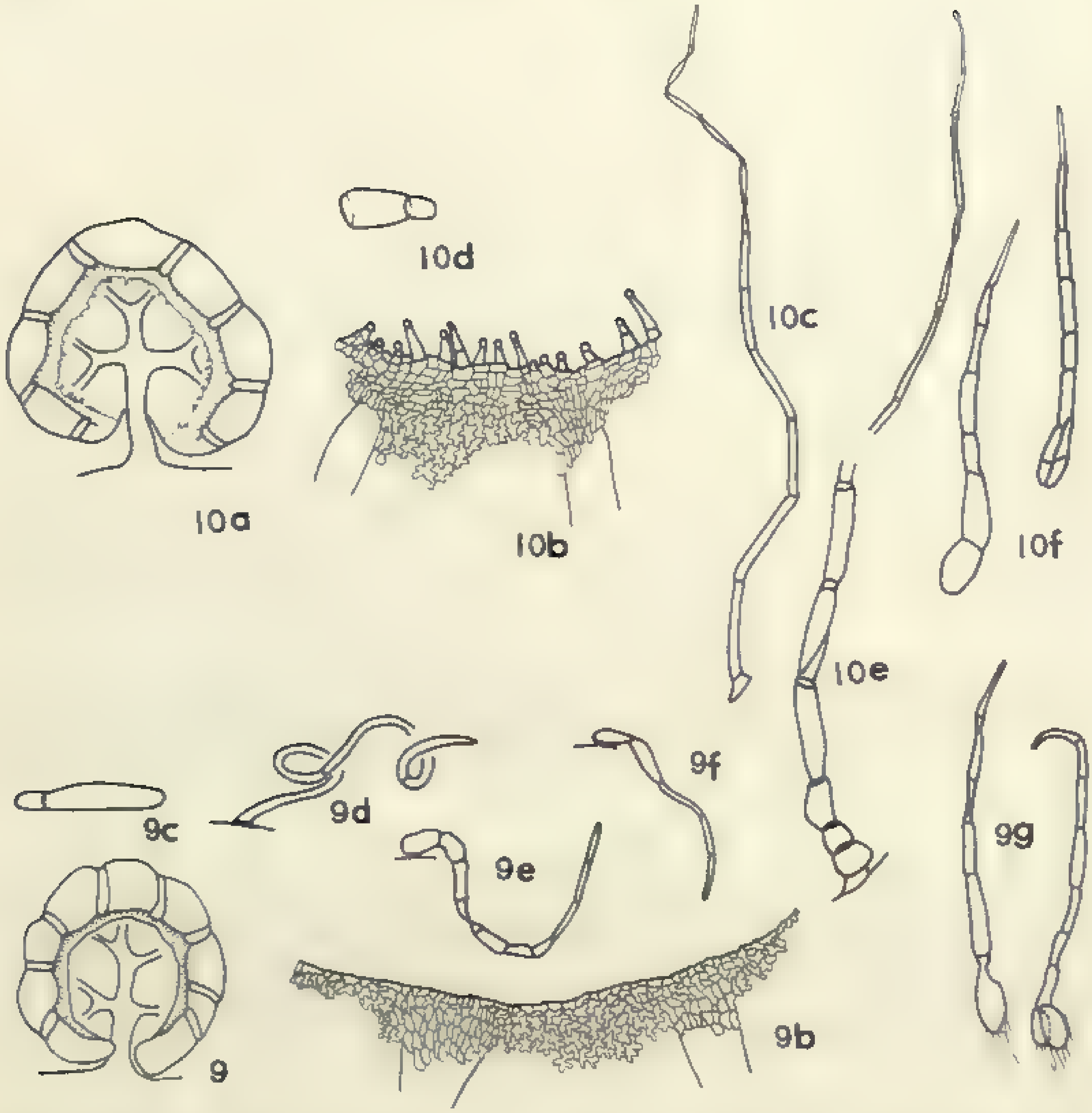
Rhizome long creeping, dichotomously branching, slender ca. 1-2 mm. in diameter with sparse roots, the internodes variable in length, the trichomes usually rigid, appressed, sometimes lax, patent, lustrous light to dark brown, usually darker than the rhizome surface, 1.0-1.5 mm. long with usually 1 (-5) cells near the base, apex acuminate. *Petiole* often bent or curled near the rhizome, sometimes appressed, 3-11 cm. long, about 1 9 to 1 3, rarely 1/2 as long as the lamina, atropurpureus, in old leaves often blackish and crustose, terete or somewhat ellipsoidal, ca. 0.75-1.0 mm. in diameter at the apex, filiform below, the trichomes sparse, brown or bicolorous with clear cells at the base, apical cells acuminate. *Lamina* once pinnate, ca. 11-45 cm. long, ca. 0.2-0.6 cm. wide, about the same size throughout with the base slightly narrowed, ca. 70-300 pinnae, indeterminate, the apical bud vermiform, usually larger than the mature pinnae, glutinose with appressed trichomes. *Rachis* similar in color to the petiole, terete, ellipsoidal or trigonous the upper surface with an obtuse angle, glutinose or crustose, the trichomes more abundant on the lower surface, generally longer adjacent to the pinnae but not exceeding them in length, clear or tan, the apical cell bulbous or sometimes acuminate. *Pinnae* alternate or subopposite, approximate or distant, in 2 ranks sometimes overlaying the rachis, (basal ones smaller, distant, sterile, usually persistent) ovate, sometimes lobed, usually with a central furrow on the upper surface, the margins enrolled, inequilateral at the base, 1.5-4.0 mm. long, 1.5-3.0 mm. wide, gray or bright green, rigid herbaceous; *upper surface* vernicose or crustose with short, appressed glands, the epidermal cell walls unthickened; *lower surface* tomentose with whitish or tan, crispate trichomes of one or few cells, *stalk* bent, ca. 0.25-0.75 mm. long, atropurpureus, not articulate, pinnae usually subsessile. *Veins* broad to moderately broad, more or less sunken on the upper surface, dichotomous with branches at wide angles, the branches moderately long, the ends clavate or flabellate extending into the border. *Border* moderately broad, firm-membranous or similar to the pinna in texture, entire or slightly undulate, opaque white or lutescent. *Sporangia* crowded along the veins, obscuring the lower pinna surface, the stalk short to moderately long with some intercalary divisions, the annulus of 19-23 indurated cells. *Spores* pale amber colored or tan, smooth, the equatorial wing moderately broad, the three angles not projecting.

I am pleased to name this species for Edith Scamman who has collected complete and ample specimens of it from Costa Rica. Her collections and studies of the Costa Rican ferns have contributed appreciably to our knowledge of that area.

It is surprising that this distinctive species has not been recognized earlier for collections of it were made by Jameson and Spruce and rather widely distributed. Some correspondence between these two was provoked by the report by Jameson of the species growing in Sphagnum. A letter from Spruce accompanying his collection at the British Museum indicates he did not believe that Sphagnum occurred in the Andes and had forced Jameson to admit to this. This abuse of Jameson is rather curious for Sphagnum does occur in the Andes and bits of it are often found among the rhizomes in collections of *Jamesonia*.

Jamesonia Scammanae is one of the three widest ranging species; it has the greatest altitudinal range and it is relatively specialized in its shortened pinna stalks, in the glandular-crustose indument and elaborate but entire pinna borders. It is distinct from other species in these characters and in the glutinose, vermiform leaf buds although there is a general resemblance to *J. imbricata* var. *glutinosa* in the small, widely spaced, glutinose pinnae. In several more detailed characters of the pinnae as the broad veins, which are dichotomous at wide angles, the central furrow on the upper surface, the cordate base, and especially in the dense, crispate trichomes on the lower surface and in the light colored spores there is a greater resemblance to *J. bogotensis*.

Central Bolivia to Costa Rica, at 1830-4300 m. Additional specimens examined: COSTA RICA. *Carson*, in 1956 (GH). CARTAGO: Cerro de la Muerte, *Carpenter 289* (US); *Holm & Iltis 476* (B, BM, S-PA, US); Cerro de Buena Vista, *Pittier & Tonduz 3350* (B, BM, P, US); *Rogers CR25* (GH); *Scamman 6078* (GH), *6078B* (GH), *7052* (GH); *Williams 16086* (US). SAN JOSE: Dos Burros Peaks, *Dayton 3083* (US); Cerro de las Vueltas, *Standley 43842* (US), *43875* (US). COLOMBIA. CALDAS: Páramo de Las Letras, *Barclay & Juajibioy 6280* (GH); Páramo Ruiz, *Tryon & Tryon 6142* (GH). CAUCA: Páramo de Puracé, *Tryon & Tryon 5960* (COL, GH), *5980* (GH). TOLIMA: Páramo de Herveo, *Hanbury-Tracy 627* (K). ECUADOR. *A. Mille 40* (US); *Stübel 350* (US).



FIGS. 9 AND 10. FIG. 9. *J. Scammanae:* a, pinna, × 10, from *Scamman & Holdridge 7929* (GH); b, pinna margin with two vein ends, × 35, from *Vargas 1060* (GH); c, gland from upper pinna surface, enlarged; d, trichome from lower pinna surface, × 40; the last two from *Asplund 9922* (GH); e, rachis trichome, × 30, from *Cook & Gilbert 1833* (US), f, petiole trichome, × 30; g, rachis trichomes, × 30; the last two from *Scamman 6078* (GH) FIG. 10. *J. peruviana:* a, pinna, × 10; b, pinna margin with two vein ends, × 35; the last two from *Pennell 13873* (GH); c, trichome from upper pinna surface, × 30, from *Macbride 4404* (F); d, gland from lower pinna surface, enlarged, from *Pennell 13873* (GH); e, rachis trichome with five cells omitted from the mid-portion, × 30; f, rhizome trichomes, × 30; the last two from *Macbride 4404* (F).

CARCHI: Páramo del Angel, *Barclay & Juajibioy 9410* (GH); *Fagerlind & Wibom 1509* (S). IMBABURA: *Wiggins 10420* (US). PICHINCHA: Antitana, *Jameson* (B, BM, G, GH), Guamini, *Jameson 768* (BM, E, K); *Spruce 5660* (BM, G, K, LE, P). TUNGURAHUA: Cord. de Llanganates, *Asplund 9922* (GH, S). PERU. *Lechler 2032* (B, E, K, LE, P). APURIMAC: *Santander* et al in 1935 (UC); *Vargas 1060* (GH). CUZCO: *Bües 1008* (US); *Cook & Gilbert 1242* (US), *1833* (US); Cerro de Cusilluyoc, *Pennell 13870* (F, GH, US); Paucartambo, *Soukup 386* (F); *Vargas 11165* (F, K, UC). HUANUCO: *Macbride & Featherstone 2182* (F, GH, US). JUNIN: *Bryan 183* (F, US); *Kunkel 485* (GH). LIMA: *Saunders 399* (BM). BOLIVIA. COCHABAMBA: *Cárdenas 668* (GH, US); *Herzog*

789 (US). LA PAZ: *Asplund 1074* (BM, S-PA); *Mandon 1552* (BM, GH, K, LE, P); *Rusby 141* (GH, US); Pongo, *Tate 111* (US).

10. **Jamesonia peruviana** A. F. Tryon, sp. nov. Fig. 10. Map 10

Trichomata rhizomatis rigida plus minusve appressa, castanea vel atropurpurea, apex laminae indeterminata, gemmae tomento fulvo vel stramineo, pinnae imbricatae, reniformes vel orbiculares, rigide herbaceae vel leviter coriaceae, pinna adaxialiter tomentosa trichomatibus longis, sapienter paucim pinnas circumjectis, abaxialiter trichomatibus brevibus, capitatis, nervis latis, dichotomis, angulis latis marginem non attingentibus, limbo lato, papillis plus minusve uniformibus, sporae fulvae vel stramineae, leviter papillatae.

TYPUS: Peru, Huanuco, Tambo de Vaca, 13,000′ *J. F. Macbride 4404*, F; isotypus, US.

Rhizome long creeping, dichotomously branched, slender, ca. 1.0-1.5 mm. in diameter with moderately dense, delicate roots, the internodes variable in length, the trichomes rigid, more or less appressed, castaneus or atropurpureus, darker than the rhizome surface, ca. 1.0-1.5 mm. long, with 1 or 2 cells at the base, apex acuminate. *Petiole* usually bent and somewhat appressed to the rhizome for a short distance before ascending, 1-3 cm. long, possibly longer, 1 27, 1 14 as long as the lamina, castaneus, terete, ca. 0.5-1.0 mm. in diameter at the apex about the same size throughout. with sparse, clear trichomes. *Lamina* once pinnate, ca. 17-40 cm. long, 0.3-0.5 cm. wide, broadest at the apex, narrower toward the base, with ca. 250-600 pinnae, indeterminate, the apical bud larger than the mature pinnae, with trichomes patent or somewhat appressed. *Rachis* castaneus, often slightly lighter colored than the petiole, ellipsoidal, or trigonous and the upper surface with an obtuse angle, tomentose, the trichomes long, two or more times longer than the pinnae, discrete, tan or straw colored, with the lower cells clear, the apical cell bulbous, rarely acuminate. *Pinnae* subopposite, usually stacked in 2 ranks, imbricate, deciduous, (the basal ones, minute and distant or often absent) reniform or orbicular-cordate, concave on the upper surface, the margin enrolled, inequilateral at the base with the acroscopic lobe often larger and bent, 1.5-2.5 mm. long, 2-3 mm. wide, yellow-green, rigid herbaceous or slightly coriaceous; *upper surface* with long, discrete, gold colored trichomes, strongly bent near the base of the trichome, appressed and usually enveloping several pinnae, the epidermal cell walls sometimes slightly thickened; *lower surface* with sparse, short, 1 or 2 celled, capitate trichomes and a tuft of longer, tan or clear trichomes on the stalk and adjacent veins, sometimes somewhat pubescent along all veins, *stalk* straight, ca. 0.75 mm. long, tan, frequently articulate. *Veins* broad, slightly sunken especially on the upper surface near the stalk, dichotomous with wide angles, the branches short or moderately long, the ends clavate or nearly acute, extending to the border. *Border* broad, firm membranous with more or less uniform papillae or cilia, tan or rust colored. *Sporangia* usually few on veins adjacent to the stalk, sometimes obscuring the lower surface, short stalked with many intercalary cell divisions, the annulus of 16-23 indurated cells. *Spores* tan or straw colored, papillose or sparsely verrucose, the equatorial wing moderately broad, the 3 angles prominently projecting.

The species is unique in having, on the upper surface of the pinnae, long, appressed but discrete trichomes which cover several pinnae, and a fringe of fairly uniform cilia or papillae along the pinna border. The northernmost collection from Libertad differs from the others in having acuminate rather than bulbous tipped rachis trichomes and fairly dense pubescence on the lower pinna surface. Some collections are mixed with *Jamesonia scalaris* and with *J. Alstonii* and there is a resemblance between the latter and *J. peruviana* in the stacked alignment of the pinnae on the rachis and the ciliate pinnae margins. There is also a resemblance to *J. rotundifolia* in the long, gold colored trichomes on the upper pinnae surface. I have seen only two rhizomes and they are probably difficult to collect for the plants are reported to grow among grasses in boggy places.

