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Edited by<br>Reed C. Rollins and Robert C. Foster

NO. CLXXIX

# A REVISION OF THE AMERICAN SPECIES OF NOTHOLAENA 

By<br>Rolla Thyon

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

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# A REVISION OF THE AMERICAN SPECIES OF NOTHOLAENA 

By<br>Rolla Tryon<br>MISSOURI BOTANICAL GARDEN<br>Illustrated by Bernadette Velick

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C. A. Weatherby working on Notholaena at Kew in July, 1939 (photo F. Ballard).

## MR. C. A. WEATHERBY'S WORK ON NOTHOLAENA.

Una F. Weatherby

In 1935 we visited some of the larger herbaria in Holland and Belgium and also the ones in Paris and London, studying and photographing the type specimens of various ferns Mr. Weatherby was interested in, especially some of the Notholaena group. After our return a more careful study was made of the specimens of this group as found in our American herbaria. In 1937 we returned to Europe for more study of the types and this time we added those in the herbaria of Berlin, Vienna and Prague.

By 1939 he had decided upon a complete revision of the Notholaena group, saying many species were masquerading under that name but did not belong there.

Though there was much talk of war we decided to go back to Europe and get as many notes and pictures as possible for fear that if there was a war the herbaria might be destroyed. We spent some time in London and in Paris where we were when the war began. Trunks and baggage were left behind but the notes and photographs we carried in our hands and got them safely home with us.

During the war years he felt it was his duty to devote his time to any war work he could do. He put aside his work on Notholaena though he made numerous notes on it and charts of each species or related groups for comparison. After the war the work was again interrupted while he did some nomenclatorial work for the International Botanical Congress. He disliked purely nomenclatorial work, but having been given the job he felt it his duty to do it. He said that plants like people must have names if one was to talk about them intelligently and it was necessary for the name to be accurate to prevent confusion. So at his sudden death he had a large pile of notes, charts, etc. concerning his Notholaena monograph but many matters were still undecided. These I turned over to Dr. Tryon who came from St. Louis to help me place some of Mr. Weatherby's botanical possessions.

After several years he has succeeded in working these up for publication. All taxonomic decisions are purely his. He has done a marvelous job in bringing order out of the mass of notes and the excellent drawings prepared by Mrs. Velick add greatly to their value.-Cambridge, Massachusetts, March 18, 1956.

## Introduction

Some time after the death of C. A. Weatherby in 1949, Mrs. Weatherby turned over to me his manuscript and notes on Notholaena. A careful perusal revealed that the treatment was fairly well along toward completion, to the extent, at least, that it was certainly not worthwhile for one to begin a similar study de novo, and accordingly it was decided, in consultation with Mrs. Weatherby, that the study should be completed. However, Mr. Weatherby's own wishes did not allow the monograph to be published under his authorship, since he had not finished it to his own satisfaction. So I have accepted the difficult position of publishing what is principally the work of another, appreciating on the one hand the reasons for this, and, on the other, the necessity of making what would have been Mr. Weatherby's major publication in taxonomy available to fern students and floristic botanists.

In a number of smaller papers, Mr. Weatherby had already used portions of the manuscript and in these seventeen species were fully treated and fifteen more partially so. The appropriate reference is given after each species to his own publications on it. The remainder of the manuscript I have checked and elaborated when necessary, the keys have often been recast, two new species that Mr. Weatherby did not see material of are described and finally the treatments of the last two species have been added, since they clearly belong with the ones immediately preceding. In the taxonomic treatment I have been guided in difficult cases by Mr. Weatherby's annotations at the Gray Herbarium and by the general mode of treatment in his publications. In all cases the judgment is my own although I have made every effort to follow the manuscript and in the cases where a species was dealt with in one of his papers his treatment has been essentially copied. Maps and illustrations have been furnished for the species and it is hoped that these will increase the usefulness of the paper.

The meaning of the different symbols used on the distribution maps is as follows: a solid dot is used for a specimen that is from a particular locality, a circle is used for a specimen with only general locality data and an $\mathbf{X}$ is used when the record is taken from the literature. In the latter case the source of the report is given in the discussion of the species concerned.

My work has proceeded more slowly than I would have liked but most of it was completed in 1954. The necessary time needed
to put the final touches on the treatment has been supported by the National Science Foundation in relation to work on the Ferns of Peru; some twenty-five percent of the species occur in that country. Mrs. Una F. Weatherby has generously supported the cost of preparation of the illustrations and of the plates. I am indebted to Mrs. Bernadette Velick for her accurate and artistic work on the illustrations.

## The Genus Notholaena

There need be no apology for a lack of a definition of the genus Notholaena. The difficulties of such a definition are well known to fern students and are in fact perhaps the principal reason for the present study. It is not likely that an adequate classification of the genera of the Cheilantheae, Cheilanthes, Notholaena, Pellaea, Doryopteris and related smaller genera, can be achieved without a previous knowledge of the species concerned and it is in this manner that this paper is a contribution to an understanding of the genus. It seems that the basic problem will be to determine the lines of evolution so that the meaning of characters is sufficiently clear, which characters are of generic value, which are convergent and which are only of specific expression.

The group of species, included here in Notholaena, grades suspiciously into Cheilanthes on the one hand (via N. peruviana, N. brachypus and a few others among species nos. 1-18) and into Pellaea on the other (via species nos. 44-58). The first mentioned species are similar to Cheilanthes in having a slightly to moderately developed margin-indusium and the others are similar to Pellaea in rhizome scales and their imparipinnate lamina. The last two species in this treatment, N. parvifolia (Pellaea microphylla) and N. formosa, have not been placed in Notholaena previously, usually residing in Pellaea, but their obvious affinity with the species preceding them necessitates their transfer. It is unfortunate to make new names under Notholaena when the generic situation is in such doubt but if they were maintained in Pellaea other species that would necessarily go with them would require new names and these would have to be made with equal doubt. The uncertainty of the definition of Notholaena is not all of the difficulty, for if Cheilanthes and Pellaea were well defined the task might be more certain, but the problems in those genera are, in their own way, as perplexing as those in Notholaena.

Characteristically, Notholaena has a flat unmodified margin
although sometimes it is revolute and sometimes it is modified into a marginal indusium. The species with wax may be distinguished from Pellaea by that character and from Cheilanthes by the unmodified margin. The species without any indument ( $N$. Jonesii, N. Lumholtzii, N. nivea var. tenera, N. parvifolia and $N$. formosa) may be distinguished from both genera by their unmodified margin, although they may resemble closely some species of Pellaea. The fact that $N$. nivea has a variety lacking indument demonstrates that this character alone is not sufficient to place a species in a genus other than Notholaena and such species are included here on the basis of their close relation in other characters to wax-bearing species. The species with hairs or scales (some also have wax) may be distinguished from Pellaea by their indument as well as by their usually unmodified margin. The latter character separates them from Cheilanthes. The few species with a slightly to moderately developed marginal indusium are transitional to Cheilanthes but retained here because of apparent relations to species without a modified margin.

Although Mr. Weatherby had paid considerable attention to the grouping of species within Notholaena, it has not been possible for me to define clearly any segregates or sections, or to place individual species with certainty elsewhere, to the end that the genus would have a better organization and circumscription. The synopsis of the genus presents such groups of species as have certain characters in common, but lacking sufficient understanding of the meaning of the characters I have not tried to do more.
The American element of Notholaena comprises 59 species, 7 of which are divided into 17 varieties. The United States has 19 species, with 13 in Texas; Mexico has 34 species; Central America 7; the Greater Antilles 8; and South America 20, with 9 species and 4 varieties in Peru.

## Systematic Treatment

Notholaena R. Br. Prod. Fl. Nov. Holl. 145. 1810. Hook. Sp. Fil. 5: 107-121. 1864; Hook. \& Baker, Syn. Fil. 370-374. 1868; Christ, Farnkr. Erde, 150-153. 1897; Diels, in Engl. \& Prantl, Nat. Pflanzenfam. 14: 272-274. 1899; C. Chr. Ind. Fil. 459-464. 1906; C. Chr. in Verdoorn, Man. Pterid. 539. 1938; Maxon \& Weath. Some species of Notholaena, new and old, Contrib. Gray Herb. 127: 3-17. 1939; Weath. The Argentine species of "Notholaena," Lilloa 6: 251-275. 1941; Weath. in Johnston, Plants of northern Mexico, I, Journ. Arn. Arb. 24: 312-318. 1943; Weath. A new Argentine variety in Notholaena, Amer.

Fern Journ. 36: 7-9. 1946; Weath. "Notholaena" in Brazil, Journ. Arn. Arb. 27: 361-370. 1946.

Cincinalis Desv. Berl. Mag 5: 311. 1811, not Gled. 1764.
Aleuritopteris Fée, Gen. Fil. 153. 1850-52, in part.
Gymnogramma Desv. sensu Mett. Cheil. footnotes 6-13 \& text (Abhandl. Senckenb. nat. Ges. 3: 5-7). 1859, in part.
Cheilanthes Sw. sensu Mett. Cheil. no. 1 et seq. (Abhandl. Senckenb. nat. Ges. 3: 19 et seq.). 1859, in part; Domin, Bibl. Bot. 20 (Heft 85): 133-136. 1913, in part; Copel. Gen. Fil. 65. 1947, in part.

Pellaea Link sensu Prantl, in Engl. Bot. Jahrb. 3: 417. 1882, in part.
Chrysochosma Kümmerle, Mag. Bot. Lapok. 13: 35. 1914. Type species (chosen by C. Chr. Ind. Fil. xli. 1906): Acrostichum Marantae L. The generic name has been spelled Nothochlaena by various authors.

## SYNOPSIS OF AMERICAN NOTHOLAENA

a. Indument of lamina of scales or hairs, or both, never ceraceous. b.
b. Indument of scales, at least in part. 1. N. peruviana, 2. N. arequipensis, 3. N. squamosa, 4. N. lonchophylla, 5. N. sinuata, 5 a . var. sinuata, 5 b . var. integerrima, 5c. var. cochisensis, 6. N. brachypus, 7. N. Hassleri.
b. Indument of hairs only. c.
c. Lamina deltoid or pentagonal, basal pinnae much the largest, usually strongly inequilateral. 8. N. venusta, 9. N. eriophora, 10. N. goyazensis, 11. N. geraniifolia.
c. Lamina ovate to linear, basal pinnae not much enlarged nor strongly inequilateral. 12. N. Pohliana, 13. N. cinnamomea, 14. N. obducta, 15. N. aurea, 16. N. tomentosa, 17. N. Fraseri, 18. N. Buchtienii, 18a. var. Buchtienii, 18b. var. ventanensis, 19. N. Parryi, 20. N. Newberryi, 21. N. mollis.
a. Indument of lamina wholly or in part ceraceous, or absent. d.
d. Scales of the rhizome rigid, sclerotic. e.
e. Scales of rhizome more or less spinescent-ciliate, lamina commonly narrowed to both ends, much longer than the stipe. f.
f. Segments without scales or trichomes beneath. 22. N. Ekmanii, 23. N. affinis, 24. N. cubensis, 25. N. rigida.
f. Segments with scales or trichomes beneath, at least on the margin. 26. N. trichomanoides, 27. N. Aschenborniana, 28. N. Galeottii, 29. N. Schaffneri, 29a. var. Schaffneri, 29b. var. Nealleyi.
e. Scales of rhizome not spinescent-ciliate, or if so then the lamina not narrowed at the base and not longer than the stipe. g.
g. Basal pinnae not markedly larger than those immediately above, not strongly inequilateral, lamina commonly longer than broad. 30. N. Grayi, 31. N. aliena, 31A. N. Weatherbiana, 32. N. Lemmonii, 32a. var. Lemmonii, 32b. var. australis, 33. N. Rosei, 34. N. leonina.
g. Basal pinnae much the largest, deltoid and strongly inequilateral, lamina often as broad as long, or broader. 35. N. galapagensis, 36. N. candida, 36a. var. candida, 36b. var. Copelandii, 37. N. sulphurea, 38. N. Standleyi, 39. N. aurantiaca, 40. N. californica, 41. N. neglecta.
d. Scales of rhizome lax, concolorous, not sclerotic (partially so in no. 42). h .
h. Ultimate segments non-articulate, sessile and the base of uniform color, or petiolulate and the dark color of the petiolule passing into the base of the segment. 42. N. Greggii, 43. N. bryopoda, 44. N. Palmeri, 45. N. pallens, 46. N. pilifera, 47. N. chilensis, 48. N. peninsularis, 49. N. Jonesii, 50. N. Lumholtzii, 51. N. limitanea, 51a. var. limitanea, 51b. var. mexicana, 52. N. dealbata, 53. N. Fendleri.
h. Ultimate segments articulate, the dark color of the petiolule stopping abruptly in a transverse line. $54 . \mathrm{N}$. delicatula, 55. N. incana, 56. N. nivea, 56a. var. nivea, 56b. var. oblongata, 56 c. var. tenera, 56d. var. flava, 57. N. parvifolia, 58. N. formosa.

## KEY TO SPECIES OF AMERICAN NOTHOLAENA

1. Indument of lamina, including upper and lower surface but excluding rachis, of scales or of hairs, or both, not ceraceous. 2 .
2. Indument of scales, at least in part. 3.
3. Indument of scales only (some in no. 5 dissected into capillary lobes, giving the appearance of tomentum). 4.
4. Lamina lanceolate or broader, bipinnate, pinnae few; stipe commonly at least half as long as lamina, with one vascular bundle. 5.
5. Scales of rhizome entire or minutely serrulate with very short ascending teeth; scales of upper surface of lamina soon deciduous, lance-subulate, flat, or if narrow and subpiliform then 1 mm . or less long, scales of the lower surface eroseserrulate with mostly deltoid teeth. 6.
6. Lamina lanceolate, mostly $12-18 \mathrm{~cm}$. tall; rhizome scales entire or nearly so; scales of lamina dark chestnut brown; dilated soriferous vein-ends projecting into small, hyaline, marginal lobes
7. N. peruviana.
8. Lamina deltoid-ovate, mostly $2-4.5 \mathrm{~cm}$. tall; rhizome scales minutely serrulate; scales of the lower surface of lamina bright or pale brown; soriferous vein-ends in slight unmodified crenations of the margin....2. 2. N. arequipensis.
9. Scales of rhizome remotely antrorse-serrulate; scales of upper
surface of lamina piliform, more or less persistent, more than 1 mm . long, scales of the lower surface pectinate-serrulate with often piliform (although broad-based) teeth. 7.
10. Lamina ovate or elliptic, about equalling, or shorter than, the stipe; piliform scales of the upper surface of the lamina brown, those of the lower surface lance-ovate or ovate, 3-4 mm. long; s. Bolivia and Argentina....3. N. squamosa.
11. Lamina lanceolate, much longer than the stipe; piliform scales of the upper surface of the lamina whitish, those of the lower surface lance- or linear-subulate, up to 2 mm . long; Peru
12. N. lonchophylla.
13. Lamina linear with numerous merely lobed (or sometimes entire) pinnae; stipe much shorter than lamina, with two vascular bundles
14. N. sinuata.
15. Indument of both hairs and scales; fertile margin slightly modified; spores rugose. 8.
16. Stipe very short; rhizome scales concolorous or nearly so, not sclerotic; hairs of lamina slender, not moniliform, lanate, on both surfaces; Mexico and Central America ...6. N. brachypus.
17. Stipe nearly as long as lamina; rhizome scales with sharply contrasting dark sclerotic central band and pale margins; hairs of lamina thick, moniliform, on upper surface only; Paraguay
18. N. Hassleri.
19. Indument of hairs only. 9.
20. Lamina deltoid or pentagonal (subpedate), as broad as long or nearly so, usually much shorter than the stipe (sometimes not in no. 9), lowest pinnae much the largest, usually strongly inequilateral; Brazil, no. 9 also in Colombia. 10.
21. Stipe thinly villous with straight, distinctly moniliform, often gland-tipped, hairs; lamina with 1-3 wholly free pinnae, only the basal deeply divided
22. N. venusta.
23. Stipe lanate with long, tortuous, matted, slender, non-glandular hairs, or glabrous; usually none of the primary segments of the lamina wholly free. 11.
24. Indument of both surfaces of lamina of long, slender, tortuous, obscurely articulate hairs; only the basal segments deeply lobed .................... 9. eriophora.
25. Indument of lower surface of lamina of fine, short, densely felted tomentum overlaid by long, straightish, conspicuously articulate hairs; median segments, as well as the basal, lobed. 12.
26. Indument of the upper surface of lamina of fine, whitish, tortuous, more or less matted hairs, median segments simply pinnatificl, with entire lobes; rhizome scales bright brown in mass.
27. N. goyazensis.
28. Indument of upper surface of lamina of coarse, straightish, golden to whitish, not much matted hairs; median segments subbipinnatifid, their lobes more or less cut; rhizome scales fuscous in mass ........11. N. geraniifolia.
29. Lamina ovate to linear, equalling or exceeding the stipe, the lowest pinnae not greatly enlarged nor strongly inequilateral. 13.
30. Indument of simple or pectinately branched hairs, not stellate. 14.
31. Indument of lower surface of lamina of long, loosely matted hairs, thin, not concealing the leaf-tissue. 15.
32. Hairs of rachis short, spreading or retrorse, unlike those of lamina; lamina tapering evenly from base to long-attenuate apex; Brazil
33. N. Pohliana.
34. Hairs of rachis long, like those of lamina; lamina not conspicuously broader at base; Guatemala
35. N. cinnamomea.
36. Indument of lower surface of lamina dense, concealing the leaf-tissue. 16.
37. Lamina 2 -pinnate, much longer than the stipe, segments appressed-ascending-pubescent beneath 14 . N. obducta.
38. Lamina not much longer than the stipe, or if so, then uniformly pinnate-pinnatifid. 17.
39. Lamina gradually reduced at base, usually much longer than the stipe, uniformly pinnate-pinnatifid; rhizome short, ascending, knotted............15. N. aurea.
40. Lamina not conspicuously reduced at base (sometimes with a single pair of distant, reduced pinnae); rhizome usually slender, horizontal. 18.
41. Stipe and rachis sulcate, glabrous; upper surface of lamina glabrous or glabrate; Chile. 16. N. tomentosa.
42. Stipe and rachis terete, deciduously or persistently pubescent; upper surface of lamina thinly to densely pubescent. 19 .
43. Rhizome scales pale, or with dark center and light margins; lamina pinnate-pinnatifid to quadripinnate, if more than 2 -pinnate, then lanate-pubescent above. 20:
44. Lamina usually pinnate-pinnatifid, upper surface arachnoid-tomentose. 21.
45. Rhizome with numerous pale scales with conspicuously tortuous capillary tips, giving a tomentose appearance; no scales on rachis or upper part of stipe; median pinnae mostly deltoid, veins not visible on the upper surface; Ecuador to Bolivia
46. N. Fraseri.
47. Rhizome usually with few and inconspicuous pale, capillary-tipped scales, not appearing tomentose; a few deciduous scales among the tomentum on upper part of stipe and lower part of rachis; median pinnae mostly lanceolate or deltoid-lanceolate, the veins usually subimpressed and visible on the upper surface; Bolivia and Argentina
48. N. Buchtienii.
49. Lamina usually tri-quadripinnate, upper surface lanate; sw. United States and Baja Calif.
50. N. Parryi.
51. Rhizome scales dark, hardly, if at all, margined; lamina tri-quadripinnate, ultimate segments small, roundish, upper surface arachnoid-pubescent; s. Calif. \& Baja Calif...........20. N. Newberryi.
52. Indument of stellate hairs; lamina tri-quadripinnate, the ultimate divisions small, suborbicular; s. Peru \& Chile . 21. N. mollis. 1. Indument of lamina, including upper and lower surfaces but excluding rachis, lacking, or wholly, or at least in part, ceraceous (in nos. 26-28 the wax often concealed by scales, in no. 31A, by hairs). 22 .
53. Indument of lamina ceraceous and of scales or hairs (or both in no. 28 ), or lacking. 23.
54. Indument lacking. 24.
55. Ultimate segments non-articulate, the dark color of the stalk passing into at least the basal part of the segment. 25 .
56. Stipe and rachis castaneous to brownish; Utah and Ariz. to s. Calif.
57. N. Jonesii.
58. Stipe and rachis blackish; Sonora
59. N. Lumholtzii.
60. Ultimate segments articulate, the dark color of the stalk stopping abruptly in a transverse line at its apex. 26.
61. Upper side of rachis channeled or flat; rhizome scales not viscid; lamina $3-4$-pinnate, ultimate segments broadly ovate to subdeltoid, the base mostly equilateral; Texas and N. Mex. s. to Tamaulipas
62. N. parvifolia.
63. Upper side of rachis rounded. 27.
64. Base of ultimate segments equilateral, mostly cuneate to truncate; rhizome scales not viscid; lamina $2-3$-pinnate; Peru to Argentina ... 56c. N. nivea var. tenera.
65. Base of ultimate segments mostly inequilaterally cordate; rhizome scales viscid; lamina $3-4$-pinnate, ultimate segments oblong to oblong-ovate; Nuevo León and Tamaulipas, south to Chiapas
66. N. formosa.
67. Indument of scales or hairs, or both, in addition to wax. 28 .
68. Indument on lower surface of lamina ceraceous and of large trichomes. 29.
69. Lower surface of the lamina and the rachis with large, brown, stiff trichomes; rhizome scales dark-sclerotic, rigid, strongly pectinate-ciliate; sporangia borne at the vein-ends; s. Texas to Puebla, Jamaica
70. N. Schaffneri.
71. Lower surface of the lamina and the rachis with filiform, weakish, whitish trichomes; rhizome scales thin, bright brown, entire; sporangia borne on the outer $1 / 2$ or $1 / 3$ of the veins; Morelos
72. N. pilifera.
73. Indument on lower surface of lamina ceraceous and of scales and sometimes also tomentose (in no. 31A the tomentum more evident than the few scales). 30.
74. Scales on lower surface of lamina long-ciliate or dissected. 31.
75. Lamina linear, its scales with a narrow central portion and long, slender branches, or stellate; pinnae entire or very shallowly (rarely deeply) lobed, lateral veins very oblique; West Indies
76. N. trichomanoides.
77. Lamina broader, the pinnae cut nearly to their rachis, lateral veins at a broad angle. 32.
78. Upper surface of lamina with stellate trichomes; Texas to s. Ariz. and Mexico. ... 27. N. Aschenborniana.
79. Upper surface of lamina with sparse, weak, simple hairs; Jalisco and San Luis Potosí's. to Oaxaca 28. N. Galeottii.
80. Scales on lower surface of lamina entire or nearly so. 33.
81. Wax orange; scales on lower surface of lamina large, broadly ovate; lamina pentagonal, the basal pinnae much the largest and strongly inequilateral; Jalisco
82. Wax white to yellow; scales on lower surface of lamina lanceolate, or narrower; lamina much longer than broad, the basal pinnae not much the largest nor strongly inequilateral. 34.
83. Upper surface of lamina somewhat ceraceous. 30. N. Grayi.
84. Upper surface of lamina with sparse hairs, slightly or not ceraceous. 35.
85. Lower surface of lamina scaly (many scales may be piliform but they do not form a tomentum), the upper thinly pubescent and sparingly ceraceous; rachis scaly, with the few hairs not forming a tomentum
86. N. aliena.
87. Lower surface of lamina tomentose, with only a few scales, the upper surface persistently (although in age thinly) tomentose, non-ceraceous; rachis scaly and tomentose

31A. N. Weatherbiana.

## 22. Indument of lamina wholly ceraceous. 36 .

36. All ultimate segments adnate for their whole breadth; rhizome scales dark-sclerotic, with or without pale margins. 37.
37. Lamina commonly longer than broad, the lowest pinnae not markedly larger than those immediately above nor strongly inequilateral. 38.
38. Stipe and rachis sulcate on the upper side. 39 .
39. Scales of the rhizome spinescent-ciliate, rigid; Cuba
40. Scales of the rhizome entire. 40.
41. Stipe and rachis blackish or castaneous, glabrate; lamina usually with a reduced pair of pinnae at base; s. Ariz. and Mexico
42. N. Lemmonii.
43. Stipe (except at base) and rachis stramineous, glandularpuberulent above; Guadalajara region, Jalisco
44. N. Rosei.
45. Stipe and rachis terete or angled. 41.
46. Rhizome scales spinescent-ciliate, rigid. 42.
47. Lamina linear to linear-lanceolate, the obtuse, deltoid to oblong pinnae with five (or fewer) pairs of lobes. 43.
48. Stipe usually bearing toward base lance-deltoid, longacuminate scales; rachis with short, weak, brown, nonglandular trichomes, at least on the upper side; both stipe and rachis blackish; Mexico and Central America.
49. N. affinis. 43. Stipe mostly without scales, like the rachis castaneous to pale brown and without trichomes; Cuba
50. N. cubensis.
51. Lamina oblanceolate, the deltoid-lanceolate, acute pinnae with 8-10 pairs of lobes; Nuevo León and Tamaulipas
52. N. rigida.
53. Rhizome scales entire, glandular-margined; Monterrey,

## Nuevo León

34. N. leonina.
35. Lamina often as broad as long, or broader, the lowest pinnae much the largest, deltoid and strongly inequilateral by the prolongation of the basiscopic pinnule on the lower side. 44.
36. Lamina above lowest pinnae fully pinnate, the rachis not winged, the pinnae decreasing in size upward. 45.
37. Scales of rhizome and base of stipe with entire to eroseciliate margins, glandular, if at all, only at apex; lamina in well-developed fronds ovate-pentagonal or narrower, not less than half as long as the stipe. 46.
38. Rhizome scales bright castaneous to brownish, they and the scales at the base of the stipe with very narrow pale margins; stipe castaneous; indument of lamina pale yellow to whitish; Galápagos Is 35. N. galapagensis. 46. Rhizome scales dark brown to blackish, they and especially those at the base of the stipe with broad pale margins; stipe blackish to black; indument of lamina white; s. Texas to central Mexico
39. N. candida.
40. Scales of rhizome and base of stipe with erose-denticulate, deciduously glandular margins; lamina broadly pentagonal, usually not more than a third as long as the stipe; Mexico to Chile
41. N. sulphurea. 44. Lamina above lowest pinnae usually pinnatifid, the lower pinna-segments usually shortened; indument of lamina commonly yellow; sw. United States and Mexico. 38. N. Standleyi. 36. At least some of the ultimate segments constricted and petiolulate at the base, not adnate for their full breadth; rhizome scales various but most often thin, bright brown, concolorous. 47.
42. Lower pinnae much the largest, strongly inequilateral, the basiscopic pinnule much produced; rhizome scales with sclerotic center and pale margins. 48.
43. Lamina broadly pentagonal, acute; stipe and rachis castaneous; pinnules glandular on upper surface, their margins crenulate and rather slightly revolute; sw. Ariz., s. Calif. and Baja Calif.
44. N. californica.
45. Lamina narrowly deltoid, long-acuminate; stipe and rachis blackish; pinnules glabrate on upper surface, their margins entire, strongly revolute; se. Ariz., s. Texas and adjacent Mexico
46. N. neglecta.
47. Lower pinnae not much the largest nor strongly inequilateral; rhizome scales usually non-sclerotic, concolorous. 49.
48. Stipe and rachis sulcate; pinnae acuminate with numerons, approximate, small, cordate-based, mostly simple pinnules with strongly revolute margins. 50 .
49. Rhizome scales subulate, with sclerotic central hand and pale, entire margins, those of the stipe lance-ovate; lamina about equalling stipe....................42. N. Greggii.
50. Rhizome scales linear, bright brown and subconcolorous with subsclerotic central band, those of the stipe subulate; lamina longer than stipe ............. 43. N. bryopoda.
51. Stipe and rachis terete; pinnae acute or obtuse, with mostly compound and not crowded pinnules with plane or slightly revolute margins; rhizome scales non-sclerotic (rarely sub-
sclerotic), bright brown and concolorous. 51.
52. Ultimate segments non-articulate, the dark color of the stalk passing at least into the basal part of the segment, or the segments sessile. 52.
53. Rachis and pinna-rachises markedly flexuous, the branching of the pinnae and the upper part of the lamina appearing dichotomous; s. Wyo. to s. central N. Mex.
54. N. Fendleri.
55. Rachis and pinna-rachises straight or essentially so, the branching obviously pinnate. 53.
56. Most primary pinnules subpetiolulate or sessile. 54.
57. Stipe and rachis blackish. 55.
58. Rachis glabrate, without scales; scales of the stipe ovate, relatively short-acuminate; San Luis Potosí.
59. N. Palmeri.
60. Rachis ceraceous-glandular, with a few small, brown to pale brown scales; scales of the stipe lance- or linear-attenuate; s. Baja Calif.
61. N. peninsularis. 54. Stipe and rachis castaneous to dark castaneous. 56.
62. Rachis ceraceous-glandular, with a few small, reddish scales; upper surface of segments ceraceousglandular; Mexico
63. N. pallens.
64. Rachis slightly ceraceous-glandular to glabrous, without seales; upper surface of segments glabrous; Juan Fernández Is. .......47. N. chilensts.
65. Most primary pinnules long-petiolulate. 57.
66. Stipe comparatively stout, it and the rachis reddishbrown to blackish; segments coriaceous, the veins not visible; Utah s. to n. central Mexico
67. N. limitanea.
68. Stipe slender, it and the rachis bright chestnut brown; segments subherbaceous, the veins usually visible; Nebr. to Mo. and s. central Texas .. 52. N. dealbata.
69. Ulimate segments articulate, the dark color of the stalk stopping abruptly in a transverse line at its apex. 58.
70. Ultimate segments herbaceous, often cuneate at the base, usually ceraceous-glandular on the upper surface; stipe castaneous to dark reddish-brown; veins sporangiferous for nearly their whole length; spores rugose; Coahuila and Nuevo León. ......... 54. N. delicatula.
71. Ultimate segments usually coriaceous, commonly truncate to subcordate at the base, glabrous on the upper surface. 59.
72. Stipe blackish; veins usually sporangiferous for their whole length; spores minutely and inconspicuously roughened; Mexico and Central America, Hispaniola.
73. N. incana.
74. Stipe light to dark castaneous; veins usually sporangiferous only on their outer third or half; spores strongly rugose; Colombia to Argentina and se. Brazil
75. N. nivea.
76. Notholaena peruviana Desv. Prod. 220. 1827. Weath. Lilloa 6: 273. 1941. тype: Peru, Dombey r!, photo gh!, fragment Bl.

Fig. 1. Map 2.
Cheilanthes peruviana (Desv.) Moore, Ind. Fil. 250. 1861.
Notholaena sinuata var. bipinnata Hook. Sp. Fil. 5: 108. 1864. type: Baños, Andes of Peru, Brackenridge (Wilkes Exped.), k!, photo ch!.

Notholaena Brackenridgei Baker, Syn. Fil. 371. 1868. type: Peru, Brackenridge (evidently the same specimen as above).

Rhizome erect, stout; scales linear-ligulate, long-attenuate to a capillary tip, tortuous and crisped in drying, with the margins entire or


Maps 1-4. Map 1, Notholaena in America. Map 2, N. peruviana. Map 3, N. arequipensis. Map 4, N. squamosa.
nearly so. Fronds $13-30 \mathrm{~cm}$. tall; stipe somewhat shorter than the lamina, with one vascular bundle. Lamina narrowly lanceolate, not narrowed below, with 8-13 pairs of pinnae, bipinnate, texture coriaceous, the veins immersed, upper surface with a few scattered scales, lower surface densely covered with imbricate, dark brown, lanceolate to ovate, somewhat pectinate-serrulate scales, their cells oblong or a little narrower, the cell walls comparatively thick and brown, the lumen lighter colored. Pinnae triangular-ovate, completely pinnate in the lower part. Veins simple or once-forked, the sporangia (with 32 spores) borne on the rather punctiform vein-ends, the margin modified, narrow, often lobed.
$N$. peruviana is very close to the next species, N. arequipensis, but appears to be separable from it. Although the degree of modification of the margin varies in N. peruviana, it does not actually intergrade with $N$. arequipensis.

Rocky places and in crevices of rocks, ca. 3000 m., Peru. Such specimens as Cuming (bм, ny) and Miller (bм) from Chile were probably not collected within the present boundaries of that country. Looser ${ }^{1}$ does not report it.

Representative specimens: Peru. Matthews 604 (bм, G, к) ; Weberbauer 1528 (в); Dombey (в, Р); Cuming 939 (к); Brackenridge (Wilkes Exped.) (к, us). Lima: Safford 999 (p, us), 1000 (Us); Macbride \& Featherstone 284 (F). Arequipa: Dora Stafford 824, 933 (вм).
2. Notholaena arequipensis Maxon, Smiths. Misc. Coll. 65: 9. 1915. Weath. Lilloa 6: 271.1941. type: near Arequipa, Peru, Aug. 15, 1914, Rose \& Rose 18797 us!, photo ch!.

Fig. 2. Map 3.
Rhizome erect or ascending, 1 cm . or less in diameter; scales vellowish brown to bright castaneous, linear, long-attenuate, distantly denticulate, the teeth minute, low, acutish, cells oblong to linear, thinwalled. Fronds numerous, up to 8 cm . tall; stipes somewhat longer than lamina, terete, with a single vascular bundle, castaneous, sub-appressed-paleaceous. Lamina deltoid-oblong, obtuse or acutish, bipinnate, upper surface with a few pale, lax, tortuous, flattish, linear, mostly deciduous scales, lower surface densely covered with large, widely imbricate, appressed, ovate-oblong, long-acuminate, light reddish-brown, erose-denticulate scales, their cells large, elongatepolygonal, the central ones of the lower portion with colored, sclerotic partition walls. Pinnae about 4 pairs, petiolate, the basal pair the largest, rounded-deltoid, with 2-3 pairs of segments below the trilobate or tripartite obtuse apex, the basal segments sessile, triangular, pin-

[^0]

Fig. 1-4. Fig. 1. N. perctiana: A, frond, X 0.5; B, underside of segments, X 4.5; C, scale from underside of segment, X 9; all from $/$. B. Stecre (mo): D, scale from rhizome, X 4.5, from Macbride \& Featherstone 421 (F). Fig. 2. N. arequipensis: A, frond, X $0.5 ; \mathrm{B}$, segment, X 4.5 ; both from Pennell 13116 ( F ). Fig. 3. N. squamosa: A, frond, X $0.5 ; \mathrm{B}$, segment, X $4.5 ; \mathrm{C}$, scale from underside of segment, X 9, D, scale from rhizome, X 4.5; all from Castillón 11615 (GH). Fig. 4. N. lonchophylla: A, frond, X 0.5 ; B, scale from underside of segment, X 9 ; C. segment, X 4.5; D, scale from rhizome. X 4.5; all from Matheu's 610 ( K ).
nately lobed or parted, the other simpler, subsessile. Veins once-forked or simple, sporangia (with 32 spores) borne on clavate or abruptly and laterally dilated vein-ends close to the somewhat revolute, unmodified margin.

A critical species, at present sufficiently separable from N. peruviana, but more ample material may not uphold such a treatment. Rocky places and in crevices of rocks, 2300-3500 m., southern Peru to northwestern Argentina.

Specimens seen: Peru. Arequipa: Rose \& Rose (Mr. d Mrs. J. N.) 18797 (US); R. S. Williams 2638 (GH, NY, us); Jaffriel 2561 (GH). Chile. Arica: 1948, O. Barros V. (Looser). Argentina. Jujuy: R. E. Fries 698 (us).
3. Notholaena squamosa (Hook. \& Grev.) Lowe, Ferns Brit. \& Exot. 1: 49. 1856, as to basonym, not as to plant figured. Weath. Lilloa 6: 268. 1941.

Fig. 3. Map 4.
Cheilanthes squamnsa Gill. ex Hook. \& Grev. Icon. Fil. t. 151. 1829. type: Cerro del Morro (San Luis), Argentina, March, 1828, Gillies, e, isotype k !.

Notholaena Gilliesii Fée, Gen. Fil. 159. 1850-52, based on C. squamosa.

Pellaea Lilloi Hicken, Anal. Soc. Cient, Argent. 62: 210. 1906 (reprint, 1907, page 20). type: Tucumán, Argentina, Lillo 5021 si!, photo GH !. In all technical characters this agrees with N. squamosa; it appears to be only a dwarfed and aberrant state of that species.

Notholaena Lilloi Hicken, Apuntes Hist. Nat. Buenos Aires 1: 117. 1909, based on P. Lilloi Hicken.

Rhizome short, erect or oblique; scales thick, subsclerotic, linear, tapering to a long capillary point, chestnut-brown, pectinate-serrulate, the teeth often antrorse, composed of very narrow, dark-walled cells. Fronds numerous, densely cespitose, up to 3 dm . tall; stipe from half as long to somewhat longer than lamina, terete, with a single vascular bundle, brown lustrous, when young covercd with pale, erose-serrulate scales in size and texture similar to those of blade, in age glabrate. Lamina coriaceous, oblong-lanceolate to broadly ovate, subabruptly narrowed to an obtuse apex, the lower pinnae slightly or not at all reduced, bipinnate except near apex, upper surface with sparse piliform scales or rarely glabrate, lower surface densely covered with soft, imbricate, brown, lance-ovate to ovate, pectinate-fimbriate, caudatetipped scales composed of narrowly to broadly oblong cells with large, pellucid lumina, no small, dissected scales beneath the larger ones. Pinnae 5-8 pairs, oblong or ovate-lanceolate, subobtuse, pinnules oblong, broadly obtuse, truncate or subcordate at base, entire or the larger with a pair of lobes at base. Veins often simple, the sporangia
(with 32 spores) borne on their clavate to subpunctiform tips, the margin slightly revolute, unmodified.

This species was long referred to as Notholaena scariosa. However, C. A. Weatherby has discussed the misapplication of that name ${ }^{2}$ which properly becomes Cheilanthes scariosa (C. ornatissima Maxon).

Crevices of rocks, eastern slope of the Andes from southern Bolivia to San Luis and reported by Hicken ${ }^{3}$ from Sierra de Ventana.

Representative specimens: Bolivia: Mecoya, April, 1864, Pearce ( $\mathbf{x}$ ); Fiebrig 3122 (в, BM, G, GH, K, P). Argentina. Jujuy: Budin (GH, LiL); Castillón 24 (GH, lil). Salta: Lorentz \& Hieronymus 140 (B, BM); Venturi 6829 (us). Tucumán: Rodríguez 414 (GH, LiL); Lorentz 299, 782 (в); Venturi 3120 (GH, us); Castillón 25, 28 (Lil), 29, 653 ( $\mathbf{G H}$, lil). Catamarca: Castellanos 30/312 (Gh); Lorentz 178 (b); Schickendantz 362 (в). La Rioja: Hieronymus \& Lorentz 440 (в). San Luis: March, 1828, Gillies (k).
4. Notholaena lonchophylla Weath. ms. spec. nov.

Fig. 4.
Rhizoma breve horizontale vel adscendens, paleis lineari-ligulatis pallide castaneis concoloribus apicem versus tortuosis sparse antrorseque denticulatis cellulis angustis elongatis parietibus tenuibus dense obtectum. Frondes approximati, stipes subcrassus $3-4 \mathrm{~cm}$. longus quam lamina multo brevior subpallide brunneus, paleas deciduas eis laminae similes gerens. Lamina lanceolata $9-11 \mathrm{~cm}$. longa $2-2.6 \mathrm{~cm}$. lata coriacea pinnato-pinnatifida vel bipinnata basi vix angustata superne in apicem obtusim gradatim angustata, pagina superiore paleis albis piliformibus (vix applanatis) basi subpustulatis sparsi obsita caetera glabra, inferiore dense paleacea, paleae ca. 2 mm . longae linearisubulatae longe acuminatae subpallide brunneae vel albescentes pecti-nato-dentatae, dentibus longis e basi dilatato angustissimis subpiliformibus, cellulis oblongis lumina magna parietibus crassis. Pinnae ad 20 jugae oblongae obtusae profunde pinnatifidae vel pinnatae superne sessiles inferne petiolulatae lobis vel pinnis oblongis late obtusis integris basas latitudine tota adnatis vel basalibus plus minusve petiolulatis lobatis. Sori transverse in oblongis apicibus nervorum subdilatatis ad marginem extremum immutatum gesti.

Specimen examined: Peru: 1835, Matthews 610 (k, photo GH).
5. Notholaena sinuata (Sw.) Kaulf. Enum. Fil. 135. 1824. Weath. Lilloa 6: 258. 1941; Journ. Arn. Arb. 24: 315. 1943. Map 5.

Rhizome short, horizontal, $3-5 \mathrm{~mm}$. thick; scales castaneous, linear

[^1]or linear-subulate, soft, pectinate-ciliate to entire, composed of elongate cells with narrow lumina. Fronds closely approximate, up to 4.5 dm . tall; stipe stout, terete, at maturity usually less than $1 / 4$ length of blade, with two vascular bundles, castaneous, densely and usually persistently clothed with linear, whitish, strongly pectinate scales. Lamina linear, pinnate-pinnatifid, the upper surface sparsely beset with narrow, whitish, very strongly pectinate scales like those of the stipe (sometimes reduced to stellate processes), or glabrate, lower surface thickly covered with castaneous or pale brown, imbricate, deltoid to lanceolate, acuminate, short-fimbriate scales composed of elongate cells, overlying a dense tomentum of smaller scales dissected into long, capillary segments; rachis similarly scaly. Pinnae numerous, 12 or more pairs, shortpetiolulate, broadly oblong to deltoid-ovate or subquadrate, subacute to obtuse, up to 2 cm . long and 1 cm . broad, entire or cut to about halfway to the costa into $4-6$ pairs of deltoid to oblong, obtuse entire lobes. Veins 1-2-forked, leaving costa and forking at acute angles, sporangia (with 32 spores) borne along the terminal portion of the unmodified veins, margin unmodified.

The two vascular bundles in the stipe serve to distinguish this species in addition to the characters mentioned in the key.

In the United States and Mexico one variety sometimes grows with or near one or both of the others and correspondingly mixed collections are not infrequent. In the lists of cited specimens I have included only those herbaria in which I have seen the collection unless there is no doubt as to its uniformity.

Crevices of cliffs, rocky banks and hillsides, apparently preferring limestone, but recorded also from sandstone, lava and granite, from about 300 m . to 3000 m ., southwestern United States, south along the Cordillera to northwestern Argentina; Hispaniola.

## KEY TO VARIETIES

Pinnae 1 cm . or more long, ovate, commonly subacute and cut $1 / 3-1 / 2$ to the midrib into 4-6 pairs of oblong lobes; scales of the upper surface of the lamina with narrow central portion or reduced to stellate processes, usually soon deciduous, those of the lower surface lanceolate, up to 1.5 mm . long; rhizome scales pectinate-ciliate or serrulate 5a. var. sinuata. Pinnae mostly less than 1 cm . long, very obtuse, with $1-3$ pairs of broadly ovate lobes or entire; scales of the upper surface with relatively broad central portion usually persistent till full maturity of the frond.
Pinnae oblong, entire or with about 3 pairs of shallow lobes; scales of lower surface and rhizome as in var. sinuata ...5b. var. integerrima. Pinnae subquadrate, nearly or quite as broad as long, with 1 or 2 (rarely
3) pairs of lobes; seales of the lower surface ovate, 0.5 mm . long; rhizome scales entire or nearly so

[^2]
## 5a. Notholaena sinuata var. sinuata

Fig. 5a. Map 5 (South America) and Map 6.
Acrostichum sinuatum Lag. ex Sw. Syn. Fil. 14. 1806. type: not seen but identity not doubtful.

Notholaena Tectaria Desv. Mém. Soc. Linn. Paris 6: 219. 1827. type: Peru, p!, photo Gh!, see Weath. in Contrib. Gray Herb. 114: 29. 1936.

Gymnogramma sinuata (Sw.) Presl, Tent. Pterid. 219. 1836.
Notholaena chalcolepis A. Br. ex Kze. Linnaea 13: 135. 1839. type: Mexico, 1827, Karwinsky, B!, photo GH!, (data from isotype at $\mathbf{P}$ !, photo $\mathbf{G H}$ !).

Notholaena laevis Mart. \& Gal. Mém. Acad. Bruxelles 15: 46.1842. type: Galeotti 6350, br!, the type consists of three small, old fronds, with the scales weathered off the upper surface and the pinnae quite as deeply lobed as is usual in dwarfed individuals of var. sinuata.

Notholaena sinuata var. integra Liebmann, Vid. Selsk. Skr. (Mexicos Bregner) 5: 213. 1849, based on N. laevis.

Notholaena sinuata var. laevis (Mart. \& Gal.) Hook. Bot. Mag. 74: t. 4599. 1853, as to name, not as to plant figured.

Notholaena crassifolia Moore \& Houlst. Gard. Mag. Bot. 3: 20. 1851. (Lowe, Ferns Brit. \& Exot. 1: t. 14 A. 1856). Type: spec. cult. Henderson.

Notholaena pruinosa Fée, Mém. Fam. Foug. 8: 78. 185̃7. type: Mexico, Schaffner 167 c.

Gymnogramma sinuata var. integra (Liebm.) Mett. Cheil. footnote 7. 1859.

Notholaena sinuata var. pruinosa (Fée) Fourn. Mex. Pl. 1: 120. 1872.

Notholaena deltoidea Baker, Syn. Fil. ed, 2. 514. 1874. type: Mexico, Leybold k!, photo ch!, the specimen is a juvenile state of $N$. sinuata.

Cheilanthes sinuata (Sw.) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Cheilanthes deltoidea (Baker) Domin, Bibl. Bot. 20 (Heft 85) : 133. 1913.

Notholaena sinuata var. pinnatifida Farw. Amer. Midl. Nat. 12: 283. 1931. Type: Bear Mts., New Mexico, Oct., 1880, Rusby B 1 (місн).

Notholaena sinuata f. pinnatifida (Farw.) Broun, Ind. N. Amer. Ferns, 120. 1938.

In central and northeastern Mexico a phase with entire pinnae occurs (for example, Stanford et al. 2616 and Lyonnet 94 and 1582) which has not been recognized in this treatment although later evidence may indicate it should be a variety or form. Notholaena crassifolia and N. pruinosa were described on the


Maps 5-7. Map 5, N. sinuata (all in South America is var. sinuata). Map 6, var. sinuata (north of South America). Map 7, var. integerrima. Map 8, var. cochisensis.
basis of this phase and some later authors misapplied the name $N$. laevis to it.

Texas to Arizona, south to northwestern Argentina; Hispaniola. Some specimens labeled as collected in Chile were evidently not taken within the present boundaries of that country. Looser ${ }^{5}$ does not report it.

Representative specimens: United States. Texas: E. J. Palmer 11235 (bм, GH, мо); Lindheimer 505 (Gн, мо), Exsicc. 1277 (GH, мо); Wright 814 (BM, GH, MO) ; Moore \& Steyermark 3017 (GH, MO); Jermy 344 (MO); Mueller 8263 (GH); Waterfall 4571, 4806 (GH, MO). New Mexico: Metcalfe 953 (mo); Maguire et al. 11926 (Gн); Wooton 101 (b, gh, mo). Arizona: W. W. Brown 19 (Gh, mo); Goodding 2387a (GH, MO); Palmer 274 ( MO); M. E. Jones 24681 (GH, MO); Blumer 1527, 2142, 3272 (Gh). Mexico. Baja California: Carter et al. 2047 (мо); Shreve 7048 (Gh, mo). Sonora: Hartman 81, 130 (GH); Gentry 1195 (сн, к, мо); Shreve 6747 (мо). Chinuahta: Palmer 82 (GH). Coahuila: Wynd \& Mueller 510 (GH, mo); Johnston 9097 (GH, мо); Palmer 1400 (GH, мо); Stanford et al. 105, 20.3 (GH, мо). Tamaulipas: Stanford et al. 663 (Gh, mo), 2616 (mo); Palmer 190 (Gh, mo). Sinaloa: Gentry 5844 (Gh, mo). Durango: Palmer 462 (b, GH, MO), 883 (b, bм, GH, mo, us). Zacatecas: Lloyd \& Kirkwood 23 (мо), 136 (сн). San Luis Potosí: Schaffner 947 (ch); Parry d Palmer 995, 996 (Gh, mo), 997 (mo). Querétaro: Arsène 10646 ( $\mathbf{G h}, \mathrm{mo}$ ). Hidalgo: Pringle 11269 ( $\mathrm{B}, \mathrm{Gh}, \mathrm{mo}, \mathrm{p}, \mathrm{us}$ ). Distrito Federal: Lyonnet 94 (Gh, mo), 1582 (Gh). Puebla: Rosenstock Fil. Mex. Exsicc. 35 (mo). Veracruz: Purpus 904.3 (Gh, mo, us); Bourgeau 2770 (Gh). Guerrero: Hinton 9724 (Gh, mo). Oaxaca: C. L. Smith 2027 (mO); Conzatti 837 (GH, P). Chlapas: Ghiesbreght 212 (bm, GH, y); Schumann 1880 (P). Guatemala: Skutch 1149, 1964 (Gн); Seler 3039 (в). Costa Rica: Bernoulli \& Cario 239 (в, р) ; Warszewicz 48 (в). Haiti: Leonard 7831 ( $\mathrm{GH}, \mathrm{us}$ ). Dominican Republic: H. von Schrenk 46 (mo). Venezuela: Tamayo 263 (us); Engel 139 (b); Mocquerys 1115 (P); Linden 511 (bм, P). Colombia: Stübel 222 (b); Mutis 2779 (us). Ecuador: Mille 269 (p); Stiibel 728 (в); Jameson 6 (bм); Rose d Rose 2.3968 ( $\mathrm{GH}, \mathrm{us}$ ). Peru. Huánuco: Macbride 3190 (F, US); Macbride \& Featherstone 2310 ( $\mathrm{F}, \mathrm{GH}, \mathrm{US}$ ). Junín: Killip \& Smith 21808 (us). Lima: Goodspeed 11.307 (GH, mo); Macbride \& Featherstone 282 ( F , us). Cuzco: Stork, Horton \& Vargas 10449 (mo). Arequipa: Pennell 13071 (F, GH). Bolivia: Buchtien 3114, 3115 (us) ; Steinbach 5045 (GH); Bang 786 (B, GH, mo, us); Julio 97 (Gh, us); Herzog 1223 (в). Argentina. Jujuy: Burkart \& Troncoso 11461 (mo). Salta: Hieronymus d Lorentz 195 (b). Tucumán: Lorentz 217 (b), 218 (b, us); Venturi 838 (ch, lil, us). Catamarca: Castillón 11622 (Gh).
${ }^{5}$ Looser, G., "El 'Notholaena' en Chile," Darwiniana 7: 62. 1945.

5b. Notholaena sinuata var. integerrima Hook. Sp. Fil. 5: 108. 1864. Weath. Journ. Arn. Arb. 24: 313. 1943. type: Mexico, Liebmann k!, photo $\mathbf{~ G H !}$.

Fig. 5b. Map 7.
C. A. Weatherby (l.c.) has discussed the general misapplication of Hooker's name to what is now known as var. cochisensis, the proper choice of type and his redefinition of the variety.

Southern Oklahoma to Arizona south to Veracruz.
Representative specimens: United States. Oкlahoma: 1925, F. C. Greene (Gн); April 20, 1928, Featherly (mo). Texas: Lindheimer 414, Exsicc. 1278 (GH, мо); Cory 869, 29692, 43284 (GH); E. J. Palmer 11791 (GH, мо); Wright 815 (GH, mO, us); Waterfall 4838 (Gн, мо); Reverchon 1184 (мо); Tracy 8051, 8321 (мо); Jermy 674 (мо). New Mexico: Earle \& Earle 564 (mo); Eastwood 8268 (GH); Goodman 2329 (Gh, mo). Arizona: Palmer 275 (mo); Blumer 1530 (GH, MO); Goodding 373 (GH); Eggleston 10972, 10982 (GH); W. W. Brown 18 (Gh, mo). Mexico. Sonora: S. S. White 4585 (Gh). Chihuahua: Pringle 464 (Gн, mo). Coahulla: Gregg 297 (мо), 365 (GH, мо); Palmer 1406 (Gн), 1407, 1409 (GH, мо); Wynd \& Mueller 321 ( $\mathrm{gh}, \mathrm{mo}$ ); Stanford et al. $429 a$ ( $\mathrm{Gh}, \mathrm{mo}$ ). Nuevo León: Mueller d Mueller 1071 (GH); Palmer 1404 (Gh, mo). Durango: Gentry 8323 (Gh). Zacatecas: Lloyd \& Kirkwood 24 (mo), 137 (Gh). San Luis Potosí: Johnston 7573 (Gh); Palmer 447 (bm, gh, mo). Hidalgo: M. T. Edwards 712 (mo). Veracruz: Aug. 9, 1924, Fisher (mo).

5c. Notholaena sinuata var. cochisensis (Goodd.) Weath. Journ. Arn. Arb. 24: 314. 1943.

Fig. 5c. Map 8.
Notholaena sinuata var. crenata Lemmon, Ferns Pacific Slope 7. 1882 , nomen nudum.

Notholaena cochisensis Goodd. Muhlenbergia 8: 93. 1912. type: Montezuma canyon, Huachuca Mts., Arizona, Aug. 1910, Goodding 373.

Notholaena sinuata f. crenata (Lemmon) Clute, Fern Bull. 15: 46. 1915.

This variety was long called var. integerrima; C. A. Weatherby (l.c.) has discussed the reapplication of the name. This has been reported as poisonous to stock and this property might reinforce its morphological characters sufficiently for specific status were it not for its intergradation with var. integerrima.

Texas to southern California, south to Aguascalientes.
Representative specimens: United States. Texas: Waterfall 3909 (GH), 4447 (GH, MO) , 4543,4741 (GH), 4794 (GH, MO), 4969 (GH), 5043 (GH, мо) ; Reverchon 1184 (GH); E. J. Palmer 34167 (GH, мо); Moore \& Steyermark 3240 (GH, MO); M. E. Jones 5133 (GH); Cory


Fig. 5-7. Fig. 5. N. sinuata: 5a. var. sinuata: A, frond, X 0.5: B, segment, X 4.5; C, sorus, enlarged; D, scale from upper surface of pinna, enlarged: all from Wooton in 1895 (mo). 5b. var. integerrima: scale from underside of pinna, X 9. from Cory in 1938 (мо). 5c. var. cochisensis: A, frond, X 0.5; B, scale from underside of pinna, X 18; C, scale from upper surface of pinna, enlarged; all from Stanford et al. 355 (м0). Fig. 6. N. brachypus: A, frond, X (0.5, from Pringle 1787 (mo); B, underside of segments, X 4.5, from Shimek (мo): C. segment, X 4.5, from Pringle 1787 (mo). Fig. F. N. Hassieri: A, frond, X ().5: B, upper surface of segment, X 4.5; C, segment, X 4.5; all from Hassler 10996 (мо).

871, 873, 874 (GH). New Mexico: Metcalfe 954 (mo); Waterfall 3733 (GH, mo). Arizona: Eastwood 5971 (GH); Blumer 1522 (b, GH, mo, us); Goodding 373 (GH); Thornber 2051 (GH); Phillips 2615 (Gh); Palmer 276 (mo). Nevada: April, 1924, Hewett (us). California: Munz et al. 3550, 4224 (us). Mexico. Sonora: Hartman 25 (Gн). Chihuahua: Johnston 7853, 7880a (GH); Palmer 357 (GH, мо); Harvey 1358 (Gh, мо). Coahuila: Wynd \& Mueller 659 (GH, мо); Gregg 297 (Gн); Stanford et al. 42, 194, 355 (GH, Mo); Wynd 745 (GH, MO); Johnston 9096 (GH, Mo); Palmer 359 (GH, MO), 1401 (GH), 1405 (GH, P, US), 1408, 1410 (GH). Durango: Johnston 7792 (GH). Zacatecas: Lloyd \& Kirkwood 138 (Gh, mo); Stanford et al. 548 ( $\mathrm{GH}, \mathrm{mo}$ ). Aguascalientes: Rose \& Painter 7720 (GH, us).
6. Notholaena brachypus (Kze.) J. Sm. Ferns Brit. \& For. 172. 1866.

Fig. 6. Map 9.
Cheilanthes squamosa var. brachypus Kze. Linnaea 18: 340. 1844. TYPE: Mexico, Leibold 52, b!, photo of specimen at $\mathbf{k}$, GH!.

Cheilanthes brachypus Kze. Linnaea 18: 341. 1844, nomen provisorium; Linnaea 23: 307. 1850.

Rhizome short, thick, erect; scales linear-attenuate, brown or castaneous, capillary-tipped, entire or somewhat pectinate-serrulate. Fronds $4-28 \mathrm{~cm}$. tall; stipe usually very short or obsolete, with one vascular bundle. Lamina narrowly elliptic or lance-elliptic, gradually narrowed below, pinnate-pinnatifid with 10-21 pairs of pinnae, under surface with dense, rusty, lanate tomentum beneath the imbricate, ovate-lanceolate, long-attenuate, entire or somewhat serrulate scales, upper surface with thin tomentum of similar hairs, rachis brown, covered with scales similar to those of the lamina. Pinnae lanceolate, obtuse or acutish, the median deeply cut into 5-10 pairs of oblong, obtuse lobes. Veins simple or once-forked, sporangia (with 32 spores) borne on their dilated ends, margin modified into a hyaline band somewhat incurved over the sporangia.

The short stipe, dense tomentum beneath the scales on the under surface and the modified margin are characteristic of this species.

Damp shaded banks, rocky places and on rocks, 200-1600 m., central Mexico, Sinaloa to Veracruz; Guatemala to Costa Rica.

Representative specimens: Mexico. Leibold 52 (b, к). Sinaloa: Oct. 31, 1904, Brandegee (us). San Luis Potosí: Parry \& Palmer 998 (GH, K, us, y). Tepic (Nayarit): Mexia 511 (bm, us), 769 (G); Pennell 19940 (us). Jalisco: Pringle 1787 (b, bм, F, G, GH, K, мо, P, US, Y), 11784 ( $\mathbf{B}, \mathbf{F}, \mathbf{G H}, \mathbf{K}, \mathbf{P}$, US); Palmer, all in 1886, 57 (GH, US, Y), 80 (BM, GH, K, P, US, Y), 733 (BM, K, P, US, Y); R. S. Ferris 5814 (GH, us); Rose \& Painter 7314 (us). Colima: Palmer 1230 (GH, K,
us, y). Michoacán: Arsène 42 (b, bm, p). Morelos: Pringle 11785 (GH, P, Us); Deam 31 (GH, US); Rose, Painter \& Rose 6875 (GH). Veracruz: Purpus 5693, 7870 (us). Guatemala: Muenscher 12120 (US); Standley 58224 ( $\mathbf{F}$ ); Lehmann 1691 (в, вм, к, us); Salvin d Godman 1862 (к); Heyde \& Lux 3200 (в, GH, к, US), 4091 (GH, мо, P, US); Tuerckheim 8825 (P). Salvador: Padilla 168 (Us); Standley 20948, 21328 ( $\mathrm{GH}, \mathrm{US}$ ), 22536 (US); Calderón 1785 (GH, US). Nicaragua: Lévy 1131 ( $\mathbf{B}, \mathrm{F}, \mathrm{P}$ ); Jimenez 349 (US); Chaves 287 (Us); Maxon 7656 ( $\mathrm{ch}, \mathrm{us}$ ), 7676 (us); Maxon, Harvey \& Valentine 7622 (us). Costa Rica: C. Hoffmann 666 (в); Brenes 15699 ( $\mathbf{F}$ ); Brade 359 (NY).
7. Notholaena Hassleri Weath. Lilloa 6: 274, pl. iv. 1941. type: Paraguay, Hassler 10996 к!, photo ch!.

Fig. 7. Map 10.
Rhizome horizontal or ascending, short; scales linear-subulate, ca. 2.5 mm . long, at least the older with shining dark brown or blackish sclerotic central band and well-developed, pale brown, minutely and closely serrulate hyaline margin. Fronds densely and irregularly clustered, $8-20 \mathrm{~cm}$. tall; stipes stout, about as long as or somewhat shorter than the lamina, terete, blackish-castaneous, with one vascular bundle, densely beset with lance-ovate, acuminate, cordate-based, pectinate-serrulate, thin, brownish to whitish scales with large translucent thin-walled oblong cells. Lamina lanceolate or oblong-lanceolate, not narrowed at base, above rather abruptly contracted to an acute pinnatifid apex, bipinnate-pinnatifid or subtripinnate at base; rachis on both surfaces and costae and costulae beneath densely beset with scales like those of the stipe, leaf-tissue otherwise glabrous on the lower surface, on the upper rather sparsely beset with short, thick, whitish, moniliform trichomes with very short cells. Pinnae 8-10 pairs, the lower rather distant, oblong, or linear-oblong (or the lowest narrowly subsessile), obtuse to acutish, pinnules deltoid-ovate, obtuse. Veins simple, sporangia borne on the outer third of the slightly or not at all thickened veins which stop just short of the somewhat modified (with short, rounded, hyaline lobes) margin.

Specimens examined: Paraguay: Hassler 10996 (b, BM, G, K, мо), 12980 ( P )
8. Notholaena venusta Brade, Anais Prim. Reun. Sul-Amer. Bot. 2: 7, t. 4, figs. 1, 2. 1940. Weath. Journ. Arn. Arb. 27: 363. 1946. type: Diamantina, Minas Geraes, Brazil, June, 1934, Brade 13494 rb, not seen.

Fig. 8. Map 11.
Notholaena capillus St. Hilaire in herb.; ex Christ, Bull. Herb. Boiss. II. 2: 381. 1902, pro syn. based on St. Hilaire B' 1220.

Rhizome about 2 mm . in diameter; scales about 2 mm . long, sometimes serrulate toward the apex with narrow, ascending teeth. Fronds $3-20 \mathrm{~cm}$. tall; stipe terete, $0.4-0.5 \mathrm{~mm}$. in diameter, $6.5-9 \mathrm{~cm}$.


Maps 9-11. Map 9, N. brachypus. Map 10, N. Hassleri: Map 11, N. venusta.
long, castaneous, shining, with one vascular bundle. Lamina pentagonal to somewhat elongate-deltoid, $3-4 \mathrm{~cm}$. long, $2-3 \mathrm{~cm}$. wide, commonly fully pinnate to about the third pair of pinnae from base; tomentum of the upper surface grayish, of slender, tortuous and matted long hairs, that of the lower surface rufous, of similar hairs underlaid by a dense felt of shorter and finer hairs, rachis castaneous. Basal pair of pinnae deeply pinnatifid and more or less inequilateral by the elongation of the basal segment on the lower side, their divisions oblong, obtuse, entire or the developed basal segment shallowly undulate-lobed; median pinnae oblong or linear-oblong, entire or shallowly lobed, rather distant, decreasing rather gradually to a somewhat prolonged, obtuse, narrow, pinnatifid lamina-apex. Veins immersed, ultimate veinlets 1-2-forked, sporangia (with 64 spores) borne on the rather abruptly dilated, somewhat flabellate tips at or very near the unmodified margin.

Eastern Brazil.
Specimens seen: Brazil. Minas Geraes: St. Hilaire B' 1220 ( $\mathbf{p}$, photo GH); Magalhães Gomes 1099 ( P ); Schwacke 14250 (GH, P). Piauhy: 1836, Gardner 2392, in part ( P ).
9. Notholaena eriophora Fée, Gen. Fil. 159, t. 13, fig. 3. 1850-52. Weath. Journ. Arn. Arb. 27: 365. 1946. type: Shady cliffs on the hills near Oeiras, Piauhy, Brazil, March, 1839, Gardner 2.390, at rb?, not seen, isotypes! (see below).

Fig. 9. Map 12.
Notholaena palmatifida Kze. Farnkr. 1: 148. 1844, nomen nudum. Based on Gardner 2390.

Polypodium eriophorum (Fée) Hook. Ic. Pl. 10: t. 991 (Cent. Ferns t. 91). 1854.

Cheilanthes eriophora (Fée) Mett. Cheil. no. 14. 1859.


Fig. 8-11. Fig. 8. N. venusta: A, frond, X 0.5: B, trichomes on stipe, enlarged; C, segment, X 4.5; all from C. B. Williams (mo). Fig. 9. N. eriophora: A, frond, X 1, redrawn from Hook. Cent. Ferns t. 91 (Gardner 2390): B, underside of segment. X 4.5: C, trichomes on stipe, enlarged; $D$, segment, X 4.5; the last three from Gardner 2390 (GH). Fig. 10. N. goyazensis: A, frond, X 0.5, from Williams 6871 ( $(\mathrm{iH})$ : B, upper surface of segment, X 2.5, from Glaziou 16643 (GH); C, segments, X 4.5, from Williams 6871 (GH). Fig. 11. N. geraniffolia: A, frond, X 0.5; B. upper surface of pinna, X 2.5; C, underside of pinna, X 2.5; D, segments, X 4.5; all from Glaziou 14408 (GH).

Rhizome $2-3 \mathrm{~mm}$. in diameter. Fronds ca. $5-12 \mathrm{~cm}$. tall; stipe terete, $4-11 \mathrm{~cm}$. long, $0.4-0.5 \mathrm{~mm}$. in diameter, with one vascular bundle. Lamina pedate-pinnatifid, $2-3.5 \mathrm{~cm}$. long and as broad or somewhat broader, rather thin, indument of both surfaces of whitish to rufescent hairs. Basal pair of segments usually much produced on the lower side and strongly inequilateral, their basal divisions on the lower side themselves lobed and somewhat inequilateral, all divisions broadly obtuse; upper part of lamina cut to near rachis into 3-4 oblong, obtuse entire segments, tapering evenly into a broad, short, 3-4-lobed obtuse apex. Veins 1-2-forked, sporangia (with 64 spores) borne on their apices a little back from the unmodified margin.

Northeastern Brazil and Colombia (Macarena Mts.), sometimes on sandstone rocks and perhaps confined to them. The report from Colombia is taken from Alston in Mutisia 7: 8. 1952; it is based on Philipson 2293.

Specimens seen: Brazil. Glaziou 14409 (в, к, p, us); Herb. Kew 1037 (у). Piauhy: Ule 46, 7423 (в); Gardner 2390 (bм, с, сн, к, ny, P, us). Ceará: Schwacke 2545 (b).
10. Notholaena goyazensis Taubert, in Engl. Bot. Jahrb. 21: 421. 1896. Weath. Journ. Arn. Arb. 27: 366. 1946. type: Serra Dourada, Goyaz, Brazil, Jan. 1893, Ule 3222, whereabouts unknown.

Fig. 10. Map 13.
Cheilanthes goyazensis (Taubert) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Rhizome about 4 mm . in diameter; scales $3-4 \mathrm{~mm}$. long, $0.1-0.2$ mm . wide at base, remotely serrulate toward apex, those of the young growth bright brown and concolorous, the older with castaneous, sclerotic central band. Fronds ca. $8-15 \mathrm{~cm}$. tall; stipe $3-10 \mathrm{~cm}$. long, with one vascular bundle, with the tomentum about 1 mm . in diameter, in age glabrate and blackish castaneous. Lamina $4.5-6 \mathrm{~cm}$. long, usually about as wide, pinnate-pinnatifid or, in the basal pinnae only, sub-bipinnatifid; tomentum of upper surface whitish or grayish, that of the lower surface at first whitish, in age dull brown or pale ferrugineous. Basal pinnae usually connected with those above by a narrow wing along the rachis, inequilaterally elongate-deltoid, the basal segments on the lower side much produced and pinnatifid with oblong, obtuse lobes, median segments of lamina linear-oblong, equilateral, pinnatifid with oblong, obtuse entire lobes, the basal lobes adnate to the rachis and forming a broad, basally narrowed wing along it, the 2-4 upper segments rather abruptly contracted into an obtusish, short or sometimes produced, pinnatifid lamina-apex. Veins at an acute angle to the costule, simple or 1-forked, the sporangia (with 64 spores) borne on their subflabellate tips at the margin which is bordered by a very narrow hyaline band.

Eastern Brazil, on sandstone and perhaps other rocks.
Specimens seen: Brazil. Minas Geraes: Glaziou 16643 (b, Gh, к, P) ; April, 1905, Silveira (p) ; L. O. Williams 6871 (GH, us). Goyaz: Glaziou 22625 (в, G, P) ; Damazio 1859 (b, NY, Р, US).
11. Notholaena geraniifolia St. Hil. ex Weath. Journ. Arn. Arb. 27: 367. 1946. Type: prope S. Miguel da Ti[Je]quitinhonha, Minas Geraes, Brazil, St. Hilaire B' 1489 p!, photo gh!. Fig. 11. Map 14.


Maps 12-17. Map 12, N. eriophora. Map 13, N. goyazensis. Map 14, N. geraniifolia. Map 15, N. Pohliana. Map 16, N. cinnamomea. Map 17, N. obducta.

Rhizome horizontal, ca. 2 mm . in diameter; scales sub-appressed, narrowly linear with dark brown subsclerotic central band and narrow paler hyaline, remotely serrulate margins, and capillary tip (ca. $3-4 \mathrm{~mm}$. long, 0.2 mm . wide). Fronds subapproximate ca. $10-22 \mathrm{~cm}$. tall; stipe slender, somewhat angled and subterete, deep castaneous, shining, with an inconspicuous, sparse, thin, pale, scarcely matted tomentum or nearly glabrous, much longer (3-5 times) than the lamina, with one vascular bundle. Lamina pentagonal, almost as broad as long 5 cm . or less each way, deeply bipinnatifid (the lower pinnae) or at base tripinnatifid, upper surface densely subappressed hirsutulous with comparatively coarse golden-brown shining, almost straight and little entangled hairs, the lower with dense, close, lanate tomentum of very fine, tortuous and closely matted, strongly ferruginous hairs. Lower pinnae enlarged, inequilaterally deltoid, the basal pinnules on the lower side much elongated and deeply pinnatifid, upper pinnae (about 4 pairs) pinnatifid, abruptly reduced to a short, pinnatifid acutish lamina-apex, ultimate lobes linear-oblong. Veins once- or twice-forked, the few sporangia (with 64 spores) on a somewhat elevated punctiform receptacle at their tips, margins with a small hyaline lobe immediately outside of the vein-end.

## Eastern Brazil, on rocks.

Specimens seen: Brazil. Minas Geraes: St. Hilaire B' 1489 (p); A. Maublanc 584 (p); Glaziou 14408 ( $\mathbf{~}, \mathrm{G}, \mathrm{GH}, \mathrm{K}, \mathrm{P}$ ). Bahia (?): bei Calderão, Ule 7239 (в).
12. Notholaena Pohliana Kze. Farnkr. 1: 45. 1840. Weath. Journ. Arn. Arb. 27: 369. 1946. type: Goyaz, Brazil, Pohl, at w?, not seen. A specimen of Gardner 3554 at $\mathrm{G}!$ det. by Kze. may be taken as authentic.

Fig. 12. Map 15.
Cheilanthes Pohliana (Kze.) Mett. Cheil. no. 13. 1859.
Fronds ca. 30 cm . tall; stipe slender, terete, blackish, dull, glabrous or beset with short, pale, retrorse, sometimes branched trichomes. Lamina tapering regularly from base to long-attenuate apex, 8-17 cm . long, $2.5-4 \mathrm{~cm}$. wide, with up to 18 pairs of pinae, texture herbaceous, both surfaces loosely beset with long, simple, distinctly articulate, pale brownish hairs; rachis like stipe. Lower pinnae with 3-5 pairs of free, oblong or deltoid-ovate, obtuse, entire or sometimes lobed pinnules 6 mm . or less long, and 3-5-lobed deltoid, obtuse terminal segments. Veins 3 - 4 -forked, sporangia borne on the only slightly clavate vein-ends, margin unmodified.

Glaziou 15735 from "Environs de Rio de Janeiro et d'Ouro Preto" was probably not actually collected at both localities; I am considering Ouro Preto as the correct one.

Eastern Brazil, presumably on rocks.


Fig. 12-15. Fig. 12. N. Pohliana: A, frond, X 0.5 : B, segments, X 4.5 ; both from Gardner 3554 (us). Fig. 13. N. cinnamomea: A, frond, X 0.5; B. portion of rachis, enlarged; C, segment, X 4.5; all from Salvin (Gh). Fig. 14. N. obdecta: A , frond, X 0.5 ; B, underside of segment, X 7: C, segment, X 7: all from Rojas 13656 (mo). Fig. 15. N. aurea: A, frond, X 10.5 : B, underside of pinna, X 4.5; C, segment, X 9; all from E. J. Palmer 30608 (мо).

Specimens seen: Brazil. Minas Geraes: Glaziou 15735 (в, к). Goyaz: Gardner 3554 (в, BM, F as 3551, G, K, P, us).
13. Notholaena cinnamomea Baker, Syn. Fil. ed. 2, 515. 1874. type: Motagua ("Montagua"), Guatemala, 1862, Salvin \& Godman k!, photo $\mathbf{~ c h !}$.

Fig. 13. Map 16.
Cheilanthes cinnamomea (Baker) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Rhizome short, erect; scales subulate ca. 3 mm . long, attenuate to a capillary apex, deep brown, shining, subsclerotic, with very narrow, pale, thin, entire margin, the cells very narrow and elongate without lumina. Fronds ca. $15-30 \mathrm{~cm}$. tall, cespitose; stipe terete, with one vascular bundle, shorter than or about equal to the lamina, rather slender, beset with narrowly linear, pale or dark brown, entire or remotely toothed scales and hairs like those of lamina. Lamina herbaceous, ovate or lanceolate $6-12 \mathrm{~cm}$. long, $2.5-5 \mathrm{~cm}$. wide, bipinnate-pinnatifid, nearly glabrous on the upper surface, beneath loosely beset with long weak pluricellular (but not obviously articulate) brownish hairs pinnately branched at base. Pinnae 8-9 pairs, lance-oblong, obtuse $0.8-1.3 \mathrm{~cm}$. wide, the lowest not or but slightly smaller, pinnules, 5 to 7 pairs, deltoid-ovate or oblong, very obtuse, inequilateral at base, distal side much wider. Veins 1-2forked, sporangia (with 64 spores) borne on their terminal portions which are slightly or not at all thickened, margin unmodified.

Guatemala, moist shaded bank, 450 m .
Specimens seen: Guatemala: 1862, Salvin \& Godman (BM, к, US); Volcan de Fuego, Salvin (GH).
14. Notholaena obducta (Kuhn) Baker, Syn. Fil. ed. 2, 515. 1874. Weath. Lilloa 6: 266.1941.

Fig. 14. Map 17.
Cheilanthes obducta Mett. ex Kuhn, Linnaea 36: 83. 1869. TYPE: Bolivia, d'Orbigny 386 в!, photo GH!.

Notholaena Balansae Baker, Journ. Bot. 16: 301. 1878. тYPE: Paraguay, Balansa 330 к!, photo GH!.

Cheilanthes Balansae (Baker) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Notholaena Herzogii Rosenst. in Fedde, Rep. Sp. Nov. 6: 175. 1905. type: Bolivia, Th. Herzog 117, probably at s-pa, not seen, isotype, s!, photo GH !

Rhizome short-repent, about 8 mm . in diameter, scales narrowly linear, soft, pale brown with rather large oblong cells or with shining, sclerotic, castaneous central band and narrow, pale brown margin. Fronds several, approximate, up to 55 cm . tall; stipe terete, with a single, vascular bundle, stoutish, castaneous, covered with subappressed deciduous trichomes similar to those of lamina. Lamina
lanceolate, bipinnate, with numerous (15-25) pairs of oblong-lanceolate pinnae, upper surface glabrous or nearly so, lower surface densely clothed with long, straightish, subappressed, relatively thick, brownish, pluricellular, compound trichomes, with 3-6 elongate lower cells attached at their bases only, the remainder of each cell free, more or less reflexed and imbricate; rachis similar to stipe. Pinnae simply pinnate, with $8-10$ pairs of oblong, broadly obtuse, entire pinnules, which are sessile or nearly so, subcordate and nearly equilateral at the broad base. Veins 1-, or the basal, 2-forked, sporangia (with 32 spores) borne on the abruptly dilated vein-ends a little within the unmodified margin which is narrowly revolute over them.

The peculiar trichomes make this an exceptionally well-marked species.

Colombia (upper Magdalena valley); Bolivia, northern Argentina and Paraguay, dry or shaded rocky places or in sandy soil, mostly at 1000 m . or less.

Representative specimens: Colombia: Lehmann 6056 (B, GH, P, US). Bolivia: R. S. Williams 1374 (Us); d'Orbigny 386 (в, P). Paraguay: Balansa 330 (K, P); Rojas 3347 (p); Anisits 2147 (ny, us). Argentina. Jujuy: Schreiter 5129 (GH, lil); Venturi 5111 (Gh, us). Salta: Hieronymus \& Lorentz 269 (в); Eyerdam \& Beetle 22899 (GH). Tuccmán: Venturi 846, 1871 (gh, lil, us). Catamarca: May 15, 1910, Castillón (P), 714 (GH, LiL). Entre Ríos: Stuckert 6582 (GH).
15. Notholaena aurea (Poir.) Desv. Mém. Soc. Linn. Paris 6: 219. 1827. Weath. Lilloa 6: 260. 1941; Journ. Arn. Arb. 24: 312. 1943.

Fig. 15. Map 18.
Pteris aurea Poir. Encycl. Meth. 5: 710. 1804. Type: Peru, Joseph de Jussicu (sheet 1333 in hb. Jussieu) p!, photo GH!.

Acrostichum bonariense Willd. Sp. Pl. 5: 114. 1810. type: "Bonaria," B!, photo Gu!.

Cheilanthes ferruginea Willd. ex Link, Enum. Pl. Berol. 2: 463. 1822. TYPE: "America meridionali," b!, photo ch!. Not Cincinalis ferruginea Desv. which is N. trichomanoides.

Notholaena rufa and vars. minor \& major Presl, Rel. Haenk. 1: 19. 1825, the species-name superfluous. TYpe: Mexico, Haenke, pr! (sheets 78.539 and 78540), photo GH!.

Pellaea ferruginea (Link) Nees, Linnaea 19: 684. 1847.
Notholaena ferruginea (Link) Hook., Second Century Ferns, sub t. 52. 1861; not Desv., 1813, which is N. trichomanoides.

Notholaena ferruginea var. canescens Kze. ex Fourn. Mex. Pl. 1: 120. 1872, nomen nudum (Schaffner 47 p !, is so labeled by Fourn.).

Notholaena bonariensis (Willd.) C. Chr., Ind. Fil. 6. 1905; 459. 1906.

Notholaena chiapensis Rovirosa, Pteridographia Mex. 229, t. 48, fig. 1-6. 1909. type: Chiapas, Mexico, Rovirosa 1077, location unknown; isotype, GH!, PH-photo mo!, us!.

Rhizome short-repent; scales lance-linear, with shining, castaneous, sclerotic central band and narrow or relatively broad, pale brown, entire, hyaline margin. Fronds ca. $20-60 \mathrm{~cm}$. tall; stipe $1 / 3$ as long as blade or less, terete, castaneous or blackish, with a single vascular bundle, clothed, as is the rachis, with coarse, straightish, subappressed, whitish, septate hairs. Lamina linear-elliptic, long-attenuate at base, pinnate-pinnatifid almost to the gradually or abruptly narrowed obtusish apex, upper surface rather sparsely clothed with straightish, rather coarse, whitish or golden tinged pluricellular hairs, the lower covered with dense tawny tomentum (white when young) of fine matted hairs. Pinnae numerous (up to 40 pairs), oblong or deltoid-oblong, obtuse or acutish, cut $1 / 2-3 / 4$ to the costa into oblong or linear-oblong, entire obtuse lobes. Veins oblique, 1-2-forked, sporangia (with 32 spores) borne on their clavate to subpunctiform ends, margin modified with a very narrow subhyaline band.

Notholaena aurea is a distinctive, and, considering its broad distribution, a remarkably uniform species. C. A. Weatherby ${ }^{6}$ has discussed the proper application of Poiret's long-overlooked Pteris aurea.

The literature records mapped are from Morton in Kearney \& Peebles, Arizona Flora, 1951, Correll in Lundell, Flora of Texas $1^{1}, 1955$ and Hicken, Cat. Polipod. Argent. in Rev. Mus. La Plata 15.

Southwestern United States, Mexico, Central America, West Indies and through the Andean region to northern Chile and Argentina; growing in a variety of moist or dry, usually rocky, habitats, ca. 700-4000 m.

Representative specimens: United States. Texas: C. H. Mueller 8261 (GH); Havard 1219 (P); Moore \& Steyermark 3056 (GH, US), 3238 (GH, us); E. J. Palmer 30608 (GH, p, us), 31975 (us), 34101 (Gh). New Mexico: Wooton 102 (Gh, p, us), in 1902 (US); June 9, 1906, Standley (us). Arizona: Goodding 2574 (GH); M. E. Jones 4329 (GH, P, US) ; Rothrock 612 (GH, Y), 613 (GH, US, Y); Blumer 2122 (GH), 2141 (us); Parish 267 (us); Shreve 5066 (us); Peebles et al. 1338, 1345 (us); Eggleston 14224 (us). Mexico. Baja California: Brandegee 658 (GH, US); 1930, M. E. Jones (Us). Sonora: Hartman 171 (GH), 238 ( $\mathrm{GH}, \mathrm{US}$ ), 253 (GH), 328 ( $\mathrm{GH}, \mathrm{US}$ ). Chihuahua: Goldman 152 (GH, US); Pringle 462 ( $\mathbf{F}, \mathbf{G H}, \mathbf{M O}, \mathbf{P}, \mathrm{Y}$ ) , 899 ( $\mathrm{GH}, \mathbf{P}, \mathrm{US}$ ).

[^3]Coahulla: Gregg 219 (b, GH, mo); Wynd \& Mueller 511 (GH, us); Palmer 369 (GH, us), 1399 (GH, p, us, Y). Nuevo León: C. H. d M. T. Mueller 332 ( $\mathbf{G H}$ ), 955 ( $\mathbf{F}, \mathbf{G H}$ ). Tamaulipas: Bartlett 10076 (us). Durango: Palmer 240 ( $\mathbf{F}, \mathrm{GH}, \mathrm{us}$ ), 354 ( $\mathrm{GH}, \mathrm{us}$ ), 463 ( $\mathrm{GH}, \mathrm{US}$ ), 464 ( $\mathrm{b}, \mathrm{F}, \mathrm{GH}, \mathrm{US}$ ), 508 ( $\mathrm{GH}, \mathrm{US}$ ), 890 ( $\mathbf{F}, \mathrm{GH}, \mathrm{US}$ ). ZaCatecas: Rose 2747 (Gh, us), M. E. Jones 541 (us). San Luis Potosí: Schaffner 35 (GH, US), 946 (GH, K, US, Y) ; Parry \& Palmer 993, 994 (F, GH, P, US, Y). Jalisco: Palmer 551 ( $\mathbf{P}$, us, y), 632 ( $\mathbf{G H}, \mathbf{P}, \mathrm{us}$ ). Guanajuato: Dugès 5 (Gh). Querétaro: Arsène 10648 (us). Hidalgo: Rose d Painter 6681 (us). Michoacán: Seler 1243 (b, GH, us) ; Pringle 3.382 ( $\mathrm{F}, \mathrm{ch}$, mo). Mexico: Schaffner 34 (b, bm, p, us), 35 (b, f, p, us); Bourgeau 257 ( $\mathrm{B}, \mathrm{NY}, \mathrm{P}, \mathrm{US}$ ); Rose \& Painter 6474, 6613, 6800, 6990, 7126, 7858 (us). Distrito Federal: Pringle 11268 (b, F, GH, mo, p, us), 11788 ( $\mathrm{B}, \mathrm{GH}, \mathrm{P}, \mathrm{US}$ ) ; Hinton 3309 (GH, K); Seler 3525 (B, GH, US). Morelos: Rose \& Rose 11059, 11097 (us). Puebla: Pittier 445 (us); J. G. Smith 56 (us). Veracruz: Seaton 121 (Gh, us); Bourgeaul 3153 (b, Gh, k, ny, P, y). Guerrero: Hinton 9486 (f). Oaxaca: Purpus $3143 a$ ( $\mathrm{GH}, \mathrm{US}$ ) ; Conzatti \& Gonzales 465 ( $\mathrm{GH}, \mathrm{P}$ ) ; Rose d Rose 11341 (us). Chiapas: Ghiesbreght 275 (GH, y). Guatemala: Bernoulli \& Cario 243 (в, к, P); Skutch 799, 807 (GH); Heyde d Lux 6284 (b, GH, US); Lehmann 1527 (b, BM, K, Us); Standley 58588, 65566, 65765, 66479, 82388 (F); Tonduz 756 (F, к, us). Honduras: T. J. Dyer A280 (us). Costa Rica: Brade 136 (b, p). Jamaica: Watt 217 (BM, GH, P, US) ; Maxon \& Killip 1418 ( $\mathbf{B}, \mathbf{F}, \mathrm{GH}, \mathrm{US}, \mathrm{Y}$ ). Haiti: Ekman H1153 (k, us), H1196 (F, GH, us); Leonard 4369, 4450 (GH), 4585 (GH, US), 4799 (GH, US). Dominican Republic: Ekman H11944 (b, F, K, US), 13875 (b, US); Fuertes 1913 (GH, P, US). Venezuela: Moritz 250 ( $\mathbf{(}), 350$ (в, вм, к, р); Linden 514 (в, вм, к, p) ; Gehriger 239 (us). Colombia: Mutis 3088 (us); Killip du Smith 16386, 16486, 16857, (GH, us); Hartweg 1514 (в, вм, us); Lindig 130 (BM, K, P) ; Lehmann 4446 (b, K, P, US), 7588 (B, GH, K, US). Ecuador: Jameson 31, 32 (в), 46 (к), 218 (вм, P); Lehmann 631 (в); André 564 (k, Ny); Spruce 5325 (bM, GH, Ny, P, y); Mexia 7429 (us). Peru. Amazonas: Matthews 205 (bm, к), 3289 (b, bar, us). Húnuco: Macbride d Featherstone 1921, 2050 (us). Juxin: Safford 991 (GH, P, us); Killip \& Smith 21809 (us). Ayacucho: Killip do Smith 22256 (us). Cuzco: Cook \& Gilbert 361, 695 (us); Hitchcock 22548 (us). Bolivia: D'Orbigny 166, 372, 404 (p); Buchtien 261 (B, GH, P, us), 471 ( $\mathrm{P}, \mathrm{US}$ ), 3113 (US), 5007 (US); Bang 205 (b, P, US), 752 (GH, P, US) ; Mandon 1572 (BM, GH, K, NY, P); Fiebrig 2860 (b, GH, P, PR, US); Rusby 332 (GH, P, US), 336 (B, GH, P, US); Herzog 1717, 2496 (B, US). Chile: Johnston 545 (GH, US). Argentina. JujuY: Parodi 9794 (GH); Venturi 7397, 9006 (us). Salta: Venturi 68.38 (us); Lorentz d Hieronymus 1.58 (b, p, us), 160 (b, p). Tucumán: Rodríguez 547 (GH, LiL); Venturi 1719 (Lil, US), 4190 (GH, Lil, us); Lillo 1043 (GH, LIL) , 5061 ( $\mathrm{GH}, \mathrm{LIL}$ ).


Maps 18-22. Map 18, N. aurea. Map 19, N. tomentosa. Map 20, N. Fraseri. Map 21, N. Buchtienii, large dots var. Buchtienii, small dot var. ventanensis. Map 22, N. Parryi.
16. Notholaena tomentosa Desv. Journ. Bot. Appl. 1: 92. 1813; not (Link) Keys. 1873, which is Cheilanthes tomentosa. Weath. Lilloa 6: 274. 1941.
Cincinalis tomentosa Desv. Berl. Mag. 5: 312. 1811. type: Concepción, Chile, 1782, Dombey P!, photo ch! (see Weath. in Contrib. Gray Herb. 114: 22. 1936).

Notholaena hypoleuca Kze. Linnaea 9: 54. 1834; not Goodding, 1912, which is N. Grayi. type: near Valparaiso, Chile, Poeppig I 262 (Diar. 41), not seen; isotypes: B !, photo cH , P !, photo ch !.
Cheilanthes hypoleuca (Kze.) Mett. Cheil. no. 11. 1859.
Rhizome slender $2-3 \mathrm{~mm}$. diam., short-creeping, branched; scales subulate, dark castaneous, sclerotic, shining, without pale border. Fronds ca. $10-30 \mathrm{~cm}$. tall, approximate; stipe slender, castaneous, glabrous, strongly sulcate as is the rachis, mostly longer than lamina, with one vascular bundle. Lamina narrowly lanceolate, pinnate-pinnatifid or bipinnate (rarely subtripinnate) at base, not or little narrowed below, $2-13 \mathrm{~cm}$. long, $1.5-3 \mathrm{~cm}$. wide, upper surface with thin, lower with dense, lanate tomentum of slender weak much entangled hairs, whitish or pale brown. Pinnae 8-12 pairs, rather distant, oblong-lanceolate, narrowed to blunt apex, with about 5 pairs of oblong, obtuse segments or pinnules, the basal only really separated and then often with 2-3 pairs of deltoid obtuse lobes cut $\frac{1}{2}$ to midvein. Veins 1 -2-forked, sporangia (with 32 spores) borne on their terminal, subelavate portions, margin not or very slightly modified.
Edwyn Reed (к) from Juan Fernández Islands and Rusby 334 ( NY ) from Bolivia are not included on the map, awaiting confirmation of these range extensions. The record from Antofagasta is taken from Looser in Darwiniana 7: 65. 1945.
Chile, in rocky places.
Representative specimens: Chile. Bertero 564 (G, P); Cuming 200 (в, вм) ; Macrae 1825 (вм, к). CoQuimbo: Rose 19457, 194.59 (us). Aconcagua: Cuming 490 (bm, GH, к) ; Bertero 1249 (g, Gh, p), 1950 (Р) ; Gaudichaud 30 (в, F, Р) ; Lechler 2815 (в); Looser 44, 717 (Gн); Rose 19124 (us); Poeppig I 262 (b, bм, G, p). Santiago: Skottsberg 968 (bм); Looser 732 (GH). Maule: Stuibel 1192 (в).
17. Notholaena Fraseri (Kuhn) Baker, Syn. Fil. ed. 2, 514. 1874. Weath. Lilloa 6: 273. 1941.

Fig. 17. Map 20.
Cheilanthes Fraseri Mett. ex Kuhn, Linnaea 34: 83. 1869. type: Ecuador, Fraser Wagner and Peru, Ruiz \& Pavon. A sheet at b! (photo Gu!) containing both collections, cited and labelled by Mettenius, is taken as authentic.

Rhizome short or moderately long-repent, often branched and intertangled, $2-3 \mathrm{~mm}$. diam.; scales narrowly linear-subulate with
castaneous, subsclerotic, shining central band, narrow paler entire or remotely serrulate margins or pale and hyaline throughout, all with very long capillary, pale brown apex, crisped and contorted in drying (no pectinate teeth seen), excluding capillary apex $1.5-2 \mathrm{~mm}$. long, cells of central band elongate, very small almost without visible lumina. Fronds ca. $20-40 \mathrm{~cm}$. tall, stipes comparatively stout, approximate and forming a loose cluster; terete, mostly about half as long as lamina, with one vascular bundle, dark-castaneous to blackish tomentose with somewhat matted hairs like those of lamina or glabrate. Lamina narrowly linear, about the same width to near apex, not narrowed, or not much, at base, acute at apex, pinnate-pinnatifid or bipinnatifid at base, the pinnatifid tip relatively very short with $2-3$ pairs of lobes, lower surface densely tomentose with comparatively coarse much matted pale brown hairs, the upper with a thin covering of fine white hairs or glabrate, texture coriaceous, veins not visible on the upper surface; rachis like stipe, permanently tomentose or rarely glabrate. Pinnae up to 25 pairs, deltoid-ovate, petiolulate, up to $2.5 \times 1.3 \mathrm{~cm}$., somewhat articulate, tapering from the commonly inequilateral base to the blunt or acutish apex, pinnatifid $1 / 2-2 / 3$ to rachis into 3-5 pairs of deltoid-oblong to narrowly oblong, obtuse lobes, these entire, crenate, or the basal on the lower side of the pinnae more or less elongate and themselves lobed. Veins at acute angle to costa, 1-2-forked, sporangia (with 32 spores) borne at the dilated tips, margin slightly modified.

A critical species, separated from the next, N. Buchtienii, by the numerous and tortuous capillary tips of the rhizome scales giving the rhizome a tomentose appearance, the lack of scales on the rachis and upper part of the stipe, the deltoid shape of the median pinnae and the immersed veins.

Ecuador to Bolivia, in rocky places, frequently shaded, from 900 to 3600 m .

Representative specimens: Ecuador: April 6, 1921, Popenoe (us). Peru. Cajamarca: Weberbauer 4139 (b). Huánuco: Macbride du Featherstone 2328 (G, GH, us). Cuzco: F. L. Herrera 3295 (GH, us); Cook d Gilbert 553 (us) ; Mexia 8055 (F, GH, us); Vargas 3150, 10449 (F, GH). Bolivia: Stübel 1233 (B); Bang 1093a, in part (GH).
18. Notholaena Buchtienii Rosenst. in Fedde, Rep. Sp. Nov. 5: 238. 1908. Weath. Lilloa 6: 263. 1941. type: Sirupava, Suryungas, Bolivia, Buchtien 472, presumably at s-PA, not seen; isotype P !, photo GH !.

Map 21.
Rhizome repent, about 3 mm . in diameter, short or up to 10 cm . long, scales narrowly linear, about 3 mm . long, with relatively broad, castaneous, shining, sclerotic central portion and narrow, pale hyaline,

subentire or serrulate margin, tipped with a long, weak hair. Fronds approximate, up to 40 cm . long; stipe about equalling or shorter than lamina, with a single vascular bundle, castaneous, deciduously tomentose, usually with a few small scales mingled with the tomentum on its upper part. Lamina linear-lanceolate, not or only a little narrowed at base, obtuse or acutish at the short pinnatifid apex, below this pinnate-pinnatifid, upper surface more or less arachnoid-tomentose with fine white hairs or glabrate, lower surface densely rufescenttomentose, texture comparatively thin, the veins somewhat impressed and usually visible on the upper surface (except as hidden by the tomentum). Pinnae $8-20$ pairs, lanceolate or deltoid-lanceolate, tapering from near the base to the obtuse apex, deeply pinnatifid or the lower pinnate at base, segments oblong or oblong-lanceolate, obtuse, entire or cut not more than $1 / 2$ to costule into $2-4$ pairs of broad, obtuse lobes. Veins oblique, 1-2-forked, sporangia (with 32 spores in var. Buchtienii), borne on their clavate to flabellate-dilated tips, margin slightly modified.

This species is close to the previous one, N. Fraseri. It differs in the few capillary-tipped rhizome scales, the presence of a few (although deciduous) scales on the upper part of the stipe and on the rachis, the lanceolate or deltoid-lanceolate median pinnae and the subimpressed, visible veins.

Bolivia and Argentina, in rocky places and on walls, 600 to 3000 m.

## KEY TO VARIETIES

Well-developed fronds usually more than 15 cm . tall, indument of the lower surface rather deep rusty brown, of the upper surface thinly arachnoidtomentose when young, soon glabrate .......18a. var. Buchtienii. Well-developed fronds to 15 cm . tall, indument of the lower surface pale brown, of the upper densely and persistently whitish-tomentose

> 18b. var. ventanensis.

## 18a. Notholaena Buchtienii var. Buchtienii.

Fig. 18. Map 21. Notholaena Fraseri var. robusta Hieron. in Engl. Bot. Jahrb. 22: 400. 1896. type: Argentina (Córdoba), Galander, B!.

Representative specimens: Bolivia: Pearce (к) ; R. S. Williams 1374 (US); Cárdenas 829 (GH) ; Buchtien 472 (B, BM, G, P, US), 4225 (F, G, ny, us). Argentina. Jujuy: Eyerdam \& Beetle 22229 (GH). Salta: Venturi 9984 (Gh); Lillo 3860 (Gh, lil). Tucumán: Venturi 750 (GH, lil, us), 4194 (Gh, lil); Monetti 1661 (Gh, lil). Catamarca: Jörgensen 12.35 (GH); Castillón 1491 (GH, LiL). Córdoba: Lorentz 14a, 15 (в); Hicronymus 269 (в); Rose \& Russell 21417 (US).

18b. Notholaena Buchtienii var. ventanensis Weath. Amer. Fern Journ. 36: 7. 1946. type: Partido de Tornquist, Sierra de la Ventana,

Estancia Funke, Cerros Grietas, November 14, 1943, Cabrera 8101 GH!. Map 21.

A local variant, known only from Sierra de la Ventana; the following specimen, in addition to the type, belongs here: Lorentz 60 ( $\mathbf{B}, \mathbf{G H}$, P, PR, US).
19. Notholaena Parryi D. C. Eaton, Amer. Nat. 9: 351. 1875. Type: St. George, Utah, Parry 263 y!.

Fig. 19. Map 22.
Cheilanthes Parryi (D. C. Eaton) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Rhizome short, erect, stout, often branching and forming dense clumps; scales lance-linear with narrow shining blackish sclerotic central band and broad entire deep brown thin margins. Fronds clustered, ca. $8-15 \mathrm{~cm}$. tall; stipe slender, castaneous with a few brownish scales toward base, beset somewhat sparsely with weak, divergent, articulate, often gland-tipped hairs, as long as lamina or nearly so, with one vascular bundle. Lamina mostly lanceolate or narrowly ovate, $3-12 \mathrm{~cm}$. long, $1.6-4 \mathrm{~cm}$. wide, bipinnate-pinnatifid, beset sparsely above and densely below with long, relativelv coarse, loosely curled and intricate, white to pale rufescent hairs which are few-celled, the cells very long; rachis similar to stipe. Pinnae 5-8 pairs, the lower distant but not reduced, segments broad-oblong to ovate, very obtuse, the lower deeply 2 - to 3 -lobed. Veins simple to 2 -forked, sporangia (with 64 spores) borne on their clavate terminal portions, margin unmodified.

Southwestern Utah to New Mexico, California and Baja California, calcareous or igneous rock crevices and among rocks, 200-2300 m.

Representative specimens: United States. Utah: Palmer 1, 2 (ch, y) ; Parry 263 (F, GH, MO, P, US, Y); Cottam 4235 (US); M. E. Jones 1606 (b, bM, F, GH, P, US), 5110 (us). Nevada: Coville \& Funston 367 (US, y); Purpus 613Z (Us). Arizona: Shreve 7630 (F); Goldman 2823 (Us); Palmer 555 (F, Y); Peebles 6486 (Us); Harrison \& Kearney 6575 (us); Goodding 2130 (Gh). California: Parish 504 ( $\mathbf{B}, \mathbf{P}, \mathrm{PR}, \mathrm{US}$ ), 6113 (P); Johnston 1046 (US), 2321 (US); Mearns 2805 (us); Eastwood 3019 (us); Howell 3985 (F); Palmer 431 (bм), 432 (bm, F, Gh, P). Mexico. Baja California: Shreve 6857 (F).
20. Notholaena Newberryi D. C. Eaton, Bull. Torr. Bot. Cl. 4: 12. 1873. TYPE: San Diego, California, Nov. 8, 1851, Dr. Newberry y!. Fig. 20. Map 23.
Cheilanthes Newberryi (D. C. Eaton) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.


Rhizome horizontal, branched, 3-5 mm. in diameter, forming dense clumps; scales lance-linear or narrower, sclerotic, shining, blackish, castaneous, no pale thin margin, tapering to a long sclerotic filiform tip which in its turn ends in a weak pale trichome. Fronds clustered, ca. $7-20 \mathrm{~cm}$. tall; stipe terete, about equalling lamina, with one vascular bundle, castaneous, covered with fine lanate tomentum. Lamina lanceolate, not reduced below, 3-4-pinnate, both surfaces finely lanate-tomentose, thinner and whitish above, very dense and pale brownish beneath, ultimate segments suborbicular. Veins mostly simple, rather thick, sporangia [with 64 spores (Guadalupe Is.) or 32 (mainland)] borne on the clavate to punctiform tips, margin unmodified.

Southern California and Baja California, dry rocky places and crevices of rock, up to 1300 m .

Representative specimens: United States. California: Abrams 3.351 (BM, F, G, GH, P, US) ; M. E. Jones 3091 ( $\mathrm{B}, \mathrm{BM}$, GH, P, US) ; Parish 50.3 (B, GH, P, US, Y), 4754 (US); Johnston 2277 (US); Munz \& Harwood 5375 (us) ; Parry \& Lemmon 430 ( $\mathrm{F}, \mathrm{GH}$ ); Palmer 431 ( $\mathrm{F}, \mathrm{GH}$ ). Mexico. Baja California: (Mainland): Wiggins 4242 (к); Johnston 3009 ( F, us); McKeever 6 (us); (Guadalupe Island): Mason 1532 (us) ; Rose 16016 (us) ; Franceschi 39 ( $\mathbf{~ , ~ F , ~ F ~ K ) ~ ; ~ P a l m e r ~} 105$ (GH, P), 855 (GH, US); Anthony 255 (GH).
21. Notholaena mollis Kze. Linnaea 9: 54. 1834, not Hort. 1893 (see under dubious names). Weath. Lilloa 6: 273. 1941. type: Playa Ancha, near Valparaiso, Chile, June, 1827, Poeppig, Hb. Kze., not seen; "squamis stellatis" leaves no doubt as to the application of the name; in addition Bertero 1766 p! and Gaudichaud 44 c ! were det. Kze.

Fig. 21. Map 24.
Cheilanthes mollis (Kze.) Presl, Tent. Pterid. 160. 1836.
Notholaena Doradilla Colla, Mem. Accad. Torino 39: 46, t. 73. 1836. type: evidently Bertero 1766. The plate shows the unique stellate trichomes.

Notholaena stellapilis J. Sm. in Hook. Journ. Bot. 4: 50. 1841, nomen nudum. Specimen ex Hb. J. Sm., k!.

Cheilanthes Doradilla (Colla) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Rhizome short-creeping, knotted; scales narrow-linear, some black-ish-castaneous and shining with very narrow pale margins mixed with thin, straw-colored or pale brown ones, all entire and tipped with an articulate trichome. Fronds crowded or few, ca. $8-30 \mathrm{~cm}$. tall; stipe stout, usually shorter than lamina, terete or slightly angled, with one vascular bundle. Lamina lanceolate, with rather numerous approximate pinnae, above tapering to a long pinnatifid tip, not narrowed at base or more often with a few (2-3) pairs of distant reduced
pinnae, bi-tripinnate, upper surface thinly, lower (with rachis) densely covered with whitish to ferruginous stellate hairs. Pinnae oblong-lanceolate, obtuse, pinnules oblong with a relatively large very obtuse suborbicular or cordiform terminal lobe and 1-2 pairs of rather distant smaller suborbicular lobes. Veins 1-2-forked, rather thick, sporangia (with 32 spores) borne on the flabellate tips, margin unmodified, strongly revolute.

This is one of the most distinctive species, the stellate pubescence beneath at once distinguishing it from all others.

Chile and extreme southern Peru (Mollendo), rocky hillsides and crevices of rocks. Bertero ( $\mathbf{P}$ ) from Juan Fernández Is. is not accepted as to locality, pending confirmation of the occurrence of the species there.

Representative specimens: Peru. Arequipa: Weberbauer 1545 (в). Chile. Pearce 289 (bm). Tarapacá: Rose 19451 (us). Antofagasta:


Fig. 22-23. Fig. 22. N. Ekmanii: A, frond, X 0.5; B, portion of rachis, enlarged; both from Ekman 10011 (GH); C, underside of pinna, X 4.5 ; D, pinna, X 4.5; the last two from Ekman 2313 (GH). Fig. 23. N. Affinis: A, frond, X 0.5 ; B, portion of upper side of rachis, enlarged; C, pinnules, X 4.5; D, scale from rhizome, X 18; all from Orcutt 3315 (мо).

Weberbauer 823 ( $\mathbf{F}, \mathrm{G}, \mathrm{GH}, \mathrm{US}$ ) ; Johnston 3581 ( $\mathrm{GH}, \mathrm{US}$ ), 5124 ( $\mathrm{G}, \mathrm{GH}$ ), 5764 (Gн). Coquimbo: Gaudichaud 44 (b, G, p); Johnston 6269 (Gh); Rose 19245 (us). Aconcagua: Cuming 653 (bм, K), 654 (вм); Bertero 1766 (в, G, GH, P).
22. Notholaena Ekmanii Maxon, Amer. Fern Journ. 16: 9. 1926. type: Sierra de Nipe, edge of Rio Piloto, Oriente, Cuba, July, 1914, Ekman 2313 us!, photo GH!.

Fig. 22. Map 25.
Rhizome short-horizontal or ascending, $2-3 \mathrm{~mm}$. in diameter, branching, nodose; scales rigid, shining, linear-acicular, dark castaneous to blackish, with long, stiff, capillary tips and rather widely spaced, long, spinescent, marginal cilia. Fronds ca. $10-25 \mathrm{~cm}$. tall, approximate, erect, forming dense tufts; stipe much shorter than lamina, with one vascular bundle, castaneous, somewhat shining, shallowly and narrowly sulcate above, with a few reduced pectinate scales below, these passing into broad-based stiff, shining, dark castaneous trichomes. Lamina narrowly linear, commonly narrowed at base, abruptly obtuse at apex with terminal pinna similar to others, glabrate above, thickly white ceraceous beneath, texture coriaceous; rachis like stipe sulcate above and more or less setose. Pinnae many, petiolulate, articulate to the petiolule, broadly rectangular-oblong or deltoid-oblong, subcordate at base, broadly rounded-obtuse at apex with 2-5 pairs of broadly oblong very obtuse lobes, the basal pair wider and sometimes produced into short auricles on one or both sides of the pinna. Veins very oblique to costa, 2 -forked, sporangia (with 64 spores) borne on their clavate tips, margin unmodified.

Eastern Cuba, on rocks in exposed locations, 200-630 m.
Specimens examined: Cuba: Ekman 2313 (G, Ny, us), 6004 (Us), 10011 (F, Us); Aug. 1914, J. F. Kemp (Ny, US).
23. Notholaena affinis (Mett.) Moore, Ind. Fil. 233. 1861.

Fig. 23. Map 26.
Cheilanthes affinis Mett. Cheil. no. 2. 1859. Type: Mexico, Aschenborn B!, photo GH!.

Alcuritopteris affinis (Mett.) Fourn. Mex. Pl. 1: 21. 1872.
Rhizome short-horizontal or ascending; scales subulate ca. 3 mm . long, blackish-castaneous, sclerotic, shining, short pectinate-ciliate. Fronds ca. 6-16 cm. tall, approximate; stipe much shorter than lamina, terete, with one vascular bundle, blackish, shining, below beset with lance-ovate scales mostly with pale, translucent, central portion and thick, shining, castaneous, sclerotic, finely and sharply pectinateciliate margins, otherwise glabrous. Lamina linear-lanceolate, pin-nate-pinnatifid, narrowed to both ends, upper surface glabrous, or glabrate, the lower with pale yellow to yellow (rarely white) cera-
ceous indument; rachis similar to stipe but obtusely somewhat angled on upper sides with two lines of short, stiff, subarticulate, brown and shining trichomes on the angles, at least in the upper portion. Pinnae twenty or more pairs in well-developed fronds, deltoid-ovate, very short-petiolulate, articulate on petiolule, obtuse or acutish, cut equilaterally $1 / 2$ to $3 / 4$ to midrib into $3-4$ pairs of oblong, obtuse lobes with narrow sinuses, the lower lobe longest, the lowest $2-4$ pairs distant and much reduced. Veins 1-2-forked, somewhat thickened, sporangia (with 64 spores) borne on their clavate to sub-punctiform tips, margin unmodified.


Maps 23-28. Map 23, N. Newberryi. Map 24, N. mollis. Map 25, N. Ekmanii. Map 26, N. affinis. Map 27, N. cubensis. Map 28, N. rigida.

Central Mexico to Honduras, shaded rocky places.
Specimens examined: Mexico. Hidalgo: March 8, 1937, M. Broun (ph). Oaxaca: Orcutt 3315 ( $\mathrm{gh}, \mathrm{K}, \mathrm{mo}$, us); Matuda 205 (us). Guatemala: Lehmann 1674 (в, к, P, US); 1862, Salvin \& Godman (GH, K) ; Maxon \& Hay 3417 (Ny). Honduras: Horton \& Morrison 8860 (GH).
24. Notholaena cubensis Weath. ms., sp. nov. Fig. 24. Map 27.

Rhizoma breve horizontale ad 5 mm . diametro, paleis rigidis brunneis vel atropurpureis marginibus spinescenter ciliatis saepe crassioribus obscurioribus. Frondes $5-25 \mathrm{~cm}$. altae caespitosae, stipes quam lamina brevissimus nitidus teres castaneus vel rubelle brunneus cera albis paleis paucis eis rhizomatis similibus nisi anguste lanceolatoovatis fasciculo vasculari uno. Lamina angusta ad basem reducta pinnato-pinnatifida vel bipinnato-pinnatifida pagina superiore plus minusve ceraceo-glandulosa pagina inferiore similis, rhachide eis stipitis similibus nisi pallidior sine paleis. Pinnae oblongae vel ovato-deltoideae obtusae ad basem plus minusve aequilaterales plerumque 4 -jugis pinnularum vel loborum obtusorum. Venulae 1-2-furcatae sporangia in apicibus gerentes, margem immutatus.
typus: Cuba orientali, 1859, 1860, C. Wright 1075 ch!.
In particular, the lighter colored rachis and the lack of trichomes on the rachis distinguish this species from N. affinis, to which the Wright collections have previously been referred.

Specimens examined: Cuba: Wright 1075 (в, GH, к, MO, Р, y), 1076 ( $\mathrm{GH}, \mathrm{K}, \mathrm{MO}$ ).
25. Notholaena rigida Davenp. Gard. \& Forest 4: 519, fig. 80. 1891. type: Sierra de la Silla, Monterrey, Nuevo León, Mexico, Pringle 2599 ch!.

Fig. 25. Map 28.
Cheilanthes rigida (Davenp.) Domin, Bibl. Bot. 20 (Heft 85) : 133. 1913.

Rhizome horizontal, rather slender; scales lance-subulate, very dark brown or blackish, sclerotic, shining, pectinate-ciliate and with minute glands along the margins, $3-4 \mathrm{~mm}$. long. Fronds $25-35 \mathrm{~cm}$. tall, approximate; stipe stout, dark castaneous, terete or nearly so, with one vascular bundle, somewhat ceraceous and at base with scales similar to those of rhizome, but broader. Lamina much longer than stipe, lance-elliptic, acute at both ends, two or three pairs of lowest pinnae reduced, pinnate-pinnatifid, texture subcoriaceous, upper surfaces slightly glandular, lower whitish ceraceous. Pinnae about 15 pairs, deltoid-lanceolate, acute, somewhat inequilateral, cut down nearly to the midrib into linear, oblong, obtuse, broadly adnate segments


Fig 24-26. Fig. 24. N. cubensis: A, frond, X 0.5, from Wright 1076 (mo); B, pinna, X $0.5: \mathrm{C}$, underside of segment, X $4.5 ; \mathrm{D}$, segment, X 4.5 ; the last three from Wright 1075 (GH). Fig. 25. N. rigida: A, frond, X 0.5 ; B, underside of pinnule, X 4.5; C, pinnule, X 4.5; all from Pringle 2599 (mo). Fig. 26. N. trichomanoides: A, frond, X 0.5 : B, two scales from underside of pinna, enlarged; C , underside of a portion of a pinna, X 4.5; all from Proctor 4961 (мо).
which are broadest at the base and connected (except sometimes the lowest pair) by a narrow wing along costa, the apical entire, the basal with shallow rounded lobes and crenulate margins. Veins 1 -2-forked, sporangia (with 64 spores) borne on their clavate to flabellate tips, margin unmodified.

Nuevo León and Tamaulipas, Mexico, limestone ledges.
Specimens examined: Mexico. 1889, Jebert (p). Nuevo León: Pringle 2599 ( $\mathbf{B}, \mathrm{BM}, \mathrm{F}, \mathrm{G}, \mathrm{GH}, \mathrm{K}, \mathrm{MO}, \mathrm{P}, \mathrm{US}, \mathrm{Y}$ ), 15617 ( $\mathrm{F}, \mathrm{GH}, \mathrm{US}$ ). Tamaulipas: Palmer 142 ( $\mathrm{GH}, \mathrm{K}, \mathrm{us}$ ).
26. Notholaena trichomanoides (L.) Desv. ${ }^{7}$ Journ. Bot. Appl. 1: 92. 1813. Fig. 26. Map 29.
Pteris trichomanoides L. Sp. Pl. 2: 1074. 1753. lectotype: Santo Domingo or Jamaica, linn, the photo at GH! shows two specimens, one a leaf and the other a plant; the latter has the pinnae scaly beneath and is accordingly taken as the type.

Trichomanes nivea Burm. Fl. Ind. 238. 1768. type: in Hb. Delessert, G!.

Acrostichum pterioides Bernh. Schrift. Acad. Erfurt 1802: 18, fig. 11; a substitute name for $N$. trichomanoides.

Cincinalis trichomanoides (L.) Desv. Berl. Mag. 5: 311. 1811.
Cincinalis ferruginea Desv. Berl. Mag. 5: 311. 1811. type: in Hb. Desvaux, p!, photo ch!; see Weath. in Contrib. Gray Herb. 114: 22. 1936. Not Notholaena ferruginea (Link) Hook., which is N. aurea.

Notholaena ferruginea Desv. Journ. Bot. Appl. 1: 92. 1813.
Cheilanthes trichomanoides (L.) Mett. Cheil. no. 1. 1859.
Notholacna trichomanoides var. subnuda Jenm. Journ. Bot. 24: 35. 1886. type: Jamaica, Sloane (Sloane Hb. vol. 1, p. 72), Bm!.

Notholaena trichomanoides var. pilosa Kuhn \& Christ, in Engl. Bot. Jahrb. 24: 133. 1897. TYPE: specimens cited: Eggers $3447^{\text {b }}$; Picarda 394, 1085; Garber 40, in part; Sintenis 3040, 3101, 3132.

Notholaena trichomanoides var. pinnatifida Jenm. Bull. Misc. Inf. Ror. Bot. Gard. Trinidad, no. 21, append.: 104. 1899.

Notholaena trichomanoides var. sulphurea Brause, Ark. Bot. 177: 69. 1921. TYPE: Haiti, Ekman 245, not seen; isotypes: k!, ny!, us!.

Rhizome short, horizontal or ascending, knotted (branches very short); scales blackish-castaneous, subulate, $3-4 \mathrm{~mm}$. long, 0.2-0.3 mm . wide, sclerotic, shining, strongly pectinate-ciliate. Fronds ca. $10-40 \mathrm{~cm}$. tall, approximate; stipe rather stout, with one vascular bundle, pale brown or pale castaneous, much shorter than lamina, beset in lower part with long ciliate scales which are pale and thin
${ }^{7}$ As Weath., Lilloa 6: 253. 1941, has pointed out, this combination, usually credited to Robert Brown, was not actually made by him.
in the central portion and with dark thick edges, and with other scales similar to those of lamina. Lamina linear, with many pairs of pinnae, coriaceous, upper surface glabrous except for a few substellate scales with long sub-capillary segments, below white-ceraccous and either densely beset with ferrugineous scales with narrow body and longpectinate margins, or these reduced to substellate processes, or nearly absent; rachis like stipe but with only stellate scales. Pinnae very obtuse, oblong, the lower smaller and deltoid-ovate, entire or with obtuse lobes, cut $1 / 2$ to midrib in apical portion, at base with blunt auricles on one or both sides, (rarely fully pinnate) petiolulate, articulate (at least with swollen pulvinus at point of junction with petiolule). Veins usually 1 -forked, sporangia (with 64 or 32 spores) borne on their slightly to flabellate-dilated tips, margin unmodified.

Two principal variants of this species occur. One has the ceraceous indument of the lower surface concealed, or nearly so, by a dense covering of dissected scales and this must be considered the typical phase on the basis of Linnaeus' description. The other has the ceraceous indument visible due to the presence of few scales, or their occurrence only on the margins. The earliest subspecific epithet for this phase is var. subnuda Jenm. Although the two kinds are relatively well defined, with rather few intermediates, I hesitate to give them recognition. They are not parallel to other varieties in this treatment, lacking a distinctive range (both grow on all four islands and are often collected together) and they differ by but one character.

Both of these phases also show variation in the degree of division of the pinnae. They are most commonly entire or slightly lobed, but occasionally will be pinnatifid and, in the scaly phase, rarely pinnate. This variation is less sharply defined than that of the indument and there are more intermediates.

Cuba, Jamaica, Hispaniola and Puerto Rico, dry or moist rocky places or on rocks, less often on earth, up to 1000 m .

Representative specimens: Cuba: Wright 776 (в, G, GH, к, мо, צ), 1048 (в, вм, GH, MO, P, y) ; Ekman 132.32, 16548, 17199 (US); Shafer 10545 ( $\mathrm{BM}, \mathrm{NY}, \mathrm{US}$ ), 13733 ( NY , us). Jamaica: Maxon \& Killip 1405, 1414, 1416, 1417, 1421 (в, GH, us, Y); Perkins 1066 (в, GH); Wilson 526 (в); Eggers 3447 (b, F, P, US) ; Clute 236 ( $\mathbf{F}$, us); Harris 7326 (bM, F, K, US). Haiti: Ekman 245 (k, Ny, us), 1820 (us), 3278 (k), 3765 (F, K); Leonard 2990, 4566, 5039, 7667 (GH, US). Dominican Republic: Fuertes 1.356 (bM, F, GH, K, P, PR, US); Türchhcim 3614 (bM, F, GH, P, US) ; Ekman 12641 (b, GH, PR, US). Puerto Rico: Sintenis 3040 ( $\mathrm{B}, \mathrm{F}, \mathrm{P}, \mathrm{PR}, \mathrm{US}$ ) , 3101, 3122, 3148 (в); Britton, Britton d Brown 5966 ( $\mathrm{F}, \mathrm{US}$ ), 6002 (US).


Maps 29-34. Map 29, N. trichomanoides. Map 30, N. Aschenborniana. Map 31, N. Galeottii. Map 32, N. Schaffneri, large dots var. Schaffneri, small dots var. Nealleyi, half dots intermediate. Map 33, N. Grayi. Map 34, N. aliena.
27. Notholaena Aschenborniana Kl. Linnaea 20: 417. 1847. Weath. Journ. Arn. Arb. 24: 315. 1943. тype: Chapultepec, Morelos, Mexico, Aschenborn 593 b!, photo GH ! of isotype at p!. Fig. 27. Map 30.

Notholaena bipinnata Liebm. Vid. Selsk. Skr. ser. 5, 1: 214. (repr. 62). 1849. type: Tehuacán, Puebla, Mexico, 5400 ft., Dec. 1841, Liebmann c, not seen; isotype us!.

Cheilanthes Aschenborniana (Kl.) Mett. Cheil. no. 7. 1859.
Rhizome ascending, branched, multicipital; scales subulate, blackish, sclerotic, shining, ca. 3 mm . long, pectinate-ciliate. Fronds 20-45 cm . tall, clustered; stipe much shorter than lamina, stout, terete, with one vascular bundle, dark-castaneous or blackish, thickly beset with bright brown, ciliate scales (the cilia pale, long and weak) and stellate scales or trichomes with long, weak branches. Lamina bipinnate, lanceolate, acute, more or less narrowed at base, texture coriaceous, upper surface rather loosely beset with skeletonized or stellate scales with long, weak divisions, lower surface densely covered with brown, long-ciliate and substellate scales like those of stipe and rachis but smaller, wholly concealing the ceraceous indument. Pinnae numerous, lanceolate, acutish, sessile, with 10 or more pairs of oblong, obtuse, sessile but not adnate pinnules. Veins simple to 2 -forked, sporangia (with 32 spores) borne on their clavate to somewhat flabellate terminal portions, margin unmodified.

The stellate trichomes on the upper surface separate this species from the next, N. Galeottii, which it superficially closely resembles.

Western Texas and southern Arziona, south to Morelos and Puebla, dry rocks and cliffs, preferring or perhaps confined to limestone, ca. $1500-3000 \mathrm{~m}$. The literature records in Texas are from Correll in Lundell, Flora of Texas $1^{1}, 1955$.

Representative specimens: United States. Texas: 1905, Girty (us). Arizona: May 20, 1884, Pringle (b, G, GH, K, MO, P, US). Mexico. Chihliatia: Pringle 466 (bM, G, GH, K, MO, P, PR, US, y ), 469 (GH, us). Coahulla: M. E. Jones 531 (us); Palmer 402 ( $\mathbf{F}, \mathrm{GH}, \mathrm{K}$, Us); Gregg 314 (мо); Johnston 7660, 8384, 8850a, 8928, 8931a, 9094 (Gh). Nuevo León: Mueller 519 (Gh), 975 (F, GH); Orcutt 1144 (us). Tamallipas: Runyon 718 (us). San Luis Potosí: Pringle 3399 (Gh, P); Whiting 998 (US); Purpus 5486 (F, GH). Hidalgo: Edwards 882 (us).
28. Notholaena Galeottii Fée, Gen. Fil. 159. 1850-52. type: Caputalpan, Oaxaca, Mexico, Galeotti 6565, location ?, seen at BM, $B R$, and K .

Notholaena Arsenii Christ, Not. Syst. 1: 232. 1910. lectotype:


Fig. 27-29. Fig. 27. N. Aschenborniana: A, frond, X 0.5; B. upper surface of segment, X 4.5 ; C , underside of segment and venation, X 4.5 ; all from M. T. Edwards 882 (mo). Fig. 28. N. Galeottil: A, frond, X 0.5. from V. H. Chase 7412 ( mo ) : B, upper surface of pinnule, X 4.5; C, underside of pinnule and venation, X 4.5; D, scale from rhizome, X 14; B to D from Purpus 5486 (мo). Fig. 29. N. Schaffneri: 29a. var. Schaffneri: A, frond, X 0.5 , from Pringle 3880 (мо); B, scale from rhizome, X 9, from Pringle 5410 (mo). 29b, var. Nealleyi: A, underside of pinnule and venation, X 4.5; B, scale from rhizome, X 9; both from O. M. Clark 4129 (мо).

Tetele, Puebla, Mexico, Arsène 2046 p!; paratype: same locality, Arsène 1686, not seen.

Notholaena hyalina Maxon, Amer. Fern Journ. 5: 4. 1915. type: San José Pass, San Luis Potosí, Mexico, Pringle 3297 (us).

Rhizome subhorizontal, short-creeping; scales subulate, black, shining, ca. 3 mm . long. Fronds ca. 15-40 cm. tall; stipe much shorter than lamina, stout, terete, with one vascular bundle, almost black, densely beset with rigid brown spinose-ciliate scales, those of the lower part with pale centers. Lamina bipinnate, to bipinnatepinnatifid, lance-elliptic, acute or subacuminate, somewhat narrowed at base, broadest about the middle, texture coriaceous, upper surface sparsely beset with weak, simple, white hairs, or glabrate, lower densely covered with stiff-ciliate scales like those of rachis, entirely obscuring the ceraceous indument; rachis like stipe. Pinnae about 20 pairs in well-developed fronds, lanceolate, acute, slightly inequilateral, the pinnules on the lower side longer, with $7-10$ pairs of oblong, obtuse or acutish pinnules mostly cut half-way to midrib into 2-4 pairs of shallow, broadly rounded lobes. Veins simple to 1-forked, sporangia (with 32 spores) borne on the slightly dilated tips, margin unmodified.
N. Galeottii is easily distinguished from the related N. Aschenborniana by the sparse, weak, simple trichomes on the upper surface of the segments; in $N$. Aschenborniana there are stellate trichomes.

Jalisco and San Luis Potosí south to Oaxaca, shaded or exposed rocks and rocky banks, $1500-2200 \mathrm{~m}$.

Representative specimens: Mexico. San Luis Potosí: Orcutt 1843 (US) ; Purpus 5406 (bм); Schaffner 43 (P); Pringle 3297 (b, F, G, GH, k, mo, p, us, y). Jalisco: M. E. Jones 533 (us). Hidalgo: Coulter 1679 (к) ; V. H. Chase 7192, 7412 (f); Distrito Federal: Schaffner 84 (b, Ny). Morelos: Arsène (Rosenst. Fil. Mex. 10) (b, bM, PR); Copeland 98a (us). Puebla: Arsène 2046 (p); Endlich 1980 (b); Copeland 98 (us); Rose, Painter \& Rose 10126 (us). Guerrero: Pringle 13848 (p); Rose, Painter \& Rose 9.392 (us). Oaxaca: Galeotti 6565 (bм, BR, K) ; Purpus 4018 (US); Conzatti 475 (GH, P), 2003 (f), 4234 ( cs ) ; Pringle \& Conzatti 1392 (GH).
29. Notholaena Schaffneri (Fourn.) Underw. ex Davenp. Gard. \& Forest 4: 519. 1891. Weath. Journ. Arn. Arb. 24: 315. 1943. Map 32.

Rhizome short, branched, ascending; scales narrow-subulate, almost black, rigid and shining, strongly pectinate-ciliate. Fronds ca. $5-25 \mathrm{~cm}$. tall, approximate; stipe much shorter than lamina, terete, with one vascular bundle, castaneous to blackish, densely beset with
scales similar to those of rhizome but much thinner, brown and with long, stiff shining trichomes. Lamina elliptic-lanceolate, narrowed to acute apex and at base to 2-3 pairs of reduced lower pinnae, bipinnatepinnatifid throughout, texture coriaceous; upper surface sparsely ceraceous-glandular, lower densely white-ceraceous and with long brown trichomes on the rachillae and midnerves; rachis like stipe. Pinnae up to 30 pairs, oblong-lanceolate, slightly inequilateral, tapering to a rather blunt apex, with up to 15 pairs of linear-oblong obtuse pinnules with 2-5 pairs of suborbicular, broadly rounded lobes. Veins simple to 2 -forked, sporangia (with 64 spores) borne on the somewhat to distinctly flabellately dilated tips, margin unmodified.

Southern Texas south to Puebla, Jamaica; rocky places and shaded ledges, $100-1700 \mathrm{~m}$.

The following specimens are intermediate between the two varieties: Veracruz, Mexico, Purpus 6199 (GH, mo, us) and Jamaica, Wilson, Webster \& Rogers 428 ( MO, us).

## KEY TO VARIETIES

Rhizome scales narrowly linear-attenuate, densely and conspicuously pec-tinate-ciliate; median pinnae with $4-6$ pairs of free pinnules

29a. var. Schaffneri. Rhizome scales linear-subulate, sparsely and inconspicuously pectinate-ciliate; median pinnae usually with 1-3 pairs of free pinnae. 29b. var. Nealleyi.
29a. Notholaena Schaffneri var. Schaffneri. Fig. 29a. Map 32.
Aleuritopteris Schaffneri Fourn. Bull. Soc. Bot. France 27: 328. 1880. type: San Miguelito Mts., San Luis Potosí, Mexico, Schaffner 2 P!, photo Gu!, isotype GH!.

Notholaena Nealleyi var. mexicana Davenp. Bot. Gaz. 16: 54. 1891. type: near Guadalajara, Jalisco, Mexico, Pringle 1864 Gh!.

Notholaena Schaffneri var. mexicana Davenp. Gard. \& Forest 4: 519. 1891.

Cheilanthes Schaffneri (Fourn.) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Nuevo León south to Jalisco and Puebla.
Representative specimens: Mexico. Nuevo León: Orcutt 1.304 (us). Tamallipas: Bartlett 10731, 11007 (us); Fisher 3318 (us). Zacatecas: Rose 2662 ( $\mathrm{GH}, \mathbf{k}, \mathrm{us}$ ) . San Luis Potosí: Schaffner 962 ( GH, к, y). Jalisco: Pringle 1864 ( $\mathrm{GH}, \mathrm{K}, \mathrm{mo}, \mathrm{P}, \mathrm{y}$ ), 3880 (b, bM, F, G, GH, K, MO, P, us, Y), 11789 ( $\mathbf{B}, \mathbf{F}, \mathrm{GH}, \mathrm{K}, \mathrm{P}, \mathrm{Us}$ ) ; Palmer 555 ( $\mathbf{B M}, \mathrm{GH}, \mathbf{K}$, ny, p, us, y). Distrito Federal: Schaffner 30 ( b, gh, Ny, p). Puebla: Purpus 3146 (BM, F, GH), 4029 (B, US).

29b. Notholaena Schaffneri var. Nealleyi (Coulter) Weath. Journ. Arn. Arb. 24: 315. 1943.

Fig. 29b. Map 32.
Notholaena Nealleyi Seaton ex Coulter, Contrib. U.S. Nat. Herb.

1: 61. 1890. type: Limpia Canyon, Jeff Davis Co., Texas, Nealley 560 us!, photo ch! (as published, the collection was said to be 894 from the Chinati Mts.).

Cheilanthes Nealleyi (Coulter) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Southern Texas and Coahuila. The literature record in Texas is from Correll in Lundell Flora of Texas $1^{1}, 1955$.

Representative specimens: United States. Texas: Nealley 123 (GH, us), 560 (us); Fisher 6, 305 (us). Mexico. Coahuila: Johnston 7167 (GH); Johnston \& Muller 205 (GH).
30. Notholaena Grayi Davenp. Bull. Torr. Bot. Cl. 7: 50, pl. 4. 1880. Weath. Journ. Arn. Arb. 24: 316. 1943. type: Mts. of se. Arizona, Feb. and March, 1880, Courtis Gh!, photo mo!. Fig. 30. Map 33.

Notholaena hypoleuca Goodding, Muhlenbergia 8: 94. 1912; not Kze. 1834, which is N. tomentosa. Type: Mule Mts., Arizona, Aug. 1911, Goodding 1004 us!, photo GH!.

Cheilanthes Grayi (Davenp.) Domin, Bibl. Bot. 20 (Heft 85) : 133. 1913.

Rhizome ascending, branched, forming rather dense clumps; scales subulate, blackish-castaneous, sclerotic, narrow-celled, with filiform but hard, stiff, sparsely pectinate-serrulate apex and below with very narrow pale margin sparsely ciliate with very slender, weak, pale, deciduous hairs. Fronds ca. $8-22 \mathrm{~cm}$. tall; stipe comparatively stout, pale brown, terete, sparsely beset with scales like those of rhizome but smaller and paler and somewhat glandular, ceraceous, about as long as lamina, with one vascular bundle. Lamina pinnate-pinnatifid, or bipinnate-pinnatifid at base of pinnae, linear-lanceolate, with rather abruptly narrowed obtuse apex, not reduced below, texture coriaceous, upper surface gray-green and sparsely ceraceous, lower with dense ceraceous indument and with pale red-brown, thin, entire-margined scales on midribs and midnerves; rachis like stipe but rather densely ceraceous-glandular and slightly channeled, with scales like those of lamina. Pinnae somewhat distant, 6-10 pairs, deltoid-ovate to deltoidoblong, often as wide as long, the basal pinnules longest, obtuse, with about 4 pairs of segments or pinnules below the broad, lobed apex, these oblong, obtuse, all but the lowest oblique and broadly adnate, entire or shallowly, or the lowest somewhat deeply lobed. Veins 1-2-forked, sporangia (with 32 spores) borne on the flabellately dilated tips, margin more or less revolute, unmodified.

Southern Texas to Arizona, south to Jalisco, cliffs and rocky slopes, ca. $1000-1500 \mathrm{~m}$. The literature records in Texas are from Correll in Lundell, Flora of Texas $1^{1}, 1955$.


Fig. 30-31. Fig. 30. N. Grayi: A, frond, X 0.5; B, upper surface of pinnule, X 4.5; C, underside of pinnule, X 4.5; D, venation of pinnule, X 4.5: all from W. W. Brown 16 (mo). Fig. 31. N. aliena: A, frond, X 0.5 ; B, upper surface of pinna, X 4.5; C, underside of segments (one with scales removed, one with wax and scales removed), X 4.5; all from Pringle 463, in part (GH).

Representative specimens: United States. Texas: Ingram 2392 ( p , us) ; E. J. Palmer 1.3504 (b, us); Nealley 551 S (f, Ny, us). New Mexico: Feb. 1881, Rusby ( $\mathrm{gh}, \mathrm{y}$ ); Feb. 1886, Rusby (b). Arizona: April 7, 1884, Pringle (G, GH, P, US); July 17, 1881, Pringle (G, GH, P, us, y); Feb. 1881, Rushy ( $\mathbf{F}, \mathrm{P}$, US, Y); M. E. Jones 4250 ( $\mathrm{F}, \mathrm{G}, \mathrm{P}, \mathrm{US}$ ); 1880, Courtis (GH, K, y). Mexico. Sonora: Kennedy 7027 (us); Wiggins 7400 (us). Chihuahua: Pringle 463 ( $\mathrm{F}, \mathrm{GH}$ in part, mo, us); Johnston 7880, 7902, 7984 (GH). Coahulla: Palmer 1388 (GH, к, us, y); Johnston \& Muller 926 (Gh). Sinaloa: Oct. 28, 1904, T. S. Brandegee (Gн). Jalisco: Pringle 1864, 5373 (Gн).
31. Notholaena aliena Maxon, Contrib. U.S. Nat. Herb. 17: 605. 1916. Weath. Journ. Arn. Arb. 24: 316. 1943. type: Soledad, sw. of Monclova, Coahuila, Mexico, 1880, E. Palmer 1389 us!, photo GH!. Fig. 31. Map 34.
Rhizome short-creeping, multicipital; scales subulate, blackish castaneous, sclerotic, narrow-celled, with filiform but stiff apex, the margins freely ciliate with weak hairs, with very narrow pale band below apex. Fronds $8-12 \mathrm{~cm}$. tall; stipe comparatively stout, brown
to dark brown, terete, beset with weak, often gland-tipped, hairs and also scales similar to those of the rhizome but paler and less sclerotic, sparingly ceraceous, about as long as lamina, with one vascular bundle. Lamina pinnate-pinnatifid, or bipinnate-pinnatifid at base of pinnac, linear-lanceolate, slightly or not reduced below, texture coriaceous, upper surface slightly ceraceous, with weak whitish hairs (subarachnoid), lower densely whitish ceraceous and midribs and midveins with pale brown, thin, mostly ciliate scales, rachis similar to stipe but slightly channeled. Pinnae ca. $7-10$ pairs, lance-deltoid, the basal pinnules longest or nearly so, rather oblong, entire or pinnatifid into broad lobes. Veins simple to 1 -forked, sporangia (with 16 spores) borne on the subpunctiform tips, margins slightly revolute, unmodified.

This species differs from the closely allied N. Grayi by the whitish hairs on the upper surface of the lamina and the ciliate scales beneath. In N. Grayi the upper surface is ceraceous and the scales beneath are entire.

Southern Texas (one collection) and adjacent Mexico, rocky places.

Specimens examined: United States. Texas: Cutler 661 (mo). Mexico. Chinuahua: Pringle 463 in part (Gh). Coahulla: Palmer 1.389 ( $\mathrm{gh}, \mathrm{k}, \mathrm{us}$ ). Tamaulipas: Bartlett 10999 (us).

## 31A. Notholaena Weatherbiana Tryon, sp. nov.

Rhizoma breve horizontale, paleis subulatis brunneis vel nigrescentibus plerumque scleroticis marginibus longe ciliatis apice filiformi. Frondes 6-15 cm. altae caespitosae, stipes teres rubelle castaneus vel saturate brunneus quam lamina brevior vel aequalis fasciculo vasculari uno tomentosus paleaceus paleis eis rhizomatis similibus nisi plerumque pallidioribus et non scleroticis. Lamina anguste lanceolata vel lanceolata bipinnato-pinnatifida coriacea pagina superiore tomentosa pagina inferiore dense tomentosa ceraceo-glandulosa pallide flava paleis paucis, rhachide eis stipitis similibus nisi leviter canaliculatis. Pinnae 6-11-jugae deltoideae vel oblongo-deltoideae plus minusve subaequilaterales 4-6-jugis loborum obtusorum. Venulae 1-2-furcatae sporangia 32 -sporis in apicibus gerentes, margem immutatus leviter revolutus.
typus: Southwestern Chihuahua, Mexico, Aug.-Nov. 1885, E. Palmer 215 мо!.

This species was not recognized until the manuscript was too advanced to allow a map and drawings to be completed. The figure of the leaf of N. aliena, its closest relative, may be taken as representing the general aspect of this species. From N. aliena
it is sufficiently distinguished by the tomentum on the rachis and upper and lower surfaces of the lamina and the lack of ceraceous glands on the upper surface. In addition to the tomentum, the rachis is moderately scaly and the lower surface of the lamina has a few scales.

The single specimen seen bears no information as to the habitat or the exact locality. Specimens at $\mathbf{b}, \mathrm{k}$ and us of this collection are $N$. incana.

Specimen seen: Mexico. Chihuahua: Palmer 215 (мо).
32. Notholaena Lemmonii D. C. Eaton, Bull. Torr. Bot. Cl. 7: 63. 1880. type: Santa Catalina Mts., near Ft. Lowell, Arizona, April 18, 1880, Lemmon Y!, photo GH!.

Map 35.
Rhizome short, subhorizontal or ascending; scales lanceolate or subulate, dark-castaneous sclerotic and shining, cells not visible, with stiff capillary tip and narrow pale margin with weak cilia. Fronds $10-3.5 \mathrm{~cm}$. tall, clustered; stipe rather stout, shallowly and broadly sulcate above, castaneous to blackish, glabrous except for a few ovate, acuminate, cordate-based scales with brown, sclerotic centers and broad, pale, entire, thin margins, shorter than lamina, with one vascular bundle. Lamina lanceolate or linear-lanceolate or linear, with 10-15 pairs of pinnae, bipinnatifid or partially bipinnate, not narrowed at base or with one pair of somewhat reduced pinnae, rather abruptly narrowed to acute apex, coriaceous, upper surface glabrous, the lower densely white or pale yellowish ceraceous; rachis like stipe, glabrous, strongly sulcate above. Pinnae deltoid to lanceolate, somewhat inequilateral with the lower side broader, broadest near base, acute or subacuminate, with 5 to 7 pairs of linear-oblong, obtuse segments which are broadly adnate and sometimes dilated at base and shallowly lobed, the lobes broad and rounded and connected by a narrow wing along the costa, or the lowest pair separate. Veins 1-2-forked, sporangia (with 64 spores in var. Lemmonii), borne on the flabellately dilated tips, margin revolute, unmodified.

Southeastern Arizona to southern Baja California; south-central Mexico; on slopes and cliffs of igneous rocks, ca. 1000-1500 m.

## KEY TO VARIETIES

Mature stipe and rachis blackish or dark castaneous, rhizome scales lance-
subulate, 2 mm . or more long
32a, var. Lemmonii.
Mature stipe and rachis pale castaneous, rhizome scales lanceolate, scarcely
1 mm . long
32 b . var. australis.

32:. Notholaena Lemmonii var. Lemmonii Fig. 32. Map 35.
Cheilanthes Lemmonii (D. C. Eaton) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

## Southeastern Arizona to southern Baja California.

Representative specimens: United States. Arizona: Spring of 1880, Lemmon ( $\mathbf{F}, \mathrm{GH}, \mathbf{K}, \mathrm{MO}, \mathrm{US}, \mathrm{Y}$ ), in 1881 (BM, G, GH, K, P, US); 1881, Pringle (Gh, K, mo, p, us). Mexico. Baja California: Brandegee 6 (y), 659 (GH, us); Johnston 4019 (us). Sonora: Palmer 266 (BM, GH, K, Us, y) ; Drouet \& Richards 3773 (y), 3809 (y); Wiggins 6160 (Us), 6479 ( $\mathbf{F}, \mathbf{G H}, \mathrm{US}$ ), 7063 (us), 7337 (GH, Us). Chihuahua: Palmer 84 (BM, GH, K, MO, US, Y).

32b. Notholaena Lemmonii var, australis Tryon, var. nov. Map 35.
A varietate typica differt stipitibus rhachidibusque maturis pallide castaneis paleis rhizomatis lanceolatis vix 1 mm . longis.
typus: Coxcatlan, Puebla, Sept. 1909, Purpus 4178 us!.
Other specimens examined: Mexico. Puebla: Schenck 161 (b); Purpus 4026 (в). Oaxaca: Rose, Painter \& Rose 10093 (us); Aug. 14, 1910, Hitchcock (us); Kenoyer 1620 (Gн).
33. Notholaena Rosei Maxon, Contrib. U.S. Nat. Herb, 16: 59. 1912. TyPe: Chapala, Jalisco, Mexico, Oct. 5, 1903, Rose \& Painter 7665 us!, photo GH!.

Fig. 33. Map 36.
Notholaena Lemmonii var. straminea Davenp. Gard. \& Forest 4: 519. 1891. type: near Guadalajara, Jalisco, Mexico, Pringle 28.30 Gh!.

Rhizome short-horizontal; scales lanceolate, acuminate, dark brown or blackish, shining, sclerotic with very narrow irregular, pale, thin margin from which long weak cilia are given off which sometimes become entangled in a sort of loose arachnoid web. Fronds $10-50 \mathrm{~cm}$. tall; stipes stoutish, castaneous at base, stramineous above, somewhat sulcate, with short, stiff gland-tipped hairs on upper side, glabrous on other faces, shorter than lamina, with one vascular bundle. Lamina lanceolate, broadest at base, coriaceous, upper surface sparingly and deciduously whitish ceraceous, the lower densely so; rachis glandular above, like stipe. Pinnae petiolulate 10 or more pairs, the lower 2 or 3 pairs reduced, the basal greatly so, lanceolate or deltoidlanceolate, somewhat inequilateral, the lower side widest, fully pinnate toward base, with pinnatifid apex, lower pinnules linear-lanceolate, deeply pinnatifid below into 3 or 4 pairs of obliquely deltoidovate, obtuse lobes with entire obtuse tip like that of pinna. Veins simple to 1 -forked, sporangia (with 64 spores) borne on the clavate tips, margin revolute, slightly modified.

Rocky hillsides near Guadalajara, Jalisco.
Specimens examined: Mexico. Jalisco: Pringle 2830 (GH); Rose d Painter 7665 (NY, us) ; Palmer 701 (bM, GH, K, MO, Ny, P, US, Y).


Fig. 32-35. Fig. 32. N. Lemmonii var. Lematonii: A, frond, X 0.5, from Pringle in 1881 (м10); B, portion of upper side of rachis, enlarged, from Wiggins \& Rollins 303 ( mo ): C , underside of pinnule and venation, X $4.5 ; \mathrm{D}$, scale from rhizome. X 18: the last two from Pringle in 1881 (mo). Fig. 33. N. Roser: A, frond, X 0.5 : B, portion of stipe, enlarged; C , portion of upper side of rachis, enlarged; D , underside of segments and venation, X 4.5; all from Palmer 701 (mo). Fig. 34. N. leovina: A, frond, X $0.5 ; \mathrm{B}$, underside of pinnule and venation, X 4.5 ; both from Palmer 1381, A ( Gh ) and B (mo). Fig. 35. N. galapagensis: A, frond, X 0.5 ; B, underside of segment and venation, X 4.5 ; C, scale from rhizome, X 9 ; all from Stewart 930 (GH).
34. Notholaena leonina Maxon, Contrib. U.S. Nat. Herb. 16: 58. 1912. Type: Monterrey, Nuevo León, Mexico, Feb. 1880, Palmer 1381 us!, photo GH!.

Fig. 34. Map 37.
Rhizome short, ascending or horizontal, branched; scales lancesubulate with central castaneous, sclerotic, shining, central band and paler, deciduously glandular-ciliate or papillate, thin margin, tipped with a weak, deciduous gland-tipped hair, the glands apparently secreting wax. Fronds $5-10 \mathrm{~cm}$. tall, numerous and clustered; stipes slender, blackish with a few ovate brown scales, glandular-papillate like those of rhizome and somewhat ceraceous-glandular, longer than lamina, with one vascular bundle. Lamina deltoid to deltoid-oblong,


Maps 35-39. Map 35, N. Lemmonii, large dots var. Lemmonii, small duts var. australis. Map 36, N. Rosei. Map 37, N. leonina. Map 38, N. galapagensis. Map 39, N. candida, large dots var. candida, small dots and x's var. Copelandii, half dot intermediate.
narrowed rather evenly and shortly to the blunt tip, bipinnate to bipinnate-pinnatifid or nearly tripinnate at base, texture coriaceous, upper surface thinly, lower densely, ceraceous. Pinnae about 5 pairs, the upper ovate, obtusish with 2-3 pairs of oblong or ovate-oblong, obtuse, entire adnate segments, the lowest distant with the basiscopic pinnules somewhat produced and deeply lobed or pinnate. Veins 1 -forked, sporangia (with 32 spores) borne on the flabellately dilated tips, margin strongly revolute, unmodified.

## Monterrey, Nuevo León.

Specimens examined: Mexico. Nuevo Leóx: Palmer 1381 (Gh, k, Mo, P, US, Y).
35. Notholaena galapagensis Weath. \& Svenson, Bull. Torr. Bot. Cl. 65: 319, t. 9, fig. 2. 1938. type: Iguana Cove, Albemarle Is., Galápagos Islands, Dec. 30, 1899, Snodgrass \& Heller 23 ch!. Fig. 35. Map 38.

Rhizome short, oblique; scales bright-castaneous to brownish, shining, lance-subulate, acuminate, with a very narrow, almost obsolete, paler, serrulate margin which sometimes bears a few cilia, a weak, short, articulate, early deciduous trichome at tip, texture sclerotic, cells narrow, without lumina, their walls thick and somewhat prominent. Fronds $7-15 \mathrm{~cm}$. tall, clustered; stipes slender, castaneous, somewhat shining, terete, near the base with lance-ovate, cordate-based, acuminate, thin, slightly serrulate, nearly concolorous scales their cells elongate-linear except at base, with thin walls, longer than lamina, with one vascular bundle. Lamina ovate or deltoidovate, the lower or second pair of pinnae longest, pinnate-pinnatifid or bipinnate at base, acute or somewhat produced at the pinnatifid apex, texture coriaceous, the veins hidden, upper surface glabrous, lower surface pale vellow or whitish ceraceous. Pinnae 5-7 pairs, the upper narrowly lanceolate or linear, acute, cut nearly to the midrib into deltoid to oblong, oblique, obtuse, mostly entire lobes, the lowest 1 or 2 pairs distant, ovate-lanceolate or deltoid-ovate, inequilateral with 1 or 2 basal pairs of pinnules free and 2 or 3 on the lower side at base somewhat elongate, linear-oblong and deeply lobed, the apex produced into a narrow, shallowly pinnatifid tip, blunt or acutish at the extreme apex. Veins simple or 1 -forked, sporangia (with 64 spores) borne on the clavate to flabellately dilated tips, margin slightly revolute, unmodified.

The lighter colored scales and stipe, the narrowly margined scales and the yellowish indument separate this species from the related $N$. candida.

Galápagos Islands, in rocky places up to 500 m .
Representative specimens: Galápagos Islands. Cuming 110 ( $\mathrm{GH}, \mathrm{K}$ ).

Albemarle: Snodgrass \& Heller 23 (GH); Stewart 930 (GH, us), 931, 932 (us). Indefatigable: Svenson 79 (us). James: Scouler (k). Narborough: Stewart (cas).
36. Notholaena candida (Mart. \& Gal.) Hook. Sp. Fil. 5: 110. 1864. Map 39.

Rhizome short, horizontal, branched; scales lanceolate or lancesubulate, $4-5 \mathrm{~mm}$. long, central dark brown to blackish, sclerotic band rather narrow, paler margin entire to ciliate. Fronds rather few, mostly $10-30 \mathrm{~cm}$. tall; stipe stoutish, blackish to black, terete, rather dull, its scales at base ovate-lanceolate, with a brown center and pale margins, cordate, somewhat longer than the lamina, with one vascular bundle. Lamina ovate-pentagonal, except for the lowest pinnae, bipin-nate-pinnatifid, acute, the apex strongly produced, or not and acuminate, coriaceous, upper surface glabrous, the lower densely white ceraceous. Pinnae 5-10 pairs, lanceolate or linear, acute or acuminate, with 10-12 pairs of linear-oblong, subacute, adnate segments, these entire, crenulate or often broadly and obtusely lobed $2 / 3$ to midribs. Veins 1-2-forked, sporangia (with 64 spores) borne on the flabellate tips, margin somewhat revolute, unmodified.

## Southern Texas to Sonora, south to Honduras.

## KEY TO VARIETIES

Rhizome scales slightly toothed or entire; basal pinnae with two to five elongated and pinnatifid lower pinnules, the other pinnae rather evenly tapering from base to apex; apex of the lamina gradually and evenly contracted

36a. var. candida.
Rhizome scales ciliate; basal pinnae with a single greatly elongated and deeply pinnatifid inner lower pinnule, the other pinnae with more or less parallel sides to near the apex; apex of the lamina abruptly contracted to a more or less well defined terminal pinna

36b. var. Copelandii.
36a. Notholaena candida var. candida. Fig. 36a. Map 39.
Cheilanthes candida Mart. \& Gal. Mém. Acad. Brux. 15: 73, t. 20, fig. 1b. 1842. type: Guadalajara, Jalisco, Mexico, Galeotti 6442 br!. Another specimen of the same number from "Jalisco" is at Br! and others from "Oaxaca and Jalisco" at Br ! and k !.

Aleuritopteris candida (Mart. \& Gal.) Fée, Gen. Fil. 154. 1850-52.
Ceropteris monosticha Fée, Mém. Fam. Foug. 7: 44, t. 22, fig. 2. 1857. type: Orizaba, Schaffner 155, not seen.

Cheilanthes furfuracea Presl ex Koch, Wochen. Gärtn. Pflanzenkr. 1: 3. 1858, based on Cheilanthes candida Mart. \& Gal.

Allosorus furfuraccus Presl ex Koch, Wochen. Gärtn. Pflanzenkr. 1: 3. 1858, in synon.

Cheilanthes monosticha (Fée) Mett. Cheil. no. 4. 1859.
Notholaena monosticha (Fée) Moore, Ind. Fil. 231. 1861.
Notholaena sulphurea var. alba Mett. ex Kuhn, Abhandl. Ges. Halle


Fig. 36-38. Fig. 36. N. candida: 36a, var. candida: A, frond, X 0.5: B, scale from rhizome, X 9: both from Palmer 82 (mo). 36b. var. Copelavdif: A, frond, X (0.5: B, segment, X 4.5; C, scale from rhizome, X 9; all from Meyer $\mathcal{E}$ Rogers 2496 (mo). Fig. 37. N. sulphlrea: A, frond, X 0.5; B, underside of segment and venation, X 4.5; C, scale from rhizome, X 9; all from Meyer \& Rogers 2882 (мо). Fig. 38. N. Standleyi: A, frond, X 0.5 ; B. underside of segment, X 4.5: C. pinna showing venation, X 2.5; all from Cutler 741 (M0).

11: 32. 1869, ex synon. princip., "Mexico."
Chrysochosma candidum (Mart. \& Gal.) Kümm. Magyar Bot. Lapok. 13: 42.1914.

The relation of var. candida and var. Copelandii is discussed under the latter variety.

Western Mexico from northern Sonora to Jalisco, then to Hidalgo and south to Honduras, limestone or igneous cliffs and rocky places, $500-1500 \mathrm{~m}$.

Representative specimens: Mexico. Baja California: Brandegee 657 (Gh, uc). Sonora: Palmer 341 ( $\mathbf{F}, \mathrm{gh}$, us). Chihuahua: Palmer 82 (bm, Gh, ph, us). Sinaloa: Palmer 1569, 1570, 1575 (us). JaLisco: Pringle 11786 ( $\mathbf{B}, \mathbf{F}, \mathbf{~ G H}, \mathbf{K}, \mathbf{P}, \mathrm{Us}$ ) ; Barnes d Land 141 ( $\mathbf{F}, \mathbf{K}$, us); Rose \& Painter 7412 (us); Galeotti 6442 (br, K, p). Hidalgo: V. H. Chase 7155, 7415 ( F ). Puebla: Purpus 3145 (bм, f); Rose, Painter d Rose 9949 (us). Veracruz: Purpus 2771 (b, p). Oaxaca: 1900, Gonzales (p). Guatemala: Maxon \& Hay 3368 (us); O. F. Cook 270 (us); Salvin \& Godman (к); Standley 59221 (F); Bernoulli d Cario 307 ( P ). Honduras: Rodriguez 3259 ( F ).

36b. Notholaena candida var. Copelandii (C. C. Hall) Tryon, comb. nov. Weath. Journ. Arn. Arb. 24: 316. 1943 (as N. candida). Fig. 36b. Map 39.
Notholaena Copelandii C. C. Hall, Amer. Fern Journ. 40: 181, t. 16. 1950. түpe: near Monterrey, Nuevo León, Mexico, Pringle 20.38 uc, not seen; isotype, F !.

There is no doubt that in the northeastern portion of its range Notholaena candida is represented by a distinctive variant but it does not seem possible to maintain this as a species. Each of the characters mentioned by Mrs. Hall in her key which expresses the "typical" conditions shows gradual intergradation from one extreme to the other and to a certain extent without correlation with other characters or geography. The other characters mentioned behave in the same manner; for example, the monosporangiate and oligosporangiate sorus occurs in both varieties, although more commonly in var. Copelandii. Purpus 4877 and 5484 from San Luis Potosí are, at mo and GH , both intermediate between the varieties, having the basal pinnae of var. Copelandii and the lamina apex of var. canclicla. The former collection is also at B, BM, F, and US and the latter at F and us; I have not personally examined them.

Southern Texas to southern Tamaulipas, limestone rocks and rocky slopes, to 1500 m . Reports for New Mexico are evidently based on erroneous or too inclusive labels; for example Wright

820 from Uvalde Co., Texas. The literature records in Texas are from Correll in Lundell, Flora of Texas $1^{1}, 1955$.

Representative specimens: United States. Texas: E. J. Palmer 13609 (в), 10145 (Us), 11011 (Us) ; Reverchon 1626 ( $\mathbf{B}, \mathbf{F}, \mathbf{G H}, \mathbf{P}, \mathrm{US}$ ) ; Jermy 349 (us); Wright 820 (2124) (Gh, к, mo, us, y). Mexico. Coahulla: Palmer 1380 (GH, P, us); Johnston 7205, 8849, 9319 (GH). Nuevo León: Pringle 2038 (F), 13722 (GH, us); Orcutt 1147 (us); Fisher 3 (us). Tamaulipas: Palmer 191 (b, f, gh, us); Bartlett 10586 (bm, f, us); Fisher 3323 (us); Runyon 722 (F); Meyer \& Rogers 2496 (мо).
37. Notholaena sulphurea (Cav.) J. Sm. Bot. Voy. Herald 1: 233. 1854.

Fig. 37. Map 40.
Pteris sulphurea Cav. Descr. 269. 1802. тype: Chimapan (Zimapan), Hidalgo, Mexico, Née ma, seen and verified by C. Chr., see Dansk. Bot. Ark. 93 : 23. 1937; isotype G ! and F !.

Allosorus sulphureus (Cav.) Presl, Tent. Pterid. 153. 1836.
Notholaena cretacea Liebm. Vid. Selsk. Skr. s. 5, 1 (Mex. Bregn.): 216. 1849. type: San Lorenzo, Tehuacán, Puebla, Liebmann c, not seen, fragment $\mathbf{G H}$ !; isotypes k !, $\mathbf{P}$ !.

Aleuritopteris sulphurea (Cav.) Fée, Gen. Fil. 154. 1850-52.
Cheilanthes Borsigiana Reichenb. f. \& Warszew. ex Koch, Wochen. Gärtn. Pflanzenkr. 1: 2. 1858. type: Peru, Warszewicz b!, photo ch!.

Cheilanthes cretacea (Liebm.) Mett. Cheil. no. 5. 1859.
Notholaena candida var. lutea Hook. Sp. Fil. 5: 111. 1864, not Pteris lutea Cav. type: Huánuco, Peru, Mathews 981 к!.

Notholaena sulphurea var. flava Mett. ex Kuhn, Abhandl. Ges. Halle 11: 32. 1869, ex synon. "Peru."

Aleuritopteris cretacea (Liebm.) Fourn. Mex. Pl. 1: 121. 1872.
Notholaena sulphurea var. Borsigiana (Koch) Salomon, Nomencl. Gefässkryp. 258. 1883.

Cheilanthes lepida Phil. Anal. Univ. Chile 94: 355. 1896. type: Copiapó (Caldera, Atacama), Chile, Guill. Geisse sco, not seen, photo Gh!, also in Darwiniana 7: t. 1. 1945.

Chrysochosma sulphureum (Cav.) Kümm. Mag. Bot. Lapok. 13: 41. 1914.

Chrysochosma Borsigianum (Koch) Kümm. Mag. Bot. Lapok. 13: 44. 1914.

Notholaena lepida (Phil.) Looser, Darwiniana 7: 65. 1945.
Rhizome short-horizontal; scales with castaneous sclerotic center and rather narrow, brown, deciduously glandular-ciliate margins. Fronds numerous, crowded, $10-20 \mathrm{~cm}$. tall; stipe terete, blackish, rather dull, below with lance-ovate, also glandular-ciliate, scales, usually much longer than the lamina, with one vascular bundle. Lamina pentagonal, bipinnate-pinnatifid at base, pinnate-pinnatifid above the basal pinnae, coriaceous, upper surface sparingly ceraceous
or glabrous, the lower densely yellow to white ceraceous. Basal pinnae inequilateral, very large, their basiscopic pinnules much produced, segments adnate. Veins 1-2-forked, sporangia (with 32 or 64 spores) borne on their clavate tips, margin thick, somewhat revolute, unmodified.
N. sulphurea differs from N. candida in its pentagonal lamina which is usually not more than $1 / 3$ as long as the stipe and in its glandular-margined (although deciduously so) rhizome scales. $N$. Standleyi is similar in its pentagonal blade but has the pinnae above the basal pair connected at the base so that the lamina is deeply pinnatifid, while in $N$. sulphurea the pinnae are free and the lamina fully pinnate.

The color of the indument varies from white to yellow. It is always of a brighter color on the young fronds and darker on the old; both colors are present on a few specimens, the young fronds being white and the old ones yellow. As the names indicate, the type of $N$. sulphurea is yellow-ceraceous and the type of N. cretacea white. The leaf architecture is also variable, the apex being more or less developed into a terminal pinna or not; and the basal pinnae being rather evenly inequilateral or the lower basal pinnules much produced and the next relatively small.

Sparingly distributed from northeastern Mexico to Chile, in open rocky places and on cliffs, $1500-2500 \mathrm{~m}$.

Representative specimens: Mexico. Nuevo León: V. H. Chase 7769 (F) ; Meyer \& Rogers 2882 (мо). San Luis Potosí: Pringle 3398 (F). Hidalgo: Kenoyer 691 ( F ) ; Née ( $\mathrm{f}, \mathrm{g}$ ). Puebla: Liebmann (k, p, us); Arsène 2356 ( $\mathbf{P}$ ); Purpus 3142 ( $\mathrm{BM}, \mathrm{F}, \mathrm{GH}, \mathrm{US}$ ), 3145 (US), 4028 (us). Oaxaca: Conzatti \& Gomez 2360 (p). Guatemala: Bernoulli \& Cario 307 (в). Panama: 1847, Seemann (вм). Colombia: 1846, Purdic (bar, y). Peru. Huánuco: Macbride 3205 (f), 3707 (f, us); Macbride \& Featherstone 2051 (G, GH, us); Stork \& Horton 9395 ( $\mathbf{F}$ ); Pearce 501 (k); Mathews 981 (k). Lima: Safford 993 (us); Macbride \& Featherstone 426 ( c , Us). Chile: Gillies (k).
38. Notholaena Standleyi Maxon, Amer. Fern Journ. 5: 1. 1915, based on N. Hookeri D. C. Eaton. Weath. Journ. Arn. Arb. 24: 316. 1943.

Fig. 38. Map 41.
Notholaena candida var. quinquefido-palmata Hook. Sp. Fil. 5: 111. 1864. type: La Cuesta, New Mexico, Bigelow k!, photo ch!.

Notholaena Hookeri D. C. Eaton, in Wheeler, Rept. U.S. Geol. Surv. W. 100th Merid. 6: 308, t. 30. 1879, based on N. candida var. quinquefido-palmata Hook.; not Lowe, 1856, which is N. chilensis.

Cheilanthes Hookeri (D. C. Eaton) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.


Maps 40-44. Map 40, N. sulphurea. Map 41, N. Standleyi. Map 42, N. aurantiaca. Map 43, N. californica. Map 44, N. neglecta.

Chrysochosma Hookeri (D. C. Eaton) Kümm. Mag. Bot. Lapok. 13: 41.1914.

Notholaena sulphurea var. quinquefido-palmata (Hook.) Farwell, Amer. Midl. Nat. 12: 284. 1931.

Rhizome short-horizontal, freely branched, multicipital; scales ca. 3 mm . long with broad, thick, blackish, shining, sclerotic central band and dark brown, entire, thin margin, lance-subulate, acute. Fronds numerous, ca. $10-20 \mathrm{~cm}$. tall, approximate; stipe terete, castaneous, shining, with one vascular bundle, with a few ovate, entire, cordatebased scales with narrow, sclerotic central band and very broad, brown margins. Lamina pentagonal, with the basal pinnae pinnate-pinnatifid and larger than the part above, coriaceous, upper surface glabrous, the lower densely vellow ceraceous. Basal pinnae inequilateral, the much elongated basal pinnules on the lower side deeply pinnatifid into linearoblong to elliptic, entire, obtuse, segments. Veins 1-2-forked, sporangia (with 16 to 32 spores) borne on their usually slightly clavate tips, margin unmodified, slightly reflexed.

The differences from the related and often similar $N$. sulphurea are discussed under that species.

Southeastern Colorado to Texas and southern Nevada, south to east-central Mexico, on cliffs and rocky slopes and at the base of limestone, sandstone or igneous rocks, $400-2200 \mathrm{~m}$. The literature records in Texas are from Correll in Lundell, Flora of Texas $1^{1}, 1955$.

Representative specimens: United States. Colorado: May 1, 1926, F. C. Greene (us). Окlahoma: O. M. Clark 3800 (в); Stevens 462 (k, us), 1043 ( GH, us). Texas: M. E. Jones 3749 (bM, K, P, us); Reverchon 1218 (b, P, us); Moore \& Steyermark 3022 (GH, US) ; E. J. Palmer 30.553, 34151, 3423.3a (Us); Wright 821 (вм, Gн, к, мо, us). New Mexico: Bigelow (к, y); Wooton 100 (b, к, p, us); Mulford 117 (k); Arsène 17379 (us), 18762 (k, p, us). Arizona: A. du R. A. Nelson 1172 (к) ; Eastwood 15947 (bм, к) ; April 7, 1881, Pringle (GH, к, P, us, y). Nevada: April, 1924, D. F. Hewett (us). Mexico. Baja California: Rose 16721 (us); Shreve 7042 (Gh, us). Sonora: Wiggins 6050 (vS) ; Lumholtz Exped. 361 ( $\mathbf{F}, \mathrm{GH}, \mathbf{K}$, US), 48.3 (k, US). CHirhuahua: Pringle 467 (F); Stewart 794, 2618 (GH); Johnston 7895,
 к, Us), 754 ( $\mathrm{GH}, \mathrm{US}$ ), 1.379 ( $\mathbf{\kappa}, \mathrm{P}, \mathrm{US}, \mathrm{Y}$ ); Wynd \& Mueller 467 (GH, US); Stewart 330, 347, 624 (GH); Johnston 7744 (GH); Stanford et al. 89 (Gh). Tamaulipas: Burtlett 10708 (us). Durango: Purpus 4632 (us); Palmer 2.57 (GH, us); Reko 5226 (us). San Luis Potosí: Orcutt 1852 (us); Parry 992 ( $\mathbf{f}, \mathbf{k}, \mathbf{P}, \mathrm{us}, \mathrm{y}$ ). Hidalgo: Rose, Painter d Rose 9107 (us). Puebla: Purpus 4027 (b, BM, F, GH, K, US).
39. Notholaena aurantiaca D. C. Eaton, Proc. Amer. Acad. 22: 462. 1887. Type: near Guadalajara, Jalisco, Mexico, 1886, Palmer 83 y!, photo GH !. Fig. 39. Map 42.
Rhizome very slender, $1-2 \mathrm{~mm}$. in diameter, creeping; scales lancesubulate from a shallowly cordate base, thick, rigid, dark castaneous to blackish, ca. 2 mm . long, tapering to a stiff, spinescent apex, shining, entire. Fronds approximate but not densely clustered ca. 6-16 cm . tall; stipe slender, castaneous, terete, more or less densely beset with small ( 1 mm . or less) lanceolate, acute, thin, entire, pale brown or whitish scales, much longer than lamina, with one vascular bundle. Lamina pentagonal, broader than long, bi-tripinnatifid, with 5-10 pairs of pinnae, the basal much enlarged, texture thin, upper surface sparsely beset with thick and blunt, usually short, trichomes, the lower with orange-ceraceous indument covered by numerous cinnamoncolored, thin, deltoid-ovate, acute, entire, scales. Pinnae, above the basal pair, lanceolate to narrowly oblong, pinnatifid, acute, the segments ca. $4-10$ pairs, entire or lobed, deltoid to ovate-deltoid. Veins mostly 1 -forked, sporangia (with 32 spores) borne on their slightly clavate tips, margin unmodified.

## Dry, shaded cliffs, Jalisco.

Specimens examined: Mexico. Jalisco: Palmer 83 (bir, ch, к, mo, P, US, Y) ; Pringle 1840 ( $\mathrm{F}, \mathrm{GH}, \mathrm{Y}$ ), 2587 ( $\mathrm{B}, \mathrm{BM}, \mathrm{F}, \mathrm{G}, \mathrm{GH}, \mathrm{K}, \mathrm{MO}, \mathrm{P}, \mathrm{US}$ ), 5405 (GH, P), Oct. 16, 1903 (P).
40. Notholaena californica D. C. Eaton, Bull. Torr. Bot. Cl. 10: 27. 1883. lectotype: Spring Vallev, San Diego Co., California, 1878, Miss A. L. Burbeck Y!, photo Gi!.