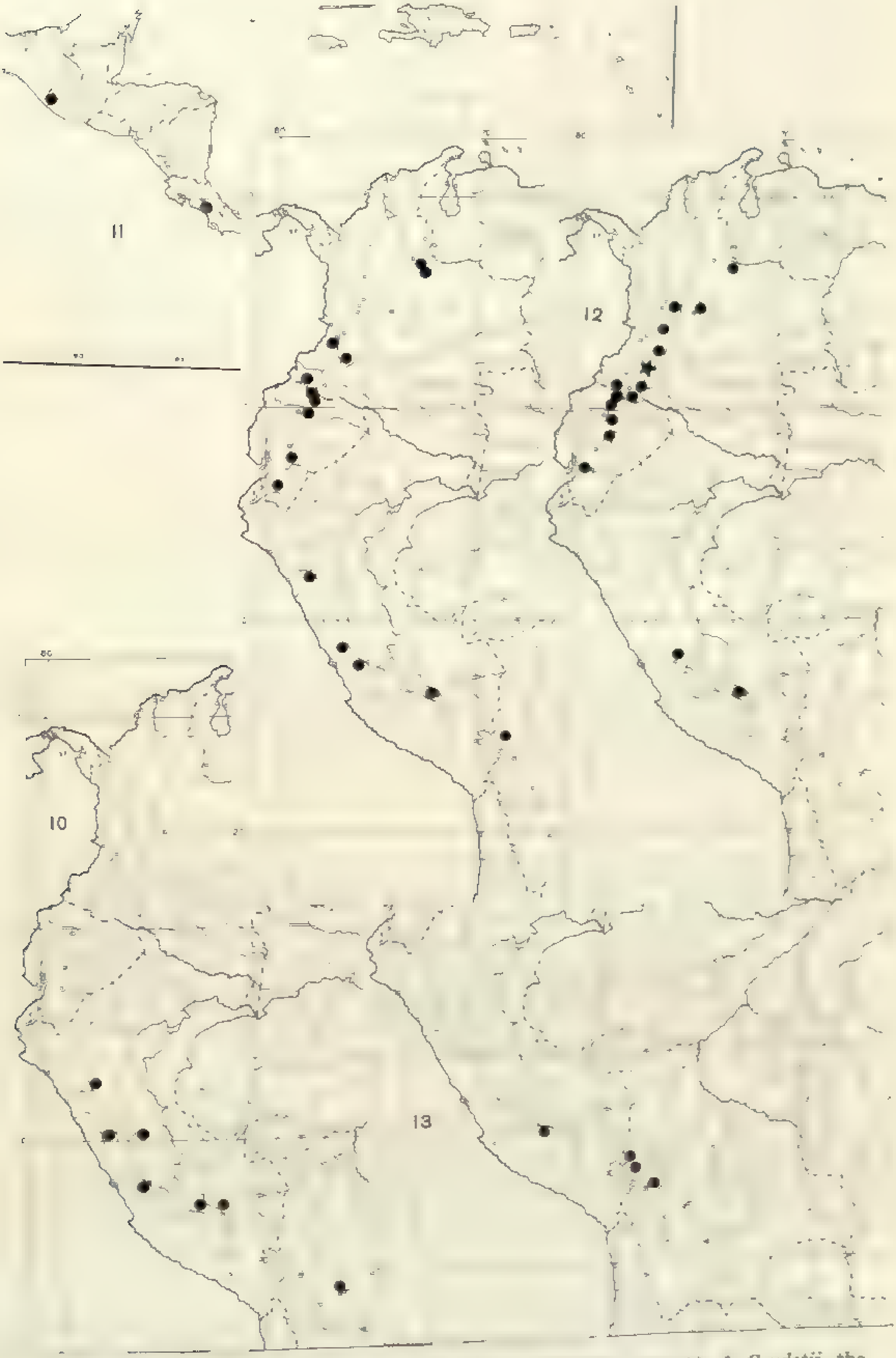
The collections are from Peru with the exception of one specimen from central Bolivia, reported from 2900 m. which is the lowest altitude for the species. The Peruvian material ranges from 3400-4300 m. Additional specimens examined: PERU. *Domby 18* (G, L, P); *Lechler 2153* (G); *Née* (F); *Pavon 137* (G). ANCASH: *Weberbauer 3302* (B, G, US). CUZCO: *Bües 1530* (US), *1531* (US), *1598* (US), *2161* (US); *Pennell 13873* (F, GH, US). HUANUCO: *Bryan 648* (F, US); JUNIN: *Macbride & Featherstone 1883* (F, G, GH, US); *Pearce*, in May 1863 (K). LA LIBERTAD: *Lopez & Sagástegui 3346* (GH). BOLIVIA. COCHABAMBA: *Brooke 6196* (U, US).

11. **Jamesonia Alstonii** A. F. Tryon, sp. nov. Fig. 11. Map 11

Trichomata rhizomatis rigida, appressa, pallida usque obscurofusca vel nigricantia, laminae 0.4-1.0 cm. latae, latitudum prope uniformum, rhachis et gemma tomento fulvo vel stramineo, pinnae ovatocordatae vel orbiculato-cordatae, coriaceae, pinna adaxialiter glabra, infrequens glandulosa, abaxialiter trichomatibus parce bulbosis, nervis latis, dichotomis, angulis latis, marginem non attingentibus, limbo lato vel modice lato, cretaceo vel luteo-albido irregulariter dentato, integro vel ciliis brevibus bulbosis, sporae pallidae succineae, leviter verrucosae.

TYPUS: Colombia, Depart. del Valle, Cordillera Occidental, Los Farallones, vertiente oriental, bajo el filo de la Cordillera en el cerro de La Torre: La Laguna, 3500-3550 m. Aug. 1, 1945, *J. Cuatrecasas 21884*, GH; isotypi: COL, US.

Rhizome usually long creeping, sometimes compact, dichotomously branched, ca. 2.0-3.5 mm. in diameter with moderately dense, long roots, the internodes variable in length, the trichomes rigid, appressed, sometimes light brown, usually dark brown or blackish, darker than the rhizome surface, ca. 1.5-2.5 mm. long, with usually 1 (-4) cells

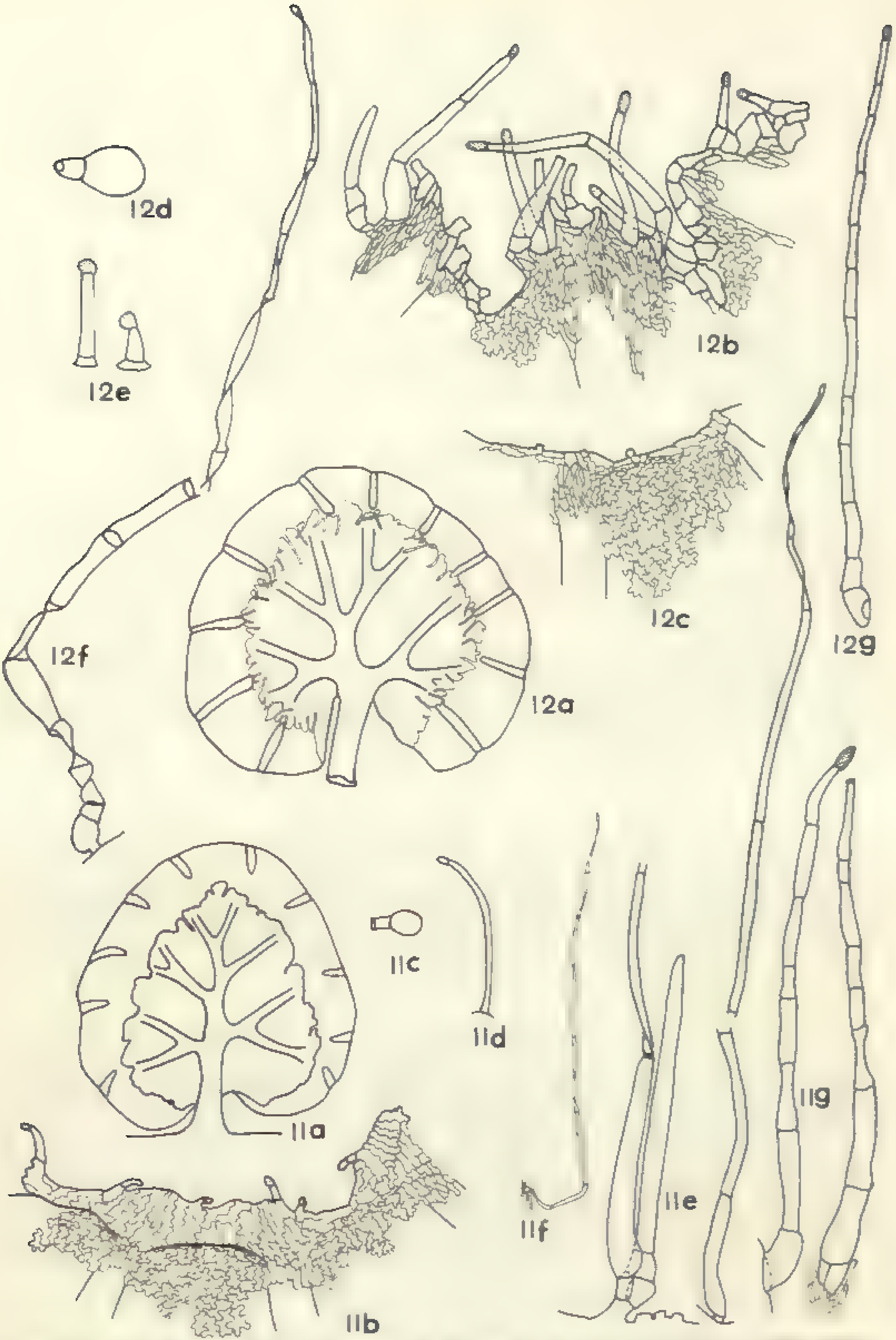


Maps 10-13. Map 10, *J. peruviana*. Map 11, *J. Alstonii*. Map 12, *J. Goudotii*, the star at the locality of the variant, hybrid collection. Map 13, *J. boliviensis*.

near the base, apex acuminate or bulbous. *Petiole* bent, sometimes appressed to the rhizome for a short distance before ascending, 2-6 cm. long, 1/10-1/5 as long as the lamina, atropurpureus, terete, ca. 1-2 mm. in diameter at the apex, often more slender below, sparsely pubescent, the trichomes similar to those of the rachis or darker brown. *Lamina* once pinnate, 15-40 cm. long, 0.4-1.0 cm. wide, about the same size throughout or the base slightly narrowed, with ca. 100-450 pinnae, indeterminate, the apical bud larger than the mature pinnae, with trichomes matted or slightly appressed. *Rachis* atropurpureus, terete, ellipsoidal or trigonous and the upper surface with an obtuse angle, tomentose, often matted, the trichomes usually exceeding the length of the pinnae, tan or straw colored, with the basal cells often clear, the apical cell acuminate or bulbous. *Pinnae* alternate or subopposite, usually stacked in two ranks, imbricate, (the basal ones smaller, distant, sterile, often deteriorated or absent, sometimes, flat, with dentate margins) ovate-cordate or orbicular-cordate, plane, the margin more or less enrolled, inequilateral at the base, 3.5-4.5 mm. long, 2-5 mm. wide, yellow-green, coriaceous; *upper surface* glabrous, rarely glandular, the epidermal cell walls thickened; *lower surface* with sparse, short trichomes having bulbous terminal cells, usually with a tuft of longer trichomes on the stalk and adjacent veins, *stalk* straight, ca. 0.5 mm. long, tan to light brown, lighter adjacent to the pinna. *Veins* broad, in the plane of the upper surface or slightly sunken, dichotomous with wide angles, the branches short or moderately long, the ends acute or somewhat clavate, usually extending to the border. *Border* usually moderately broad, extended at the vein ends, rigid herbaceous, (the cells mostly longer than broad) dentate with sparse, short, bulbous cilia or entire, lutescent or whitish. *Sporangia* abundant, usually obscuring the lower pinna surface and sometimes extending under the enrolled margin or fewer mostly adjacent to the pinna stalk, the stalk short or equal to the capsule length, of 2 or 3 tiers with intercalary cell divisions, the annulus of 15-22 indurated cells. *Spores* light amber colored, smooth or slightly papillose especially on the proximal face, with a moderately broad equatorial wing, the three angles slightly projecting.

Although A. H. G. Alston did not collect this species on his expedition to the Andes of Venezuela and Colombia in 1939 he made excellent specimens of several others. His interest in the genus is also evident in a preliminary key to the species and notes on his observations on specimens, at the British Museum.

There is a greater resemblance between *Jamesonia Alstonii* and *J. Goudotii* than there is between any other two species in the genus and they are distinct from others in having pinnae of a coriaceous texture with the cell walls of the upper epidermis thickened. Considering its extensive distribution, *J. Alstonii* is morphologically relatively uni-



FIGS. 11 AND 12. FIG. 11. *J. Alstonii:* a, pinna, × 10, from *Cuatrecasas 21884* (GH); b, pinna margin with three vein ends, the heavy lines indicating a fold in the tissue, × 35, from *Asplund 16886* (GH); c, gland from the upper pinna surface, enlarged, *Stork & Horton 10007* (F), d, capitate trichome from lower pinna surface, × 30; e, rachis trichomes, the right one with four cells omitted from the mid-portion, × 30, f, petiole trichome, × 30; the last three from *Cuatrecasas 21884* (GH); g, rhizome trichomes, × 30, from *Killip & Smith 17477* (GH). FIG. 12. *J. Goudotii* a, pinna, × 10, from *Cuatrecasas 19110* (GH); b, pinna margin with two vein ends, × 35, from *Mexia 7552* (GH); c, pinna margin with two vein ends, × 35, from *Penland & Summers 814* (US), d, gland from upper pinna surface, enlarged, from *Asplund 9942* (GH); e, capitate trichomes from lower pinna surface, × 45, from *Cuatrecasas 20303* (GH); f, rachis trichome with six cells omitted from the mid-portion, × 30; g, rhizome trichome, × 30, from *Asplund 8779* (GH).

form although there is some variation in the size of the leaves and the border of the pinnae. The specimens from Mexico and Costa Rica may have a few trichomes on the upper surface of the pinnae and rather narrow, dentate pinnae borders. The collection of Stork and Horton from Peru is exceptional in having capitate glands on the upper pinna surface.

The pinnae in *Jamesonia Alstonii* are generally longer and with broader borders than in *J. Goudotii* although these characters may vary in each of these species. The bicolorous rachis tomentum and clavate form of the lamina in *J. Goudotii* distinguish it from *J. Alstonii.*

Jamesonia Alstonii has the widest distribution in the genus ranging from western Bolivia near Lake Titicaca to Chiapas, Mexico on Volcan Tacaná and has an altitudinal range of 2850-4200 m. It occurs on the three Cordilleras in Colombia, occurring at 2890 m. the lowest altitude in the south of Colombia while in the north in Santander and Boyacá it occurs at 4200 m. Additional specimens examined: MEXICO. CHIAPAS: Volcán Tacaná, *Matuda S-234* (GH, K, US), *2864* (GH, K, US). GUATEMALA. SAN MARCOS: Volcán Tajumulco, *Sharp 46113* (US); *Steyermark 36114* (GH, US). COSTA RICA. CARTAGO: *Carlson 3516* (GH); *Rogers CR24* (GH). COLOMBIA. BOYACA: Páramo del Alto Escobal, *Cuatrecasas 1766* (COL, US); *Grubb & Guymer P36* (BM, COL, GH, US). CAUCA: *Haught 5101* (COL, US). NARINO: Volcán de Cumbal, *Ewan 16133* (GH, US). SANTANDER: Páramo de Santurbán, *Killip & Smith 17475* (COL, GH, US); *St. John 20772* (GH, US). VALLE: Cerro La Torre, *Cuatrecasas 17859* (GH, US), Alto del Buey, *17963* (GH, US). ECUADOR. *Espinosa 2217* (US). CANAR: *Rose & Rose 22755* (US). CARCHI: *Asplund 16886* (GH, S). COTOPAXI: *Couthouy,* in 1855 (GH). IMBABURA: *Wiggins 10286* (US). PICHINCHA: Guamani, *Ewan 16437* (GH, US); *Jameson,* in 1856 (GH), in 1857 (G); *Mille 41* (US), *172* (P, U); *Spruce 5659* (B, BM, G, K, P). PERU. CUZCO: *Bues 1378* (US), JUNIN: Mito, *Macbride & Featherstone 1883* (B, GH, US). LA LIBERTAD: *Stork & Horton 10007* (F, G, K, UC). PASCO: Huayllay, *Mathews 979* (E, G, K). BOLIVIA. LA PAZ: *Cárdenas 1025* (GH).

12. **Jamesonia Goudotii** (Hieron.) C. Chr. Ind. Fil. 373. 1905.

Fig. 12. **Map 12**

Gymnogramma Goudotii Hieron. Engl. Bot. Jahrb. **34:** 476. 1904. TYPE: *Goudot*, Colombia B!, photos: COL, F, GH, NY, US; isotypes G! P!.

Rhizome long creeping, dichotomously branched, 1.5-4.0 mm. in diameter with moderately dense to dense, long roots, the internodes variable in length. the trichomes rigid, appressed, light brown to lustrous black, darker than the rhizome surface, ca. 2-3 mm. long, with usually 1 (-3) cells near the base, apex bulbous often exuding. *Petiole* usually bent and somewhat appressed to the rhizome for a short distance before ascending, ca. 0.5-21 cm. long, 1/20 to nearly equal the length of the lamina, atropurpureus, terete or oval ca. 1-3 mm. in diameter at the apex, the same size throughout, sparsely pubescent with trichomes similar to those of the rachis. *Lamina* once pinnate, 5-40 cm. long, 0.5-1.2 cm. wide, broadest at the apex narrowed toward the base, with ca. 50-350 pinnae, the central portion rarely broadest, indeterminate, the apical bud usually larger than the mature pinnae, with trichomes erect or slightly appressed. *Rachis* similar or lighter colored than the petiole, terete, ellipsoidal or trigonous and the upper surface with an obtuse angle, rarely channeled, tomentose, the trichomes up to twice as long as the pinnae, bicolorous usually clear in the basal portion, brown above, the apical cell usually bulbous, sometimes acuminate. *Pinnae* alternate, subopposite, usually stacked in 2 ranks, imbricate, (the basal ones smaller distant, sterile, finally deciduous or sometimes persistent) reniform, orbicular-cordate or long-ovate and auriculate, plane, the margin incurved, sometimes strongly so, forming a pouch-like structure, inequilateral at the base 3-8 mm. long, 3-7 mm. wide, light or yellow-green, coriaceous; *upper surface* usually glabrous, sometimes glandular, rarely pubescent with light tan or bicolorous trichomes the epidermal cell walls thickened; *lower surface* with sparse, short, bulbous, clear or tan trichomes on the veins, with a tuft of longer trichomes on the pinna stalk and adjacent veins, *stalk* straight, ca. 1.0 mm. long, tan or slightly darker, always lighter colored adjacent to the pinnae. *Veins* broad, in the plane of the upper surface or slightly sunken, dichotomously branched at wide angles, the branches moderately long, the ends clavate or flabellate, extending to or nearly to the margin. *Border* irregularly dentate, usually extended at the vein ends rarely entire or nearly so, (the cells mostly broader than long) usually ciliate, the cilia with the terminal cell bulbous and sometimes bicolorous, rigid herbaceous, clear, whitish or lutescent. *Sporangia* abundant sometimes obscuring the lower surface and extending under the incurved margin, the stalk from 1 2 as long to equal the capsule length, the lowest tier sometimes thickened and dark brown, the annulus of 17-21 indurated cells. *Spores* tan or light amber colored, usually papillose to verrucose, with a broad, sometimes crenate or irregularly lobed equatorial wing, the 3 angles broad, slightly projecting; rarely large and shriveled.

The close relationship between this and *J. Alstonii* is evident in the form, indument, border and particularly in the texture of the pinnae. There are two collections from Páramo de las Papas, in southern Colombia, near Valencia which resemble *J. Goudotii* in having ruddy brown tomentum on the rachis, irregularly dentate and ciliate borders and coriaceous pinnae. However, the pinnae are auriculate with whitish trichomes on the upper surface, the rachis is slightly channeled and the spores are exceptionally large and irregular. This material appears to be intermediate between *Gymnogramma Mathewsii* var. *glabriuscula* and *J. Goudotii.* Specimens of the former were mixed in one of the collections of the intermediate. *Jamesonia Goudotii* has also been collected on this páramo.

A specimen of *J. Goudotii,* from the market in Huancayo, Peru, was sent to me by *G. Kunkel, 486.*

Jamesonia Goudotii has a similar but more limited range (from southern Peru to northern Colombia) than *J. Alstonii* and has a slightly higher altitudinal range of 3000-4700 m. Additional specimens examined: COLOMBIA. Bordoncillo, *Lehmann 529* (B, BM, G, K, LE, P, US). ANTIOQUIA: *Mayor 68* (S-PA, US). BOYACA: *Bischler 2760* (COL). CALDAS: *Bischler 1491* (COL); *Barclay & Juajibioy 6354* (GH); *Cuatrecasas 9232* (GH); Páramo del Quindio, *Pennell & Hazen 9932* (GH, US). CAUCA: *Cuatrecasas 19110* (GH, US); Páramo de Moras, *Pittier 1388* (US). CUNDINAMARCA: Guadalupe, *Haught 5072* (S-PA, US). HUILA-CAUCA: Páramo de las Papas, *Idrobo,* et al. *3107* (COL, GH). NARINO: Volcán de Chiles, *Ewan 16003* (GH, US), Páramo of Cerro San Francisco, *16246* (GH, US). SANTANDER: Almorzador, *Vareschi 4038* (VEN). TOLIMA: Páramo de Hervo Fresno, *Hanbury-Tracy 627A* (K); Páramo de Ruiz, *Pennell 3040* (GH, US). VALLE: Páramo de Las Vegas, *Cuatrecasas 20303* (GH, US). ECUADOR. AZUAY: *Jameson 119* (K); *Steyermark 53073* (US). CHIMBORAZO: Páramo de La Laguna Negra, *Barclay & Juajibioy 8775* (GH). IMBABURA: *Penland & Summers 814* (F, US); *Sodiro 4 92* (K). NAPO-PASTAZA: *Asplund 8779* (GH, S); *Barclay & Juajibioy 9100* (GH). PICHINCHA: *Ewan 16440* (GH, U, US). TUNGURAHUA: *Asplund 9942* (GH, S); *Rimbach 43* (L, P, S-PA, US). PERU. CUZCO: *Bües 1406* (US). JUNIN: *Weberbauer 6629* (F, GH, US).

Intermediate specimens: COLOMBIA. HUILA-CAUCA: Páramo de las Papas, *Idrobo,* et al. *3108* (COL), *3336* (COL, GH).

13. **Jamesonia boliviensis** A. F. Tryon, sp. nov. Fig. 13. Map 13

Trichomata rhizomatis rigida, appressa, atropurpurea vel nigricantia, apex laminae indeterminata gemmae tomento patente, fulvo vel rufo-fusco, pinnae imbricatae, orbiculato-cordatae vel ovato-cordatae, inequilaterales, planae, rigidae herbaceae, epidermis supra cellulis subcrassioribus, pinna adaxialiter et abaxialiter trichomatibus glandulosis brevibus nervis ultra marginem protrusis, limbo angusto, ciliis glandulosis, sporae pallidae, succineae, papillatae.

TYPUS: Peru, Dept. Apurimac, Bosques de Ampay, 3200 m. June 1938, *C. Vargas 1060a,* GH; isotypus: US.

Rhizome long creeping, dichotomously branched, ca. 1.5-2.5 mm. in diameter with sparse roots, the internodes variable in length, the trichomes rigid, appressed, lustrous atropurpureus or blackish, darker than the rhizome surface, 1-2 mm. long, 2 or usually 1 cell at the base, apex bulbous or decapitated. *Petiole* bent, appressed to the rhizome for a short distance before ascending, 1.0-7.5 cm. long, about 1 8 to 1 5 as long as the lamina, atropurpureus, terete, ca. 0.5-1.0 mm. in diameter at the apex, often more slender below, with short capitate trichomes and longer trichomes similar to those of the rachis. *Lamina* once pinnate, 9-30 cm. long, 0.3-0.7 cm. wide, about the same size throughout or the base slightly narrower, with ca. 100-225 pinnae, indeterminate, the apical bud the same size or slightly larger than the mature pinnae, with patent trichomes. *Rachis* castaneus, terete or trigonous and the upper surface with an obtuse angle, pubescent or tomentose, and sometimes matted on the lower surface, the trichomes as long or slightly longer than the pinnae, rust-brown, with the basal cells often clear, the apical cell bulbous or acuminate. *Pinnae* alternate, subopposite, in 2 ranks laterally disposed, imbricate, (the basal ones smaller, often incompletely developed, distant, sometimes persistent) orbicular-cordate or ovate-cordate, plane, the margin incurved, inequilateral at the base, 2-4 mm. long, 2-4 mm. wide, bright or yellow green, rigid herbaceous; *upper* and *lower* pinna surfaces with short, capitate trichomes, the latter with longer trichomes on the stalk and adjacent veins, the cell walls of the upper epidermis slightly thickened, *stalk* straight, ca. 0.5 mm. long, atropurpureus, lighter adjacent to the pinnae. *Veins* broad, in the plane of the upper surface or slightly raised or sunken, dichotomous with wide angles, the branches short or moderately long, the ends acute or clavate, protruding from the margin. *Border* narrow, a row of cells mostly broader than long, with capitate cilia. *Sporangia* abundant, obscuring the lower pinna surface or fewer and mostly adjacent to the pinna stalk, the stalk short, about 1/4 the capsule length, with 2 tiers, the lower with intercalary cell divisions, the annulus with 18-24 indurated cells. *Spores* light amber colored, papillose, the equatorial wing broad, the 3 angles slightly projecting.

This species has been obscure since most of the collections of it are mixed with other species as *Jamesonia scalaris*, *J. Scammanae*, *J. blepharum* and with *Eriosorus elongatus*. The fine collection of César Vargas is the most complete and ample material.

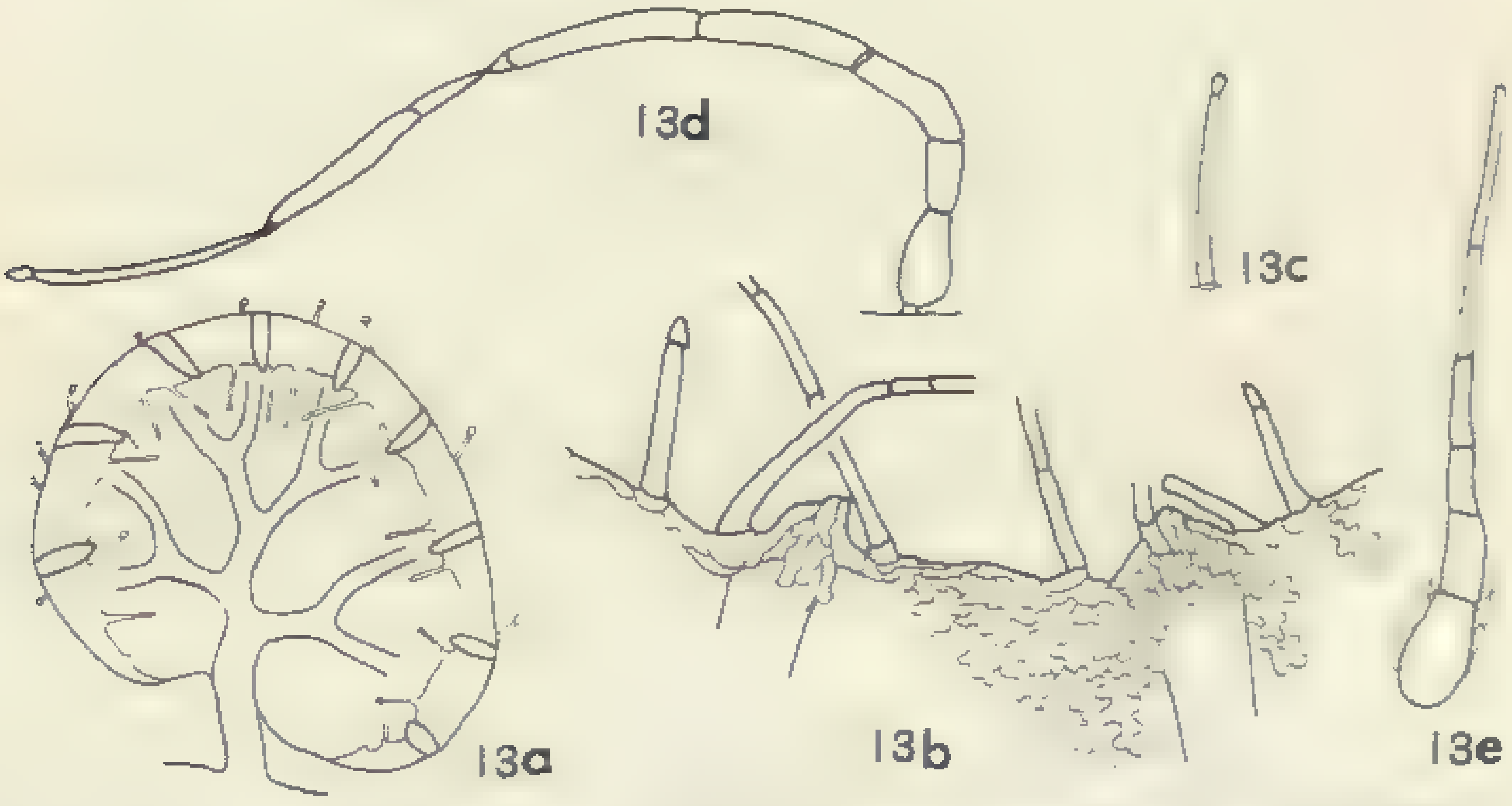


FIG. 13. *J. boliviensis*: a, pinna, × 10; b, pinna margin with two vein ends, × 35; c, capitate trichome from lower pinna surface, enlarged; d, rachis trichome, × 30; e, rhizome trichome, × 30; all from *Vargas 1060a* (GH).