Fig. 40. Map 43.
Notholacna albida Prantl, in Engl. Bot. Jahrb. 3: 405. 1882, nomen nudum.

Notholaena candida var. accessita Jepson, Man. Fl. Pl. Calif. 27. 1925. type: Upper Vallecito, San Diego Co., California, Jepson 8031 uc or Jeps, not seen, illustrated in Amer. Fern Journ. 32: t. 10, fig. c. 1942.

Notholaena sulphurea var. californica (D. C. Eaton) Farwell, Amer. Midl. Nat. 12: 283. 1931.

Notholaena sulphurea var. accessita (Jepson) Farwell, Amer. Midl. Nat. 12: 283. 1931.

Notholaena californica ssp. nigrescens Ewan, Amer. Fern Journ. 32: 93, t. 10, fig. b. 1942. type: San Gabriel Canyon, Los Angeles Co., California, L. C. Wheeler 878 ewan hb., not seen.

Notholaena californica f. accessita (Jepson) Ewan, Amer. Fern Journ. 32: 95. 1942.

Rhizome short, horizontal, multicipital; scales linear-subulate ( $4-5 \mathrm{~mm}$. long) with shining, castaneous, excurrent, sclerotic central
band, the apical capillary portion rather long and distinctly, although sparsely, pectinate-denticulate, the lower part with a narrow, paler, erose-denticulate, subciliate, thin margin. Fronds ca. $3-13 \mathrm{~cm}$. tall; stipe terete, rather slender, castaneous, more or less ceraceous-glandular, with a few lance-subulate scales rather like those of rhizome but with more nearly entire margin, commonly much longer than lamina, with one vascular bundle. Lamina broadly pentagonal, acute to shortacuminate, with 4-5 pairs of pinnae, the lowest inequilaterally broadly deltoid, coriaceous, upper surface ceraceous-glandular, lower whitish to usually yellow ceraceous. Pinnae above basal pair lanceolate, segments sessile but not adnate, oblong to suborbicular, very obtuse. Veins 1 -forked, sporangia (with 32 spores) borne on their definitely clavate tips, margin revolute, unmodified.

Arizona and southern California to southern Baja California, in rock crevices and on rocky hillsides, $300-1000 \mathrm{~m}$.

Representative specimens: United States. Arizona: Aug. 1882, Lemmon (G, P, Y); 1894, Toumey (NY, y); Wiggins 6577 (F, US). California: 1876, Parry \& Lemmon (bM, F, GH, us); Parish $502 a$ (B, PR, US), 4739 (US); Kimball 21 ( $\mathrm{MO}_{2}$ US); Johnston 1052 (US); Vasey 691 (us); 1878, Burbeck (Gh, K, y). Mexico. Baja California: Palmer 748 (P, US); Orcutt 1461 (F, GH, Y); Shreve 6830, 7047 (US); Johnston 3460 (US), 3916 (F, US), 4007, 4020, 4032, 4185 (US). Sonora: Palmer 552 (bm, Gh, k, us, y).
41. Notholaena neglecta Maxon, Contrib. U.S. Nat. Herb. 17: 602. 1916. Weath. Journ. Arn. Arb. 24: 316. 1943. TYpe: vicinity of Saltillo, Coahuila, Mexico, 1902, Palmer 324 us!, photo gh!. Fig. 41. Map 44.

Rhizome horizontal, short-creeping; scales lance-subulate ( 2 mm . long) with rather broad, castaneous or blackish, sclerotic central band which is produced into a somewhat flexuous, stiff, capillary tip sometimes with a few rigid, narrow teeth, with a thin, brown, erosedenticulate sparsely and moderately short-ciliate margin nearly as broad. Fronds ca. 3-10 cm. tall; stipe mostly terete, blackish, glabrous except for a few ovate to lanceolate, entire, pale, brown scales with dark center, longer than lamina, with one vascular bundle. Lamina elongate-pentagonal, acuminate, tri- to quadripinnate at base with about six pairs of pinnae, coriaceous, upper surface glabrous or very slightly ceraceous-glandular, the lower with whitish ceraceous indument; rachis blackish to castaneous. Upper pinnae lanceolate, pinnate, the basal much larger and strongly inequilateral, the basiscopic pinnules on the lower side much produced; segments sessile but not adnate, cordate at base, very obtuse, oblong to suborbicular. Veins simple or 1-forked, sporangia (with 32 spores) borne on their clavate to clavate-punctiform tips, margin unmodified, strongly revolute.


Fig. 39-43. Fig. 39. N. aurantiaca: A, frond, X 0.5; B, underside of segment and venation, X 2.5; both from Palmer 83 (mo). Fig. 40. N. califorvica: A, frond, X $0.5 ; \mathrm{B}$, portion of rachis, enlarged; C , upper surface of segment, $\mathrm{X} 7: \mathrm{D}$, segment, X 4.5; E, scale from rhizome, X 9; all from Kimball 21 (mo). Fig. 41. N. neglecta: A, frond, X 0.5, from Palmer 324 (мо); B, upper surface of segment, X 9; C, segment, X 9; the last two from Pringle 452 (mo). Fig. 42. N. Greggii: A. frond, X 0.5 ; B, segment, X 7; C, scale from rhizome, X 18; all from Palmer 1383 (мо). Fig. 43. N. bryopoda: A, frond, X 0.5, from Pringle 8802 (mo); B, segment, X 7; C, scale from rhizome, X 8; the last two from Johnston 8354 (мо).

Southern Texas and southeastern Arizona, Chihuahua and eastern Coahuila, limestone cliffs and rocks. The literature records in Texas are from Correll in Lundell, Flora of Texas $1^{1}, 1955$.

Specimens examined: United States. Texas: Ripley \& Barneby 4103 (ch, us). Arizona: Aug. 1882, Lemmon (bm, f, us); Goodding 1384 (us) ; R. D. Camp 2540 ( $\mathrm{F}, \mathrm{us}$ ). Mexico. Chihuahua: Pringle 452 (b, bм, f, G, GH, K, мо, P, pr, us, y). Coahula: Palmer 324 (bm, ch, mo, us), 424 (bм, gh, us); Johnston \& Muller 822 (сн); Stewart 2894 (Сн); Johnston 8775, 9.319a (сн); M. E. Jones 520 (мо, us).
42. Notholaena Greggii (Kuhn) Maxon, Contrib. U.S. Nat. Herb. 17: 606. 1916. Weath. Journ. Arn. Arb. 24: 317. 1943.

Fig. 42. Map 45.
Pellaea Greggii Mett. ex Kuhn, Linnaea 36: 86. 1869. type: Mapimi, Durango, Mexico, April 17, 1847, Gregg 467 в!, photo Gh!.

Notholaena Pringlei Davenp. Bull. Torr. Bot. Cl. 13: 132, t. 58. 1886. lectotype: (by Maxon in Contrib. U.S. Nat. Herb. 17: 607. 1916) : Santa Eulalia Mts., Chihuahua, Mexico, April 23, 1885, Pringle 441 Gh!, photo mo!.

Allosorus Greggii (Kuhn) O. Ktze. Rev. Gen. 2: 806. 1891. (ms. in Herb. by Mett., in synonymy of Pellaea Greggii by Kuhn).

Cheilanthes Davenportii Domin, Bibl. Bot. 20 (Hंeft 85) : 133. 1913, based on N. Pringlei Davenp., not Ch. Pringlei Davenp.

Rhizome short-repent or suberect; scales subulate with black, shining, sclerotic central band and pale brown, hyaline, nearly entire margin, the capillary tip short and weak. Fronds ca. $4-20 \mathrm{~cm}$. tall, clustered; stipe somewhat sulcate or angled above, pale brown, dull, glandular with a few lance-ovate scales with narrow brown center and broad, pale margins, about as long as lamina, with one vascular bundle. Lamina narrowly deltoid or deltoid-lanceolate, the lowest pinnae longest, bipinnate to bipinnate-pinnatifid, with $6-8$ pairs of pinnae, apex long-acuminate, pinnate to very tip, coriaceous, upper surface ceraceous-glandular, lower white-ceraceous; rachis like stipe, without scales. Pinnae lanceolate, nearly equilateral, with about 5 pairs of sessile but not adnate, non-articulate, cordate-ovate, obtuse, entire to pinnatifid pinnules. Veins simple or 1 -forked, sporangia (with 64 spores) borne on their clavate to punctiform tips, margin strongly revolute, unmodified.

Southern Texas, Coahuila, Chihuahua and Durango, rocky calcareous slopes and ledges, frequent on gypsum but not confined to it, $200-1800 \mathrm{~m}$.

Specimens examined: United States. Texas: Moore d Steyermark 3448 (Gh, us). Mexico. Chimuahua: Pringle 441 ( $\mathbf{~}$, bm, G, GH, к, mo, p, us, y), 856 (mo); Stewart 2614 (GH). Coahuila: Hinton

16562 (GH); Palmer 1382 (GH, K, P, US, Y), 1383 ( $\mathbf{B}, \mathrm{GH}, \mathrm{K}, \mathrm{P}, \mathrm{US}, \mathrm{Y}$ ); M. E. Jones 519 (us); Wynd 747 (GH, us); Purpus 4633 (GH); Johnston \& Muller 206, 774, 817, 833, 994 (GH); Johnston $8503(\mathrm{GH})$; Stewart 2693, 2743, 2831, 2906 (GH). Durango: Gregg 467 (b, GH, aro); Shreve 9113 ( GH ); Chaffey 58 in part (us).
43. Notholaena bryopoda Maxon, Proc. Biol. Soc. Wash. 15: 205. 1905. Weath. Journ. Arn. Arb. 24: 317. 1943. type: 15-20 miles south of Doctor Arroyo, Nuevo León, Mexico, Pringle 8802 us!, photo ch!. Fig. 43. Map 46.
Cheilanthes bryopoda (Maxon) Domin, Bibl. Bot. 20 (Heft 85): 133. 1913.

Notholaena brachypoda Conzatti, Fl. Tax. Mex. 12: 72. 1939, no latin description; based on a sheet of Pringle 8802. (N. brachypoda Davis, Life and Work of C. G. Pringle, 591. 1936, nomen).

Rhizome very compact, strongly multicipital; scales subulate with brown, shining, subsclerotic, usually narrow central band and broad, pale, hyaline margins, the tip filiform, the margins entire. Fronds $4-15 \mathrm{~cm}$. tall, clustered; stipe terete at base to shallowly sulcate above, brown to dark brown, with long-subulate, brownish scales, otherwise glabrous, shorter than the lamina, with one vascular bundle. Lamina bipinnate to tripinnate, with some 6-8 pairs of pinnae, the apex very gradually reduced, broadest at base, upper surface glabrous, the lower pale yellow ceraceous; rachis similar to stipe, shallowly sulcate, glabrous. Pinnae mostly strongly ascending, the basal longest, segments oblong to long-oblong, very short-stalked, subcordate. Veins simple to 1 -forked, sporangia (with 64 spores) borne on their longclavate tips, margin strongly revolute, unmodified.

Coahuila and Nuevo León, most commonly on gypsum and perhaps confined to it.

Specimens examined: Mexico. Coahuila: Johnston d Muller 243 (GH); Stewart 839, 2732 (GH); Johnston 8354, 8488 (GH). Nuevo León: V. H. Chase 7678 (f); Pringle 8802 (в, bм, f, G, GH, K, mo, P, PR, US).
44. Notholaena Palmeri Baker, Hook. Icon. Pl. 17 (s. 3, 7) : t. 1678 \& text. 1887. Type: Mts. of San Luis Potosí, Mexico, 6-8000 ft., Parry \& Palmer 991 k!, photo cu!.

Fig. 44. Map 47.
Rhizome short-creeping, compact; scales lanceolate to lanceolatelinear, light brown, concolorous, or somewhat darker toward the base, entire. Fronds clustered, (3-) 10-15 cm. tall; stipe terete, blackish, slightly ceraceous, shining, shorter than the lamina, with one vascular bundle. Lamina mostly bipinnate, to tripinnate at the base, linear, with about $8-12$ pairs of pinnae, the basal somewhat reduced and often distant, the upper surface sparingly white cera-
ceous, the lower densely so; rachis similar to stipe. Pinnae oblong-ovate, segments non-articulate, mostly oblong, obtuse, the apical sessile, the basal stalked and with the dark sclerotic color of the stalk entering their base. Veins 1-2-forked, sporangia (with 64 spores) borne nearly the whole length of the vein, margin unmodified.

This species differs from $N$. pallens, into which all collections previously associated with the type of N. Palmeri are placed, by its blackish stipe and rachis and the lack of scales on the glabrate rachis. In N. pallens the stipe and rachis are castaneous to dark castaneous and the rachis is ceraceous-glandular with a few small reddish scales.

San Luis Potosí, ca. 2500 m.


Fig. 44-45. Fig. 44. N. Palmeri: A, frond, X 0.5; B, scale from stipe, X 9: C, underside of segment, X 7; all from Palmer 991 (Gh). Fig. 45. N. paldens: A, frond, X 0.5 ; B, portion of rachis, enlarged; C, underside of segment (wax removed at base). X 7; all from Palmer 465 (GH).

The only collection: Mexico. San Luis Potosí: Parry \& Palmer 991 (GH, K, P, MO, US, Y).
45. Notholaena pallens Weath. ms., spec. nov. Fig. 45. Map 48.

Rhizoma breve erectum vel plus minusve decumbens, paleis ad 7 mm . longis brunneis concoloribus firmis nec siccitate tortis lanceolato-
subulatis integris ad apicem capillarem gradatim angustatis dense onustum. Frondes dense caespitosae $4-20 \mathrm{~cm}$. altae, stipes ex comparatione robustus teres castaneus fasciculo vasculari uno ceraceo-glandulosus et paleas parvas lineari-lanceolatas longe acuminatas saturate brunneas sparse gerens. Lamina linearis vel lanceolatolinearis plerumque quam stipes valde longior bi- vel subtripinnata apice obtusa ad basem leviter angustata pagina superiore ceraceoglandulosa pagina inferiore dense albo-ceracea, rhachide eis stipitis similibus nisi plerumque dense glandulosis et sparsissimis paleaceis. Pinnae ca. 12-jugae fere aequilaterales late deltoideo-ovatae pinnula terminali rhomboidea obtusa trilobata pinnulis lateralibus $1-2$-jugis oblongis obtusis sessilibus (non adnatis) segmentis non articulatis jugo basali plerumque lobatis vel pinnatis. Venulae 1-2-furcatae sporangia 64 -sporis per $1 / 2$ longitudinem gerentes, margem immutatus.
typus: Sandia Station, Durango, 6800 ft ., Oct. 12, 1905, Pringle 10149 GH !.

This species has been universally accepted as N. Palmeri except by a single anonymous commentator at Berlin who, without the type collection of that species at hand, expressed doubt as to the proper inclusion of Pringle 10149 and W. Schumann in it. The differences from N. Palmeri are presented in the key and in the discussion under that species.

Chihuahua south to Puebla, cliffs and ledges, often or perhaps usually on limestone, $2300-2800 \mathrm{~m}$.

Representative specimens: Mexico. Chihuahua: Pringle 1440 ( F , gh, k, p, ny, us). Durango: Palmer 471 ( $\mathrm{F}, \mathrm{gh}, \mathrm{P}, \mathrm{Ny}, \mathrm{us}$ ); Pringle 10149 (B, F, G, GH, MO, NY, P, PR); Palmer 465 (P, US). Jalisco: Palmer 541 (k, ay, p, us, y) ; Pringle 11899 (Gh, us). Guanajuato: Haage d Schmidt 1897 (k). Hidalgo: Pringle 13643 ( $\mathbf{p}$, us). Puebla: Purpus 3147 ( $\mathrm{F}, \mathrm{GH}, \mathrm{NY}, \mathrm{US}$ ), 4026 ( G in part, P ).
46. Notholaena pilifera Tryon, spec. nov.

Fig. 46. Map 49.
Rhizoma breve horizontale, paleis lanceolatis integris plerumque pallide brunneis concoloribus vel obscurioribus ad basem. Frondes ca. $8-10 \mathrm{~cm}$. altae, stipes teres nigrescens valde curvus quam lamina plus minusve brevior decidue cera albis paleis paucis eis rhizomatis similibus nisi lanceolato-subulatis trichomatibus longis laxis articulatis fasciculo vasculari uno. Lamina oblonga ad basem non vel leviter reducta plerumque bipinnata vel bipinnato-pinnatifida pagina superiore decidue ceraceo-glandulosa pagina inferiore dense ceraceo-glandulosa trichomatibus laxis articulatis, rhachide eis stipitis similibus. Pinnae 7 -10-jugae deltoideae vel oblongae obtusae non articulatae segmentis basis plus minusve brevi petiolulatis segmentis


Maps 45-53. Map 45, N. Greggii. Map 46, N. bryopoda. Map 47, N. Palmeri. Map 48, N. pallens. Map 49, N. pilifera. Map 50 , N. chilensis. Map 51, N. peninsularis. Map 52, N. Jonesii. Map 53, N. Lumholtzii.
apicis late sessilibus. Venulae 1-2-furcatae sporangia 64 -sporis per $1 / 2-2 / 3$ longitudinem gerentes, margem immutatus.
typus: Pueblo del Tepozteco, Morelos, Mexico. José Sanchez S. 98 us!.

This species is related to N. Palmeri, N. pallens, and N. peninsularis; it is distinguished from them in the key. The trichomes on the stipe and rachis and lower surface of the lamina are its most distinctive feature; the stipes are strongly curved in the type-collection but this may be a character of the individual rather than the species.

Morelos.
Specimens seen: Mexico. Morelos: Sanchez 98 (GH, us).
47. Notholaena chilensis (Fée \& Remy) Sturm, Enum. Pl. Vasc. Crypt. Chilens. 16. 1858.

Fig. 47. Map 50.
Cincinalis chilensis Fée \& Remy, in Gav, Hist. Chile (Bot.) 6: 497. 1853. type: Juan Fernández Is., collector and whereabouts unknown.

Notholaena Hookeri Lowe, Ferns Brit. \& Exot. 1: 59, 33, t. 13. 1856, not D. C. Eaton, 1878, which is N. Standleyi. lectotype: spec. cult. Riley k!, photo GH!; also at k! are Hb. Wentworth and Wollaton Hall, also cult.

Cincinalis Hookeri (Lowe) J. Sm. Ferns Brit. \& For. 178. 1866.
Pellaea chilensis (Fée \& Remy) C. Chr. Ind. Fil. 479. 1906. (Fée, Gen. Fil. 129. 1850-52, nomen nudum).

Rhizome stout, upright; scales linear, 3 mm . long, bright brown, thin, dull, entire margined, tipped with an articulate trichome. Fronds clustered, ca. $5-15 \mathrm{~cm}$. tall; stipe dark castaneous, terete, glabrous, about as long as the lamina, with one vascular bundle. Lamina ovate, broadest at the base or at the second pair of pinnae, acute, tripinnate, with about 5 pairs of pinnae, coriaceous, the upper surface glabrous, the lower densely white ceraceous. Pinnae ovate-lanceolate or ovate, acutish, short-petiolulate, terminal segments rhomboid, 3lobed, the next pair oblong, entire, the other pinnules pinnate with the ultimate segments oblong, obtuse, rather broadly sessile at the subcuneate base, non-articulate, color at the base uniform. Veins 1-2forked, sporangia (with 64 spores) borne on the apical $1 / 3$ or $1 / 4$ of the vein, margin more or less revolute, unmodified.

Juan Fernández Islands, dry, exposed, rocky places, 20-40 m.
Representative specimens: Chile. Juan Fernández Is.: (Masatierra) Bertero 1410 (G), 1519 (B, P), 1549 (GH, K); Skottsherg 100 ( $\mathbf{F}, \mathbf{K}$, P, US), 473 (B); Philippi 1090 (B). (Masafuera) Germain; and Skottsberg 410 are cited by C. Chr. \& Skottsb. Pterid. Juan Fernánd. Is., Nat. Hist. Juan Fernánd. \& Easter Is. 2: 30. 1920.


Fig. 46-49. Fig. 46. N. pilifera: A, frond, X 0.5; B, portion of rachis, enlarged; C, underside of segment (wax removed at base), X 4.5; all from Sanchez 98 (GH). Fig. 47. N.chilensis: A, frond, X 0.5 ; B, underside of segment (wax removed at base), X 7; both from C. \& I. Skottsberg 100 (s-pa). Fig. 48. N. peninsularis: A, frond, X $0.5: \mathrm{B}$, portion of stipe, enlarged; C , underside of segment (wax removed at base), X 2.5; all from Brandegee in 1890 (GH). Fig. 49. N. Jonesit: A, frond, 0.5 ; B. underside of segment, X 4.5 ; both from Phillips 2934 (мо).
48. Notholaena peninsularis Maxon \& Weath. Contrib. Grav Herb. 127: 15. 1939. Type: Sierra de la Laguna, from San Bernardo to El Sanz, Baja California, Mexico, 3500 ft., Jan. 21, 1906, Nelson du Goldman 7430 us!, photo GH!.

Fig. 48. Map 51.
Rhizome short, horizontal or ascending; scales concolorous, castaneous or pale brown, slender, drying tortuous, linear-subulate, longacuminate, entire, to 5 mm . long. Fronds many, ca. $15-30 \mathrm{~cm}$. tall; stipe terete, blackish or dark castaneous, shining, more or less scaly below, scales similar to those of the rhizome but smaller, shorter than to about as long as the lamina, with one vascular bundle. Lamina ovate or ovate-lanceolate, bipinnate-pinnatifid, lowest pair of pinnae slightly reduced, obtusely or subabruptly narrowed to the apex, the upper surface sparsely and minutely ceraceous-glandular, the lower surface densely white-ceraceous; rachis similar to the stipe, more or less ceraceous-glandular, and sparsely beset with small, slender, linear-acuminate scales. Pinnae remote, ca. 8-10 pairs, lanceolate or oblong, obtuse, petiolulate, pinnules oblong-ovate or most of the larger ones deltoid, segments non-articulate (or mostly so), the dark color of the stalk passing into the base of the segments, rarely stopping abruptly at the base. Veins 1-2-forked, sporangia (with 64 spores) borne on the apical $1 / 2$ or $1 / 3$ of the vein, margin unmodified.

This species is separated from its non-articulate relatives by its blackish stipe and rachis, the latter ceraceous and bearing a few scales, and most of the primary pinnules being sessile or short-petiolulate. From N. incana, to which it is also closely related, it differs especially by the ceraceous and slightly scaly rachis.

Southernmost Baja California, dry rocky places, ca. 1200 m .
Specimens examined: Mexico. Baja California: Nelson du Goldman 7430 (us); Jan. 21, 1890, Brandegee (GH); Jan. 24, 1890, Brandegee (us); Brandegee 650 (GH, Ny), 656 (us); M. E. Jones 24154 ( $\mathrm{mO}, \mathrm{NY}$ ).
49. Notholaena Jonesii Maxon, Amer. Fern Journ. 7: 108. 1917. type: Panamint Canyon, Inyo Co., California, 4000 ft ., May 4, 1897, M. E. Jones us!, photo ch!. Fig. 49. Map 52.
Pellaea Jonesii (Maxon) Morton, Amer. Fern Journ. 40: 251. 1950.
Rhizome short, erect; scales linear-subulate, bright brown, thin, concolorous. Fronds cespitose, ca. $5-15 \mathrm{~cm}$. tall; stipe terete, castaneous, shining, glabrous, usually shorter than to about as long as the lamina, with one vascular bundle. Lamina ovate-lanceolate to ob-long-ovate, acute, not narrowed at base, bipinnate, or rarely tripinnate
at base, with 4-6 pairs of pinnae, coriaceous-fleshy, both surfaces glabrous. Pinnae ovate or deltoid-ovate, obtuse or acutish, with 2-3 pairs of deltoid to ovate, obtuse, cordate to truncate pinnules, these entire or rarely lobed, or the basal pinnate, segments nonarticulate, dark color of the stalk passing into the base. Veins 1-2forked, sporangia (with 64 spores) borne on the apical $1 / 3$ of the veins, margin unmodified.

This species and the next, $N$. Lumholtzii, both lack indument and are easily distinguished from their close relatives by this character. N. parvifolia and N. formosa which also lack indument have articulate segments. In $N$. Jonesii the stipe and rachis are castaneous to brownish, the axes of the lamina not glaucous, while in N. Lumholtzii the stipe and rachis are blackish and the axes, especially the pinna-rachises, are glaucous.

Arizona, southwestern Utah and southern California, crevices and ledges of limestone and igneous cliffs, $900-1900 \mathrm{~m}$. The literature records in Arizona are from Morton in Kearney \& Peebles, Arizona Flora, 1951.

Representative specimens: United States. Utah: M. E. Jones 5004d (us); Palmer 500 (GH, K, y). Arizona: Phillips 2928, 2934 (GH, mo). California: Parish \& Parish 1242 (GH, us); Munz, Johnston \& Harwood 4232 (US); L. C. Wheeler 2000 (us); Duran 2633 (G, GH, мо).
50. Notholaena Lumholtzii Maxon \& Weath. Contrib. Gray Herb. 127: 16. 1939. type: Huehuerachi, Sonora, Mexico, 4000 ft ., Dec. 7, 1900, Hartman (Lumholtz Exped.) 298 us!. Fig. 50. Map 53.

Rhizome short, erect; scales linear-ligulate, long-acuminate, ca. 4 mm . long, entire, slender, in drying more or less crispate, rufousbrown, concolorous. Fronds tufted, $7-15 \mathrm{~cm}$. tall; stipe slender, terete, black, more or less glaucous, glabrous, shorter than the lamina, with one vascular bundle. Lamina deltoid-lanceolate or deltoidovate, bipinnate, pinnate toward the apex, no part pinnatifid, herbaceous or subcoriaceous, glabrous, glaucous-green; rachis similar to the stipe. Pinnae subopposite or alternate, remote, about 7 pairs, oblong, pinnules remote, all simple, entire, the terminal deltoid, truncate at the base or broadly cuneate, the apex obtuse, lateral 1-4 pairs mostly oblong or deltoid-ovate, obtuse, short-petiolulate, nonarticulate, dark color of the stalk passing into the segment. Veins 1 -2-forked, sporangia (with 64 spores) borne on the apical $1 / 2$ or $1 / 3$ of the vein, margin unmodified.

The differences from the closely related $N$. Jonesii are discussed under that species.

Sonora, 1300 m .


Fig. 50-53. Fig. 50. N. Lumholtzii: A, frond, X 0.5; B, underside of segment, X 4.5; both from Hartman 298 (GH). Fig. 51. N. limitanea: 51 a. var. limitanea: A, frond, X $0.5 ; \mathrm{B}$, underside of segment, X 4.5 ; both from Pringle 1583 (mo). 51 b . var. mexicana: frond, X 0.5, from Rushy in 1880 (mo). Fig. 52. N. dealbata: A, frond, X 1, from Bush 132 (mo); B, underside of segment (wax removed along midnerve), X 7, from Steyermark 22966 (mo). Fig. 53. N. Fendleri: A, frond, X 0.5, from O. M. Clark 10035 (mO); B, underside of segment (wax removed at base), X 7, from O. M. Clark 9704 (MO).

Specimens seen: Mexico. Sonora: Hartman (Lumholtz Exped.) 298 (GH, US); Lloyd (Lumholtz Exped.) 489 (GH).
51. Notholaena limitanea Maxon, Amer. Fern Journ. 9: 70. 1919. type: Tortugas Mt., southeast of Las Cruces, Dona Ana Co., New Mexico, 1400 m ., Sept. 14, 1902, Wooton us!, photo GH!.

Map 54.
Rhizome compact, short-creeping; scales linear, chestnut brown, entire, thin, concolorous. Fronds mostly $10-25 \mathrm{~cm}$. tall; stipe terete, reddish-brown, glabrous, with a few scales similar to those on the rhizome only at the very base, somewhat shorter to somewhat longer than the lamina, with one vascular bundle. Lamina usually bi- to tripinnate, or 5-pinnate at base, linear-lanceolate to deltoid, with 4-13 pairs of pinnae, the apex gradually narrowed, broadest but sometimes not markedly so at the base, upper surface glabrous or sparingly white-ceraceous, the lower densely white-ceraceous; rachis similar to stipe. Pinnae patent to strongly ascending, with usually numerous and crowded ultimate segments, the segments small, roundish to oblong, petiolulate or narrowly sessile, non-articulate, the color of the stalk passing into the segment or the base of the segment of uniform color. Veins 1-2-forked, sporangia (with 32 spores in both varieties), borne on the apical $1 / 2$ or $1 / 3$ of the veins, margin unmodified.

Southeastern Utah south to Hidalgo.

## KEY TO VARIETIES

Lamina broadly deltoid-ovate, 4-5-pinnate, the basal pinnae at least half as long as the lamina, spreading

5la. var. limitanea.
Lamina narrowly deltoid-oblong to oblong-lanceolate, $3-4$-pinnate, the basal pinnae $1 / 4$ to $1 / 3$ as long as the lamina, often curved-ascending

5lb. var. mexicana.
51a. Notholaena limitanea var. limitanea. Fig. 51a. Map 55.
Pellaea dealbata var. limitanea (Maxon) C. Chr. Ind. Fil. Suppl. 3: 131. 1934.

Pellaea limitanea (Maxon) Morton, Amer. Fern Journ. 40: 351. 1950.

Southeastern Utah, Arizona, south to Chihuahua, dry or moist ledges, cliffs or rocky hillsides, predominantly calcareous or sometimes igneous rocks, ca. 1300-2700 m.

Representative specimens: United States. Utah: Rydberg \& Garrett 9386 (us); Cutler 3161 (Gh, us). Arizona: Blumer 1526 (F, K, us); Rothrock 657 ( $\mathbf{F}$, US, y) ; Darrow d Haskell 2.313 (mo). New Mexico: Metcalfe 1003 (us); Eastwood 8235 (us); Mulford 454 (mo). Mexico. Sonora: Hartman (Lumholtz Exped.) 267 (GH, K); Lloyd (Lum-
holtz Exped.) 490 ( $\mathbf{g h}, \mathbf{k}$ ); Shreve 6735 (us). Chimuahua: LeSueur 1127 (GH, us); Pringle 1583 (mo); Knobloch 1146, 1369, 5401, 5502, 8027 (MSC).

51b. Notholaena limitanea var. mexicana (Maxon) Broun, Ind. N. Amer. Ferns 119. 1938. Weath. Journ. Arn. Arb. 24: 312. 1943.

Fig. 51b. Map 56.
Notholaena limitanea ssp. mexicana Maxon, Amer. Fern Journ. 9: 72. 1919. type: Santa Eulalia Mts., Chihuahua, Mexico, Sept. 15, 1885, Pringle 451 us!.

Notholaena nivea var. mexicana (Maxon) Farwell, Amer. Midl. Nat. 12: 283.1931.

Pellaea limitanea var. mexicana (Maxon) Morton, Amer. Fern Journ. 40: 251. 1950.

Southeastern Arizona and adjacent New Mexico south to Hidalgo, dry or moist cliffs or rocky hillsides, predominantly calcareous, sometimes acidic rocks, ca. 1700-3000 m.

Representative specimens: United States. Texas: Marsh 245 (us). New Mexico: Sept. 28, 1880, Greene ( $\mathrm{K}, \mathrm{p}$ ); Oct. 12, 1880, Rusby (Gh, y). Arizona: Blumer 2.388 (f), 2390 (us). Mexico. Chihuahua: Pennell 17.355, 18943 (PH); Pringle 451 ( $\mathbf{B}, \mathrm{G}, \mathrm{GH}, \mathrm{MO}, \mathrm{P}, \mathrm{Y}$ ). COAhulla: Palmer 376 (us); Johnston 7269, 9046a (GH); Pringle 3031 (f, mo) ; Stanford et al. 107 (Gh). Nuevo León: Schneider 1057 ( F ). Tamallipas: Stanford et al. 684 (mo). Durango: Reko 4224 (us); Palmer 465 (b, bm, gh, mo, us). Zacatecas: Stanford et al. 574 (GH) ; Pennell 17450 (PH); Lloyd 207 (Us); Kirkwood 140 (F). SAN Luis Potosí: Lundell 5793 (us); Whiting 751 (mo). Hidalgo: O. M. Clark 7022 (м0).
52. Notholaena dealbata (Pursh) Kze. Amer. Journ. Sci. s. 2, 6: 82. 1848.

Fig. 52. Map 57.
Cheilanthes dealbata Pursh, Fl. Amer. Sept. 2: 671. 1814. type: banks of the Missouri, Bradbury $\mathbf{k !}$ !.

Notholaena pulchella Kze. Bot. Zeit. 1: 6.33. 1843. type: "Hort. Reg. Berl. \& Hort. Lips., ex rupibus Missouri." not seen, whereabouts unknown.

Cincinalis dealbata (Pursh) Fée, Gen. Fil. 160. 1850-52.
Gymnogramma dealbata (Pursh) Mett. Cheil. footnote 8. 1859.
Pellaea dealbata (Pursh) Prantl, in Engl. Bot. Jahrb. 3: 417. 1882.
Notholaena nivea var. dealbata (Pursh) Davenp. Cat. Davenp. Herb. Suppl. 44. 1883.

Pellaea dealbata var. Stubeliana Hieron. Hedwigia 48: 225, t. 12, fig. 15. 1909. TYPE: Said to be Stübel 1048, in part, from Peru but the specimen at B ! is perfectly good $N$. dealbata and was erroneously associated with the Stübel label.

Pellaea Stubeliana Hieron. Hedwigia 48: 225. 1909, in synonymy.


Maps 54-60. Map 54, N. limitanea. Map 55, var. limitanea. Map 56, var. mexicana. Map 57, N. dealbata. Map 58, N. Fendleri. Map 59, N. delicatula. Map $60, \mathrm{~N}$. incana.

Rhizome short, slender; scales linear, pale brown, entire, thin and delicate, concolorous, ca. 3 mm . long. Fronds clustered, numerous, mostly $5-15 \mathrm{~cm}$. tall; stipe very slender, terete, glabrous, shining, bright chestnut, as long as or longer than the lamina, with one vascular bundle. Lamina broadly to narrowly deltoid, often nearly as broad as long, 4-5-pinnate, with 3-5 pairs of pinnae, upper surface glabrous or very slightly white-ceraceous, glaucous, the lower white or rarely vellowish ceraceous, usually densely so. Pinnae deltoid, long-petiolulate, segments small, ovate to oblong, entire, non-articulate, dark color of the stalk passing into the segment. Veins 1-2-forked, sporangia (with 64 spores) borne (one or two of them) back of the vein-tip, margin unmodified.

Nebraska and Missouri south to central Texas, exposed or shaded calcareous cliffs and ledges; the literature records in Missouri are from Steyermark (ms.).

Representative specimens: United States. Missouri: Bush 1.32 ( F , US), 798 (в), 819 ( $\mathbf{G H}, \mathbf{K}$ ) , 850, 7706 ( $\mathbf{F}, \mathbf{G H}, \mathrm{US}$ ); E. J. Palmer 30421, 34733, 39290 ( $\mathbf{F}, \mathrm{US}$ ); Steyermark 8371 (мо), 5749, 22.502, 22966 (f). Arkansas: E. J. Palmer 4538 (us), 5951 (f, us), 17200 (k); Harvey 22, 39 (us, y). Nerraska: Nov. 10, 1895, Williams d́ Wilcox ( $\mathrm{gh}, \mathrm{k}, \mathrm{us}$ ). Kansas: Fendler 1017b (в, мо); Hitchcock 96.3 ( $\mathrm{gh}, \mathrm{mo}$, us, y) ; E. J. Palmer 41806 (us). Oklahoma: Stevens 48 (G. GH, K. us); Carleton 494 (us). Texas: Lindheimer 608 (b, Mo), 1279 (MBG dist.) (b, G, GH, K, MO, P, us) ; Reverchon 1183 (f, us); E. J. Palmer 10377 (US), 11114 (US), 11805 (GH, US), 14200 (в); Jermy 670 (US); Tharp 2162 (us).
53. Notholaena Fendleri Kze. Farnkr. 2: 87, t. 136. 1851. type: Trapp formations of the Rio del Norte near Santa Fe, New Mexico, May, 1847, Fendler 1017a, presumably originally at lz and now destroyed; isotypes: b!, bм!, Gh!, к!, mo!. Fig. 53. Map 58. Gymnogramma Fendleri (Kze.) Mett. Cheil. footnote 13. 1859. Pellaea Fendleri (Kze.) Prantl, in Engl. Bot. Jahrb. 3: 417. 1882. Cincinalis Fendleri (Kze.) Fée, Gen. Fil. 160. 1850-52.

Rhizome stout, often horizontal or oblique; scales linear, chestnut brown, entire, thin, concolorous, 5 mm . or more long. Fronds numerous, densely clustered, ca. $10-30 \mathrm{~cm}$. long; stipe relatively stout, terete, castaneous, glabrous, as long as or longer than the lamina, with one vascular bundle. Lamina broadly deltoid, often broader than long, 4-6-pinnate, upper surface glabrous or ceraceous-glandular, the lower densely white-ceraceous; rachis (and pinna-rachises and costae) markedly flexuous, the divisions of the next order arising from the angles and strongly divergent so as to give the appearance of dichotomous branching. Pinnae alternate, up to 11 of them,
broadly deltoid, both they and the pinnules long-petiolulate, ultimate segments ovate to oblong, obtuse, broadly cuneate at base, non-articulate, dark color of stalk passing into the base. Veins 1-2forked, sporangia (with 64 spores) borne (usually one or two of them) back of the vein-tip, margin unmodified.

The strongly flexuous rachis and other axes make this an exceptionally well-marked species.

Southeastern Wyoming south to New Mexico, dry rocky bluffs and cliffs, ca. 1750-2500 m.

Representative specimens: United States. Wyoming: Nelson 2020 (mo, Ny). Colorado: M. E. Jones 12 (b, bm, p); Hall \& Harbour 69.3 ( $\mathbf{F}, \mathrm{GH}, \mathrm{MO}, \mathrm{Y}$ ) ; Clokey 3287 ( $\mathbf{F}, \mathrm{GH}, \mathbf{M O}, \mathrm{Us}$ ) ; Clements 73.2 (в, GH, Mo, us) ; Patterson 163 (b, F, GH, K, MO, P, US). New Mexico: Fendler 1017 ( в, вм, сн, к, мо); Eggleston 16960 (us); Arsène \& Benedict 15433 (F, us); O. M. Clark 9669, 9704, 10035 (mo); Griffiths 553 (us).
54. Notholaena delicatula Maxon \& Weath. Contrib. Gray Herb. 127: 7. 1939. Weath. Journ. Arn. Arb. 24: 312. 1943. type: Lerios, 45 miles east of Saltillo, July, 1880, Palmer 1.387 us!. Fig. 54. Map 59.

Rhizome short, erect or oblique; scales slender, brown, concolorous, linear-subulate, long-acuminate, about 4 mm . long, entire. Fronds clustered, $10-35 \mathrm{~cm}$. tall; stipe castaneous, slender, terete, glabrous, somewhat shining, nearly equal to the lamina, with one vascular bundle. Lamina mostly deltoid, tripinnate or toward base nearly quadripinnate, herbaceous, the upper surface minutely ceraceousglandular, the lower white-ceraceous; rachis similar to stipe. Pinnae about 4-8 pairs, deltoid or narrowly so, terminal segments rhombic or flabelliform, others roundish, oblong or subdeltoid, segments articulate where the dark color of the stalk abruptly terminates at the base of the segment. Veins $1-2$-forked, sporangia (with 64 spores) borne on nearly the whole length, or on the apical $1 / 2$ of the vein, margin unmodified.

As Maxon and Weatherby mentioned in their publication of this species, it is not entirely distinct from N. incana, although from the few collections available it seems sufficiently so. Additional material may indicate it should be considered a geographic variety of $N$. incana, or may confirm its specific status.

Coahuila and Nuevo León, in exposed or shaded, rocky places, $1200-3400 \mathrm{~m}$.

Specimens examined: Mexico. Coahuila: Palmer 1385 (Gh, mo, us, y), 1387 (GH, K, P, US, Y) ; Johnston 9046 (GH). Nuevo León: Palmer 1386 (GH, P, US); Pringle 2581 ( $\mathbf{~}, \mathbf{B M}, \mathbf{G H}, \mathbf{K}, \mathbf{M O}, \mathbf{P}, \mathrm{US}, \mathrm{Y}$ ).


Fig. 54-55. Fig. 54. N. delicattla: A, frond, X 0.5, from Pringle 2581 (mo); B, underside of segment, X 7, from Palmer 1385 (mo). Fig. 55. N. incana: A, frond, X 0.5 : B , underside of segment, X 4.5 ; C , segment, X $4.5 ; \mathrm{D}$, scale from rhizome, X 7; all from Lyonnet 35 (мо).
55. Notholaena incana Presl, Rel. Haenk. 1: 19, t. 1, fig. 2. 1825. Maxon \& Weath. Contrib. Gray Herb. 127: 5. 1939. lectotype: (by Maxon \& Weath. l.c.) : Mexico, Haenke pr!, photo Gh!.

Fig. 55. Map 60.
Gymnogramma candida Mett. Cheil. footnote 9. 1859. lectotype: Valle de Mexico, Schmitz 231 b!, photos bm!, gh!, us!.

Pellaea candida (Mett.) Prantl, in Engl. Bot. Jahrb. 3: 417. 1882.
Rhizome short, thick, erect or oblique; scales chestnut brown, concolorous, linear-ligulate, long-attenuate, entire, up to 1 cm . long. Fronds clustered, mostly $15-40 \mathrm{~cm}$. tall; stipe rather stout, blackish, shining, terete, glabrous, usually about equalling the lamina, with one vascular bundle. Lamina rather narrowly deltoid, tripinnate, at least toward base, with 6-9 pairs of subopposite pinnae, coriaceous, glabrous and gray-green above, densely white-ceraceous beneath. Pinnae deltoid to ovate, long-petiolulate, ultimate segments broadly oblong to ovate, broadly obtuse, truncate or subcordate at base, articulate where the dark color of the stalk abruptly terminates at the base of the segment. Veins 1 -2-forked, sporangia (with 64 spores) borne on the whole length, or on the apical $2 / 3$ of the vein, margin unmodified.

Maxon and Weatherby (l.c.) have discussed the type-specimen of N. incana and the application of the name. Dr. Maxon was prepared to name this segregate of N. nivea for Mettenius and such a name appears on a number of labels but the identity of Presl's name was established and the manuscript name never published.

Sonora and Chihuahua south to Guatemala; Hispaniola; on cliffs or rocky banks, or in clay soil, ca. $1800-3000 \mathrm{~m}$. A specimen of this species at Kew: Santa Rita, Arizona, March, 1881, Lemmon is provisionally questioned as to locality and not mapped; the species is not reported by Morton in Kearney \& Peebles, Arizona Flora, 1951.

Representative specimens: Mexico. Sonora: Drouet et al. 3667 (F, мо); Shreve 67.35 (мо); Schott 16 (f). Chihuahua: Palmer 115 ( $\mathrm{G}, \mathrm{GH}, \mathrm{y}$ ), 215 (bic, k, us). San Luis Potosí: Schaffner 961 ( $\mathbf{g}$, GH, $\mathrm{k})$; Virlet d'Aoust 21 ( P ). Jalisco: Barnes \& Land 132, 231 ( $\mathbf{F}$ ). Michoacán: Arsène 5341 (p), 5756 (us). Mexico: Pringle 5248 (мо, P), 11267 (B, G, GH, K, US), 15021 (G, US); Bourgeau 754 (G, K, p); Distrito Federal: Schaffner 2.34 (b, K, p), 262 ( $\mathbf{~}$ ); Hinton 4195 (f, gi, mo), 6244 (f, mo). Morelos: Pringle 15698 (us). Puebla: Arsène 1993, 2145 (p). Guerrero: Mexia 9014 (f, gh). Oaxaca: Ghiesbreght 415 (P); Conzatti \& Gonzales 463 (G, GH). Chiapas: Ghiesbreght 226 (G, GH, K, Y). Guatemala: Salvin 238 (G, GH); Ber-
noulli \& Cario 251 ( $\mathrm{B}, \mathrm{K}, \mathrm{P}$ ). Dominican Republic: Ekman 13770 (us); R. A. \& E. S. Howard 9113 (us).
56. Notholaena nivea (Poir.) Desv. Journ. Bot. Appl. 1: 93. 1813. Maxon \& Weath. Contrib. Gray Herb. 127: 8. 1939. Map 61.

Rhizome short, thick, erect or somewhat oblique; scales concolorous, castaneous, linear-subulate, $2.5-3 \mathrm{~mm}$. long, thin and delicate, often much crisped in drying, margins entire or with the walls of the marginal cells projecting. Fronds crowded, mostly $10-30 \mathrm{~cm}$. tall; stipe rather slender, bright to dark castaneous, terete, glabrous, usually dull, shorter than or about equalling the lamina, with one vascular bundle. Lamina lanceolate or deltoid-lanceolate to ovate, subtripinnate, with up to 12 subopposite pairs of pinnae, coriaceous, the upper surface glabrous, the lower densely yellow- or white-ceraceous or glabrous; rachis like stipe. Pinnae petiolulate, ovate to lanceolate, pinnules rather long, petiolulate, ultimate segments oblong to suborbicular, obtuse, subpetiolulate at the truncate to subcordate base, entire, articulate where the dark color of the stalk abruptly terminates at the base of the segment. Veins 1-2-forked, sporangia (with 32 spores in all varieties), borne on the apical $1 / 2$ to $1 / 4$ of the vein, margin unmodified.

Maxon and Weatherby (l.c.) have discussed the variability of the varieties and some of the intermediates between them. It is evident that none of the variations are entitled to specific rank and equally so that they are entitled to recognition of some kind. Considering the number and kinds of characters involved and the fact that each variety has a reasonable range, the varietal treatment seems justified.

Colombia to Argentina and eastern Brazil, in crevices and on ledges of cliffs, on rocky banks, less often in clay soil, ca. 13004200 m .

## KEY TO VARIETIES

a. Indument white. b.
b. Lamina more or less completely tripinnate, ultimate segments suborbicular to broadly oblong, the terminal often lobed, stipe castaneous, rhizome scales often strongly crisped ............... 56a. var. nivea.
b. Lamina bipinnate above, subtripinnate in lower pinnae, ultimate segments oblong and entire (or subdeltoid and trilobate), the terminal commonly simple, stipe bright castaneous, rhizome scales not strongly crisped

56b. var. oblongata.
a. Indument yellow or none, ultimate segments oblong to elliptic-oblong. c.
c. Indument none, lamina usually only bipinnate except toward base, terminal segments entire to lobed, stipe castancous to dark-castaneous, rhizome scales not strongly crisped

56 c . var. tenera.
c. Indument yellow, lamina fully tripinnate when well-developed, terminal segments usually entire, stipe dark-castaneous, rhizome scales not crisped

56d. var. flava.


Maps 61-65. Map 61, N. nivea. Map 62, var. nivea. Map 63, var. oblongata. Map 64, var. tenera. Map 65, var. flava.

56a. Notholaena nivea var. nivea. Maxon \& Weath. Contrib. Gray Herb. 127: 8. 1939 (as N. nivea).

Fig. 56a. Map 62.
Pteris nivea Poir. Encycl. 5: 718. 1804. type: Peru, Jos. de Jussieu (Hb. Jussieu sheet no. 1047) p!, photo GH!.

Acrostichum albidulum Sw. Svn. Fil. 16, 205, t. 1, fig. 2. 1806. type: Née, specimen so named, "Cav. misit" in Hb. Swartz, s-pa!.

Cincinalis nivea (Poir.) Desv. Berl. Mag. 5: 313. 1811.
Gymnogramma nivea (Poir.) Mett. Cheil. footnote 11. 1859.
Pellaea nivea (Poir.) Prantl, in Engl. Bot. Jahrb. 3: 417. 1882.
Cincinalis tarapacana Phil. Anal. Mus. Nac. Chile Bot. 1891: 91. 1891. Type: Sibava, Tarapaca, Chile, Philippi, not seen; isotypes B!, k!.

Pellaea nivea f. nivea (Poir.) Hieron. in Engl. Bot. Jahrb. 22: 390. 1896.

Notholaena albidula C. Chr. Ind. Fil. 459. 482. 1906, nomen in synonymy; basonym A. albidulum Sw. implied but combination not made by Sturm as cited and questionably made by C. Chr.

## Ecuador to western Argentina.

Representative specimens: Ecuador: Spruce 5632 (b, BM, GH, K, NY, p); Heinrichs 36 (b, ny); Mille 171 (p). Peru. Ancachs: Weberbauer 3009, 3061 (b). Huánuco: Ruiz 45 (b). Junín: Killip d Smith 21812 (ny, us), 22161 (us). Lima: Macbride 3207 ( f ); Matthews 755 (k, P) ; Safford 990 (GH, P, Ny, us); Killip \& Smith 21561 (GH, Ny, us); Weberbauer 1.35 (b). Huancavelica: Stork \& Horton 10823 (f). Cuzco: Weberbauer 4866 ( в); Hitchcock 22528, 22549 (us); Herrera 144 (us); Cook d Gilbert 196, 221 (us). Apurimac: Stork du Horton 10718 (F). Puno: Mexia 7788 (F, GH, MO). Bolivia: Shepard 181 (GH, Ny, P, US) ; Buchtien 600 (Ny, US), 1142 (US); Bang 19 (b, BM, GH, K, NY, P, US ), 2600 (GH, NY, US); Fiehrig 3024 (b, BM, GH, K, P, US). Chile: Sibaya, Philippi (b, к); Werdermann 1068 (b, K, Ny, us). Argentina. Los Andes: Catalano 2 (GH); Budín 7 (GH). Salta: Lorentz dHieronymus 53 (b, us). Tucumán: Lorentz \& Hieronymus 955 (в). Catamarca: Castellanos 30/313 (Gh). La Rioja: Hieronymus d Niederlein 555 (в). Córdoba: Stuckert 1764 (p). San Juan: Jan. 1876, Echegaray (в).

56b. Notholaena nivea var. oblongata Griseb. Abh. König. Ges Wiss. Gött. 24 (Symb. Fl. Argent.): 342. 1879. Maxon \& Weath. Contrib. Gray Herb. 127: 10. 1939; Weath. Journ. Arn. Arb. 27: 369. 1946. Type: said to be from Salta, not seen; a specimen at k ! "comm. Grisebach $1878^{\prime \prime}$ is taken as authentic. Fig. 56b. Map 63.

Southern Peru; Argentina; Santa Catharina, Brazil.
Representative specimens: Peru. Cuzco: Soukup 76 (Gh). Apurimac: Herrera 1498, in part ( GH ). Puno: Lechler 1830 (b). Argentina. Tucumán: Burkart 5168 (GH); Venturi 1649, in part (GH, us). Cata-
marca: April 12, 1910, Castillón (Gh, p). Córdoba: Lossen 242 (Ph); Osten 10510 (s-Pa). Brazil. Santa Catharina: Spannagel 172 (Ny, Ph).

56c. Notholaena nivea var. tenera (Hook.) Griseb. Abh. König. Ges. Wiss. Gött. 24 (Symb. Fl. Argent.) : 342. 1879. Maxon \& Weath. Contrib. Gray Herb. 127: 11. 1939.

Fig. 56c. Map 64.
Notholaena tenera Gill. ex Hook. in Curtis, Bot. Mag. t. 3055 \& text. 1831. type: a cultivated specimen from spores sent by Gillies from Mendoza, Argentina, k!, photo GH!.

Cincinalis tenera (Hook) Fée, Gen. Fil. 160. 1850-52.
Pellaea tenera (Hook.) Prantl, in Engl. Bot. Jahrb. 3: 417. 1882.
Pellaea nivea f. tenera (Hook.) Hieron. in Engl. Bot. Jahrb. 22: 390. 1896.

Notholaena tenera var. major Christ ex Stuckert, Anal. Mus. Nac. Buenos Aires s. 3, 1: 300. 1902. type: Rio Primero, vicinity of Córdoba, Stuckert Hb. Argent. 5971, not seen; isotype p!.

Pellaea peruviana Copel. Univ. Cal. Bot. Publ. 19: 302, t. 59. 1941. type: Abancay region, Apurimac, Peru, Oct. 1935, pupils of V. Santander C. Uc!, photo vc!.

## Central Peru to Argentina.

Representative specimens: Peru. Junín: Killip \& Smith 22162 (ny, us). Lima: Savatier 589 (к); Macbride \& Featherstone 82 ( $\mathbf{F}, \mathrm{GH}$ ); Safford 992 (us); Killip \& Smith 21578 ( Ny ). Cuzco: Herrera 717 (Us), 3156, 3174 (F). Bolivia: Mandon 1550 (bм9, GH, K, NY, P), 1863 (в); Rushy 326 (GH, Ny, US), 327 (Ny, us); Buchtien 1141 (us), 3112 (GH, us). Argentina. Jujuy: Venturi 49.31 (GH, us); Schulz 974 (ch). Tucumán: Lorentz 888 (b); Venturi 1064 (ch, us), 10369 (ny). Catamarca: Schickendantz 44 ( $\mathbf{p}$ ), 364 (b); Jörgensen 12.37 (GH). La Rioja: Hieronymus d Viederlein 4.39, 732 (в). Córdoba: Stuckert 5971 (P); Lossen 242, in part (mo). Mendoza: Wilcheck 2 ( P ). Buevos Aires: Bettfreund 1006 (b).

56d. Notholaena nivea var. flava Hook. Sp. Fil. 5: 112. 1855. Maxon \& Weath. Contrib. Gray Herb. 127: 12. 1939; Weath. Journ. Arn. Arb. 27: 370. 1946. type: uncertain, but identity clear. Map 65.

Acrostichum flavens Sw. Syn. Fil. 16, 204. 1806. Type: South America, Vée, presumably at s-pa, not seen, but identity not doubtful.

Acrostichum tereticaulon Desv. Berl. Mag. 5: 310. 1811. тype: (perhaps Peru, Dombey) p!; see Weath. Contrib. Gray Herb. 124: 14. 1939.

Cincinalis (?) flavens (Sw.) Desv. Berl. Mag. 5: 329. 1811.
Gymnogramma flavens (Sw.) Kaulf. Enum. 77. 1824.
Notholaena chrysophylla Kl. Allg. Gartenzeit. 23: 265. 18.55. type: cultivated specimen said to have been originally collected in Peru by Warszewicz, B!.

Notholaena flavens (Sw.) Moore, Ind. Fil. lxx. 1857.


Fig. $56-58$. Fig. 56 . N. nivea: 56 a. var. Nivea: A, frond, X 0.5: B, underside of segment. X 4.5 : both from Buchtien 600 (110). 56h. var. oblovgata: underside of segment, X 4.5, from Loosen 242, in part (mo). 5(ic. var. texfra: underside of segment. X 4.5 , from lenturi 10369 (mon). Fig. 57 . N. parvipolia: A, frond, X 0.5 : B, proton of rachis, enlarged; $C$, underside of segment, $X 4.5$ : all from Tryon \& Tryon 5036 (mo). Fig. 58. N. formosa: A, frond, X 0.5, from C. L. Smith 2080 (Mo): R, underside of segment, X 4.5 , from Meyer \& Rogers 2609 (mo).

Pellaea nivea f. flavens (Sw.) Hieron. in Engl. Bot. Jahrb. 22: 390. 1896.

Pellaea flavens (Sw.) C. Chr. Ind. Fil. 480. 1906.
Pellaea nivea var. flavens (Sw.) [incorrectly attributed to Hieron. by] Hicken, Apunt. Hist. Nat. Buenos Aires 1: 117. 1909.

Colombia to western Argentina; Minas Geraes, Brazil.
Representative specimens: Colombia: Mutis 2102, 2104 (us). Ecuador: 1896, Sodiro (P); Seemann (x). Peru. Húnuco: 1863, Pearce (k). Lima: Macbride 3706 (f, us). Bolivia: White (Mulford Exped.) 619 (K, NY, US); Rusby 143 (NY); Weddell 3918 (P); Stübel 1228 (в); Cárdenas 141 (GH). Argentina. Jujuy: Pearce (bm, K). Salta: Lorentz d Hieronymus 209 (B, us). Tucumán: Venturi 1386 (GH, us), 5138 (us). Catamarca: 1910, Castillón (GH, p). La Rioja: 1906, Uniche (в). Córdoba: Stuckert 11714 (в); Hieronymus 270 (в). Brazil. Minas Geraes: Schwacke 12764 (p); Damazio 1728 (Ny, us).
57. Notholaena parvifolia Tryon, nom. nov. Weath. Amer. Fern Journ. 8: 107. 1918, and Journ. Arn. Arb. 24: 311. 1943 (as Pellaea microphylla).

Fig. 57. Map 66.
Pellaea microphylla Mett. ex Kuhn, Linnaea 36: 86. 1869 (prior to Sept. 10); not Pellaea microphylla Fée, Crypt. Vasc. Brésil 1: 43. 1869 (after Nov. 7); not Notholaena microphylla (Sw.) Kevs., 1873 which is Cheilanthes microphylla, nor Notholaena microphylla Bolle, 1858, which is Cheilanthes persica, according to C. Chr. Ind. Fil. type: New Mexico, C. Wright 825 в!, photo Gh!.

Rhizome compact, short-creeping; scales linear, chestnut brown, entire, thin, concolorous. Fronds ca. $10-25 \mathrm{~cm}$. tall; stipe slightly grooved on the upper surface, reddish-brown, darker at base, glabrous except for a few scales similar to those on the rhizome at the base, somewhat shorter to about the same length as the lamina, with one vascular bundle. Lamina quadripinnate below to bipinnate near apex, deltoid or ovate-deltoid, with some 5-9 pairs of alternate or subopposite pinnae, rather abruptly contracted to the apex, upper and lower surfaces glabrous, glaucous; rachis lighter than stipe in color, grooved or channeled-flattened on the upper side, it and the pinna-rachises not or slightly flexuous. Pinnae strongly patent to somewhat ascending, the basal much enlarged, the segments small, numerous, spaced, roundish to oblong or deltoid-oblong, petiolulate, articulate where the dark color of the stalk abruptly terminates. Veins 1-2-forked, sporangia (with 64 spores) borne on the apical $1 / 4$ of the vein, margin strongly revolute, unmodified.

This is the only species in which the treatment of this alliance of species as Notholaena causes any serious nomenclatural concern. In the next species a new combination is needed but the


Maps 66-67. Map 66, N. parvifolia. Map 67, N. formosa.
epithet remains the same. It is hoped that the choice of the new epithet will be sufficiently suggestive of the species-name under Pellaea.

The distinguishing features of this species from the next, N. formosa, are discussed under the treatment of the latter.

Texas and southern New Mexico, south to Tamaulipas, limestone cliffs and ledges and rocky calcareous slopes, up to ca. 2200 m . The literature records in Texas are from Correll, in Lundell, Flora of Texas $1^{1}, 1955$ and in New Mexico from Dittmer, Castetter and Clark, The Ferns and Fern Allies of New Mexico (Univ. New Mex. Publ. Biol. 6), 1954.

Representative specimens: United States. Texas: Waterfall 4522 (GH); Cory 885, 8403, 26675 (GH); Moore \& Steyermark 3514 (GH, мо); E. J. Palmer 11554, 12991 (сн, мо); R. M. \& A. F. Tryon 5036 (mo). New Mexico: Standley 40757 (Gh); C. Wright 825 (GH, mo). Mexico. Chihuahua: Pringle 440 (GH, mo), 458 (GH); Johnston 7854 (GH); Stewart 986 (GH); Johnston \& Muller 44, 1136 (GH). Coahuila: Hinton 16510 (GH); Stanford et al. 416 (GH, MO); Palmer 404, 1423, 1424 (GH, MO); Johnston 7206 (GH), 8389, 8930 (GH, MO); Stewart 271, 346, 2767 (Gh). Nuevo León: C. H. \& M. T. Muller 956, 1070 (Gh). Zacatecas: Stanford et al. 47 (Gh, mo). Tamaulipas: Stanford et al. 882 (мо).
$4^{3 / 0}$ 58. Notholaena formosa (Liebm.) Tryon, comb. nov. Weath. Amer. Fern Journ. 8: 107. 1918 (as Pellaea pulchella).

Fig. 58. Map 67.
8039 Allosorus pulchellus Mart. \& Gal. Mém. Acad. Sci. Brux. 15: 47,
t. 10, fig. 1. 1842, not Allosorus pulchellus Presl, 1836. ${ }^{\text {TYPE: }}$ south of Sola, Oaxaca, Mexico, Galeotti 6352 br!. Purpus $4882 a$ GH! is annotated by C. A. Weatherby as "compared with type at Brussels, more glaucous but in essential agreement."

Allosorus formosus Liebm. Vid. Selsk. Skr. s. 5, 1: 220 (Mex. Bregn., reprint 68). 1849, based on Allosorus pulchellus Mart. \& Gal.

Pellaea pulchella (Mart. \& Gal.) Fée, Gen. Fil. 129. 1850-52.
Platyloma pulchella (Mart. \& Gal.) Moore, Ind. Fil. 45. 1857.
Cincinalis pulchella (Mart. \& Gal.) J. Sm. Ferns Brit. \& For. 178. 1866.

Pellaea formosa (Liebm.) Maxon, Contrib. U.S. Nat. Herb. 24: 61. 1922.

Cassebeera pulchella (Mart. \& Gal.) Farwell, Amer. Midl. Nat. 12: 281. 1931.

Rhizome compact, short-creeping; scales linear, chestnut brown to brown, entire, thin, concolorus, oily-viscid. Fronds ca. $15-40 \mathrm{~cm}$. tall; stipe terete, reddish-brown to atropurpureous, often glaucous, glabrous, or with some scales similar to those on the rhizome, definitely shorter than to longer than the lamina, with one vascular bundle. Lamina mostly tripinnate, to quadripinnate at the base, ovate to longdeltoid to ovate-lanceolate, with 6-9 subopposite to alternate pairs of pinnae, apex acute, upper and lower surfaces glabrous, usually glaucous; rachis similar to stipe. Pinnae somewhat ascending, the basal largest, segments numerous, spaced, deltoid-oblong to elliptic, or narrowly so, petiolulate, articulate where the dark color of the stalk abruptly terminates. Veins 1-2-forked, sporangia (with 32 spores) borne on the apical $1 / 4$ of the vein, margin strongly revolute, unmodified.

Distinguished from the related $N$. parvifolia, which, like N. formosa, lacks indument, by its rounded rachis, its oily-viscid rhizome scales and its inequilaterally based segments. In N. parvifolia the rachis is grooved or channeled-flattened, the rhizome scales are dry and the segments equilateral at the base.

Tamaulipas and Nuevo León south to Oaxaca and perhaps Chiapas, cliffs and ledges of limestone, perhaps confined to it, ca. 1500-2700 m.

Representative specimens: Mexico. Nuevo León: C. H. \& M. T. Muller 971 (Gh); Meyer \& Rogers 2609 (mo). Tamaulipas: Stanford et al. 882 (GH). San Luis Potosí: Pringle 3401 (ch, mo); Orcutt 5405 (мо); Purpus $4882 a$ (gh, mo). Hidalgo: T. C. d E. M. Frye 2558 (GH, mo); M. T. Edwards 717 (mo). Veracruz: Spence 78 (GH); Bourgeau 2894 (GH). Oaxaca: Pringle \& Conzatti 1395 (GH); C. L. Smith 2080 (мо). Chiapas: "Chiapas etc.," Ghiesbreght 227 (Gh).

## Dubious and Excluded Names

Notholaena andromedaefolia (Kaulf.) Keys. Polyp. Cyath. Hb. Bung. 29. $1873=$ Pellaea andromedaefolia (Kaulf.) Fée.
Notholaena argentea Moore \& Houlst. Gard. Mag. Bot. 3: 20. 1851, is probably Cheilanthes farinosa (Forsk.) Kaulf.
Notholaena argyrostigma J. Sm. in Hook. Journ. Bot. 4: 50. 1841, nomen nudum.
Notholaena asplenioides Christ, in Engl. Bot. Jahrb. 24: 132. 1897. Described from the island of Guadeloupe which is not within the range of Notholaena; it is perhaps a Pityrogramma.
Notholaena atropurpurea (L.) Keys. Polyp. Cyath. Hb. Bung. 30. $1873=$ Pellaea atropurpurea (L.) Link.
Notholaena candida var. aurea Hook. Sp. Fil. 5: 111. 1864, nomen nudum. It is perhaps N. nivea var. flava, but I cannot place the name with certainty without examination of the specimens cited: Ruiz \& Pavon, Peru and Seemann 946, Ecuador.
Notholaena cheilanthoides Spreng. Nova Acta 10: 227, t. 17, figs. 3-4. 1821 $=$ Cheilanthes microphylla Sw.
Notholaena cordata (Cav.) Keys. Polyp. Cyath. Hb. Bung. 29. 1873, not (Thbg.) Desv. $1813=$ Pelifaea sagittata (Cav.) Link.
Notholaena ferruginea (Kze.) D. C. Eaton, Mem. Amer. Acaad. n.s. 8: 201. 186.), based on Gymnogramma ferruginea Kze.; not Notholaena ferruginea Desv. 1813, which is N. trichomanoides, nor (Link) Hook. 1861, which is $N$. aurea $=$ Pityrogramma ferhuginea (Kze.) Maxon.
Notholaena Filarszkyi Kümmerle, Mag. Bot. Lapok. 13: 38. 1914. I cannot place this name from the description although it suggests Cheilanthes pilosa Goldm. The type is given as Warsceuicz 12 from "Cord. Ecuad. \& Nov. Gran."
Notholaena lanuginosa (I). C. Eaton) Keys. Polyp. Cyath. Hb, Bung. 28. 1873, not (Desv.) Poir. $1816=$ Cheilanthes Feei Moore. Evidently the first valid publication of Nuttall's herbarium name, Cheilanthes lanuginosa, was by Eaton in Gray's Manual, Addenda ci. 1863. There it would appear to be a superfluous name but of the two synonyms cited, C. vestita Hook. is a sensu name, not a nomenclatorial synonym, and C. gracilis Mett. is a later homonym.
Notholaena lendigera (Cav.) J. Sm. in Curtis, Bot. Mag. 72 (s. 3, 2) Comp. 10. $1846=$ Cheilanthes lendigera (Cav.) Sw.

Notholaena "lentigera (Sw.)" J. Sm. in Hook. Journ. Bot. 4: 50. 1841, evidently an error for lendigera $=$ Cheilanthes lenigiera (Cav.) Sw.
Notholaena lutea (Desv.) Moore, Ind. Fil. 11. $1857=$ Pityrociramma aurea (Willd.) C. Chr., see Weath. Contrib. Gray Herb. 124: 14. 1939.
Notholaena Matheusii (Kze.) Griseb. Abhandl. Ges. Wiss. Gött. 19: 276. $1874=$ Cheilanthes Pruinata Kaulf.
Notholaena microphylla (Sw.) Keys. Polyp. Cyath. Hb. Bung. 28. 1873, not Bolle, 1858 = Cheilanthes microphylla Sw.
Notholaena microptcris (Sw.) Keys. Polyp. Cyath. Hb. Bung. 28. $1873=$ Cherlanthes micropteris Sw.
Notholaena mollis Hort. Gard. Chron. s. 3, 13: 638. 1893, not Kze. 1834, which is Notholaena mollis. The description: "fronds light green, silverypowdered on the underside; habit dense, compressed as are the divisions of the fronds." is not sufficient for me to place the name.
Notholaena myriophylla (Desv.) J. Sm. in Hook. Journ. Bot. 4: 50. 1841,
based on Cheilanthes myriophylla Hook. which is presumably the same as Desv. = Chellanthes myriophylla Desv. The combination was properly made by Keys. Polyp. Cyath. Hb. Bung. 28. 1873.
Notholaena pulveracea (Presl) Kze. Linnaea 13: 135. 1839 = Chetlanthes farinosa (Forsk.) Kaulf.
Notholaena rufidula Desv. Mém. Soc. Linn. Paris 6: 221. 1827, is probably Woodsla llvensis (L.) R. Br.
Notholaena scariosa (Sw.) Baker, in Mart. Fl. Bras. $1^{2}: 540.1870=$ Cheilanthes scariosa (Sw.) Presl, see Weath. Contrib. Gray Herb. 124: 19. 1939.

Notholaena squamata Moore \& Houlst. Gard. Mag. Bot. 3: 20. 1851. I cannot place this name from the description. Said to be from Mexico and Peru, the former country would undoubtedly place it with N. brachypus, the latter country perhaps as $N$. peruviana.
Notholaena ternifolia (Cav.) Keys. Polyp. Cyath. Hb. Bung. 30. $1873=$ Pellaea ternifolia (Cav.) Link.
Notholaena tomentosa (Link) Keys. Polyp. Cyath. Hb. Bung. 28. 1873, not Desv. 1813, which is Notholaena tomentosa $=$ Chellanthes tomentosa Link.
Notholaena vestita (Spreng.) Desv. Journ. Bot. Appl. 1: 93. $1813=$ Cherlanthes lanosa (Michx.) D. C. Eaton.

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Edited by

Reed C. Rollins and Robert C. Foster

## NO. CLXXX

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## Introduction

This paper is the first in a series of detailed systematic studies of the genus Sida. It reviews the previous work on the genus and the changing concepts of its limits and evaluates the twenty section names which have been published. Of the nearly twelve hundred published specific and subspecific names, 112 are here individually assigned to five of the previously established sections or to the three new ones proposed here, and these, involving 28 species and 9 varieties, are monographed. The remainder are reserved for consideration in later papers in this series.

The genus is one of the warm-temperate and tropical zones, with the primary center in the New World tropics and a secondary center in Australia. About one hundred and twenty species are confined to the New World and about thirty-five to Australia. One species is found only in Europe and Asia Minor; there are several endemic species in Africa, and a few others are found in Asia and the Pacific Islands. Eleven species of weedy behavior are shared by the New World and the Old. Of these, S. rhombifolia, S. spinosa and S. acuta are aggressive weeds found nearly throughout the range of the genus. S. leprosa of the New World has the greatest, although a discontinuous, latitudinal range, from nearly $48^{\circ}$ north to nearly $48^{\circ}$ south.

## Survey of Previous Studies

Linnaeus originally described 10 species in Sida, which he based on Malvinda Dill. and Abutilon of Tournefort and of Dillenius. Of these, only the first four remain in Sida, S. spinosa, S. rhombifolia, S. alnifolia and S. cordifolia; two species are now in Wissadula, and one each in Abutilon, Bogenhardia, Anoda and Malachra. The genus as he defined it would include the presently accepted genera of subtribes Abutilinae and Sidinae of tribe Malveae, and Malachra of tribe Urenae, which he separated from Sida in 1767.

Adanson (1763) proposed the substitution of the name Abutilon for Sida, apparently because it was the classically correct one. He cited Malvinda Dill., Abutilon Dill., and Sida L. as synonyms of Abutilon, which was thus superfluous when published. Miller (1754) had already used Abutilon as a generic name, and is
sometimes cited as the author of the genus In the first work in which he consistently used the binomial system (1768), under the heading "Abutilon", he merely said "see Sida". Under "Sida", he indicated that he thought Abutilon a separate genus and gave the distinguishing characters. He did not list nor describe any species in Abutilon, and one of the species of Sida he described is now considered an Abutilon. I have considerable doubts that this publication of Abutilon in the abridged 4th edition of his Dictionary (1754) should be considered as valid, but if it is acceptable, and there is nothing in the present Rules specifically against it, then the problem created by the Adanson use of the name, invalidating it for use in its presently accepted context, is avoided.

Cavanilles (1785) began his extensive writings on the Linnaean Monadelphia with a monographic dissertation on Sida, which he added to and corrected in subsequent publications. He described Anoda (1785) and Cristaria (1799) as segregate genera, but his concept of the genus was still wide enough to include Abutilon and other pluriovulate genera. In his various publications, he attributed a total of 109 specific names to Sida.

Medicus (1787), whose attitude toward Linnaeus' work is summarized by his comment on the Genera Plantarum (p. 147), "der irrigste Wegweiser.... den ich kenne", divided Sida into the pre-Linnaean genera on which it was based, Malvinda and Abutilon, and reserved Sida for species not now considered as belonging in the genus. He also established the new genus Wissadula, which was represented in Sida of Linnaeus by S. periplocifolia. In 1789, he described a new genus, Lamarkia, for the taxon now called $S$. humilis Cav. His use of Sida, Malvinda and Abutilon was followed by Gaertner (1791) and Moench (1794), but by few others, as the authoritative stature of the work of Linnaeus increased.

Kunth (1822) maintained Abutilon as a separate genus and is of ten credited with being its author. In addition, he described two new genera, Gaya and Bastardia, for species formerly in Sida or new in this work.

De Candolle (1824) in the Prodromus made the species of Gaya and Bastardia the constituents of a new section, Abutiloides, and reduced Abutilon Kunth to a section. Rather inconsistently, he described Periptera as a new genus separated from Sida. Only a
few subsequent authors followed de Candolle in regard to Gaya and Bastardia, although many continued to consider Abutilon as a section of Sida containing the pluriovulate species. De Candolle's third section, Malvinda, based on Medicus' genus of that name, was almost exclusively composed of species which are still retained in Sida. This section has undergone progressive limitation since its founding and is narrowed still further here. Despite this, it remains by far the largest section of the genus, with about a hundred species, and is the one which contains the typical element, S. rhombifolia L., and most of the common and weedy species. Under the present Rules, it must be called section Sida.
Sprengel (1826) treated 176 species, returning or newly transferring to Sida a number of species of Anoda, Bastardia, Cristaria and Gaya. G. Don (1831) distributed 180 species into three sections: Malvinda DC., Abutiloides DC. and his new Malacroideae, the last of which I have accepted here. Rafinesque (1836), declaring that certain species, still kept in Sida, should be considered distinct, proposed Diadesma as the name of a new genus to accommodate them, without ever describing it. Wight (1837) described a new genus, Dictyocarpus, for Sida cuneifolia Roxb., which has won no acceptance. The confused nomenclatorial history of this species, which includes its misidentification as a species of Riedleia and thus to the occasional citation of that genus of the Sterculiaceae as a synonym of Sida, is discussed under Sida Grayana (S. cuneifolia Gray). Steudel proposed a new monotypic genus, Fleischeria, for a species soon identified with and here called S. calyxhymenia J. Gay.
D. Dietrich (1847) arranged 358 species in the following groups whose category was not specified: Malvinda, Abutiloides, Malacroideae, Abutilon, Cristaria, Anoda and one unnamed. He restored its Linnaean extension to Sida, including in it everything then known in the genera Sida, Gaya, Bastardia, Abutilon, Periptera and Cristaria.

The next subdivisions of the genus were made by Gray (1849) when he published the section Pseudonapaea for two species now known as S. hermaphrodita (L.) Rusby and Abutilon Hulseanum (Gray) Torr. \& Gray. In the same paper Gray established the section Psendomalvastrum for the two involucellate species S. bederacea and S. sulphurea, here considered as synonyms of S. leprosa. He and Baker separately added other species, two of
which, S. cuneifolia Gray and S. Helleri Rose, are here considered to belong in a new section. In the Plantae Wrightianae (1852), Gray described a third section, Physalodes, for certain species with inflated fruiting calyces, including his own S. physocalyx. The aberrant Sida Sherardiana was made the basis of a new genus Malvella by Jaubert \& Spach (1855) but its separation from Sida is now maintained by very few botanists. I have included it in section Psendomalvastrum.

Grisebach, in his Flora of the British West Indian Islands (1859), divided the genus into three sections, Malvinda, Steninda and Wissada, without indicating that de Candolle was the author of the first. This led Schumann and, later, Baker to cite Grisebach as the author of that section. Section Steninda was established with only one species, S. linifolia. Although Baker (1892) greatly modified the section-concept, the section is restored here to Grisebach's definition of it and includes only S. linifolia and its immediate allies. Section Wissada was established to accommodate S. divergens Benth., which is usually placed as an anomalous element in Wissadula. Baker (1892) transferred the section-name with the species to $W$ issadula and added a new species, $W$. Balansae, the latter now considered synonymous with Briquetia denudata (Nees \& Mart.) Chod. \& Hass., based on Sida denudata Nees \& Mart.

Miquel (1859) used the conventional sign for section in conjunction with four Latin adjectival plural names, each followed by a brief phrase descriptive of the leaves, to divide the species of Sida in his Flora van Nederlandsch Indië. Since he did not name the category of these divisions and obviously did not intend to describe formal sections, I have not listed these. All of the species in his work are usually placed in section Sida.

In 1860-62, Mueller in his Plants Indigenous to the Colony of Victoria described three new sections, Eusida, Notho-Plagianthus and Lawrencia. Section Eusida was intended for 'typical' species of the genus, as opposed to those of the other two sections, but as specified it included only certain aberrant Australian species which are not in section Sida as I understand that section. The species of section Notho-Plagianthus, together with the synonyms given, are now treated as Plagianthus pulchellus Gray, thus removing the sectional name from the genus. The section Lawrencia is now treated as a section of Plagianthus. In this same
work, Mueller included a fourth and last section, Abutilon, with two species, both now referred to the genus Abutilon.

Grisebach in his Plantae Lorentzianae (1874) added a fourth section Sidastrum, to the three he previously recognized and in this he included several species usually referred to Malvastrum; none of these is here considered as belonging in Sida. Baker (1892) used the name Sidastrum for a monotypic genus based on $S$. quinquenervia Duchass. which has no relation to this section and which Kearney (1954) and others have retained in Sida.

In 1887 Gray published two new sectional names, Abutilastrum and Calyxhymenia. The first was a nomen nudum, Gray merely indicating that it was appropriate for a new section which included S. Lindeniana, now referred to Robinsonella, while the second was superfluously published for his own section Physalodes (1852), since it included the same group of species.

A certain amount of confusion in the nomenclature of the sections was created by Schumann. In his treatment of the Malvaceae in Engler and Prantl (1890) he listed the names, without descriptions, of 5 sections of Sida (as he gave them): Psendomalachra K. Schum., Pbysalodes A. Gray, Steninda Griseb., Malvinda Griseb. and Pseudomalvastrum K. Schum. The first was a nomen nudum, the fourth should have been attributed to de Candolle and the last to A. Gray. In 1891, in the Flora Brasiliensis, he listed and described seven sections, adding to the previous list two new ones, Bastardiopsis K. Schum. and Thyrsinda K. Schum. He still attributed Malvinda to Grisebach and Pseudomalvastrum to himself and changed the attribution of Physulodes, wrongly, from Gray to Grisebach. His section Pseudomalachra, based on the same taxa which Don had made the basis for his section Malacroideae, was superfluous when published. He also published here a new section-name without description, in his observations on S. myriantha, using the following words, "Hae tres species, nempe S. myriantha Pl. \& Lind., S. Lindeniana Turcz. et indescripta ex Insula Tabago probabiliter sectionem bene distinctam efformant, cui apte nomen Dendrinda attribuendum est". Thus another nomen nudum in addition to Gray's Abutilastrum was published for a section including $S$. Lindeniana.

The last survey of the whole genus was that by E. G. Baker (1892). He indexed a total of 634 specific and subspecific names,
excluded 340 of them and distributed the rest in 108 species divided among 6 sections, or listed them as "dub. vel. ignot." or "incert. sect.". Descriptions were given only for the sections, and the synoptic key in the text was only to groups of species. This synopsis has been the basis for most of the recent work in the genus and even his nomenclature has been perpetuated, despite changes made necessary by the changes in the Rules.

The six sections which he recognized were, as he gave them: Pseudomalvastrum Gray (4 spp.), Abutilastrum Gray (5 spp.), Calyxhymenia Gray (10 spp.), Steninda Griseb. (12 spp.), Pseudomalachra K. Schum. (2 spp.) and Malvinda Griseb. ( 75 spp .). He took up Gray's name Abutilastrum for a section including S. Lindeniana, S. myriantha, S. lepida of Australia, S. Eggersii (with reservations as to its place in the section, since the carpels were very little inflated) and $S$. densiflora. As was his custom in this work, he provided a Latin diagnosis of the section, thus validating Gray's name. Since he included S. densiflora, which had been made the basis for the monotypic section Bastardiopsis by Schumann the previous year, section Abutilastrum was superfluous when published. Section Bastardiopsis was later transferred to the genus Bastardia and then raised to generic rank by Hassler (1910). Section Calyxhymenia Gray, as previously noted, was superfluous for section Physalodes Gray, and section Psewdomalachra K. Schum. for section Malacroideae G. Don. Section Malvinda should have been attributed to de Candolle. Baker, as already mentioned, greatly altered the original concept of Steninda and placed in it a number of Australian species which have nothing in common with the typical element, S. linifolia, save terete or subterete calyces. He did not accept Schumann's section Thyrsinda, returning the two species Schumann included to section, Malvinda. The list of sections in Dalla Torre and Harms follows Schumann in incorrectly attributing section Malvinda to Grisebach and Pseudomalvastrum to Schumann and uses Calyxhymenia A. Gray instead of the earlier Physalodes A. Gray.

Greene (1906) separated several species, here considered as belonging in sections Pseudomalvastrum or Incanifolia, as the elements of a new genus, Disella. For a time, some botanists of the western United States followed Greene in this, but few if any do so now.

In addition to those studies of the genus in several geographic areas which have already been mentioned because of their importance in the delimitation of the genus and its sections, certain others are of interest. The first of these was St. Hilaire and Naudin's survey (1842) of the species then known from Brasil, 11 of them new. This was followed by Schumann's work in Martius' Flora Brasiliensis (1891) already referred to, and by Monteiro's preliminary survey (1935) consisting mainly of keys, which is the only published fascicle of a proposed monograph of the Brasilian Malvaceae.

Baker (1937) reviewed Monteiro's paper, calling attention to some of the errors an isolated worker inevitably commits when he does not have access to types, to material from outside his immediate area, nor to a good library. Monteiro later (1949) published an account of the Brasilian, Uruguayan and Argentine species of section Sida, in which he provided keys to a series of 4 named but not formally established subsections and to the 48 species of these which he recognized from the area. He depended to a great extent on Rodrigo's (1944) paper for the species found in Argentina and Uruguay. Although his paper shows some of the same inadequacies, it is considerably more accurate and useful than his earlier one.

Rodrigo's paper also shows the effects of a lack of references and authentic material. In attempting to make up the latter deficiency, she assembled photographs of "types" of all the species treated. These are excellently reproduced in her paper, but unfortunately some of them do not illustrate the actual types. The plate illustrating the "type" of S. ciliaris L. actually shows the type of S. muricata Cav. in the Madrid herbarium; that of S. linifolia Cav. shows a Boldo collection from Cuba, whereas the type was collected by A. de Jussieu; and that of S. prostrata Cav. shows a Née collection purportedly from Chile, whereas the type is a Commerson collection from Uruguay.

The first treatment covering all the truly North American species of the genus was that in Gray's Synoptical Flora (1897), which considers 21 species in 4 sections. Since then, Small has added 2 and Fernald 1 new species to those known from the United States, all 3 of which are in close relationship to the complex centering on S. Elliottii Torr. \& Gray of section Sida.