It is a distinctive species and remarkable for the genus in having a single kind of capitate trichome or cilia on each of the pinna surfaces and the margin. Such uniformity of indument does occur in species of *Eriosorus* but in the other species of *Jamesonia* there has been specialization of the pinna indument.

The collection from Peru is from the lowest altitude at 3200 m. and the other collections from northern Bolivia are from 3400 and 4200 m. Additional specimens examined: PERU. APURIMAC: *Santander,* et al. in Oct. 1935 (UC). BOLIVIA. LA PAZ: Unduavi, *Buchtien 2733* (US); *Cárdenas 1025* (GH), *1026* (GH); Pelechuco, *Pearce* in 1865 (K); Tolapampa, *R. S. Williams 1152* (US), *1153* (GH, US), Pelechuco, *2628* (US).

14. **Jamesonia scalaris** Kunze, Bot. Zeit. 2: 738. 1844.

Fig. 14. Map 14

TYPE: *Ruiz 49,* Peru, Pillao B!, photos COL, F, GH, NY, US; isotypes HAL, P! US!.

Gymnogramma scalaris (Kunze) Kl. Linnaea **20**: 407. 1847.

Psilogramme scalaris (Kunze) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 334. 1882.

Jamesonia imbricata (Sw.) Hook. and Grev. var. *scalaris* (Kunze) Sodiro, Crypt. Vasc. Quit. 387. 1893.

Rhizome wide creeping, dichotomously branched, ca. 1.5-2.0 mm. in diameter with moderately dense roots, the internodes variable in length, the trichomes rigid, appressed or somewhat patent, light to dark brown or atropurpureus, about the same color as the rhizome surface or slightly darker, 1.5-2.0 mm. long usually with 2 (-5), cells near the base, apical cell bulbous, exuding. *Petiole* bent or curled near the rhizome, usually appressed to the rhizome for a short distance before ascending 2.5-6.5 cm. long, 1 16-1 5 as long as the lamina, castaneus or atropurpureus, terete, ca. 0.75-1.0 mm. in diameter at the apex, filiform below, the trichomes sparse, short, brown or bicolorous, basal cells clear, apical cell bulbous. *Lamina* once pinnate, 10-33 cm. long, 0.2-0.6 cm. wide, about the same size throughout or the base slightly narrowed, with ca. 50-270 pinnae, indeterminate, the apical bud about the same size or smaller than the mature pinnae, not glutinous, the trichomes patent or slightly appressed. *Rachis* similar in color to the petiole, terete, elliptical or trigonous and the upper surface with an obtuse angle, pubescent, the trichomes more abundant on the lower surface, not exceeding the length of the pinnae, clear, tan or bicolorous, the upper cells darker, the apical cell bulbous. *Pinnae* alternate, approximate, usually not imbricate or slightly so near the apex, in 2 ranks sometimes overlaying the rachis, (the basal ones minute, distant, often persistent) ovate-cordate, usually lobed, patelliform, the upper surface often depressed near the stalk, the margin enrolled, equilateral or nearly so at the base, 2-4 mm. long, 1.5-3.0 mm. wide, bright green, herbaceous; *upper surface* with papillate glands, the epidermal cell walls unthickened; *lower surface* with 1 or few

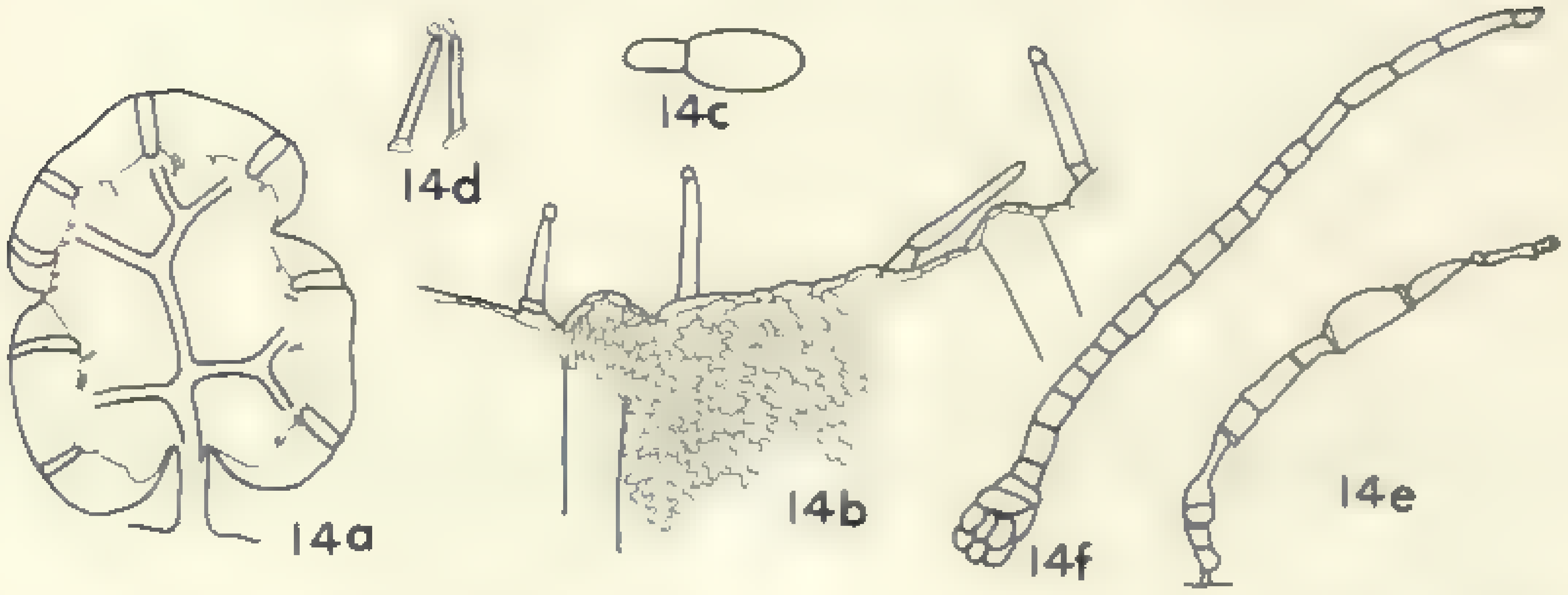


FIG. 14. *J. scalaris:* a, pinna, × 10, from *Asplund 13718* (GH); b, pinna margin with two vein ends, × 35; c, gland from upper surface of pinna, enlarged. d, capitate trichomes from lower pinna surface, enlarged; the last three from *Bues 2163* (US); e, rachis trichome, × 30 from *Asplund 13718* (GH), f, rhizome trichome, × 30, from *Bües 2163* (US).

celled, erect, clear, capitate trichomes, sometimes tomentose, usually with a tuft of clear trichomes on the stalk or adjacent veins, *stalk* straight or slightly bent, ca. 0.75-1.50 mm. long, atropurpureus, usually lighter adjacent to the pinna, articulate in older leaves. *Veins* slender or moderately broad, in the plane of the upper surface or raised, dichotomous with wide angles, the branches short or moderately long, the ends clavate or somewhat acute, extending to the margin or protruding. *Border* narrow, a row of cells broader than long, with capitate cilia. *Sporangia* mostly adjacent to the pinna stalk, the stalk short or moderately long, of 2 or 3 tiers with intercalary cell divisions, the annulus of 17-20 indurated cells. *Spores* dark brown, smooth or slightly verrucose especially on the distal face, the equatorial wing narrow, the 3 angles prominently projecting.

Jamesonia scalaris was the first to be described among the species with small pinnae and subsequently the name has been applied to most specimens of that form. The species is quite distinct in the lobed and patelliform pinnae with glands on the upper surface and narrow, ciliate borders. The basal pinnae of the lamina are sometimes minute with stalks up to twice as long as the pinnae and the amount of indument on the lower surface of the pinna may vary from sparse to dense. It has been collected with *J. peruviana*, *J. Scammanae* and *J. brasiliensis* and resembles the last in the symmetrical form of the pinnae, the dark spores, and the narrow, ciliate pinnae borders. In the last character it is also similar to *J. boliviensis*.

It occurs from central Peru to northern Bolivia, at 2300-4700 m. Additional specimens examined: PERU: *Hill 553* (K). CUZCO: *Bues 1533* (US), *1783* (US), *1784* (US), *1787* (US), *1931* (US), *2161* (US), *2163* (US), *2190* (US); Marcapata, *Stafford 989* (K); Paucartambo, *Vargas*, in June 1937 (GH). HUANUCO: Punta de Panao, *Asplund*

13718 (GH, S), *Macbride 4524* (F, US). JUNIN: Cerró Goyllarisquisca, *Asplund 11922* (GH, S); *Pavon 137* (G). LA LIBERTAD: *Lopez & Sagástegui 3435* (GH). PUNO: Ayapata, *Lechler 2036a* (B, E, G, K, LE, P). BOLIVIA: COCHABAMBA: *Brooke 6196* (US); *Steinbach 9569* (F, GH, K, S-PA, U). LA PAZ: Unduavi, *Buchtien 2732* (S-PA, US), *8898* (US).

15. **Jamesonia imbricata** (Sw.) Hook. & Grev. Icon. Fil. 1: 2. 1831.

Rhizome long creeping, dichotomously branching, ca. 1-5 mm. in diameter with sparse, long roots, the internodes variable in length, the trichomes patent, tan or rigid, appressed and ruddy brown to blackish, 0.5-3.0 mm. long with 1-5 cells near the base, apex acuminate or bulbous. *Petiole* usually bent and appressed to the rhizome for a short distance before ascending, 1-15 cm. long, 1/20-1/5 as long as the lamina, rarely twice as long, castaneous or atropurpureus, terete or somewhat flattened on the upper surface, ca. 0.5-2.0 mm. in diameter at the apex, stouter or filiform below, glabrous or with sparse trichomes similar to those of the rachis. *Lamina* once pinnate, ca. 7-80 cm. long, 0.2-1.2 cm. wide, nearly the same size throughout or more slender at the base or apex, ca. 50-400 pinnae, indeterminate or sometimes determinate, the apical bud about the same size or larger than the mature pinnae, with trichomes patent or appressed. *Rachis* atropurpureus or castaneus, terete or trigonous and the upper surface with an obtuse angle, pubescent, the lower surface usually more densely tomentose, the trichomes as long or slightly longer than the pinnae but not enveloping them, tan or rust colored, the tips clear or darker, the apical cell bulbous or acuminate. *Pinnae* alternate or subopposite, overlaying the rachis or laterally stacked in 2 ranks, distant, approximate or imbricate, (the basal ones smaller, distant, sterile, sometimes plane, membranous and strongly dentate, persistent or deciduous) orbicular, ovate or long-ovate, truncate and equilateral or inequilateral at the base, patelliform, or the upper surface concave or furrowed, margins enrolled or incurved, 0.75-6.0 mm. long, 1-4 mm. wide, bright or yellowish green, rigid herbaceous; *upper surface* with few, short, appressed glands or more abundant glands and vernicose, the epidermal cell walls unthickened; *lower surface* glabrous or tomentose with curled or crispate trichomes, clear, opaque white, tan or rust colored, of 1 or few cells, *stalk* usually bent or twisted or sometimes nearly straight, 1.0-1.5 mm. long, tan, brown or atropurpureus. *Veins* slender or moderately broad, in the plane of the upper surface, sunken or raised, dichotomous with acute angles and long branches, or wide angles and moderately long branches, the ends clavate or slightly flabellate, extending to the border. *Border* broad or narrow, entire, dentate and or ciliate, membranous, clear, opaque white, tan or rust colored. *Sporangia* usually abundant near the pinna stalk, fewer on the distal portions of the veins, the stalk short, of 2 tiers, the lower clear or with a cushion of darker cells with intercalary divisions, the annulus with 17-21 indurated cells. *Spores* tan, light or dark brown, smooth, the equatorial wing narrow or broad and the angles not or scarcely projecting.

The species is principally represented by var. *glutinosa* which is geographically wide spread and the most distinctive, although polymorphic, member. The two other varieties are associated with it for in each of them there is found two of the critical characters of var. *glutinosa* — glands on the upper surface of the pinnae and bent pinnae stalks. Variety *imbricata* combines these characters with some of the features of *J. robusta* and var. *meridensis* with some of those of *J. canescens*. The association of these characters in var. *imbricata* and var. *meridensis* and their geographic distributions suggest that they may be of hybrid origin. I have observed var. *meridensis* in the field and it is sufficiently distinct on several characters of habit to warrant taxonomic recognition. Variety *imbricata* is insufficiently known and may be reinterpreted as additional, complete material is available; it is, however, a taxon of historical interest in the genus.

KEY TO THE VARIETIES OF JAMESONIA IMBRICATA

a. Spores tan or light brown; upper surface of the pinnae plane or somewhat concave, the base more or less cordate; veins dichotomous with wide angles, the branches widely diverging and usually short .... b

b. Rhizome trichomes amber-colored or light brown, lax, patent; pinnae plane on the upper surface or somewhat concave near the stalk; Colombia, Ecuador, Peru .... 15A. *J. imbricata* var. *imbricata.*

b. Rhizome trichomes dark brown or blackish, rigid, appressed; pinnae usually with a central furrow on the upper surface; Venezuela and northern Colombia. ...... 15C. *J. imbricata* var. *meridensis.*

a. Spores dark brown; pinnae convex on the upper surface (patelliform), the base truncate and incurved near the stalk, veins dichotomous usually with acute angles, the branches somewhat parallel and long. .... 15B. *J. imbricata* var. *glutinosa.*

15A. **Jamesonia imbricata** var. **imbricata** Fig. 15A. Map 15A

Pteris orbiculata Poir. in Lam. Encycl. 5: 710. 1804, not Houtt. Nat. Hist. 14: 108. 1783. TYPE: *J. Jussieu*, Pérou (Herb. Jussieu no. 1332) P!, photo GH; isotype: P!, photo, GH.

Pteris imbricata Sw. Syn. Fil. 102. 1806. Based on *Pteris orbiculata* Poir.

Cheilanthes imbricata (Sw.) Desv. Mém. Soc. Linn., Paris **6**: 303. 1827.

Allosorus imbricatus (Sw.) Presl. Tent. 153. 1836.