The Mexican species were treated in the 2 editions of Sessé and

Moçino's Flora Mexicana $(1889,1894)$ and by Hemsley (1879), but the first organized treatment was that of Standley (1924). Hemsley added only a varietal nomen nudum, while the 2 editions of Sessé \& Moçino's work contained a number of new names and overly brief descriptions. Baker, who made a special trip to Madrid to examine the types of certain Cavanilles' species, mentioned in a brief article on his trip the availability of the Sessé and Moçiño specimens there but completely ignored many of their species in his Synopsis. Standley keyed out 28 species and gave summaries of their characters, bibliography and designation of type-specimens.

Kearney (1954) has published a tentative key, with brief notes and partial synonymy, for 55 North American, Mexican, Central American and West Indian species. The paper contains very few of the defects which might reasonably be expected in a geographically restricted treatment of a large, variable and wide-ranging genus and is a much-needed and valuable contribution.

The species of Australia were last summarized in Bentham \& Mueller's Flora Australiensis (1863). The many species described and the changes made in the classification of others since then are only partly covered by regional floras. The species are mostly endemics, only 6 of them occurring outside Australia. For other parts of the Old World, only conventional treatments in floristic works are available, with the exception of Gagnepain's (1909) brief and inadequate "Essai d'une classification des Sida asiatiques" in which he keys a mere 10 species and confesses his inability to separate S. rhombifolia from S. spinosa. Hu (1955) in her study of the Malvaceae of China has published a number of new combinations and taxa in Sida, all of them in section Sida.

Special studies of the morphology, anatomy and cytology of the genus are almost completely lacking. Hochreutiner has published some observations, his (1920) paper on carpellary structures in the family being of special interest. Kearney (1951) in his useful survey of the American genera of Malvaceae has provided an excellent summary and discussion of the taxonomically useful characters of these genera, with a fairly complete bibliography. Metcalfe and Chaik (1950) summarize the slight amount of information on the anatomy of the genus, while the literature of economic botany has innumerable references, particularly to the use of a number of species as locally important fiber plants.

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This paper was completed at the United States National Herbarium in 1956 while on sabbatical leave from the Atkins Garden and Research Laboratory. I wish to thank the Head Curator, Mr. Jason Swallen, for permitting me to work there and to acknowledge once again the helpful assistance of Dr. Lyman Smith, now of that herbarium.
The Directors and Curators of the following herbaria have generously permitted me to borrow from the collections in their care (the herbaria designated in the text by the symbols given here):

Chicago Natural History Museum (formely Field Museum) (F); Dudley Herbarium, Stanford University (DS); Gray Herbarium, Harvard University (GH); Missouri Botanical Garden, St. Louis (MO); Muséum d'Histoire Naturelle, Paris (P); New York Botanic Garden (NY); Pomona College (POM); Rocky Mt. Herbarium, University of Wyoming (WYO); Royal Botanic Garden, Kew, England (K); Southern Methodist University, Dallas (SMU); United States National Herbarium (US); University of Arizona (ARIZ); University of California (UC); University of Mexico, Herbario Nacional (MEXU); University of New Mexico (UNM) ; University of Utah (UAC); Vegetation Type Map Herbarium, at University of California (VTM).

Other citations, primarily to indicate the location of type, use the symbols of Index Herbariorum (ed. 3).

## Taxonomic Treatment

Sida L. Species Plantarum ed. 1, 2: 683-686. 1753.
Abutilon Adans., Fam. 2: 283. 1763.
Malvinda Medic., Malv. 23. 1787.
Lamarkia Medic., Phil. Bot. 1: 28.1789.
Diadesma Raf., New Fl. Am. 1: 41. 1836. (nom. nud.).
Dictyocarpus Wight, Madras Jour. Sc. 5: 309. 1837.
Fleischeria Steudel in Lehmann, Pl. Preiss. 1: 236.1845 , non Steudel and Hochstetter 1838.

Malvella Jaub. \& Spach, Illustr. Pl. Or. 5: 47 t. 446. 1855.
Sidastrum E. G. Baker, Brit. Journ. Bot. 30: 137-8. 1892.
Disella Greene, Lflts. Bot. Obs. \& Crit. 1: 209. 1906.
Herbs, shrubs or small trees, annual to perennial. Stems fibrous to woody, pubescent or glabrous, simple or freely branching. Stipules present, free, sometimes deciduous. Leaves alternate, distichous or spiralled, from simple--linear and entire to palmately lobate or orbicular-reniform and serrate. Inflorescence solitary and axillary to paniculate and terminal; individual flowers never large and showy. Epicalyx none or, in 2 few species, of $1-5$ bracteoles at the base of the calyx (a false involucel of $6-8$ linear bracts on the upper pedicel in one species). Calyx valvate, 5 -lobed, terete or angled, campanulate or urceolate, in some species greatly accrescent after anthesis. Petals five, adnate at the base to the lower part of the stamen-tube. Stamens fused in a column, the free portion of the filaments terminal or some of them subterminal, the anthers 5 to 40 or more, unilocular, usually everted in anthesis. Ovary superior, enclosed by the stamen-tube and the fused bases of the petals. Styles free at least in the upper part, isomerous with the carpels. Stigmas terminal, capitellate or capitate, sometimes oblique, never decurrent. Mature fruit a single whorl of schizocarps usually separating freely from the axis and each other, in an open, closed or greatly expanded calyx. Schizocarps uniovulate, indehiscent or dehiscent along the mid-dorsal line, rarely along the inner margin or by breakdown of the lateral or basal walls; apex muticous or variously rostrate, two-beaked or biaristate (in some specimens of S. rhombifolia a single arista by fusion), the aristae sometimes subapical; apical wings absent; basal hooks absent; lateral walls persistent, membranous, reticulate, rugose or clathrate; endoglossum absent. Seed rounded, somewhat cordiform, without an arilloid envelope, separating freely in maturity or adherent to the lateral walls of the carpel, pendulous from the upper inner angle, the funicle, raphe and radicle thus superior. Columella (receptacle) truncate, usually slender and slightly conical, the base occasionally flared; remnant vascular traces from the base to the individual carpels persisting in a few species. Cotyledons variously plicate or contortuplicate.

The name used by pre-Linnaean authors in many applications, by Theophrastus for a Nymphaea, and by other classical authors supposedly for some "marsh-mallow" or water plant; from the Greek Eid $^{\prime}$.

## Type species: Sida rhombifolia L.

Britton and Wilson (1924) named S. alnifolia L. as the type species without giving any reasons for their choice. Hitchcock and Green (1935) named S. rhombifolia L. Their list of Linnaean
generic lectotypes having been published as a supplement to the third edition of the International Rules led Rodrigo (1944) to assume that it carried the authority of the Rules, and she cited these as the authority for her designation of S. rhombifolia. Hu (1955) also designated S. rhombifolia. Neither S. spinosa nor $S$. cordifolia has been selected; they are the first and last of the four species originally named by Linnaeus which are still considered to be in Sida. Both are represented by at least one specimen in the Linnaean Herbarium, according to Savage (1945).

Although there is some question of the reliability of Jackson's (1912) dating of the presence of the various specimens in this herbarium, in all probability the single specimen representing S. rbombifolia was there before the publication of the Species Plantarum ed. 1. The species is well known and widely distributed, nearly throughout the natural range of the genus and beyond it as a weed or waif. It is in every respect a typical species of the genus, and for these several reasons, I have accepted Hitchcock and Green's selection of it as the generic type.

## THE SECTIONS

The following sections of the genus have been named:
Malvinda (Medic.) DC., Prod. 1: 459. 1824. (The typical section, Sida). Abutiloides DC., op. cit. $467=$ Gaya \& Bastardia spp. Abutilon (Kunth) DC., 1. c. - Abutilon spp. Malacroideae G. Don, Gen. Syst. 1: 498. 1831. Pseudomalvastrum A. Gray, Mem. Am. Acad. 4: 23. 1849. Pseudonapaea A. Gray, l.c. Physalodes A. Gray, Smithson. Contr. Knowl. 3, art. 5: 20. 1852. Steninda Gris., Fl. Brit. W. Ind. 76. 1859. Wissada Gris., op. cit. $77=$ Wissadula sp. Notho-Plagianthus F. Muell., Pl. Vict. 160. 1860-62 = Plagianthus sp. Lawrencia F. Muell., op. cit. 162 $=$ Plagianthus, sect. Lawrencia. Eusida F. Muell., op. cit. 163. Sidastrum Gris., Pl. Lorentz. 42. $1874=$ Malvastrum spp. Calyxhymenia A. Gray, Proc. Am. Acad. 22: 294. $1887=$ sect. Physalodes. Abutilastrum A. Gray, op. cit. 295 (nom. nud.). Dendrinda K. Sch., Marr. Fl. Bras. 12 (3): 347. 1891. (nom. nud.). Bastardiopsis K. Sch., op. cit. $280=$ Bastardiopsis sp. Pseudomalachra K. Sch., l. c. = sect. Malacroideae. Thyrsinda K. Sch., op. cit. 281. Abutilastrum A. Gray, valid. Bak. f., Jour. Bot. 30: 38. 1892.

Those which I am accepting are in bold-face. Reasons for the rejection of the others are either summarized by reference above to present disposition of the contained species or were given in the survey part of this paper. In addition to those accepted, three new sections are proposed here for species formerly in section Psendomalvastrum or section Sida.

## Key to the sections

A. Pedicels of the inflorescence adnate to the petioles of foliaceous bracts; in-
florescence often subumbellate-congested at athe apices of branchlets;
calyx terete, not accrescent
I. Section Malacroideae G. Don, Gen. Syst. 1: 498. 1831.

Section Pseudomalachra K. Schumann, Engl. \& Prantl, Nat. Pfl. 3, Abt. 6: 43. 1890.

Subshrubs or herbs. Pedicels adnate to the petioles of foliaceous bracts, flowers of ten subumbellate-congested at the apices of the
branches. Calyx not accrescent, epicalyx absent. Carpels of ten stellate-pubescent, strongly muricate to nearly smooth, dehiscent mostly along the inner margin.

Don established this as the first new section since those of the Prodromus, with the brief characterization "heads of the flowers involucrated", and remarked that "this section of Sida agrees with Malachra as it is now constituted. There is much difference of opinion about the character of that genus". He included the elements represented by the names S. fulva, S. anomala, and S. plumosa, and these three elements are also represented in K. Schumann's section Pseudomalachra. It might seem that the very brief diagnostic phrase given by Don was insufficient, yet this section contains the only species of the genus in which the pedicels are regularly adnate to the petioles of foliaceous bracts which, with their stipules, give the appearance of involucres. Schumann's characterization of the section in Mart. Fl. Bras. (1891) is more exact and is the basis for the one used here. Don's name has been nearly completely ignored and Schumann's used, particularly in recent works. Type species: Sida ciliaris L.

## Key to the Species

A. Stem-leaves long-hirsute on both surfaces; dorsum of the carpels densely puberulent, the outer margin a 3-peaked ridge; petals $12-13 \mathrm{~mm}$. long; anthers $15-20$; stamen-tube with ascending strigose hairs; plants procumbent

1. S. Brittonii.
A. Stem-leaves glabrous or appressed-pudescent on the upper surface . B
B. Petals $18-22 \mathrm{~mm}$. long, $10-14 \mathrm{~mm}$. wide; anthers $30-40$; dorsum of the carpels strongly verrucate and rugose; plants procumbent
2. S. centuriata.
B. Petals 5—1/ mm. long, 2-11 mm. wide; anthers $10-30$. . . . . C
C. Stamen-tube heavily patent-stellate-pilose; petals $13-16 \mathrm{~mm}$. long, ca. 5 mm . wide; carpels $7-8$, verruculate, submuricate; plants procumbent
3. S. surumuensis.
C. Stamen-tube glabrous to sparsely pilose . . . . . . . . . D
D. Petals $14-17 \mathrm{~mm}$. long, $8-11 \mathrm{~mm}$. wide; stem-leaves cuneate-oblong, rarely more than 1 cm . long, crowded and clustered; anthers ca. 20; carpels 5 ; plants semidecumbent
4. S. paradoxa.
D. Petals $5-15 \mathrm{~mm}$. long, to 7 (rately to 9) mm . wide; stem-leaves suborbicular to elliptic to linear, not crowded and clustered; carpels 5-8 muticous to short-aristate, the dorsum variously sculptured, often muricate; plants prostrate to erect
5. S. ciliaris.

## I. Sida Brittonii León, Torreya 19: 172. 1919.

Perennial prostrate herb. Stems hirsute-strigose, diffusely branched at the base, 3-4 dm. long, tips of the branches sometimes arching. Leaves oblong to elliptic or obovate, rounded at the apex, serrate above the middle, $1-2 \mathrm{~cm}$. long, 4-9 mm. wide, with long, scattered, villous or hirsute hairs on the upper surface and margins, and with that plus densely stellate-strigose hairs on the prominent midnerve of the lower surface. Stipules linear or somewhat spatulate, long-ciliate. Petioles 4-7 mm . long. Calyx 5 mm . long; lobes ovate, acute, long-ciliate, divided slightly more than halfway to the base, densely hirsute within. Petals yellow, $12-13 \mathrm{~mm}$. long, ca. 5 mm . wide, obliquely spatulate, the margins minutely ciliate. Column terete, stout, $2-2.5 \mathrm{~mm}$. from base of the petals to the filaments, with appressed, ascending, strigose hairs; filaments $1-2 \mathrm{~mm}$. long. Anthers $15-20$, dotted. Styles five, ca. 7.5 mm . long, ca. 4 mm . free; stigmas capitellate. Carpels five, strongly tetrahedral, $2.5-2.9 \mathrm{~mm}$. high, $1.3-1.5 \mathrm{~mm}$. radially, biapiculate, the apiculations ca. 1 mm . high; indument of upper dorsum rather densely multicellular-puberulent; outer dorsal spines reduced to a sharp 3-peaked ridge; lateral walls coarsely reticulate-rugose.

TYPE: León E Roca 7466, "dry savanna, Chirigota, Pinar del Río Prov., Cuba", (Colegio de La Salle, Cuba).
distribution: Pine and oak woods and palm savannas of Pinar del Río Prov., w. Cuba.

This species, known only from Pinar del Río Province, Cuba, is remarkable for the long-hirsute indument of the leaves and the pubescence of the carpels. There are specimens of $S$. ciliaris var. ciliaris from Brasil which are superficially similar to specimens of S. Brittonii. Schumann based S. ciliaris var. guianensis on specimens of this kind, but his variety and the specimens represent no more than a tendency in that species and have no close relation to this one.

Cuba: Pinar del Río: Britton et al. 63.4.2, near Herradura (ny). Britton et al. 6996, near Coloma (ny). Earle 748. Herradura (NY). Ekman 10710, Herradura (NY). Ekman 11054. Mantua (F). Ekman 18244, between Caldura and Pinar del Río (ny). Herman 729, near Herradura (pom, f, us). Killip 32370, nr. El Payuco, bet. Guane and Remates (us). León \& Roca 7466, La Chirigota (ISOTYPE, NY). Palner \& Riley 360, nr. Coloma (us). W'right 2046, Asiento Viejo de San Julián (NY, GH, US).

## 2. Sida centuriata Clement, sp . nov.

Herbae perennes procumbentes. Caules 25 cm . vel breviores, cum pilis parvulis stellatis strigosis vestiti. Stipulae $5-8 \mathrm{~mm}$., linearilanceo-
latae. Petioli 5- 8 mm . Folia (7-) $10-23 \mathrm{~mm}$. long., (4-) 8-12 mm . lat., elliptica vel anguste ovata, basi cordata, apice subacuta, truncata. Pedicelli 3 mm . Calyx $4.5-5.0 \mathrm{~mm}$. long., cupuliformi-campanulatus, lobis lanceolatis ca. 4 mm . long., $2.0-2.5 \mathrm{~mm}$. lat. ad basem. Petala $18-22 \mathrm{~mm}$. long., $10-14 \mathrm{~mm}$. lat., obovata, conspicue obliquogibbosa, cum partibus paginae exteriore in alabastro expositis puberulentibus. Columna staminalis subangulata pilis sparsis stellatis patentibus. Filamenta 2-3-seriata. Antherae $30-40$. Styli 11 mm ., perfecte liberi. Carpella $7-8$, a dorso conspicue verrucata et rugosa, omnino minute stellato-pubescentia et pulverulentia, a latere rugulosa, caeco-membranacea, nec cancellata.

Perennial procumbent herbs from a woody root. Stems terete, $1-1.3$ mm . diam. at base, to 25 cm . long, covered with small, stellate-strigose, appressed hairs. Stipules linear-lanceolate, $5-8 \mathrm{~mm}$. long, ca. 0.7 mm . broad with scattered, marginal, pilose hairs, stellate-pubescent on the lower surface, glabrescent or glabrous on the upper. Petioles 5-8 mm. long, channeled adaxially, indument like that of the stem. Leaves (7-) 10-23 mm. long, ( $4-$ ) 8-12 mm. broad, elliptic, or long-ovate, cordate at the base, palmately 3 -nerved, the nerves conspicuous on the lower surface; indument of small, yellowish, appressed. 6-7-rayed, stellate hairs, denser on the lower surface; margins serrate on the upper third to half; apex subacute to truncate. Pedicels 3 mm . long. Calyx cupuliform-campanulate, $4.5-5 \mathrm{~mm}$. long, lobes ca. 4 mm . long, 2-2.5 mm . wide at the base, lanceolate, acute, tube with many fine veins, lobes with a single midvein and a double set of intramarginal veins separately confluent below the sinuses; exterior densely stellate-hirsutulous with a few long marginal and apical pilose hairs, interior of the tube glabrous, of the lobes hirsutulous. Petals obovate, strongly oblique, $18-22 \mathrm{~mm}$. long, $10-14 \mathrm{~mm}$. wide, 1.5 mm . wide at the claw, the margins with regularly scattered, short, fimbriate hairs, outer surface puberulent where exposed in bud. Stamen-tube subangulate, 3 mm . high from claw to level of filaments, with scattered, patent, stellate hairs. Filaments in 2-3 series, the lowest ca. 1.5 mm . long, longest 3 mm . long, flattened, tapering to the apex, recurved in anthesis. Anthers dotted, $30-40$, ca. 0.8 mm . wide, 0.7 mm . high, globose, the sinus deep and constricted. Styles $7-8$, free to the base, 11 mm . long, recurved in anthesis. Stigmas capitellate, the apex of the style dilated below them. Ovary 1.5 mm . in diam., 1.0 mm . high, densely stellate-puberulent. Carpels $7-8$; the dorsum strongly verrucate and rugose, the spines chiefly on the outer angle of the dorsum, everywhere finely-stellate-pubescent and pulverulent; lateral walls rugulose, opaquely membranous, not cancellate. Seed plump, brownish-black, densely yellowish-stellate-puberulent
except the funicle; hilar depression rather shallow. Columella ca. 2 mm . high, subcylindrical, truncate, angulate.
tYpe: K. Fiebrig 4051, "N. Paraguay: Zwischen Río Apa und Río Aquidaban. Centurion, Okt. 1908." (GH).
distribution: Known only from the type locality.
S. centuriata is obviously in close relationship to S. ciliaris, differing from it primarily in having much larger flowers, with minor differences in the indument of the leaves and the carpels. The smallest open flowers on the three sheets cited have the petals 18 mm . long, the largest 22 mm . long.

Paraguay: Fiebrig 4051, Oct. 1908, Centurion, between R. Apa and R. Aquidaban, n. Paraguay. (TYPE, GH). Fiebrig 4213, Nov. 1908, same locality. (AA, Us).

## 3. Sida surumuensis Ulbrich, Notizbl. 6: 320. 1915.

Procumbent perennial herb. Stems few-branched, terete, tips ascendent, fulvid-scabrous to glabrescent, to 30 cm . long. Stipules $4-5 \mathrm{~mm}$. long, linear, setose-fimbriate, persistent. Petioles $2-3 \mathrm{~mm}$. long, channeled adaxially. Leaves narrowly linear, $10-20 \mathrm{~mm}$. long, $1-2 \mathrm{~mm}$. wide, cordate at the base, subacute, the single nerve prominent beneath; indument of small, vitreous, stellate hairs on both surfaces or scattered on the lower surface only. Pedicels $1-2.5 \mathrm{~mm}$. long, densely stellatestrigose. Calyx $5-6 \mathrm{~mm}$. long, cupuliform-campanulate, densely and finely stellate-tomentose, the margins pilose; lobes $3-3.5 \mathrm{~mm}$. long, 2- 2.5 mm . wide at the base, acute or acuminate, one-nerved. Petals orange, yellow, or white, $13-16 \mathrm{~mm}$. long, $4.5-5.5 \mathrm{~mm}$. wide, obliquely obovate, the inner margin concave, the outer convex; apex obtuse or subtruncate, margins with scattered very short ciliate hairs, the small portion exposed in bud with scattered stubby puberulence. Stamen-tube 2.5 mm . long from base of petal to level of filaments, heavily patent-stellate-pilose; filaments multiseriate, $1-2 \mathrm{~mm}$. long. Anthers 25 , dotted. Styles 7 mm . long, all but 1 mm . free; stigmas flat-tened-capitate. Carpels 7-8, verruculate, biapiculate, submuricate, with scattered, small, stellate hairs; ca. 2 mm . high; lateral walls rugulose.

TYPE: Ule 8227, "auf trockenen Campo bei der Serra do Mel, Rio Branco, Surumú. Brasil Aug. 1909." (B).
distribution: Northern Río Branco State, Brasil, and adjacent British Guiana.

This species is distinguishable from $S$. ciliaris by its somewhat verticillate linear leaves and large flowers. Superficially, it resembles $S$. ciliaris var. mexicana, differing from it, however, in
the longer and broader petals as well as in minor features of the habit, indument, and androecium. A certain amount of variation in the indument is found in the three localities from which the species is known, the type being rather heavily stellate-pubescent on both surfaces of the leaves, while that of British Guiana has the leaves glabrous or glabrescent on the upper surfaces. One of Tate's two collection from Brasil resembles the type, the other the Guiana material.

British Guiana: A. C. Smith 2340, basin of Rupununi R., nr. mouth of Charwair Cr., lat. ca. 2 $35^{\prime}$. 1-4 Nov. 1937 (us, MO, F).

Brasil: Rio Branco: E. Ule 8227, nr. Serra do Mel, Surumú, (isotypes: NY, UC, US; TYPE photographs: GH, F, US). G. H. H. Tate 85, Limão (NY). G. H. H. Tate 125, Limão, (Ny).

## 4. Sida paradoxa A. P. Rodrigo, Notas Mus. La Plata 2: 105,

 figs. $3^{3}, 5$, Pl. 4. 1937.Perennial semidecumbent herb. Stems leafy, many-branched, slightly woody, $20-25 \mathrm{~cm}$. high, the indument of whitish stellate hairs. Roots strong, woody, deep. Leaves numerous, and clustered at the nodes, emer-ald-green in life; stipules lanceolate, $5-7 \mathrm{~mm}$. long; petioles as long as or shorter than the blades; blades oblong or slightly cuneate, truncate, 4-8, rarely to 11 mm . long, $1.5-3.5 \mathrm{~mm}$. wide, the base obtuse or narrowly subcordate, the apex tridentate, the lateral teeth larger, the central one shorter, usually no more than an apiculation; upper surface glabrous, lower surface with scattered to dense white stellate hairs, the midnerve prominent. Flowers solitary or usually in clusters of two to four, rarely five, at the ends of the branches, the foliaceous bracts of the inflorescence linear, slightly spatulate, sparsely stellate-pubescent. Peduncles $2-4 \mathrm{~mm}$. long. Calyx angulate, 8 mm . high, 3 mm . wide, covered with fine, white, stellate hairs, 5 -nerved; lobes cordate-acuminate, two-thirds the height of the calyx, margins fine-ciliate; inner surface of the lobes with ascending, appressed, fine hairs; inner surface of the tube glabrous. Petals yellowish pink, veined in red, with a tuft of white ciliate hairs at the base, strongly oblique, obtuse, widest near the apex, 14 to 17 mm . long and $8-11 \mathrm{~mm}$. wide, the corolla to 25 mm . in diameter. Stamen-tube glabrous, very short, $1-1.5 \mathrm{~mm}$. long, the filaments $1.5-2.0 \mathrm{~mm}$. long; stamens ca. 20. Styles five, pink, 6-7 mm . long; stigmas capitate; ovary conoid. Mature carpels five, 3 mm . high, biaristate, the aristae $1-1.5 \mathrm{~mm}$. high, they and the dorsum with numerous small, stellate, whitish hairs; dorsum rugose, the outer margins few-spined; lateral walls reticulate; pulverulent; dehiscence along inner margin, nearly complete. Columella 3 mm . high, knobbed at apex, flared
at base. Seeds 2 mm . high, 1.8 mm . wide, with minute, scattered, cinereous stellate hairs.

TYPE: A. P. Rodrigo 605, Mercedes, Arroyo La Garza, center of Corrientes Prov., Argentina (Museo La Plata).
distribution: Known only from the type-area.
I have seen only one sheet of this species, but this and Rodrigo's original and subsequent descriptions and illustrations (1937, 1944) convince me that $S$. paradoxa is a distinct species. It probably arose as a local segregate of $S$. ciliaris and differs from it mainly in having numerous, small, clustered leaves and large flowers. The specimen cited does not have the long-aristate carpels described and figured by Rodrigo and its leaves are shorter.

Argentina: Pedersen 121, Corrientes, Estancia Sta. María (us).

## 5. Sida ciliaris L., Syst. ed. 10, 1145. 1758.

Perennial herbs or subshrubs. Stems sublignescent to herbaceous, numerous, prostrate to ascending or erect from a branching or single stout woody root, clothed with appressed, rigid, stellate or submalpighiaceous hairs, often becoming hirsute to tomentose toward the apices. Leaves extremely variable, linear to linear-oblong to oblong to ovate to suborbicular; the base truncate to rounded to narrowly cordate; the apex truncate to obtuse to acute; the margins variably serrate, only at and near the apex or merely tridentate, to slightly more than halfway toward the base; 3-5 palmate nerves from the base; indument variable, the upper surface glabrous to glabrescent, the hairs simple or stellate or mixed, appressed, the under surface usually more densely covered with stellate or submalpighiaceous hairs, scabrous to softly villous, the margins occasionally short-ciliate. Petioles $3-9 \mathrm{~mm}$. long, ca. 0.6 mm . diam., lower portion flattened adaxially, upper portion terete or subterete, geniculate at the apex; the indument variable, of flavid, cinereous or white, stellate or submalpighiaceous and ciliate hairs. Stipules linear to spatulate, $6-12 \mathrm{~mm}$. long, the apex acuminate to bluntly acute, ciliate; stipules of the involucre somewhat longer and longer-ciliate, the hairs flavid, cinereous or white. Pedicels from less than 1 to ca. 2 mm . long, involucrated in two- to eight-flowered heads at the apices of the stems, rarely solitary in lower axils. Calyx $5-7 \mathrm{~mm}$. long, campanulate, terete; lobes ovate or triangular to lanceolate, $2-4 \mathrm{~mm}$. long, acute; indument villous, of simple hairs, to subtomentose, of stellate hairs, or mixed, the hairs or individual rays occasionally to 2.5 mm . long, white, cinereous or ferrugineous-flavid, the lobes puberulent near the margins within,
the tube glabrous within. Petals 3-15 mm. long, 2-7 (-10) mm. wide, white, yellow, or variously rose or purple, often darker at the base, ovate-spatulate or broadly rotund-triangular, slightly to markedly oblique, the apex obtuse or retuse, the margins ciliolate, the base glabrous or sparsely pilosulous. Stamen-tube slender, terete, 3-5 mm. high, glabrous or sparsely pilose with spreading, simple, hyaline hairs; filaments 2-3 (-4) mm. long, slender, reflexed in anthesis; anthers $10-40$, minutely dotted or plain. Ovary five- to eight-lobed, glabrous or minutely hairy, conoid or subglobose, the apex truncate to apiculate. Styles 4-8 mm. long, 2-5 mm. free; stigmas capitellate. Carpels 5-8, extremely variable in the sculpturing, muticous or rostellate or biaristate, the dorsum muricate or reticulate or rugose, glabrous to densely stellatepilosulous, thick or fragile; the lateral walls finely to coarsely reticulate, membranous between the reticulations or rugosities or cancellate; 2-3 mm . high, $2.5-3 \mathrm{~mm}$. radially. Seeds usually with scattered stellate puberulence, denser near the hilum, $2-2.5 \mathrm{~mm}$. radially, light brown, yellowish or nearly white in maturity, rarely purpurascent.

## Key to the Varieties

A. Leaves suborbicular to ovate, obtuse or truncate (becoming lanceolate and acute in specimens intermediate between vars. ciliaris and anomala); petals 3-10 mm . long, $2--4 \mathrm{~mm}$. wide; plants prostrate to ascending B
B. Carpels 5-8, briefly biaristate, muricate to verruculate, the lateral walls rugose and reticulate or cancellate; leaves glabrous or glabrescent above, with scattered pilose hairs above in some large-leaved specimens; indument of the involucre sparse to moderate, white or cinereous; solitary axillary flowers sometimes present . . . . Sa. S. ciliaris var. ciliaris.
B. Carpels 5 , rarely 6 , muticous or submuriculate, the lateral walls membranous, weakly reticulate; indument of the involucre dense, flavid or fulvous; flowers numerous in the involucres, never solitary 5 b. S. ciliaris var. fulva.
A. Leaves linear to narrowly oblong to elliptic or lanceolate, the margins serrate usually in the upper part only or merely tridentate; petals 5-15 mm . long, 2- 10 mm . wide

C
C. Leaves narrowly oblong, often cuneate, truncate to acute; petals $8-15 \mathrm{~mm}$. long, $7-10 \mathrm{~mm}$. wide, strongly oblique; carpels $5-8$, muricate, biaristate . . . . . . . . . . . Sc. S. ciliaris var. anomala.
C. Leaves linear to linear-lanceolate or elliptic, apex acute; petals slightly oblique, 2-4 mm. wide
D. Carpels 5, rarely 6, biapiculate, muriculate; leaves linear-elliptic to elliptic, to 17 mm . long and 4.5 mm . wide; petals $5-6 \mathrm{~mm}$. long, $2-3 \mathrm{~mm}$. wide; stamen-tube glabrous; plants procumbent

5d. S. ciliaris var. involucrata.
D. Carpels usually 7, short-aristate, muricate; leaves linear to linear-lanceolate, to 21 mm .; petals $1-14 \mathrm{~mm}$. long, $3.5-4 \mathrm{~mm}$. wide; stamen-tube with scattered hairs; plants ascending to erect . . Se. S. ciliaris var. mexicana.

## 5a. Sida ciliaris var. ciliaris.

S. muricata Cav., Ic. 6: 78, f. 2. 1801.
S. erosa Salzm. ms. in Tr. and Pl., Prod. Fl. Nov. Gran. 1: 176. 1862. (nomen nudum).
S. ciliaris var. guianensis K. Schum., Mart. Fl. Bras. 12 (3): 284. 1891.
S. ciliaris f. flava O. Ktze., Rev. Gen. 3 (2): 22. 1898.
S. longistipula Merr., Phil. Journ. Sci., Bot. 13: 301918.
type: Browne, Jamaica (Linnaean Herbarium).
In publishing this species, Linnaeus cited a plate in Sloane's Natural History of Jamaica. Unfortunately, the plate shows a plant which is very doubtfully of this species, since it much more resembles $S$. spinosa. The phrase in the type-description "seminibus muricatis", however, can refer only to $S$. ciliaris, and the additional phrase "fol. ....retusis" certainly does not refer to the acute leaves of the cited figure, which finds no match in the Jamaican material of the species which I have seen. Linnaeus had purchased Browne's Jamaica collections before the species was described, and undoubtedly his original description was based on the specimen which he labelled "Sida ciliaris" and "Br.", for Patrick Browne (Savage 1945).
distribution: Florida Keys and Texas; Bahamas and Antilles (except Puerto Rico); Mexico to Bolivia and Argentina; Philippines (introd.).

5b. Sida ciliaris var. fulva (St. Hil.) K. Schum., Mart. Fl. Bras. 12 (3): 284. 1891.
S. plumosa Cav., Diss. 1: 7. t. 12, f. 4. 1785.

Malachra plumosa (Cav.) Desr., Lam. Encyc. 3: 363. 1791.
S. fulva St. Hil., Fl. Bras. Mer. 1: 176. 1827.

TYPE: The type of S. plumosa, the oldest name for the taxon, is a Commerson specimen from Brasil loaned by Thouin to Cavanilles in Paris. There is a probable isotype of this collection in Madrid. distribution: Southern Brasil.

5c. Sida ciliaris var. anomala (St. Hil.) Hochr., Ann. Cons. Jard. Bot. Gen. 6: 35. 1902.
S. anomala St. Hil., Fl. Bras. Mer. 1: 177. 1827.
S. ciliaris var. anomala K. Schum., in Engl. \& Prantl, Nat. Pfl.

3, Abt. 6: 43. 1890. (nom. nud.).
S. anomala f. albiflora Chod. \& Hass., Bull. Herb. Boiss. ser. 2.

5: 290. 1905. (including subforms).
S. anomala f. roseiflora Chod. \& Hass., l.c. (incl. subforms).
S. anomala f. violaceiflora Chod. \& Hass., op. cit. 291.
type: St. Hilaire C2/2470 "près le village de Sando" Paisandú, Uruguay ( P , specimen in F labelled "Santos" probably of this collection; St. Hilaire was never in Santos).
distribution: Colombia, Venezuela, Brasil, Uruguay, Paraguay and Argentina.

5d. Sida ciliaris var. involucrata (A. Rich.) Clement, stat. nov.
S. involucrata A. Rich., Ess. Fl. Cub. 162. 1845.
? S. tridentata Cav., Icones 4: 6. 1797.
TYPE: de la Sagra "crescit in incultis insulae Cuba" ( P , fragment in F).
distribution: Bahamas, Cuba, Hispaniola and Lesser Antilles; Yuca$\tan$ peninsula of Mexico.

5e. Sida ciliaris var. mexicana (Moric.) Shinners, Field and Laboratory 21: 94. 1953.
S. anomala var. mexicana Moricand, Pl. Nouv. Am. 36, t. 24. 1837.
S. fasciculata Torrey \& Gray, Fl. N. Am. 1: 231. 1838, non Willd.

Malvastrum linearifolium Buckley, Proc. Acad. Sci. Phila. 1861: 442. 1862.
S. ciliaris var. fasciculata (Torr. \& Gray) Gray, Proc. Am. Acad. 22: 294. 1887.

TYPE: Berlandier exsicc. 66, "circa Tampico de Tamaulipas" (G). distribution: Texas and Mexico to Panama.
The species is variable nearly throughout its range and is especially so in South America. A major problem arises in the satisfactory disposition of the element usually identified as $S$. anomala. The type-specimen of S. anomala, from Uruguay, is not what most authors consider it to be. Its leaves are oblong, slightly cuneate and mostly truncate, rather than linear and acute; its carpels muricate only on the dorsal margins rather than on the whole dorsum and on the lateral walls; and its petals $5-8 \mathrm{~mm}$. long rather than around 10 mm . It is, as it is usually described,
few-stemmed and apparently erect, and is, in sum, intermediate between the extremes usually separated as $S$. ciliaris and $S$. anomala. There is no truly linear-leaved material in South America, although this character has appeared in most keys because Schumann, whose key has usually been taken over outright by later authors, included S. anomala var. mexicana, here considered a variety of $S$. ciliaris, as a synonym of $S$. anomala. I do not think that $S$. ciliaris var. mexicana and $S$. ciliaris var. anomala have any close relationship but are, instead, two separate tendencies in the species, both having narrow leaves and large flowers. Both intergrade with the typical smaller-flowered, broader-leaved material, and in the South American material, such combinations as large flowers and small obovate and truncate leaves occasionally occur, as in Swallen 9507 (Us). Despite the number of intermediates, I have attempted here to define thesc tendencies as separate varieties, but it should be understood that they are only tendencies. Only those specimens representing the non-typical varieties in or near their maximum expression have been listed under them in the specimen-citation.

Other tendencies in the species in South America have been named. Of these, only S. ciliaris var. fulva has any constancy, although a few intergrades between it and the typical state are present. S. ciliaris var. guianensis, even in the specimens cited by Schumann, varies continuously from the large-leaved, six-carpelled extreme to the typical, and I have not retained it. The colorforms and pubescence-subforms of Kuntze and Chodat \& Hassler, described under both S. anomala and S. ciliaris, are of no real worth in a species where color-variation is common, even in local populations, and pubescence-variation is still more common.

The species appears to be one of hybrid origin which is still in the process of segregation and recombination in much of its area. Only in a few areas such as Jamaica is there any constancy in the nature of the population. In the southern part of its range, as in the northern, a tendency to narrow leaves and large flowers is strongly evident, and to a lesser extent in the intervening area. Centering in Cuba, there is a third narrow-leaved element, here named as var. involucrata, but the flowers here are small, about the size of the typical. The other species of this section are undoubtedly segregates from this complex which have achieved genetic or geographic isolation, and I can think of no group in
the genus where genetic and cytological studies of inter- and intra-specific variation might be more rewarding.

## 5a. Sida ciliaris var. ciliaris

United States: Florida: Blodgett. Key West (gh, us 2). Chapman, Key West (Gh). Curtiss 5445, Long Key (GH 2, uc, us). Hitchcock. March 1906. Key West (F). Hitchoock 28, 30 March 1906, Key West (F). Lansing 1983, Key West (F). Rugel 96. Key West (GH. Us). Simpson 472, Long Key (GH, Us). Small 10108. Big Pine Key (GH); Small 10217, Key West (us). Texas: Cory 5910, w. of Menthalia, Gonzales Co. (GH). Heller 1567. near Gregory, San Patricio Co. (Ny, us). Palmer 91. Sutherland Springs, Wilson Co. (GH, us).

Mexico: Baja California: Jones 24127. Todos Santos (us). Jones 24661, Todos Santos (ром). Campeche: Steere 1812, Champoton (f). Colima: Ferris 6095 , vicinity of Manzanillo, Colima (Ds, GH, us). Guerrero: Hinton 6490, Coyuca, Coyuca (GH, ny, us). Palmer 30. Acapulco and vicinity (GH, mo, NY, us). Jalisco: Mexia 1155. Puerto Vallarta (Gh, mo, ny, pom, uc). Pringle 4497, near Guadalajara (mexu 2, mo, UC, Ny, GH). Rose 2581, between Huajuquilld and Mosquitac (us). Rose 3696. Bolanos (GH, us). Mexico: Hinton 1469. Dist. of Temascaltepec, Calera (f, mexu 2. us). MichoacÁn: Hinton 15181. Apatzingan (gh, ny). Oaxaca: Conzatti 1600. Oaxaca (us). Gonzáler 288, El Forties (Gh). Nelson 1231, Valley of Oaxaca (us). Orcutt 5028. Puerto Angle (Ds). Smith, L. C. 510, Cuicatlán (GH). Sinaloa: Brandegee. 8 Oct. 1893, Mazatlán (UC). Brandegee, 13 Sept. 1904, vicinity of Culiacán (GH, uC). Brandegee, 1 Nov. 1904, vicinity of Culiacán (us). Mexia 64, hill "La Neveria". near Mazatlán (UC). Mexia 168, "La Noria" (mo. uc). Mexia 350. "La Noria" (ром, мо, vc). Narváez Montes \& Salazar 666, San Ignacio (us). OHegat 4361. Cerro de la Neveria (mexu, us). Ortega 4640. Mazatlán (mexu 2, us). Rore 13694, vicinity of Mazatlán (GH, NY, us). Wight 1258, Mazatlán and vicinity (DS, F, GH, MO, UC).

British Honduras: Peck 175, near Manatee Lagoon (GH). Peck 452, near Manatee Lagoon (GH). Espat 35, Bakers. near Belize R. 18 miles from Belize (F).

Guatemala: Heyde 175, Guatemala (us). Heyde \& Lux 3948. Carrizal. Dept. Santa Rosa (Gh. ny, mo, us). Standles 24379, vicinity of Los Amates, Dept. de Izabál (ny, GH. us). Standley 59629, near Fiscal, Dept. Guatemala (NY, F). Standley 73600, vicinity of Zacapa, Dept. Zacapa (F). Standley 73928, Dept. Zacapa: Baños de Santa Marta, north of Zacapa (f). Stundley 74373. Dept. Chiquimula: Quebrada Shusho, above Chiquimula (F). Standle) 75038. Dept. Jutiapa: vicinity of Jutiapa (F). Standley 78805, Dept. Santa Rosa: southeast of Chiquimulilla (F). Standley 80467, Dept. Guatemala: near Fiscal (F). Steyermark 29077, Dept. Zacapa: near Estanzuela (F)

El Salvador: Standley 19835, nr. Ahuachapan, Dep. Ahuachapan (GH, us).
Honduras: Rodriguez 312, Yeguaré, Dept. Morazán (F). Yuncker, Dawson \& Youse 5812, Siguatepeque (MO, GH, F).

Nicaragua: Maxon et al. 7584. near Granada (us).
Costa Rica: Brenes 22814, "Los Loros". Pacific coast (F)
Panama: Pittier 4843, Aguadulce. Prov. of Coclé (Ny, GH. us). Standley 26288, near Punta Paitilla, Prov. of Panama (us). Standley 30786. Nuevo San Francisco, Prov. of Panama (us). Standley 31863, between Las Sabanas and Matias Hernández, Prov. of Panama (us).

Bahamas: Brace 132, New Providence (Ny). Hitchcock, 12/3/90, Inagua (mo). Millspaugh \& Millspaugh 9099, East Caicos, Jacksonville and vicinity (US, NY, F). Wilson 7820, Great Ragged Island (GH).

Cuba: Ekman 8243. Prov. Oriente, María Pilar, on Río Baconao (Ny). Bro. Hiram 2274, Boca del Jaibo (Ny). Shafer 2482, Cayo Romano, Camagüey (GH, NY, US).

Jamaica: Alexander, 1850 (NY). Britton 785, vicinity of Kingston (NY, F). Cambell 6023 (Ny). Harris 9768, Long Acre Point, west of Black River (ny, us). Harris 12044, near Spanish Town, St. Catherine (GH, MO, NY, US). McNab (GH, NY).

Haiti: Ekman H8396, St. Michel, towards l'Halaye (us). Leonard 2855, vicinity of St. Marc, (US, GH, NX). Leonard 7312, vicinity of St. Michel de l'Halaye, Dept. du Nord (US). Leonard 7307, vicinity of St. Michel de l'Halaye, Dept. du Nord (GH, NY, US). Leonard 12610, vicinity of Jean Rabel (GH, NY, Us). Leonard 9855, vicinity of Gros Morne, Dept. de l'Artibonite (UC, US). Leonard \& Leonard 15107, vicinity of Bassin Bleu (US). Leonard \& Leonard 11052, vicinity of Port de Paix (us, mo). Nash 938, Cap Haitien (Ny). Potter 5026, Port au Prince (GH).

Dominican Republic: Abbott 866, Guayubin, Prov. de Monte Cristi (us). Ekman H15996, Valle del Cibao, Prov. de Santiago, Hato del Yague (us). Fuertes 20, Prov. Barahona (us, NY). Fuertes 1018. Prov. Barahona (Ny). Valeur 246, Moncion, Prov. of Monte Cristo (mo, us, F, NY, pom, DS, UC). Wright, Parry \& Brummel 46, Santiago de los Caballeros (us). Bertero, "Santo Domingo" (mo).

St. Croix: Haunen 159 (ny). Ricksecker, A. E. 3, Bassin yard (US, NY, GH, mo). Ricksecker, J. J. 260, Bassin yard (us, MO). Thompson 42, Anna's Hope (GH). Thompson 136, Anna's Hope (ny). Thompson 317, Anna's Hope (GH). Thompson 333, Coakley Bay (GH). St. Jan: Britton \& Shafer 329, Betheania (US, NY). Virgin Gorda: Fishlock 163, "valley" (NY). Anegada: Britton and Fishlock 1022, "rocky plain near the settlement" (NY). Fisblock 33, "near a small pond" (Gн). Tortola: Britton \& Shafer 687, road, Town to Sea Cow Bay (us, Ny). St. Thomas: Britton, Britton \& Shafer 36, Belgian Road (Us, F, Ny). Kuntze 139 (Ny). Holion (ny). Eggers, 16 May 1876 (mo). Eggers, July 1887 (us). Eggers 194, Jollyberg (Us). St. Martin: Brition \& Cowell 87, "waste places" (Ny). St. Barthélemy: Questel 187, Gustavia (NY). Questel 298, Gustavia (ny). Questel 813, Sous le Fort (ny). St. Eustatius: Boldingh 1153 B (ny). Antigua: Box 1073, High Point (GH, us). Guadeloupe: Duss 2790 (US). Duss 2790.4116, "St. Francis, Désirade. Les Saintes. 1892" (ny). Duss 4141, along the Marne (Ny). Steblé 148, Marie-Galante, sands of Grand Bourg (us). Stehlé 194. Désirade (NY). Stehlé \& Quentin 5294, Désirade, "près du Phare" (us). Martinique: Duss 8ú2, St. Anne (ny). Stehlé 5443, near Madiana (us). Barbados: Gooding 583, Gibbon's Christ Church (NY).

British Guiana: Schomburgk 405, Pirara (Isotype of S. ciliaris var. guianensis, us). Brasil: Allemao 96, Ceará (us). Dablgren 854, Ceará, Fortaleza region, Kagado (F). Drouet 2317, State of Ceará, Municipio de Fortaleza (GH, F). Drouet 2333, Ceará, Fortaleza (F, GH, NY). Gardner 2052, Prov. de Piauhy (GH, US, F, Ny 2). Kuntze 1799, La Guayra (ny). Pickel 3991, Pernambuco, Russinha (GH, NY, F). Suallen 9507, Bonito, Mato Grosso (Us).

Paraguay: Hassler 1238, "Duarte" (ny). Hassler 2491, Cerros de Paraguary (GH). Hassler 7508, near Concepción (GH). Hassler 12660, Cordillera de Altos (US, MO, GH). Jörgensen 4387 (F, NY 2). Kuntze, Sept. 1892, Concepción de Paraguay (NY). Kuntze, Sept. 1892, "Sud-Paraguay" (NY). Morong 240, Asunción (NY, UC). Rojas 2485, Gran Chaco, Loma Clavel (GH).

Argentina: Aguilar 480, Chaco, Dep. Resistencia, Margarita Belén (us). Jörgensen 2312, Formosa, in Territorio de Formosa (GH).

Bolivia: Bang 934, vicinity Cochabamba (Gr, us). Cârdenas 4115, nr. Serrano, Chuquisaca (us). Fiebrig 2551, Padcaya (us, NY).

Ecuador: Asplund 5619, Prov. Guayas, Salinas (US). Eggers 14813 (F). Jameson 580, environs of Guayaquil (us). Svenson 11238, Prov. Guayas, Salinas (NY).

Philippines: Ramos 27311 and 32704, Burgos, Luzon (us). Ramos 27492, Bangui, Luzon (Us).

## 5b. S. ciliaris var. fulva

Brasil: Barreto 5245, Cruz das Almas, Andrelardia (F). Burchell 958 (GH). Commerson (photograph of probable TYPE, P: F). Cummerson (photo. of ISOTYPE in herb. Cav., Madrid: us). Gardner 12, Rio Comprido, Rio de Janeiro (NY, us, GH). Hoebne 19516, Canelleiras, Ouro Fino (Ny). Lutzelburg 339, Bahia (NY). Martius Aug. '70, "in aridis ad vias Sebastianopolis", Rio de Janeiro (photo. us). Riedel 1332, Rio de Janeiro (GH, us). Riedel 2026, near Ytú (Us). Rose 19688, vicinity of Bahia (US). Schwartze 14684, "east of Rio" (US). Smith, L. B., 1637, Rio de Janeiro, vicinity Monte Serrat, Mi. Itatiaya (GH, Us). Usteri, 18 March 1906 (Ny).

## 5c. S. ciliaris var. anomala

Colombia: Lebmann 2276, Tolima (us). Lehmann 6051, Neiva (F). Lehmann 8719, El Gigante and Altamira, Río Magdalena (NY, UH). Venezuela: Holt and Gehriger 37, Anzoátegui, Soledad (us). Brasil: Dias du Rorha 4, Ceará (us). Drouet 2196, Ceará, Mun. de Maranguape (F, GH). W'eddell 3073, Prov. Mato Grosso, nr. Kiamentino (F). Uruguay: St. Hilaire, cat. C2/2470, Paisandú (TYPE, P, specimen in F labelled "Santos" probably of this collection). Paraguay: Fiebrig 910, without locality (F, GH). Hassler 6388, Cerros de Tobaty (GH). Hassler 6615, Central Cordillera, Río Y-acá ( GH ). Jörgensen 4287, Villa Rica (us). Argentina: Jörgensen 2315, Chaco Territory, Las Palmas (GH, us). Lorentz 1762, Dec. 1877, Concepción del Uruguay, Entre Ríos Prov. (Gн). Veniuri 9120, Formosa (us).

## 5d. S. ciliaris var. involucrata

Mexico: Yucatan: Gaumer 779. Izamal (GH, ds, us, Ny, uC, mo). Gaumer 1565, Chichankanab (F). Gaumer 2509, Izamal (GH, F). Schott 116, Merida (mo, us, f labelled "Habana"). Steere 4998, Chichen-Itzá (mexu). Bahamas: Brace 131, New Providence (F). Brace 4909, Ruaria Hill, Long Cay (NY). Brace 4257, Acklin's Island, Spring Point (ny, us, f). Britton 3369, Tea House, New Providence (f, uS, GH, MO, NY). Britton \& Brate 201, Farringdon Road, New

Providence (ny, F). Britton \& Millspaugh 2248, Little Harbor Cay, Berry Islands (ny, us). Britton \& Millspaugh 5467, Eleuthera, Governor's Harbor and vicinity (ny). Coker 340, Eleuthera (ny). Curtiss 96, Near Nassau, New Providence (us, mo, nY, GH). Hitchcock, Nov. 1890, Fortuno Is. (mo). Nash \& Taylor 964. Inagua, Mathew Town (Ny). W'ight 22, near Fort Charlette, Nassau (GH, NY). W'ilson 7376, Atwood Cay (Ny). Wilson 7820, Great Ragged Island (Ny, mo).
Cuba: Baker \& W'ilson 2342, Batabanó, Prov. Habana (f, pom, us). Britton \& Earle 7566, Prov. of Pinar del Río, Bay of Mariel (ny). Curtiss, March 1904, Isle of Pines (ny). Ekman 869, Prov. Habana, Vedado (F, us). Howard 5772, Santiago de Cuba, Oriente Prov. (Gh). León 358, near Habana (ny). León 4679, north of Marianao, Habana (ny). Palmer \& Riley 1050, near Nueva Gerona, 1sle of Pines (ny). Haiti: Leonard \& Leonard 15852, vicinity of Port au Prince (us).

## 5e. S. ciliaris var. mexicana

United States: Texas: Berlandier 3035, without locality (us). Bigelow, San Antonio (ny). Bush 293, Brazos R., Columbia (GH, ny, us). Cory 14187, Queen City Falfurrias (GH). Cory 55767, 6 mi . WSW of Giddings, Lee Co. (Us). Drummond 37 (Type of S. fasciculata, Ny). Drummond 47 (GH). Drummond 50 ( GH ). Fisher 2058, Houston (UC, Us). Hanson 57, Gregory (us), Junction H. S. (Tharp) 7189, Goliad Co. (us). Lundell \& Lundell 8767, nr. Redfish Bay, Willacy Co. (Ds). Lundell \& Lundell 10036, nr. San Manuel, Hidalgo Co. (Ds). McDonald, nr. Bastrop (us). Metz 745, 20 mi . south of San Antonio, Bexar Co. (uc). Nealley, Nov. 1884. Houston (GH). Runyon 2441, Yturria, Willacy Co. (DS, UC). Snyder, 1905, Cypress (UC). Tharp 1170, Brownsville (Us). Tharp 1392. Austin (US). Thalp et al. 49172.18 mi . southeast of Yoakum, Lavaca Co. (Us) Thuron 12, Hockley (us). W'right, Eagle Lake (us).

Mexico: Berlandier 66, nr. Tampico, Tamaulipas (ISOTYPE, mo). Haenke, Mexico (мо). Mell 2108, San Gerónimo, Oaxaca (Ny, us). Mexia 963, trail from Los Labrados to La Marisma, Sinaloa (Ds, GH, MO, NY, UC, us 2). Oriega 4639, Mazatlán, Sinaloa (US). Ortega 7279, Sinaloa (F). Rose 1892, between Concepción and Acaponeta, Nayarit (us). Rose 2581, Nayarit (us). Sessé and Mofiño. "S. linearis" (F). W'ooton, 1919, Hda. Buena Vista, Tamaulipas (US). British Honduras: Lundell 6989, Baker's Pine Ridge, Belize Distr. (ny). Honduras: Molina R. 278, Maraita (us). Rodriguez 510, road to Tatumbla, Dep. Morazán (F). Rodriguez 3297, San Lorenzo, Dep. Valle (F). Rodriguez 3438, San Lorenzo (F). Williams and Molina 10211, nr. Galeras, Dep. El Paraiso (uc). Costa Rica: Shannon 5006, Volcán Orosí, Prov. Guanacaste (us).
Panama: Allen 817. Nata (F, GH, MO, NY, US).
II. Section Physalodes A. Gray, Smiths. Contr. Knowl. 3, art. 5: 20. 1852.

Section Calyxhymenia A. Gray, Proc. Am. Acad. 22: 294. 1887.
Calyx much inflated after anthesis, the lobes deeply divided, the margins plicate; carpels muticous, lateral walls persistent.

The section was founded by Gray in the following words:
"this species [S. physocalyx Gray], S. hastata, St. Hil., and S. physalodes, [sic] Presl, form a section remarkable for the bladdery inflated calyx, which may be distinguished by the name of Physalodes". In the later paper, he described section Calyxhymenia as follows: "To the peculiar sections named in Pl. Fendlerianae.... a third may be added, Calyxhymenia, for species which have the ebracteolate calyx much accrescent around or under the fruit, and membranaceous or scarious, - the name taken from S. calyxhymenia, Gay, of Australia, .... Our species, S. physocalyx, Gray, Pl. Lindh. 2, 163, in which the 5 -parted and angulate bladdery fruiting calyx imitates that of Nicandra, has rather peculiar and very thin-walled reticulated indehiscent carpels with a beak-like apex. The homonymous S. physocalyx F. Mueller from Australia is much later, and will find another name".

Schumann later showed that S. physocalyx Gray and S. hastata St. Hil. were synonymous, the first described from Texas, the other from Brasil. He apparently did not realize that St. Hilaire's name was a later homonym for S. hastata (Cav.) Willd. (1801), and for S. bastata Sims (1811), since he placed Gray's name in the synonymy, which has been done by almost all workers since. The nomenclatorial type of the section is, then, S. physocalyx A. Gray, while the type-collection of that species and thus of the section is St. Hilaire's "In provincia Cisplatina" Uruguay, in the Paris herbarium. A photograph of this is reproduced in Rodrigo (1944).

All of the previously known American species of the section are represented in the flora of Argentina and Uruguay, and Rodrigo's analysis of them (1944) is satisfactory in most respects. She added S. decumbens St. Hil. \& Naud. to the section on the grounds that it has the calyx inflated after anthesis and muticous carpels. Hochreutiner had transferred the species to Anoda because of the disappearance of the lateral walls of the carpels in maturity, but Kearney (1954) retains it in Sida. Even if it be kept in Sida, it does not belong in the section. I have here added to the section a new species from Mexico.

Baker placed a number of Australian species in the section, and of these, S. calyxhymenia Gay ex DC., and S. physocalyx F. Muell. non Gray definitely belong here. Study of types, authentic material and published descriptions of the other species assures
me that they do not belong here. S. Kingii F. Muell. has a somewhat accrescent calyx, but the spinulous fruits are quite unlike those of any species of this section. The calyx of S. cleisocalyx is not at all accrescent, while that of S. inclusa and of S. platycalyx is of a very different type with numerous ribs. S. inclusa, furthermore, has a tremendous globose fruit, beset with spines clothed in stellate pubescence. S. Clementii Domin was related to $S$. calyxhymenia by its author, but the material I have seen of it differs in a number of details from that species and the calyx is only slightly accrescent. Type species: Sida physocalyx A. Gray.

Key to the Species
A. Carpels ten to seventeen . . . . . . . . . . . . . . . . B
B. Carpels ten to fourteen. (New World) . . . . . . 6. S. physocalyx.
B. Carpels fifteen to seventeen. (Australia)
7. S. Brownii.
A. Carpels five or eight, rately nine

C
C. Carpels eight or rarely nine . . . . . . . . . 8. S. macrodon.
C. Carpels five

D
D. Flowers clustered four to sixteen in the upper axils . . 9. S. urticaefolia.
D. Flowers solitary or paired in the axils, rarely in threes . . . . . . E
E. Plants erect, leaves rounded at the base, flowers usually solitary in the axils. (Australia) . . . . . . . . . . . 10. S. calyxbymenia.
E. Plants prostrate, leaves cordate at the base; flowers usually paired in the axils. (New World)
F. Petals 5 mm . long, stamens ca. twenty. (Mexico) . . . 11. S. Standleyi.
F. Petals $8-9 \mathrm{~mm}$. long, stamens $30-40$. (S. America) 12. S. flavescens.
6. Sida physocalyx A. Gray, Bost. J. Nat. Hist. 6: 163. 1850. S. hastata St. Hil., Fl. Bras. Mer. 1: 190. 1827, non Willd., Sp. P1. 3: 763. 1801.
S. hastata var. tomentosa R. E. Fries, K. Sv. Vets. Handl. 42, 12: 35. 1908.
S. hastata var. glabriuscula R. E. Fries, 1.c.
S. inflata Larrañaga, Escritos 2: 218. 1923.

Perennial herb from a thick, fusiform, woody taproot; stems decumbent or prostrate, $10-30 \mathrm{~cm}$. long, few- to many-branched, dark green, covered more or less densely with 4 -rayed submalpighiaceous hairs, hyaline or yellowish. Leaves suborbicular, ovate, or oblong, or long-elliptic, to 6 cm . long and 5 cm . wide, the base cuneate to truncate, sometimes oblique; the apex rounded to acute; the margins serrate, sometimes irregularly; nerves 5, palmate from the base, prominent beneath; the indument variable, that of the upper surface from glabrescent to moderately stellate-tomentellous, the hairs fine or coarse, sometimes like
those of the stem; indument of the lower surface like that of the upper, usually much denser; occasionally both surfaces with simple, appressed, pilose hairs, intermingled, of various lengths. Petioles $1.0-2.2 \mathrm{~cm}$. long, always shorter than their leaves, the indument like that of the stem. Stipules linear-lanceolate, persistent, yellowish-ciliate, ca. 3 mm . long, ca. 0.8 mm . wide. Pedicels solitary and axillary, $12-20 \mathrm{~mm}$. long, filiform, finely stellate-hirsute, articulated in the upper fourth. Calyx greatly accrescent during the whole period of growth, strongly plicate. the lobes and subjacent tube flat or concave, during anthesis ca. 5 mm . high, 4 mm . wide, the base of the tube rounded, later impressed; the lobes soft-awned, the lobal face of the calyx almost cordate in appearance; the indument like that of the leaves. Petals white, yellow or rose, veins and base darker, gibbous, the outer portion rotund, one margin concave, the other convex; $1.2-2.0 \mathrm{~cm}$. high, $5-9 \mathrm{~mm}$. wide, the claw $1.0-1.5 \mathrm{~mm}$. wide, entirely glabrous. Stamen-column 5 mm . high, terete, with five pairs of strongly marked traces; the base of the column broadly dilated, glabrous; the filaments $1-2 \mathrm{~mm}$. long. Anthers ca. 40 , pale, not dotted. Ovary 1.3 mm . high, ca. 2.5 mm . wide, the lower third impressed, the apex subapplanate. Styles $5-6 \mathrm{~mm}$. long, $2.5-3 \mathrm{~mm}$. free; the stigmas capitellate. Carpels $9-14$, ca. 5 mm . radially, 3 mm . high, forming a flat-topped fruit, blackish, the rostrum prolonged as a long horizontal beak over the apex of the columella; the dorsum manynerved, impressed transversely over the hilar depression of the seed, sharply impressed radially on the outer surface, the outer margins crested; the lateral walls horizontally compressed-rugose; dehiscence by the tardy disintegration of the apex. Seed black, with minute, rather thickly scattered, stellate, white, appressed puberulence, $2-3 \mathrm{~mm}$. high and wide, the funicle black, glabrous, flattened. Columella capstan-shaped, 1.0 mm . high, 1 mm . wide at the top, 2 mm . at the base, the sides concave in outline, the top stellate in vertical view, black.

TYPE: St. Hilaire "Assez commun sur les bords des chemins dans la province Cisplatine". Uruguay (P).
distribution: Texas, New Mexico, Arizona; northern Mexico, Brasil?, Uruguay, Argentina, Bolivia.

The problem of typification of the section rests on the typification of $S$. physocalyx and has been discussed previously. The distribution of the species is unusual but not unprecedented; Schumann (1891) pointed out that S. leprosa has a rather similar bicentric range, as do species of the genera Mentzelia, Daucus, Cuphea and Bouchetia. Two closely allied species of this same section also show this pattern when their ranges are mapped together. The presence of the species in Bolivia is based on a
single O. Kuntze collection which is not in mature fruit, but it occurs in adjacent Jujuy province, Argentina, and will probably be found again.

Fries' two varieties, based almost solely on the leaf-pubescence, were supposedly geographic, his var. glabriuscula found throughout the range and var. tomentosa confined to the South American part of it. In actuality, both are seen to occur at random throughout the range when a long series of specimens is studied, and there are so many intergrades that they are not even worthy of being considered forms.

Larrañaga's field notes, unfortunately published, named as $S$. inflata a plant he had observed on April Fool's Day 1814 which had solitary flowers in the axils, an inflated calyx and eleven carpels and which was undoubtedly S. physocalyx.

The extraordinary carpel-shape in this species finds its parallel in that of S. aprica Domin of Australia. Examination of authentic material of that species from Kew shows that it does not belong to this section, the calyx being very little inflated, nor does that species resemble $S$. physocalyx very closely in any other details.

United States: (only enough U.S.A. specimens to indicate the range are listed here). OKLAHOMA: Harmon Co.: Stevens 1103, near Hollis (ny, gh). TEXAS: Baylor Co.: Reverchon 104 (us). Bell Co.: W'olff 992, northwest of Belton (us). Bexar Co.: Clemens 601, San Antonio (mo, pom). Brewster Co.: Warnock W99, Altuda Pass, Glass Mts. (ch). Brown Co.: Palmeer 26804, Brownwood (mo). Cameron Co.: Hanson 8, Brownsville (mo, ny, gh, us) Comanche Co.: Eggert, 10 May 1900, Comanche (mo 2). Culberson Co.: Waterfall 5345, 9 miles east of Van Horn (mo, gh). Edwards Co.: Cory 37900, Substation No. 14 (GH). El Paso Co.: Ferris \& Duncan 2369, east of Ft. Bliss on Alamagordo Road (mo, ny). Garza Co.: Ruth 1318 (us). Hidalgo Co.: Camaron 109, Mc Allen (F). Hudspeth Co.: Waterfall 4966, east side of Eagle Mts. (mo, Gh). Jeff Davis Co.: Hinckley 1200, Davis Mts. (f, ny). W'aterfall 4727, 2 miles southwest of Chispa (GH). Kerr Co.: Heller, $12-19$ June 1894, Kerrville (ariz, gh, uc, ny 2, mo). Kleberg Co.: Sinclair 175, Kingsville (ch). Kinney Co.: Mearns 1455, Fort Clark (us, ds). Midland Co.: Tracy 7815, Midland (ny 4, gh, mo, us). Mitchell Co.: Eggert, 9 June 1900, Colorado (мо 2). Pecos Co.: Tharp 43-702 (uc, mo). Presidio Co.: Hinckley 1500, 25 miles west Marfa (ariz, Gh). Stephens Co.: Reverchon 104. 710 (mo). Sutton Co.: Cory 2049 (Gh). Taylor Co.: Tolstead 7460, near Abilene at Lake Lytle (uc). Terrell Co.: Pulmer 33510, neat Feodora (ny). Tom Green Co.: Tueedy 220, Dove Creek (us). Travis Co.: Taylor 3054, Austin (uc). Hall 60. Coronado R. (mo, pom. ny, F). Livalde Co.: Munz 13302, 7 miles southeast of Livalde (ром). Wilson Co.: Palmer 9197, Southerland Springs (ds, mo). Zapata Co.: Cluver 131f. Las Comitas Ranch (ny). Without definite locality: Wright. 1848 ( $\mathrm{GH}, \mathrm{mo}, \mathrm{ny}$ ). Type-sheet of S. physocalyx

Gray has following: Cult., Harvard Botanic Garden. from Texas seed sent by Wright; Gregg, valley near San Pablo, Mexico; Lindbeimer, llano, west Texas; and IV'right, 1848, Texas. NEW MEXICO: Chaves Co.: Earle 352, 20 miles south of Roswell (us, mo 2, ny). Doña Ana Co.: Standley 3414. near Tortugas Mountain (US). W'ooton 560, in the Organ Mountains (NY, us, MO, ARIZ). Wrthout definite locality: Wright, 1851 (ny, us). ARIZONA: Cochise Co.: W'olf 2543. 5 miles north of Douglas (DS, GH). Peebles. Harrison \& Kearney 3514, near Ft. Huachuca (us). Pima Co.: Abrams 12678, Tucson (DS, pom, Ny). Kearney \& Peebles 14971, Baboquivari Canyon. Baboquivari Mts. (GH). Santa Cruz Co.: Beattie 4. Tubac (mo). Yavapai Co.: Purpui 57. Beaver Creek (mo, us, Uc).

Mexico: Sonora: Thurber 419, Fronteras (Gh). Chihuahua: LeSueur 743, Meoqui Pass (GH, F). Siewart 675, 20 kilometers northwest Jaco along road to Victoria (GH). W' bite 1108, Carretas (GH). W' bite 2164. 3 miles north Cd . Jiminez (GH). Coahulla: Jobnston \& Muller 852. 1 mile east Bufido (GH). Marsh 1800. Allende (GH). Palmer 87. Parras, 112 miles west Saltillo (GH, US). Stewart 551. 4 kilometers west Castillon (GH). Stewart 1164. Llano de Guaje. near Tanque de La India (GH). Steurart 1766. 16 kilometers west San Guillermo (GH). Nuevo León: Heard. W'ebster \& Burkley 14565. 2 miles north of Sabinas Hidalgo (GH). Thurber 851. Parras (GH).

Brasil: Sello, without number or locality (us).
Uruguay: Rusengurt B-4710. Durazno (GH, mo, us). St. Hilaire, "sur les bords des chemins dans la province Cisplatine" (TYPE, P).

Argentina: Bridarolli 3210. Carapari. Dept. de Oran (GH). Eyerdam \& Beetle 23092. Campana. Prov. Buenos Aires (GH, UC). Hauthal. Ventana, Prov. Buenos Aires 1892 (NY). Jörgensen 1825. Catamarca. Dept. Andalgalá, El Guacho (GH). Palmer. 1853-1856. La Plata (us). Parodi 11328, Campana, Prov. de Buenos Aires (GH). Parodi 11278. Vera, Prov. de Santa Fé (F). Venturi 4840, Dept. of Tumbaya, Prov. de Jujuy, Volcán (us). Venturi 1722. Tucumán. Dept. Trancas (us).

Bolivia: Kuntze, 1892, Parotani (NY).
7. Sida Brownii Clement, nom. nov.

Sida physocalyx F. Muell., Fragm. 3: 3. 1862, non A. Gray, Bost. Journ. Nat. Hist. 6: 163. 1850.

Erect subshrub to 4.5 dm . high, stems few, densely soft-stellate tomentose, the rays pale yellow, very fine and short. Leaves orbicular or ovate, subcordate at the base, $2.5-5 \mathrm{~cm}$. long, to 3.2 cm . broad; the apex rounded or acute; the margins irregularly crenate; the indument dense, fulvid or canescent-tomentose; petioles densely tomentose, like the stem, terete, $1.0-1.5 \mathrm{~mm}$. diam. Stipules filiform, $1.3-1.5 \mathrm{~cm}$. long. Pedicels solitary in the axils, somewhat crowded in the upper leaf-axils, articulated above the middle, $2.4-2.7 \mathrm{~cm}$. long, sharply bent at the articulation ca. 1 cm . below the fruiting calyx and flexuous above it, erect below. Calyx plicate, fulvid-tomentose externally, the lobes cordate, sparsely stellate-pilose internally, the tube glabrous internally; lobes connivent above the corolla. Petals yellow, obcordate, scarcely 6 mm . long,
glabrous or sparsely ciliate at the base. Stamen-tube short, glabrous. Filaments ca. 2 mm . long. Styles yellow, free nearly to the base, capillary, ca. 6 mm . long; stigmas terminal, depressed-capitate. Fruiting calyx ca. 2 cm . high, $6.5-7 \mathrm{~cm}$. in diameter when split and flattened, pentagonal in section, the angles strongly winged by the plicate edges of the lobes and subjacent tube, the lobes broadly cordate, 3.5 cm . broad, the whole reticulate-veined, yellow, the external indument reduced, glabrous within. Mature carpels 15-17, forming a depressed discoid fruit ca. 1.3 cm . in diameter; individual carpels $4.5-5 \mathrm{~mm}$. radially, 3 mm . high; dorsum thick, pale brown, glabrous, coarsely verrucate on the outer surface and margins; lateral walls lighter in color and thinner; the rostrum prolonged as a sharp-pointed horizontal beak. Seed 2 mm . high and wide, red brown, smooth, dull, glabrous; the funicle greatly prolonged, 1.5 mm . long, extending 0.8 mm . beyond the seed; dehiscent apparently by the separation of the top of the dorsum from the lateral walls. Columella 2.5 mm . high, 3 mm . broad at the base, 4 mm . in diam. across the middle with acuminate flanges from the domed upper half projecting between the carpels, constricted below this and dilating again to the base; edge of the base rounded, its lower surface with many radial grooves.

TYPE: "In locis rupestribus montium Hammersly Range legit $N$. Brown in expeditione Fr. Gregorii." (Fragment in K).
distribution: Western Australia.
The only material which I have seen of this species has been two terminal scraps about 15 cm . and 10 cm . long, sent by Mueller to Hooker at Kew and to Gray at Harvard. The description given above has been based on Mueller's original diagnosis, supplemented wherever possible by details from the fragments.

The species must have a new name, as Gray pointed out, and it seems fitting to name it for the collector.

The extraordinary inflation of the calyx in this species makes it perhaps the most striking of all the Sidas when in fruit. It does not closely resemble any other species of the genus in any of its characters, and is especially distinct in the ornate structure of the columella, the extremely slender and elongate stipules and the accrescence of the calyx.

Australia: Collector unknoun, "Hb. Mueller", Gascoyne River, Western Australia (GH). Brown, Hammersley Range, Western Australia (TyPE fragment, $\mathbb{k}$ ).

## 8. Sida macrodon DC., Prodr., 1: 464. 1824.

S. cymbalaria Hochr., Bull. Herb. Boiss., ser. 2, 5: 291. 1905, as to description, in part as to specs. cited.

## S. macrodon var. cymbalaria (Hochr.) Hassl., 1.c. 7: 729. 1907. <br> S. physaloides Presl, Rel. Haenk. 2: 105. 1835.

Perennial herbs or subshrubs, prostrate or semidecumbent, freely branching from the base; stems (5-) 10-20 (-60) cm. long, lax, terete, the tips ascendent, $1-2 \mathrm{~mm}$. diameter, the indument of minute, shining, white, simple hairs, tomentulose ca. 2 mm . long, and pulverulent. Leaves suborbicular to rotund-ovate, the base cordate, the apex obtuse, the margins coarsely serrate, (7-) $12-20$ ( -45 ) mm. long, (7-) $10-20(-30) \mathrm{mm}$. wide, broadest below the middle; discolorous, green above, yellowish or cinereous below, appressed-tomentose on both surfaces; the younger leaves with setose-villous margins; seven-nerved, prominent beneath; petioles terete, (3-) 8-20 (-25) mm. long, ca. 0.5 mm . diameter, about as long as the leaves or shorter. Stipules linear to linear-lanceolate, $3-4 \mathrm{~mm}$. long, $0.5-1.0 \mathrm{~mm}$. wide, acute, indument like that of stems and more or less ciliate. Pedicels axillary, solitary or rarely paired, $2-3 \mathrm{~cm}$. long, 0.5 mm . in diameter, terete, gracile, tomentellous, articulated in the upper fourth. Calyx broadly campanulate, subpentagonal, $6-8 \mathrm{~mm}$. high; the lobes erect, $3-4 \mathrm{~mm}$. high, acute; the indument subtomentose, the margins short-ciliate. Petals white, rose, or salmon pink, $8-12 \mathrm{~mm}$. long, $6-9 \mathrm{~mm}$. wide, symmetrical or slightly oblique, rotund, emarginate, tapering quickly to the narrow claw, the margins short-ciliate. Stamen-tube $2-3.5$ (-4) mm. high, terete, with ten paired traces obvious externally at the base; glabrous or scattered-pilose (rarely heavily spreading-short-pilose). Filaments $1-2 \mathrm{~mm}$. long. Anthers 20 , pale, not dotted. Ovary 0.7 mm . high, 1 mm . in diam., eight-lobed, glabrous. Styles $8-10 \mathrm{~mm}$. long, $4-5 \mathrm{~mm}$. free; stigmas capitate. Fruiting calyx open, greatly inflated, the base of the tube impressed, the lobes erect, not plicate, to 1.2 cm . long. Carpels $7-9$ rarely 6 , muticous, united by a web around the outer dorsum, subrugulose when fully mature, indehiscent; the apex fragile, prolonged upward; dorsum with a distinct midnerve, cinereous; 2.5 mm . high, 2 mm . wide; the exocarp firmly adherent to the seed at the base, occasionally on the sides. Seed plump, glabrous, subrotund, filling all but the apex, blackish, paler near the hilum, 2 mm . in diameter. Columella conical, the sides concave, angulate in section, woody, persistent, 2 mm . high.

TYPE: "Mr. Stevens 1820. Bresil" (G).
distribution: Southern Brasil, Paraguay, northern Argentina, Bolivia, Peru.

Although de Candolle described the species as having ten carpels, and the type-sheet bears a note that there are ten muticous carpels, I have seen no material which has more than nine and Rodrigo (1944) reported no more than eight. The species
is variable enough in its other characters, although no discrete varieties are recognizable.
S. physaloides Presl is customarily placed in the synonymy of S. macrodon although it is described as having only five carpels. It was based on a Haenke collection from Huánuco, Peru, and I have seen a photograph of a probable isotype which is in the Vienna Herbarium. It is undoubtedly very close to $S$. macrodon, and, in the absence of any material from Peru, I am retaining it as a synonym of S. macrodon. Bang 2164 from Bolivia is nearly identical with the Haenke specimen in gross appearance. I have seen four sheets of it from U. S. herbaria, while Fries (1907) reported on duplicates in European herbaria, and we are in agreement that the material belongs to $S$. macrodon. The sheet in the U.S. National Herbarium has seven carpels; other sheets were too scrappy to permit carpel-counts.

Hochreutiner (1905) cited three collections from Paraguay for his new species S. cymbalaria: Hassler 4325, with pink flowers, Hassler 6806, with white flowers, and Hassler 7047, which Chodat and Hassler in the same paper made the type of $S$. cymbalaria f. viridescens. Hassler (1907) reduced Hochreutiner's species to a variety of $S$. macrodon, pointing out that Hochreutiner's description was based on only one of the three collections cited: Hassler 4325. The other two collections Hassler then cited as the basis for his S. rubifolia ssp. psendocymbalaria of section Sida. The differences which Hochreutiner claimed existed between his $S$. cymbalaria and other species of the section are actually no more than those often found between individuals of S. macrodon.
S. macrodon var. intermedia Griseb. (1874) is a synonym of S. flavescens Cav.

Brasil: Archer 4143, Bututan São Paulo (us). Bornmiuller 595. Panambi (Neu Württemberg). Rio Grande do Sul ( GH ). Burchell AA18-2. without locality (Gн). Hatschbach 2697. Rio do Salto, Paraná (us). Hoehne \& Gehrt 36563. Suzanno, São Paulo (us). Lund. near Lagoa Santa (us). Novaes 490, Campinas, Jundiahy (Us). Sello, without locality (Us). Stevens, 1820, without locality (Photograph of TYPE, G: F, us). Warming. Lagoa Santa (Us). W'idgren, 1845, Minas Geraes (us).

Paraguay: Hassler 9377. near Caaguazú (GH). Hassler 5085. Sierra de Maracayu (GH). Hauthal 38, Rio Ibitimi (ny).

Argentina: Ekman 133, 1908, "Posadas, Bonpland" (Ny).
Bolivia: Bang 2164, "Yungas. Coripati", La Paz: (GH, mo, us 2)

Peru: Haenke, "ad Huanacio" (Photograph of Isotype? of S. phyraloides Presl, Vienna: f).

## 9. Sida urticaefolia St. Hil., Fl. Bras. Merid. 1: 148, t. 37. 1827.

S. flavescens Cav. sensu Schum., Mart. Fl. Bras. 12, pt. 3: 290. 1891.

Erect perennial, to 40 cm . high, the stems few-branched, covered with a double indument of dense, minute, stellate pubescence and scatteredspreading, pilose-stellate hairs, the rays ca. 1 mm . long. Leaves $3.5-7.0$ cm . long, $2.0-4.3 \mathrm{~cm}$. wide, nerves prominent on the lower surface, the lower suborbicular and obtuse the upper oblong-ovate, often oblique, the base truncate to shallowly cordate, the apex obtuse to acute, the margins coarsely serrate, the serrations irregular; the upper surface scabrid with a thick scattering of appressed, yellowish or golden, 5-7rayed, fine, stellate hairs; the lower surface densely covered with minute, stellate, cinereous or yellowish hairs and slightly larger, many-rayed, yellow, stellate hairs, the bases of the rays often bulbous; the petioles $1.4-2.3 \mathrm{~cm}$. long, terete, the indument like that of the upper portions of the stem, ascending, straight, to 1.0 mm . thick. Stipules $4-7 \mathrm{~mm}$. long, $0.7-1 \mathrm{~mm}$. wide, lanceolate or falcate, entire or with one or two blunt lobes on the inner curve, the upper ones occasionally linear. always acuminate. Pedicels $4-16$ in the axils, rarely fewer in the lower axils, $2-12 \mathrm{~mm}$. long, mostly ca. 7 mm . long, slender, the indument like that of the upper stems but the long-rayed stellate-pilose hairs more numerous. Calyx campanulate, densely stellate-hirtellous to pilose, strongly 5 -angled, ca. 4 mm . high in early anthesis, rapidly accrescent to ca. 9 mm . in late anthesis; the lobes changing shape and dimension during the accrescence, from broadly deltoid to cordate, mucronate, ca. 2 mm . wide at the base, elongating from 1 to 2 or more mm .; interior markedly reticulate, shining, the tube glabrous, the margins finely stellate-hirtellous. Petals white to salmon pink or rose, strongly obliqueovate, the margins somewhat irregular, the apex often retuse, the margins with regularly scattered short-ciliate hairs, increasingly dense towards the claw; the claw ca. 1.5 mm . wide. Stamen-column $2.0-2.5$ mm . long, terete, glabrous, thick, the lower third dilated; filaments $1-1.5 \mathrm{~mm}$. long, slender, not paired; anthers $20-30$, verruculate, not dotted, ca. 0.5 mm . wide; the valves usually not reflexing in age, the septum prominent. Styles five, ca. 4 mm . long, 3 mm . free; the stigmas depressed-capitate, dark red. Ovary 1 mm . high and wide, light brown, five-lobed, ovate, glabrous. Fruiting calyx 7-8 mm . long; the lobes 3- 3.5 mm . long, $3.5-4 \mathrm{~mm}$. wide; reticulated, membranous, translucent, grayish-tan, persistent after the fall of the fruits, rarely abscissing at the inconspicuous articulation ca. 3 mm . below the calyx. Carpels
five, obtuse, muticous, dark reddish-brown, ca. 2 mm . high by 1.8 mm . wide, the entire dorsum convex, reticulate, with a distinct midnerve, the margins with the lateral walls slightly ridged; lateral walls membranous. Seeds glabrous, black, nearly spherical, ca. 1.5 mm . in diameter.

TYPE: St. Hilaire, C2/2683, Feb. 1821, "Pâturages de la province des Missiones, près du village de S. Borga", western Rio Grande do Sul state, Brasil (P).
distribution: Southern Brasil, Paraguay, and northern Argentina.
Study of St. Hilaire's type and of a photograph of material he sent to Berlin (labelled as Isotype) has given me some certainty about the application of the name to the cited material, despite uncertainties resulting from a study of his description alone. Schumann confused this species with S. flavescens Cav., and some later authors have followed his example. Rodrigo's key (1944), unfortunately, does not sufficiently emphasize the diagnostic characters of the plant, although her description is quite clear; she makes a main key-heading of the habit of the plant, a character which is not easy to recognize on most specimens.
'The map of collectors' travels in vol. 1 of Martius' Flora Brasiliensis shows St. Hilaire's route extending into what is now the Gobernación de Misiones of Argentina. It is clear from St. Hilaire's own account (1946) that he collected only on the Brasilian side of the Uruguay River in an area around San Borja once under the influence of the Missions of Paraguay, seven of which were on that side of the river.

Brasil: Bornmüller 183 and 423, near Panambi (Neu Württemberg), Rio Grande do Sul (GH). Rambo S1611, Passo do Socorro, Rio Grande do Sul (us). St. Hilaire "Brasil" (photo. of fragment sent by him to Kunth, B: GH, us). St. Hilaire, near San Borja, Rio Grande do Sul (p: type).

Paraguay: Hassler 6943. Cordillera Central, near the Y-aca (GH, us). Kuntze, Sept. 1892. "Süd-Paraguay" (NY).

Argentina: Kuntze, Dec. 1891, Dique, near Córdoba (ny). Montes 3376, Puerto Rico, Dep. Cainguás, Gob. Misiones (us). Parodi 11183, Reconquista, Prov. Santa Fé. (GH). Rodrigo 2498, Enrique Urion, Dept. Tapenaga (ny). Schwindt 916, Cainguás, Gob. Misiones (us).