Pteris imbricata "Cav. Hort. Matrit.", cited by Swartz was not published, see C. Christensen, Dansk Bot. Ark. **9**^{3}: 7. 1937.

Gymnogramma imbricata (Sw.) Kl. Linnaea **20**: 407. 1847.

Jamesonia imbricata (Sw.) Hook. & Grev. var. *gracilis* Hook. Sp. Fil. 5: 106. 1864. Based on *Pteris imbricata* Sw.

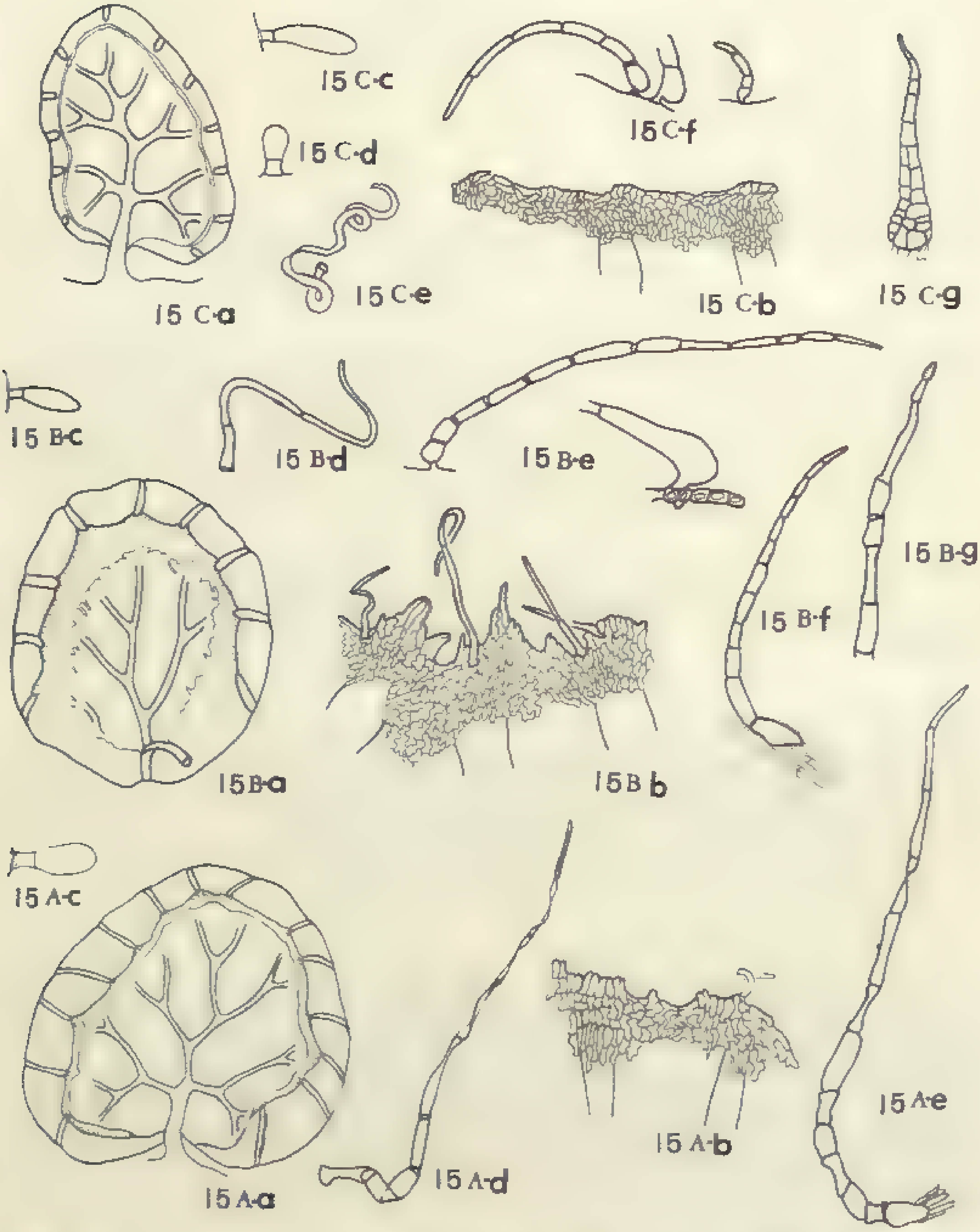


FIG. 15. *J. imbricata:* 15A. var. *imbricata:* a, pinna, × 10; b, pinna margin with two vein ends, × 35; c, gland from upper pinna surface, enlarged; d, rachis trichome, × 30; all from *J. Jussieu* (P); e, rhizome trichome, × 30, from *Fosberg 20809* (GH). 15B. var. *glutinosa:* a, pinna × 10, from *Idrobo, et al. 3150* (GH); b, pinna margin with three vein ends, × 35, from *Ewan 16364* (GH); c, gland from upper pinna surface, enlarged, from *Tryon & Tryon 6085* (GH); d, trichome from lower pinna surface, × 40, from *Ewan 16364* (GH); e, rachis trichome, × 30, at right the basal cell and epidermal cells of the rachis enlarged, from *Cuatrecasas 7968* (GH); f, rhizome trichome, × 30, from *Idrobo et al. 3150* (GH); g, apex of rhizome trichome, × 30, from *Tryon & Tryon 6044* (GH). 15C. var. *meridensis:* a, pinna, × 10; b, pinna margin with two vein ends, × 35; c, gland from upper pinna surface, enlarged, d, gland from lower pinna surface, enlarged; e, trichome from lower pinna surface, × 40; f, rachis trichomes with detail of the basal cell, × 30; g, rhizome trichome, × 30; all from *Tryon & Tryon 5801* (GH).

Psilogramme imbricata (Sw.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 334. 1882.

Rhizome trichomes lax, patent, amber-colored or light tan, lighter than the rhizome surface, with usually 1 (-3) cells at the base, the apex acuminate. *Lamina* indeterminate, the bud of the same size or slightly larger than the mature pinnae, with tan or light brown, patent trichomes. *Pinnae* orbicular or ovate, the upper surface plane or more or less sunken, slightly inequilateral at the base and somewhat cordate; *upper surface* glandular, sometimes with a few short trichomes; *lower surface* tomentose with rust-colored or tan, lax, crispate trichomes, *stalk* more or less bent. *Veins* dichotomously branching with wide angles, the branches widely diverging, moderately long. *Border* rust-colored or tan, entire or dentate and sparsely ciliate. *Spores* tan or light brown, sometimes shriveled.

The name *Jamesonia imbricata* has unfortunately been misapplied to specimens of several other species. The de Jussieu collection, at Paris, upon which the name is based, has an unusual combination of characters and there are only a few other collections similar to it. The leaves in the type collection are about the same width throughout with the pinnae imbricate near the apex and distant in the basal portion of the lamina. The pinnae are ovate-cordate or somewhat truncate at the base with a dense tomentum of rust-colored, crispate trichomes on the lower surface and appressed glands on the upper surface. The borders of the pinnae are moderately broad, slightly dentate and sparsely ciliate. There are a few other collections similar to this from Colombia and Ecuador which resemble *J. robusta* in the light color of the rhizome trichomes, and in the rust colored tomentum on the lower pinna surface. They differ from that species in the shape of the pinnae and in the glands on the upper surface. In these latter characters and also in the bent pinna stalks and somewhat truncate pinna base there is a resemblance to *J. imbricata* var. *glutinosa*. On the basis of these characters and the occurrence of each of these taxa in the range of var. *imbricata*, it is considered a possible hybrid between *J. robusta* and *J. imbricata* var. *glutinosa*.

Colombia, Ecuador, Peru; subparamo, in cutover forest at 3385 m. in Colombia and in dense grass in southern Ecuador at about 3400 m. Additional specimens examined: COLOMBIA. CAUCA: Páramo de Guanacas, *Lehmann 4420* (K, US). CUNDINAMARCA: *Fosberg 20809* (GH, US). ECUADOR. AZUAY: Páramo de Silván, *Barclay & Juajibioy 5399* (GH).

15B. **Jamesonia imbricata** var. **glutinosa** (Karst.) comb. nov.
Fig. 15B. Map 15B

Jamesonia glutinosa Karst. Fl. Columb. **2:** 85, t. 143. 1865. TYPE: *H. Karsten,* Colombia, monte Guadalupe, Bogotá, 2900 m. LE!, photo GH.

Gymnogramma glutinosa Karst. ex. Mett. Ann. Sci. Nat. V, **2:** 209. 1864, nom. nud.

Jamesonia ciliata Karst. Fl. Columb. **2:** 85, t. 143, fig. 13. 1865. TYPE: *H. Karsten,* Venezuela, Mérida LE!, photos GH, W.

Psilogramme glutinosa (Karst.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 333. 1882.

Gymnogramma ciliata (Karst.) Hieron. Engl. Bot. Jahrb. **34:** 477. 1904.

Gymnogramma Mayoris Rosenst. Mém. Soc. Neuchâtel. **5:** 55, t. 5. 1912. TYPE: *E. Mayor 74,* Colombia, Páramo de Cruz Verde, 3500 m. S-PA!, photo BM; isotypes: P! US!.

Jamesonia Mayoris (Rosenst.) C. Chr. Ind. Fil. Suppl. 47. 1913.

Rhizome trichomes patent or slightly appressed, ruddy to dark brown, the same color or more ruddy than the rhizome surface, with 1-3 cells near the base, the apex acuminate or often bulbous. *Lamina* indeterminate or sometimes determinate, the bud usually smaller than the mature pinnae, with tan or brownish, often bicolorous on the bud, appressed or patent trichomes. *Pinnae* orbicular, patelliform, with the base equilateral, truncate and incurved adjacent to the stalk; *upper surface* glandular, usually vernicose; *lower surface* with opaque white to tan, curled trichomes, sometimes glabrous or nearly so, *stalk* strongly bent. *Veins* dichotomously branching usually with acute angles, the branches long and somewhat parallel. *Border* whitish or tan, entire or dentate and sometimes ciliate. *Spores* dark brown.

Karsten's epithet was published a year later than that of Mettenius but the latter attributes the species to Karsten without a reference. It seems that Mettenius was aware of Karsten's treatment of this species before it was published in the Flora Columbiae.

Karsten's type of *Jamesonia ciliata* from Mérida in the herbarium at Leningrad is accompanied by his notes comparing the species with his *J. glutinosa* and with *J. scalaris.* The specimen has patelliform pinnae with glands on the upper surface and moderately broad, dentate pinnae borders or narrow ciliate ones. There are other collections similar to this from the Sierra Nevada de Cocuy in Boyacá and from Monserrate, near Bogotá, in Colombia. In *J. imbricata* var. *glutinosa* the pinna borders are variable and on the same leaf the basal pinnae may have narrower, more ciliate borders than the younger ones near the apex. Two characters which appear less variable and better characterize the variety are the strongly bent pinna stalks and the symmetrical pinnae with the bases truncate and incurved near the stalk.

Plants intermediate between var. *glutinosa* and one of the other species have been most perplexing. Field studies on the populations of these growing on one páramo have been helpful in interpreting the complexity. Where I have found var. *glutinosa* growing with other species there were usually plants having characters intermediate between the two. On Páramo Palacio and Guasca, north of Bogotá, var. *glutinosa* occurs with *J. rotundifolia* and there are many intermediate plants. On Páramo Chisaca, south of Bogotá, var. *glutinosa* occurs with *J. bogotensis* and there are some plants appearing intermediate between them. The relationships of var. *glutinosa* are particularly complicated in regard to the group of *J. robusta, J. bogotensis, J. canescens* and also with *J. rotundifolia.* Intermediates with any of these and var. *glutinosa* may be so modified by the latter that it is not possible to clearly establish which of the former species may be involved.

Variety *glutinosa* occurs at relatively low altitudes ranging from 2000-3550 m. from Venezuela to southern Ecuador. The lowest record is from Trujillo, Venezuela. Additional specimens examined: VENEZUELA. TACHIRA: Páramo de Tamá, *Cardona 307* (US, VEN); *Steyermark 57403* (US, VEN). TRUJILLO: *Funck & Schlim 844* (BM, G, K, LE); Páramo Cristalino, *Jahn 139* (US, VEN); *Steyermark 55356* (US, VEN). COLOMBIA. *Mutis 3084* (US), *3085* (US), *3086* (US), *3098* (US). BOYACA: *Barclay & Juajibioy 7555* (GH); *Dawe 916* (K); *Grubb & Guymer P118* (BM, GH, US). CALDAS: *Bro. Tomás 2054* (US). CAUCA: *Barclay & Juajibioy 5754* (GH), *5780* (GH); Páramo de Puracé, *Cuatrecasas 14610* (GH, US); *Grant 10636* (GH, US); Páramo de Gabriel López, *Lehmann V.* in Nov. 1961 (GH); *Pennell 6907* (GH, US); *Tryon & Tryon 5991* (COL, GH, S, US), *5993* (COL, GH, NY). CUNDINAMARCA: Guadeloupe, *Apollinaire*, in 1908 (GH); *Cuatrecasas 5414* (GH, US), *7968* (COL, GH, US); *Dawe 12* (US); Grant *9413* (US); *Haught 5658* (US), *5947* (G, US); Páramo de Chisaca, *Jaramillo*, in Oct. 1961 (GH); *Lindig 118* (GH, K); Monserrate, *Little & Little 9446* (COL, US); *Perez-Arbelaez 1520* (US); *Rusby & Pennell 1264* (GH, US); Páramo de Palacio, *Tryon & Tryon 6028* (BM, COL, GH, US), *6033* (GH), *6044* (COL, B, GH, LE, NY, US), Alto de Aguila, *6075* (GH), Cruz Verde, *6085* (COL, F, GH); HUILA-CAUCA: Páramo de Las Papas, *Idrobo, et al. 3150* (COL, GH). NORTE DE SANTANDER: *Apolinar-Maria 21* (US); Páramo de Tamá, *Cuatrecasas* et al. *12606* (GH); Páramo de Santurbán, *Killip & Smith 19593* (GH, US). PUTUMAYO: *Alston 8348* (BM, GH); Páramo de San Antonio del Bordoncillo, *Cuatrecasas 11724* (GH, US); *Ewan 16364* (GH, US); *Schultes & Villarreal 7826* (GH). SANTANDER: Páramo de Santurbán, *Barclay & Juajibioy 10433* (GH). VALLE: *Cuatrecasas 17839* (GH, US), *20256* (GH, US), *21886* (GH, US). ECUADOR. AZUAY: Páramo del Castillo, *Camp 5158* (F, G, GH, K, US).

Specimens examined intermediate between var. *glutinosa* and *Jamesonia rotundifolia*: COLOMBIA. CAUCA: *Lehmann V.* in Nov. 1961 (GH). CUNDINAMARCA: Páramo de Palacio, *Cuatrecasas* et al. *25642* (US); *Fosberg & Villareal 20594* (US); *Schultes 18784* (US); Páramo de Palacio, *Tryon & Tryon 6035* (GH), *6036* (GH), *6045* (GH), *6049* (COL, GH), *6051* (GH), *6054* (COL, US). SANTANDER: Páramo de las Coloradas, *Killip & Smith 18433* (GH, US).

Specimens examined intermediate between var. *glutinosa* and *Jamesonia bogotensis*. COLOMBIA. CUNDINAMARCA: *Bischler 1515* (COL); Páramo de Chisacá, *Cuatrecasas & Jaramillo 25760* (US); Páramo de Chisacá, *Tryon & Tryon 6182* (GH, US).

15C. **Jamesonia imbricata** var. **meridensis** A. F. Tryon, var. nov.

Fig. 15C. Map 15C

Trichomata rhizomatis rigida appressa, obscuro-fuscae vel nigricantia saepe paucis cellulis lata prope basem, pinnae expositae, longiovatae plerumque longiores quam latae, pinnae adaxialiter glandulosae, medio sulcatae, abaxialiter tomentosae trichomatibus crispatis, densis, limbo modice lato, involuto, sporae pallido-fuscae, laeves.

TYPUS: Venezuela, State of Mérida, above Mérida, among rocks near the shore of Laguna de Anteojos, 3900 m. September 16, 1961, *Rolla M.* and *Alice F. Tryon 5800A* (GH).

Rhizome trichomes rigid, appressed, dark brown or blackish, darker than the rhizome surface with 1-5 cells near the base, the apex acuminate. *Lamina* indeterminate, the bud usually larger than the mature pinnae, with tan or yellow, patent trichomes. *Pinnae* long-ovate, usually with a central furrow on the upper surface, inequilateral at the base, cordate, the basal lobes sometimes raised above plane of the upper surface; *upper surface* glandular, sometimes also pubescent; *lower surface* tomentose with tan to rust colored, crispate trichomes and some capitate glands, *stalk* slightly bent or nearly straight. *Veins* dichotomously branching with wide angles, the branches short, widely diverging. *Border* rust brown, tan or clear, dentate. *Spores* tan or light amber colored.

At the northern end of the Andes, in Venezuela, around Laguna de Anteojos, and at Aguada above Mérida there are large colonies of these plants growing nearby those of *J. canescens*. The two are entirely distinct in habit and *J. canescens* is more abundant over the páramo. Variety *meridensis* has bright green leaves with large, yellow apical buds and exposed, shining glutinose pinnae. There is a resemblance to var. *glutinosa* in the somewhat truncate pinna base, bent pinna stalks and glandular indument although the light colored spores and inequilateral form of the pinnae base are similar to *J. canescens*. There are some specimens from páramos north in the state of Mérida which resemble var. *meridensis* in having sparsely indumented leaves with small pinnae but these are treated under *J. canescens* since they are not glandular.

Mérida, Venezuela and Magdalena, Colombia, at 4200-4350 m. Additional specimens examined: COLOMBIA. MAGDALENA: Cerro Avión, *Cuatrecasas & Castaneda 25149* (US); *Romeral-Castañeda 7375* (COL, GH). VENEZUELA. MERIDA: *Alston 6851* (BM, GH); *Farenholtz 1830* (GH, U); *Funck & Schlim 1098* (BM, G, GH, L, LE, P); *Gehriger 79a* (G, VEN); *Moritz 338* (B, BM, K, LE, P, US); Laguna de Anteojos, *Tryon & Tryon 5791* (F, GH, NY), *5799* (B, BM, GH), *5810* (GH), *5811* (GH, NY, S), La Aguada, *5801* (GH, S), *5803* (COL, F, GH, P), *5807* (GH); Laguna de Anteojos, *Vareschi & K. M. 6862* (VEN), *6863* (VEN).

16. **Jamesonia brasiliensis** Christ, Farnkr. Erde 75. 1897.

Fig. 16. Map 16

TYPE: *Ule*, in Mar. 1894, Brazil, Agulhas Negras, Serra de Itatiaia, 2200 m. P!, photos: COL, F, GH, NY, US; isotypes: BM! P!.

Rhizome long creeping, dichotomously branched, slender, ca. 1.0-1.5 mm. in diameter with sparse, roots, the internodes variable in length, the trichomes lax, patent, ruddy brown, about the same color or slightly darker than the rhizome surface, 1.5-2.0 mm. long with 1 or 2 cells near the base, apical cell bulbous. *Petiole* bent or curled near the rhizome, and appressed for a short distance before ascending 0.5-10.0 cm. long, from 1/12 to 1/3 the length of the lamina, castaneus, terete or plane on the upper surface, slender, ca. 0.5-1.0 mm. in diameter at

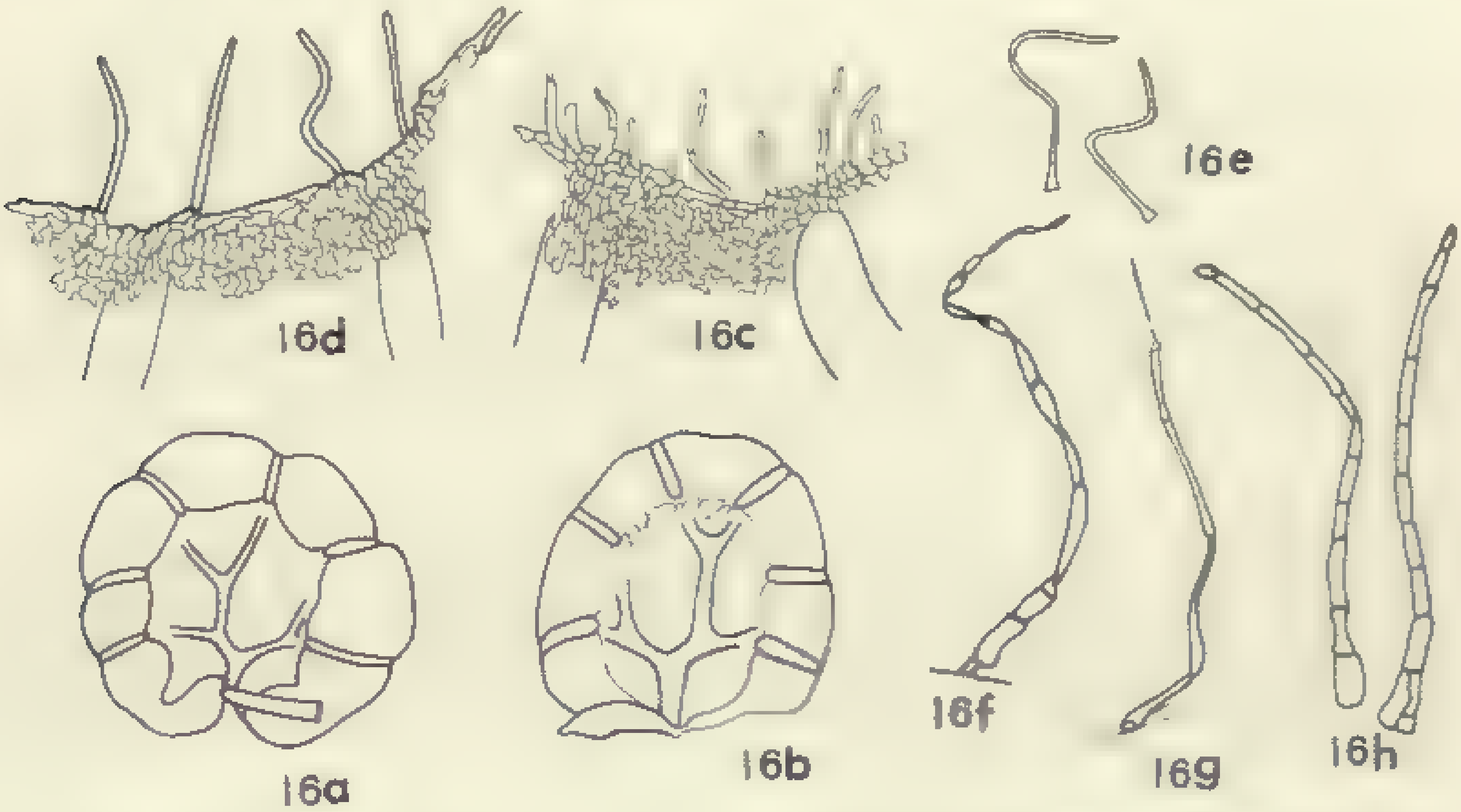


FIG. 16. *J. brasiliensis:* a, pinna, × 10, from *Dusen*, in 16/6 1902 (US). b, pinna, × 10; c, pinna margin with two vein ends, × 35; the last two from *Tate 327* (US); d, pinna margin with two vein ends, × 35, from *Rose & Russell 20505* (US); e, trichomes from lower pinna surface, × 35, from *Dusen*, in 16 6 1902 (US); f, rachis trichome, × 30, from *Rose & Russell 20505* (US); g, petiole trichome, × 30, from *Brade 6485* (US); h, rhizome trichomes, × 30, from *Rose & Russell 20505* (US).

the apex, glabrous or with sparse, clear trichomes similar to those of the rachis. *Lamina* once pinnate, ca. 15-40 cm. long, 0.3-0.6 cm. wide, nearly the same size throughout or the base and sometimes the apex slightly narrower, with ca. 175-250 pinnae, indeterminate, the apical bud slightly larger than the mature pinnae, with trichomes patent or slightly appressed. *Rachis* castaneus, ellipsoidal or trigonous with an obtuse angle on the upper surface, densely pubescent on the lower surface, the trichomes as long or longer than the pinnae, often matted, clear or light tan, concolorous, the apical cell acuminate. *Pinnae* alternate or subopposite, in 2 ranks overlaying the rachis, imbricate, (the basal ones smaller, distant sterile, persistent) orbicular, sometimes crenate in outline, patelliform, the margin strongly enrolled, equilateral at the base, 2.0-3.5 mm. long, 2.0-3.5 mm. wide, bright green, herbaceous; *upper surface* sparsely pubescent with long, clear trichomes or glabrous, the epidermal cell walls unthickened; *lower surface* with moderately dense tomentum of clear, curled, one or few celled trichomes, *stalk* bent, ca. 0.25-0.50 mm. long atropurpureus. *Veins* slender, in the plane of the upper surface or slightly raised, dichotomous with wide angles, the branches long or moderately long, the ends clavate or acute, extending to the border. *Border* usually moderately broad, sometimes extended at the vein ends, entire or slightly undulate, ciliate, membranous, clear or opaque white. *Sporangia* few, on veins mostly adjacent to the pinna stalk, not on the distal portion, the stalk short, of 2 tiers with intercalary cell divisions, the lower tier may be brown and with 1 or few trichomes, the annulus of 12-18 indurated cells. *Spores* dark brown, smooth, the equatorial wing moderately broad, the 3 angles not or scarcely projecting.

Jamesonia brasiliensis was long considered to be an endemic on Mount Itatiaia but there are a few collections from Bolivia which are without doubt this species. They differ slightly from the Brazilian material in having the pinnae glabrous on the upper surface and the collection of Tate has smaller pinnae of a more rigid texture. These Bolivian specimens are of great interest for they connect the outlying Brazilian specimens with the rest of the genus which is Andean in distribution. The species appears to be most closely related to *J. imbricata* var. *glutinosa* on the basis of the symmetrical pinnae with bent pinnae stalks and dark brown spores. The concentration of species of *Jamesonia* in the Andes suggests that *J. brasiliensis* has migrated eastward into Brazil.

Northern to central Bolivia and Mount Itatiaia, Brazil, at 2200-2600 m. Additional specimens examined: BOLIVIA. COCHABAMBA: Comarapa, *Herzog 1944* (B, S, US); *Steinbach 9596* (US). LA PAZ: Cocopunco, *Tate 327* (US). BRAZIL. RIO DE JANEIRO: Serra de Itatiaia, *Brade 6485* (B, S-PA, US); *Dusén 400* (B, BM, GH, K, LE, P, S,

MAPS 14-19. Map 14, *J. scalaris*. Map 15, *J. imbricata*, the triangles at the localities of var. *imbricata*, the dots at the localities of var. *glutinosa*, the stars at the localities of var. *meridensis*. Map 16, *J. brasiliensis*. Map 17, *J. verticalis*. Map 18, *J. blepharum*. Map 19, *J. cinnamomea*.

S-PA, US); *Glaziou 5327* (B, K, P), *7016* (B, K, P, S, US); *Rose & Russell 20505* (US), *20514* (US).

17. **Jamesonia verticalis** Kunze, Bot. Zeit. 2: 739. 1844.
Fig. 17. Map 17

TYPE: *Hartweg 1504*, Colombia BM!, photos: COL, F, GH, NY, US; isotypes: B! GL! K! P!.

Gymnogramma verticalis (Kunze) Kl. Linnaea **20**: 410. 1847.

Jamesonia imbricata (Sw.) Hook. and Grev. var. *verticalis* (Kunze) Hook. Sp. Fil. **5**: 107. 1864.

Gymnogramma verticalis (Kunze) Kl. var. *humilis* Karst. Fl. Columb. **2**: 86, t. 143. 1865. TYPE: *Lindig 311*, Colombia, Manzanos, 2800 m. B!; isotypes: BM! K! (photos: COL, F, GH, NY, US) P!.

Jamesonia imbricata (Sw.) Hook and Grev. var. *Pearcei* Baker, Syn. Fil. 514. 1874, as "var. J. Pearcei". TYPE: *Pearce*, Andes of Ecuador, 10,000′ K!, photos: COL, F, GH, NY, US.

Psilogramme verticalis (Kunze) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 332. 1882.

Gymnogramma verticalis (Kunze) Kl. var. *frigida* Hieron, Engl. Bot. Jahrb. **34**: 475. 1904. TYPE: *F. C. Lehmann 5002*, Colombia, near Popayan, 2800-3200 m. B!; photos: COL, F, GH, NY, US; isotypes BM! GH! K! P! US!.

Gymnogramma tolimensis Hieron. Engl. Bot. Jahrb. **34**: 475. 1904. TYPE: *F. C. Lehmann 2401*, Colombia, montis Alto de Oteras, montis Tolima, 3200 m. Jan. 11, 1883 B; isotypes: K! LE!, photos: COL, F, GH, NY, US.

Jamesonia tolimensis (Hieron.) C. Chr. Ind. Fil. 374. 1905.

Jamesonia Pearcei (Baker) C. Chr. Ind. Fil. 374. 1905.