## 10. Sida calyxhymenia J. Gay ex DC., Prodromus 1: 462. 1824.

Perennial shrub 6-15 dm. high, the stems erect, terete, branching, densely stellate-incanous-tomentose, the branches numerous and crowded, erect to spreading. Leaves ovate-oblong, $23-43 \mathrm{~mm}$. long, $8-12$ mm . wide, the upper leaves narrower in proportion, $8-12 \mathrm{~mm}$. long, ca. 2 mm . wide, rounded at the base, obtuse to subacute at the apex,
the margins repand-undulate to subentire, flavescent from the dense short-stellate tomentum, above, velutinous-incanous beneath and less dense; three-nerved from the base, the midnerve lightly impressed above, prominent beneath, the petioles terete, their indument like that of the stems, $6-8 \mathrm{~mm}$. long, the upper ones shorter. Stipules subulate, stellatetomentose, glabrescent towards the apex, deciduous, $2-3 \mathrm{~mm}$. long. Pedicels solitary and axillary or rarely paired, terete, short and erect in flower, elongating later and flexuous, densely incanous-tomentose, 1216 mm , long, articulated $2-4 \mathrm{~mm}$. above the base in fruit, not visible beneath the tomentum. Calyx $6-8 \mathrm{~mm}$. high in anthesis; lobes $4-5$ mm . high, $4-5 \mathrm{~mm}$. wide slightly below the middle; cordate in outline, acute, greatly accrescent, flavid-velutinous; lower margins of the lobes plicate; sinuses closed; accrescent to 1 cm . in height, becoming membranous; reticulately veined, with three main veins per lobe. Petals erect, ca. 6 mm . high and wide, obovate, the claw ca. 0.8 mm . wide, densely white-flexuous-fimbriate, the margins with scattered very slender cilia, the remainder glabrous. Stamen-tube glabrous, with 5 conspicuous pairs of traces, slender, tapering, ca. 4 mm . high; filaments $1.5-2.0$ mm . long, filiform; anthers $10-20$, ferrugineous, not dotted, reniformglobose, ca. 0.5 mm . wide. Styles five, 6 mm . long, $2-3 \mathrm{~mm}$. free reflexed, dark; stigmas capitellate, dark red. Carpels five, 3 mm . high, 1.5 mm . radially; the rostrum prolonged vertically, ca. 1.5 mm . long; dorsum wrinkled, scattered-puberulent, transversely impressed in the hilar depression of the seed; lateral walls rugose-reticulate, paler; dehiscence along the midline of the dorsum and the inner margin. Seed glabrous, 2- 3 mm . high, dark reddish-brown, the hilar depression rather deep, the rostrum prolonged briefly upward; funicle flattened. Columella ca. 3 mm . high, crowned with the remnant style-base, 5 -angled; the angles subalate; the base dilated into a very small crispate disk.

## Key to the Varieties

Plants cinereous-tomentose; calyx flavid-velutinous externally; leaves $23-43 \mathrm{~mm}$. long . . . . . . . . . . . 10a. S. calyxhymenia var. calyxhymenia. Plants ferrugineous-tomentose; calyx tomentose externally; leaves shorter 10b. S. calyxbymenia var. ferragined.

## 10a. Sida calyxhymenia var. calyxhymenia.

Fleischeria pubens Steudel in Lehmann, Plantae Preissianae 1: 236. 1845 and emend. Steetz, op. cit. 2: 365. 1848.

TYPE: Leschenault et al. 1795, "cueillie à la Rivière des Cygnes, sur la côte occidentale de la Nouvelle Hollande" (K).
distribution: Western Australia.

10b. Sida calyxhymenia var. ferruginea Pritzel,

Engl. Bot. Jahrb. 35: 362. 1904.

COTYPES: George 1902, "e. gr. in distr. Austin pr. Murrinmurrin" and Diels 3269, "pr. Cue, fl. m. Jun."
distribution: Known only from the cotypes.
'The variety is known to me only from the description, there being no material of the species which I have examined which can accurately be termed "ferrugineous" in the color of the indument. Domin has tentatively identified an E. Clement collection (к) from between the Ashburton and Yule rivers of Western Australia as possibly belonging to this variety. While it has a reddish cast and leaves shorter than the typical, it cannot be identified certainly since it has no fruit. In addition, the stamencolumn is shorter and not so markedly nerved, although the petals are very similar to those of the typical.

Fleischeria was established by Steudel (1845) as a new genus, with the single species $F$. pubens, distinct from Sida in having a "petaloid" calyx and the corolla shorter than the calyx. It was Steetz's opinion, expressed at the time he emended the generic and specific diagnoses (1848), that Sida was too vast and diverse, and that since $F$. pubens was so markedly distinct from all the other Australian species which might be placed in Sida, it was best to treat it as generically distinct. There is no indication that either Steudel or Steetz recognized the conspecificity of $F$. pubens with S. calyxhymenia. Oddly, the name Fleischeria had been used in 1838 by Steudel and Hochstetter in Endlicher's Genera Plantarum for species usually referred to Scorzonera of the Compositae.

Australia: Queensland: Blake 19195, Mt. Howitt Station. Gregory South District (к). Western Australia: Burbidge 265. Glenorn Station, Malcolin (к). Clement. n.w. Australia, between the Ashburton and Yule Rivers ( $\mathbf{x}$ ). Clement. n.w. Australia, between the Ashburton and Gray Rivers ( K ). Drummond. 1839, Swan River (к 2). Drummond 52. 1843. Swan River (k). Gardner 2422, Mt. Sir Samuel (к). Gardiner 2263, east of Cue (к). Gardner 3248. Wandagee, Minilya River (к). Ince, without locality (к). Koch 2975, Merredin, Pemberton (mо, к). Leschenault, Swan River, (TYPE, к; ISOTYPE, GH). Mitchell, Northwestern Division (k). Morris 2341. Stephen's Creek, 10 miles n. of Broken Hill (к). Oldfield, Murchison River (GH, к). Preiss 1662, Mount Mathilde, York District (Isotype of Fleischeria pubens Steud. к). Southenn Australia: Holms, "Arco-cillinna Well." (k). Without definite locality: Anketell, "Trans Australian Railway Survey, 4-8-1910" (к). Anketell, "Trans Australian Railway Survey, 12-8-1901" (k).

## 11. Sida Standleyi Clement, sp. nov.

Herbae perennes prostratae 40 cm . vel minores; folia $1.3-3.4 \mathrm{~cm}$. long., $1.4-2.8 \mathrm{~cm}$. lat., plurima ovata caetera suborbicularia, apice acuta, basi cordata, marginibus grosse serratis. Petioli $1.0-1.8 \mathrm{~cm}$. Stipulae filiformes sive lineari-lanceolatae. Pedicelli 5-20 mm., filiformes articulati prope apicem bini et in axillis superioribus soli. Calyx accrescens conspicue 5 -gonus, lobis acuminatis nervo expresso. Petala ca. 5 mm , rotunda gibbosa, margine exteriore subretuso. Columna staminales teres, pilis subulatis patentibus sparsesque munita. Antherae 20. Styli 3.5 mm , 5 in ovario. Calyx marcescens, aetate fructus maturandi membranaceus et ad 1.0 cm . alt. accrescens. Carpella 5 in fructu, $2.5-2.8 \mathrm{~mm}$. alt., ca. 1.7 mm . lat. secundum radium, a dorso convexa glabra, parietibus lateralibus planis albo-pulverulentibus. Semen cum parietibus adnatum nisi ad aspicem.

Perennial prostrate herb. Stems $20-40 \mathrm{~cm}$. long, slender, $1-2 \mathrm{~mm}$. in diam., terete, fibrous-woody near the base, densely clothed in minute, greenish, soft, many-rayed, stellate hairs, appressed, and scattered longerrayed stellate hairs, the rays yellowish, spreading, and simple, spreading, pilose hairs. Leaves $1.3-5.4 \mathrm{~cm}$. long, $1.4-2.8 \mathrm{~cm}$. wide, mostly ovate; some of the lower leaves suborbicular; the base cordate, symmetrical; the apex acute; nerves $7-9$, palmate from the base, the midnerve with 2-3 lateral nerves subopposite or alternate, all prominent beneath, yellowish; the margins coarsely serrate, the serrations ovate, acute or bluntly mucronate; indument of the upper surface minutely stellate-tomentellous, somewhat scabrous; that of the lower surface similar, the hairs softer, slightly longer-rayed, denser. Petioles $1.0-1.8 \mathrm{~cm}$. long, $0.5-0.8$ mm . diam., terete, spreading or ascendent; indument like that of the upper stem, often with more numerous, long, pilose hairs. Pedicels filiform, 5-20 mm. long, articulated $1.5-4 \mathrm{~mm}$. below the calyx, solitary or usually paired in the axils. Calyx accrescent, strongly 5 -angled, ca. 7 mm . high; the base of the tube impressed; the lobes acuminate, with a prominent mid-nerve, 3 mm . high, 4 mm . wide, fine. white, stellate-hirtellous outside, the same inside but the lower part of the tube glabrous. Petals 5.0 mm . long and broad, rotund, gibbous; the outer margin slightly retuse; the claw ca. 0.6 mm . wide, densely ciliate, the rest of the petal glabrous, $5-6$-veined. Stamen-tube 1.5 mm . high from the base of petal to level of filaments, terete, with scattered, spreading, hyaline, subulate hairs; the interior with 5 pairs of traces; filaments ca. 0.8 mm . long, slender, flexuous. Anthers $20, \mathrm{ca} .0 .3 \mathrm{~mm}$. wide, the surface subpapillose. Styles five, 2.8 mm . free, 3.5 mm . long; stigmas de-pressed-capitate. Ovary 0.5 mm . high and wide, ovate, pale, glabrous, strongly five-lobed. Fruiting calyx tan, membranous, to 1 cm . high; indument persistent. Carpels five, $2.5-2.8 \mathrm{~mm}$. high, 1.7 mm . radially;
the dorsum convex, light brown, glabrous, rough, dull, with an impressed midline; lateral walls flat, ca. 1 mm . wide, as high as the carpel, white-pulverulent, indehiscent; the walls adnate to the seed except at the apex. Seed dark red-brown, glabrous, paler near the hilum; the funicle prominent, reddish. Columella 2 mm . high, the lower fourth dilated, woody, angulate, truncate.

TYPE: H. H. Bartlett 10167, "Cerro de los Armadillos, vicinity of San José, Sierra de San Carlos, Tamaulipas, Mexico. 3100 ft. 8 July 1930" (F).
distribution: Mexico: Sierra de San Carlos, Tamaulipas and Sierra Madre, nr. Monterrey, Nuevo León.
S. Standleyi is closely allied to S. flavescens of Argentina, Paraguay and Uruguay, the carpels being almost indistinguishable, although the petal-size and stamen-number are quite different. It is curious that S. physocalyx, also of section Pbysalodes, has a distribution similar to that of S. Standleyi and S. flavescens combined.

The specimens cited were given an herbarium name by Dr. Paul C. Standley, but I think it more appropriate to name the species for him.

Mexico: Tamaulipas: Bartlett 10167, Cerro de los Armadillos, vic. of San José, (type, f). Nuevo León: Mueller \& Mueller 79, Diente Canyon, Sierra Madre, nr. Monterrey, (f, MExU 2).
12. Sida flavescens Cav., Diss. 1: 14, t. 13, f. q. 1785.
S. prostrata Cav., op. cit. 1: 13, t. 13, f. 3.
S. intermedia St. Hil., Fl. Bras. Mcr. 1: 188. 1827.
S. macrodon var. intermedia (St. Hil.) Griseb., Pl. Lorentz. 43. 1874.
S. prostrata var. flavescens Bak. f., Jour. Bot. 30: 294. 1892.
S. prostrata var. genuina Hassl., Ostenia 337. 1933.
S. prostrata var. flavescens Hassl., l.c.

Prostrate perennial herbs, many-branched from freely branching, deep, woody taproot; the stems $25-40 \mathrm{~cm}$. long, terete, $1-2 \mathrm{~mm}$. in diam., densely stellate-velutinous, the hairs minute, whitish or cinereous, and with scattered to dense, longer, slender-rayed, spreading or somewhat appressed, white or flavid hairs. Leaves $1.5-3.2 \mathrm{~cm}$. long, $1.0-3.1 \mathrm{~cm}$. wide, cordate, sometimes oblique; the apex subacute or acute; the margins irregularly or fairly regularly serrate, the serrations obtuse, 2.5-6 mm . wide at the base; indument of the upper surface greenish, densely stellate-puberulent; that of the under surface the same, plus scattered to
dense longer-rayed stellate hairs, the rays flavid, slender, soft; nerves 7-9, palmate from the base, prominent beneath; petioles $10-15 \mathrm{~mm}$. long, usually about half as long as their leaves, channeled adaxially; the indument like that of the stem. Stipules to 5 mm . long, 1 mm . wide, linear, lanceolate, or falcate, occasionally with a small lateral lobe, varying even within one pair; indument like that of the stems. Pedicels axillary; solitary, paired or in threes, usually paired, $5-8 \mathrm{~mm}$. long, articulated $1-3 \mathrm{~mm}$. below the calyx. Calyx five-angled, the tube rounded at the base; the sides and lobes parallel; $3-4 \mathrm{~mm}$. high during anthesis, accrescent to $7-9 \mathrm{~mm}$. in fruit; external indument greenish to flavid, thickly to densely stellate-puberulent, with longer-rayed stellate hairs on the prominent midnerves; the lobes erect, ovate, acuminate, ca. 2 mm . high in flower, to 5 mm . high in fruit. Petals rose, 8-9 mm . long, 5-7 (-9) mm. wide, obliquely obovate-retuse, the margins short-ciliate all around; the cilia longer and denser towards the base; claw ca. 2 mm . wide. Stamen-column ca. 1.5 mm . high, terete, stout, glabrous or with few, short, scattered bristles; filaments ca. 1 mm . long, not paired, flexuous; anthers $30-40$, ca. 0.5 mm . wide, not dotted. Ovary five-lobed, truncate-pyramidal, ca. 1 mm . high and wide, glabrous, light brown. Styles $3.2-4.5 \mathrm{~mm}$. long, 3.5 mm . free; stigmas capitate. Fruiting calyx pale tan, membranous-reticulated; the indument persistent. Carpels five, muticous, light brown, forming a pyriform fruit, 3 mm . high, 2 mm . radially, glabrous; the lateral walls flattened, whitepulverulent; midline of the dorsum visible only near the apex; partially dehiscent by the inner margin, the walls separating with difficulty from the base and lower dorsum. Seed reddish brown, the surface dull, densely and minutely pitted, 2 mm . high, 1.5 mm . radially; funicle lighter in color, corded. Columella 2 mm . high, tapering slightly, finely ribbed, pale; the apex irregular, crowned by the short persistent style-base.

TYPE: Commerson, "in rupibus Montevideo", Uruguay. (P).
distribution: Southern Brasil, Uruguay, northern and central Argentina, perhaps Bolivia and Chile.
S. flavescens Cav. and S. prostrata Cav. were first combined by Willdenow (1801) in the following words, extracted from the intercalated description, "Sida flavescens S. (prostrata) Cav. Diss. 1 p. $13 \ldots$. $\beta$ S. (flavescens) .... Cav. Diss. 1. p. $14 \ldots$... De Candolle (1824) gave Willdenow as the author of the combined species, citing both of Cavanilles' species in the synonymy. Under the present rules, Willdenow's combination of the elements under the name $S$. flavescens must be followed. As is evident from the synonymy, later authors have apparently gone on the basis of page priority or have followed Garcke (1896).

Schumann, however, used $S$. flavescens, with a synonym-citation including $S$. prostrata and referring to Willdenow and de Candolle. He also included S. urticaefolia in the species, although it is quite distinct.

The types of both of Cavanilles' species were Commerson collections from Montevideo, both originally sent to Thouin. That of $S$. prostrata was lent by de Jussieu to Cavanilles for study, that of $S$. flavescens by Thouin. The specimens in the Madrid herbarium, photographs of which are reproduced in Rodrigo's paper (1944), are certainly not the types, that ostensibly of $S$. prostrata being a Née collection from Chile, although accompanied by a drawing which closely resembles that of the Dissertationes, while that of $S$. flavescens gives no clue as to its origin and is accompanied by a sheet bearing a handwritten diagnosis, in what looks like Cavanilles' hand, which is worded quite differently from the published diagnosis. There can be no doubt that the actual types are in Paris, where the bulk of the Commerson and half the Dombey collections were sent. I have studied the types of both S. flavescens Cav. and S. prostrata Cav. and the brief descriptions on the original labels are repeated in Cavanilles' published description and attributed to Commerson. Cavanilles apparently took some material to Madrid with him when he left Paris in 1789, and distributed duplicates to Berlin, Copenhagen and other herbaria, but the types themselves, usually loaned to Cavanilles from the herbaria of such men as de Jussieu, Thouin, and de Lamarck or grown from seed in the Jardin des Plantes, remained in Paris.

The type of St. Hilaire's S. intermedia, so named because it was supposedly intermediate between S. macrodon and S. urticaefolia, was collected by its author from fields near the Salto Grande in Uruguay. It is a small plant which is a ratoon or sprout-growth from an old base, and there can be no doubt that it is conspecific with $S$. flavescens.

Baker's treatment of this species-complex was perhaps the most original, for he took up the name $S$. prostrata for his assemblage of entities, with $S$. urticaefolia as an outright synonym of the typical element, and with $S$. flavescens reduced to the rank of a variety.

The distribution of the species given above is based in part on specimens seen, which are from Uruguay and Argentina only, in
part on that given by Rodrigo (1944). This seems reasonably safe, since her concept of the species is the same as mine, despite the difference of name.

[^4]
## III. Section Pseudomalvastrum Gray, Mem. Am. Acad. 4: 23. 1849 (Pl. Fendl.).

Low or prostrate herbs or subshrubs. Leaves usually oblique, reniform to elongate-triangular. Indument of scattered to dense lepidote scales or appressed stellate hairs. Peduncles commonly recurving in fruit, mostly solitary in the axils. Epicalyx present, of $1-3$ filiform to setaceous bracteoles; calyx terete. Carpels tumescent, the dorsum stellate-puberulent to hirsute, indehiscent or dehiscent irregularly along the middorsal line. Funicle curved over the rostrum of the seed, usually dilated towards the columella.

The section was originally described by Gray for only two species, $S$. hederacea and $S$. sulphurea, with the comment " $S$. sulphurea... from Mendoza [Argentina] is a nearly related species [to $S$. hederacea]; and some others from the same region usually referred to Malva probably belong here." There is a marginal note in his hand on the type-sheet of S. bederacea (GH) "cf. Malva leprosa Orteg. ex Hook.", but that species was not transferred into the genus or the section until 1890, when Schumann made the transfer in his discussion of the section. Meanwhile, in 1852 Gray had described S. lepidota and its varieties depauperata and sagittaefolia, commenting that S. lepidota was "a well-marked though somewhat polymorphous species of the Section Pseudomalvastrum."

In Schumann's treatment of the section mentioned above, he recognized only one other species, S. Sherardiana, as belonging
to the section, apparently considering S. bederacea and S. lepidota as subspecific entities under $S$. leprosa, without, however, mentioning either.

Two years later Baker reshuffled the names and entities in the section, selecting $S$. hederacea as the species-name for the leprosahederacea complex, and adding S. cuneifolia Gray to the section, although it has no bracteoles and is sufficiently unlike the rest of the section to form a new section with S. Helleri. Hochreutiner (1902) attempted to unscramble the nomenclatorial snarl created by Baker with only partial success, falling into the trap of following Baker's acceptance of S. bederacea var.? parvifolia Hemsley as legitimate, although it was published without description, and transferring it to $S$. leprosa as a still illegitimate variety.

In 1906 Greene transferred S. cuneifolia Gray, S. hederacea, S. lepidota and S. lepidota var. sagittaefolia to the new genus Disella. The genus was based on the presence of an epicalyx, despite the fact that the first-named species never has one. Very few botanists have accepted Disella. Kearney (1954) includes the section in his key, lists and keys out S. hederacea, S. lepidota, S. Grayana and S. Helleri, and comments in his notes that the section is heterogeneous and poorly defined. Type species: Sida leprosa (Ort.) K. Schum.

## Key to the Species

Leaves mostly symmetrical, reniform, with a deep and narrow sinus. Carpels heavily hirsute, with a prolonged rostrum hooking over the apex of the columella
13. S. Sherardiana.

Leaves reniform to semisagittate, usually oblique, often strongly so. Carpels moderately hirsute or hirtellous or puberulent, the rostrum not prolonged, never more than slightly hooked over the apex of the columella 14. S. leprosa.
13. Sida Sherardiana (L.) Benth., Jour. Linn. Soc. 6: 101. 1862.

Malva Scherardiana L., Sp. Pl. ed. 2, 1675. 1763.
Malva Sherardiana L., Syst. ed. 12 and later.
Malva cymbalarifolia Desr. in Lam., Encyc. 3: 753. 1791.
Malva cymbalariaefolia Desr. (orth. var. in DC. Prod. 1: 431. 1824).

Malvella Sherardiana (L.) Jaub. \& Spach, Illustr. 5: 47. 1853-57.

## Malvella cymbalariaefolia (Desr.) B. D. Jackson, Index Kew. 3:

 156. 1894, erroneously attrib. to Boiss. Fl. Or. 1: 835. 1867.Prostrate or decumbent perennial herbs. Stems numerous from a woody taproot, the entire plant covered with a dense, soft, whitish, long-rayed, stellate indument. Stipules oblong or ovate, acutish, 2-3 mm . long, ca. 0.8 mm . wide, persistent, yellowing in age, spreading. Petioles to 27 mm . long, subcomplanate, assurgent. Leaves reniform, variably crenate or crenate-serrate except in the deep rather narrow sinus, ( $10-$ ) $12-25$ (-28) mm. wide, (5—) 9-14 (-23) mm. long; indument occasionally thin on the upper surface of large-leaved specimens; nerves $6-7$, palmate, prominent beneath. Pedicels solitary in the axils, slender, sinuate, terete, not articulated, $10-50 \mathrm{~mm}$. long, accrescent after anthesis; indument double, of long- and short-rayed stellate hairs. Calyx subcampanulate, plicate in specimens with ovate lobes, invaginated around the receptacle in fruit, $6-8 \mathrm{~mm}$. high; lobes 3-5 mm . long, 3-5 mm. wide, broadly lanceolate or ovate, acute, with four main nerves on each, folding over the fruit, somewhat accrescent after anthesis; inner surface glabrous at the base, finely pubescent on the lobes, not dotted. Epicalyx of 2-3 thin, lanceolate, spreading bracteoles ca. 2 mm . long. Petals rose, pink to yellowish-brown on drying, broadly spatulate, obtuse, $5-8 \mathrm{~mm}$. wide, $7-12 \mathrm{~mm}$. long, sparsely hirsute near the claw, inserted slightly above the base of the column. Stamentube 2 mm . high from the base of the ovary to the level of the filaments, short-obpyriform, sparsely hirsute, strongly geniculate at the base; filaments ca. 2 mm . long, not paired. Anthers numerous, ca. 0.8 mm . wide when open, pale, not dotted. Ovary ca. 1 mm . high and wide, densely hirsute. Styles deeply inserted between the apices of carpels, free almost to the base, connate, subclavate apically, $5-6 \mathrm{~mm}$. high; stigmas strongly oblique, obtuse, only slightly thicker than the subjacent portion of the styles. Carpels $7-16,3-4 \mathrm{~mm}$. high, $4-5 \mathrm{~mm}$. radially, forming a flat-topped fruit; dorsum pale yellowish-brown, muticous, inflated; rostrum prolonged into a vertical flange hooking downward to the top of the very short columella; lateral walls nearly white, rugosereticulate. Seeds plump, grayish, glabrous, minutely verruculate, 2 mm . high and radially; funicle thin, flat; hilar depression shallow.
TYPE: Specimen in Linnaean Herbarium, listed in 1767 enumeration.
distribution: Central Spain, Greece, Asia Minor and the Caucasus.
The species was named by Linnaeus for John Sherard, an English botanist of his time, but was misspelled in the original publication. In Linnaeus' later works, however, the name was consistently spelled as it is used here.
The species was first transferred from Malva by Jaubert and

Spach as the basis for a new genus Malvella, distinguished primarily by the characters of the carpel; the genus has found little acceptance, whereas Bentham's transferral of the species to Sida, because of the pendulous ovule and despite the presence of bracteoles, has been generally considered as correct. S. Sherardiana is closely allied to the $S$. leprosa-hederacea complex of the western hemisphere in the inflation of its carpels and in general features of leaf-shape, indument and habit. It is the only species of the genus native in Europe.

Spain: Bourgeau, Cerro Negro near Madrid (GH, UC). Gruelsius, Cerro Negro near Madrid (сн). Greece: "Triv.", "Macedonia" (мо). Turkey: Sintenis 677, Dardanelles (GH). U.S.S.R.: Bohenacker, May 1836, "Cauc. ...... prope Sheki Geor." (мо). Newodowakij, 12 June 1911, Prov. Tiflic, Karajazy (ch). Turkey in Asia: Balansa 724, "Village de Tchaousli, près de Mersina (Cilicia)" (uc). Hildreich, Oct. 1845, near Timboukchan (GH). Pichler, Sept. 1875, "circa Brufsa" (Mo). Szovits, "Armenia" (US, GH, NY). Syria: Boissier, June 1846, near Aleppo (uC). Kotschy?, near Ain el Ombarek in vicinity Aleppo (mo 2). Post 460 , Ramoth (us). Sintenis 1418, Kiredjik near Zambur (мо). Palestine: Eig \& Grizi 357, el-Qubab (GH). Meyers 790. Jerusalem (F). Without collector or date, Arimathea (мо). Iraq: Rolland 11.f. "Mesopotamia" (GH).
> 14. Sida leprosa (Ort.) K. Schum., Engl. \& Prantl, Nat. Pflf. 3, Abt. 6: 43. 1890.

Low perennial herbs from branching woody roots. Stems $5-40 \mathrm{~cm}$. long, often assurgent at the tips, woody, terete basally, complanate or terete above, densely clothed with silvery, lepidote to free-rayed or appressed, stellate hairs; branches few to many from any part of the axis. Stipules lanceolate, linear-subulate or subfalcate; indument like that of the stem; $1-2 \mathrm{~mm}$. long, to 0.5 mm . wide, deciduous, appressed. Petioles 4- 30 mm . long, channeled on the adaxial surface; indument like that of the stem, dense. Leaves extremely polymorphic, reniform to ovate-subcordate with the margins nearly entire to serrate, or obliquely triangular and semicordate, with the margins irregular, or narrowly triangular with the upper margins entire and the semisagittate base laciniate; leaves $8-34 \mathrm{~mm}$. long, 2- 50 mm . wide; indument variable, like that of the stem, scattered to dense, scabrous, denser on the younger leaves; nerves mostly 5, palmate from the base, prominent beneath, usually paler than the surface. Pedicels solitary in the axils or occasionally from the axils of much shortened branchlets, terete or subcomplanate, flexuous to recurved, $10-50 \mathrm{~mm}$. long, not noticeably articulated; indument like that of the stem, dense, the hairs silvery or yellowish or cinereous. Epicalyx of (0-) 1-3 filiform to subulate, appressed or spreading bracteoles $1-3 \mathrm{~mm}$. long, often hidden in the indument of
the calyx, deciduous, occasionally at the apex of the pedicel, usually on the base of the calyx; indument like that of the calyx. Calyx campanulate, terete, $3-8 \mathrm{~mm}$. high, deeply divided into deltoid or ovate, acute or acuminate lobes $2-6 \mathrm{~mm}$. long; indument dense, like that of the stem, the interior glabrous except the lobes. Petals $10-16 \mathrm{~mm}$. long, $7-11 \mathrm{~mm}$. wide, white to rose to sulfur yellow, varying within one colony at times, often with the portion exposed in bud more deeply colored and with scattered to dense, minute, stellate hairs, obliquely obovate, the inner margin often auriculate, the outer margin concave, the apex obtuse, rounded; veins fine, numerous; claw glabrescent to softly ciliate, inserted on the stamen-tube above the level of the ovary. Stamen-tube $3-4.5 \mathrm{~mm}$. high, glabrous, 10 -striate, somewhat 5 -ribbed, ca. 2 mm . diam. at the claws; filaments numerous, crowded, falsely multiseriate, often paired, $1-4$ long, recurved in anthesis. Anthers $40-50$, ca. 0.6 mm . wide when open, not dotted. Styles erect, $10-12$ mm . long, slightly clavate at the apex; stigmas capitellate, sometimes oblique. Ovary densely stellate-puberulent, occupying about two-thirds of the cavity, ca. 1 mm . high, 1.5 mm . diam. Carpels 6-10 (rarely more, and the additional ones usually aborted), muticous, tumescent, $2.7-3.2 \mathrm{~mm}$. high, indehiscent, or dehiscent irregularly along the middorsal line; dorsum dull red-brown, moderately to densely stellate-puberulent; lateral walls membranaceous to thick, smooth, straw-colored, white-pulverulent; outer margins sporadically umbonate; outer dorsum tumescent or somewhat invaginated; apex nearly horizontal or somewhat ascendent; inner margin vertical or somewhat concave. Seed 2.22.5 mm . high, ca. 2 mm . radially, dark red-brown, plump, with scattered puberulence; funicle paler, terete inwardly, prominent; hilar depression shallow, abrupt. Columella variable, slender to broadly conical, truncate, ca. 2 mm . high, flanged, pale straw-colored.

## Key to the Varieties

A. Leaves reniform to broadly and obliquely ovate and acute, mostly broader than long; indument steflate or lepidote
B. Indument lepidote, leaves to 10 mm . long, rarely longer; calyx $3-4 \mathrm{~mm}$. high; flowers sulfur yellow, sometimes tinged with rose

14a. S. leprosa var. leprosa.
B. Indument stellate, leaves to 40 mm . long, rarely less than 10 mm. ; calyx $4-7 \mathrm{~mm}$. high; flowers cream-colored or light yellow, often tinged with red, rately white

14b. S. leprosa var. hederacea.
A. Leaves obliquely triangular and acute, mostly longer than broad; indument lepidote
C. Leaves deltoid, semicordate, mostly $10-30 \mathrm{~mm}$. long, the upper margins irregularly notched and toothed . . . 14c. S. leprosa var. depauperata.
C. Leaves narrowly elongate-triangular, semisagittate, mostly $20-50 \mathrm{~mm}$. long, the upper margins entire and straight 14d. S. leprosa var. sagittaefolia.

## 14a. Sida leprosa var. leprosa.

Malva leprosa Ortega, Dec. 8: 95. 1798.
Malva sulphurea Gillies, Hook. Bot. Misc. 3: 149. 1833.
S. sulphurea (Gillies) Gray, Mem. Am. Acad. 4: 23. 1849.

Malvastrum sulphureum (Gillies) Griseb., Symbol. Fl. Argent. 43. 1879.
S. hederacea var. ? parvifolia Hemsl., Biol. Centr. Amer. 1: 104. 1879. (nom. nud.).
S. hederacea var. sulphurea (Gillies) Bak. f., Jour. Bot. 30: 138. 1892.
S. leprosa var. sulphurea (Gillies) Hochr., Ann. Cons. Jard. Bot. Gen. 6: 33. 1902.
S. leprosa var. parvifolia (Hemsl.) Hochr., 1.c. (nom. nud.).

Indument usually lepidote, occasionally semi-lepidote, the inner portions of the rays fused, the outer portions free. Leaves to 10 mm . long, 12 mm . wide, reniform. Calyx $3-4 \mathrm{~mm}$. high. Petals often greenishblack on drying, sulfur yellow or yellow flushed with rose in life.

TyPe: Collector unknown, "Hab. in insula Cuba" (Madrid). The species is not known from Cuba and a photograph of a probable isotype in Geneva sent by Cavanilles is very much like the Argentina material.
distribution: Uruguay, Paraguay, Argentina and Chile; Mexico.
14b. Sida leprosa var. hederacea (Dougl.) K. Schum., Mart. Fl. Bras. 12(3): 342. 1891.
Malva bederacea Dougl. ex Hook., Fl. Bor. Am. 1: 107. 1831.
Malva californica Presl, Rel. Haenk. 2: 121. 1835.
Malva plicata Nutt. ex Torr. \& Gray, Fl. N. Am. 227. 1838.
Malva obliqua Nutt. mss. cited by Torr. \& Gray, 1.c., as basonym for following:

Sida? obliqua (Nutt. mss.) Torr. \& Gray, 1.c.
S. hederacea (Dougl.) Torr. ex Gray, Mem. Am. Acad. 4: 23. 1849 (Pl. Fendl.).
Disella hederacea (Dougl.) Greene, Lflts. Bot. Obs. \& Crit. 1: 209. 1906.

Indument of free-rayed stellate hairs, becoming partially or completely lepidote in intermediates to var. depauperata. Leaves to 40 mm . long, 50 mm . wide, rotund-reniform to ovate-subcordate, the margins variably and irregularly crenate to acute-serrate. Calyx $4-7 \mathrm{~mm}$. high. Petals usually pale brown or pale brown and rose on drying, white, cream-colored or rose in life.

TYPE: Douglas, "in the interior districts of the Columbia [River]." (K).
distribution: Washington and western Idaho, U.S.A. to Baja California, Mexico (eastward from Arizona to Texas, Oklahoma and Kansas, U.S.A. and south to Querétaro, Mexico, mostly as intermediates to var. depauperata). Reported as a weed in South Australia by Black (1952).

14c. Sida leprosa var. depauperata (Gray) Clement, comb. nov.
S. lepidota, A. Gray, Smithson. Contrib. Knowl. 3, art. 5: 18. 1852 (Pl. Wright. 1).
S. lepidota var. depauperata Gray, l.c.

Disella lepidota (Gray) Greene, Lflts. Bot. Obs. \& Crit. 1: 209. 1906.

Indument of silvery many-rayed scales, like those of var. leprosa, becoming mixed with stellate hairs, some of which in intermediates to var. bederacea have the bases of the rays fused. Leaves mostly $1-3 \mathrm{~cm}$. long, rarely to 4.5 cm . long, obliquely deltoid, acute, semicordate, occasionally yellow, often tinged with various shades of red.

TYPE: Wright 45, "Hillsides between El Paso and the Mountains, Aug. 1848." (GH).
distribution: Arizona, New Mexico and Texas, U.S.A.; Baja California ( 1 coll.), Sonora, Chihuahua and Coahuila, Mexico.
14d. Sida leprosa var. sagittaefolia (Gray) Clement, comb. nov.
S. lepidota var. sagittaefolia A. Gray, Smithson. Contr. Knowl. 3, art. 5: 18. 1852.
S. sagittaefolia (Gray) Rydb., Bull. Torr. Club 33: 145. 1906.

Disella sagittaefolia (Gray) Greene, Lflts. Bot. Obs. \& Crit. 1: 209. 1906.

Indument like that of var. depauperata, always lepidote, scattered to dense. Leaves to 54 mm . long, $2-6$, rarely to $10, \mathrm{~mm}$. wide, elongatetriangular to nearly linear; base strongly oblique, coarsely laciniate; upper margins entire, usually straight; apex acute, blunt. Petals (9-) 12-15 (-17) mm. long, 8-10 mm. broad, yellow or white, often suffused with red, the depth of color strongest on the portion exposed in bud, or that portion specked with red, or only the base reddened.

TYPE: Wright 47, "Mountain valleys, 60 miles west of the Pecos; Aug." 1848 (GH). The only collection listed in Prof. I. M. Johnston's annotated list of Wright's field notes and numbers which could possibly be this distribution number is no. 869. Aug. 21, 1849, collected 80 miles west of the Pecos.
distribution: Arizona, New Mexico and Texas, U.S.A.; Sonora, Chihuahua, Coahuila and Durango, Mexico.

The present organization of this species-complex into a single species with four varieties may seem at first to be the ultimate in reduction, an oversimplification of the situation, yet it has been impossible to find absolute criteria of any kind which would effectively distinguish the entities as species. The host of intermediates between $S$. leprosa var. hederacea and $S$. leprosa var. depauperata in the area of overlap of their ranges bears uncontestable witness to the fact that genetic divergence of the types cannot have proceeded very far, although typical examples of each variety are amply distinct from one another in general appearance. In the case of $S$. leprosa var. depauperata and $S$. leprosa var. sagittaefolia, there are few intermediates between them, and they apparently do not occur together in the field. Yet their ranges are strikingly similar and they have no differential characters save those pertaining to leaf-shape. Apparently a genetic barrier exists but morphological differences, save of leafshape, do not. These specimens have the margins of the leaf above the base straight and entire, but the proportions of the leaf have changed, broadening towards that of var. depauperata. Wooton 402 from Doña Ana Co., New Mexico, of which I have seen seven specimens, represents the transition from one variety to the other quite well, having all but the extremes represented on each of several sheets. The UC and ARIZ specimens are close to var. depauperata, while the NY and US sheets are close to var. sagittaefolia. Other transitional specimens are Warnock 549 and Sperry 1465 from the Dog Flats of Brewster Co., Texas, Havard 134, Presidio Co., Texas, and Mulford 1149, Hudson's Hot Springs, New Mexico (which I have been unable to locate on any map). Jobnston and Mueller 1224 from western Coahuila represents an absolute extreme of leaf-size in this complex. The proportions are those of an intermediate between the varieties, the leaves measuring up to 4.5 cm . long and 1.2 cm . broad (measured as before) or 2.5 cm . broad, measured along the axis of the base. I have seen no other specimens which approach the size of this. The stems are to 40 cm . long, the petals white, tinged with maroon, and the plant is in every respect, save leaf-size, a good specimen of var. depauperata, the inappropriateness of the name never more evident than here, where its largest leaf is 4.5
times as long as the largest leaf of an Argentina specimen of the typical variety.

The typical variety of the species is found in Chile, Argentina and Uruguay and is rather variable in leaf-form, even as var. bederacea is in North America. It appears again in the region around Mexico City, near San Luis Potosí (Parry \& Palmer 75), these very scrappy specimens the basis for the nomen nudum $S$. hederacea var.? parvifolia Hemsl., and in Coahuila (Fisher 44105), collected along the railroad, near cultivated fields, which may account for its presence so far north. It has been impossible to distinguish this material from the South American, and the parallel distribution of S. physocalyx immediately comes to mind. Other material gradually intermediate between var. leprosa and var. depauperata or var. hederacea (and one cannot be certain which) appears in a chain from near Zaragoza and Mohovano, Durango, Mexico (Jobnston 7791 and Purpus 4538), through eastern Chihuahua (Stewart 682) and northern Chihuahua, Mexico (Rose \& Hough 4203, Pringle 7742), to Presidio Co., Texas (Hinckley 1860) and Cochise Co., Arizona (Blumer 1689), U.S.A. The last most nearly resembles var. depauperata, but the leaves are obruse at the apex rather than acute, and the base and upper margins shallowly and minutely toothed rather than laciniate and sharply toothed as in var. depauperata.

## 14a. S. leprosa var. leprosa.

[^5]definite locality: Hicken 738, La Plata? (ny). Moreno \& Tonini 353, "Patagonia, 50/3" (Ny). Lorentz 168, Feb.-April 1881 "Sierras Pampeanas" (US, GH).

Uruguay: Canelones: Rosenguitt B-3073, Canelones (ny)
"Cuba"? (see discussion of TYPE): Collector unknou'n, (photograph of TYPE in Madrid Herbarium: us). Collector unknown, (photograph of ISOTYPE? in Delessert Herbarium: f).

Mexico: Coahulla: Fisher 44105, Viesca (gh). San Luis Potosí: Parry \& Palmer 75, region of San Luis Potosí (Gh, mo). State of Mexico: Pringle 11934, Tlalnepantla (GH). Rose 8398, Tlalnepantla (GH). Schaffner 187, "Vallée de Mexico" (Gh). Federal District: Patoni-Ochotorena 4998 (mexu). Pringle 9415, Mexico City (GH 2). Bourgeau 32, edge of fields near Mexico City (GH).

## S. leprosa var. leprosa [intermediates to var. depauperata or var. bederacea.]

Mexico: Chinuahua: Pringle 7742, Rancheria (mexu 2). Rose \& Hough 4203, Rancheria (GH, uc). Stewart 682, n.w. of Jaco (GH). Coshuila: Purpus 4538 , "Movano, Coahuila" (uc). Durango: Jobnston 7791, road from Bermejillo to Zaragoza and north to Mohavano (GH).

United States: Arizona: Blumer 1689, Paradise, Chiricahua Mts., Cochise Co. (GH 2, ariz, F, ny 2, mo, ds, us). Texas: Hinckley 1860, Sierra Tierra Vieja (GH).

## 14b. S. leprosa var. bederacea.

United States: WASHINGTON: Oranogan Co.: Fiker 1424, between Omak \& Okanogan (us). Walla Walla Co.: Nuttall, Walla Walla (ny 2, gh). Douglas?, Walla Walla ( gh ex Hb. Hook.). Yakima Co.: L. Smith 110, Sunnyside-Mabton Road ( gh ). OREGON: Gilliam Co.: Palmer 37961, near Arlington (mo). Malheur Co.: Griffiths \& Morris 931, Ontario (ny). Norrow Co.: Peck 22667. 5 miles west Boardman (uc). Without definite locality: Nuttall, Oregon plains (Gh 2). IDAHO: W'ashington Co.: Davis 3006, 5 miles south Weiser (UC, Ds). CALIFORNIA: (selected citation sufficient to show range): Alameda Co.: Brewer 849, Corral Hollow (gh, mo, uc, us). Amador Co.: Braunton 1186, near Ione (ny 2, uc, mo 2, us). Colusa Co.: Heller 12393, near Colusa (GH, ny, mo, ds). Stinchfield 294, College City, Tule levee (pom, ny, ds). Contra Costa Co.: Rose 38310. Byron (uc, mo). Abrams 5728, Concord Road between Walnut Creek and Martinez (ds). Inyo Co.: Coville \& Funston 951, 2 miles south Lone Pine (us). Kern Co.: Bauer 8 Oct. 1927, near Bakersfield (ds). Kings Co.: Kearney 24, near Hanford (mo, us). Lake Co.: Blankinship 1 Sept. 1926. Kelseyville (mo). Lassen Co.: Burtt Daty 3330, Noney Lake Valley (uc). Los Angeles Co.: Abrams 2959, near Mesmer (uc, ny, pom, mo 2, DS, us). Munz 6622a, San Clemente Island (POM). Trask 258, west end San Clemente Island (us). Merced Co.: W'olf 725, 9 miles east Los Banos (ds). Monterey Co.: Abrams 4020. Morocco Junction (us, ds). Orange Co.: Buoth 1174. Santa Ana River, half mile from ocean (UAC, UC, POM). W olf 3855, Bryant Ranch (uc, ds). Riverside Co.: Roos 2308, La Sierra (pom). San Benrto Co.: Abrams 6667. Pajaro River on Los Boba road (ds).

San Bernardino Co.: IV beeler 2079, Chino Creek (gh, ny, uc, mo). San Diego Co.: Chandler 5396, Escondido (UC. Ny, Ds). Orcutt 1097, San Diego (GH, UC, US 2). Youngberg 11 July 1934, Lindo Lake, Lakeside (pom, UC, DS). San Joaquin Co.: Burtt Davy 826, Stockton (uc 2). Michener \& Bioletti 12, San Joaquin Bridge (mo, vc, gh, us 2). San Luis Obispo Co.: Brandegee 2 Oct. 1912. San Miguel (uc, us). Solano Co.: Jepson Sept. 1891. Vacaville (ny, us 2). Baker 3223. Suisun (gh, ny, pom, mo). Santa Clara Co.: Dudley, 4 Oct. 1895, Lake Lagunita, Stanford Univ. (ds). Stanislaus Co.: Hoover 108, Crow's Landing (uc). Ventura Co.: Feudge 1156, Upper Ojai Valley (pom). Yolo Co.: Keck 1732, 6 miles south Woodland (ds). Without definite locality:Haenke (mo, gh). NEVADA: Churchill Co.: Aller 302, 1 1/2 miles northwest Fallon (uc, mo). Allen 442, 30 miles southeast Toy (ny). Kennedy 1767. Carson Sink region (pOM, Ds). Tidestrom 10780, near Carson Lake (GH, ny, us). Humboldt Co.: Torrey 56. "sterile saline plains. $1865^{\prime \prime}$ ( $\mathrm{Ny}, \mathrm{mo}, \mathrm{GH}$ ). Lander Co.: Hitchcock 598, Battle Mountain (us). Lyon Co.: Allen 247, 6 miles north Yerinton (ny, ds). UTAH: Cache Co.: C. P. Smith 1819, LoganO.S.L. RR. (uac). Salt Lake Co.: Jones 1007. Salt Lake City (uac, gh, ny 3. pom, mo, us). San Juan Co.: Eastuood 15, San Juan River below Recapture Creek (gh, mo). Uintah Co.: Grabum 7322, 20 miles south Vernal (mo). OKLAHOMA: Beaver Co.: Ortenburger 10 July 1926, near Gate (us). ARIZONA: Apache Co.: Griffiths 5829, Hawthorn to Canyon du Chelly (us). Coconino Co.: W"ard. 26 May 1901, 10 miles below Tanner's Crossing, Little Colorado (us. ny). Graham Co.: Ounes, 31 May 1939. Safford (ariz). Navajo Co.: Peebles \& Fulton 9551, near Leupp (us). W゙ard. 20 June 1901, Woodruff (us, ny). Pinal Co.: Peebles 9409. near Sacaton (uc. es, pom). Yuma Co.: County Agriculture Agent, June 1925 (ARiz). Peebles, Havrison \& Keariney 4935. near Dome (us). Suingle S. 258, Yuma (Ariz). Thornber, 26 Sept. 1912, Yuma (ariz). W'ilkinsun, 27 Aug. 1905. Yuma (ariz). Without definite locality: Millspaugh 151, to the Grand Cañon (f). NEW MEXICO: Bernallllo Co.: Herrick, 7 Sept. 1894, Albuquerque (us). Doña Ana Co.: Archer 445. 5 miles north of Mesilla Park (smu). Cbild 524, Archer Ranch, Brazito (mo). Eggleston 20221. Mesilla Park (Us). Ferris 1147, 5 miles from Las Cruces (Ds). Fusberg S3457. Mesilla Valley, Lower Sonoran Zone (uC. pom). W' onton. June 41893, Mesilla Valley (us 2, mo). W'ooton 16. Mesilla (wyo, pom, mo, ariz, uc, us, ds, GH, ny). W'ooton, May, 1899. Mesilla Valley (ariz, wyo). W"ooton, 26 May, 1899, Mesilla Valley (DS, UC). W'ooton. 15 Oct. 1901, Mesilla Valley (pom). W'outon \& Standley 3283, Mesilla Valley (F, ds 2, ny, wyo, mo 2). Socorro Co.: Herrick 831, Magdalena (us). TEXAS: Baylor Co.: Reterchon. Sept. 1879. "banks of the Brazos" (GH. mo). Eastland Co.: Oyiter. 28 May 1883, vicinity Eastland (ny). El Paso Co.: Barlou', 1 July 1911, Rio Grande Valley at Canutillo (F). Cory 2064 (GH). Cory 52932.7 miles east El Paso (GH. smu). Dewes. 15 June 1891, west of El Paso (us). Earle 474. El Paso (wy 2). Ferris \& Duncan 2358. between Fabens \& Ysleta (Ds). Jones. 11 Sept. 1885, El Paso (uac, us, ny, uc 2, f. pom, ds). Mearns 677, El Paso (us). Meams 1522. Ft. Hancock (us). Palmer 31097, near El Paso (mo). Sbinner: 8926. south east side of El Paso (smu). Stearns 12. vicinity of El Paso (us). Vase). May 1881, El Paso (us 2). W"arerfall 3959. $31 / 2$ miles southeast of Clint (GH). W' hitehouse 8398, El Paso (F). Howard Co.: Palmer 12477, Big Springs (UC 2,
mo). Hudspeth Co.: IF'aterfall 3985, Rio Grande Valley, near Ft. Quitman (GH). Waterfall 4590, along Rio Grande. McNary-Ft. Quitman levee road (ariz, gh, mo, smu). Jeff Davis Co.: Waterfall 5328, 3 miles west Chispa ( $\mathbf{\text { gh } ) . ~ L u b b o c k ~ C o . : ~ R e e d ~ 3 0 8 0 , ~ v i c i n i t y ~ L u b b o c k ~ ( u s ) . ~ P o t r e r ~ C o . : ~ R e v e r c h o n ~}$ 3824, Amarillo (mo 2, pom, NY, GH, us). Reeves Co.: Nealley 715, 42, Pecos Flat, near Pecos City (us, f). Taylor Co.: Tolstead 7545, 18 miles southwest of View, on Edwards Plateau. (gh 2, smu 2). Young Co.: Reverchon, 29 Oct. 1902. banks of Brazos, near Graham (mo). Without definite locality: $\mathbb{W}^{\prime}$ right 44, "western Texas" (GH 2, UC, NY). II'right 45, "western Texas" (Us, UC, GH 2). Young. 12 Sept. 1917, Llano Estacado, near Paloduro Canyon (mo).

Mexico: Guadalupe Island: Thoburn, Green \& W'ing, July 1897, near northeast landing (ds). Revillagigedo Islands: Howell 8359, Sulphur Bay, Clarion Island (ds). Baja California: Brandegee. 5 April 1889, San Gregorio (uc). Orcutt, 31 Aug. 1889, Ensenada (mo 3). Brandegee 50, San Jose del Cabo (uc). Sonora: Palner (ds). Thurber 424, Fronteras (gh). Chihuahua: Pringle 5278, Paso del Norte (mexu). Stearns 12, "state of Chihuahua" (F). Coahulla: Palmee 92, Lorenzo de Laguna (gh). Querétaro: Deam 95, Querétaro ( GH ). W'ithout definite locality: Thurber, " 1852 " (GH).

## 14c. S. leprosa var. depauperata.

United States: ARIZONA: Cochise Co.: Darrou: Pbillips \& Pultz 1321, 4 miles west Chiricahua. (Ariz). Gondding 2275. Douglas (UC, mo). Gould \& Pultí 3143, southeast of Chiricahua (ARIZ, uc. us). Griffith 1991, 6 miles south Benson (ny). Jones, 26 Sept. 1884, San Simon (GH). Lemmon 523, Apache Pass (GH. UC). Shreve 6361, south of Rodeo (F). Thornber 2562, Sulphur Spring Valley (ariz). Thornber 260, San Pedro Valley, Benson (ariz). Thornber 4642. Bowie (ariz). Mohave Co.: Lemmon 3255, Kingman (Gh). Pima Co.: Lemmon 14. Tucson (Gh). Yavapai Co.: Meaths 191. Ft. Verde (ny 2). Without definite locality: Rothrock 188 , Deer Springs (F, GH, us). NEW MEXICO: Catron Co.: Metculfe, Aug. 1901, Mangas Springs (ariz, us). Doña Ana Co.: Standley, 17 June 1906. Mesilla Valley, College Farm (gh). W'ontoin, 22 April 1894. Mesilla Valley (ds, Ariz, uc, mo, pom). Wooton \& Standley 3236. Mesilla Valley (us, f, ds). Grant Co.: Eggleston 16509, along Gila river and on mesa above Cliff (F). Eggleston 19992, Shelley "Poison Pasture" Cliff (GH). Holzinger, 31 July 1911, Hanover Mt. (us). Holzinger, 27 Aug. to 12 Scpt. 1911, Fierro (mo). Luna Co.: Abrams. 24 July 1919, mesa near Little Florida Mts. (Ds, pom). Eggleston 16261 and 16262, Nutt (MO, F). Mulford 1024. Deming (mo. ny). Sierat Co.: Beats. Sept. 1914, Lake Valley (us). Without definite locality: Mulford $1076 a$. Meenjani Road (mo). W'onton. S July 1906, Cactus Flat (us 2). W'right S89, sandy soil between the Rio Grande and Mimbres, June (gh, type \& isotype, ny. uc, mo, us). TEXAS: Brewster Co.: Sperry 1335, Dog Canyon Wash (us). Culberson Co.: Earle \& Tracy 400. R. near Kent (ny, us). El. Paso Co.: Wright, Oct. 1904, El Paso (ds). Howard Co.: Tracy 7817. Big Springs (mo, ny 3, gh, us). Jeff Davis Co.: W'atetfall 4404, north edge of Davis Mts. (ariz, mo, gh, smu). Lubbock Co.: Reed. 28 Aug. 1929, Lubbock (mo). Presidio Co.: Havard. Oct. 1893, Marfa (us). Reeves Co.: Cory 52140,20 miles southwest Pecos (GH. Smu). Hanson. 17 Dec. 1918. Pecos (ny). Hanson 45, Pecos (GH, Mo).

Taylor Co.: Tolslead 72.4. Camp Barkelcy (mo, uc). Without definite locality: Hatatd. 1881 (us). I"right 45. "west Texas", (Type no. of S. lepidota var. depauperata). (UC, Gif, MO, NY, US).

Mexico: Baja California: Brandegee. 3 Sept. 1893. San José del Cabo (GH). Sonori: Schott. 25 Junc 1855. El Potrero (f). Chihuahua: Stearni, 1911. valleys, near Ciudad Juárez. (ny 2). W' bite 2613. Carretas (ghe). Coahulla: Aguirre \& Rtko 116. Paila (N). Jotonston \& Muller 122千. north end of Bolson de los Lipanes ( GH ).
S. leprosa var. depauperata [intermediates to var. sagittaefolia.]

United States: New Mexico: Mulford 11ヶ9, "Hudson's Hot Springs" (MO. Ny). II voton 402 , plains south of the white Sands, Doña Ana Co. (Ny, ahiz, uc, mo, pom, us, ds). Texas: Sperry 1465. Dog Flats, Brewster Co. (Gh). W'arnock C549. same locality (us). Haraid 134. Presidio Co. (GH).

## 14d. S. leprosa var. sagittaefolia.

United States: ARIZONA: Cochise Co.: Parish. 2 May 1884. Lowell (Ni, UC, dS, us 2). Lemmon \& uife, 11, 1880 Ft. Lowell (UC). Maricopa Co.: Lemmon Herbarium 11. Aug. 1880, nr. Gila Bend (GH). Mohave Co.: Eastuood 18455. road from Kingman to Peach Springs (US). McKelvey 2267, between Hackberry and Peach Springs (pom). Pima Co.: Caller: 1 Oct. 1933. Tucson (Ariz). Cory 3255. Tucson (GH). Goodding \& Lusher 140-45. Menenger's Dam (ariz). Gould 3062. 10 miles cast of Tucson on Nogales Road (ariz, vac, uc, mo, us, GH). Griffiths 8962. Baboquivari Valley (mO). Jones, 25 Aug., 1903. Tucson (pOM). S. B. \& W'. F. Parish, April 1884, Tucson (UC). Peebles, Harison, Kearney 3849, Papago Reservation (us). Pringle. 29 June 1881, (mo, 13635), Santa Cruz Valley near Tucson (Ny, GH). Sbrete 7376, near Tucson (mo, F, DS). Spulding. 21 March 1906. Altar Valley (east side of Baboquivari Mts.), (ariz). Pima Co.: Thornber 54. Santa Cruz Valley, Tucson (ariz. us). Thomber 453. Santa Cruz bottoms (ariz 2, mo, UC, dS. US). Thornber 2648. Hart's Ranch (ARIz). Thornber 4107, Santa Cruz Valley (ariz). Pinal Co.: Eastuood 6316. Maricopa (us). Gilman 363. Sacaton (ariz). Peebles 7390. near Casa Grande (us). Thornber 7347. Casa Grande (ariz). Yavapai Co.: Coues \& Palmer 524. Rio Verde. Ft. Whipple (mo, gh 2). Purpus 8268, Plains, Beaver Creek (mo, uc, us). Without definite locality: Engelmann, 23 Sept. 1880, Mesa, Arizona Desert (mo). Potts, southern Arizona (mo). Purpus 72, Black Mesa (mo, UC, us). NEW MEXICO: SoCorro Co.: Rusby 51, alluvial flats, north of Socorro (UC, uIS, F). Without Definite locality: Rusby 51. dry plains near Alamilln (mo. ny). Rusb; 51, Mogollon Mts. (ny). Rusby 51. dry plains. Jornada del Muerto (mo). Edu:ards. 1848 (NY, GH). Rusby, 1881 (NY). Wright 1331 (GH 2. UC, NY 3. MO. US). TEXAS: Borden Co.: Pobl 4424, 4 miles north of Murphy School (smu). Brewster Co.: Cory 53130. $53 / 4$ miles northwest of Alpine (SMU). Cory 53131. $53 / 4$ miles northwest of Alpine (GH, SMU). Ingram 2829, 16 miles east Alpine (Us). Palmer 34031a, Alpine (mo). Schulz 11 Oct. 1931 (F). Thatp 18 Aug. 1935, Ft. Stockton, Alpine (MO, GH, UC. SMU). Tharp 175 (MO, UC. GH). Tharp 3581.

Marathon (us). Crosby Co.: Erlanson 1166, 20 miles southwest Spur (smu). Howard Co.: Letterman 104, Big Springs (mo, us). Kinney Co.: Cory 16781, 9 miles south Spafford (GH). La Salle Co.: Cory 28518. $73!4$ miles west Fowlerton (GH). Lubbock Co.: Reed 3137. Lubbock (us). Midland Co.: Trac; 7814, Midland (mo, ny 3, Gh, us). Pecos Co.: Cory 17513, $41 / 2$ miles northeast Hovey (GH). Presidio Co.: Diusbel 11159, near Marfa (ny, F). Hinckley 701, $12 \mathrm{~m} . \mathrm{s}$. Marfa (Ny, F). Hinckley July 1936, San Esteban Lake, Marfa (GH). Hinckley 713. Marfa (F). Nealley 43. "The Chenatic" (F). Zavalla Co.: Palmer 13545. Crystal City (mo). Tharp 6037, Crystal City (us). Without definite locality: V. Havard 188, Mts., Western T'exas (us). Nealley 788 (Ds). W'right 47, "mt. valleys west of the Pecos" (UC, MO, GH TYPE 2, ny, US).

Mexico: Sonora: II'iggins 6370, 1/2 kilometer west Punta Piedras, 15 miles west of Empalme (ds). W'iggins 8391. 32.5 miles west Sonoyta (Ds). Chihuahua: LeSuess 383, El Carmen (F, GH, SMU). Palmer 220, near Chihuahua, (Ny, GH, mo, us). Pringle 27, Llanos, Escalón (mexu). Stewart 2366, 1 kilometer north Escobillas. (GH). Stewart 2589, near Trinidad, road from Guimbalete west to south end of Sierra del Diablo (GH). Thurber 846, El Gallote (GH 2, Ny 2). IV'bite 2030, 6 miles west Guimbalete, road to Escalón (GH). W' bite 2046. Escalón (GH). W'ilkinson, 1885, Santa Eulalia Plains (Ny). Coahulla: Fisher 44136. 3 miles northeast Torreón (GH). Fisher 44152. 3 miles east Torreón ( CH ). Jubnston \& Muller 784́, Llano de Juaje, between Lomas del Aparejo and Tanque la India (GH). Marsh 1412, trail from Encantada Mesa to Fresno Mesa, Sierra de Santa Rosa, northwest of Muzquiz (GH, F). Marsb 1529, vicinity Encantada Ranch Hq. and east to escarpment of the Sierra del Carmen, northwest of Muzquiz (GH, F). Marsh 1530, vicinity Encantada Ranch Hq. and east to escarpment of the Sierra del Carmen, northwest of Muzquiz (GH. F). Stewart 432, 18 miles south Castillon, road to Santa Elena Mines, via Jesus Maria and San Rafael (GH). Stewait 559, 8 kilometers west of Castillon (GH). Stewait 1165. 1 kilometer east of La India, Llano de Guaje, north of Tanque de La India (GH). Steurart 2777. Rancho Parritas, 5 kilometers south base of mountains along east margin of Valley de Acatita (GH). Durango: Palmer 536, Mapimi (Gh. NY, UC 2, MO 2, mexu). Patoni-Ochotorena 324, near San Juan de Guadalupe, south of Sierra de Ramirez (mexu). Without definite locality: Schoti 9 July 1855, Escopeta Valley (F).
IV. Section Incanifolia Clement, sect. nov.

Herbae prostratae, omnino molle stellato-canescentes; folia symmetrica, crassius griseo-viridia; flores axillares subsessiles; lobis calycis angustoovatis; carpella 5, paullum inflata et ad modum carpellorum Abutilonis acuminata.

Prostrate herbs, everywhere softly stellate-canescent; leaves symmetrical, dark gray-green; flowers subsessile in the axils; calyx lobes longovate; carpels five, slightly inflated, peaked.

The two species of the section have customarily been placed in section Pseudomalvastrum, although they are never bracteolate and have symmetrical leaves which are softly canescent, rather
than asymmetrical leaves which are scabrous. The carpels are always five in number here and always more than five in section Pseudomalvastrum. Type species: Sida Grayana Clement in Kearney.

## Key to the Species

Carpels 5.5 mm . high, with two protracted blunt apical peaks from the middle of the upper dorsum (similar to those of Abutilon); stamen-column 3.5 mm . high, the lower half with coarse, scattered, stellate hairs; petioles $3-6 \mathrm{~mm}$. long; stipules 5-6 mm. long, oblanceolate, acute . . . 15. S. Grajana.
Carpels 5 mm . high, the apex peaked but not protracted; stamen-column 3.0 mm . high, glabrous; petioles $6-12 \mathrm{~mm}$. long; stipules 7 mm . long, ovate, obtuse
16. S. Helleri.

## 15. Sida Grayana Clement in Kearney, Lflts. West. Bot. 7: 140. 1954.

S. cuneifolia A. Gray, Bost. Journ. Nat. Hist. 6: 165. 1850, non Roxb., Fl. Ind. 3: 170. 1832.

Disella cuneifolia (Gray) Greene, Lflts. Bot. Obs. 1: 209. 1906.
Perennial assurgent subshrub. Stems many from a slender, tapering, pale, woody taproor, freely branching, up to 45 cm . long, woody; the whole plant covered with a canescent, soft, fine-rayed, stellate pubescence with a characteristically soft feel; the wood slightly yellowish, with a high waxy luster when cut; leaves suborbicular to rotund-cuneate, $3(-5)$-nerved, the nerves prominent beneath, variably crenate to serrate, except on the base, concolorous, $6-14 \mathrm{~mm}$. long, 6-16 mm. wide; stipules oblanceolate, acute, spreading, slightly folded on the median nerve, $5-6 \mathrm{~mm}$. long, ca. 1 mm . wide, persistent; petiole terete, 3-6 mm. long; flowers solitary or clustered on much shortened branchlets in the axils; pedicels $2-3 \mathrm{~mm}$. long, terete, erect, articulated near the base, elongating slightly in fruit; calyx campanulate, terete, 5-7 mm . long, lobes ovate to lanceolate, acute, $3-4.5 \mathrm{~mm}$. long, $1-1.8$ mm . wide, erect, closing slightly over the fruit, with one main nerve and several fine small ones, stellate-pubescent within except the tube; petals yellow, obovate, subtruncate, slightly oblique, $5-6 \mathrm{~mm}$. long, 3 mm . wide, the claw 1.5 mm . wide, rather coarsely veined, inserted just below the level of the top of the ovary; stamen-column slender, terete, 3.5 mm . long from base of ovary to level of the filaments, with scattered, coarse, stellate hairs on the lower part and tufted stellate hairs between the claws of the petals. Stamens $18-20$, reniform with a deep, narrow sinus, pale yellow, with many fine red-brown dots, 0.5 mm . wide open and closed; filaments $1-1.5 \mathrm{~mm}$. long, not paired; pollen 0.03 mm .
diam. Ovary globose, densely stellate-hirsute apically, thinning basally, ca. 1 mm . high, 1 mm . wide, almost filling the cavity. Styles $4.5-5.5$ mm . long, 4- 4.5 mm . free, subconnate in bud, protruding in early anthesis, reflexing later; stigmas capitellate, 0.1 mm . in diameter; carpels 5.5 mm . high, 2 mm . radially; apex peaked, with two blunt, stellatepubescent, slightly introrse aristae, dehiscence between them by a wellmarked suture, the dehiscence often continuing to the base; lateral walls membranaceous, pale, smooth, 2 mm . high, 1 mm . wide, basal; dorsum stellate-hirsute, denser and longer-rayed apically, nearly glabrous basally; inner surfaces straw-colored, shiny, perfectly glabrous except on the strigose margins of the suture. Seed globose, glabrous, dark redbrown, minutely verruculate, filling all but the apex of the carpel; the funicle broad and flat, with a few setulose hairs of the same color. Columella slender, narrow-flanged, 2.5 mm . high, pale, base of the styles persistent.

TYPE: Wright, 1848, " 35 miles northeast of Eagle Pass, Rio Grande, Texas. Place overgrown with plants indicative of salt, Sept." (GH, fragment us).
distribution: Southern Texas; Tamaulipas and Nuevo León, Mexico.
The name Sida cuneifolia was first used by Roxburgh (1814), without accompanying description, for a plant growing in the Calcutta garden. He later (1832) provided a description and validated the name. In 1834, Wight and Arnott identified this plant with Riedleia truncata (Willd.) DC. (1824), based on Melochia truncata Willd. (1800), but in 1837, Wight, with better material available, showed that Willdenow's plant and Roxburgh's were actually of the Malvaceae rather than the Sterculiaceae and proposed a new genus, Dictyocarpus, closely related to Sida, for the species. Bentham and all others since have agreed that it belongs in Sida. Sida Schimperiana Hochst. ex A. Rich. (1847) is apparently the same thing, described from African material, and this name is often applied to the Indian material. Sida cuneifolia Roxb. is the first available name, there already being a Sida truncata, of Cavanilles (1785), and should be used. It is earlier than Gray's Sida cuneifolia by 28 years, and I have renamed the latter species for its author.

Hochreutiner (1902, p. 33) remarks under S. cuneifolia Gray, "Nous voudrions signaler ici une plante de Lemue, provenant de Litakoun, Afrique australe, et qui nous paraît être identique à la plante américaine". I have seen no African material which resembles this species nor have I read of any anywhere else.

United States: TEXAS: Bexar Co.: Parks f819, Near San Antonio (mo). Cameron Co.: Cory 51383. Loma Alto, 8 airline miles northeast of Brownsville (smu, us, GH). Hanson. 19 May 1919, 10 miles cast Brownsville ( GH ). Hunt 16 , Brownsville (ds). Runyon 455, Brownsville (us). Runyon 654, Brownsville (us). Shiller M-115, Brownsville (mo, GH). Dimmit Co.: Jones 28239, Carriso Spring (UC, POM. mo, ds). Tharp 593. 10 miles south of Big W'ells (us) Jim Hogg Co.: Hanson 30. 25 miles south of Hebronville (mo. us). la Salle Co.: Cory 14980, 2 miles south of Los Angeles (ch). Mavehics Co.: Wright. 1848, 35 miles northeast of Eagle Pass. Rio Grande (GH, us). Webb Co.: Manson, 26 April, 1919, valley, 7 miles east of Laredo (ny). Wrthout definite locality: Parks M-115 (mo). Wright 48, "western Texas, 1849" (Gh 3, us). Berlandier 645 \& 2055, Rio Frio (сн).

Mexico: Nuevo Lén: Berlandier 3104. (Gh, ny 2, mo, us). Tamaulipas: Bartlett 10969, vicinity El Mulato (F).

## 16. Sida Helleri Rose, Contr. Herb. Franklin \& Marshall Coll. 1: 66. 1895

Perennial prostrate shrub, 3 cm . or less high, to 60 cm . in diameter. Stems woody, numerous from near the base, only slightly branching; flowering shoots prostrate to erect, herbaceous, clothed with a soft, very slender-rayed, stellate indument, the older stems becoming woody and glabrous. Leaves suborbicular, crenate to obtusely serrate except the rounded, subcuneate or truncate bases, finely stellate-pubescent, scattered above, dense beneath, $8-13 \mathrm{~mm}$. long, $10-16 \mathrm{~mm}$. wide, three-nerved, the nerves inconspicuous above, prominent and straw-colored beneath. Petioles 6-12 mm. long, terete or slightly ribbed under the dense indument. Stipules obtuse, ovate, foliaceous, usually persistent, appearing as bracts at the base of the pedicels, 7 mm . long, 3 mm . wide, 1 -nerved, slightly folded, erect. Flowers subsessile, solitary in the axils. Calyx campanulate, terete, accrescent after anthesis, $4-5 \mathrm{~mm}$. high in flower, $5-8 \mathrm{~mm}$. high in fruit; the lobes ovate, without apparent nerves, remaining erect in fruit, obtuse or subacute, densely stellate except the inside of the tube proper, $3-3.5 \mathrm{~mm}$. long, $1-1.5 \mathrm{~mm}$. wide; epicalyx none. Petals "pale copper-colored", broadly obovate or obliquely suborbicular, broadly and shallowly emarginate, glabrous throughout, $4-5$ mm . long, $3-4 \mathrm{~mm}$. broad, inserted on the stamen-column above the top of the ovary, venation very fine. Stamen-column slender, faintly ribbed, glabrous, 3 mm . high from the base of the ovary to the level of the filaments; filaments all from the same level, not paired, ca. 1 mm . long. Anthers 20 , ca. 0.8 mm . wide open, ca. 0.5 mm . wide closed, minutely dark-verruculate; pollen ca. 0.05 mm . diam. Styles five, 5 mm . long, 3 mm . free, reflexed in anthesis; stigmas capitellate. Ovary 1.5 mm . high and wide, subspherical, densely strigose laterally, densely hirsute apically; the styles inserted high within the ring of ovules. Fruit deeply five-lobed; carpels five, 5 mm . high, 3 mm . radially, inflated
apically, partially dehiscent by a medio-dorsal suture, the margins thickened; dorsum obtusely peaked apically, the peak hirsute to the funicular opening, remainder of the dorsum short-strigose; lateral walls chartaceous, smooth, 2 mm . wide radially, 3 mm . high. Seed plump, filling the lower two thirds of the carpel, puberulent; the wall woody, hard, dark red-brown; funicle flattened, puberulent, lighter red-brown. Columella 3 mm . high, 5 -flanged, the basal portion of the stylar column often persistent.
type: Heller 1533, shores of Corpus Christi Bay, Nueces Co., Texas (US).
distribution: Southern Gulf coast of Texas, United States.
United States: Texas: Heller 1533, shores of Corpus Christi Bay, Nueces Co. (us 2, ny, uc, ARIZ, GH, F). Sbiller 350, near Brownsville, Cameron Co. (us).

## V. Section Oligandrae Clement, sect. nov.

Herbae annuae; folia palmatilobata; carpella aristis elongatis retrorse barbatis; antherae 5-20; carpella 5-10; calyx accrescens non tamen inflatus; epicalyx deest; flores paniculati (flores inflorescentia foliosa paniculata); parietes laterales carpellorum ad semina firmiter adherentes.

Annual herbs. Leaves palmately lobed. Calyx somewhat accrescent but not inflated; epicalyx absent. Stamens 5-20. Carpels 5-10, longaristate, the aristae retrorsely barbed, the lateral walls firmly adherent to the seed.

A well-defined natural section of western Bolivia, Peru and Ecuador, section Oligandrae is composed of species previously placed in section Sida. Fries (1947) treated the species as an "Artgruppe" with this name but did not formally establish a new section.

The treatment here presented is at best preliminary because of the lack of material of certain species and the relatively few specimens of others. In addition, it is felt that were collections available from intervening parts of the disjunct ranges of certain species, the distinctions between them might easily be removed. Still another barrier to satisfactory treatment has been the unavailability of type or authentic material of two species which are, then, maintained "de fide" only. Type species: Sida palmata Cav.

## Key to the Species

A. Carpels 7-9; stamens $10-20$
B. Leaves 3-5-lobed, lobes deltoid or slightly narrowed at the base; margin regularly dentate
17. S. palmata.
B. Leaves mostly $7-9$-lobed, lobes lanceolate, usually markedly narrowed toward the base and deeply divided . . . . . . 18. S. jatrophoides.
A. Carpels 5 C
C. Stamens 10, stamen-tube villous
D. Leaves mostly 3-lobed; aristae of the carpels $12-1$ mm. long
19. S. decandra.
D. Leaves mostly 5-7-lobed; aristae ca. 5 mm . long . . . . 20. S. rupo.
C. Stamens 5, stamen-tube glabrous

E
E. Leaves shallowly lobed; aristae 4 mm . long . . . . 21. S.lomageiton.
E. Leaves deeply lobed

F
F. Aristae of the carpels ca. 14 mm . long . . . . . 22. S. lomana.
F. Aristae of the carpels $4-6 \mathrm{~mm}$. long . . . . . . . . . . . . G
G. Stamen-column $1.5-2 \mathrm{~mm}$. high; petals with a tuft of stellate hairs in the outer margin, visible in the bud
23. S. patuliloba.
G. Stamen-column ca. 3.5 mm . high; petals without marginal tuft but with scattered, appressed, stellate hairs on the outer surface 24. Soligandra.

## 17. Sida palmata Cav., Diss. 1: 20, t. 2, f. 3. 1785.

S. ricinoides l'Hérit., Stirp. Nov. 115, t. 55. 1788.

Malvinda palmata Moench, Suppl. 203. 1802.
S. Ricini Spreng., Syst. 3: 116. 1826.

Erect annual herb, 10-18 dm. high. Stems terete, covered with a white tomentum of spreading, stiff, unicellular hairs $1-3 \mathrm{~mm}$. long, and denser, finer, softer, spreading hairs to 0.5 mm . long. Stipules not seen, possibly absent. Petioles of the upper leaves $5-15 \mathrm{~cm}$. long, faintly ribbed, with a tomentum like that of the stems. Leaves 3 - 5 -lobed, reniform in circumscription; upper leaves to 10 cm . long and 15 cm . wide, outer pair of lobes smaller, deltoid or ovate, acuminate, divided about halfway to the base or slightly more; base cordate, the sinus deep and narrow; nerves five from the base, straw-colored, prominent on both surfaces; indument of the upper surface hirsute, of simple, appressed, thin, hyaline, unicellular hairs of two sizes: to 2.5 mm . long and to 0.5 mm . long, more prominent on the veins; indument of the lower surface densely tomentose, the stellate hairs of two types: scattered, mostly 3 -rayed hairs, the rays ca. 0.5 mm . long, and denser, much smaller, finer, many-rayed hairs. Lower leaves caducous. Inflorescence of few-flowered terminal panicles, additional solitary flowers from the lower axils rarely present. Pedicels terete, ca. 3 mm . thick, conspicuously articulated $6-9 \mathrm{~mm}$. below the calyx, flexed above or around the articulation, elongating in fruit to as much as 5 cm .; pedicels of the uppermost part of the panicle much abbreviated, ca. 0.5 cm . long in anthesis; tomentum like that of the stem. Calyx green, cupuliform-campanulate, $5-6 \mathrm{~mm}$. long in anthesis; lobes deltoid, acute, ca. 3 mm . long, 2.5 mm . wide at the base, without prominent nerves; tomentum of the ex-
terior like that of the stem with additional scattered, mostly 3-rayed, stellate hairs; margins finely ciliate; interior finely puberulent, becoming sericeous-hirsute on the lobes. Petals obovate, truncate, $5-6 \mathrm{~mm}$. long, ca. 4 mm . wide, finely veined; the outer upper surface sprinkled with fine, multicellular, twisted, simple hairs; claw 1 mm . wide, finely villous on the margins. Stamen-tube 1.5 mm . high from base of the petals to the filaments, conoid, assurgent-villous on the lower portion, with ten paired traces; filaments erect, reflexing after anthesis, 1.5 mm . long, somewhat paired. Stamens ten, fifteen or twenty, ca. 0.5 mm . wide when open, yellow, not dotted. Ovary obturbinate, subangulate, glabrous, olivaceous, less than 1 mm . high and wide, 5-beaked, each beak split. Styles $3-4 \mathrm{~mm}$. long, $1.5-2.5 \mathrm{~mm}$. free, slender, reflexed in anthesis; stigmas subcapitellate, minutely papillose. Fruiting calyx accrescent after anthesis to 1 cm . high, remaining green; the lobes $5-6 \mathrm{~mm}$. long and wide, erect, acute or acuminate; the midnerve of each lobe becoming prominent. Carpels seven to nine, 4 mm . high, subquadrate viewed laterally; dorsum finely downy-pubescent, the outer surface invaginated and with a conspicuous midnerve; lateral walls membranous or scarious, subrugose, not or slightly adherent to the seed; aristae 5 mm . high, erect, retrorsely setose, slightly divergent, never reflexed. Columella conical, truncate, 3.5 mm . high, occasionally splitting or flattening on drying and pressing; base of the styles persistent; remnant traces to the lateral walls of the carpels sometimes persistent, curving upward and outward from the base of the columella. Seed dark brown, 3 mm . high, 2 mm . radially, dull, pulverulent; the rostrum assurgent, thickly covered with collapsed, obtuse, hyaline cells; funicle flattened at the hilum, becoming terete along the rostrum.

TYPE: Specimen cultivated in the Jardin des Plantes, Paris, from seed collected by Dombey, presumably near Lima, Peru (P).
distribution: Ecuador and Peru.
The nomenclatorial confusion surrounding the application of the name S. palmata is discussed under S. jatrophoides, with which this species has of ten been confused, even by its author. Cavanilles' original description and illustration were sufficiently precise so that the name can be applied only to the taxon which has 7-9 carpels, ten or more stamens, and the leaves divided into three or five lobes, the lobes about half as long as the leaves and triangular or at most slightly narrowed at the base. In all the material of this section available to me, the only specimens which fit the original description of S. palmata are from near Huigra, Ecuador, although the species was said by Cavanilles to have been observed by Commerson near Lima. It was originally described
from living material grown in the Jardin des Plantes, presumably from seed collected by Dombey in Peru. I have seen no modern collections of the species from that country, and all the material from around Lima which has more than five carpels is unquestionably S. jatrophoides.

Ecuador: Chimborazo: Camp E-2999, near Huigra (us). Hitchoock 20335, Huigra (Ny. us, GH). Hitchcock 20620. Huigra (Us, GH). Rose 22176, vicinity of Huigra (GH, NY, US).

Peru: Dombey, (Photograph of specimen in G: F, GH). Dumbe), Lima (Photograph of specimen in M: $\boldsymbol{F}$ ).
18. Sida jatrophoides l'Héritier, Stirp. Nov. 117, t. 56. 1788.
S. palmata Cav., Diss. 2: 48. 1786 and Diss. 5: 274, t. 131, f. 3. 1790 in part, non Cav. Diss. 1: 20. 1785.

Erect annual herb, 5-6 dm. high. Stems woody, glabrescent or shorthirsute, hairs of the indument of two lengths, spreading, white. Stipules early deciduous, not seen. Petioles subangulate, to 7 cm . in length, the indument like that of the stem. Leaves cordate in circumscription, the sinus deep and narrow, palmately 7-9-lobed; lobes acute, ca. 6 cm . long or less, divided almost to the base, at least two-thirds of the way, often with secondary lobules or sublaciniate, lanceolate, narrowing below the middle; nerves 7-9, prominent on both surfaces, pale; upper surface with few, scattered, appressed, simple or few-rayed stellate hairs, these flavid golden or brownish mostly pointing apically; margins ciliate; lower surface paler than the upper, with scattered, mostly 3-4. rayed, yellowish, stellate, appressed hairs. Inflorescence of few-flowered terminal and subterminal glomerules elongating to form lax panicles, a few flowers occasionally solitary in the axils as well; pedicels very short, to 1.5 cm . long, slender, densely tomentose, terete, articulated near the apex. Calyx campanulate, densely long-sericeous, the hairs occasionally to 4 mm . long, yellowish; flowering calyx $4-5 \mathrm{~mm}$. high, the lobes lanceolate, acute to subacuminate, ca. 3 mm . high, $1-1.5 \mathrm{~mm}$. wide; indument of appressed, sericeous, apically pointing hairs. Petals broadly obovate, slightly oblique, $3.5-5 \mathrm{~mm}$. long, $2.5-3 \mathrm{~mm}$. wide, contorted after anthesis, scattered-pulverulent; claw ca. 1 mm . wide, the margins few-ciliate; veins not prominent. Stamen-tube conical, $1.5-2 \mathrm{~mm}$. long from base of the petals to filaments; traces ten, paired, prominent on the interior; filaments ca. 0.5 mm . long, reflexed, slender. Anthers $10-15$, ca. 0.6 mm . long, verruculate, pale yellow. Ovary shortturbinate, multiapiculate, ca. 1 mm . high and wide. Styles ca. 2.5 mm . long, the upper half free; stigmas subcapitellate. Fruiting calyx 5-6 mm . high; lobes erect or spreading, acuminate, ca. 2 mm . wide at the base; green. Carpel 2 mm . high, 1.5 mm . radially, muticous, awned, or
briefly apiculate; dorsum yellowish, with rather dense dark brown verruculations, invaginated slightly on the outer surface; lateral margins rugose; lateral walls membranous, pulverulent, firmly adherent to the partly visible seed near the base, a vascular trace from the columella paralleling the lower and outer margin of the wall; apex of the dorsum prolonged into two yellowish, laterally flattened, pyramidal projections from which the aristae may develop; the latter, when present, ca. 6 mm . long, yellowish, flattened, dilated basally, with few retrorse hairs; inner margin not differentiated from the lateral walls in texture; all walls except the apex adherent to the sced. Seed almost black, plump, the hilar sinus shallow, abruptly ridged on the outward edge; funicle flattened at the hilum, dark. Columella conoid-truncate, ca. 2 mm . high, flanged; remnant traces to the lateral walls of the carpels sometimes present.

TYPE: Specimen cultivated in the Jardin des Plantes, Paris, from seed c)llected by Dombey in Chancay, Peru (P).
distribution: Western Peru.
There are two distinct elements in the $S$. palmata group, one with 5 -lobed leaves, the lobes cut approximately half-way to the base, the margins crenate-serrate, S. palmata Cav. 1785 only; and a second with $7-9$ lobes, the lobes divided almost to the base, the lobes markedly narrowed toward the base, S. jatrophoides l'Hérit.

Cavanilles and many later authors have consistently confused the two entities, taxonomically and nomenclatorially. Cavanilles emended his original description of $S$. palmata, the 5 -lobed element, in two subsequent Dissertations. His long feud with l'Héritier seems to have affected his usual good judgment for he sank the latter's $S$. ricinoides and S. jatrophoides in his own $S$. palmata. It is clear from a comparison of the descriptions, the plates, and photographs of authentic material in various European herbaria (Paris, Geneva, Copenhagen, Berlin and Madrid) that S. ricinoides is identical with $S$. palmata. The original descriptions of both were based on material grown in the Jardin des Plantes from seed sent by Dombey. S. jatrophoides is the same as the taxon described by Cavanilles under the name $S$. palmata in the first Mantissa. Although Cavanilles said that his material was grown "ex seminibus Mexicanis", it was probably from more Dombey seed from Peru, as was the type-material of S. jatrophoides. In the second Mantissa, Cavanilles added to the original description of $S$. palmata still further information from living
material and published a plate which is a very good match for l'Héritier's plate of S. jatrophoides. Since Cavanilles thought both clements belonged to $S$. palmata and did not therefore name the second, $S$. jatrophoides must be used for the element with deeply 7-9-lobed leaves.