Rhizome creeping or somewhat erect near the apex, dichotomously branched, stout ca. 3-5 mm. in diameter with dense roots, the internodes short, with petioles congested, the trichomes rigid, appressed, lustrous ruddy or dark brown, the same color or slightly darker than the rhizome surface, 2.0-2.5 mm. long with 1-4 cells near the base, apex bulbous, exuding, rarely acuminate. *Petiole* usually bent and appressed to the rhizome before ascending, 2.5-45.0 cm. long, 1 4 as long as the lamina or frequently up to 4 times longer than the lamina, dull, glutinous, atropurpureus, the upper surface channeled, the lower surface convex, ca. 1-3 mm. in diameter at the apex with dense, rigid, appressed trichomes. *Lamina* pinnatisect or pinnate at the base, ca. 8-40 cm. long, 0.7-4.5 cm. wide, broadest above the base with ca. 50-160 pinnae, usually determinate, the apex pinnatisect, acuminate. *Rachis* similar or lighter colored than the petiole, the upper surface sulcate, the lower surface convex, densely pubescent, crustose, the trichomes rigid, appressed, or somewhat patent, tan or bicolorous short or longer and tufted at the base of the pinna, with cells at the base dark brown, the apical cell bulbous. *Pinnae* alternate or subopposite, approximate, in 2 ranks laterally disposed, usually adnate, (the basal ones smaller, distant, fertile, persistent) long-ovate to oblong, rarely orbicular, the base broad to narrowly attached along the central channel of the rachis or the acroscopic side partly free and imbricate, usually auriculate or lobed, sometimes entire, plane or slightly patelliform, 0.8-2.2 cm. long, 0.2-1.0 cm. wide, yellow-green, sometimes brownish along the veins adjacent to the rachis, coriaceous; *upper surface* vernicose with appressed glands, the epidermal cell walls slightly thickened; *lower surface* with rigid, erect, capitate, clear, tan or light brown, short trichomes of one or few cells, especially abundant along the veins. *Veins* broad, in the plane of the upper surface or usually raised, dichotomous with acute angles, the branches long, nearly parallel, the vein ends broad, clavate to flabellate extending nearly to the margin. *Border* usually undifferentiated or narrow, sometimes protruding at the veins, fimbriate with cilia similar to the trichomes of the lower pinna surface. *Sporangia* abundant along the veins especially adjacent to the rachis in the central portion of the pinnae, fewer on the distal portion of the veins, the stalk short, of 2 tiers the lower one usually brownish, several cells broad sometimes with 1 or more trichomes, the annulus of 17-19 indurated cells. *Spores* dark brown, smooth to slightly verrucose especially on the distal face, the equatorial wing moderately broad, the 3 angles not or slightly projecting.

There is remarkable plasticity in the form of the leaves in *J. verticalis* especially in the length of the petiole, the size of the pinnae and the elaboration of the margin. In one collection the length and breadth of the leaves vary considerably and on a single leaf there is a broad range in pinna size. There are some collections from Cauca and Cundinamarca, Colombia with mostly small, entire pinnae with strongly enrolled margins which have been distinguished as var. *frigida* and var. *humilis*. They are not recognized here because of the variability in these characters and the occurrence of intermediate specimens.

Jamesonia verticalis differs from other species in *Jamesonia* in the elongate pinnae which are mostly adnate but the relationship appears to be closest to *J. cinnamomea*. A collection of *Fosberg 20954*, from Páramo de Sumapaz, in Meta, south of Bogotá is included in *J. verticalis* on the adnate pinnae and short stalks of the sporangia but it resembles *J. cinnamomea* in the orbicular pinnae form.

Jamesonia verticalis is regarded as the least specialized member of a group including *J. cinnamomea* and *J. blepharum*. The adnate pinnae in *J. verticalis*, however, appear to be a character that is more specialized than in the other two. This group represents an independent line in *Jamesonia*, originating from a species similar to *Gymnogramma Mathewsii*. There are similarities between this species and *J. verticalis* in the form of the pinnae, the channeled petioles, the short, rigid trichomes on the lower surface of the pinnae and the rectangular form of the epidermal cells.

Jamesonia verticalis has a broader geographic and altitudinal range than *J. cinnamomea*, occurring in all three of the Cordilleras of Colombia and in southern Ecuador, at 1800-3500 m. Additional specimens examined: COLOMBIA. Santa Ana, *Langlassé 99* (B, G, GH, K, P, US). ANTIOQUIA: Cerro de la Vieja, *Bro. Daniel 1729* (US); Páramo de Sonsón, *Ewan 15708* (GH, US); *Kalbreyer 1325* (B, K). CALDAS: Cerro Tatama, *Pennell 10471* (GH, US). CAUCA: Alto del Duende, *Cuatrecasas 18859* (GH, US); *Hartweg 1048* (K); *Lehmann 1268* (K, L, US), *4428* (B, K, P, US), *5705* (B, K, P, US); Mount El Derrumbo, *Pennell 7492* (GH, S, US); Páramo de Buena Vista, *Pittier 1149* (US); El Tambo, *von Sneidern 1127* (B, S, US). CUNDINAMARCA: *Grant 10201* (US); *St. John 20526* (GH, US). HUILA: *Cuatrecasas 8793* (COL, US); *Juzepczuk 6602* (LE); *Stübel 182* (B, US), *298* (B). META: Páramo de Sumapaz, *Fosberg 20954* (US). PUTUMAYO: *Alston 8402* (BM, GH); *Fosberg 20344* (US); Alta de Cruz, *Foster & Foster 2053* (COL). VALLE: *Cuatrecasas 18023* (GH, US). ECUADOR. *André 4534* (F, GH, K, US). AZUAY: Páramo del Castillo, *Camp E4815* (F, GH, US), *4884* (U, US); *Crespi 52* (US).

18. **Jamesonia blepharum** A. F. Tryon, sp. nov. Fig. 18. Map. 18

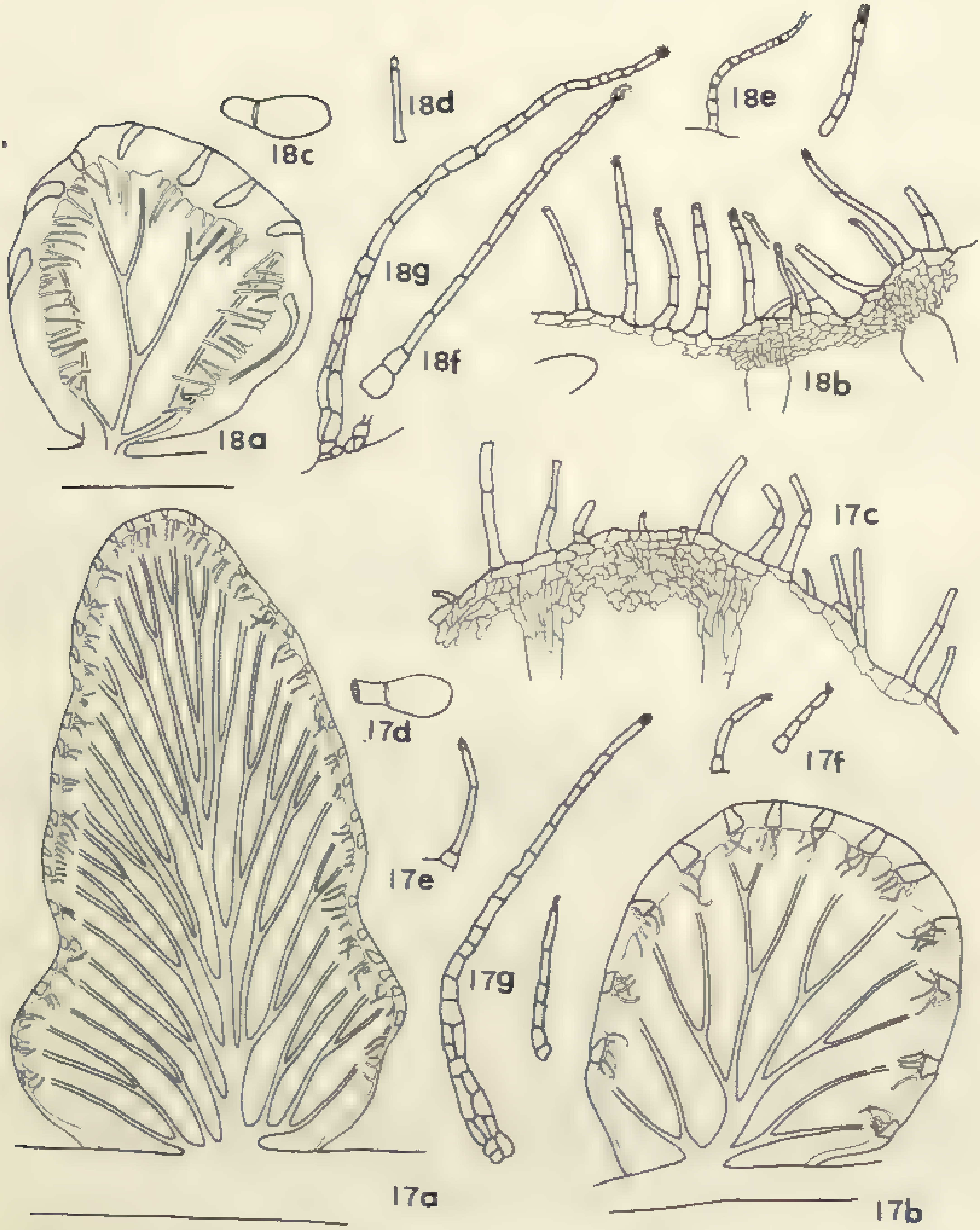
Trichomata rhizomatis rigida, appressa, pallida usque obscurofusca vel atropurpurea, laminae saepe determinatae vel gemmae quam pinnae minores, glutinosae trichomatibus appressis, rachis aliquid sulcata vel adaxialiter infrequens plana, pinnae adnatae vel subsessiles, orbiculares, patelliformes, rigide herbaceae, pinna adaxialiter vernicosa trichomatibus glutinosis, abaxialiter trichomatibus capitatis, glandulosis, nervis copiosis, nervis gracilibus, dichotomis angulis acutis, ramis longis aliquanto parallelibus, sporae obscurofuscae, raro pallidae, laeves vel papillatae.

TYPUS: Peru, Pampayacu, Jan. 16, 1927, *Ryozo Kanehira 148*, GH; isotypus: US.

Rhizome long creeping, dichotomously branched, ca. 1.0-2.5 mm. in diameter with sparse, long roots, the internodes variable in length, with petioles sometimes congested, the trichomes rigid, appressed, lustrous light to dark brown or atropurpureus, usually darker than the rhizome surface, ca. 1.0-1.5 mm. long with usually 1 or 2 cells near the base, apical cell acuminate or bulbous and exuding. *Petiole* often bent and appressed to the rhizome before ascending, 3.5-22.0 cm. long, from 1/6 to nearly 1/2 as long as the lamina, usually dull blackish, sometimes lighter, nearly castaneus, terete or channeled on the upper surface, ca. 1.0 mm. in diameter or slightly less at the apex, usually with appressed, glutinous trichomes. *Lamina* once pinnate, ca. 10-55 cm. long, 0.5-1.0 cm. wide, with 60-220 pinnae, the lamina nearly the same size throughout or the base and apex more slender, sometimes determinate, the apical bud usually smaller than the mature pinnae, with appressed or patent, glandular trichomes. *Rachis* similar in color or lighter than the petiole, shallowly sulcate, rarely plane on the upper surface, usually crustose or vernicose and with appressed, rarely patent trichomes especially on the lower surface, longer and tufted at the base of the pinnae, often with basal cells lighter colored, the apex usually bulbous, sometimes exuding, rarely acuminate. *Pinnae* alternate, approximate or distant, rarely slightly imbricate, usually laterally disposed in 2 ranks overlaying the upper surface of the rachis, (the basal ones smaller, usually sterile, distant, persistent) orbicular, entire, usually patelliform, equilateral at the base or nearly so, adnate or subsessile, 1-8 mm. long, 1-6 mm. wide, yellow-green, rigid herbaceous; *upper surface* vernicose with appressed glands, the epidermal cell walls sometimes thickened; *lower surface* with clear or tan, short, erect, capitate, glandular trichomes, or longer trichomes of several cells, longer on the veins, sometimes curled and more or less matted, *stalk* oblique not exceeding 1.0 mm. long, atropurpureus often broad and decurrent on the upper surface of the rachis. *Veins* slender, in the plane of the upper surface or slightly raised or sunken, dichotomous with acute angles, the branches long, nearly parallel, the ends clavate or flabellate extending nearly to the margin. *Border* narrow, a row of cells broader than long, with cilia similar to the trichomes on the lower pinna surface. *Sporangia* abundant, sometimes obscuring the lower pinna surface, the stalk short, of 2 tiers, the lower one a cluster of brown cells, the annulus of 17-19 indurated cells. *Spores* dark brown, rarely tan, smooth or papillose, the equatorial wing broad, the 3 angles scarcely projecting.

The name *Jamesonia ciliata* was formerly applied to this material and Hieronymus cites the Lehmann collection from Ecuador under that name. The epithet was, however, originally applied by Karsten to a collection of another species from Venezuela. *Jamesonia blepharum* is known from only a few collections from widely disjunct stations. The collections from Peru, Ecuador and Colombia are relatively uniform with the exception of the Philipson collection from north of Bogotá which has tan spores. The Bolivian collections are diverse and somewhat intermediate to this species and *J. cinnamomea*. *Williams 1152*, in part, and *Steinbach 8370* have pinnae with broader borders and lax, whitish trichomes on the lower surface of the pinnae; while *Cárdenas 1024* has unusually long, lax leaves with dense, white, crispate trichomes on the lower pinna surface. These collections resemble *J. cinnamomea* in having relatively long stalked pinnae but I am placing them in *J. blepharum*, with some reservation, on the relatively smaller pinnae, the short stalked sporangia and dark, appressed rhizome trichomes.

Jamesonia blepharum is most closely related to *J. cinnamomea* in several characters and intermediate to this and *J. verticalis*.



FIGS. 17 AND 18. FIG. 17. *J. verticalis:* a, pinna, × 5, from *Cuatrecasas 18859* (GH); b, pinna, × 5, from *St. John 20526* (GH); c, pinna margin with two vein ends, × 35, from *Fosberg 20344* (US); d, gland from upper pinna surface, enlarged, from *Cuatrecasas 8793* (US); e, capitate trichome from lower pinna surface, enlarged, from *Cuatrecasas 18023* (GH); f, petiole trichomes, the apical cells with exudate, × 30, from *Cuatrecasas 8793* (US); g, rhizome trichomes, the apical cells with exudate, × 30, from *Pittier 1149* (US) FIG. 18. *J. blepharum*: a, pinna, × 10; b, pinna margin with three vein ends, × 35; c, gland from upper pinna surface, enlarged; d, glandular trichome from lower pinna surface, enlarged; e, rachis trichomes, the right with exudate at the apex, × 30; f, rhizome trichome with exudate at apex, × 30; all from *Kanehira 148* (GH); g, rhizome trichomes showing the basal cells, × 30, from *Philipson et al. 2443* (COL).

At disjunct stations from central Bolivia to northern Colombia, from 1500-3400 m. Additional specimens examined: COLOMBIA. CUNDINAMARCA: Páramo de la Calera, *Philipson* et al. *2443* (BM, COL). ECUADOR. LOJA: *Lehmann 5707* (K, P, US). PERU. CUZCO: *Bües 1824* (US), *1908* (US), *1914* (US). BOLIVIA. LA PAZ: *Cárdenas 1024* (GH); Tolapampa, *Williams 1152* (US). SANTA CRUZ: Comarapa, *Steinbach 8370* (GH, K, S).