Peru: Dombey, " 670 " ( P ), Dombey, "Peroú" ex herb. de Franqueville (P). Dombey, ex herbs. Cosson. Maire (P). Dombey. "Chile et Peroú" (F). Dombè, (Photoglaph of ?ISOTYPE, B: F, GH). Dombey. (Photograph of ?ISOTYPE, M: F). Rose \& Rose 18619. vicinity of Santa Clara (us). Stork 11470, between Ambar and Huacho, Prov. Cajatambo, Lima (UC, GH). W'eberbauer $7 \neq 27$. mountains between Moquegua and Terata, Prov. Moquegua. (MO, US, GH, F. NY). IF'eberhauer 5247. hills of San Agustin, Lima (F, US, GH), (cited by Clbrich in type descr. of S. rupo). Collector unknou'n. (photograph of isotype, C: GH, F). Collector unknou'n. (photograph of spec. B: GH, F). Collector wnknou'n, cult. Paris (GH, ex Hb. J. Gay).

## 19. Sida decandra R. E. Fries, K. Sv. Vet. Akad. Handl. ser. 3, 24(2): 16. 1947.

Erect annual herb. Young branches clothed in multicellular, pilose, stellate-pilose and rigid-setaceous hairs. Petioles to 7 cm . long, stellatehirsute and setose; lamina to 10 cm . long and broad, membranaceous, concolorous; upper surface with numerous long appressed-pilose and smaller, deciduous, stellate-pilose hairs; lower surface stellate-hirsute; circumscription more or less 5 -angled; base cordate; lobes 3, divided almost to the base; lobes lanceolate and narrowed towards the base, coarsely crenate-serrate; lateral lobes often with a small minor lobe. Stipules linear-subulate, green, ca. 0.7 mm . wide at the base, acute, 3-4 mm . long. Flowers very numerous, aggregated into rather dense oblong panicles; pedicels flexuous, erect, 3-4 mm. long, accrescent in fruiting to 15 mm . Calyx 5 mm . long, campanulate, hirsute without, divided about halfway into lanceolate lobes about 2 mm . wide at the base. Corolla equaling the calyx, violaceous on drying, red in life (according to the collector). Androecium 3 mm . long; stamen-tube $2-2.5 \mathrm{~mm}$. long, cylindric, slightly dilated towards the base, 0.5 mm . thick at the apex, ca. 1 mm . thick at the base, with sparse, short, rigid, pilose hairs below the middle. Anthers ten. Ovary glabrous, conical. Styles ca. 3 mm . long, divided to the middle; stigmas capitate, papillose. Carpels five, truncate at the base, ovoid-trigonous, 3.5 mm . long; dorsum flattened and briefly hirsute; margins somewhat muricate; aristae 2 , slender, customarily divergent, 12-14 mm. long, violaceous, with minute, yellowish, lax, retrorse hairs. Seed castaneous, orbicular, flattened (not mature), 2 mm . in diameter.

TYPE: Asplund 6797, June 1939, Ecuador, Prov. Chimborazo, Alausi.

Alt. 2300 m. (Herb. Regnell., Stockholm.)
distribution: Known only from the type.
I have seen no material of this species, but it is obvious from the description that it is close to S. rupo as that species is understood here, differing from it chiefly in the length of the aristae, the sparseness of the pubescence of the stamen column, and the shape of the leaves. With additional material, it may prove to be no more than a variety.
20. Sida rupo Ulbr., Engl. Bot. Jahrb. 54, Bbl. 117: 75. 1916.

Annual herb, few-branched, erect, 5-12 dm. high. Stems 10 mm . thick at the base, terete, with long-pilose patent hairs; the younger portions subtomentose and hirsute. Stipules not seen. Petioles $4-10$ cm . long, longer than the leaves; pubescence like that of the stems. Leaves deeply 5-7-lobed, $4-5$ to 8 cm . long, almost equally broad; lobes ovate, acute or acuminate, narrowing towards the base; the margins irregularly subcrenate-serrate; both surfaces sparsely pubescent, with simple and stellate hairs; young leaves subtomentose; nerves 5-7, prominent on both surfaces. Flowers in the upper axils and terminating the branches, forming lax panicles; pedicels $2-7 \mathrm{~mm}$. long, articulated $1-3 \mathrm{~mm}$. below the calyx, elongating to as much as 14 mm . after anthesis, fulvid-tomentose and sparsely villous. Calyx campanulate, ca. 5 mm . long, divided almost halfway into ovate-lanceolate lobes; fuscidtomentose and villous on the outside. Corolla purple, campanulate or cylindric; petals obovate, glabrous, $6-8 \mathrm{~mm}$. long, obtuse. Sta-men-tube conical, almost 3 mm . high, rather densely stellate-pilose, ca. 1.5 mm . long. Anthers ca. 10, ovoid, pale yellow. Ovary subconoidglobose, glabrous, subangulate. Styles five, white, 4 mm . long, 1.5 mm . free, filiform; stigmas capitate, small, glabrous. Fruiting calyx cupuliform, enfolding the fruit. Carpels five, obliquely pyriform, ca. 3-4 mm . high, 2 mm . thick, glabrous, brown, rugulose-loriform, the apex with 2 aristae ca. 5 mm . long, yellow, armed with retrorse pilose hairs. Seeds obliquely ovoid, ca. 2.5 mm . high, 2 mm . thick, black, verruculose, glabrous, pulverulent at the base; the funicle indurate.

TYPE: Weberbauer 5392, May 1910, between Pampano and Huaytara, on the Río Huaytara, ca. 50 miles inland from Pisco, Peru. On stony slopes, $17-1800 \mathrm{~m}$. (B).
distribution: Known only from the type.
No material which matches the description of this species has been seen. Ulbrich listed two collections, Weberbauer 5392 and 5247. Examination of several sheets of the latter number shows
clearly that they cannot belong to the species as described, since they have $7-10$ carpels, rather than 5 , and a carpel number of either 5 or $7-10$ in the same species is without parellel in the genus. The specimens match S. jatrophoides well in all other particulars and are referred here to that species. If Weberbauer 5392 has 5 carpels as described, it alone should be considered the type.

## 21. Sida lomageiton Ulbr., Engl. Bot. Jahrb. 54, Bbl. 117: 73. 1916.

Annual erect herb. Stems terete, simple or few-branched, hirsute, with spreading or retrorse bristles, double-coated above, the longer to 1.5 mm . long, stiff. Stipules linear-lanceolate, $1.5-2 \mathrm{~mm}$. long, hirsute, deciduous. Petioles $0.7-3 \mathrm{~cm}$. long, ca. 0.5 mm . diam., hirsute and tomentose, shorter than the blades. Leaves broadly subcordate in circumscription, 3 -lobed, to 5 cm . long and wide, lobed halfway; lobes ovate-acute, irregularly subcrenate-serrate; nerves 5 , palmate from very near the base, inconspicuous above, prominent beneath; the upper surface with scattered single and fewer few-rayed stellate hairs; the under surface densely covered with mostly stellate hairs, many of them 3 -rayed, golden; the veins with dense setaceous hairs. Flowers subpaniculate, axillary and in shortened branches, appearing subglomerate when young; pedicels $2-5 \mathrm{~mm}$. long, elongating after anthesis to 10 mm . or longer; articulated ca. 2 mm . below the calyx; pubescence like that of the stem. Calyx campanulate, 6 mm . long, divided halfway into acute, ovatelanceolate lobes ca. 3 mm . long, 2 mm . wide at the base, three-nerved, densely pubescent, with branched and single hairs; accrescent, but not inflated in fruit, glabrous within. Petals $4-5 \mathrm{~mm}$. long, ca. 2.5 mm . wide, as long as the calyx, obovate-subspatulate, purple, obtuse; apex clothed on the outside with large, scattered, stellate hairs. Stamen-tube subcylindric, glabrous, conically dilated towards the base, ca. 3 mm . high, whitish; filaments 5, very short. Anthers five, ovoid, yellowish, not dotted, 0.5 mm . long and wide. Ovary obpyriform, subangulate, glabrous. Styles five, $3.5-4 \mathrm{~mm}$. long, white, the upper 3 mm . free; stigmas depressed-capitate, glabrous, yellow. Fruiting calyx only slightly enlarged, enfolding the fruit except the aristae. Carpels "subclavatepyriform", glabrous, ca. 4.5 mm . long; the apex divided into two corniculate aristae ca. 4 mm . long; these divergent, attenuate, retrohispid; lateral walls firmly adherent to the seed, verruculate; margins strongly transverse-rugose. Seeds filling the carpel except the apex, ca. 3 mm . high, 2 mm . radially, very short-pilose on the funicle, pulverulent, dark red-brown.

TYPE: Weberbauer 5240, Sept. 1909, Mt. San Augustin, nr. Lima, Peru. In the Loma formation, $300-400 \mathrm{~m}$.
distribution: Known only from the type-locality.
Ulbrich pointed out no distinguishing features between this and its nearest relative, S. oligandra of Bolivia, and in gross aspect there are few. The habital difference is very striking, however, and the leaf-shape of the isotype is rather distinct.

Peru: Weberbauer 5240, Lima, Mt. San Augustin, Loma formation, Sept. 26, 1909, flowers purple. (Photograph of TYPE, B: GH, F), (ISOTYPES: F, US, MO, GH).

## 22. Sida lomana Bruns, Mitteil. Inst. Bot. Hamburg 8: 1: 58, t. 9. 1929.

Annual herb, simple or few-branched, $30-50 \mathrm{~cm}$. tall. Stems terete, branching above, densely covered with a double coat of stellate and simple hairs, the latter 2 mm . long. Stipules persistent, subulate, linear, 5 mm . long, 1 mm . wide, pilose. Petioles $4-10 \mathrm{~cm}$. long, densely pilose, shorter than the blades. Leaves cordate in circumscription, deeply 3-5lobed, 10 cm . or more long, equally broad; the margins irregularly sub-crenate-serrate, 5-7-nerved, sparsely covered everywhere with simple hairs; lobes of about equal length, ovate, acute or acuminate, narrowed roward the base. Flowers crowded in the upper axils forming dense panicles; pedicels 2 cm . long, elongating after anthesis to 5 cm ., articulated near the apex, densely pilose. Calyx campanulate, 4 mm . long, accrescent after anthesis to 8 mm .; lobes 3 mm . long, 2 mm . wide at the base, one-nerved, hispid. Corolla pale purple, subcampanulate, ca. 6 mm . long; petals obovate, obtuse, 6 mm . long, 5 mm . wide, covered near and to the apex with scattered stellate hairs. Stamen-tube conoid, 5 mm . long, glabrous; filaments filiform, 1.5 mm . long. Anthers five, subglobose, 0.5 mm . long and wide. Ovary subglobose, glabrous. Styles five, white, ca. 4 mm . long, connate at the base; stigmas subcapitellate. Fruiting calyx accrescent around the fruit, but not inflated. Carpels five, obliquely pyriform, 5 mm . long and wide, glabrous, rugose, brown; the apex divided into two divergent and reflexed aristae ca. 14 mm . long (f. Bruns), $\{-6 \mathrm{~mm}$. on specimens cited; the basal portion of the aristae conoid, glabrous, 3 mm . long (f. Bruns), ca. 1 mm . on specimens; the terminal portion 11 mm . long ( f . Bruns), $3-5 \mathrm{~mm}$. on specimens; with yellow retrorse hairs. Seed ellipsoid, 2.5 mm . long.

SYNTYPES: Günther \& Buchtien 193, 1946, Nov., 1923, Posco, Peru; 194. Aug. 1923, Mejía, Peru; 194a, Mejía, Hacienda Challascapa, Peru, Oct., 1923 (Hamburg).
distribution: Known only from the cotype localities.

This species as described is very close to $S$. oligandra and $S$. lomageiton. Not having seen any authentic material, I must accept Bruns' statements that the aristae are ca. 14 mm . long although the figures he published to illustrate the species indicate a length of 5-6 mm. Cook \& Gilbert 49, collected in the same general area and matching the original description quite well in some respects, has the aristae about $5-6 \mathrm{~mm}$. long. Similarly, a photograph of one of the syntypes in the Hamburg herbarium (Günther \& Buchtien 194) shows the aristae on that specimen to be never longer than ca. 6 mm . In a number of other species, full development of the aristae is not reached until very late in the maturation of fruit, and this may be the explanation of the discrepancy in measurements noted here.

Peru: Cook \& Gilbert 49. Posco between Mollendo and Arequipa (is). Guentber \& Bucbitien 19f, Mejia, Lemas (photograph of ssixtppe. M: f).
> 23. Sida patuliloba R. E. Fries, K. Sv. Vets. Akad. Handl. ser. 3, 24, n. 2: 15, t. 1, ff. 4-6. 1947.

Erect annual herb from a slender, branching, woody root. Stems and branches terete, wrinkling longitudinally on drying, their indument of dense, soft, spreading, simple, white hairs and dense or scattered seta-ceous-stellate hairs to 1.5 mm . long. Stipules linear or linear-subulate, 2- -4 mm . long. Petioles ascendent, channeled adaxially, to 5 cm . long, those of the upper leaves shorter, their indument like that of the stem, often denser, occasionally on one surface only. Leaves cordate or trian-gular-cordate in circumscription, $2-8 \mathrm{~cm}$. long, and about as wide, concolorous or somewhat paler beneath, deeply three- or five-lobed; the lobes three-quarters or more the length of the leaf, obtuse to acute, narrowed towards the base, rather coarsely serrate; the lateral lobes of the younger leaves at nearly right angles to the midlobe; the upper surface with many, fine, nearly appressed, bifurcate or simple hirsute hairs pointing apically; the lower surface with many, fine, mostly 3 -rayed, stellate hairs, the rays whitish and nearly appressed; the base cordate; the nerves $5-7$, prominent beneath, yellowish, lightly impressed above. Calyx campanulate, densely hirsute, 3-4 mm. high, accrescent after anthesis to $7-9 \mathrm{~mm}$.; the lobes erect, lanceolate or long-triangular. $2.5-3 \mathrm{~mm}$. long, ca. 1 mm . wide at the base. Petals obovate, slightly oblique, often purple on drying, red in life, membranaceous, fine-nerved, with a tuft of stellate bristles on the outer portion of the margin exposed in bud, ca. 3.5 mm . long, $2.0-2.5 \mathrm{~mm}$. wide; the claw broad. Stamen-column $1.5-2 \mathrm{~mm}$. high, terete, pale, translucent, with five traces, glabrous; the lower portion markedly dilated over the apex of
the ovary; the petals inserted about halfway up the height of the ovary; the filaments less than 0.5 mm . long, reflexed. Anthers five, 0.4 mm ., pale yellow, not dotted; the valves reflexing in maturity. Styles five, 5 mm . long, ca. 4.5 mm . free; the stigmas capitate. Ovary pale brown, glabrous, five-beaked around the style-base. Carpels five, glabrous, subtrigonous, 3 mm . high; the dorsum tuberculate on the outer surface; the apex protracted into two brief, vertical, triangular wings each bearing a long, extrorse, tapered arista $4-5 \mathrm{~mm}$. long furnished with minute, retrorse, subulate, stiff hairs; lateral walls flat, pulverulent; dehiscence incomplete between the aristae; the walls firmly adherent to the seed elsewhere. Seed 3 mm . high, plump, dark reddish brown; the hilar depression deep; the entire surface with a thickly scattered, brownish, stellate pulverulence. Columella 2 mm . high, pale, usually flattened, not apparently winged.

TYPE: Asplund 11242, 30 May 1940, "Peru: Dep. Lima, Matucana, 2400 m. ü d. M." (R).
distribution: Near Huigra, Ecuador and Lima, Peru.
S. patuliloba is in many respects similar to S. lomageiton, and much of the material here cited was originally identified as that species. A study of a series of isotypes of S. lomageiton indicates that that species is quite distinct in a number of ways, the leaves being shallowly lobed, the lobes of different outline and toothing, while the slightly larger flowers are in crowded, heavily hirsure panicles rather than in the lax panicles of S. patuliloba. Further collections from the area around Lima, Peru, may show an intergradation of the characters here used to separate the two as species. Macbride and Featherstone 102 from Matucana, Peru, is a well-marked leaf-form with 5 distinct lobes to the leaf.

Ecuador: Rose 22414, vicinity of Huigra (us, GH, NY).
Peru: Lima: Macbride \& Featherstone 161, Matucana (GH, F, us). Pennell 14474, along Rio Chillon, near Viscas (NY, US, GH, F). Pennell 14597, Canta ( $\mathrm{F}, \mathrm{GH}$ ). Macbride \& Featberstone 102, Matucana (F, GH), Leaf form. La Libertad: López Miranda 392, Cerro Campana (us). Ayacucho: Killip \& Smith 23343, Huanta (Us).
24. Sida oligandra K. Schum., Mart. Fl. Bras. 13,

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\text { pt. 3: 321. } 1891 .
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Annual herbs (possibly perennial at times). Stems $7-40 \mathrm{dm}$. high, woody at the base in larger specimens, terete or slightly angled, indument of intermixed stellate and long-pilose hairs, becoming glabrescent. Petioles about as long as the leaves or less, $1.5-8 \mathrm{~cm}$. long, mostly $3-4 \mathrm{~cm}$. long. Stipules filiform, caducous, pilose, $4-7 \mathrm{~mm}$. long, ca. 0.4 mm . wide at the base. Leaves $3-5$-lobed, divided more than half-
way to the base, to 6 cm . long and wide on usual specimen; lower leaves (seldom found on specimens) much larger, to 13 cm . long and wide; lobes usually 5, variable, divided about halfway to the base to almost all the way, the latter especially in young upper leaves, lanceolate-oblong in outline, sometimes deltoid, occasionally narrowed towards the base, somewhat obtuse to acuminate. Flowers solitary in the axils of lower leaves or forming dense to lax panicles at the apices of branches; the degree of laxness of the panicle seemingly a furiction of age. Pedicels $1.5-2 \mathrm{~cm}$. long, elongating, after anthesis to 3 cm ., articulated ca. 2 mm . below the calyx; the articulation inconspicuous before anthesis, terete, pilose. Calyx campanulate, tomentose, $5-6 \mathrm{~mm}$. long before anthesis, divided halfway to the base into lancerlate-acute lobes; lobes; 3 -nerved, the marginal nerves confluent below the sinuses, but inconspicuous under the fairly dense tomentum of 5-6-rayed stellate hairs; the margins of the lobes clothed with stiff, tufted, 2-4-rayed, stellate hairs. Petals as long as the calyx, $5-6 \mathrm{~mm}$. long, 2.5 mm . wide, obovate, slightly oblique, glabrous at the base; the upper portion sprinkled with stellate hairs. Stamen-tube terete, glabrous, 3.5 mm . long; filaments ca. 0.5 mm . long. Anthers five, minute, 0.3 mm . diam. Ovary conical, 5 -peaked, glabrous or the beaks sometimes pilosulose. Styles five, 4 mm . long, 2.5 mm . free; stigmas subcapitellate. Fruiting calyx to 8 mm . long, accrescent but not inflated, enfolding the fruit except the aristae. Carpels five, $3-4 \mathrm{~mm}$. long, trigonous; the dorsum rotund, muriculate-verruculate; the apex prolonged into two divergent, reflexed, retrorsely pilose aristae, ca. 6 mm . long; base of the latter dilated. Seed ca. 2 mm . long and wide, tuberculate, dark brown, almost black, adhering to the lateral walls of the carpel. Columella slender, tapering very slightly, 3.5 mm . high; flanges not prominent.

Type: Mandon 818, near Mt. Sorata, Prov. Larecaja, Bolivia. "in sepibus et graminosis" (B).
distribution: Type locality only.
The name $S$. oligandra has bren used indiscriminately for any material of the section which was not of the extreme "jatrophoid" leaf-type or which had only 5 carpels. As far as I can judge from the scanty material in this section, it can be applied only to the type-material.

Bolivia: Mandon 818, Prov. Larecaja, near Sorata. (Photograph of TYPE, B: F, GH), (isotypes: $\mathbf{F}, \mathrm{GH}, \mathrm{NY} 2$ ).
VI. Section Pseudonapaea Gray, Mem. Am. Acad. 4: 23. 1849 (Pl. Fendler.).

Calyx terete ; flowers umbellate corymbose, white; leaves palmately divided; carpels gibbous, the rostrum ascendent.

As founded, the section was composed of two species, Sida hermaphrodita (L.) Rusby and S. Hulseana Torr. \& Gray. The latter species was referred to Abutilon as A. Hulseanum Torr. by Baker in his list of species excluded from Sida, although he nowhere treats that species in his synopsis of Abutilon. The section has no close affinities with any other in the genus, nor with Napaea save in habit. Type species: Sida hermaphrodita (L.) Rusby, the only species.
25. Sida hermaphrodita (L.) Rusby, Mem. Torrey Club 5: 223.1894.
Napaea hermaphrodita L., Sp. Pl. 1: 685. 1753.
Sida Napaea Cav., Diss. 5: 277, t. 132, f. 1. 1788.
Erect perennial herb. Stems few or single from a woody root, terete, $1-5 \mathrm{~m}$. high, glabrous or with scattered, small, stellate hairs. Stipules linear-lanceolate, deciduous, $7-9 \mathrm{~mm}$. long, densely short-stellatetomentose at the base, 3-nerved, erect or slightly spreading. Petioles terete or slightly channeled on the adaxial surface, $0.5-2 \mathrm{~mm}$. diam., to 8.5 cm . long, mostly glabrous. Leaves palmately (3-) 5 (-7)-lobed, $5-7$-nerved, broadly cordate in circumscription with a wide and shallow sinus, acute or acuminate, to 24 cm . in length; lobes to 18 cm . in length, coarsely incised-dentate. Inflorescense of axillary few- to manyflowered corymbs or terminal corymbose panicles, to 5.5 cm . long; peduncles terete, $15-30 \mathrm{~mm}$. long to point of branching, glabrous or with scattered stellate hairs, terete; pedicels $3-15 \mathrm{~mm}$. long, terete, inconspicuously articulated ca. 4 mm . or less below the calyx. Calyx shortcampanulate, terete, 5 mm . high, densely stellate-velutinous, without prominent veins, glabrous within; lobes erect, deltoid, acute, 1.5 mm . high, 2.5 mm . broad. Petals white, concave, obliquely obovate, obtuse, 8-9 mm . long, 5 mm . broad, occasionally retuse; claw moderately narrow, densely stellate-hirsute on both surfaces. Stamen-tube cylindrical above the ovary, 5 mm . long to level of first filaments, slightly 10 -ribbed; the lower two-thirds with scattered to dense, spreading, flattened (collapsed?), lanceolate, white hairs, with a few stellate hairs at the base of the column; filaments in several series, ca. $50,0.5-2 \mathrm{~mm}$. long, the lower longer, paired or single, slender, tapering. Anthers pale, not dotted, 0.5 mm . wide. Styles connate, or reflexing slightly after anthesis, 7 mm . long. 5 mm . free; stigmas subcapitellate or merely rounded papillose apices of the styles. Ovary short-pyriform, 1.5 mm . high, 2 mm . diam., filling the cavity, somewhat angulate, with stellate flattened hairs on the upper surface of the angles. Carpels 8-10, one-beaked from an upward prolongation of the rostrum becoming vertical in ripe-
ning; dorsum and beak subglabrous to moderately stellate-pubescent, the hairs with fine assurgent rays; base of rostrum hooked over the top of the columella; the entire carpel $6-7 \mathrm{~mm}$. high, 3 mm . radially, the beak 2.5 mm . high; lateral walls membranous, pulverulent, 3 mm . high, 2 mm . wide; dorsum thinning radially and downward; carpel dehiscent by the disintegration of the lateral walls. Seed plump, glabrous, red-brown; rostrum ascendent; hilar sinus shallow; funicle persistent, flattened at the hilum. Columella conical, truncate, flanged, ca. 3.5 mm . high, usually with the base of the style persistent.
type: Probably specimen from Hortus Cliffortianus or Hortus Upsaliensis. (Linn. Hb., 1753).
distribution: Lower Susquehanna R. Valley of Pennsylvania and Maryland, flats of the Potomac (escape?), valley of the Kanawha R. and tributaries, W. Va., and upper Eastern Tennessee. Cultivated as "River Mallow", escaping but apparently not persisting.

United States: Pennsylvania: Crauford. shores of the Susquehanna R., York Furnace, York Co. (Ny). Diffenbuiugh. Aug. 1861, hanks of Susquehanna, York Co. (F, GH). Durand, "Penns" (Ny). Durand, 1863, banks of the Schuylkill below Philadelphia (GH). Garber, banks of the Susquehanna, York Co. (Ny 2, mo 2, f). Palmer, 1883. on the Susquehanna R., Rockville, York Co. (Us, Ny). Porter, 2 Sept. 186.3. banks of the Susquehanna, opposite Safe Harbor, Lancaster Co. (wy, uc, GH). Porter: Sept. 1867. rocky bank of Susquehanna R., York Co. (us). Porter, 19 Sept. 1868, York Co. (us). Smith, Aug. 1905, York (UC). Collector unkliou'n, Lancaster (mo). Mariland: Killip 32667, Plummers Island. along river, Montgomery Co. ( GH ). Tatn all +55 f. Susquehanna R., 0.1 mile below Pennsylvania state line, Cecil Co. ( GH 2 2). W'ashington. D.C.: Chase 2533, istand in Potomac R. (F). Steele, 27 July 1896, flats of the Potomac R. (GH, mo, ny 2). Vase). 1887 (gh). West Virginia: Broun. "Kanawha Co. Court House" (GH). Ebj. Aug. 1890, Wild Cat. (мо 2). Holton, "Virginia" (wy). Millspuugh 016. Great Kanawha R., Kanawha Co., 1890 (Ny). Millspaugb, 1891 (wy). Millspoutgh, 1892, banks of the Great Kanawha R. from Nuttallburg to the mouth ( F ). Tosh 1158, in drain to New River 3 miles below McCreery, 15 miles east Beckley (UC). Collector wiknown, "Virginia" (photograph of specimen of Sida Napalea Cav., M: F, us). Tenxessee: Gattinger. June 1883. Cumberland Mts. near Kentucky line (us). Gattinger, July 1884. W'olf Creek near Hot Springs. Cocke Co. (us). Gattinger. July 1884, "upper east Tennessee" (Ny). Gattinger 14 July 1884 (Ny). Guttinger, July 1885, "upper cast Tennessee" ( GH ). Gattinger, "upper east 'Tennessee" ( GH ).

## VII. Section Hookeria Clement, sect. nov.

Calyx teres urceolatus nec accrescens, lobis patentibus aetate maturandi; epicalyx deest; folia palmatilobata; antherae 10-20; carpella mutica, indehiscentia; flores singuli in axilla vel bini raro plures ex pedunculis solitaribus vel pluribus.

Calyx terete, urceolate, not accrescent; lobes patent in fruit, epicalyx
none. Leaves palmately lobed. Arithers 10-20. Carpels muticous, indehiscent. Flowers axillary solitary or paired (rarely several) from solitary or several peduncles. Two species. Eastern Africa from Ethiopia to Cape of Good Hope, and southwestern Australia.

The species of this section have customarily been placed in section Sida with other species having palmately lobed leaves. The combination of this character with those of the fruit and inflorescence is sufficiently striking and unlike that found in any other section of the genus to warrant the recognition of a distinct section, which is most closely allied to section Psendonapaea of eastern North America. Type species: Sida Hookeriana Miq. ex Lehm.

## Key to the Species

Annual herbs $3-6 \mathrm{dm}$. high; antlers $10-15$; funicle lateral on the upper surface of the seed; Australian
26. S. Hookeriana.

Perennial subshrubs 6-12 dm. high; anthers 20 ; funicle centered on the upper surface of the seed; African
27. S. ternata.
26. Sida Hookeriana Miquel ex Lehmann, P1. Preiss.

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\text { 1: } 242.1844 .
$$

S. leiophloia Miq. ex Lehm., op. cit. 241.
S. rupestris Miq. ex Lehm., op cit. 242.

Erect or decumbent annual herbs, 3-6 dm. high, essentially glabrous or with scattered small hairs, the younger parts sometimes stellatepubescent. Stems single or few from the base, simple or weakly branching. Leaves cordate in circumscription, $3-3.5 \mathrm{~cm}$. long, about as broac, deeply divided into 3 or 5 ovate or cuneate deeply toothed lobes; upper surface with few, scattered, stellate hairs; lower surface glabrous; margits with short, subulate, contour hairs. Stipules lanceolate, $3-3.5 \mathrm{~mm}$. long, 1 mm . wide, 1 -nerved, erect, herbaceous, becoming patent in age, strilw-colored, at length deciduous. Petioles terete, $1.5-5.6 \mathrm{~cm}$. long, ca. 0.5 mm . diam. Flowers solitary or several from the axils, or 2 or more from one peduncle, the point of branching articulated and marked by a pair of straw-colored stipular bracts; peduncles terere, 2-4 cm . long, filiform, erect; pedicels when solitary to 4.8 cm . long, when paired from a peduncle, one $1.5-3.5 \mathrm{~cm}$. long, the other $0.2-1.0 \mathrm{~cm}$. long. Calyx campanulate or somewhat urceolate in flower, 10 -veined, $5-6.5$ mm . high, pulverulent within; lobes $3-4 \mathrm{~mm}$. long, 3 mm . wide, ovate or broadly larceolate, aclite 10 acuminate, slightly accrescent after anthesis; intramarginal veins of the lobes abruptly corifluent below the sinus, the midvein prominent to the tip; lobes patert in fruit, becoming
straw-colored, the veins becoming more prominent. Petals white, 6 mm . long, 3 mm . wide, obovate, glabrous except for a slight tuft at the base of the claw, inrolling after anthesis; claws narrow, separated from one another at the point of insertion on the column. Stamen-tube $2-2.5$ mm . long from base of claw to filaments, glabrous, or sparsely hirtellous, subterete, pale; filaments very short. Anthers $10-15,0.5 \mathrm{~mm}$. wide when open, ca. 3 mm . long. Styles 3 mm . long, 0.5 mm . free, recurved at anthesis; stigmas capitellate. Ovary 0.5 mm . high, filling the cavity, 10 -angled, glabrous. Carpels ten, ca. 2 mm . high and wide, forming a flat-topped fruit with an annular depression sunk in the hilar depressions of the seeds, muticous, rostellate; upper dorsum thick, the outer portion thinning; lateral walls very thin, pulverulent, cancellate or rugulose, becoming rugose along the outer margins; all but the upper dorsum firmly or loosely adherent to the seed. Seed strongly trigonous, the outer surface invaginated, $1.5-2 \mathrm{~mm}$. high and wide, dark brown; funicle lateral. Columella ca. 2 mm . high, truncate-conical; midveins of the carpels often persistent from its base.

TYPE: Preiss 1894, Rottnest Island, near Perth, Western Australia (Hamburg).
distribution: Extreme southwestern Australia.
Australia: Western Australia: Andreu's 13, Darlington, 15 mi . e. of Perth. (к). R. Brown 5109, without locality (k). Collies, Swan River (K). Drummond, Swan River (к). Koch 1820, Wooruloo (k). Koch 1890, Lowden, Warren District (GH). Koch 1986, Lowden (k). Oldfield, Vasse River ( $\mathbf{x}, 2$ ). Preiss 1894, Rottnest Island (isotype, mo).

## 27. Sida ternata L. f., Suppl. 307. 1781.

## S. triloba Cav., Diss. 1: 11, t. 1, f. 11. 1785.

S. permutata Hochst. ex A. Rich., Tent. Fl. Abyss. 1: 67. 1847.

Subshrubs 6-12 dm. high from a woody branching root. Stems few, slender, woody at the base, subsimple or branching. Leaves concolorous, palmately 3 -lobed, rarely 5 -lobed, $3-7 \mathrm{~cm}$. long, $3.5-6 \mathrm{~cm}$. broad, extremely variable in form, cordate in circumscription; basal sinus broadly U-shaped; nerves 5-7; margins serrate to crenate, divided from a third to almost to the base, depth of lobing usually greater on the upper leaves; lobes deltoid to lanceolate, obtuse to acuminate, the central lobe longest, $3-7 \mathrm{~cm}$. long, the lateral lobes $2.5-5 \mathrm{~cm}$. long. Petioles $1.5-4.0(-7.0) \mathrm{mm}$. long, glabrescent, channeled adaxially, occasionally deflexed near the apex, ca. 1 mm . in diameter. Stipules lanceolate, $4-5 \mathrm{~mm}$. long, 1 mm . broad, 3-5-nerved, herbaceous, thin, tardily deciduous, usually glabrous. Pedicels solitary and axillary, filiform, $15-55 \mathrm{~mm}$. long, not articulated, glabrous or occasionally finely stellate-hairy when young, arching at the tip in flower. Calyx campa-
nulate, terete, $5.5-8 \mathrm{~mm}$. long, glabrous or sparsely puberulent, glabrous within, dull; lobes ovate or acuminate, $2.5-5 \mathrm{~mm}$. broad, $3.5-5$ mm . long, erect in flower, patent in fruit, 3-nerved, the adjacent intramarginal nerves confluent below the sinus. Petals pale yellow or whitish, barely exceeding the calyx, $5-6 \mathrm{~mm}$. long, $3-5 \mathrm{~mm}$. wide, suborbicular to oblong, rarely retuse; claw narrow, rarely hirtellous. Stamen-tube terete, glabrous, $1.5-2 \mathrm{~mm}$. high from base of claw to filaments; filaments paired at the base, ca. 1 mm . long, slender. Anthers 20, not dotted, 1 mm . wide when open. Ovary subglobose, glabrous, ca. 1.5 mm . in diameter, occupying three-fourths of the cavity. Styles slender, 3.54.5 mm . long, $2-2.5 \mathrm{~mm}$. free, recurving in anthesis; stigmas dark, capitellate. Carpels (7-) 8-10 (-13), muticous, glabrous, rostrate, forming a flat-topped fruit $3-3.5 \mathrm{~mm}$. high, $3.5-4 \mathrm{~mm}$. in radius; dorsum thick above, straw-colored, becoming light brown in age, thinning from the distal margin to the base, marked with a fine median line; lateral walls membranous, pulverulent, rarely partly adherent to the seed; dehiscent by disintegration of the thinner walls. Seed glabrous, dark dull brown; funicle flattened; hilar sinus shallow. Columella coarsely ribbed, truncate, $1.5-2 \mathrm{~mm}$. high, pale.
type: Thunberg, Cape of Good Hope, (Linn. Herb.).
distribution: Upper reaches of the Nile in Ethiopia; Sumaliland, Kenya, Uganda, Tanganyika, Rhodesia, to Cape of Good Hope in Union of South Africa.

The name revived for this species was known to Cavanilles at the time he described S. triloba, for he indicated in the description that his might be the same plant as $S$. ternata, if by "foliis ternatis" the younger Linnaeus meant the type of division illustrated by fig. 64 of the elder Linnacus' Philosophia Botanica (p. 290), but a different plant if he meant that shown by fig. 65, in which the lobes are divided all the way to the base and petiolate. Since the lobes, though often divided to the base, are never petiolate, most authors have taken up Cavanilles' names, although Thunberg listed both species in his Flora Capensis. I have restored the name given by Linnaeus f. despite the brevity of his description: "foliis ternatis, foliolis serratis. Habitat in Cap. bonae spei. Thunb." since it unmistakably applies to this species.

Specimens distributed by Hochstetter from Schimper's Abyssinian collection bore label names, one of which was validated by A. Richard in his Tent. Fl. Abyss. as S. permutata Hochst. ex A. Rich., with the other in synonymy. I can find no constant
characters to separate these plants of Ethiopia from S. ternata. They appear to be only the terminals in a series of very slight geographic variations, having a greater number of 5 -lobed leaves, the carpels somewhat more numerous, and the petals (reportedly) rose-purple.

The specimens cited by Richard for S. permutata were Schimper 1911, Schimper 7, and Dillon \& Petit (without number). I have seen examples of the first two, and Schimper 7 fits the description, whereas Schimper 1911 (GH) is a Pavonia. Apparently Schimper 364, the type no. of Pavonia Kraussiana Hochst. (fide Ulbrich in his Monograph of the African species of Pavonia, p. 126), became mixed with Schimper 1911 in some cases, for Ulbrich in the same work, (p. 180) refers Schimper 364 to $S$. triloba. To complete the confusion, Schimper 364 was distributed with the label name Urena mollis. The Kew specimen of Schimper 1911 bears a note in Hochreutiner's hand that the labels should be exchanged, and a note in another hand that they had been, although what the original label was is not stated.

There is a form of this species in Kenya which has 9-13 carpels, the walls of which are rugulose and the seeds with a deeper hilar sinus. Since I know it only from one specimen (Curtis 721, 10 Jul. 1932, "Buffalo Country", Kenya Colony, British East Africa, in GH), I refrain from naming it. In all other characters, it comes within the range of variation of the species.

Ethiopia: Gilletl 5163. Galla Pass (k). Schimper 7. Tut-Adegi, Scholoda, (UC, K, GH). Schimper 401, Scholoda (US, UC). Schimper 1911. Scholoda, 4 Oct. 1842 (k). Roth 101, Ankober (k).

Eritrea: Schueinfurth \& Riva 911, Gorge de Degorra (k).
Kenya: Bally 7699, Chyulu South (K). Curtis 721. in Buffalo country (GH). Fries \& Fries 695, "occid.: in siloc montana, loco aperto, 2300 m ." (к). Hill 649, upper Kipkarren (k). van Someren 2458. Nairobi Dist. (k). W'hyte. Oct. 1898, Eldama ravine (k).

Uganda: Maitland 1002. (к). Chandler-Hau'nk 2610. Kirwa Kigezi (x). Rogers 353, Kigezi District, edge of Lake Chibapi (к).

Tanganyika: Burtt 4364. Olomoti Volcano, gorge of Munge River (x).
South Africa: Transvaal: Rogers 23817. Irene (us). Gulfin 994, Rimer's Creek, Barberton (k). Natal: Rogers 504. Port Shepstone (k). Orange Free State: Port 662, Dist. Kroonstad (gh, us). Cape Province: Conper 351. British Kaffraria (к). Cooper 563, Dist. Drege 7331. Somerset East Div. (к). Gill. Fish River (k). Kuntze 94 (к). Long 978. Addo Heights (k). MacOu:an 301. near Grahamstown (GH 2). Prior, Nov. 1847, on Uitenhage Karroo (k). Thode A2601, Enon, (k).
VIII. Section Steninda Grisebach, Fl. Brit. W. Ind. 76. 1859.

Calyx-tube subterete; carpels briefly two-beaked, indehiscent; flowers in terminal corymbs; leaves entire, linear to lanceolate. One species: S. linifolia Cav.

The section was founded by Grisebach (1859) for the single species in the following words, "Calyx 5 -fid, tube subterete. Carpids bluntish, indehiscent. - Flowers in terminal corymbs. Leaves quite entire." Schumann (1890) maintained the section as founded, but Baker (1892) changed the concept completely, omitting the essential characteristics "leaves quite entire" and "flowers in terminal corymbs". In their place, he established a series of negative criteria: "calyx non angulatus post anthesin non accrescens.... carpella indehiscentia vel fere indehiscentia.... nunquam aristata.... bracteolae O.... flores petiolis haud adnati." The result of this series of exclusions was that the section, sensu Baker, was now available for any number of species otherwise difficult to place in the genus. While he did not take full advantage of the opportunity thus afforded, he did include ten species from Australia and one from New Caledonia. None of these has the leaves entire, eight have the flowers solitary or subsolitary, and all have only generic affinity with S. linifolia.

The closest species to $S$. linifolia in the morphology of its flowers and carpels seems to be S. blepharoprion Ulbr. in which, however, the flowers are strictly solitary from the upper leafaxils and the calyx strongly angulate. It is most satisfactorily placed in section Sida.

## 28. Sida linifolia Cav., Diss. 1: 14, t. 2, f. 1. 1785.

Annual or biennial herb, erect from a strong fibrous root-system. Stems terete, $2-10 \mathrm{dm}$. high, $2-5 \mathrm{~mm}$. diam. at the base, few-to manybranched; branches virgate; entire stem covered with simple, forked or stellate hairs, glabrescent, hispidulous or long-villous. Stipules linear or narrowly lanceolate, $4-7 \mathrm{~mm}$. long, $0.5-1.0 \mathrm{~mm}$. wide, entire or serrulate at the bases of the regularly spaced, patent or subpatent, pilose hairs, these present also on the prominent midnerve. Petioles $3-6 \mathrm{~mm}$. long, flattened adaxially, sparsely pilose. Leaves (2-) 4-6 (-11) cm. long, (2-) 3-10 (-15) mm. wide, linear to lanceolate, long-acuminate, usually broader below the middle, minutely mucronulate, quite entire, rounded or truncate at the base or rarely narrowly cordate, 3nerved, the lateral nerves marginal, joined by the secondary veins from
the midnerve; indument like that of the stem, usually denser beneath, appressed or partially so. Inflorescence of 8-12 (-20)-flowered corymbs, the upper ones usually congested, the lower laxer; occasionally solitary from the upper axils in addition. Peduncles terete, $6-12 \mathrm{~cm}$. long, patent-pilose, articulated $2-3 \mathrm{~mm}$. below the calyx, appressedpilose above the articulation; bracts subulate, acute, caducous. Calyx campanulate, subterete, ten-nerved, $4.8-7.0 \mathrm{~mm}$. high; indument hirsute; lobes erect in flower, partly enclosing the fruit, triangular, acute, 2- 4 mm . high, $2.5-3 \mathrm{~mm}$. broad at the base, with a prominent midnerve; interior glabrous except the margins, straw-colored in fruit, shining. Petals $8-15 \mathrm{~mm}$. long, 4-5 mm. wide, obovate, white or yellow; base reddish, purple, or nearly black; quite glabrous. Stamentube subterete, ca. 2 mm . long, glabrous near the base, becoming histricine near the summit, the hairs subulate, hyaline, simple; base broadly dilated; filaments slender, paired, $0.5-1.0 \mathrm{~mm}$. long, pale. Anthers numerous, sinall, 0.5 mm . long or less, pale, not dotted. Styles $5-6 \mathrm{~mm}$. long, ca. 4 mm . free, slender, reddish; stigmas capitellate, dark red, minutely hispidulous. Ovary 1 mm . diam., $0.6-0.8 \mathrm{~mm}$. high, somewhat lobed; upper surface with an annular depression; apex multidenticulate. Carpeis five to nine, $2.5-3.5 \mathrm{~mm}$. high, $1.6-2.0 \mathrm{~mm}$. radially, rotund-trigonous, dull brownish black, papyraceous; apex with two triangular, blunt, divergent beaks; lateral walls flat, very thin, fragmenting in maturity, the seed thus escaping, cinereous-pulverulent. Seed 2 mm . high, ca. 1.7 mm . radially, dark brown, dull, the sides subimpressed, the hilar depression rather deep. Columella 2 mm . high, persistent, stellate in section, tapering slightly, pale.

## Key to the Varieties

Stems glabrescent to hispidulous; leaves linear to narrowly lanceolate, $30-110$ mm . long, $2-12 \mathrm{~mm}$. wide; petals $8.0-9.2 \mathrm{~mm}$. long; calyx-lobes $2.0-2.5$ mm . high; carpels 5-9

28a. S. linifolia var. linifolia.
Stems and rest of plant villous; leaves $25-60 \mathrm{~mm}$. long, - -15 mm . wide. lower ones broadly lanceolate; petals ca. 15 mm . long; calyx lobes ca. 4.0 mm . high; carpels usually 6

28b. S.linifolia var. brevis.
28a. Sida linifolia var. linifolia.
S. graminifolia A. Rich., Act. Soc. Hist. Nat. Paris 1: 111. 1792.
S. viminea Fisch. ex Link, Enum. Hort. Berol. 2: 202. 1822.
S. campi Vell., Fl. Flum. 278. 1825.
S. linearifolia Thonn. in Schum. \& Thonn., Beskr. Guin. Pl. 2: 77 (303). 1827.
S. linifolia var. angustifolia St. Hil., Fl. Bras. Merid. 1: 181. 1827.
S. angustissima Miq., Stirp. Surin. Sel. 102. 1850, non St. Hil.
S. longifolia Brandegee, Zoë 5: 212. 1905.
S. linifolia f. flaviflora Chod. \& Hass.; Bull. Herb. Boiss. ser. 2, 5: 292. 1905.
S. Fiebrigii Ulbr., Engl. Bot. Jahrb. 54, Bbl. 117: 72. 1916.
tYpe: J. de Jussieu, "In insula Caienae \& in Peru." (p).
distribution: Antilles; Mexico to Brasil, Paraguay and Bolivia; Sierra Leone to nothern Angola and Tanganyika; Fiji.

28b. Sida linifolia var. brevis (Hochr.) Clement, comb. nov.
S. Hassleri Hochr., Ann. Cons. \& Jard. Bot. Gen. 6: 33. 1902.
S. Hassleri var. brevis Hochr., l.c.
S. linifolia var. Hassleri (Hochr.) Hassl., Add. Pl. Hassl. 15. 1917.
type: Hassler 4728. "near Igatimi", Sierra de Maracayu, Paraguay (G).
distribution: Northeastern Paraguay.
On the basis of two Hassler collections from Paraguay, Hochreutiner described S. Hassleri and its variety brevis. Hassler later considered these as no more than specimens of a rather broadleaved variety of S. linifolia which he called S. linifolia var. Hassleri (Hochr.) Hassler. The earliest available varietal name in S. linifolia for this taxon is brevis, however, and I have made the combination here.

This variety, found at the southern limit of the species, is connected to the typical by such intermediate specimens as Jörgensen 4586 and Fiebrig 572, both of Paraguay and the latter the type-collection of S. Fiebrigii Ulbrich. The characters given by Ulbrich to distinguish it from S. linifolia var. brevis (which he recognized as $S$. Hassleri) merely place it as intermediate between that and the typical variety. His statement that the calyx-lobes are only 2 mm . high is not confirmed by actual measurements on the isotypes or on the photograph of the type.

The species is remarkably consistent in the remainder of its very extensive range, even the African material being very little different from that of eastern South America. Schumann and Arechavaleta have stated that the species occurs in Uruguay and was collected there by Tweedie. No material from that country was known to Rodrigo (1944), nor have I seen any. The only Tweedie specimen I have seen is from Rio de Janeiro, Brasil.

The citation of the author of the species as "Cavanilles" rather than "Jussieu" is the result of a survey of the general practice of the former in the Dissertationes. He almost invariably cited the person who loaned him the material upon which he described his new species, and the citation is an indication of the typespecimen rather than of authorship. Cavanilles' practice was to use the herbarium or field notes attached to specimens in framing his descriptions, but these, even when quoted and attributed, as in the case of the specimen loaned by de Jussieu, are never the first and decisive paragraph, which is always Cavanilles' own description and is the one on which the species rests.

## 28a. Sida linifolia var. linifolia.

(About one-half of the New W'orld material I have seen is listed here. Because of the great uniformity of the species throughout most of its range. only enough specimens to define the distribution have been listed for Mexico, Central America, Colombia and Venezuela).

Mexico: Chapas: Matud. 3777 . Aguacate Palenque, (ny, f, gh, mo). Guerrero: Hinton 11.397. Valtecitos. Dist. Montes de Oca (ny, gh). Palmer 279, Acapulco and vicinity (u's). Jaliscio: Pringle. 6 Sept. 1893. Guadalajara (mexu). Pringle 54 . Tequila (mext 2. ght). Mexico: Hinton 2239. Ixtapan, Dist. of Temascaltepec (ny, us, gil). Sinalon: Debes.a 1576. Cuncordia (us). Montes \& Sollizal gil. San Ignacio (us). Sonora: Gentr) 29.35. Alamos, Rio Fuerte (F, gh, mo). Vera Crez: Mutudıı 1.fiz. Cuitláhuac (mo). Mell. 28 Nov. 1928. Minatitlán (us). Purpus 1947, Zacuapan (UC, NY, GH, us, Mo).

Guatemala: He)de \& Iux. 39+9. Chiapas. Dept. Santa Rosa (mo. us, ny, Gh). Standle) 24519. vicinity of Quirigua Dept. de Izabal (Gh, ny, us). Standley 74930. Dept. Jutiapa. vicinity of Jutiapa (F). Stundle; 76798. Dept. Jalapa, northeast of Jalapa (F). Sturdley 80471. Dept. Guatemala, near Fiscal (F). Steyermark 30610. Chiquimula. Volcan Ipala, near Amatillo (F). Steyermark 42194. Dept. Zacapa, between Monte Grande and Santa Rosalia (F)

British Honduras: O'Neill 8770. Sibun Road, 9 miles southwest of Belize ( GH ). Peck 24.3. Pine ridge near Manatee Lagoon (GH). Lundell 11. Honey Camp. Orange Walk (f). Gentle 1362. Maskall Pine Ridge (mo. us, ny, f).

Honduras: Rodriguez 3695. Las Mesas. Dept. Morazán (f). Thieme 5142. San Pedro Sula, Dept. Santa Barbara (us, ch). W'illiams \& Molina R. 10242, 3 kilometers west of Guinope. Dept. El Paraiso (UC). Yuncker. Dausson \& Youse 6034. near Siguatepeque. Dept. of Comayagua (Ny. us. GH. Mo. F)

El Salvador: Calderón 978. near Chalchuapa (Ny, us. GH). Calderón 2472. El Roblar, Dept. Chalatenango (Ny, us, F). Standles 20423, vicinity of Santa Ana. Dept. de Santa Ana (us, GH ).

Costa Rica: Brener 14586. "Carrillosc. de Poas" (F). Brener 17302. "entre los ríos Pilas y Tacaros" (F). Ridley 7098. near Saymateo (US).

Panama: Davidson 752. Boquete. Chiriquí Prov. (F). Erlanson 288. San José Island. Pearl Archipelago (us). Pittier 3595. Taboga Island. Gulf of Panama
(us). Pitticr 4590, near Cheop, Prov, of Panama (us, Ny). Standley 26298, near Punta Paitilla, Prov. of Panama (us). Standley 26320. Ancon Hill, Canal Zone (us). Standley 28177, Rio Tapia, Prov. of Panama (us). Siundle, 29161, between Fort Clayton and Corozal (us).

Cuba: Shafer 11707. Prov, of Pinar del Río, Los Palacios to Herradura (ny, mo, us). B.iker 2110 . Herradura, Prow. Habana (pom). Combs 595, Prov. of Santa Clara, Dist. of Cienfuegos (N1, Mo, GiI). Curliss 279. near Nueva Gerona, Isla de Pinos (Ny, Mo, chi, us). Ekm.,in 995s. Prov. Oriente. Sierra de Vije, on the Lojo trail (Ny). Shafer 5.\{2. Sicrra Cuhitas to Santa Rosa, Camagüey Prov. (Ny, GH, us). Shafer 10.i21. Prov, of Pinat del Rio. palm-barrens west of Guane (F, GH, Nr, mo, us). Jamaica: IL.umi 12250. upper Clarendon (mo, ny). Haiti: Ekm.an H. 9417. St. Michel de 1Halaye (us). Holdridge 1862, La Victoire (us). Leomuld $86 \neq$ f. vicinity of Dondon. Dept. du Nord (us, NY, GH). Dominican Republic: Abbot 676. Pimentel. Prov. Pacificador (us). Allard 13066. vicinity of Piedra Blanca, Prox, of La Vega (us). Jiménez 1055, El Rubio, Prov. of Santiago (U'S). I'aleur 510. Dist. of Sahancta, Prov. of Monte Cristy (mo 2, us, F). Martinique: Stebl' +72 . Muntc-Bello. Petit Bourg (nx). Tobago: Broadway 2052. "Botanic Station, wild" (an). Eggers 5474. near Bacolet (us). Trinidad: Broaduaj. 12 Junc 1908, St. Margarcte (N1). Brobdu:ay 2565. Yoco, roadside to Galera Point (mo 2).

Colombia: Daniel 4170. Medellin. Antioquia (us). Killip 35598, Dept. El Valle, Cisneros (us). Killip \& Smith 16304, Dept. Santander, northwest of Bucaramanga (GH, US). Pennell $3.66 \%$ Dept. of Tolima. west of San Lorenzo (mo, Gif, US, Ni). Sneidern 2+5. Dist. Cauca, El Tambo (us).

Venezuela: Killip 87581. "Bolivar: La Paragua" (us) Pittier 12485, Mesa de El Sombrero, Guarico (us. NY). Pillicr 11982. Carabobo, Carabobo (us). Pittier 2818. Federal Dist. around Caracas (Gif. Ny). Pittier 1.4529. State of Anzoátegui, Pariaguán (us).

British Guiana: Icnman 22. Ipelemanta, Arapoo R. (us). Sanduith 1227, Mazaruni Station (NY). Sibomburgk 131. near Anna-y (US). Dutch Guiana: Hoitman 816 (cin). French Guiana: Biodduci 191. vicinity of Cayenne (NY, US, GH). Melinon 217, Maroni, 1876 (NY, F, US).

Brasil: Baticto 80-5. Capitão Eduardo. Belo Horizonte (f). Barreto 8056, Lagoa Santa. Santa Luzia (F). Curzalbu 652. Campinas, São Paulo (GH). Dahlgren. Ceará (F). Drouet 2036. Belém. Patá (us). Drouet 2216. Fortaleza (mo. F, Gh. Ny, u's). Huébhe 286. Butantan, São Paulo (Ny). Mexia 5594. Corinto. Minas Geräes (us, Mo. Gil. Ny, F). Monteino C. 1002, State of Pará, Belém. Souza (u's. F). Pickel. Sept. 1931. Tapera. Pernambuco (ds, us, gh, f). Pebl 317. Mt. Corcovada (gir, f). Smith. L. B. 7108 , Araruama. Rio de Janeiro (us). Tate 128. Liman (NY). Tueedie 131. Rio de Janciro (GH).

Paraguay: Fielirig 572. Cordillera de Altos (photograph of TYPE of $S$. Fiebrigii, b: gif, F, US). (isotypes, (GH, F). Fiebrig 4721, "N. Paraguay. Zwischen Rio Apa und Rio Aquidaban" (cir). Jörgentes - 4586 , Santa Barbara (Ny, us, DS). Peru: W'illiam 7:93. San Roque. Dept. San Martín (f). IF'illiams 5847. Dept. San Martín near Tarapoto (f, us). Bolivia: Círdenas 2699. Reg. Oriente, Río Grande (F). Steinbach 5331. Buena Vista, Prov. Sara, Dept. Santa Cruz. (GH, F) Rusby 1314, San Pedro, vicinity Reyes (Ny).

Sierra Leone: Broun \& Broun 6.4. Freetown (us). Deighton 247. Freetown
(к). Glanwille 145, Makump (к). Thomas 3804, Bumbuna (к). Gold Coast: Brou'n 380. Accra (к). Kitson 1166, Tafo (к). Togo: W'arnecke 267, rear Lomé (к). Nigeria: Lely 279. Naraguat (к). Neuberry 98, Ibadan (к). Vogel, 1843, Secorra (к). French Equatorial Africa: Debeaux 186. Libreville, Gabon (к). Le Cestre 4218, Yalinga (Ht. Oubangui) (к). Angola: Monteiro, Jan. 1873, Boma (к). Fiji Islands: II'ilkes Exped., 1838-42, Ovalau (GH, us).

## 28b. Sida linifolia var. brevis.

Paraguay: Hassler 5738, "In altoplanitis Yeruti", Sierra de Maracayú. (Photograph of type of S. Hassleri var. genuina Hochr. G: F), (isotype, GH). Hassler 4728, near Igatimí, Sierra de Maracayú. (isotype of S. Hassleri var. bretis Hochr., GH). Jörgensen 4852. "in the campo, Estancia Primera (us).

## Literature Cited

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## News Names and Taxa

Hookeria, sect. nov.; Incanifolia, sect. nov.; Oligandrae, sect. nov.; Sida centuriata, sp. nov.; Sida ciliaris var. involucrata, stat. nov.; Sida Brownii, nom. nov.; Sida Grayana, nom. nov.; Sida leprosa var. depauperata, comb. nov.; Sida leprosa var. sagittaefolia, comb. nov.; Sida linifolia var. brevis, comb. nov.; Sida Standleyi, sp. nov.

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## INTERSPECIFIC HYBRIDIZATION IN LESQUERELLA (CRUCIFERAE)

Reed C. Rollins

The results of initial studies on naturally occurring populations of hybrid plants of Lesquerella were presented before a session of the Eighth International Botanical Congress in Paris (Rollins, 1954). At that time, data had been accumulated that pointed unmistakably to the involvement of $L$. densipila and L. Lescurii in the hybrid origin of the several large populations of plants found along the flood plain of the Harpeth River in middle Tennessee. However, experimental proof of the compatibility of these species had not been fully obtained and there were a number of questions about the geographical relationships both of the species and the hybrid populations that required further field work and further study. In screening measurement data from samples of two populations of plants from the Stones River flood plain, previously identified as $\bar{L}$. densipila var. maxima (Rollins, 1952), I was impressed by the wide range of variation present. By using Fisher's discriminant function and an analysis of variance, ${ }^{1}$ it was readily shown that these populations, if they were the result of interspecific hybridization, could not have been derived from any pair of known species from central Tennessee. However, the probability of L. densipila being one of the parental species was demonstrated. Thus, questions regarding the possibility of a second series of hybrid populations along Stones River remained open and a further complication was introduced, namely, the question as to whether there was yet another undetected species of Lesquerella in the Central Basin of Tennessee.

A second puzzle arose from the failure in 1953 to find Lesquerella densipila and L. Lescurii coming completely together in the area where their ranges appeared to approach each other most closely. At that time, there had been certain deterrents, such as inaccessibility by roads and the lack of time, that left open the question as to how and where cross-pollination takes place between these two species. It was highly desirable to conduct a further search of the upper Harpeth River and Arrington Creek areas for additional populations of $L$. densipila, of $L$. Lescurii and of their hybrids.

In the spring of 1955 , I returned to middle Tennessee with
${ }^{2}$ I am indebted to Dr. R. C. Foster for having carried out these statistical procedures.
several tasks in view. The first and major objective was to locate the exact place where L. densipila and L. Lescurii come together, or, alternatively, to rule out the possibility of an actual point of contact of the ranges of the two species. A second objective was to find out what insects were pollinating Lesquerella in the area. Such information would be of importance especially if the species were found not to come into contact areally. Thirdly, it was needful to determine more accurately the geographical distribution of both $L$. densipila and L. Lescurii, especially in certain critical areas such as that mentioned above and in the upper drainage area of Stones River. Furthermore, there was a need to search for an unknown species of Lesquerella. If such a species existed, as there was reason to believe, it was most likely to be found on the upper part of Stones River. Answers to several of the questions remaining from previous studies were provided by materials gathered and information obtained as a result of the 1955 field work.

## MATERLALS AND METHODS

The present study combines an examination and evaluation of field populations of Lesquerella occurring in the Central Basin of Tennessee and the results of experiments with samples of these same populations in the greenhouse in Cambridge, Mass. Our concentrated effort has been toward determining the extent and nature of interspecific hybridization in the wild material and to offer as much in the way of explanation for the existing situations as has become evident.

Much of the analytical work in connection with hybrid indices has been carried out using mature siliques. An important aspect of the silique has been shape. Therefore, it has been necessary to protect carefully all samples so that the natural shapes of the individual siliques were maintained. This was done by placing the samples loosely in envelopes with the infructescences projecting above, where they would dry without receiving any kind of pressure. Once fully dry, the shape of the silique is permanent. In sampling field populations, a single infructescence only was taken from a given plant. Each infructescence provided ten to twenty siliques for analyses. The plants sampled were picked at random by arbitrarily taking from the plant nearest the toe of one foot every other step as one walked across the population. The largest populations were extensive enough to provide several hundred samples from one trip in a straight walk across them.

Others required several trips taken at different angles to avoid sampling from the same place twice. Every wild population sampled consisted of thousands of plants. No attempt was made to estimate the total number of plants or to estimate the minimum number of infructescences required to give an adequate sample of a given population. However, as will be seen from the graphs, a relatively large number of infructescences were taken in each instance, probably several times the minimum requirement in most cases.

Seeds were collected from many of the wild populations for use in germination tests and to establish living collections for cytogenetic studies. In a number of instances, young buds were fixed for cytological studies.

At the time of the initial flowering in the greenhouse of each of the species, L. densipila, L. Lescurii, and L. perforata, and of the hybrids, potted plants were isolated and self-pollinated, or bagged and self-pollinated. The flowers so treated failed to set seed, showing that a high degree of self-incompatibility was present. The results of these preliminary trials led to the use of the plants in various combinations of crosses without resorting to the emasculation of the individual flowers. The particular combinations of pollinations made are given in tables 2 and 4 . The plants grew vigorously in the greenhouse, responding well to artificial conditions and not suffering noticeably from manipulative procedures. The plants began flowering ten to twelve weeks after planting and the pollinations were carried out over a period of two months in March and April, 1954. The progenies were grown during the early months of 1955 . There were approximately two thousand progeny plants, each grown individually in a separate three inch pot. These were grown to maturity and data were taken periodically during their period of growth. Mature infructescences were harvested from each plant for final detailed analyses.

## THE WILD SPECIES POPULATIONS

The species and hybrids of Lesquerella under consideration are endemic to the Central Basin, as shown in Map 1. All four species shown are extremely abundant at given locations and a population may consist of hundreds of thousands of individuals. Lesquerella densipila occupies cedar glade-like situations (Quarterman, 1950) in southeastern Williamson County, in Maury County and southeast of Murfreesboro in Rutherford County, but it has


Map 1. The distribution of the auriculate-leaved Lesquerellas and of their hybrids in central Tennessee. In each case, this is the total presently known distribution. The Central Basin covers much of the area shown.
been found most frequently near streams in level fields that are part of the flood plain of the stream. It is particularly abundant along the Duck River and its tributaries and along the upper part
of the Harpeth River. In the drainage area of the West Fork of Stones River, this species appears to be less abundant than in the other two river systems mentioned.

Lesquerella Lescurii occurs in cedar glade-like situations at many stations, but also occupies many flood-plain sites on the Cumberland River, Arrington Creek in Williamson County, the Little Harpeth River in Davidson County and Stewarts Creek in Rutherford County. In general, the distribution of L. Lescurii is in the northern portion of the Central Basin and is distinct from that of $L$. densipila (cf. Map 1).

Lesquerella stonensis is known at present only from the area of the East Fork of Stones River. Here it occurs on the flood plain except at one location on an upland limestone knoll less than a mile from the river. The presence of this recently discovered species on the upper Stones River was presumed on the basis of comparative data derived from the hybrids of it and L. densipila. L. stonensis was sought and found in 1955. L. perforata is known only from three stations near Lebanon, where it is abundant. All three localities are flood plain or low level field-like areas. It is completely isolated from the other species. The detailed distribution of all four species has been documented with herbarium specimens and many of these have been cited in previous papers (Rollins, 1952, 1955). So far as I have been able to discover, these four species are the only ones of the auriculate-leaved group of Lesquerellas found in central Tennessee. A fifth, unrelated species, L. globosa (cf. Rollins, 1952) found along the Cumberland and in Maury County belongs to another section of the genus and need not receive attention in the present connection.

## THE WILD HYBRID POPULATIONS

Three species in two combinations have been involved in producing wild hybrids, $L$. densipila $\times L$. Lescurii and L. densipila $\times L$. stonensis. The most extensive hybrid populations are those of $L$. densipila $\times L$. Lescurii, found along the Harpeth River. These populations extend from just below the junction of Arrington Creek with the Harpeth River in Williamson County to about four miles above the point where the Harpeth enters the Cumberland River in Cheatham County (Map 1). It is hard to ascertain the full extent of flood plain area occupied by Lesquerella hybrids, for there are stretches of the river that are difficult to get at. I have searched the most accessible parts
of the river flood plain from Arrington Creek to the Cumberland River, and from the hybrid population farthest down stream to the Cumberland, I have searched the area thoroughly. Apparently the hybrids have not reached the Cumberland, for only pure L. Lescurii has been found there up to the present. There are long stretches of the river banks and flood plain where no hybrids are to be found. The largest populations appear to be on low lying land on the upper side of long river bends. This suggests that the seeds tend to settle-out in areas of quiet water at a time when the river is at flood stage. The river follows a tortuous course, providing many places which seem ideal for the development of hybrid populations, but all such places are not occupied.

The largest hybrid population I have seen was sampled as collection 55115 and is found below the junction of Arrington Creek, along the Harpeth River (cf. Map 1). It was estimated that over 600 acres were well sprinkled with hybrid plants and many of these acres held hundreds of thousands of plants each. This hybrid population, barely down river from where L. densipila and L. Lescurii come together, is just below the area where these species become intermixed. A graph depicting the results of an analysis of this population is given on page 13. Most of the plants studied were found to be intermediate to some degree between the species and only a few had the combination of characters found in either L. densipila or L. Lescurii. The more or less bimodal nature of graph 55115 , as compared to the graphs for the other hybrid populations, probably reflects the continuing entrance through migration of each of the species directly into this population.

The hybrid plants are found almost exclusively on the flood plain but there are two known locations where they have begun to move off it. At one of these, the hybrids are found along the margin of the grade of U. S. Highway 70. Here, plants were seen on three different years, 1953, 1955, and 1956. The other location is at the edge of a field near U. S. Highway 70, approximately one half mile from the Harpeth River toward White Bluff. In the latter instance, it is probable that seed was moved from the flood plain area to the higher ground by farming operations.

## LeSQUERELLA DENSIPILA $\times$ L. LESCURII

The Hybrid Index
In developing a hybrid index, characters of the fruit were used. The assignment of values to these characters was arbitrary:
except that I was guided somewhat in my stress on characters of the fruit by the knowledge that these are the most important classificatory characters in the Cruciferae. The object was to set up a system of analysis that would reflect the pattern of changes actually seen in the hybrids, leaving aside the matter of an ideal model. For example, it was easily observed that the complete range of variation from globose siliques, characteristic of L. densipila, to the strongly flattened ones of L. Lescurii, was present among the hybrids. Various silique shapes were combined in what appeared to be a random way, with trichome characters and other silique features differing radically in the two species.

The same index has been used throughout the study of $L$. densipila $\times$ L. Lescurii hybrids, the essential features of which are repeated from my previous publication (1954).

L. Lescurit

L. DENSIPILA

## A. Nature and Size of Trichomes on Exterior of Siliques.

| 1 si b-0 | m si $\mathrm{b}-1$ | 1 si-2 | m si -3 | s si -4 |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| s br - 0 | s br, sf-1 | sf-2 | sf, s si - 3 | s si - 4 |  |
| $\mathrm{b}=\mathrm{bulb}$ $\mathrm{mi}=\mathrm{min}$ | $\mathrm{br}=\mathrm{brar}$ |  | $\mathrm{red} ; 1=\mathrm{lon}$ | $\mathrm{m}=\mathrm{medi}$ |  |


| Strongly |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| flattened | Flattened | Slightly <br> flattened | Subglobose | Globose | Slightly depressed- |
| :---: |
| 0 |


| None | At base only |  |
| :---: | :---: | :---: |
| 0 | 1 | Extending up style |

D. Trichomes on Replum Margin.

None
0

Definitely projecting 0

Many to abundant 0

Few
1
E. Shape of Replum Apex.

Barely projecting

1

Numerous
2

Rounded 2
F. Trichomes on Interior of Valves.

Few to scarce

1

None 2

As pointed out above, each of the values was arbitrarily assigned to a model. The characteristics of L. Lescurii were





Figure 1
assigned zero throughout and those of $L$. densipila were assigned the highest number in each category A through F. Intermediates from one of the hybrid populations were selected to represent all of the different types that could be recognized. Each type was given a value and a model of it was selected for use as a standard. The samples from every hybrid population and from the hybrid cultures were actually compared with the same set of models to obtain the ultimate index number.

The results of the analyses are presented in the graphs of fig. 1-3. This method of presenting the results is not a highly critical or an analytical one because a particular index number can be reached by a variety of combinations of the assigned values. The exact nature of the graph, particularly if it were converted into a curve, could be markedly affected by the arbitrary values assigned. However, the method adequately shows the intermediacy of the hybrid plants which combine as individuals the characters scored. This is the crux of the present study; not an examination of the way in which each trait is inherited.

## Wild Hybrids

The overall picture, with considerable added data, is the same as that presented previously (1954). Fig. 1 is the same as that of the previous paper with the numbering of the graphs changed by placing the year date 53 before each of them. Other graph numbers beginning with 55 signify that the collections were made in 1955. Some populations were sampled in 1953 and again in 1955. Graphs for two such populations are given in fig. 2. Graphs 53128 and 55130 were made from the scores of samples taken in 1953 and 1955 respectively, from the same population. Graphs 53130 and 55131 similarly were made from samples of the two different years from the same population.

Graphs 53128 and 55130 are quite comparable. Evidently the general character combinations remained roughly the same in the population, even though the second group of samples was of plants two generations away from the first. Graphs 53130 and 55131 are roughly comparable, although the latter tends slightly in the direction of L. Lescurii and, in this respect, is similar to

[^6]graphs 53128 and 55130. This may indicate that plants of L. Lescurii, which are known to be abundant on the Little Harpeth





Fic. 2. Graphs prepared from hybrid index numbers derived from scoring plants of two hybrid populations taken in two different years and a third population sampled in 1955. Graphs 53128 and 55130 are from the same population. Graphs 53130 and 55131 are from the same population. The number of plants scored to produce each graph is as follows: 53128-129 plants; 53130-80 plants; 5512 110 plants: 55130-165 plants: 55131-91 plants. Map 1 shows the location of each population.

River (cf. population 53134, Map 1), only a few miles distant, are actually contributing secondarily to the genetical makeup of these populations. It will be noted that graphs 55129, 55127, 53133 and 53135, all showing an intermediacy between the


Fig. 3. Graphs prepared from hybrid index numbers derived from scoring plants from two hybrid populations, one population of L. Lescurii, one population of pure L. densipila, and two populations of L. densipila showing evidence of introgression. The number of plants scored to produce each graph is as follows: L. Lescrurii, graph 53134-50 plants; L. densipila, graph 53139-25 plants; introgressed L. densipila, graph 53137-50 plants, graph 53138-50 plants: hybrid populations, graph 55115 - 185 plants, graph 55129-106 plants. Map 1 shows the location of each prpulation.
graphs of the species, are from populations above the entrance of the Little Harpeth River. On the other hand, graphs 53129 and 53130 are also intermediate and they are from populations below the mouth of the Little Harpeth.

Graph 55115 is of special significance because it reflects the situation in the first hybrid population below pure L. densipila
on the Harpeth River and the junction of Arrington Creek where pure stands of L. Lescurii are found. Evidently, plants of both species come together at the junction of Arrington Creek with the Harpeth River, producing the hybrid population less than half-a-mile below that point from which the samples for graph 55115 were taken. This graph indicates that neither species had been fully assimilated into the hybrid complex as completely as apparently occurs farther downstream on the Harpeth.

## Experimental Hybrids

The graphs of fig. 4 were produced from families of plants grown from seed produced by controlled pollinations. Graphs $54-5$ and 54-12 were prepared from families of $F_{1}$ hybrids of the species cross $L$. densipila $\times$ L. Lescurii. In general, the $F_{1}$ plants were relatively uniform and somewhat intermediate between the species. Deviations from a uniform pattern were slight and scarcely noticeable in the families as a whole upon casual inspection, but the study of individual characters did reveal the variations reflected in the graphs. Plants of Family 54-5 were usually golden yellow flowered, the siliques subglobose, the trichomes on the silique medium length and simple with an understory of short branched and short forked types; there were no trichomes on the style and few on the replum margin; the apex of the replum was barely projecting and the trichomes on the interior of the valves were few to scarce. Plants of family 54-12 differed rather consistently in having a few trichomes at the base of the style and in the absence of trichomes on the interior of the valves. Otherwise they were similar to the plants of family 54-5.

The variation found in these interspecific $F_{1}$ families is apparently attributable to the heterozygosity present in the parent plants. Both L. densipila and L. Lescurii are self incompatible, which means that each plant is obligately outcrossed within its own natural population. Thus a fair amount of heterozygosity is certain to be present.

It is interesting to note that the variation pattern can readily be pushed toward one species or the other by selecting the hybrids to be crossed. Graph $54-25$ was prepared from the index numbers of a progeny produced by crossing an intermediate hybrid plant and one showing marked tendencies in the direction of L. Lescurii, both from the same hybrid population. The graph shows a definite trend toward L. Lescurii. On the other hand.
graph 54-26 shows an opposite trend toward L. densipila. This progeny was produced by crossing an intermediate hybrid plant with one showing marked tendencies in the direction of $L$. den-


Fic. 4. Graphs prepared from hybrid index numbers derived from scoring plants produced by crossing as follows: L. densipila (53140) $\times$ L. Lescurii (53134). graph 54-5. plants scored 25; L. densipila (53136) $\times$ L. Lescurii (53137). graph 54-12, plants scored 30; L. Lescurii (53134) $\times$ intermediate hybrid (53129), graph 54-10, plants scored 74 : L. densipila (53140) $\times$ intermediate hybrid (53129), graph 54-11, plants scored 86; intermediate hybrid (53125) $\times$ hybrid showing L. Lescurii tendencies (53135), graph 54-25, plants scored 41 : intermediate hybrid ( 53129 ) $\times$ hybrid showing L.. densipila tendencies (53129). graph 5t-26. plants scored 30.
sipila. Again, the plants selected were from the same hybrid population.

The results of backcrossing intermediate hybrids to each of
the species are shown in graphs 54-10 and 54-11. Of course, it is impossible to select an exactly intermediate hybrid from a group of highly variable individuals but an effort was made to select plants as nearly intermediate to the species as possible for backcrossing purposes. Index numbers of the backeross progeny to $L$. Lescurii are shown in graph 54-10. In graph 54-11 are shown scores from plants of the backeross to $L$. densipila.

## Seeds and Pollen

The size of the hybrid population varies with the size of the available flood plain land. The largest population covered an
Table 1. Seed quality in species and interspecific hybrids of Lesquerella from wild sources in Tennessee.

Same \& Coll. No.
L. densipila

| 53137 | 50 | 49 | 98.0 |
| ---: | ---: | ---: | ---: |
| 53138 | 50 | 37 | 74.0 |
| 53139 | 50 | 42 | 84.0 |
| 53140 | $\underline{50}$ | $\underline{46}$ | $\underline{92.0}$ |
| Total | $\underline{200}$ | $\overline{174}$ |  |

L. Lescurii

| 53127 | 20 |
| ---: | ---: |
| 53131 | 50 |
| 53134 | 50 |
| 53136 | 38 |
| Total | $\boxed{158}$ |

L. densipila

| $\times$ L. Lescurii |  |  |  |
| :---: | :---: | :---: | :---: |
| $53129-53$ |  |  |  |
| $53130-79$ | 29 | 24 | 80.0 |
| $53130-8$ | 35 | 25 | 86.2 |
| $53130-23$ | 23 | 30 | 85.7 |
| $53130-15$ | 45 | 14 | 60.8 |
| $53130-73$ | 33 | 18 | 40.0 |
| $53130-9$ | 28 | 10 | 30.3 |
| $53135-248$ | 63 | 8 | 28.5 |
| $53135-204$ | $\underline{29}$ | $\underline{11}$ | 76.1 |
| Total | $\underline{315}$ | $\underline{188}$ | $\underline{59.9}$ |

L. densipila
$\times$ L. stonensis
53141
53142
Total
$\begin{array}{r}50 \\ 50 \\ \hline 100\end{array}$
L. perforata

53145

No. germinated
\% germination

7
35.0
94.0
76.0
73.6
$\overline{75.94}$
$\times$ L. Lescurii ${ }^{\circ}$
53129-53
29
25
86.2

53130-8
35
30
85.7

53130-23
14
40.0

10
30.3

53130- 9
28
8
28.5

53135-248
$\frac{11}{188}$
$\frac{37.9}{59.68}$

| 53142 | $\frac{50}{100}$ |
| :---: | :---: |

* Each number under this combination represents an individual plant.
estimated 600 acres of land and the smallest was of several hundred individuals. However, most populations were large, ranging upward from several hundred thousand of plants. The marked success of the hybrids as colonizers is apparent froms the vigor of the plants and the numbers produced. The capacity to reproduce is excellent. Table 1 gives the germinability of the seeds of wild hybrids of $L$. densipila $\times$ Lescurii and of wild hybrids of $L$. densipila $\times$ stonensis, as compared with seeds of L. densipila, L. Lescurii and L. perforata. Although the percentage of germinable seeds in one hybrid plant was 28.5 , in another it was as high as 86.2 . This is much better than would ordinarily be expected in interspecific hybrids and certainly would easily permit the maintenance of the hybrid plants. In table 2 the germinability of seeds produced from various combinations of crosses is shown. The controls were different, hand

Table 2. Germinability of seed produced by reciprocal pollinations between plants of the same and different species and including various interspecific hybrid combinations in Lesquerella.

Name \& Coll. No."
No. seeds
No. germinated
\% germination
L. densipila
$\times$ L. densipila
$53140 \times 53140$
$53140 \times 53139$
Total
L. densipila

$$
\times \text { L. Lescurii }
$$

$53140 \times 53127$
393
298
278
93.2
$53140 \times 53139$
464
$\overline{762}$
399
85.9
$\overline{677}$
$\overline{88.84}$

| $53140 \times 53134$ | 804 | 747 | 92.9 |
| ---: | ---: | ---: | :--- |
| $53138 \times 53134$ | 411 | 387 | 94.1 |
| $53137 \times 53136$ | $\underline{545}$ | $\overline{531}$ | $\underline{97.4}$ |
| Total | $\underline{2153}$ | $\overline{94.00}$ |  |

L. densipila $X$ wild hybrid
$53140 \times 53129-5-3295229$
L. Lescurii
$x$ wild hybrid
$531.34 \times 53129-5-3$
3.5.5
3.50
98.9

Wild hybrid
$X$ wild hybrid

| $53135-248 \times 53135-248$ | 661 | 658 | 99.5 |
| :---: | :---: | :---: | :---: |
| $53129-53 \times 53129-53$ | $\underline{224}$ | 208 | 92.8 |
| Total | $\overline{885}$ | $\overline{866}$ | $\overline{97.85}$ |

Table 2. (continued)
Name \& Coll. No.*
No. seeds
No. germinated
\% germination
L. densipila
$\times$ L. perforata
$53140 \times 53145$
492
394
98.0
L. densipila
$\times \mathrm{L} . \times$ maxima
$53140 \times 53141$
441
385
87.3
L. Lescurii
$\times$ L. perforata

| $53131 \times 53145$ |
| ---: |
| $53134 \times 53145$ |


| 888 | 786 | 88.5 |
| ---: | ---: | :--- |
| 370 | $\underline{349}$ | $\underline{94.3}$ |
| 1258 | $\overline{1135}$ |  |

L. Lescurii
$\times \mathrm{L} . \times$ maxima
$53142 \times 53134 \quad 657$
635
96.6
L. perforata
$\times$ L. perforata
$53145 \times 53145$
495
469
94.7
L. perforata
$\times$ L. $\times$ maxima
$53145 \times 53142$
668
636
95.2
L. $X$ maxima
$\times$ L. $\times$ maxima
$53142 \times 53142$
50
45
90.0
L. $X$ maxima
$X$ wild hybrid
$53142 \times 53129-5-3$
366
337
92.0

[^7]pollinated plants of $L$. densipila. The high percentages of germinable seeds from all of the combinations shows a high degree of compatibility between the species, between the hybrids and between the hybrids and species.

A high degree of compatibility is further demonstrated in tables 3 and 4. In table 3, the pollen quality of wild plants is shown and in table 4, the pollen quality of plants produced by a variety of pollinations is given. Here, also, is overwhelming evidence in confirmation of the high compatibility present. Again, L. densipila was used as a control.

## Cytological Observations ${ }^{2}$

Seeds were gathered in the field from a number of individual hybrid plants which were open pollinated. Several families were grown from this seed source and meiosis was studied in the plants produced. The results of these studies are given in table 5 together with observations on the pollen of the same plants. To be scored as regular, no deviations from normal. how-

Table 3. Pollen quality in plants of species and hybrids of Lesquerella grown from seed obtained from wild sources.
Name \& No. No. of plants No.filled grains No. unfilled grains \% filled grains
L. densipila

| 53137 | 15 | 1363 | 137 | 90.8 |
| :---: | :---: | :---: | :---: | :---: |
| 53138 | 15 | 1335 | 165 | 89.0 |
| 53139 | 15 | 1403 | 97 | 93.5 |
| 53140 | 14 | 1340 | 60 | 95.7 |
| Total | 59 | 5441 | 459 | 92.22 |
| L. Lescurii |  |  |  |  |
| 53127 | 1 | 99 | 1 | 99.0 |
| 53131 | 5 | 494 | 6 | 98.8 |
| 53134 | 5 | 400 | 10 | 97.5 |
| 53136 | 5 | 303 | 17 | 94.6 |
| Total | 16 | 1296 | 34 | 97.44 |

L. densipila
$\times$ L. Lescurii

| 53129-53 | 18 | 1713 | 87 | 95.1 |
| :--- | ---: | ---: | ---: | :--- |
| $53130-8$ | 17 | 1561 | 139 | 91.8 |
| $53130-9$ | 4 | 360 | 40 | 90.0 |
| $53130-15$ | 10 | 984 | 16 | 98.4 |
| $53130-23$ | 9 | 847 | 53 | 94.1 |
| $53130-73$ | 8 | 773 | 27 | 96.6 |
| $53130-79$ | 14 | 1166 | 234 | 83.2 |
| $53135-204$ | 6 | 548 | 52 | 91.3 |
| $53135-248$ | 24 | 2126 | $\underline{274}$ | $\underline{88.5}$ |
| Total | 110 | 10,078 | 922 | 91.61 |

L. densipila
$\times$ L. stonensis

| 53141 | 15 | 1204 | 296 | 80.2 |
| :---: | :---: | :---: | :---: | :---: |
| 53142 | $\frac{15}{30}$ | $\frac{1444}{2648}$ | $\frac{56}{352}$ | $\frac{96.2}{88.26}$ |
| Total |  | 479 |  | 21 |

${ }^{2}$ I am greatly indebted to and wish to thank Dr. L. O. Gaiser for producing the slides and making man! of the observations recorded here. Many of the pollen counts given in tables $3-5$ were made br. Dr. John H. Beaman, to whom I wish to express my appreciation.

Table. 4. Pollen quality in plants grown from seed produced by reciprocal pollinations of different species and interspecific hybrid combinations in Lesquerella.

Name \& No.*
No. of plants No. filled grains No. unflled grains \% filled grains
L. densipila

$$
\times \text { L. densipila }
$$

$53139 \times 53140$
L. densipila
$\times$ L. Lescurii
$53140 \times 53127$
$53140 \times 53134$
$53138 \times 53134$
$53137 \times 53136$
Total
L. densipila
$\times$ wild hybrid
$53140 \times 53129-5-3$
2

| 182 |
| :--- |
| 196 |
| 219 |
| 149 |
| 746 |


| 18 | 91.0 |
| ---: | ---: |
| 4 | 98.0 |
| 89 | 71.1 |
| $\frac{51}{162}$ | $\underline{74.5}$ |
|  | 82.15 |

L. Lescurii
$X$ wild hybrid
$53134 \times 53129-5$
Wild hybrid
$X$ wild hybrid
53135-248 $\times 53135-248$
53129-53 $\times 53129-53$
Total
L. densipila
$\times$ L. perforata
$53140 \times 53145$
2
180
20
90.0
L. densipila
$\times$ L. $\times$ maxima
$53140 \times 53141$
$2 \quad 200$
L. Lescurii
$\times$ L. perforata
$53131 \times 53145$
$53134 \times 53145$
Total
$3 \quad 21$

| 2 | 198 |
| :--- | :--- |
| 2 | 147 |

2
99.0

4
98.0

196
98.0

4
ever slight, were permitted. Thus, if a chromosome lagged ever so slightly, the figure was scored as slightly irregular and the plant was classed as having slightly irregular meiosis. In this, we were perhaps too cautious, for it is obvious from the pollen and on the evidence given above, that very little meiotic irregularity of sufficient gravity to produce sterility is present in the hybrids. Perhaps it would give a more accurate reading if the columns under regular and slightly irregular were put together under regular.
As shown in table 5, in a progeny of 14 plants of accession

Table 5. Observations on the Meiotic Chromosomes and Pollen of Families Grown from Seed of Individual Wild Hybrid Plants.

| Population <br> \& Acc. <br> Number | Family <br> Number | Number <br> of Plants | MEIOSIS <br> Segular <br> Slightly |  |  |  |  | $\%$ | FILLED |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 53129 | 53 | 14 | 7 | 6 | 1 | 87 | 100 | 95.6 |  |
| 53130 | 8 | 11 | 2 | 8 | 1 | 57 | 100 | 89.1 |  |
| 53130 | 9 | 3 | 2 | 1 | 0 | 67 | 99 | 87.3 |  |
| 53130 | 23 | 7 | 5 | 2 | 0 | 86 | 99 | 93.2 |  |
| 53130 | 73 | 5 | 1 | 2 | 2 | 97 | 100 | 98.8 |  |
| 53130 | 79 | 5 | 3 | 2 | 0 | 56 | 99 | 77.0 |  |
| 53135 | 204 | 3 | 1 | 1 | 1 | 95 | 100 | 97.6 |  |
| 53135 | 248 | 20 | 6 | 11 | 3 | 50 | 100 | 87.0 |  |
| Totals |  | 68 | 27 | 33 | 8 |  |  |  |  |

Table 6. Observations on the Meiotic Chromosomes of L. densipila and L. Lescurii.

| Species | Accession <br> Number | Number <br> of Plants | Regular | MEIOSIS |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| L. densipila | 53137 | 1 | 1 | 0 | 0 |
|  | 53138 | 1 | 0 | 1 | 0 |
|  | 53139 | 3 | 1 | 2 | 0 |
|  | 53140 | 1 | 1 | 0 | 0 |
|  | 53131 | 2 | 1 | 1 | 0 |
| L. Lescuregular | Irregular |  |  |  |  |
|  | 53136 | 2 | 2 | 0 | 0 |

53129, 6 showed some slight irregularities. The greatest irregularity was found in plant 6 , classed as irregular, where, in the first division, chromosomes were in advance at metaphase, bridging was seen at anaphase and stragglers were observed at telophase. Some plants, such as no. 4 and 12 , showed only a slightly uneven line from a lateral view at first metaphase. Nevertheless
these were classed as slightly irregular. Irregularities observed in accessions 53129,53130 and 53135 included the following:(1) at first metaphase, chromosomes off-plate from polar view; from later view, chromosomes uneven or some in advance; (2) at first anaphase, occasional bridges or pairs of chromosomes in contact; (3) at first telophase, stragglers present or an occasional bridge; (4) at second metaphase, uneven at plate or separation in advance; (5) at second anaphase, occasional chromosomes slow to divide. Second telophase was remarkably free of any irregularities even in those plants where bridges were fairly frequent at the earlier stages of meiosis. The relatively high quality of the pollen in the same plants suggests that many of the irregularities of meiosis observed were of a very minor nature and that the majority of dividing p.m.c.'s must complete their divisions without failure.

As shown in table 6, a few plants of L. densipila and L. Lescurii were studied for comparisons with the hybrid progenies scored in table 5. The amount of meiotic irregularity among the hybrid plants is not greatly different from that observed in the species. In the few plants of the species examined, we did not see any highly irregular figures although those plants classed as slightly irregular were much the same as the hybrid plants similarly classified. Certainly, the hybrid plants do not show the amount or the extent of meiotic irregularity that is usually thought of as being characteristic of interspecific hybrids.

## Evidence of Introgression

By and large, there is remarkabiy little evidence of introgression in the field involving L. densipila and L. Lescurii, especially in view of the ease with which these species cross and the very large populations of hybrids found. Population after population throughout the range of each species has been carefully examined for evidence of introgression and in only one area has this been found. In an area in southeastern Williamson County, L. densipila on the south approaches L. Lescurii, which appears to be spreading from the north in a southerly direction. There is a heavy concentration of $L$. densipila southward and of L. Lescurii northward, as shown on Map 1. Graphs prepared from 50 samples each from populations 53137 and 53138 are given in fig. 3. Comparing these with graph 53139, which represents a population of $L$. densipila to the south and remote enough from L. Lescurii to escape any chance of cross pollination.
shows that there has been some slight introgression from L. Lescurii. Indeed, the greater variability of populations in the area of 53137 and 53138 was recognized (cf. Rollins, 1952) before we were in possession of any real evidence that interspecific hybridization might be involved in Lesquerella. At that time, the relatively longer trichomes on the exterior of the siliques of these introgressed plants over those of pure L. densipila was noted.

Although it is clear that introgression has occurred, it should not be assumed that these are hybrid populations in the sense of those so designated on Map 1. In fact, the genetic influence from $L$. Lescurii has been very slight, the shape of the siliques being relatively unaffected. The difference between an average length for the trichomes of 81 microns for pure L. densipila and of 100 microns for population 53138 is not great but does show a slight influence from L. Lescurii, which has much longer trichomes. This point is in addition to those scored to produce the index figures of the graphs.

## LESQUERELLA DENSIPILA $\times$ L. STONENSIS [L. $\times$ MAXIMA]

Wild populations of hybrids produced by the crossing of these two species were found before L. stonensis was discovered and before $L$. densipila was definitely known to be present in the drainage area of Stones River. These plants were originally described as $L$. densipila var. maxima in 1952 (1. c.) and now may be designated $L . \times$ maxima. At that time, variations in flower color from white to yellowish and variations in trichome length from 151 microns to 413 microns were pointed out. Since then, we have established that the yellow-flowered $L$. densipila does occur on the West Fork of Stones River and that L. stonensis, a white-flowered species, occurs on the East Fork of Stones River. At the junction of these two tributaries which form Stones River, L. densipila and L. stonensis come together (cf. Map 1). Below this junction only hybrid populations have been found.

Up to the present, no detailed analyses of these hybrid populations have been made except to see whether they could have resulted from the crossing of $L$. densipila and $L$. perforata. As pointed out above, this possibility was ruled out and the search set off which culminated in the discoverv of $L$. stonensis. Observations upon the hybrid populations leave no doubt about their being derived from $L$. densipila $\times$ L. stonensis. The flowercolor. while predominantly white in many plants, is somewhat creamy in others and many shades from light yellow to orange-
yellow may be seen in a given population. Genes for yellow color were shown to be present in a white-flowered hybrid by crossing it with the pure white-flowered L. perforata. In a progeny of 17 plants, one bore lemon-yellow flowers and another had an unusual amount of yellow pigmentation in the center. The other 15 plants were white-flowered.

The trichomes on the exterior of the siliques are variable in length from plant to plant, as pointed out above, but are consistently much longer than those present in pure L. densipila. Furthermore, there is variability of the silique shape ranging from globose, characteristic of $L$. densipila, to somewhat didymous, which is characteristic of L. stonensis. My overall impression is that the hybrid populations are nearer to L. stonensis than they are to L. densipila. This impression comes from the predominance of white-flowered plants, the larger more nearly didymous siliques so frequently found and the long trichomes, much closer in length and disposition to those of L. stonensis than to $L$. densipila.

Unfortunately, I have not had pure L. stonensis in cultivation so that the cross between this species and $L$. densipila has not been made. However, as shown in tables 2 and 4, the hybrid L. $\times$ maxima was crossed with L. Lescurii, L. densipila, L. perforata and with a wild hybrid plant of L. densipila $\times L$. Lescurii. In all cases, a high percentage of viable seed resulted and the pollen of the grown progenies was of high quality. It is clear that a high degree of compatibility is present and it may be assumed that $L$. stonensis would cross with $L$. Lescurii or with L. perforata if it were in contact with them.

There are undoubtedly more populations of hybrids than we have seen along Stones River (cf. Map 1). The ones we examined and sampled in 1953, 1955 and 1956 appear to persist in the same general location from year to year. Some variation in population size is notable. This may be correlated with land use. I have searched the flood plain of the Cumberland River east of Nashville at several locations without finding these hybrids. Nor was L. Lescurii present. However, it may be just a matter of time until $L . \times$ maxima moves onto the Cumberland flood plain and eventually downstream far enough to come into contact with L. Lescurii. When and if this happens, it is expected that hybridization will occur and, in this way, elements of three species may be brought into hybrid combination. The hybrid combination of L. Lescurii, L. densipila and L. stonensis may be
expected to occur in a different way. Populations of L. Lescurii have been found along Stewarts Creek, a tributary of Stones River (cf. Map 1). Seeds from these populations may move gradually downstream, eventually reaching Stones River, where they will come in contact with $L . \times$ maxima.

## OTHER CROSSES

In the wild, hybrid populations of only the two species combinations L. densipila $\times$ L. Lescurii and L. densipila $\times$ L. stonensis have been found. In the greenhouse and garden, additional crosses have been made or attempted. In the following diagram the successful crosses are indicated by solid-line arrows. The


Fig. 5. Crosses and attempted crosses between species and hybrids of Lesquerella. Solid-line arrows indicate successful, broken-line arrows unsuccessful crosses. Pollen was carried in the direction indicated by the arrowhead in each case.
attempted but unsuccessful crosses are indicated by broken-line arrows. All crosses were carried out reciprocally.

Lesquerella grandiflora is probably a distant relative of the auriculate species of Tennessee but its chromosome number is $n=9$ instead of $n=8$, as in the other auriculate-leaved species. For this reason, the complete failure of crosses involving L. grandiflora is not surprising. ${ }^{3}$ This species occurs in Texas and the details of its characteristics and distribution may be found in a previous paper (1955).

[^8]Results in terms of the fertility of the progenies of the various crosses, excepting those involving L. grandiflora, are shown in tables 2 and 4 . These data show a high degree of compatibility between all members of the successful crosses.

## GENERAL OBSERVATIONS

In Map 1, I have brought together considerable information on the geography of the species and hybrids under consideration. It is significant that in an area scarcely seventy-five miles across are found the total known ranges of four species of Lesquerella. There will undoubtedly be at least minor future additions to the ranges indicated and it is possible that the species themselves may alter their areas of occurrence through migration. However, the present information is as complete as we could make it during three seasons of field study.
In their general habit of growth, L. densipila, L. Lescurii, L. perforata and L. stonensis are similar. The plants tend to occur close together in very large concentrations of several hundred thousand individuals. Most populations are sufficiently extensive to produce yellow or white areas when the plants are in bloom. The life cycle begins in the fall with the development of a basal rosette of lyrately pinnatifid leaves. These persist through the winter months and flowering shoots begin in early spring. Seed germination is most likely to occur in late August, September, or early October, while flowering often gets under way as early as March. The height of flowering is usually reached in April. Seeds mature rapidly and ripe seeds are shed in April and May.

Fall and winter growth coupled with early spring flowering and fruiting is important to the survival of Lesquerella in the flood plain areas, one of their principal habitats. Many of these sites are under cultivation, the most frequent crop being maize. The land is ordinarily too wet from the annual spring floods to be prepared for seeding until May or sometimes early June. Thus the full development and seeding of a population of Lesquerella is permitted before farm operations begin. A radical shift in the kind of crop produced on the river flood plains in central Tennessee would almost certainly markedly affect the abundance of Lesquerella in these areas and the development of the present cycle of farming operations may have strongly influenced what we see there today. In fact, the agricultural factor may have
been important in species distribution shifts permitting interspecific hybridization.

Plants of these species possess a wide latitude of adaptability and their specific response is evidently geared to seasonal influences. For example, a given plant may produce a single flowering shoot with a short, few-flowered inflorescence if growing conditions are unfavorable. On the other hand, the same plant may produce twenty or more flowering shoots with long racemes of numerous flowers if growing conditions are favorable. Also, the plants will stand a certain amount of submergence due to flooding. Complete submergence for several days kills the plants but I have seen nicely recovered plants that had been partially inundated, which resulted only in a set-back in their growth and flowering.

The unilateral movement of seed downstream has a bearing on the distribution of the species and of the hybrids. This in turn is dependent upon the climatic and other factors controlling stream flow that produces annual spring flooding of the rivers in the Central Basin. These violent floods pick up the seeds of Lesquerella on the higher land and carry them downstream, where some of them settle-out in the quieter and shallower waters over fields and pastures adjacent to the inner curve of major bends of the rivers. Here, the resulting plants intermix with those already present and produce seeds to perpetuate the population, or be carried downstream to a new location during the succeeding flood.
The flowers of Lesquerella are indiscriminately visited by a wide variety of insects. The domestic honey bee is one of the most important pollinators, but solitary bees and a variety of diptera were seen visiting the flowers. The vigor with which the flowers are worked during sumny periods insures an effective transfer of pollen from plant to plant. This is important because all four species and the wild hybrids were found to be selfincompatible. ${ }^{+}$Outcrossing is obligate and the seed-set in any given population is dependent upon the effectiveness of the pollinators. A natural result of this, when combined with the annual habit, is the maintenance of a high level of heterozygosity in any given population.

The fruits and seeds of Lesquerella are parasitized by a weevil

[^9]belonging to the genus Ceutorhynchus." In 1953, the fruits of L. densipila were very heavily infested while those of $L$. Lescurii were almost untouched. Again in 1955, it was observed that L. densipila, L. $\times$ maxima and L. perforata were infested by the weevil, while L. Lescurii seemed free of these seed-feeding larvae. It is interesting to speculate about the possibility that the covering of long, stiff trichomes present over the ovary of flowers of L. Lescurii somehow interferes with oviposition by the adult of Ceutorhynchus and thus protects a vital reproductive structure, the seed. At first it was thought that such a factor might be of survival value and that this would in some way help provide a selective advantage for the hybrids of L. densipila $\times$ L. Lescurii over straight $L$. densipila. This may be the case but I have not been able to test it. However, in view of the tremendous seed-set in L. densipila in spite of the ravages of the weevil and the fact that the hybrids themselves are somewhat parasitized, I am inclined to discount this as having much to do with the success of the hybrids. There may be something to a possible selective advantage for $L$. Lescurii in years of critically low seed production from other causes but this point needs some direct experimentation for a solution.

## THE SPECIES QUESTION

The high degree of compatibility between the four species of Lesquerella under consideration, as shown by experiment, brings into sharp focus the question as to whether we are, in fact, dealing with species or with taxa of an infraspecific sort. The fact that three of the four species hybridize naturally in two combinations adds evidence to the demonstrated genetical closeness of these taxa. Some writers (Dobzhansky, 1951) maintain that the presence of genetical incompatibility betwen species is an essential criterion of speciation and unless it is present, the status of species has not been achieved. Certainly some barrier to gene exchange is a necessary condition for the maintenance of two sympatric species and if they are competing for the same habitat, the required barrier almost has to be genetical. However, allopatric species require only adequate spatial separation to prevent gene exchange between them. The Central Basin species of Lesquerella are essentially allopatric and must have been completely so not many decades ago. Presumably, they arose in

[^10] making the identification from the larvae.
complete isolation from each other and have remained isolated down to the present.

In plants, at least, genetical incompatibility cannot be regarded as the one essential criterion of speciation, nor is it the final test in determining whether one is dealing with species or infraspecific taxa. If incompatibility exists between two taxa and is of a complex nature not easily circumvented, it is of importance as a taxonomic criterion. However, if incompatibility is not present between what otherwise appear to be distinct species, a negative situation with regard to it as a criterion and as an interspecific barrier exists. In such a case, other barriers must operate to keep the species apart and other criteria must be relied upon to distinguish them. The latter situation appears to be present in Lesquerella and is comparable to a number of other well known cases (cf. Stebbins, 1950, p. 199-200).

But why do we call these compatible taxa species rather than subspecies? The answer comes from a number of lines of evidence. The first is morphological. Each of the species differs from the other by a pattern of character-differences and there are no intergrades between them except where hybridization must be inferred. The characteristics most readily observed in the four species are as follows:

| Silique shape | L. Lescurii Hattened | L. densipila globose | L. stonensis <br> slightly didymous | L. perforata subpyriform |
| :---: | :---: | :---: | :---: | :---: |
| Texture of silicque | leathery | leathery | leathery | papery |
| Trichomes on siliques | large, rigid | minute, stiff | medium, soft | usually absent |
| Trichomes on style | absent | at base | base to middle or above | absent |
| Trichomes on silique interior | present | absent | absent | present |
| Septum of silique | entire | entire | small perforation | large perforation |
| Veins of silique | inconspicuous | inconspicuous | inconspicuous | conspicuous |
| Flower color | yellow | yellow | white | white |

The magnitude of the differences in silique shape, and the surface covering or markings on the siliques, may be seen in plates one, two, three, and four, all from photographs of the same magnification. The differences between these four species are
of the same order and kind as those separating other species in Lesquerella.

The second line of evidence comes from the geography of the species. L. perforata is completely separated from the others. L. Lescurii, L. densipila and L. stonensis are essentially separated from each other geographically, except for relatively restricted sites where hybridization occurs. This indicates that all four species achieved their present distinctness in isolation from each other. The merging through hybridization is a secondary regressive step, and is not indicative of any direct evolutionary connection between the species involved. If it were assumed that we are dealing with subspecies, the situation would be open to the interpretation that taxa comparable to species in every respect had become differentiated evolutionally and that now, because they have begun to hybridize, they have dedifferentiated back to the subspecific level.

A third line of evidence exists in the nature of the variation of each of the species. Each has a range of morphological variation of its own, which it does not transcend except in the limited areas where hybridization takes place. Furthermore, these variation patterns are comparable to those of other species of Lesquerella found outside of the Tennessee area. In my judgement, the evidence for treating the taxa under consideration as species rather than some infraspecific rank is solid and strong. I believe that such a disposition of them better fits the facts than other possible alternatives and is, in reality, inescapable.

## DISCUSSION

A number of questions are raised by the findings concerning the species of Lesquerella of central Tennessee. For example, how could four reproductively compatible species have arisen in such a relatively small area? Recalling that the total ranges of these species are within an area approximately seventy-five miles in diameter, it is clear that, although they originated allopatrically, they could not have been separated by great distances at any time. There is no evidence whatever that any of the four species, L. Lescurii, L. densipila, L. stonensis or L. perforata, have at present or had in the past any direct connection with a species outside of the Central Basin of Tennessee. Therefore, it must be assumed that these species arose in the areas, or near them, where they now occur.

The very close genetical interrelationships of all four species,


Plate 1. Lesquerella Lescurii. Part of an infructescence. $\times 6$ ( (ollins 551/t). Photo by Frank White.


Plate 2. Lesquerella densipila. Part of an infructescence. $\times 6$ (Kollins i: Quarterman 55146). Photo by Frank White.


Plate 3. Lesquerella stonensis. Part of an infructescence, $\times 6$ (Rollins 55176 ). Photo by Frank White.


Plate 4. Lesquerella perforata. Part of an infructescence, $\times 5$ (Rollins \& Bold 55139). Photo by Frank White.
as shown by the high reproductive compatibility between them. makes it plausible to assume that they had a common ancestor. This ancestor undoubtedly reached central Tennessee from the southwest. The presence of L. lyrata as an isolated species in northwestern Alabama perhaps marks the route by which Lesquerella migrated to its most easterly stations in Tennessee. The present-day species of the southwest most likely to have been involved, either directly or as a derivative, in the ancestry of the Tennessee species is L. auriculata, which occurs in Oklahoma and Texas. This species not only has the same chromosome number ( $\mathrm{n}=8$ ) and generally similar morphological features, but possesses some presumably primitive characteristics such as a relatively large number of ovules per locule (6-10) and fertile placentae extending to the base of the silique. Furthermore, there is a wide variability in L. auriculata which probably coincides with a wide evolutional potential, if the differences within and between populations may be taken as providing some indication of this.

The Tennessee species of Lesquerella occur exclusively upon Ordovician limestones or upon soils derived from the limestone. All available evidence points to a high degree of adaptive adjustment of these Lesquerellas to the basic limestones, which probably accounts for the limited total range of the genus in the Central Basin. Also, it seems probable that this factor had something to do with the evolutional differentiation of the genus. For this reason, we look to the developmental history of the Central Basin for clues that might account for the fractionation of Lesquerella there.

According to Fenneman (1938), the Central Basin [Nashville Basin] originated from a low dome, whose gradual uplift permitted river-cutting to keep pace with the rise. This dome and a similar structure in Kentucky are the oldest geological features of the area, presumably dating from the Paleozoic. The subsequent processes of peneplanation (producing successively the Cumberland and Lexington peneplains) reduced the thickness of the strong cherty limestones more rapidly over the cap of the dome than in the adjacent areas of lower elevation, ultimately exposing the weaker Ordovician rocks beneath. The Basin was then formed by the more rapid river action on these rocks than upon the harder, more recent rocks characteristic of the rim. The development of the Basin, at least in its early stages, is thought to have been very rapid. The present flora of the Basin
presumably dates from mid-pleistocene. It is clear that the Central Basin has had a distinctive physiographical and geological history and we may assume that the presence of a number of Lesquerella species endemic to the area is in some way tied into this history. It is at least conceivable that the spatial isolation of the four species is to be associated with the streams which gradually uncovered the Ordovician limestones at different locations in the Basin. L. densipila is associated with the Duck River, L. Lescurii with the Cumberland River, L. stonensis with Stones River and L. perforata with Spring Creek. It is interesting to note that the size of the present distributional area of each species correlates with the size of the river with which it is associated. Thus, $L$. Lescurii, which has the largest distributional area is associated with the Cumberland River which, because of its great size, undoubtedly played the leading role in ultimately fashioning the Central Basin. The Duck River is next in size and $L$. densipila is likewise next in the size of its distributional area. The most restricted species, L. perforata, is associated with Spring Creek, the smallest of the four streams.

Although the exact way in which these species arose cannot be known, I think that certain points in connection with their origin and history can reasonably be inferred: (1) all four species had a common ancestor; (2) each species arose when not in contact with the others; (3) the species have remained allopatric down to the recent past; (4) each species arose in or near the area where it now exists; and (5) the origin of each species is probably tied in with the physiographical products of the river with which it is associated. In connection with point three, it is probable that the species remained separated until man came upon the scene. Along with agricultural activities in the Basin, man is most likely to have extended the ranges of those species which have now entered the same river systems and into contact with each other.
I have previously (1954) emphasized the fact that many of the hybrid populations maintain themselves largely if not wholly independent of the parental species. Certainly there has been a considerable down-river movement of the hybrids from the principal areas where the species meet, both on the Harpeth River and on Stones River. The question as to how much reciprocal introgression occurs between the species and the hybrids is still not fully explored. However, it is certain that the movement of both species and hybrids is primarily unidirectional, i.e.
downstream. There is no known intrinsic reason why the hybrids should not move away from the river flood plain and at one point on the Harpeth, as mentioned above, this is apparently taking place. If, in such an instance, the hybrids came into contact with one of the species, introgression would undoubtedly occur. But the overriding influence governing plant movement in the stream valleys is stream flooding and this is such a powerful factor that it dominates all others, affecting plant movement both in the Harpeth River system and in the Stones River system. It would appear that so far as bringing the separate species together, it became dominant only after some agent such as man introduced them into the river systems in which they now hybridize. In the case of $L$. densipila and L. Lescurii in the Harpeth River system, it appears that both species gradually spread into it, L. Lescurii from the north and L. densipila from the south. In the Stones River system, the situation seems to be different. There, it is probable that $L$. stonensis originally occurred in pure form well below the junction of the East and West Forks of the River. In spreading northward, L. densipila finally entered the drainage of the West Fork where it was eventually transported into contact with $L$. stonensis. Thus, L. densipila is, in a sense, penetrating $L$. stonensis territory. Such a supposition would account for the fact that the hybrid populations on Stones River seem not to be intermediate between the species, but appear to be closer to $L$. stonensis than to L. densipila, as pointed out above.
A major question concerning the hybrid populations along the Harpeth River is how do they maintain their relative intermediacy between the species? We can readily see that the initial mixing of $L$. densipila and L. Lescurii is accomplished by the presence of such a large population of hybrids that the species. themselves, have little or no chance of persisting. There is a constant influx of plants of both species and the incorporation of them into the giant plexus of hybrids is equally incessant. In this area just below the junction of Arrington Creek, an equal opportunity is presumably present for each species to enter the hybrid swarm. No doubt there are differences in numbers of plants, the extent of penetration by migration. etc., between the two species and variations of these from year to year. No attempt has been made to determine the relative effects of each species on the initial hybrid population structure and those at consecutively greater distances downstream, except as this is shown by
the hybrid indices from which the graphs were produced. The net result appears to be that the genetical potentialities of both species are incorporated into the hybrid populations in a tremendously diverse and complicated series of combinations and that the particular combinations possessed by each parental species are not particularly favored. In the characters worked with, it would appear that linkage is not a strong factor in producing particular character combinations.

In dealing with the question of intermediacy of the hybrid populations, three items should be reemphasized: (1) the plants are self-incompatible; (2) as a result, they are obligately outcrossing; and (3) they are annual, so that a complete turnover of genetic material occurs each year. These factors set the stage for the rapid and complete breakdown of the two species into a hybrid swarm and the subsequent rapid incorporation of the genes of any additional plants of the species that come within pollinating range. The latter point is significant for the downriver populations of hybrids, where L. Lescurii is present on the tributaries and must at times be carried down to the flood plain of the Harpeth. These plants of L. Lescurii quickly lose their identity by being overwhelmed within the hybrid populations, for among the thousands of hybrids examined I have never seen a plant I would unequivocally call $L$. Lescurii. On the other hand, the influence of $L$. Lescurii on the hybrid populations may be considerable and the shift toward L. Lescurii, shown by graph 55131 over graph 53130, both prepared from samples of the same population but in different years, the former in 1955 and the latter in 1953, may be due to an influx of L. Lescurii during the interim.

## SUMMARY AND CONCLUSIONS

There are virtually no genetical barriers between four species of Lesquerella that are endemic to the Central Basin of Tennessee. Proof of this has been obtained by experiment and it may also be inferred from the natural hybridization that takes place, involving three of the four species. These species presumably arose in isolation from each other and have persisted allopatrically until recent times when three species in two different combinations have come together to produce interspecific hybrids. L. densipila and L. Lescurii hybridize near the junction of Arrington Creek with the Harpeth River. From that point downriver for a distance of over 40 miles, there are numerous large
populations of hybrids on the flood plain of the Harpeth. The preeminent feature of these hybrid populations is that they are somewhat intermediate between the species and show little or no overlap with the parental species in their variation patterns. Although introgression is to be found, it is not a prominent aspect of interspecific hybridization in this case.

Lesquerella densipila hybridizes with L. stonensis at the junction of the East Fork and the West Fork of Stones River. From that point down-river, only hybrid populations are to be found. These interspecific hybrids appear to be more similar to $L$. stonensis than to L. densipila, but a detailed study of the hybrid populations has not been made.

The four species of Lesquerella, L. densipila, L. Lescurii, $L$. stonensis and $L$. perforata appear to have had the same ancestor which probably migrated to the Central Basin from the Southwest. A lone, related species, L. lyrata, endemic to northwestern Alabama, probably marks the migration route eastward from Oklahoma and Texas, where a putative ancestral type, L. auriculata, now resides.

The populations representing $L$. densipila, L. Lescurii, L. stonensis and $L$. perforata are held to represent species, in spite of the high compatibility shown to be present between them.

Local migrations of the species and of the hybrid populations are strongly affected by seasonal flooding of the streams of the Central Basin, the seeds being carried downstream. This unidirectional movement of the interspecific hybrids particularly is an important factor in maintaining the purity of the species. The tendency is for the species to move downstream until they come together, and for the resulting hybrids to continue to move downstream away from the areas where the pure species exist.

The hybrids have incorporated in a complex way the genes of the species entering into the combination and present a much wider variation pattern than is found in either species or in both added together. Thus many new combinations of characters that are not present in either species are available for the selective action of the forces of evolution. Up to the present, no definite evolutionary trends have been detected in the hybrid populations. This does not necessarily mean that none are present because I have not made a systematic search for them. However, the raw materials for numerous striking deviations from the parental species are present among the hybrids and perhaps only favorable circumstances are needed for some of these deviations
to emerge as definite evolutionary trends. The latter is admittedly conjectural, but it is not without some foundation, for there is no known reason why the selective forces of evolution may not act as effectively upon deviations from the parental types produced by hybridization as upon those produced in some other way.

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# A REVISIONAL STUDY OF THE GENUS MARSHALLIA (COMPOSITAE) ${ }^{1}$ 

R. B. Channell

The genus Marshallia is a relatively small group of distinctive herbs included in the Tribe Heliantheae of the Compositae. The genus is found only in the United States. It is comprised of ten taxonomic entities and is restricted in distribution largely to the Southeastern States, but extends northward along the Appalachians through West Virginia into Pennsylvania and westward into Texas and Oklahoma.

None of the members of the genus is of economic importance. Early collectors in this country sent representatives of a few species to Europe, however, where they were grown in botanical gardens and used to some extent as perennials in flower gardens. But apparently because of their limited desirability as ornamentals and the meager success in cultivating them, the stocks soon disappeared. Nevertheless, the group would appear to possess some floricultural possibilities and, indeed, certain species are still grown by local wild flower gardeners in this country even today.

Scientific interest in these plants has been almost exclusively taxonomic and has consisted largely of descriptive accounts of new species as they were discovered. The genus has been the subject of only one comprehensive revisional treatment, namely that of Beadle and Boynton in 1901. The group, however, has continued to be a source of many difficulties. The high percentage of incorrect determinations on herbarium specimens is indicative of the poor understanding of the taxonomy of the species and the inadequacy of the existing treatments. In fact, the variation encountered among specimens of the grass-leaved complex is such that it has proved impossible to apply the names in current use with any degree of accuracy. In addition, apparent discrepancies in the known range of certain species have been noted, together with the suggestion that some of the names have been erroneously applied. With the need for a critical re-examination of the nomenclature, taxonomy and distribution of the entire

[^11]genus thus evident, it was on this basis that the present revisional study was undertaken.

This treatment is based primarily upon morphology and utilizes the existing specimens of various herbaria. In addition, extensive field observations were carried out and an attempt was made to determine as completely as possible the geographic distribution of each taxon. Further observations were made in the greenhouse where representatives of eight of the ten taxa were successfully grown.

During the course of the investigation over 2000 sheets of specimens were examined, representing the Marshallia collections of 57 herbaria. In general only representative specimens are cited, although a minimum of one per county for each of the taxa recognized is included. For the rarer or more localized species all specimens examined are cited. In any case, all specimens studied have been appropriately annotated so that they may be used in conjunction with this revision whether they are cited specifically or not. The standardized herbarium abbreviations of Lanjouw and Stafleu (Index Herbariorum, ed. 3, 1956: Regnum Vegetabile, vol. 6, pt. 1) have been adopted whenever possible; those not included in their list are marked with an asterisk.

I wish to thank the curators of the following herbaria for kindly lending for study the specimens in their care:

| ALU | Mohr Herbarium, Geological Survey of Alabama |
| :--- | :--- |
| ARIZ | University of Arizona |
| BAYLU | Baylor University |
| BKL | Brooklyn Botanic Garden |
| BM | British Museum (Natural History) |
| CHARL | Charleston Museum |
| CLEMS | Clemson Agricultural College |
| CM | Carnegie Museum |
| CONN | University of Connecticut |
| CU | Wiegand Herbarium, Cornell University |
| DUKE | Duke University |
| DWC | Darlington Herbarium, Pennsylvania State Teachers College |
| F | Chicago Natural History Museum |
| FI | Herbarium Universitatis Florentinae |
| FLAS | Agricultural Experiment Station, University of Florida |
| G | Conservatoire et Jardin botaniques, Genève |
| GA | University of Georgia |
| GH | Gray Herbarium, Harvard University |
| ILL | University of Illinois |
| IND | Indiana University |
| K | Royal Botanic Gardens, Kew |


| LCU | Langlois Herbarium, Catholic University of America |
| :--- | :--- |
| LlC | Our Lady of the Lake College, San Antonio |
| LUNDELL | Lundell Herbarium, Texas Research Foundation |
| MIN | University of Minnesota |
| MISSA | Mississippi State College |
| MISSU | Lowe Herbarium, University of Mississippi |
| MO | Missouri Botanical Garden |
| NA | United States National Arboretum |
| NCSC | North Carolina State College |
| NCU | University of North Carolina |
| ND | University of Notre Dame |
| NO | Tulane University |
| NTSC | Benjamin B. Harris Herbarium, North Texas State College |
| NY | New York Botanical Garden |
| OKL | Bebb Herbarium, University of Oklahoma |
| OKLA | Oklahoma Agricultural and Mechanical College |
| P | Muséum National d'Histoire Naturelle, Paris |
| PAC | Pennsylvania State University |
| PENN | University of Pennsylvania |
| PH | Academy of Natural Sciences, Philadelphia |
| PHIL | Philadelphia College of Pharmacy and Science |
| POM | Pomona College |
| RM | Rocky Mountain Herbarium, University of Wyoming |
| sIU | Southern Illinois University, Carbondale |
| SMU | Southern Methodist University |
| TAES | Tracy Herbarium, Agricultural and Mechanical College of Texas |
| TENN | University of Tennessee |
| TEX | University of Texas |
| UALA | University of Alabama |
| UARK | University of Arkansas |
| US | United States National Museum |
| USC | University of South Carolina |
| VDB | Vanderbilt University |
| VHC | Herbarium of V. H. Chase |
| WVA | West Virginia University |
| YU | Yale University |

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It was upon the suggestion of Dr. R. K. Godfrey (Florida State University), who was familiar with the taxonomic difficulties in Marshallia, that this study was initiated.

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## History of the Genus

The original reference in literature to the plants now known as Marshallia is that which appears in Walter's Flora Caroliniana (1788). In this work three Marshallia species were described under the Old World genus Athanasia where they remained up to and even beyond the time of the description of Marshallia as a distinct genus. These species, namely Athanasia graminifolia, A. obovata and A. trinervia, appeared in the flora in consecutive order, an arrangement which suggests that Walter himself recognized their mutual affinities apart from the other species (not Marshallia) which he also assembled as Athanasia.

The first account of Marshallia as a separate genus was published in the 8th edition of Linnaeus' Genera Plantarum (page 810 ) by Schreber in 1791. The actual specimen or specimens upon which the genus is based have not been located. No reference was made in the generic description to the Walter species and no binomial combination was made at all. There is no evidence, therefore, to indicate that Walter's species were used in drawing up the generic description. In fact, certain suggestions would seem to indicate that they were not.

There is some possibility that Muhlenberg in this country conveyed specimens or written information to Schreber, either or both of which may have formed the basis of the description. This is suggested in the following passage quoted from a letter *

[^12]to Dr. Moses Marshall from Muhlenberg, dated April 9, 1792, the year following the publication of the generic description:

[^13]One might presume from the word "plant" in the quotation that only one species was involved in establishing the genus and, by inference, that Schreber did not utilize the Walter descriptions, whether they were available to him or not.

In any case, however, due to the homogeneity of the floral structure of all the species, the generic description contains a very small proportion of descriptive material which is not applicable to the entire genus. Yet, the use of the adjectives obtusis, concavis . . " (in describing the phyllaries) and the phrase ". . . apice paullulum dilatatis obtusis . . ." (in reference to the pales of the receptacle) is considered to be highly significant, for the phyllaries and pales of only one species are thus specifically characterized. On this basis Marshallia obovata (Walt.) Beadle \& F. E. Boynt. has been determined as the type species of the genus. This choice is in keeping with the type species, Marshallia lanceolata Pursh, listed by Mansfeld in the original proposal ${ }^{3}$ for the conservation of the generic name officially adopted in $1940 .{ }^{4}$ Although the epithet actually originated with Michaux, this binomial is clearly to be considered a synonym of Marshallia obovata.

Contrary to numerous printed accounts that the generic name honors the famous Humphrey Marshall, Harshberger ${ }^{5}$ discovered a copy of the reply to Muhlenberg's note, in the handwriting of Dr. Moses Marshall, which indicates that the latter (nephew of the more famous Humphrey Marshall) alone was recognized by Schreber and Muhlenberg in their transaction. Dated April 13, 1792, the year following the publication of the generic description, the following selection from the reply appears to be conclusive evidence:

[^14]honor done me through your request, by Dr. Schreber, and think myself but too undeserving."

The history of Marshallia is further complicated by the publication of the name Marshallia by J. F. Gmelin, also in 1791, for an entirely different genus (Flacourtiaceae). This name appears in the 13th edition of Linnaeus' Systema Naturae ${ }^{6}$ (volume 2. page 836) by J. F. Gmelin, a compilation which not only retained Walter's species under Athanasia but included as well the new genus Marshallia Schreb. and the binomial M. Schreberi J. F. Gmel., the first combination to be made in the genus. In spite of the fact that the precise dates of publication (in 1791) of the two respective works have not been determined, the very fact that Schreber's genus is catalogued by Gmelin with full reference to edition and page suggests the actual priority of Schreber's name. The resulting homonyms, nevertheless, have led in recent times to the conservation of the name Marshallia Schreb. This action is discussed in detail in a footnote accompanying the generic synonymy.

In 1803, Michaux (Fl. Bor.-Am. 2: 104-106), apparently unaware of Marshallia Schreb., published the genus Persoonia ${ }^{\top}$ for the same group. Three species were included: P. lanceolata, P. latifolia (both from the Carolina mountains) and P. angustifolia (from the Tennessee Territory). The descriptions of the first two species carry references indicating the questionable synonymy of Walter's Athanasia obovata and A. trinervia, respectively, but the description of $P$. lanceolata carries no reference to prior description at all.

In 1807, Persoon (Syn. Pl. 2: 403), using the specific epithets of Michaux, substituted the name Trattenikia for Persoonia, knowing that Smith (1798) had previously appropriated the latter name for a genus of the Proteaceae. The name Trattenikia ( as Trattinickia ${ }^{8}$ ), however, had already been appropriated by Willdenow (1806) for a genus of the Burseraceae. According to

[^15]the account of Trattinik himself (Arch. Gew. 1: 108-110. 1814), Persoon detected his own mistake and in a "literature communication," probably a letter, pointed out Trattenikia as being the same as Schreber's Marshallia.

Pursh (Fl. Amer. Sept. 2: 519, 520. 1815) soon came to the same conclusion concerning the synonymy of Persoonia Michx., Trattenikia Pers. and Marshallia Schreb. Accepting the latter. he made combinations of the three Michaux epithets. Pursh's citations are particularly useful in following the subsequent application of the names, for, under both M. lanceolata and M. latifolia, Pursh indicated not only the Walter equivalents (Athanasia obovata and A. trinervia, respectively) but also "v. s. in Herb. Walter," in confirmation. The notation for M. angustifolia indicates that Pursh collected material of this species himself in swamps, near Wilmington, on the coast of North Carolina. This is at variance with "Territorio Tennessee," the apparently erroneous source of the original material of P. angustifolia cited by Michaux.

A final change involving the generic name was made by Poiret (Encyc. Suppl. 4: 405, 406. 1816). Using a manuscript name of de Jussieu, Poiret renamed the genus Phyteumopsis and the Michaux epithets were once again combined with a new generic name (Phyteumopsis Juss. ex Poir.). If the substitution of a new generic name had proved necessary, then Phyteumopsis would indeed have been the legitimate name, inasmuch as it was the first available one to follow that of Marshallia Schreb. This reasoning must have influenced Dr. Mansfeld (see discussion of generic synonymy) who proposed, although without apparent necessity, the conservation of Marshallia Schreb. over Phyteumopsis Juss. ex Poir.

The genus Therolepta, erected by Rafinesque in 1825 (Neogenyton, page 3), was originally reputed to differ from Marshallia. The type species, T. pumila, was collected by Rafinesque in western Kentucky. In a later account (New Fl. N. Amer., page 78. 1838), however, Rafinesque himself interjected a note of uncertainty regarding the validity of the genus. Referring to the known assemblage of Marshallia species to that time, Rafinesque states: ". . thus we have 6 sp [ecies]. of this pretty G[enus]. A 7th might be my M. pumila now my G[enus]. Therolepta Neog. 1825." Inasmuch as no specimen has been located with which to associate the name, it seems best to maintain Rafinesque's own disposition of the genus, at least until such time as the
identity of the taxon can be shown with certainty. Torrey and Gray (Fl. N. Amer. 2: 390. 1842), however, have assigned Therolepta to the generic synonymy of Marshallia.

Although for many years the three Walter names published in 1788 (Athanasia graminifolia, A. obovata and A. trinervia) were completely supplanted by the names of Michaux, the Walter epithets have been gradually re-instated. The circumscriptions of these species by Walter have proved to be both accurate and diagnostic. From the descriptions, supplemented by photographs of the two remaining types (now preserved at the British Museum) and using a procedure of elimination, it has been possible to confirm the identity of each of the Walter species and to corroborate the relegation of the Michaux names to synonymy. These three represent the only species of Marshallia known up to the year 1824 .

Subsequent works of both regional and monographic scope summarized the current knowledge concerning the genus, incorporating new species as they were discovered and additional morphological and geographical data. These various treatments saw the gradual elimination of certain errors as well as the perpetuation of others. In this connection it seems appropriate to emphasize that erroneous application of names has been one of the major factors responsible for the nomenclatural as well as taxonomic confusion found to be so prevalent in this group. These difficulties are clearly traceable in most instances to the failure of many of the workers to consult the type collections.

The first and only real revisional treatment of the genus Marshallia was made by Beadle and Boynton (Bilt. Bot. Stud. 1: 3-10, pls. 1-11. 1901). This work was prompted by an accumulation of specimens of Marshallia at the Biltmore Herbarium (Biltmore, North Carolina) which could not be satisfactorily associated with representatives of the known species. As a result, three new species and one variety, all still in good taxonomic standing, were described. In an attempt to re-define certain of the earlier published species, Beadle and Boynton not only perpetuated the erroneous application of the Walter epithets obovata and graminifolia, but, under the former, recognized var. platyphylla (Chapman's Fl. Southeastern States, page 241. 1860), the type of which is identical with that of Athanasia obovata Walt. and, under the latter, upheld var. cyananthera Ell. (Sk. 2: 315-317. 1824) as erroneously interpreted by Fernald (Bot. Gaz. 14: 1435. 1897). Small's Marshallia lacinarioides (Bull. Torr. Bot.

Club 25: 482. 1898) was included in the treatment, but the species was reduced to varietal rank. The recognition of lacinarioides as a variety of Marshallia graminifolia by Beadle and Boynton illustrates their poor understanding of the taxonomy of the grassleaved complex, as well as their inadequate knowledge of the morphological variation and geographical distribution of Walter's graminifolia. Apparently Beadle and Boynton did not consult the Walter types. The species proposed by Rafinesque (New Fl. 4: 77. 1836) and Bertoloni (Misc. Bot. 15: in Mem. Accad. Sc. Instit. Bologna 5: 442, t. 21. 1854) were not treated by Beadle and Boynton. In the introduction of their revision the authors stated that they were unable to interpret the species proposed by Rafinesque and Bertoloni because they were unable to authenticate the names. Although from the standpoint of nomenclature and geographical distribution of the taxa the work may be justly criticized, Beadle and Boynton's revision is nevertheless much more comprehensive than the former treatments of the genus. A total of eleven taxa was included, ten of which are recognized taxonomically in the present treatment.

The over-all history of the group entails a total of 23 different specific and varietal epithets, each of which has been used in combination with the generic name Marshallia. Of these, 18 apply to the 10 entities currently known to comprise the genus Marshallia Schreb.; 5 apply to species of other genera.

## Morphological and Taxonomic Criteria

As a genus, Marshallia is based upon numerous rather welldefined morphological characters. The genus is so distinctive, in fact, that it cannot be related with certainty to any of the helianthoid genera with which it is associated. The species, however, are very similar, with a paucity of strong, contrasting differences that may be regarded as "fundamental" characters. It would appear that evolutionary pressures have been most effectively exerted upon the vegetative organs, for the floral apparatus of the various species is fundamentally the same. The structural details of the florets, for example, are so similar as to provide few characters of value in distinguishing the species or in suggesting relationships. In contrast to the relative stability of the floral apparatus, the vegetative structures are often considerably variable and must be used with caution as taxonomic criteria. While the individual plants may easily be distinguished on the basis of appearance and may even be properly classified, the problem
has been one of expressing differences on a firmly objective basis. To this end, various morphological characters have been studied and evaluated. No single criterion, however, was found to be applicable throughout the genus. The differences between taxa are usually expressed by combinations of characters which vary from one species to another.
habit.-The genus Marshallia contains scapose and subscapose as well as caulescent growth forms. While the distinction between subscapose and simple caulescent specimens is not always absolute, the two subscapose-scapose taxa, M. obovata var. scaposa and M. caespitosa var. caespitosa, have been treated as varieties differing from their distinctly caulescent counterparts by additional, though rather tenuous, morphological characters. In both cases the varieties occupy distinct geographical ranges and habitats. For these reasons both varieties named above are recognized taxonomically in the present treatment. The stemless or nearly stemless habit is considered to be a derived feature in the genus, which is in keeping with a general theory of reduction from caulescent progenitors. Correlated with the purely morphogeographical basis upon which these two pairs of varieties are recognized is the fact that the geographical areas supporting the subscapose-scapose representatives are geologically more recent than the areas supporting their caulescent counterparts.

Of the caulescent Marshallias only two representatives are regularly unbranched, M. obovata var. obovata and M. grandiflora. Marshallia trinervia, while usually simple-stemmed also, may be sparingly branched from the upper leaf axils. Marshallia Mohrii is the only species which is apparently regularly branched. The remaining taxa are typically freely cymosely branched but all of them contain a small proportion of individuals with simple stems.

In those specimens which are branched, the flowers of the central, terminal head open first, followed centrifugally by the secondary heads which arise on peduncles or branches from the leaf axils. Thus, while the individual heads are indeterminate. the overall inflorescence system in the branched plants is of a determinate type. In spite of the fact that Small (Manual of the Southeastern Flora, page 1457. 1933) has described two species (M. ramosa and M. Mohrii) as corymbosely branched, perhaps in a non-specific sense to denote the more or less flat-topped form of the plants, it is more accurate to regard the branching as cymose.

Photographs have been included of representative specimens of the various taxa for the purpose of illustrating the comparative differences in growth habit. These photographs, however, do not render the fine details of structure.

воотятоскs.-Marshallia trinervia is apparently the only species which produces evident rhizomes under field conditions. Unfortunately, these structures are not often collected and thus the character is of dubious taxonomic value when dealing with herbarium material. The other species are perennial by means of upright, non-woody, crown- or caudex-like bases. During the growing season offsets are produced, which, by the following season, have become freed of connection with the parent through the disintegration of the rootstock of the previous season and are finally established as individual plants. This feature is typical of the varieties of M. obovata. In other species, especially the varieties of M. caespitosa, the crown may persist for two or more years, in which case it may become rather fleshy and tuberous, or even rhizomatous under greenhouse conditions, with many congested, transverse nodes marking the position of numerous radical leaves.
stems.-Morphological aspects of the stems are so uniform as to provide no means of distinguishing the species. The stems are characteristically striate and more or less angled in cross section, features apparently related to the three-nerved venation and more or less clasping insertion of the leaves. The reddish color of the stem bases has been included in the descriptions of those taxa for which it is considered to be relatively uniform, but color is never more than a supplementary feature and is of no diagnostic significance.
pubescence.- The peduncles and the external surfaces of the corollas are regularly pubescent in varying degree but always with uniseriate trichomes of several moniliform cells. These hairs are usually ascending-incurving in position and vary from white to reddish purple in color. Because of its relative uniformity, pubescence has proven to be of little taxonomic significance, although the degree of pubescence on the peduncles aids in distinguishing certain species.
leaves. - In all of the species of Marshallia the leaves are alternate, simple, entire and longitudinally 1-3-nerved. The leaves are strictly glabrous throughout the genus except occasionally for a few hairs on the lower surfaces of the upper, reduced leaves of M. graminifolia, and these usually pass unnoticed.

The fresh foliage of all the species is minutely impressedpunctate. In some of the species these punctations are clearly resin glands in which resin droplets are usually visible in dried material under $10 \times$ magnification, at least over designated portions of the leaves. This is subject to apparent exception, however, for the physiological condition of the plant when collected and the method of drying and preservation often render resin droplets invisible. In other cases, the punctations apparently are not related to resin secretion or else, if resin is produced, it is not in a quantity sufficient to be detected, even with magnification. The character, therefore, is of very limited use in distinguishing the taxa. It has been employed only in a supplementary way where the differences are more or less pronounced and only in the absence of more practical diagnostic features.

Although there is considerable variation in leaf texture, it has not been possible to describe this quality, except on a comparative basis with related species in which the leaf texture is markedly different. On this basis, it is of assistance in distinguishing the very thin-leaved $M$. trinervia from $M$. grandiflora and $M$. Mohrii which have considerably thicker leaves. The comparatively thin texture of the leaves of M. trinervia is more apparent in dried than in living material. Elsewhere in the genus differences in leaf texture can be detected only after much experience. Subjective characters such as this have been omitted.

The genus may be divided into two primary units on the basis of narrow vs. broad leaves, i.e. leaves usually four to many times longer than broad vs. leaves usually less than four times longer than broad, respectively. There are admittedly minor exceptions to this seemingly artificial classification, yet, when the probable final relationships are considered using all available criteria, including morphology and geographical distribution, these units take on more natural characteristics. Nevertheless, these units are not here recognized in formal taxonomic status.

The possession of elongate, linear-lanceolate, more or less erect radical leaves, differing in no essential way from the lower cauline, is a feature of only two species of the genus, namely M. graminifolia and M. ramosa. Even in the seedling stages the radical leaves of these two species are of this form. Occasionally, however, specimens of M. ramosa do have the horizontal-spreading, obovate-spatulate type of radical leaf, but this is not considered to be typical of the species and may possibly have resulted from hybridization with M. tenuifolia. The
basis for this belief is discussed at some length under the systematic treatment of M. ramosa. The remainder of the genus is characterized by having rather broad, horizontal-spreading, obovate, spatulate or oblong-obovate radical leaves, differing conspicuously in form from the lower cauline. Unfortunately, however, the radical leaves are not always present on the specimens, often being shaded or crowded out by other plants or being the first to shrivel and die with the onset of drought. This is particularly true of M. tenuifolia (Plate 12) which can be distinguished easily from M. graminifolia (Plate 11) on the basis of the possession of basal leaves of an obovate, spreading type. For obvious reasons, therefore, the presence or absence of the obovate-spatulate type of radical leaves is not, from a practical standpoint, an ideal character for distinguishing the species. Nevertheless, M. graminifolia and M. tenuifolia differ mainly in this respect, so the character has of necessity been employed at this point in the key.

It should be emphasized that the spreading, obovate-spatulate type of radical leaves is a common feature of most species of the genus. Consequently, the radical leaves should be excluded from consideration in making the initial choice when using the key to the species. Cauline leaves should be considered exclusively, unless the specimens in question are scapose or subscapose in habit, in which case the basal leaves must of necessity be used. When dealing with scapose or subscapose specimens in which there is obvious differentiation in leaf form, the innermost leaves should be considered in preference to the very basal, radical leaves.

Leaf shape and size are useful means for distinguishing only a few of the species. In general, close relatives are very similar in this respect, with the range in variation precluding the use of either leaf shape or size. The gradual and successive diminution in size of leaves from the base of the plant upwards, constant in certain species, contrasted with more or less uniform leaves of little reduction in size from the base upwards, provides a useful means for distinguishing species. Such variation imparts rather distinctive gross features to the taxa, providing valuable means for distinguishing closely related species of the broadleaved group, as, for example, Marshallia obovata (var. obovata) and M. grandiflora.
peduncles.-The peduncles are very similar in all the taxa. They are longitudinally grooved (sulcate) and more or less
pubescent. There is some variation among species in the degree of the pubescence from the base of the peduncles to the summit. This has been used to supplement the taxonomic distinction between M. grandiflora and M. Mohrii.
phyllaries.-The phyllaries, despite their peculiar, abrupt variation even in the same taxon, have proven to be perhaps the most significant taxonomic character. The phyllaries vary in shape from linear to oblong, lanceolate, rhomboidal and ovate, with variation in the shape of the apices from obtuse to acutish, acuminate and subulate. Marshallia graminifolia and the related species, M. tenuifolia, are regularly pubescent, while the others are glabrous or nearly so. In addition, there is considerable variation in the margins, some phyllaries being white-hyaline in varying degrees, others winged, entire or somewhat erose or remotely dentate. The genus may be divided into four species groups on the basis of the form of the phyllaries, two in the broad-foliaged part of the genus and two in the narrow-foliaged part of the genus. The arrangement of the species in the natural key and in the systematic treatment is designed to emphasize these relationships. The form of the phyllaries of each taxon is illustrated in Plate 1. Five of the species have acute or acutish phyllaries, although these comprise two groups when subdivided on the basis of leaf form and flowering habit: M. trinervia (fig. 1), M. Mohrii (fig. 2) and M. grandiflora (fig. 3)-all with broad leaves and flowering in summer; M. ramosa (fig. 7) and M. caespitosa (figs. $8 \& 9$ )-both with narrow, elongate leaves and flowering in spring. The Fhyllaries of M. obovata (figs. $4 \& 5$ ) are distinctly obtuse and typically possess white-hyaline borders below the middle. Like M. ramosa and M. caespitosa, both varieties of M. obovata flower in spring but they are most closely allied to the summer-flowering species, having the broad leaves and other features suggestive of that group. Marshallia graminifolia (fig. 6) and M. tenuifolia (fig. 10) are unique in possessing subulate phyllaries. These two species flower in late summer and fall.
pales.-The pales of all of the taxa are more or less linear in outline or sometimes slightly dilated at the summit (Plate 1). The pales of a particular species group reflect the general nature of the phyllaries of the same group. Glabrous, clavate-spatulate pales, for example, are correlated with the obtuse phyllaries of the varieties of Marshallia obovata, while pubescent, subulate pales are for the most part correlated with the pubescent, subulate phyllaries of the fall-flowering, grass-leaved species. In the


Plate 1. Representative phyllary (the broader member of each figure-pair) and pale (the narrower member) of each of the species of Marshallia, to scale: Fig. 1. M. trinervia: Fig. 2, M. Mohrii; Fig. 3, M. grandiftora: Fig. H. M. olou'ata var. nbovata; Fig. 5, M. obotata var. scaposa; Fig. 6, M. graminifolia: Fig. 7, M. ramosa: Fig. 8, M. caespitosa var. caespitosa: Fig. 9, M. caespitosa var. signata; Fig. 10, M. tenuifolia.
two remaining species groups the differences in respect to the form of the phyllaries and pales are not at all pronounced. In these, however, the pales are in general merely acute, corresponding to the acute phyllaries of the two groups in question.

The presence or absence of resin glands on the phyllaries and pales tends to be a useful character in certain specific instances, but because of the apparent sporadic occurrence or absence of such glands in the same taxon, the character has been largely abandoned. The presence of resin droplets on the phyllaries and pales of M. obovata var. scaposa, however, is of assistance in distinguishing this variety from $M$. obovata var. obovata which usually does not have such droplets at all.
florets.-As stated elsewhere, the florets of all of the taxa are in general very similar and are consequently of little value in classification. The corollas are all tubular and externally pubescent, with long, narrow, equal and spirally twisted limbs. Two species, $M$. trinervia and $M$. grandiflora, are unique in having the corolla-tube more or less conspicuously dilated at the summit into a distinct throat. The corollas of the other species are either narrowly tubular and not dilated at all or, if dilated, with only very shallow throats.

Corolla color is subject to considerable variation even in the same taxon. The florets of M. obovata var. obovata, the varieties of $M$. caespitosa and M. ramosa are predominantly white or cream-colored; the remainder of the taxa have predominantly purplish or pale lavender, rarely whitish florets.
anthers.- The anthers of all the species are similar in form, having characteristic ovate, inwardly keeled terminal appendages and minutely sagittate bases. The anthers vary in color from cream to purplish, pale lavender and "blue."
pollen.-Pollen grains were examined for possible means of distinguishing the varieties of M. obovata, as well as the varieties of $M$. caespitosa. The pollen grains were found to be globular with spinescent surfaces, each grain having three germinal pores. No taxonomically significant difference in size or structure was detected.
stigmas.-The stigmas of all of the species are quite uniform in structure and size. They are divergent at anthesis, exserted beyond the anther-column, soon becoming strongly recurved in position. The stigmas are half-cylindric, externally pubescent with short hairs or papillae and have obtuse or blunt-tipped apices.
achenes.-The achenes of herbarium specimens of Marshallia are often immature, thus extreme care should be exercised when interpreting the specified shapes, sizes and degree and length of pubescence. The achenes of all the species are more or less turbinate or clavate in shape, being broadest near the middle or at the apex and varying from 1 to $4(-5) \mathrm{mm}$. in length. The achenes are generally 5 -angled and 10 -ribbed, with five alternate ribs often being more prominent than the five intervening ones. The achene-surface between adjacent ribs is usually concave and, with the apparent exception of M. grandiflora, is beset with minute resin atoms. The ribs are furnished with longitudinally biseriate trichomes, with minutely bifid apices. The length of these trichomes apparently varies with the relative maturity of the achene, but when the length of trichome is expressed in terms of relative distance between adjacent ribs, this character can be used in conjunction with others to distinguish the two varieties of M. obovata.
pappus.-The pappus of all Marshallia species consists of 5-6 (-7) distinct, membranous scales. These scales are usually obovate, oval or deltoid in outline and usually have acute or acuminate apices. There is considerable variation in the size and shape of pappus scales even in the same taxon. For the most part this renders the scales valueless as taxonomic characters, especially in distinguishing varieties where characters are most needed. In a few cases, however, the scales of certain taxa are markedly different and have been used accordingly in the key. Plate 2 illustrates the comparative variation of selected pappus scales of the ten taxa recognized in this treatment. The figures of these plates, however, do not represent the total range in the variation of the pappus of any particular taxon. The diagrams have been included to supplement the description of the scales, which could not always be easily and lucidly expressed.

Anatomically, each scale is composed of elongated prosenchymatous cells, the tips of which project so as to give the surface of the scales a minutely papillose appearance under magnification. The scales are nerveless. The margins may be regularly serrulate by projecting cell tips or irregularly lacerate.

The broken or irregular condition of the pappus-scale margin is helpful in distinguishing M. Mohrii (fig. 3) from M. trinervia (fig. 1) and M. grandiflora (fig. 2). Inasmuch as these three species have pappus scales of very characteristic shapes, they may even be distinguished taxonomically on this basis. The pappus


Plate 2. Representative pappus scales of the species of Marshallia, to scale: Fig. 1, M. trinervia; Fig. 2, M. grandiflora; Fig. 3, M. Mohrii; Figs. 4 \& 5, M. obovata var. obovata; Figs. 6 \& $7, M$. ohovata var. scaposa; Figs. 8-11, M. ramosa; Figs. 12 \& 13, M. caespitosa var. signata; Figs. $14 \& 15, M$. caespitosa var. caespitosa; Figs. 16-19, M. tenuifolia; Figs. 20-24, M. graminifolia.
scales of $M$. trinervia, in fact, are quite uniform in shape and are unique in being subaristate. There is an apparently significant difference in size between the pappus scales of the two varieties of M. obovata (figs. 4-7). Although there is a small percentage of intergradation, the varieties can usually be distinguished on this basis. The pappus scales of M. caespitosa (figs. 12-15), however, are so variable in size that the two varieties cannot be distinguished on the same basis. On the contrary, there is a very great difference in the size of the pappus scales of the M. caespitosa varieties as compared to the related species, M. ramosa (figs. 8-11). The variation in the form and size of the pappus pales of the two grass-leaved Marshallias, M. graminifolia (figs. 20-24) and M. tenuifolia (figs. 16-19), is such that it is impossible to distinguish the species on this basis.

## Generic Relationships

With certain modifications, the system of classification of the Compositae generally followed today may be said to date from the work of Cassini ${ }^{9}$ (1813-34). Utilizing modifications of the anthers and style in addition to various other characters, Cassini was the first to undertake a general revision and re-distribution of the various members. Marshallia was included in this systematic arrangement by Cassini (Dict. Sci. Nat. 55: 265. 1828) as a member of the Heliantheae-Helenieae (under the Caléinées, between the Galinsogées and the Hyménopappées). This marks the first attempt by anyone to place Marshallia in any comprehensive system of subfamilial classification. In the important treatments of the Compositae which closely followed (Lessing, ${ }^{10}$ De Candolle, ${ }^{11}$ Torrey and Gray ${ }^{12}$ ) the genus was retained in the Helenieae. It was not until 1873 that the genus was placed in its present position in the Heliantheae. This change was made by Bentham in Bentham and Hooker's Genera Plantarum, volume 2, page 198. In this work, Marshallia, together with Galinsoga, Calea, Balduina, Blepharipappus, Tridax and Dubautia, comprise the Subtribe Galinsogeae. These genera had previously been classified mostly under the Helenieae because of the possession of a scaly pappus, but their affinity, according to Bentham (Journ. Linn. Soc. 13: 446. 1873), appears to be with the Subtribe Ver-

[^16]besineae, which they resemble in habit, the paleaceous receptacle, etc. ". . . so much so that some species of Calea where the pappus is occasionally or constantly deficient, are difficult to distinguish from Sabazia and its allied Verbesineous genera." Three of the genera, Marshallia, Blepharipappus and Balduina, are exclusively North American.

In Hoffmann's treatment of the Compositae for Engler and Prantl's Die natürlichen Pflanzenfamilien (IV. 5: 24-247. 1890) the same classification was maintained, with the addition of two other genera to the subtribe: Railliardia of the Hawaiian Islands and Bebbia of the southwestern United States. The subtribal name, Galinsoginae O. Hoffmann, dates from this work. Subsequently, the genus Geissolepis Robinson (Proc. Amer. Acad. 27: 177. 1893) of Mexico was added, making a total of ten genera.

These ten genera comprising the Galinsoginae have in common the pluripaleaceous pappus (although highly variable in form and structure) and achenes which are commonly turbinate and 5 -angled. Otherwise, however, the genera are very similar to the Verbesineae. The receptacle is chaffy throughout, but otherwise the genera possess characters of the Helenieae.

It is not within the scope of this problem to discuss or attempt to evaluate the relative merits of the systematics of the Heliantheae and Helenieae. Such an undertaking would be presumptuous on the part of the writer as this would require a wide and intimate familiarity with Compositae in general. It would appear, however, that the subtribe Galinsoginae is a very heterogeneous assemblage of genera and that Marshallia is not closely related to any one of the present members. Cronquist (Amer. Midl. Nat. 53: 478-511. 1955) has correctly pointed out that Marshallia, which appears to be without a close relative, shows no direct evidence of a radiate ancestry and, unlike most helianthoid genera, has strictly cyanic flowers and wholly alternative leaves as in the Vernonieae. The deeply lobed corollas find their closest match among the Mutisieae, although a similar condition is not unknown in the Vernonieae and Eupatorieae. According to Conquist, there is no question, however, of transferring Marshallia to any of the discoid tribes. To do so would be to alienate it from genera with which its style agrees.

I concur in the belief that Marshallia is best associated with the Heliantheae, although, as stated above, it must occupy a relatively isolated position there.

Marshallia comprises a group of perennial herbs characterized
by distinct, herbaceous receptacular pales, phyllaries in 1-2 subequal series and homogamous heads of cyanic tubular florets with long, linear, equal limbs. The leaves are alternate, simple, entire, 1-3-nerved and glabrous. The peduncles and the external surfaces of the corollas are clothed with uniseriate, moniliform hairs. The pappus is comprised of 5-6 distinct, membranous, nerveless scales. Each scale is composed of long cells, the ends of which project above the surface so as to produce a minutely "scabrous" appearance under magnification. The ribs of the achenes bear longitudinally biseriate, minutely bifurcate trichomes. The herbage, as well as the corollas and achenes, are commonly beset with resin droplets. This unique combination of characters serves to set Marshallia apart as a remarkably distinctive genus, without close relationship to any other member of the tribe.

## Intrageneric Relationships

As stated previously, Marshallia may be divided into four groups of closely related species on the basis of the form of the leaves, phyllaries and pales. These four groups are shown in the following scheme, an arrangement designed to indicate their presumed relationships based upon the available information.

Group 1 is comprised of what may be regarded as the most primitive or generalized members of the genus, characterized by broad leaves, acute phyllaries and pales and a summer-flowering habit. Although the wide-ranging Marshallia trinervia also occurs on the lowlands, all the species of this group have an Appalachian center of distribution (Map 1). Of the three species, M. grandiflora and M. Mohrii are perhaps most closely related morphologically, although phases of the variation of M. trinervia often closely approach both. The very localized distribution and rarity of M. Mohrii suggests a relict species of comparatively old age. Marshallia grandiflora has the most northerly distribution of all the species and, like M. Mohrii, is confined to the southern Appalachians. Marshallia trinervia is one of the most distinctive species of the genus due to the broad, thin-textured, conspicuously acuminate, three-nerved leaves. It is also one of the least variable of the species. It often branches from the upper leaf axils and produces secondary heads in a manner suggestive of an ancestral type of M. Mohrii which apparently always bears several heads in a corymbosely branched inflorescence-system.
Marshallia obovata comprises Group 2. This species has broad
leaves like those of Group 1 but differs in the obtuse phyllaries, clavate-spatulate pales and a spring-flowering habit. Of the two varieties of $M$. obovata, the scapose variety of the geologically more recent Coastal Plain is considered to be the derived member. Marshallia obovata var. obovata is characteristically caulescent and monocephalous like M. grandiflora, the two often closely resembling one another in habit and in other features. Maps 1

M. tenuifolia

M. trimervia
:
and 2 reveal the close geographical relationship of these two taxa and further suggest that the direction of the evolution and spread of $M$. obovata may have been from the Appalachian highlands to the Coastal Plain.
Group 3 is comprised of Marshallia caespitosa, widely distributed in Texas and Oklahoma and occurring west of the Mis-

sissippi only, and M. ramosa, a localized endemic of south-central Georgia. These species have in common elongate, narrow leaves,
acute or acutish phyllaries and a spring-flowering habit. The relationships of the components of this group are discussed in the systematic treatment. The present geographical distribution of members of Group 3 (Map 3) suggests an early divergence from Group 1. The evidence of a morphological line of connection between these two groups is very fragmentary. It involves the close similarities of M. Mohrii (Group 1), itself a localized endemic, to the unusually broad-leaved specimens of M. caespitosa var. signata from Ozark County, Missouri, which represent a population presumably relict in that area. Although clearly to be classified with M. caespitosa var. signata, the disjunct Ozark County population is nevertheless atypical of the variety which is otherwise confined to Texas. The spring habit of flowering suggests a common source for Groups 2 and 3. Such a relationship may account for the presence of obtuse phyllaries in certain populations of $M$. ramosa, a species most closely related to $M$. caespitosa. The endemic nature of the distribution of $M$. ramosa, adjacent to the range of $M$. obovata, suggests a divergence from Group 1 similar to that of M. caespitosa var. signata.

Group 4 is not easily related to the remainder of the genus. The subulate-tipped, pubescent phyllaries and pales which characterize the group represent the greatest morphological divergence within the genus. The species are distributed along the outer Coastal Plain from North Carolina into Texas and flower in the late summer and early fall. Considerably variable as to quantitative morphological characters, these species are regarded as the most highly evolved members of the genus. Although representing divergent evolutionary trends evidently of considerable age, Groups 3 and 4 apparently retain some measure of genetic compatibility. Hybridization is believed to have occurred between $M$. ramosa and $M$. tenuifolia in the area where the ranges of these two species abut. The evidence for this is presented under the discussion of M. ramosa in the systematic treatment. The common feature of elongate, linear leaves further suggests a connection between Groups 3 and 4 , as well as the fact that branching, with the accompanying production of many heads, reaches its best development in these groups.

## Systematic Treatment

Marshallia Schreb.
Marshallia Schreb. Gen. Pl. 2: 810. 1791, not J. F. Gmel. 1791.

Nomen conservandum. ${ }^{13}$ Type-species: M. obovata (Walt.) Beadle \& F. E. Boynt. [M. lanceolata (Michx.) Pursh].

Persoonia Michx. Fl. Bor.-Am. 2: 104, 105. 1803, not Smith. 1798. Type-species: P. lanceolata Michx. [M. obovata (Walt.) Beadle \& F. E. Boynt.].

Trattenikia Pers. Syn. Pl. 2: 403. 1807, not Trattinikia Willd. 1806. Type-species: T. lanceolata (Michx.) Pers.

Phyteumopsis Juss. ex Poir. Encye. Suppl. 4: 405. 1816. Typespecies: P. lanceolata (Michx.) Poir.

Peremial, caulescent, subscapose or scapose, erect herbs from nonligneous caudices or rhizomes with relatively coarse fibrons roots. Pubescence, except that of the achene, consisting of uniseriate trichomes, composed of several transparent, moniliform cells, the hairs ascending-incurving in position, sometimes somewhat spreading, regularly occurring about the summit of the peduncles and on the external surfaces of the corollas. Herbage, including the phyllaries and pales. odorless, obscurely glandular-dotted or impressed-punctate. often with resin droplets. Leaves alternate, simple, entire, 1-3-nerved, not manifestly veiny, glabrous, sessile or contracted into somewhat vaginate. petiole-like bases, the cauline leaves somewhat clasping. Caulescent members with striate, somewhat angled, glabrous or puberulent stems. simple or sparsely to freely eymosely branched, terminated by long-

[^17]pedunculate heads; acaulescent members with simple scapes or peduncles. Peduncles naked or leafy-bracted, more or less terete, sulcate, glabrous or sparsely pubescent below, becoming more densely pubescent upwards, usually copiously so about the summit. Involucres hemispherical or campanulate, composed of herbaceous phyllaries, often with hyaline margins, subequal in 1-2 series, imbricate or merely approximate and not at all imbricate, glabrous or pubescent. Receptacle convex or conical, usually hollow, paleaceous, in age pitted with shallow depressions (the achene-scars) and with as many pales, palescars or pale-bases (the tenacious stubble of broken pales). Pales of the receptacle herbaceous, often hyaline-margined below, narrowly linear in outline, longer than the achenes, rigid, inwardly arched above, glabrous or pubescent, persistent or tardily deciduous. Heads homogamous, many-flowered, all the florets tubular, perfect and fertile. Corollas white, cream-colored, pale-lavender or purplish, longer than the pales, externally pubescent, the tubes slender, sometimes dilated upwards, the five equal limbs long and linear, more or less spirally twisted at anthesis, the obtuse apices strongly cellular-thickened. Filaments glabrous, filiform, shorter than the anther-column, inserted near the summit of the corolla-tube, the anthers linear-oblong, slightly or minutely sagittate at the base, each with a distinct, ovate appendage at the apex, the appendages dorsally concave and ventrally keeled, the anther-column white, cream, pale lavender or purplish in color, exserted beyond the corolla-tube. Stigmas divergent or recurved at anthesis, half-cylindric or somewhat flattened, truncate or with blunt, obsoletely thickened tips, slightly pubescent or somewhat papillose, exserted beyond the anther-column, shorter than the terete, filiform, style. Corolla and style soon deciduous after anthesis. Achenes turbinate or clavate, truncate, comewhat 5 -angled, 10 -ribbed, the ribs with longitudinally bicellular trichomes with minutely bifurcate apices, the achene-surface between the ribs concave and usually beset with minute resin atoms, these rarely absent. Pappus-scales 5 (sometimes 6 ) in number, erect or spreading in position, forming a crown at the summit of the achene, membranous-scarious in texture, translucent, white-hyaline or ferrugineous in color, ovate, ovate-lanceolate or tri-angular-lanceolate in outline, sessile, the apices acuminate, acute or somewhat obtusish, the margins regularly or irregularly serrulate or lacerate, the surfaces minutely upwardly roughened by projecting cell tips.

## NATURAL KEY

A. Leaf blades, except the lowermost, of a broad, ovate or lanceolate type, usually not more than 4-5 times longer than broad
B. Phyllaries and pales of the receptacle acute, the pales linear, only slightly if at all dilated at the summit; plants flowering in the summer
C. Leaves thin-membranous in texture, appearing distinctly so in drying, the middle and upper extending without much reduction in size to the summit of the stem, the lower cauline (often shriv-
eling in age) being scarcely longer than those above; internodes usually $10-25$ in number, not greatly reduced in length upwards; plants with creeping rhizomes, without the fiber of old leaf bases; pappus scales with very short, triangular bases, little or not at all imbricate, abruptly contracted into long, filiform acuminations, subaristate

1. Marshallia trinervia.
C. Leaves thick and firm in texture, especially in age, the middle and upper rapidly decreasing in size, the lower cauline (usually intact) being distinctly longer than those above; internodes usually 4-12 in number, successively reduced in length upwards; plants with short caudices surrounded by fiber of old leaf bases; pappus scales with ovate bases, usually more or less imbricate, gradually narrowed into acuminate apices, not at all aristate
D. Stem simple, bearing only one head; peduncle usually copiously pubescent near the summit; phyllaries usually with conspicuous white-hyaline borders at least below the middle, the adaxial surfaces smooth or at least not raised-veiny; corolla-tube regularly dilated upwards into a distinct throat $2-3 \mathrm{~mm}$. long; surface of achene between the ribs without resin atoms; pappus scales regularly serrulate, the margin usually unbroken by irregular points
2. Marshallia grandiflora.
D. Stem cymosely branched above the middle, bearing $2-10$ heads; peduncle usually only sparingly pubescent near the summit; phyllaries usually without conspicuous white-hyaline borders, the adaxial surfaces usually raised-veiny; corolla-tube not dilated upwards into a distinct throat; surface of achene between the ribs bearing minute resin atoms; pappus irregularly serrulate, the margins broken by a few sharp points . 3. Marshallia Mohrii.
B. Phyllaries and pales of the receptacle obtuse, the pales linear-spatulateclavate, usually conspicuously dilated at the summit; plants flowering in the spring and early summer
3. Marshallia obovata
E. Plants caulescent, the leafy portion usually not less than $1 / 4$ the length of the peduncles, sometimes as long or longer; lateral nerves of the leaves usually prominent to the naked eye; upper leaf surfaces, outer (abaxial) surfaces of the phyllaries and pales usually without resin glands and only occasionally beset with a few scattered resin droplets; achenes clavate at maturity, broadest below the slightly constricted summit, the hairs of the ribs usually shorter than the distance between adjacent ribs; pappus scales ( $0.5-$ ) $1-1.5 \mathrm{~mm}$. long, usually regularly serrulate, sometimes somewhat lacerate; plants typically of clayey soils in the Piedmont and Mountains from Virginia to Alabama, extending into the Coastal Plain and reaching Florida along the drainage area of the Chattahoochee between Georgia and Alabama . 4a. var. obovata.
E. Plants strictly scapose, all the leaves basal, or subscapose with a few stem leaves, but with the leafy portion usually less than 1,4 the length of the peduncle; lateral nerves of the leaves (especially from the upper surface) usually obscure to the naked eye; upper leaf surfaces, outer (abaxial) surfaces of the phyllaries and pales usually with seattered resin glands and beset with minute resin droplets; achenes turbinate at maturity, broadest at the truncate summit, the hairs of the ribs usually longer than the distance between adjacent ribs; pappus scales (1-) 1.5-2.5 (-3) mm. long,
usually irregularly lacerate, sometimes regularly serrulate; plants typically of sandy soils in the Coastal Plain from North Carolina to Florida and Alabama

4b. var. scaposa.
A. Leaf blades, except the lowermost, of a narrow, linear or linear-attenuate type, usually 4 -many times longer than broad
F. Phyllaries and pales of the receptacle merely acute, sometimes obtuse and minutely mucronate, but not subulate-tipped (or rarely so in M. ramosa), glabrous; phyllaries not winged, with or without narrow hyaline borders, linear or lanceolate in shape; plants flowering in the spring and early summer
G. Pappus scales mainly less than 2 mm . long, usually shorter than the achene; phyllaries $4-6 \mathrm{~mm}$. long; involucres usually $6-10 \mathrm{~mm}$. wide, rarely to 12 , thus heads small; peduncle only sparsely pubescent near the summit; local endemic in east-central Georgia

## 5. Marshallia ramosa.

G. Pappus scales mainly over 2 mm . long, usually as long or longer than the achene; phyllaries $6-12 \mathrm{~mm}$. long; involucres usually $15-30 \mathrm{~mm}$. wide, thus heads large; peduncle densely pubescent near the summit; plants occurring west of the Mississippi River

> 6. Marshallia caespitosa.

H
H. Plants scapose or subscapose, monocephalous; the leaves (excepting, when present, the obovate or spatulate basal leaves) extending to more or less the same level; leafy portion of stem much shorter than the peduncle ..........6a. var. caespitosa.
H. Plants caulescent, usually branched and bearing few-many heads, but sometimes simple and monocephalous; the leaves (gradually reduced above) extending to various levels on the stem; leafy portion of stem as long or longer than the peduncles, rarely shorter

6b. var. signata.
F. Phyllaries and pales of the receptacle strongly acuminate or subulatetipped, pubescent with scattered moniliform trichomes; phyllaries usually winged at least below the middle, usually shouldered and of a rhomboidal form; plants flowering in the late summer and early fall
I. Basal and lower cauline leaves with elongate, ascending, linearlanceolate, prominently 3 -nerved blades of relatively firm, thick texture; the wiry vascular fiber of old leaf bases usually intact at the base of the plant; plants of the Coastal Plain of North and South Carolina
7. Marshallia graminifolia.

1. Basal and lower cauline leaves horizontal-spreading, with spatulate, elliptic to elliptic-ovate, oblong or oblong-ovate, obtuse, 3-nerved blades of relatively thin-membranous texture, the lateral nerves not prominent; the base of the plant without the wiry valscular fiber of old leaf bases; plants of the Coastal Plain from Georgia to Florida and Texas
2. Marshallia tenuifolia.
3. Marshallia trinervia (Walt.) Trel. ex Bramner \& Cov.

Athanasia trinervia Walt. Fl. Carol. 201. 1788. (Charl-Neotype: marked "Marshallia latifolia, St. John's [Parish], Berkley, So. Ca [r]., June [18] '41," Cranmore Wallace Herbarium.)

Persoonia latifolia Michx. Fl. Bor.-Am. 2: 105, pl. 43. 1803. "Hah.
in montosis Carolinae"; A. trinervia Walt. cited as a questionable sinonym. (Lectotype-tab. 43, Michx. Fl. Bor.-Am. 2: 105. 1803.)

Trattenikia latifolia (Michx.) Pers. Syn. Pl. 2: 403. 1807.
Marshallia latifolia (Michx.) Pursh, Fl. Amer. Sept. 2: 519, 520). 1814. "In the Carolina mountains . . . v. s. in Herb. Walter."; A. trinervia Walt. cited as a synonym.

Marshallia Schreberi J. F. Gmel. sensu Tratt. Arch. Gew. 1: 108. 1814.

Phyteumopsis latifolia (Michx.) Poir. Encere. Suppl. 4: 406. 1816. "v. s. in Herb. Michx."; A. trinervia Walt. cited as a ssnonym.

Marshallia trinervia (Walt.) Trel. ex Branner \& Cov. Rep. Geol. Surv. Ark. 4: 196. 1889. Basionvm cited and M. latifolia [Michx.] Pursh as a synonvm. Credit for the earliest publication of this combination has been erroneously attributed to Porter, Mem. Torr. Bot. Club 5: 377. 1894.