19. **Jamesonia cinnamomea** Kunze, Bot. Zeit. 2: 738. 1844.

Fig. 19. Map 19

TYPE: *Hartweg 1516* BM!, photos: COL, F, GH, NY, US; isotypes B! BM! G! GH! K! LE! US!.

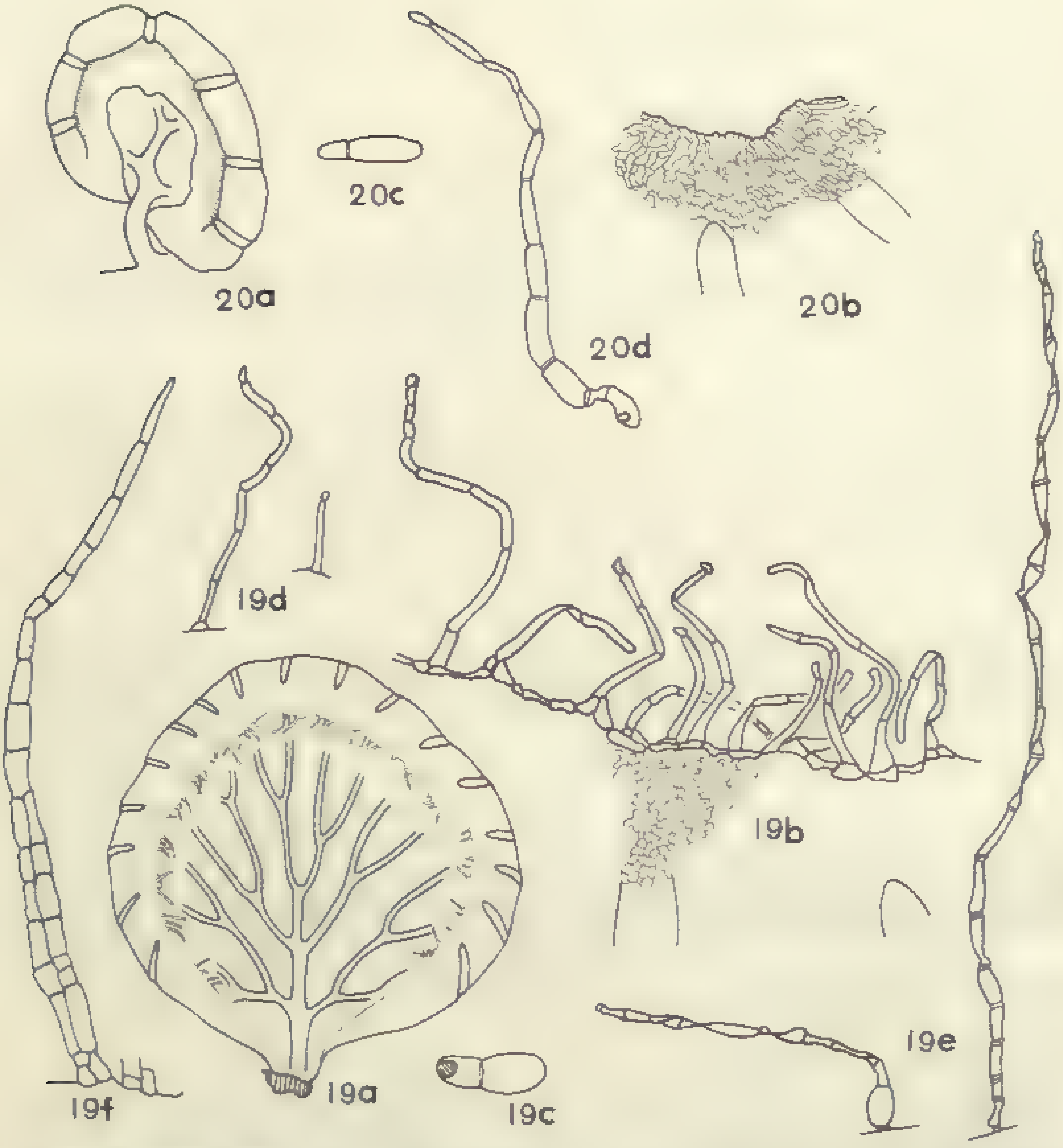
Gymnogramma cinnamomea (Kunze) Kl. Linnaea 20: 407. 1847.

Jamesonia imbricata (Sw.) Hook. and Grev. var. *cinnamomea* (Kunze) Hook. Sp. Fil. 5: 107. 1864.

Psilogramme cinnamomea (Kunze) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 334. 1882.

Jamesonia brunnea Maxon, Jour. Wash. Acad. Sci. 14: 72. 1924. TYPE: *L. Mille 42*, Ecuador, Mount Guamani, 4000 m. US!; isotype GH!.

Rhizome creeping, stout, ca. 2-5 mm. in diameter with sparse roots, the internodes short or long, with petioles sometimes congested, the trichomes lax, patent, lustrous tan or golden brown, lighter than the rhizome surface, 1.5-2.5 mm. long with usually 1 (-3) cells near base, apical cell acuminate. *Petiole* often bent and appressed to the rhizome before ascending, 7-21 cm. long, about 1.5 to twice as long as the lamina, usually dull, ruddy or dark brown, terete or the upper surface channeled and the lower surface convex, ca. 2 or 3 mm. in diameter at the apex, usually with appressed, ruddy or dark brown trichomes. *Lamina* once pinnate, ca. 38-43 cm. long, 0.8-1.5 cm. wide nearly the same size throughout or the base and apex slightly narrower with ca. 70-170 pinnae, sometimes determinate, the apical bud usually large, up to 4 times larger than the mature pinnae, with a tomentum of partly appressed, cinnamomeus trichomes. *Rachis* similar in color to the petiole, the upper surface sulcate or with 2 shallow lateral grooves, densely pubescent especially on the lower surface, with crisped, patent or rigid, appressed trichomes which are longer and tufted at the base of the pinnae, with the basal cells sometimes lighter colored, the apex usually bulbous. *Pinnae* alternate, imbricate, often approximate, in 1 or 2 closely placed rows over the rachis, (the basal ones smaller, sometimes distant, sterile, persistent) orbicular, entire, patelliform, the margin enrolled, equilateral at the base, 2-10 mm. long, 2-9 mm. wide, yellow-green, coriaceous; *upper surface* with appressed, glutinous trichomes, often vernicose, the epidermal cell walls slightly thickened; *lower surface* with clear or tan, short, erect, capitate trichomes of 1 or few cells and with longer tan to brown, curled trichomes, of several cells, near the stalk of the pinna, *stalk* oblique, usually short, rarely up to 2 mm. long, castaneus or atropurpureus often broad and slightly decurrent on the upper surface of the rachis. *Veins* broad, in the plane of the upper surface, often slightly raised,



FIGS. 19 AND 20. FIG. 19. *J. cinnamomea:* a, pinna, × 5, b, pinna margin with two vein ends, × 35; c, gland from upper pinna surface, enlarged, d, capitate trichomes from lower pinna surface, × 30, e, rachis trichomes, × 30; f, rhizome trichomes showing the basal cells, × 30, all from *Cuatrecasas 14713* (GH) FIG. 20. *J. ceracea:* a, pinna, × 10, b, pinna margin with two vein ends, × 35; c, gland from upper pinna surface, enlarged; d, rachis trichome, × 30; all from *Pennell 2607* (GH)

dichotomous with moderately wide angles, the branches long and nearly parallel, the ends clavate or acute, ending short of the border. *Border* narrow, rarely broader, with a row of cells broader than long with trichomes having the apical cell bulbous and sometimes glandular. *Sporangia* abundant, the stalk usually as long or longer than the capsule, with intercalary cell divisions and sometimes with trichomes, the annulus of 18-21 indurated cells. *Spores* dark brown, smooth, the equatorial wing broad, the 3 angles prominently projecting.

This is a most distinctive species easily recognized by the long, robust leaves with numerous, orbicular pinnae and the usually large, ruddy brown leaf bud. In a few collections the apex may be completely unrolled. Most specimens are relatively uniform but a collection from Ecuador, *Espinosa 956*, has unusual dark brown, rigid, appressed rhizome trichomes and some lobed pinnae.

The species is most closely related to *Jamesonia blepharum* and *J. verticalis* on several characters and appears to be more specialized than these in the broader pinnae margins, elongated sporangia stalks and large leaf buds. However, the lax, light colored rhizome indument and the stalked pinnae appear less specialized.

Jamesonia cinnamomea occurs from central Ecuador to southern Colombia, at 3100-5000 m. The highest altitude at which the genus is reported is a collection of this species from Mount Chimborazo, Ecuador. Additional specimens examined: COLOMBIA. CAUCA: Volcán de Puracé, *Cuatrecasas 14713* (GH, US); *Pérez Arbeláez & Cuatrecasas 5930* (COL, US); *von Sneidern 1685* (G, S). NARINO: Volcán de El Galeras, *Ewan 16321* (GH, US); Volcán de Pasto, *Jameson 12* (B, E, G, GL, K, LE, US). ECUADOR. *André 3262* (GH, K, US); *Espinosa 956* (GH); *Sodiro 28* (GH, P, S-PA, U). CHIMBORAZO: Mount Chimborazo, *Asplund 7821* (GH, S); *Heinrichs 946* (F, G); *Hitchcock 21971* (GH, US); *Rimbach 35* (GH, US), *72* (GH, US), *132* (US), *312* (B, S-PA), *538* (S-PA). IMBABURA: Volcán de Cayambe, *Drew E439* (US); Monte Cayambe, *Jameson 503* (G, GH); *Little & Paredes C. 6895* (US). TUNGURAHUA: Mount Caribuayrazo, *Asplund 8480* (GH, S).

DUBIOUS AND EXCLUDED NAMES

Jamesonia adnata Kunze, Farrnkr. 2: 80, t. 133, f. 1. 1851. TYPE: *Linden 1006*, Colombia B. = *Polypodium moniliforme* Lagasca.

Jamesonia ceracea Maxon, Jour. Wash. Acad. Sci. **14**: 73. 1924. Fig. 20. TYPE: *F. W. Pennell 2607*, Colombia, Mt. Chuscal, west of Zipaquirá US!; isotype: GH!. The collection consists of several detached, sterile leaves with small pinnae having very broad, indusioid borders and copious, ceraceous indument on the lower surface. In these characters the material is so distinctive from other species in the genus it is understandable that it was described as new. It is in fact so unique that I regard it as aberrant. There are a few collections of *Jamesonia imbricata* var. *glutinosa* with ceraceous indument on the upper surface of the pinnae but this Pennell collection is the only material that I have seen in which such indument is found on the lower pinna surface. I suspect that it is a hybrid of one of the complexes involving var. *glutinosa*.

Jamesonia crespiana Bosco, Nuovo Giorn. Bot. Ital. n. s. 45: 147, t. 10. 1938. TYPE: *C. Crespi*, Ecuador, Gualaceo — Culebrilla, 2500 m. Herb. Miss. Salesiane. This is not a *Jamesonia* since it is described as having broad, ovate rhizome scales and from the photograph it appears to be a species of *Polystichum*.

Jamesonia elongata (Hook. & Grev.) J. Smith, Hist. Fil. 168. 1875 = *Eriosorus elongatus* (Hook. & Grev.) Copel.

Jamesonia grisea Maxon ex Pittier, Man. Pl. Usual. Venez. 193. Caracas. 1926, nom. nud.

Jamesonia hispidula Kunze, Bot. Zeit. **2:** 739. 1844. TYPE: *Moritz 72*, Caracas, Venezuela. This collection was not found at either B or BM. It is out of the geographic range of *Jamesonia* and is perhaps an *Eriosorus*.

Jamesonia imbricata var. *culebriliensis* Bosco, Nuovo Giorn. Bot. Ital. n. s. **45:** 147. 1938. TYPE: *C. Crespi*, Ecuador, Gualaco et Cuebrilla, 2500 m. Herb. Miss. Salesiane. From the description of the alate rachis and dentate segments this cannot be a *Jamesonia* but I cannot place it in any genus with certainty.

Jamesonia paleacea Kunze, Bot. Zeit. **2:** 739. 1844. TYPE: *Linden 505*, Caracas, Venezuela BM!; isotype: BR, photo, GH! = *Polystichum pycnolepis* (Kunze) Mett.

LITERATURE CITED

BOWER, F. O. 1928. The Ferns. Vol. 3. The Leptosporangiate Ferns. University Press. Cambridge, England.

BRADE, A. C. 1942. A composição da flora Pteridófita do Itatiaia. Rodriguésia **6:** 26-43.

CHRISTENSEN, C. 1938. Filicinae, in Manual of Pteridology. Martinus Nijhoff, The Hague.

COPELAND, E. B. 1947. Genera Filicum. Chronica Botanica. Waltham, Massachusetts.

CUATRECASAS, J. 1934. Observaciones Geobotánicas en Colombia. Trab. Mus. Nac. Cien. Nat. Madrid Ser. Bot. **27:** 1-144.

ERDTMAN, G. 1957. Pollen and Spore Morphology Plant Taxonomy. Almqvist and Wiksells. Stockholm.

FOSBERG, F. R. 1944. El Páramo de Sumapaz. Jour. N. Y. Bot. Gard. **45:** 226-234.

————————. 1961. Southern distribution of *Botrychium oneidense* and *B. multifidum*. Amer. Fern Journ. **51:** 175-179.

HOLTTUM, R. E. 1946. A Revised Classification of Leptosporangiate Ferns. Jour. Linn. Soc. Lond. Bot. **54:** 123-158.

JAMESON, W. 1865. Syropsis Plantarum Aequatoriensium. Quito, Ecuador.

KRAMER, K. U. 1957. A revision of the genus Lindsaea in the New World with notes on allied genera. Acta Bot. Neerl. **6:** 97-290.

MANTON, I. 1958 Chromosomes and Fern phylogeny with special reference to "Pteridaceae." Jour. Linn. Soc. Lond. Bot. **56:** 73-92.

SIMPSON, G. G. 1961. Principles of Animal Taxonomy. Columbia University Press. New York.

SMITH, A C. AND I. M. JOHNSTON. 1945. A phytogeographic sketch of Latin America, *in* Plants and Plant Science in Latin America. Chronica Botanica. Waltham, Massachusetts.

SMITH, L. B. 1962. Origins of the flora of southern Brazil. Contrib. U. S. Nat. Herb. **35:** 215-249.

THOMPSON, J. M. 1918. The anatomy and affinity of certain rare and primitive ferns. Trans. Roy. Soc. Edin. **52:** 363-397.

TRYON, A. F. AND D. M. BRITTON. 1958. Cytotaxonomic studies of the fern genus *Pellaea*. Evolution **12:** 137-145.

TRYON, R. M. 1944. Dynamic phytogeography of *Doryopteris*. Amer. Jour. Bot. **31:** 470-473.

WILSON, K. A. 1959. Sporangia of the fern genera allied with *Polypodium* and *Vittaria*. Contrib. Gray Herb. no. 185: 97-127.

INDEX TO NAMES