Peremnial herb (3-) 4-7(-8) dm. in height, stems usually arising singly from a thickish, sometimes slender, short-creeping, horizontal or ascending rhizome with coarse fibrous roots; the plants sometimes apparentl! solitary but usually occurring in small to large clump-like colonies with some of the stems sterile. Stem leafy, glabrous, striate. usuall obtusely 4 -5-angled and often purplish below. becoming distinctly grooved and greenish near the peduncle. Peduncles (4-) 10-$20(-24)$ ( mm . long, terminating the stem (and branches when present). sukate, glabrous to glabrate below, becoming distinctly pubescent below the head. Leaves glabrons, entire, prominently : 3 -nerved, thin and membranous in texture, the lower narrowed into broad. petiolelike bases, the middle and upper sessile and somewhat clasping, extending without much reduction in size to the middle of the stem or above. Radical leaves nsually not intact at flowering time, when present about $1-1.5 \mathrm{~cm}$. wide and ( $1.5-5-10 \mathrm{~cm}$. long, with obovate. spatulate or elliptic, obtuse, often emarginate blades, gradually tapering below into somewhat sheathing, petiole-like bases. Lower cauline leaves often shriveled, (0.5-) 1-1.5(-2) cm. wide, (4-).5-10(-1.2) cm . long, with elliptic-lanceolate, ovate-lanceolate, oblanceolate or oblonglanceolate, obtuse or acute blades, sessile by merely marrowed bases or with broad petiole-like bases sometimes as long or longer than the blades; mid and upper cauline leaves (1-) 1.5-2.5 (-3.5) cm. wide, (4-)5-9(-10) cm. long, sessile or somewhat clasping, elliptic, oblong. ovate, ovate-lanceolate or lanceolate in outline, acute, usually with strongly acominate apices. Upper leaves sessile, acuminate, not greath reduced in size. Involucres hemispherical to broadly campanulate. (10-) $15-20(-25) \mathrm{mm}$. wide, ( $7-) 8-10(-12) \mathrm{mm}$. high, rarels suhtended by a reduced leaf-bract. Phyllaries glabrous, entire. little if at all imbricated at anthesis, subequal, marginless or with narrow white-hyaline margins below the middle, the outer usually (1-)1.5-3 mm . wide, (7-) 9-11 (-13) mm . long, linear, linear-lanceolate or lanceo-


Pian 3. Marshallia trinervia: Channell 2857, Tuscaloxa Counts. Alabama.
late, acuminate or attenuate, the midrib prominent, the veins obscure; abaxial (outer) surfaces pale green; the adaxial (inner) darker green, the whitish midrib prominent, the lateral veins obscure if visible at all. Pales of the receptacle narrowly linear, acute or acuminate-tipped, $8-9 \mathrm{~mm}$. long, persisting beyond the shedding of the achenes, finally deciduous. Receptacle plane or slightly convex, conical in age. Flowers lilac purple. Dried corollas $10-15(-17) \mathrm{mm}$. long, the tubes $6-10 \mathrm{~mm}$. long, conspicuously expanded above into a well-defined throat about $2-3 \mathrm{~mm}$. long. Anthers purple, (2.5-) $3-3.1(-3.5) \mathrm{mm}$. long. Stigmas and sometimes the style exserted beyond the anthercolumn. Pappus scales shorter than the mature achenes, $2-3 \mathrm{~mm}$. long, subaristate, with very short, triangular bases, not at all imbricate, abruptly contracted into long, filiform acuminations, regularly serrulate, minutely scabrous on the abaxial surfaces. Achenes $3-4.5 \mathrm{~mm}$. long at maturity, short-hairy on the ribs, the surfaces between the ribs with scattered resin atoms. Flowering from late May to the middle of July; fruiting in July and August. (Plate 3.)
distribution. Occurring very locally along rocky stream banks and cliffs and in damp deciduous woods, often on calcareous clayey soils; Virginia (?), western North Carolina, central Tennessee, southward throughout Alabama and southeastern Mississippi into Louisiana (?). (Map 1.)
specimens examined. From cultivation: New York Botanical Garden, Moldenke 4940 (vdB); Biltmore, North Carolina, Biltmore Herbarium (Collectors) 4215\%. Without locality: Collector unknown, April 1840 (P); Steinhauer (PH). Virginia. Without definite locality: Stebbins (NY). North Carolina. Without definite locality: Durand [?] (PH). Macon Co.-Highlands: Reinkes Place, Forest, 14 July 1938 (ncu); Harbison, 25 July 1904 (GH). South Carolina. Berkeley Co.St. John's, ex Cranmore Wallace Herbarium, June 1841 (charlNeotype). Georgia. Without definite locality: Nuttall, 1815-30 (вм). Barton Co.-deciduous woods, sandy soil of natural levee, along road on e. side of Allatoona Creek, about 1 mi . from Etowah River, 5 June 1948, Duncan 8274 (alu, cu, Flas, GA, na, nCSC, SMU). Tennessee. Coffee Co.-Tullahoma, Biltmore Herbarium (Collectors) $4215^{\circ}$ (us); oak barrens s. of Manchester, Svenson 10540 (bkl, CU). Davidson Co.-Eggert, 13 July 1897 (mo). Lewis Co.-Little Swan Creek, near Meriwether Lewis National Monument, Natchez Trace Parkway: King 147 (vdB), McDougall 1366, 1676 (us). Robertson Co.-Ridge Top. Eggert, 13 July 1897 (mo, Ny). Alabama. County Uncertain: Sand Mountain, Biltmore Herbarium (collectors) 4215d (us), $4215^{\circ}$ ( vcu, us); mountains of Alabama, Ashe [?], May 1902 (NCU). Without definite locality: Buckley, Sept. 1841 (mo), (bm, GH, NY). Bibb) Co.limestone cliffs, banks of Little Cahaba River, Pratts Ferry, Mohr. 3 June 1883 (F, us). Cullman Co.-Cullman, Mohr, 1 June 1882 (Hark). De Kalb Co.-De Soto Falls, e. of Valley Head, Wherry, 11

June 1933 (na, penn). Franklin Co.-Vicinity of Russellville, Jame's 21 (мо). Lee Co.-Auburn: Earle \& Baker, 29 June 1892 (alu), 1347 [?], 29 June 1897 (min, mo, Ny), 28 May 1898 ( $\mathbf{F}, \mathrm{GH}, \mathrm{Ill}, ~ \mathrm{Ny}$, pom, us). Mobile Co.-Dukes 88 (ny). Shelby Co.-Colena, Everts, 1879 (us); Shipman (F). Tuscaloosa Co.-Windham Springs: Channell 2857 (to be distributed); Smith, 23 June 1875 (alu, us). Wilcox Co.-Buckley, June 1840 (alu, cu, dwC). Mississippi. County unknown: south Mississippi, Hilgard, May 1859 (mo); north Mississippi, Stewart, 1863 ( 5 ); north Mississippi, Frederick Brendel Herbarium (ill); Stewart (Gh). Clarke Co.-Pachuta, Tracy 3299 (ㅊy). Forrest Co.-Hattiesburg, Channell 2610 (to be distributed). Creene Co.-1 mi. w. of Leaksville, Bailey, 19 July 1915 (missu). Perry Co.Augusta, Tracy 4384 (Ny). Scott Co.-Forest, Cook, 25 May 1925 (us); between Morton and Forest, Ripley \& Barneby 11224 (ny); near Forest, Channell 2114, 2115 (to be distributed). Louisiana. Without definite locality: Hartmann, 1877 [?] (FI).

The synonomy of this species has already been covered in considerable detail under the historical account of the genus. The correct combination, Marshallia trinervia, was first validly published in a checklist of the plants of Arkansas by Branner and Coville, who acknowledged in the introduction the assistance of Trelease in revising the nomenclature. Trelease, therefore, is cited as the author of the transfer.

The type specimen of Athanasia trinervia Walt. is apparently nonexistent, for there is no specimen of the species in the Walter Herbarium now preserved at the British Museum. The last record of a Walter specimen of this species is in the reference given by Pursh in 1814 to the effect that he had seen the dried specimen in the Walter Herbarium ("v.s. in Herb. Walter."). Consequently, there is no indication beyond the general information in the introduction of Flora Caroliniana as to the precise source of the Walter specimen. One would presume, in the absence of information to the contrary, that it was collected in the vicinity of Walter's home in South Carolina. Harper (Bull. Torr. Bot. Club, 38: 232. 1911), however, has pointed out:
"But Walter's Flora Caroliniana contains the names of a considerable number of plants that probably do not grow within many miles of his home (which was near the center of the coastal plain of South Carolina), and a few that have not even been seen in South Carolina at all, in modern times at least; and it is reasonable to assume that he had some specimens from the two adjoining states in addition to those from his own."
The list of examples enumerated by Harper is headed by Marshallia trinervia.

The herbarium collections examined during the course of this revision have yielded, however, a single specimen of Marshallia trinervia from South Carolina. This specimen is located at the Charleston Museum and bears the data: "St. John's [Parish], Berkley, So[uth]. Ca[rolina]., June [18] '41, Cranmore Wallace Herbarium." These collection data have been carefully checked and verified through the assistance of Mr. Albert Swartz (at the time associated with the Charleston Museum), who has also kindly furnished information concerning the Cranmore Wallace Collection. ${ }^{14}$

In view of the fact that the Wallace specimen is the only one of the species known to be in existence from South Carolina and since it was collected in Berkeley County, presumably near the type locality of Athanasia trinervia Walt., it has been designated as the neotype.

The name Marshallia Schreberi J. F. Gmel. (Syst. Nat. 2: 1207. 1791) has been erroneously equated by various authors with Persoonia latifolia Michx. and thus with the earlier synonym Athanasia trinervia Walt. Although M. Schreberi was the first combination to be made under the genus and first appeared without a description, reference was clearly made at the time of publication to the generic description of Schreber. This name must consequently be equated rather with the name of the single plant upon which the generic description is known to be based. M. obovata (Walt.) Beadle \& F. E. Boynt. [M. lanceolata (Michx.) Pursh].

Marshallia trinervia is the most distinctive species of the genus. being unique in having very thin-textured. ovate-lanceolate leaves, usually with strongly aciminate apices. The pappus scales (Plate 2, fig. 1) are also inique, being triangular at the very short bases, abruptly contracted into long, filiform acuminations and being somewhat subaristate in form. This species is apparently related to M. grandiflora which it sometimes approaches in habit and with which it has in common the dilated corolla-throats.

This species was reported from Arkansas by Lesquereux (Cat. Plants Ark.: Bot. \& Paleont. Rep. Ark. Geol. Surv. p. 370) in 1860. but there is apparently no specimen to substantiate the record. On this basis, the species was also included by Bramer and Coville (Rep. Ark. Geol. Surv. 1888. 4: 196) in their checklist

[^18]of the plants of Arkansas. There are, however, no modern collections of the species from Arkansas at all.

Other than the fragmentary, although easily identifiable, specimen in the herbarium of the New York Botanical Garden labeled "Va., Mr. Stebbins," no specimen is known to support the Virginia record for Marshallia trinervia. Although this specimen was apparently unknown to Fernald, the species was included in his enumeration of Virginia records (Rhodora 39: 473. 1937) on the basis of the erroneous interpretation of the Gronovian polynomial "Erigeron caule simplicissimo, saepius bifloro, folio caulino semiamplexicaule . ." (Fl. Virg. 122. 1762). According to Fernald, this entry, based by Gronovius on Clayton's specimen number 375, was annotated by Asa Gray as Marshallia in the latter's copy of Flora Virginica when he examined the Gronovian herbarium in 1839. Photographs of the actual specimen kindly furnished by the British Museum show, however, in the hand of Asa Gray, the annotation "E[rigeron]. bellidifolius" only. The explanation for the discrepancy in the two annotations is not known. In any case, the photographs clearly indicate that the specimen in question is not one of any species of Marshallia.

The specimens of the species upon which the Louisiana reports are based are without precise locality data. These records, as well as those of South Carolina, Arkansas and Virginia, need verification by modern collections.

Marshallia trinervia grows well and flowers in peaty soil under ordinary greenhouse conditions. Isolated plants, however, fail to set fertile achenes.

## 2. Marshallia grandiflora Beadle \& F. E. Bovnt.

Marshallia grandiflora Beadle \& F. E. Boynt. Bilt. Bot. Stud. 1: 7, pl. 1. 1901. "Dry soil near Saluda, Polk County, North Carolina"; Biltmore Herbarium (Collectors) 4215 a, 22 Julv 1898 (us-966506Type, ex Biltmore Herbarium, presented by Mrs. George W. Vanderbilt, 1917, marked "Type Sheet" by C. D. Beadle and F. E. Bornton; Isotypes-GH, NY, Us-335500).

Perennial unbranched herb bearing only one, long-pedunculate head, the stem usually (2-) $3-5(-8.5) \mathrm{dm}$. in height, from a short caudex with coarse fibrous roots and, in age, with the tenacious fiber of old leaf bases, sometimes bearing leafy offsets; plants often somewhat clustered, the stems rarel with leafy proliferations from the lower leaf axils and rooting from the lower nodes. Stem glabrous, obtusely angled below, striate, becoming more distinctly grooved above, light green, buff or stramineous in drving, rarely if ever reddish, leafy to the peduncle. Peduncle sulcate, glabrous to glabrate below, becoming
copiously pubescent beneath the head, rarely sparingly pubescent or glabrate above, (4-)7-15(-30) cm. long, naked, or occasionally with 1 or 2 reduced linear or lanceolate bracts of various disposition. Leaves glabrous, entire, prominently 3-nerved (broader leaves occasionally with 2 additional nerves), thickish and firm in texture at least in age, gradually diminishing in size and greatly reduced upwards; the lower contracted below into broad, winged, somewhat vaginate petioles about as long or longer than the blades; the middle and upper becoming sessile with somewhat clasping bases, the uppermost greatly reduced, becoming only 1 -nerved. Radical leaves usually intact, $(0.5-) 1-2(-3) \mathrm{cm}$. in width, (2-) 3-1.3(-20) cm . in length, with oval, obovate, spatulate or oblong, obtuse, sometimes emarginate blades, the leaves of basal offsets much larger. Lower cauline leaves 1.5-3(-4) cm . wide, $8-25(-30) \mathrm{cm}$. long, the blades elliptic, oblanceolate, ellipticoblanceolate or ovate-lanceolate, broadest near the middle, with obtuse or rounded apices, gradually narrowed below into broad, somewhat sheathing, petiole-like bases. "Middle cauline leaves sessile or becoming so, usually $1-3 \mathrm{~cm}$. wide, $5-15(-25) \mathrm{cm}$. long, with elliptic, ellipticovate, ovate-lanceolate or lanceolate, obtuse blades, becoming acutish above, rarely somewhat acuminate. Upper leaves greatly reduced in size, sometimes approximate, but usually becoming rather remote. Involucres hemispherical or campanulate, (12-) 15-25(-30) mm. in width at the broadest point and (8-) $10-15(-20) \mathrm{mm}$. in height including the pales, sometimes subtended by a remote bract. Phyllaries glabrous, entire, with usually conspicuous white-hyaline (rarely purplish) borders to the middle and above, thin in texture at flowering time, becoming thick, firm and rigid in age, the outer usually 2-3(-4.5) mm . wide and 7-12 mm. long, ovate, ovate-lanceolate, lanceolate or oblong in outline, usually acute, rarely obtusish; the abaxial (outer) surfaces green, becoming buff in age, at flowering time copiously minutely punctate with resin glands (visible under $10 \times$ magnification), superficial resin atoms absent, the midrib prominent, obscurely reticulate-veiny, in age becoming thick and smooth with neither glands nor veins apparent; adaxial (inner) surfaces green, usually smooth, in drying sometimes rugose but not raised-veiny. Pales of the receptacle linear, acute, sometimes purple-tipped, $8-15 \mathrm{~mm}$. long. Receptacle convex, conical in age. Flowers purple. Dried corollas $10-1.5 \mathrm{~mm}$. long, the tubes about 10 mm . long, the upper third regularly and conspicuously dilated into a distinct throat about $2-3 \mathrm{~mm}$. long. Anthers purple, $3-3.5(-4) \mathrm{mm}$. long, the column exserted beyond the corolla throat. Stigmas and often the style also exserted beyond the anthercolumn. Pappus scales shorter than the achene, about 2 mm . long, acuminate from a broad base, regularly serrulate, minutely scabrous on the abaxial surfaces. Achenes 4.5 mm . long at maturity; hairy on the ribs, the surface between without resin atoms. Flowering from mid June through July; fruiting in August and September. (Plate 4.)


P'atr t. Marshallia grandiftora: Bright 1690t. Fasette Count!. Pennohamia.
distribution. Occurring along rocky river and lake shores, creek banks, bluffs and flood plains in moist to wet sandy soil and in mediacid soil of Coastal Plain-like "bogs," uplands from southwestern Pemsslvania southward through West Virginia into southeastern Kentucky, east-central Tennessee and southwestern North Carolina. (Map 1.)
specimens examined. From cultivation: New York Botanical Garden. Hartling, 24 June 1918 (ill). Pennsylvania. Allegheny Co.near Pittsburgh, Leighton, Sept. 1915 (cu, pens). Favette Co.Younghiogheny River, Ohiopyle: Batholomeu, 22 June 1940 (wva); Bright 28.3, 1884 (IND), 3062, 9417 (min), 6711, 1.3515 (PENN), 9416 (NA) , 16900 (TEX), 16902 (LLC), 16904 (oKL), 21 June 1923 (CM, wva), 20 June 1936 (tex); Brown, Crawford \& Van Pell 95 (PH); Clark, 30 June 1894 (GH); Fogg 18445 (PENN); Fretz, 3 July 190.5 ( PH ) ; Henry, 24 June 1939 (CM); Jennings 9859 (PAC), 9882 (CM), 9883 (penn); Pätterson, 3 July 1905 (Cu); Ricker 1217 (us); Shafer 44 (F, US), 44 a' 11 (PENN), 1479 (GH, PH), 2195 (CM), 1 July 1900 (Ny), 29 June 1902 (Ny); Shafer \& Medsgar 44 (Cu, no, penn), $44 a(\mathrm{PH}), 1$ July 1900 ( $\mathrm{NY}, \mathrm{PH}$ ) ; Smith 6966 (PENN, PH, US); Welton, Juls 1891 (PH). West Virginia. Without definite locality: Millspaugh, 1892 ( $\mathbf{F}$ ). Barbour Co.-Tygart Junction, Greenman 217 ( $\mathbf{F}, \mathbf{G H}$ ); Tygart River, Moore 2556, 2568 (GH). Monongalia Co.-Quarry Run, Brooks 4547 (wva); Cheat River, Davis 5892 (wva). Preston Co.Big Sandy Creek, Davis 585.3 (wva); Cheat River, Albright, Smith d Carroll, 29 Jume 1947 (wva). Randolph Co.-Cheat River: Core, 20 July 1935 (wra); Hutton du Whitlach, 12 July 1941 (Flas, ch, lCu, da, ny, okl, penn, taes, Wva); Straushough, 1 Aug. 1933 (ny, okla). Stuart Camp, Orton, 10 July 1943 (wva); Shaver's Fork, Cheat Mt., Sharp, 9 July 1941 (tens); West Virginia Biological Expedition (Collectors), 9 July 1941 (wva). Summers Co.-Greenbrier River below cliff at Bacon's Falls, Fox 2479 (ga, na, scse, smu, wva). Upshur Co.-Sago: Grose \& Grose, 25 July 1946 (wva); Polloch, 24 June 1895 (F, GH, ill, MIN, MO, PH, POM, us, vhC), 4 July 1896 (bkl, Cu, GH, LC: , MIN, Mo, NCu, Ny, us). Kentucky. McCreary Co.south fork of Cumberland River, Braun, 18 June 193.5 (GH). Tennessee. Roane Co.-Emorv River, Harrimon: Sharp 2007 (tenn); (Inderwood \& Sharp 1144 (bKl); Underwood 2767 (PH). South Carolina. Without definite locality; source questionable: Smith, 1881 (cs). North Carolina. Without definite locality: western part of state. Hyams (xy). Henderson Co-Ashe Herbarium, May 1902 (ved); Biltmore Forest, Hendersonville, Clement, 12 Ang. 1936 (duke); near Hendersonville, Biltmore Herbarium (Collectors) 421.5" (us); Flat Rock, Crayton, Aug. 1919 (flas, Ny); Muddy Creek, Smith, 19-26 Ang. 1881 (bkl, duke, f, gh, phil, us, yu); bog near Flat Rock Station, Wherry, 29 July 1933 (peni). Polk Co--Saluda, Biltmore Herbarium (Collectors) 4215" (Holot!pe-us; Isotypes-GH, sy, us).

Before, and even after, the recognition of Marshallia grandiflora as a distinct species, specimens of this taxon were identified as M. trinervia and M. obovata var. platyphylla (var. obovata of this treatment) and for many years passed unnoticed under these names.

Although Marshallia grandiflora was described in 1901, specimens clearly referable to the species were distributed by the Southern Appalachian Botanical Club in 1941, under the name M. obovata var. platyphylla. This illustrates the taxonomic confusion existing between these taxa. As pointed out elsewhere, M. grandiflora was considered to be only a robust form or state of M. obovata var. platyphylla in the seventh edition of Gray's Manual.

The similarity of Marshallia grandiflora and M. trinervia has already been pointed out in the discussion of the latter species. In addition, both these species are usually simple-stemmed. Although M. grandiflora is rarely branched, when it is, the branches arise from the basal nodes. Marshallia trinervia, on the contrary, is branched from the upper leaf axils, if it is branched at all.

Marshallia grandiflora may be distinguished from both M. trinervia and $M$. obovata var. obovata by the gradual reduction in the size of the leaves from the base of the plant upwards. The leaves of $M$. trinervia and M. obovata var. obovata extend upward without much reduction in size. The phyllaries of the latter are decidedly obtuse, unlike the acute or merely obtusish phyllaries of M. grandiflora. Moreover, the achene-surface of Marshallia grandifora apparently lacks the superficial resin atoms characteristic of all other species of the genus.

In western North Carolina, the only area in which the ranges of M. grandiflora and M. obovata var. obovata overlap (see Maps $1 \& 2$ ), the general flowering period of M. obovata var. obovata is usually from two weeks to a month or more in advance of that of $M$. grandiflora. In general, on an annual basis, a similar difference in flowering period obtains throughout their ranges. Thus, these two taxa are effectively isolated both geographically and seasonally.

Marshallia grandiflora specimens transplanted to the greenhouse from Henderson County, North Carolina and Randolph County, West Virginia, did not flower during the two-year period in which they were under observation. The plants survived but showed very poor growth. Specimens of M. trinervia and M. obovata var. obovata, however, grew very well in the greenhouse
under similar conditions and flowered two consecutive years. Having the highest altitudinal range and most northern distribution of any other species of the genus, M. grandiflora may require a physiological cold treatment for successful growth and flowering in the greenhouse.

## 3. Marshallia Mohrii Beadle \& F. E. Boynt.

Marshallia mohri ${ }^{15}$ Beadle \& F. E. Boynt. Bilt. Bot. Stud. 1: 8, pl. 3. 1901. ". . . collected by Dr. Charles Mohr . . . at Cullman, Cullman County Alabama, June 24, 1893 . . " (us-Type, ex Herb. Chapman of Biltmore Herbarium Collection, presented by Mrs. George Vanderbilt, 1917, marked "Type Sheet" by C. D. Beadle and F. E. Boynton).

Perennial herb usually (3-)3.5-6.5(-7) dm. tall, the stem from an inconspicuous crown or rhizome, often producing lateral offsets at the base, sparingly cymosely branched above the middle and usually bearing (1P) 2-6(-10) heads. Stems glabrous, somewhat obtusely angled below, becoming distinctly grooved above, light green to stramineous in drying, rarely reddish at the base, leafy to the inflorescence branches or above. Peduncles sulcate, glabrous or glabrate, becoming at most only sparingly pubescent above, (3-)4-16(-20) cm . long (including the leafy portion), arising alternately from the upper leaf axils and forming a cymose inflorescence, the peduncles naked or leafy-bracted below the middle and above by the successively and gradually reduced leaves of the upper stem. Leaves glabrous, entire, prominently 3 nerved, firm in texture at least in age, gradually diminishing in size upwards, usually extending well up on the inflorescence branches as reduced bracts; the lower leaves contracted into winged, somewhat vaginate, petiole-like bases about as long or longer than the blades, the middle and upper sessile and somewhat clasping, the uppermost becoming only 1 -nerved. Radical leaves usually not intact, when present $0.5-2 \mathrm{~cm}$. or more in width, $2-10 \mathrm{~cm}$. or more in length, with obovate. spatulate or oblong, obtuse, occasionally emarginate blades, those of basal offsets usually much larger. Lower cauline leaves (0.5-) 1-3(-4.5) cm . wide, (6-) $8-20(-25) \mathrm{cm}$. long, the blades lanceolate, ovatelanceolate or elliptic, broadest near the middle, the apices obtuse. acutish or rarely acute, the blades gradually tapering below into prolonged petioles. Middle cauline leaves sessile, usually $0.5-2.5(-3) \mathrm{cm}$. wide, $3-10(-14) \mathrm{cm}$. long, elliptic, lanceolate or ovate-lanceolate. acuminate, the ultimate tips acute or sometimes obtusish. Upper leaves becoming gradually reduced in size to mere leaf-like bracts of the upper stem and inflorescence branches. Involucres hemispherical or

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Plate 5. Marshallia Mohrii: Eggert, 21 June 1897. Cullman County, Alabama.
broadly campanulate (rarely subtended on the peduncles by a reduced linear or falcate bract), usually (6-) $10-22(-25) \mathrm{mm}$. in width and (5-) $7-10(-15) \mathrm{mm}$. in height including the pales. Phyllaries glabrous, without resin atoms, entire, with or without conspicuous hyaline borders to the middle and above, thin to firm in texture at flowering time, thick and rigid, at least in age, usually ( $1-$ ) $2-3(-3.5$ ) mm . wide, ( $5-) 6-8(-13) \mathrm{mm}$. long, ovate-lanceolate, lanceolate, elliptic or ellipticoblong in outline, usually acute, sometimes attenuate, rarelv obtusish and minutely mucronate; the abaxial (outer) surfaces light brown, tan to pale greenish in color, usually smooth to smoothish under $10 \times$ magnification, the midrib evident but not prominent, the lateral veins obscure within the tissue if evident at all; the adaxial (inner) surfaces usually greenish to dark green in color, distinctly raised-veiny, the midrib and vein-reticulum light green to whitish. Pales of the receptacle linear, acute. Receptacle convex, especially in age. Florets pale lilacpurple in color. Dried corollas (8-) $10-15 \mathrm{~mm}$. long, the tubes about 5 mm . long, not regularly dilated above into well-defined throats (if occasionally at all abruptly expanded, this portion only about 1 mm . in length or less). Anthers $\dot{3}-3.5(-4) \mathrm{mm}$. long. Stigmas, and sometimes the style, exserted beyond the anther-column. Pappus scales $1-3 \mathrm{~mm}$. long, shorter than the mature achene, acute to strongly acuminate, the margins irregularly broken by a few sharp points. Achenes to about 4 mm . in length at maturity, prominently hairy on the ribs, the intervening achene-surface beset with minute resin atoms, sometimes copiously so. Flowering from mid May through June; fruiting in July and August. (Plate 5.)
distribution. Springy places and grassy glades (according to Mohr, Plant Life of Alabama), damp places in woodlands, grassy woodlands, low damp openings in flatwoods and in sandy soil of open meadows; known only from northern Alabama and northwestern Georgia (Lookout Mountain). (Map 1.)
specimens examined. Without locality: Wray [?], ex Herb. Short (PH). Alabama. County uncertain: mountains of Alabama, Ashe [?], May 1902 (ncu). Cullman Co.-Cullman: Biltmore Herharium (Collectors) $4758,7187^{\text {b }}$ (us) ; Eggert, 19 June 1897 (f, min, mo, Nd, NY, rm, us) ; Harbison 4758 (ncu); Mohr, 1 June 1882 (us), Aug. 1886 (alu), 15 Aug. 1886 (us), 5 May 1891 (Alu), 18 June 1892 (PH), 23 June 1893 (us), 24 June 1893 (us-Type); Sudworth, 6-11 June 1891 (us); Eight Miles Creek, Eggert, 21 June 1897 (MO); sandy loam, flat open woods near CCC Camp, Morgan, 17 June 1941 (LCU). Walker Co.-Without definite locality: pine woods, Earle, 20 June 1899 (F, NY). Georgia. County uncertain: Lookout Mountain: Ruth, July 1898 (ill, NY), 262 (vHC), 6.38 (NY), Rock Creek, 662 (Us), 692 (мо).

The collection data (low pine barrens, Beaufort, Carteret

County, North Carolina, 10 August 1902) borne by an Albert Ruth specimen of this species (GH) are apparently erroneous. The specimen is mentioned here because it is thought to belong to Ruth's collection of July 1898, from Lookout Mountain Georgia. The specimen resembles duplicates of the 1898 collection so closely that it seems safe to suppose that the specimen was originally a part of that series and that, inadvertently, it received the data intended for a different collection.

Prior to the original description of Marshallia Mohrii in 1901, specimens of the species were labeled M. trinervia. Since that date specimens of the species have frequently been labeled $M$. obovata var. platyphylla (var. obovata of the present treatment). These incorrect determinations are suggestive of the general similarity of the three taxa. Marshallia Mohrii may be distinguished from all other broad-leaved Marshallias, however, by the cymosely branched inflorescence of 2-10 heads, a feature unique in this species group. Unlike M. trinervia and M. grandiflora, the pappus scales of M. Mohrii have irregular, broken margins (Plate 2, fig. 3).

Marshallia Mohrii (Plate 5) is considered to be very closely related to M. grandiflora (Plate 4). Specimens of these two species are quite similar in general appearance, as well as in finer details of structure. In fact, the morphological similarities and geographical distribution are such that M. Mohrii may be regarded as a southern counterpart of M. grandiflora.

There is also an apparent relationship between Marshallia Mohrii and M. trinervia. The phyllaries of M. Mohrii for example, are very similar in quality and form to the maturing phyllaries of M. trinervia. In addition, certain specimens representing extreme elements in the two species are very similar in general appearance.

Marshallia Mohrii is apparently very rare and local in distribution. As far as is known it was last collected in 1941 by Morgan (apparently connected at the time with St. Bernard Abbey, St. Bernard, Alabama) in the vicinity of the type locality, Cullman, Alabama. Trips by the writer to the area in search of the species in the spring of two consecutive years (on one occasion assisted by Drs. Roland M. Harper and E. Gibbes Patton, University of Alabama), were not successful in terms of locating the plant. If located in the future it should be collected very sparingly and every effort should be made to protect it so as to avoid its extinction.

4a. Marshallia obovata (Walt.) Beadle \& F. E. Bornt. var. obovata
Athanasia obovata Walt. Fl. Carol. 201. 1788. (bm-Type, on page 16 Herb. Walt., analysis of type supplied by Mr. W. T. Stearn; ghphotograph examined.) South Carolina, Walter.

Persoonia lanceolata Michx. Fl. Bor.-Am. 2: 105. 1803. "Hab. in montosis Carolinae"; A. obovata Walt. cited as a questionable synonym. ( $\mathrm{p}-$ Lectotype, Herb. Richard, ex Herb. Drake.)

Trattenikia lanceolata (Michx.) Pers. Svn. Pl. 2: 403. 1807.
Marshallia lanceolata (Michx.) Pursh, Fl. Amer. Sept. 2: 519. 1814. "In the Carolina mountains . . . v. s. in Herb. Walt."

Marshallia lanceolata (Michx.) Tratt. Arch. Gew. 1: 109. 1814.
Phyteumopsis lanceolata (Michx.) Poir. Encyc. Suppl. 4: 405, 406. 1816. "v. s. in Herb. Michx."; A. ohovata Walt. cited as a questionable synonym.

Marshallia lanceolata (Michx.) Pursh var. platyphylla M. A. Curtis ex Chapm. Fl. Southern U. S., ed. 1, 241. 1860. (GH-Lectotype, collected by M. A. Curtis at Hillsborough, North Carolina.)

Marshallia obovata (Walt.) Beadle \& F. E. Boynt. var. platyphylla (M. A. Curtis ex Chapm.) Beadle \& F. E. Boynt. Bilt. Bot. Stud. 1: 6. pl. 6. 1901.

Marshallia obovata (Walt.) Beadle \& F. E. Bornt. Bilt. Bot. Stud. 1:5 (as to name only). 1901. Basionym cited but the new combination applied erroneously to a different taxon (M. obovata var. scaposa of the present treatment). The new combination is here retained for the plant on which the epithet was originally based.

Perennial herb with a simple leafy stem, (2-) 3-5 (-7) dm. in height, arising annually from a short crown or caudex with coarse fibrous roots and often in age bearing the vascular fiber of old leaf bases, propagating vegetatively by lateral offsets which soon become freed of connection with the parent plant, thus somewhat gregarious in habit. sometimes solitary but usually disposed in chump-like colonies, the individual plants usually single-stemmed, sometimes bearing intact leafy offsets at the base but rarely with additional flowering stems intact upon the same rootstock. Coarse fibrous roots 1-2 mm. in diameter, somewhat fleshy in texture when fresh. Stem simple, glabrous, striate, somewhat angled, becoming distinctly grooved above, green or greenish at flowering time, becoming stramineous in age, typicallyleafy to the middle or above, the leafy portion (5-) $8-20(-30) \mathrm{cm}$. long. often as long or longer than the peduncle, occasional genotypes (apparently depauperate individuals) leafy below the middle only, internode length and leaf size not greatly reduced upwards, the leaves more or less abruptly discontinuous upwards (without the gradual ultimate reduction in size typical of M. Mohrii and M. grandiflora). Peduncles (8-) 15-35(-45) cin. long, sulcate, glabrous or glabrate below, becoming copiously white-pubescent with ascending-incurving moniliform hairs, the pubescence usually abruptly discontinuous below the phyl-
laries. Leaves glabrous, rarely punctate with a few resin glands, entire, prominently 3 -nerved, the radical and lower cauline leaves contracted below the middle into broad, somewhat sheathing, petiole-like bases, the upper becoming sessile with narrowed, clasping bases; radical leaves obovate, spatulate or oblong-spatulate, (2-)4-12(-15) mm. wide, (2-) $3-6(-8) \mathrm{cm}$. long, with obtuse, sometimes emarginate blades; cauline leaves with oblanceolate, elliptic-lanceolate or elliptic, obtuse, rarely acutish blades, (3-)5-20(-30) mm. wide, (3-)5-12(-16) cm . long. Involucres hemispherical or broadly campanulate, 12-$25(-30) \mathrm{mm}$. wide, (5-) $7-12(-1.5) \mathrm{mm}$. high including the pales. Phyllaries subequal in about 2 rows, the outer (5-)6-10(-13) mm. long, $1-2.5(-3.5) \mathrm{mm}$. wide, typically oblong in outline with obtuse and often minutely mucronate apices, sometimes lanceolate, elliptic or linear-elliptic but rarely with acutish apices, glabrous, usually without resin atoms, bordered to the middle and above by white-hyaline margins, entire or occasionally remotely toothed, light green on the outer (adaxial) surfaces with the midrib thickened and somewhat raised above the adjacent tissue, the inner surfaces dark green except the white midrib, phyllaries becoming stramineous and firm in age. Pales of the receptacle glabrous, usually without resin atoms, $5-8 \mathrm{~mm}$. long, linear-spatulate or spatulate-clavate, usually distinctly dilated upwards, with obtuse or minutely mucronate apices, gradually narrowed below. Receptacle convex, dome-shaped or conical in age, the pales persistent beyond the sheading of the achenes, finally deciduous. Flowers pale lavender to purplish, cream-colored or even white. Dried corollas (8-) 10-12(-13) mm. long, the tube $5-7 \mathrm{~mm}$. long, sometimes dilated above into a shallow throat. Anthers usually bluish, sometimes creamcolored or white, (2.5-) $3-3.5 \mathrm{~mm}$. long, the column exserted beyond the corolla-throat. Stigmas divergent and recurved in age, usually exserted bevond the anther-column. Pappus scales ( $0.5-$ - $1-1.5 \mathrm{~mm}$. long, ovate, strongly acuminate, usually regularly serrulate, occasionally lacerate, shorter than the achene. Achene at maturity broadest below the summit, ( $2.5-$ ) $3-4 \mathrm{~mm}$. long, 10 -ribbed, the ribs shortpubescent, the hairs of the achene shorter than the distance between adjacent ribs, the concave achene-surface between ribs covered with minute resin atoms, sometimes copiously so. Flowering from April through June; fruiting from May into July. (Plate 6.)
distmibution. Occurring on heavy clayey soils in meadows, woods, along rocky stream banks and road shoulders from Mecklenburg County, Virginia, southward through the Piedmont and upper districts of North and South Carolina, Georgia and Alabama, extending into western Florida along the drainage area of the Chattahoochee. (Map 2.)
representative specimens. Without definite locality: Ameriq. Sept.: Balduin (PH-258, вм); LeConte, Herb. Richard (p-ex Herb. Drake); Michaux [?] (p); Carolina, Fraser (bm-photograph). Mon-


Plate 6. Marshallia oboeata var. obotata: Channell 2820. Lee Count!. North Carolina.
tosis Carolinae, Herb. Richard (p-ex Herb. Drake-Lectotype of Persoonia lanceolata). Elliott (charl, mo-3636, mo-Herb. Bernhardi). Montibus Carolinae et Georgiae, Buckley (GH, BM-photo-graph-Herb. Shuttleworth). Louisiana [?]. Drummond (к); Hale (PH). Virginia. Mecklenburg Co.-Near Soudan, Channell 2841 (to be distributed). Tennessee. Territorio Tennessee (probably western North Carolina), Herb. Richard (p-Herb. Drake). North Carolina. Without definite locality: Schweinitz ( $\mathbf{K}-\mathrm{Herb}$. Bentham, NY); chiefly of the mountains and upper country, Vasey, 1878 (F); region of the Yadkin River, Herb. Britton 14341 (mо); Curtis (GH, мо, Pн). Chatham Co.-Merry Oaks, Freeman, 22 May 1925 (na); Sanford, Radford d Radford 2004 ( $\mathrm{ncsc}, \mathrm{ncu}$ ). Cleveland Co.-Kings Mt., Biltmore Herbarium (Collectors) $5521^{g}$ (NY, US). Davidson Co.-Yadkin River, Radford \& Haesloop 7063 (ncu). Durham Co.-Braggtown, near Eno River, Godfrey, Fox \& Anderson 40391 (GA, gh, min, ncsc, smu); Channell 1936, 1938, 1939, 1946, 1957, 2817, 2819, 2832 (to be distributed). Forsyth Co.-Salem, Schweinitz (GH); vicinity of WinstonSalem, Schallert, variously dated (Cu, duke, Gh, LlC, MO, Nd, NY, SMU, tex, uark). Granville Co.-near Soudan, Virginia, Channell 2844 (to be distributed). Guilford Co.-Greensboro, Correll 10619 (duke, Na). Henderson Co.-swamps along Muddy Creek, Smith, 24 Aug. 1881 (min). Iredell Co.-Gray, Sargent, Rédfield \& Canby, 24 Aug. 1881 ( $\mathbf{P H}$ ) ; vicinity of Statesville, Hyams, variously dated (ny, min, mo, pHil-photograph-Herb. Martindale, pom). Lee Co.-near Sanford, Biltmore Herbarium (Collectors) 5.521", 5521 d (us); Channell 2820 (to be distributed). Montgomery Co.-Troy, Fox \& OConnell 4706 (ncsc). Moore Co.-Hillsborough: Curtis, 1848 (GH-Lectotype of Marshallia lanceolata var. platyphylla); Palmer 42241 (GH, мо). Duke Forest, Rhododendron Bluff, Channell 728 (to be distributed). Person Co.-near Roxboro, Channell 1932, 2836 (to be distributed). Polk Co. -Tryon: Tounsend, 24 May 1897 (cu, us); Churchill, May 1899 (GH, mo, tenn). Randolph Co.-vicinity of Asheboro: Wiegand \& Manning 3452 (CU, GH); Oosting 2456 (Duke, miN). Rowan Co.-Gold Hill, Small \& Heller 485 ( $\mathbf{F}$, ILL, Min, MO, PH). Vance Co. -2 mi. s.e. of Fairport, Ahles 12697 (GH, NCU, duplicates to be distributed). Wake Co--between Norrisville and Cary, Channell 1941 (to be distributed). Warren Co--Little Shocco Creek, Bell 2910, 2920 (GH, NCU, duplicates to be distributed). South Carolina. Without definite locality: Buckley (GH); McCarthy, 1888 (US); Ravenel (Fi); Herb. Walter (BM-Type). Abbeville Co-Abbeville, Gibbes, 1855 (Ny). Anderson Co.-Blecklev Woods near Anderson, Davis, 24 May 1920 (cu, lcu, min, mo, tex). Cherokee Co.-Broad Bank River near Gaffnev, Wright \& Munz 1.314 (CU, pom). Georgetown Co.-Georgetown (considered to be erroneous source of collection), Foster, 5 March 1859 (ny). Greenville Co.Laurel Creek, Radford 91 (GA). McCormick Co.-vicinity of Clark Hill Dam. Duncan 9442 (uala, cu, flas, ga, ncsc, smu). Oconee Co.-

Seneca, McCarthy, June 1888 (us); Keowee, House 2198 (wy, us); Old Stone Church, near Clemson, Morrison, 10 May 1933 (clems). Pickens Co.-Anderson $12-15$ ( min); dry woods near Clemson, House 3356, 3362 (Ny). Spartanburg Co.-Spartanburg, Wheeler, 1891 (PH). Georgia. Without definite locality: near Flint River, Herb. Muhlenberg, 1812 ( $\mathbf{P H}$ ); Nuttall ( PH ); Elliott ( $\mathbf{k}$ ); north Georgia, Vasey, 1878 (Ny) ; Chapman (f, Ny, us); Darlington (Fi); Herb. Mann (Cu). Baldwin Co.-Milledgeville, Harbison, 5 May 1914 (ncu). Cherokee Co.-bottomland of sinall stream near Etowah River, Duncan 8.315 (GA). Clay Co.-near ravine, 1 mi . s. of Fort Gaines, Thorne \& Thorne .3790 (Cu, GA, GH). Cobb Co-Marietta, Allmendinger (Ny). Early Co.-near Hilton, Thorne 3616 (cu, GA). Floyd Co.-Mount Berri, Jones 16 (ns). Fulton Co.-McPherson Park, Atlanta, Schneck, 20 May 1904 (ILL); Oakland City, Spratt, 28 May 1933 (GA); vicinity of Atlanta, Darby 60 (na). Guinnett Co.-McGuire's Mill, Biltmore Herharium (Collectors) $1248^{\text {b }}$ (BKL, F, ILL, MiN, NY, RM); Thompsons Mills and vicinity, Allard 262 (mo, Ny, us). Haralson Co.-Tallapoosa, Way 19 (us). Meriwether Co.-Pine Mt., Harper 1269 (Gh, мо, мy, us). Randolph Co.-Grier's Cave, n. of Cuthbert, Thorne d Muenscher 7918 (cu). Richmond Co.-Augusta: Biltmore Herbarium (Collectors) $5521^{a}$ (us) ; Dudgeon (Ny); Cuthbert, variously dated (conn, flas, ny, Ph). Sumter Co.-Americus, Harper 1024 (bm, gh, mo, ny, us). Alabama. Without definite locality: Buckley (GH); Montagnes des Racoons, Lesquereux (bм). Cherokee Co.-Valley of the Coosa River, Mohr, 20 May 1887 (f); Mohr, 16 May 1881 (us). Etowah Co.Coosa River, Harvey (uark); Coosa River valley, about 6 mi . n.w. of Hoke's Bluff, Harper 4052 (duke). Lee Co.-Auburn, Earle, 18 May 1901 (Ny); Duggar, 12 May 1892 (cu). Shelby Co-Shipman, 187[?] (F). Lee Co.-Auburn: Earle \& Baker, variously dated (F, ill, min, mo, ny, pom, rm, us, vhc). Russell Co.-Uchee Creek, west of Fort Mitchell, Harper 4 (GH, MO, NY, PH, Us). Florida. Without definite locality: Herb. Buckley (mo); Chapman (GH, Ny, us); Herb. Darlington (DwC); Jackson, ex Herb. Swarthmore College (PH). Jackson Co.Marianna, Knight \& Arnold, 5 April 1944 (flas).

This taxon was first described by Walter in 1788 as Athanasia obovata. In 1803, Michaux unnecessarily renamed the species Persoonia lanceolata, the epithet of which was subsequently used to the exclusion of Walter's obovata. The specific epithet lanceolata was preserved through a series of transfers which followed and was first combined with Marshallia by Pursh in 1814.

Marshallia lanceolata var. platyphylla was proposed as new in Chapman's Flora of the Southeastern States (page 241, 1860). The name was attributed by Chapman to M. A. Curtis who, judging from the labels on herbarium specimens examined during
the course of this revision, is clearly responsible for the taxon. The variety was said to differ from typical M. lanceolata in having stems leafy to the middle. One would infer, therefore, that M. lanceolata at this time was interpreted as having mostly basal or radical leaves.

In the revision of the species of Marshallia by Beadle and Boynton (Bilt. Bot. Stud. 1: 3-10. 1901) var. platyphylla was upheld and applied to the leafy-stemmed plant. The authors stated that, while the original description of Athanasia obovata was very brief, they had no hesitancy in applying the Walter epithet to the species, i.e. the scapose plant. On this basis the following transfers and combinations were made: M. obovata (Walt.) Beadle \& F. E. Boynt. and M. obovata (Walt.) Beadle \& F. E. Boynt. var. platyphylla (M. A. Curtis ex Chapm.) Beadle \& F. E. Boynt. By so defining these taxa Beadle and Boynton are largely responsible for the concepts that have subsequently come into general usage, i.e. interpreting M. obovata as comprising the scapose and subscapose plants and var. platyphylla as including the caulescent plants with larger leaves.

Investigations conducted during the present revision, however, have indicated that the type of Walter's Athanasia obovata (now preserved at the British Museum) consists of two specimens both of which are themselves leafy-stemmed. This fact was first suspected when the Gray Herbarium photograph of the type was examined. The brief original description was then re-examined in the light of this information. The entire passage referring to foliage is: "foliis radicalibus obovato-oblongis subnervosis
On the basis of this statement it cannot be concluded whether the plants are scapose or caulescent, for only the radical leaves are described.

Additional information concerning the type of Athanasia obovata, however, has been kindly supplied by Mr. W. T. Stearn of the British Museum. Mr. Stearn has furnished diagrams of the relative position of the individual leaves of the type specimens. On the basis of these diagrams there is no doubt that the typematerial belongs to the leafy-stemmed taxon. Mr. Stearn arrived at a similar conclusion after comparing the type-material with representatives of both the leafy-stemmed and scapose variants. Mr. Stearn's analyses indicate that, on the basis of leaf-characters. the Walter type-material belongs to the leafy-stemmed taxon with conspicuously 3-nerved leaves, as figured by Beadle and Boynton (1. c., pl. 6) for Marshallia obovata var. platyphylla.

The type-material, according to Mr. Stearn, essentially matches several specimens in the British Museum under the name Marshallia lanceolata. I have examined photographs or duplicate specimens of these collections and concur in this opinion.

Mr. Stearn was also kind enough to compare the Walter typematerial with a specimen in the British Museum collected by R. K. Godfrey (no. 49184, Brunswick County, North Carolina) and labeled Marshallia obovata. This is a collection of strictly scapose plants of which several duplicates have been examined during the course of the present revision. Mr. Stearn concurs in the belief that this collection differs from the Walter type and that it corresponds to Marshallia obovata as figured by Beadle and Boynton (1. c., pl. 5) with apparently 1-nerved leaves.

On the basis of these data it has been concluded that Walter's Athanasia obovata has been incorrectly interpreted in the past. It is the same taxon as that described as var. platyphylla. On taxonomic grounds, however, two varieties are here recognized as comprising the species. For reasons of priority, the leafystemmed variety must be called Marshallia ohovata (Walt.) Beadle \& F. C. Boynt. var. obovata and the scapose one must be named. Despite the fact that the new combination Marshallia obovata was misapplied to the scapose variety, that name must be retained for the leafy-stemmed taxon upon which the epithet was originally based.

Both varieties of Marshallia obovata flower in the late spring, in general earlier than the three preceding broad-leaved species. Their phyllaries (Plate 1, figs. 4 \& 5) are elliptic, linear-elliptic or oblong in outline, usually with obtuse, sometimes minutely mucronate apices. Occasionally the phyllaries may be abruptly pointed but they always have a marked tendency toward the obtuse condition. The pales are unique in being linear-spatulateclavate and are also often minutely mucronate at the apices. In general, the obtuse phyllaries and the clavate-spatulate pales serve to distinguish $M$. obovata from all other species of the genus. Occasionally the phyllaries of M. grandiflora are abruptly pointed or even obtusish, but the acute apex is nevertheless the general rule in this species. The occasional striking similarity of the phyllaries of M. obovata var. obovata and M. grandiflora, the simple habit and similar leaf-form are suggestive of relationship. Indeed, the two taxa have often been confused taxonomically as already pointed out.

The relationships of the two varieties of Marshallia obovata to
one another and further discussion of their relationships to $M$. grandiflora are presented under var. scaposa.

Marshallia obovata var. obovata occurs almost exclusively on the geologically older Piedmont and upper districts on very clayey, highly plastic soils (Map 2). The southern extension of the range of this variety into western Florida is along the drainage area of the Chattahoochee where the sandy soil has apparently been eroded away, exposing clay, thus providing suitable edaphic accommodations for the spread of the plants into the Coastal Plain.

The geographical range of Marshallia obovata var. obovata (as var. platyphylla), according to the eighth edition of Gray's Manual, extends from Florida to southern Missouri and North Carolina. The Missouri record, credited to the authority of Palmer and Steyermark, is apparently based on Palmer's collection number 34811 from Ozark County. This collection, of which three duplicates have been examined, proved to represent uncommonly broad-leaved specimens of M. caespitosa var. signata. The inclusion of M. obovata var. obovata in the Gray's Manual range on this basis is thus incorrect. According to the present study, however, the natural range of this variety extends from North Carolina into Mecklenburg County, southern Virginia. This is the first authentic report of the variety from the territory covered by Gray's Manual.

Marshallia obovata var. obovata grows well and flowers in the greenhouse in ordinary garden-type soil. Under these conditions the leafy-stemmed nature of this variety is emphasized.

4b. Marshallia obovata (Walt.) Beadle \& F. E. Boynt. var. scaposa var. nov. ${ }^{16}$

Marshallia obovata (Walt.) Beadle \& F. E. Boynt. sensu Beadle \& F. E. Boynt. Bilt. Bot. Stud. 1: 5, pl. 5. 1901. Not Athanasia obovata Walt. Fl. Carol. 201. 1788.

Perennial scapose or subscapose herb (0.5-) 1.5-3.5 (-5.0) dm. tall. the stem from a short caudex wtih coarse fibrous roots, the vascular

[^20]fiber of old leaf bases and several to many radical leaves; plants usually simple with a single scape but occasionally with 1-5 intact leafy offsets, each bearing a peduncle. Inflorescence a single head, typically borne on a simple (true) scape but sometimes apparently long-pedunculate from a short stem with a few leaves, the leafy portion $1 / 4$ the length of the peduncle or less. Peduncles (5-) $15-30(-40) \mathrm{cm}$. long, naked or sometimes with a remote linear-oblong, obtuse bract, sulcate, glabrous or glabrate below, becoming copiously white-pubescent beneath the head with ascending-incurving, moniliform hairs, the pubescence abruptly discontinuous below the phyllaries. Leaves radical or nearly so, glabrous, 3 -nerved or apparently 1 -nerved with the laterals of the upper (adaxial) surface obscure to the naked eye; lowermost (radical!) leaves (1-) $2-5(-10) \mathrm{cm}$. long, $4-10(-15) \mathrm{mm}$. wide, with obovate, spatulate or oblong-spatulate, obtuse, sometimes emarginate blades, narrowed below into broad petioles; subradical (the lower cauline or upper rosette) leaves (3-)5-10(-12) cm . long, (3-) $5-10(-15) \mathrm{mm}$. wide, with lanceolate, oblanceolate or linear-oblong, obtuse or acutish blades, narrowed below into sheathing petioles usually shorter than the blades. Heads hemispherical or broadly campanulate, (10-) 15-20(-25) mm . wide, (5-) $7-12(-15) \mathrm{mm}$. high including the pales. Phyllaries usually oblong with obtuse and often minutely mucronate apices, sometimes lanceolate, elliptic or linear-elliptic with obtuse or abruptly pointed apices, (5-) 6-8(-10) mm . long, ( $1.5-) 2-2.5(-3) \mathrm{mm}$. wide, glabrous, often with scattered resin atoms, usually green (rarely reddish) and thin in texture at anthesis, buff to stramineous and firm in age, bordered to the middle and above by narrow to quite conspicuous white-hyaline margins, usually entire, sometimes remotely dentate or erose, the midribs slightly thickened. Pales of the receptacle glabrous, usually with scattered resin atoms, $5-8(-10) \mathrm{mm}$. long, spatulateclavate or linear-spatulate, gradually narrowed below, the summit usually distinctly dilated, the apices obtuse and minutely mucronate or abruptly pointed. Receptacle convex, dome-shaped or conical in age, the pales usually persistent beyond the spreading of the achenes. Flowers white, whitish or pale lavender in color, externally pubescent. Dried corollas $10-12 \mathrm{~mm}$. long, the tube $5-6 \mathrm{~mm}$. long, expanded above into a shallow throat, the limbs spirally twisted. Anthers cream-colored, white or bluish, $2.5-3.5 \mathrm{~mm}$. long, the column exserted bevond the corolla throat. Stigmas exserted bevond the anther-column, divergent and reflexed in age. Pappus scales white or castaneous in color, usually imbricate at the base, ovate, strongly acuminate, usually with at least the upper half somewhat irregularly lacerate, sometimes regularly serrulate, (1-) $1.5-2.5(-3) \mathrm{mm}$. long, as long or shorter than the achene. Achenes obconic, 10 -ribbed, about 3 mm . long, the ribs copiously pubescent, the hairs as long or longer than the distance between adjacent ribs, the concave achene-surface between ribs usually covered with minute resin atoms. Flowering from April through the first week of June; fruiting from May to mid July. (Plate 7.)


Plate. 7. Marshallia ohoruta var. scaposa: Fig. 1, Godfrey 4918ł-Type, Brunswick County, North Carolina (to scale); Fig. 2, specimen from Harnett County. North Carolina grown in the greenhouse and showing the conspicuous rosette habit (approx. $1 / 2$ scale).
distribution. Occurring on light sandy soils in dry pinelands, edges of sandhills, dry savannas and oak woods in the Coastal Plain from North Carolina southward into Florida and Alabama. (Map 2.)
hepresentative specimens. Without locality: Herb. Wallace 55 (Charl); Herb. Rugel (phil-Herb. Martindale). Am. Sept.: Le Conte, Herb. Richard (p-Herb. Drake); Fraser (Fl-Herb. Webb). North Carolina. Bladen Co--Biltmore Herbarium (Collectors) 1258 (ConN, CU, RM, US) ; vicinity of White Lake: Blomquist 5280 (DUKE); Channell 2816 (to be distributed) ; Oosting 34109 (PENN, Ph). Brunswick Co.3 mi . w. of Leland, Godfrey 49184 (Gh-Type; duke, G, GA, Na, NCSC, vcu-Isotypes). Columbus Co.-Bolton, Schallert 11112 (ill, min, taes). Cumberland Co.-Vicinity of Favetteville: Biltmore Herbarium (Collectors) $1258^{d}$ (us), $1258^{\circ}$ ( NCSC, NY); Channell 1906. 1910 (to be distributed); Godfrey \& Fox 49450 ( NCSC). Durham Co--Radford d Radford 3036 (NCU). Hartnett Co.-Channell 2821, 2822, 2823, 2830, 2831 (to be distributed). Johnson Co.-Princeton, Mitchell. 19 May 1936 (duke). Montgomery Co.-near Eldorado, Correll 810 (duke). Moore Co--near Aberdeen, Biltmore Herbarium (Collectors) $1258^{\prime}$ (ill, min, ny, us); near Pinebluff, Palmer 42370 (GH, mo, ny). New Hanover Co.-Wilmington, Bartram \& Long 1054 (PH). Richmond Co.-Hamlet, Williamson (PH). Scotland Co.-Laurinburg, Radford \& Stewart 441 ( NCSC, NCU). Wake Co.-near Raleigh, Godfrey 77 (GH, NCSC) ; between Cary and Morrisville, Channell 1940 (to be distributed). South Carolina. Without definite locality: McCarthy, 1888 (us). Aiken Co.-vicinity of Aiken: Biltmore Herbarium (Collectors) $.5521,5521^{\circ}$ (us) ; Canby, May 1869 (P, GH, MO, NY, PH, us); Ravenel (Charl, dwC, f, us), 3 May 1867 (Gh); Smith (penn). Barnwell Co.4.4 mi . s.e. of Ellenton, Leeds 2866 (duke, mo, ph). Clarendon Co.5 mi s. of Manning, Batson, 14 April 1953 (usc). Darlington Co.-vicinity of Hartsville: Coker, 24 May 1909 (ncu); Rogers, 6 May 1910 (UNC); Norton, variously dated (NCU, US); Smith (NCU); Radford d Stewart 38.5 (NCU). Florence Co.-Florence: Biltmore Herbarium (Collectors) 1258 ( $\mathbf{~ U S}$ ) ; Bartram 2283 ( $\mathbf{P H}$ ). Horry Co. -2.8 mi . s.e. of county line, S. C. Rt. 9, Radford \& Stewart $987^{\circ}$ (NCU). Lexington Co.-Swansea, Weatherby 6126 (GH, Ny, us). Richland Co--vicinity of Columbia: Bartram, 16 May 1912 (PH); Blackman (F); Canby with Sargent 57 (GH); Philson, 12 May 1936 (duke, okla); Taylor, May 1890 ( $\mathrm{BKL}, \mathrm{F}$ ). Georgia. Bibb Co.-Macon: Greenman (PH); Shaw, May 1888 (yU). Burke Co.- Alexander, Ellis (POM). Calhoun CoArlington, Thorne \& Muencher 28.9 (GA, us), 8033 (Cu, GA, GH); Leary, Thorne 33.31 (cu). Lee Co. -3 mi . e. of Smithville, Duncan 2.314 (GA). Macon Co.-Marshallville, Earle 3140 (ny). Peach Co.near Byron, J. C. D. 28, 23 April 1927 (UARK). Florida. Without definite locality: Buckley (mo); Chapman (NY); Elliott (K); Rugel 74 (F, GH, MO, NY, Us). Alabama. Barbour Co. -15 mi s.w. of Eufaula,

Wherry, 12 April 1897 (na). Lee Co.-Auburn, Earle \& Baker ( F , ill, min, mo, ny, rm, us). Pike Co.-Troy, Leland, 17 April 1891 (GH).

As indicated in the discussion of the preceding variety (obovata), the taxon treated here as var. scaposa has never before had a legitimate name, although it has previously been recognized taxonomically by implication. This situation developed as a result of the description of var. platyphylla as a leafystemmed variant of $M$. obovata and with the subsequent erroneous restriction of the application of the epithet obovata to its scapose counterpart. Thus the taxon treated by Beadle and Boynton as M. obovata represents a new variety, different from Athanasia obovata Walt.

Marshallia obovata var. scaposa occurs almost exclusively on the geologically more recent, light sandy soils of the Coastal Plain, along or outside the Fall Line. Although the two varieties of $M$. obovata flower over the same general period and although their ranges abut, they are nevertheless effectively isolated ecologically. Variety scaposa occupies more specialized, xeric habitats on the edges of sand hills beneath pines or amongst scrub oaks, etc., while var. obovata is more widely distributed over the Piedmont in more mesic habitats and even extends into the mountains. While the Fall Line between the Piedmont and Coastal Plain forms the more or less sharp line of demarcation between the ranges of the two varieties (Map 2), the apparent overlapping of ranges at certain points is due to the uneven nature of the Fall Line in certain areas where there are interfingerings of geologically older clayey soils with younger sandy soils. At certain points along the Fall Line where there are abrupt changes in the physical nature and geologic history of the soils, the two varieties may occur in close proximity to one another. Yet morphological distinction is maintained along the line of contact with very little if any intergradation. This suggests that the varieties may in fact be isolated genetically. Experimental attempts to hybridize the two varieties in the greenhouse were unsuccessful.

There is no question but that the two taxa are very closely related morphologically. Genetically the evidence is inconclusive for additional experiments are required to determine whether or not they will actually hybridize. From the standpoint of geographical distribution the two taxa are strongly allopatric. Historically the two elements have been treated as geographical
varieties. Despite the fact that there are indications that the two taxa may probably be completely isolated genetically, and have certain qualities of distinct species, it seems best to retain the varietal status until sufficient experimental information is accumulated to justify fully their elevation to specific rank.

In considering the probable direction of evolution within Marshallia obovata there are two indications which suggest that var. scaposa is probably the younger, derived member. The first indication is the fact that the plants are scapose or subscapose in habit, a growth form which morphologically may be considered to have been derived from the caulescent through a telescopic type of reduction of the stem. The second indication concerns the distribution of the varieties, respectively, over areas with entirely different geological histories. It is significant that the distribution of the scapose variety, presumed on morphological grounds to be the more recently evolved, occupies the area of geologically more recent soils and which has only in geologically recent times become available for plant occupancy. It is perhaps significant further that the scapose variety has not been collected in any of the disjunct Coastal Plain-like habitats isolated in the Piedmont and mountains which are floristically notorious for their richness in Coastal Plain species. This may be due to the relatively recent origin of var. scaposa somewhere along, at or near the Fall Line and its subsequent spread into the adjacent coastal plain only.

If the actual course of evolution in Marshallia obovata has been in the direction supposed here, it may be concluded that var. obocata is the older representative and that it apparently has Appalachian affinities. Turning, then, to those species with an Appalachian distribution, it can be readily seen from Map 1 that M. grandiflora is conspicuous in this respect. Moreover, this is the one species which on a morphological basis is more closely related to M. obovata var. obovata, as already pointed out.

Marshallia obovata var. scaposa is apparently adapted genetically to the more rigorous xeric habitat of the Coastal Plain. Representatives of the two varieties maintained their respective differences in growth habit under similar greenhouse conditions when grown in a garden-soil mixture. In fact, the scapose nature of var. scaposa was actually emphasized as shown in Plate 7, fig. 2. by the production of more numerous radical leaves and a more striking rosette habit of growth. Variety obovata responded in a similar manner as under natural field conditions.

## 5. Marshallia ramosa Beadle \& F. E. Boynt.

Marshallia ramosa Beadle \& F. E. Boynt. Bilt. Bot. Stud. 1: 8, 9, pl. 2. 1901. ". . . grows in moist, sandy pine-lands at Eastman, Georgia (type locality), where it was collected in full flower June 5, 1900, by Mr. C. L. Boynton, of the Biltmore Herbarium." (us-Type, ex Biltmore Herbarium, presented by Mrs. George W. Vanderbilt, 1917, marked "Type Sheet" by C. D. Beadle and F. E. Boynton.)

Perennial linear-leaved herb (1-)2.5-5(-6) dm. tall, the stem from a thickish crown (caudex) with coarse fibrous roots, usually bearing wiry fiber of old leaf bases, freely crmoselv branched about the middle and above, the alternate branches ascending and producing a more or less flat-topped, compound inflorescence of (2-) 4-12 (-20 or even more) small, long-pedunculate heads, the peduncles sometimes approximate, giving an umbellate appearance; stems sometimes solitary but usually clustered with several arising from the same caudex, and often with sterile, leafy offsets at the base. Stems annual, glabrous below, becoming very sparingly pubescent on the branches, striate or angled below (sometimes squarish), becoming more distinctly sulcate above, usually green or greenish in drying, stramineous in age and often purple at the base, leafy to the inflorescence branches and above. Peduncles slender, $0.5-1 \mathrm{~mm}$. in diameter, sulcate, glabrate below, becoming sparsely pubescent near the summit, naked or leafy-bracted below the middle by the reduced, linear, obtuse leaves of the upper stem. Leaves glabrous, entire, firm in texture, the lower prominently 3 -nerved, gradually diminishing in size upwards and usually extending well upon the branches to the bases of the peduncles as reduced linear bracts; the lower leaves contracted into winged, petiole-like bases as long or longer than the blades; the middle and upper cauline leaves becoming sessile and only 1 -nerved. Radical leaves rarely intact or well developed, when present $5-10(-15) \mathrm{mm}$. wide, (2.5-) $4-8(-10) \mathrm{cm}$. long including the petioles, with oblong, oblong-spatulate or obovate, obtuse blades about as long as the petiolar portion; lower cauline leaves (3-)5-8(-10) mm . wide, (5-) 8-20 (-25 or more) cm . long including the prolonged petioles, linear, linear-attenuate or linear-lanceolate in outline, with obtuse apices; middle cauline leaves gradually reduced in size upwards, usually $3-8(-10) \mathrm{mm}$. wide, $3-10 \mathrm{~cm}$. long; the upper leaves greatly reduced (1-) 2-3(-4) mm . wide, (1-) $2-4 \mathrm{~cm}$. long, the uppermost narrowly linear, linear-oblong or linear-lanceolate, with obtuse or acutish apices. Involucres hemispherical or broadly campanulate, typically small, usually ( $7-) 8-10(-15) \mathrm{mm}$. wide and (5-) $6-8(-10) \mathrm{mm}$. high including the pales, sometimes subtended by a remote leaf-bract. Phyllaries herbaceous, thin in texture at flowering time, the midrib slightly thickened, stramineous to buff and rigid in age, glabrous or occasionally sparingly pubescent, without superficial resin atoms, without hyaline margins and entire or with conspicuous white-hyaline borders and usually remotely toothed or erose, subequal in about 2
series, the outer ( $0.8-$ ) $1-2(-2.5) \mathrm{mm}$. wide, $4-6(-7) \mathrm{mm}$. long, shorter than the pales, quite variable in outline: oblong with rounded or obtuse and minutely mucronate apices, linear-lanceolate with acute apices, elliptical with acute apices and white-hvaline borders to the middle and above or rhomboidal, broadest above the middle by conspicuous whitehyaline shoulders, with acute apices or occasionally subulate-tipped. Pales of the receptacle linear, usually merely acute, sometimes subu-late-tipped, $5-7 \mathrm{~mm}$. long, typically glabrous but occasionally sparingly pubescent with scattered hairs, without resin atoms, rigid in age, persistent beyond the shedding of the achenes. Receptacle convex and dome-shaped or weakly conical in age, $3-4 \mathrm{~mm}$. wide, about 3 mm . high. Flowers predominantly white or whitish, occasionally very pale lavender. Dried corollas $8-10 \mathrm{~mm}$. long, the tube about 5 mm . long, usually expanded at the junction of the corolla-lobes into a shallow throat $1-2 \mathrm{~mm}$. in length. Anthers usually white or cream-colored, sometimes pale lavender, $2-2.5 \mathrm{~mm}$. long, the filaments usually white, sometimes red. Stigmas divergent and curling downward in age, usually exserted bevond the anther-column, the style usually included. Pappus scales usually shorter than the achene, $1-1.5(-2)^{\circ} \mathrm{mm}$. long, regularly serrulate, acuminate from a broad base or somewhat irregularly lacerate, minutely scabrous. Achenes (1.5-) $2-2.5(-3) \mathrm{mm}$. long, prominently 10 -ribbed, the ribs hairy, the concave surfaces between the ribs covered with minute resin atoms, sometimes copiously so. Flowering from late May through June; fruiting from late June through July. (Plate 8.)
distribution. Localized endemic of the Altamaha Grit Formation of south-central Georgia (known only from Dodge, Johnson, Tattnall and Telfair Counties); occurring on dry rocky outerops, dry wire-grass pine-barrens, bases of post-oak sandhills and somewhat moist sandy pinelands. (Map 3.)
specimens examined. Without locality: Muhlenherg Herbarium 599 (PH). Georgia. Dodge Co.-vicinity of Eastman: Ashe Herbarium (ncu) ; Biltmore Herbarium (Collectors) 2370 (us), 8708 (min, us), 8708a (us). Johnson Co-near Wrightsville: Channell 1963 (to be distributed); Harper 1.342 (bKl, bm, F, GH, MO, Ny, us, wva); Pyron \& McVaugh 3081 (GA, NA). Tattnall Co.-flat rocks near Ohoopee River, Harper 1855 (ariz, F, GH, Mo, Ny, us). Telfair Co--vicinity of Lumber City: Biltmore Herbarium (Collectors) $8708^{\circ}$ (us); Wilbur 3449 (dUKE, NCSC).

Marshallia ramosa is a very localized endemic in south-central Georgia (Map 3), known only from Johnson, Telfair, Dodge and Tattnall Counties. It is isolated geographically from M. caespitosa var. signata, the taxon which it most closely resembles morphologically. In fact, both varieties of M. caespitosa occur west of the Mississippi River only.


Plate. 8. Marshallia ramosa: Channell 1963, Johnson Count!. Ceorgia.

The relationships of Marshallia ramosa to M. caespitosa var. signata were pointed out by Beadle and Boynton (Bilt. Bot. Stud. 1: 8, 9) in 1901, when the two taxa were first described. According to Beadle and Boynton, M. ramosa differs from both varieties of M. caespitosa in the extremely floriferous habit, the shorter and more obtuse phyllaries and in the smaller pappus scales. These same characters are used in the present treatment to distinguish these species.

As originally described and as represented in the type, the phyllaries of $M$. ramosa are ". . . oblong, rounded at the apex and minutely mucronate, smooth, $1-2 \mathrm{~mm}$. wide, thin in texture at flowering time, the midrib slightly thickened:" The phyllaries of the species as a unit, however, are quite variable in form, in fact, considerably more variable than indicated in the original description. They are sometimes pubescent with scattered moniliform hairs, are frequently rhomboidal in form due to the possession of broad shoulders or wings and are occasionally acute or even subulate at the apices. While some modification of the "glabrous-oblong-obtuse" form represented in the type might be expected to accompany the maturation of the phyllaries, the extreme forms encountered are not easily explainable on this basis. The kinds of variation just mentioned are exemplified by specimens of R. L. Wilbur's collection number 3449 from Lumber City, Telfair County.

It should be emphasized at this point that the element of this species represented by the type is encountered exclusively in certain populations. Living plants were taken from such a population near Wrightsville, Johnson County (R. B. Channell's collection number 1963), and transplanted to the greenhouse. It is significant that the "glabrous-oblong-obtuse" character of the phyllaries was maintained over a two-year period in the greenhouse during which time some of the plants flowered twice.

As suggested elsewhere in this work, the spring-flowering species Marshallia ramosa with the varieties of M. caespitosa form a closely related species group which is morphologically distinct from the late summer or fall-flowering species group comprised of M. tenuifolia and M. graminifolia, despite the fact that they have in common the narrow, linear-lanceolate leaf form. Moreover, as groups, the two are in large measure isolated geographically. It would appear, however, in contradistinction to the stated divergencies, that certain members of these two groups still retain genetic compatibility. The basis for this reasoning
involves the extreme, atypical morphological element of $M$. ramosa, exemplified by Wilbur's number 3449, already discussed. This element may have been derived through hybridization with M. tenuifolia, that is, from introgression of the characters of $M$. tenuifolia into M. ramosa. Marshallia tenuifolia possesses all of the characters considered to comprise the atypical element in M. ramosa and hybridization between these species would form a logical explanation for this peculiar variation pattern. The present study indicates that the geographical ranges of the two species (Maps 3\&4) overlap in Telfair County, the source of the Wilbur collection, and at other points, according to the literature.
In general, however, these species are isolated seasonally. Marshallia ramosa with $M$. caespitosa comprise a spring-flowering species-group, while $M$. tenuifolia with M. graminifolia comprise a late summer or fall-flowering group. Yet, of these species, $M$. ramosa has a relatively long flowering period which may have in some years overlapped that of M. tenuifolia, especially if the flowering of the latter were occasionally earlier than usual. This would help to explain the localized population-wise nature of the presence of characters of M. tenuifolia in M. ramosa which is clearly not a general feature of the latter as a unit. Otherwise, one must regard the introgression of the characters of M. tenuifolia into M. ramosa as antedating the evolutionary adaptation to the different flowering seasons of the two species, respectively. This, however, probably would have allowed the characters of M. tenuifolia to be considerably more general or widespread in M. ramosa than is now the case.

Finally, it is considered significant that seeds of relatively pure Marshallia ramosa from Wrightsville, Georgia planted in the greenhouse produced seedlings which from the start had leaves of an elongate linear-lanceolate type and which were retained unaltered at maturity. The radical leaves of the supposedly introgressed M. ramosa from Lumber City, conversely, are often of a broad ovate or obovate type resembling those of $M$. tenuifolia.

6a. Marshallia caespitosa Nutt. ex DC. var. caespitosa
Marshallia caespitosa (Nutt! in litt. 1825) DC. Prod. 5: 680. 1836. ". . . in Amer. bor. ad Red-River legit cl. auctor." The type locality was very probably in what is now southeastern Oklahoma. (G-Type, photograph examined; Isotypes-вm, photograph examined; x, PH, specimens examined.)

Marshallia spiralis Raf. New Fl. 4: 77. 1838. ". . . in Arkansas and west Louisiana found by Binder . . ." (Type not located.)

Peremial scapose or subscapose herb (1-) 2-4 (-6) dm. in height, the stem arising from a short caudex with coarse fibrous roots, the caudex somewhat fleshy in age and often bearing the vascular fiber of old leaf bases; plants sometimes singly disposed but usually somewhat tufted or cespitose in habit, usually with several offsets borne on the same caudex, each bearing a simple scape or peduncle. Stem very short, with a few reduced leaves at the base of the peduncle, or plants apparently stemless, with all the leaves crowded at the base. Peduncle usually more or less stout, $1-4 \mathrm{~mm}$. wide, ( $8-$ ) $15-35(-50) \mathrm{cm}$. long, sulcate, glabrate to sparingly pubescent below, becoming densely pubescent beneath the head with white or tawny, ascending-incurving, moniliform hairs, frequently with 1 or 2 remote, linear leaf-bracts. Leaves glabrous, entire, usually 3 -nerved or the upper (inner rosette leaves) apparently 1 -nerved, gradually tapering below the middle into winged, petiole-like bases. Radical (lowermost) leaves usually not intact, when present (3-) $5-10(-15) \mathrm{mm}$. wide, $2-6(-10) \mathrm{cm}$. long, with obovate, spatulate or oblanceolate, obtuse blades; imer (upper) leaves of the rosette $2-10(-12) \mathrm{mm}$. wide, $(4-) 5-15(-16) \mathrm{cm}$. long, of a linear or linear-lanceolate type, with obtuse, rarely acutish apices. Cauline leaves few in number, like the latter in form, gradually reduced in length upwards, their tips projecting only slightly if at all bevond the level of the longer basal leaves, imparting a wholly basal-leaved aspect to the plant. Involucres hemispherical or broadly campanulate, 15-$25(-35) \mathrm{mm}$. wide, ( $5-) 6-12(-14) \mathrm{mm}$. high including the pales. Receptacle convex, conical in age. Phyllaries herbaceous, green in color except for the white-hyaline margins below the middle, rigid and straw-colored in age, glabrous, entire, subequal in 1-2 series, the outer usually but scarcely imbricate, $1-2(-3) \mathrm{mm}$. wide, $6-10(-12) \mathrm{mm}$. long. linear-oblong or linear-lanceolate in outline with obtuse or acutish apices. Pales of the receptacle ( $5-$ - $7-8 \mathrm{~mm}$. long, linear with acute apices, slightly dilated at the summit. Florets usually white or creamcolored, only occasionally pale lavender. Dried corollas $10-12 \mathrm{~mm}$. long, the tube $5-7 \mathrm{~mm}$. long, sometimes slightly dilated upwards into a shallow throat. Anthers white or cream-colored, rarely bluish, (2.5-) 3-3.5(-4) mm. long, the column usually exserted bevond the corolla-tube. Stigmas exserted bevond the anther-column, divergent and recurving in anthesis. Pappus scales white to tawn in color, (1.5-) $2-2.5(-3) \mathrm{mm}$. long, shorter than the mature achene, imbricate at the base, mimutely scalbrous, irregularly serrulate, sometimes somewhat lacerate, the apices acute to scarcely acute. Achene (2-) 3-4 (-4.5) mm . long, obprramidal, somewhat angled, prominently 5 -ribbed, and usually also with 5 secondary ribs evident, the primary ribs conspicuously and copiously villous with white or tawny hairs, the trichomes minutely bifurcate at the apices, achene-surface somewhat concave between the ribs, beset with scattered resin atoms. Flowering from mid April through May; fruiting in May and June. (Plate 9.)


Plate 9. Marshallua cuespionsa var. caespitosa: Wiaterfall 11 39 I, Puhhmataha County, Oklahoma.
distribution. Prairies, open woods, fields and rocky hills; occurring locally in Jasper County, Missouri, extending southward through western Oklahoma into northeastern Texas; distributed on sandy soils over much of southeastern Texas and locally in western Louisiana.
representative specimens. Missouri. Jasper Co.-High prairies: Alba, Palmer 26946 (mo); Jasper, Palmer 3407 (GH, мо), 21565 (NY); Prosperity, Palmer 2153 (GH, MIN, MO, NY, US), 2153 A (GH, ny, us, WVA) ; Webb City, Palmer 2015 (GH, ILL, MO, NY, US). Arkansas. Without definite locality: Nuttall (F, GH, K, PH). Oklahoma. Red River, Nuttall, 1825 (GH-photograph of Type; вм, к, PH-Isotypes). Choctaw Co.-Hugo, Demaree 12591 (okl, Ny). Creek Co.-Bristow, Williams 1, 24 ( PH ). Cravin Co.-Stratford, Hudson 22 (OKL). Haskell Co.-Bebb 5468, 8 June 1940 (okl); 5 mi. s. of Kinta, Hopkins 5127 (okl). Hughes Co.-Calvin, McLean, 10 May 1935 (okla). Johnston Co. -15 mi . n. of Tishomingo, Waterfall 11426 ( OKl, OKla); 9.5 mi . w. of Wapanucka, Waterfall 8917 (OKL, OKLA). Le Flore Co.-Pine Valley, Goodman 2538 (GH, MO, NY, OKL, OKLA, RM); 5 mi. s. e. of Talihina, Robbins 2966 (okl, smu, taes). McCurtain Co.-n. e. of Broken Bow, Sears 1395 (okl). Murray Co. -3 mi . e. of Sulphur, Waterfall 6463 (OKL). Muskogee Co.-Fort Gibson, Engelmann (GH). Pontotoc Co. -3.4 mi . s.e. of Pittstown, Robbins 2.538 (okl, taes); 7 mi. s. of Ada, McCary 677 (okla). Pushmataha Co.-Tuskahoma, Dyal, Hazard \& Fisher 261 (cu); 3 mi. s. of Albion, Waterfall 11391 (OKla). Pottawatomie Co.-Wanette, Faulkner 10, 140 (okl). Seminole Co.-2 mi. n. of Seminole, Nelson 66 (okl). Sequoyha Co.-Fort Salissa and Illinois River, Engelmann 582 (mo). Texas. Without definite locality: Lindley, 1843 ( $\mathbf{K}$ ) ; Jordan, 1869 ( $\mathbf{P}$ ); Hildebrands (US); Milligan (ARiz) ; Drummond 174 (fi, G, GH, K, P, PH); Mill Creek, Lindheimer 47 (mo). Austin Co.-Industry, Wurzlow, 1891 (ilL). Bastrop Co.-Smithville, Morrs, 22 April 1930 (TEX); Bastrop, Duval 5 (us). Brazos Co.-Brazos, Lindheimer, May 1844 (mo); White Creek, 2 mi. s.e. of College Station, Cory $515 \dot{6} 9$ (GH, SMU); College Station, Parks, April 1946 (taes, tex). Burleson Co. -9.7 mi. n.e. of Lyons, Cory 5164 ( rm, smu, us). Caldwell Co.-near Luling, Perkins \&f Hall 2863 (CU). Chambers Co. -14.5 mi . n.w. of White Ranch Depot, Parks \& Cory 22504 (taes), 22506 (NA). Favette Co.Matthes 63 (G). Galveston Co.-Kemah, Fisher, 21 April 1924 (Duke, US); Nelson, 14 April 1942 (TEX). Gonzales Co.-Gonzales, Schulz 2318 (LCU). Grayson Co.-Liberty High School, Gentry 50-267 (oKl, Penn, Tex). Hardin Co. -2 mi. niw. of Sour Lake, Rosier, 24 March 1952 (Smu). Harris Co.-Houston: Hall, May 1872 (BKL), 365 (f, g, GH, ILL, K, MO, NY, PHIL, POM, US ), 366 (GH) ; Lindheimer 23, 32 ( MO), 110 (BM, GH, MO, NY, P, PH, SMU). Jackson Co.-Canado, Palmer 9221 (mo, us). Jefferson Co.-Hamshire, Stuckman 7 (TEX); Nome, Fisher .38034 (F, VHC). Lamar Co.-Paris, McMullen, 3 May 1926 (tex). Navarro Co.-Corsicana, Williams 18 (TEX); 3 mi . s.e. of Dawson,

Cory 55630 (us). Orange Co.-Orange, Warren, 4 May 1930 (Na). Polk Co.-Corrigan, Fisher 3486 (F). Refugio Co.-Refugio, Benke 5441 ( $\mathrm{F}, \mathrm{G}, \mathrm{GH}$ ). Louisiana. Without definite localitv: Drummond (k); Leavenworth (FI, GH) ; Hale (GH, P). Caddo Parish.-Shreveport, Cocks, 20 April 1916 (мо). Calcasieu Parish.-English Bayou area, Cooley \& Brass 4104 (GH, duplicates to be distributed); Sulphur, Palmer 7700 (mo, ny, us); Parkins, Pennell 10215 (ny, PH). Rapides Parish.-Alexandria, Hale, April 19?? (Pн). Vernon Parish. -7 mi. n.e. of junction of Haddenburg Ferry, Cooley \& Brass 4044 (GH, duplicates to be distributed).

In the original description of Marshallia caespitosa, De Candolle (Prod. 5: 680. 1836) ascribed the name to Nuttall in the reference "(Nutt.: in litt. 1825)." On the basis of this reference, however, it is not clear whether Nuttall supplied the name alone, or both the name and description published by De Candolle. The Nuttall type of Marshallia caespitosa, preserved at the Conservatoire et Jardin botaniques, Genève, has thus far furnished the only clue to the meaning of this citation. The Genève specimen is the only one of the series of Nuttall isotypes which bears the inscription "Mr. Nuttall 1825," in addition to "Marshallia "caespitosa, Red River." Only the latter inscription appears on the remaining isotypes. The inscription " 1825 " is presumed to indicate the year that Nuttall probably sent the specimen and perhaps information "in the form of a letter" to De Candolle. It could not refer to the year of collection, for Nuttall is known to have traveled in the Red River area of the Arkansas Territory (now southeastern Oklahoma) only in the year 1819. ${ }^{17}$ This is the area from which the isotypes were apparently collected.

In the absence of information to the effect that Nuttall actually supplied the description of Marshallia caespitosa for publication by De Candolle, the authorities' names are separated by the word ex. While this is in keeping with the citation as written by Shinners (Field and Lab. 17: 174. 1949), it is contrary to the citation currently in general use in which Nuttall alone is acknowledged. Even if Nuttall were definitely known to be the author of the description, the name of the publishing author, being the more important, should be retained (Recommendation 46A, International Code of Botanical Nomenclature, 1956).

[^21]In any case, the Genève specimen has been selected as the lectotype. Because this sheet bears the inscription "1825," cited by De Candolle, it is believed to be the one used in drawing up the description.

Marshallia spiralis Raf. is clearly a synonym of Marshallia caespitosa Nutt. ex DC. However, this binomial has not previously been interpreted. It seems desirable, therefore, to clarify the matter in some detail. The original description (New Fl. 4: 77. 1836) is as follows:

[^22]Inasmuch as no Binder collections have been located during the course of this revision, it has been necessary to rely solely upon the original description for the interpretation of the species. The original description clearly defines the plant as subscapose, with linear-lanceolate, obtuse leaves. The possibilities are thus considered narrowed, for there is only one subscapose Marshallia with linear-lanceolate, obtuse leaves. This species, M. caespitosa, is definitely known to occur in Arkansas and Louisiana and is the only species which is not excluded by Rafinesque's circumscription of M. spiralis.

On the basis of this information it seems safe to conclude that Marshallia spiralis Raf. represents the same species as that published by De Candolle as M. caespitosa. Moreover, Rafinesque was apparently unaware of the previous description of $M$. caespitosa, for, in summarizing the Marshallia species known to him in 1836 (New Fl. 4: 77), the latter was not taken into account.

The geographical distribution of Marshallia caespitosa is given by Rydherg (Flora of the prairies and plains of central North America, page 839. 19:32) as "Ark.-Kans.-Tex.-La." No specimens were located during the present study, however, which substantiate the report of either variety of this species from Kansas. The Arkansas record for the species is supported by Nuttall collections which lack definite locality data. These reports need verification by modern collections.

The relationships of the two varieties of Marshallia caespitosa are discussed under var. signata.

6b. Marshallia caespitosa Nutt. ex DC. var. signata Beadle \& F. E. Boynt.

Marshallia caespitosa Nutt. var. signata Beadle \& F. E. Boynt. Bilt. Bot. Stud. 1: 9, 10, pl. 8. 1901. "Based on A. A. Heller's no. 1618 from Kerrville, Kerr County, Texas, April 19-25, 1894." (us-966507Type, ex Biltmore Herbarium, presented by Mrs. George W. Vanderbilt, 1917, marked "Type Sheet" by C. D. Beadle and F. E. Boynton; Isotypes-ariz-25260 \& 58432, BKL-5917 \& 016055 , CU, F, GH, iLL, MIN, MO, NY, PH, POM, RM, US.)

Perennial, caulescent, linear-leaved herb, (1.5-) 2-5(-6.5) dm. in height, the stem from a short crown or caudex with coarse fibrous roots and often the vascular fiber of old leaf bases, the caudex becoming fleshy in age, sometimes 1 cm . thick and 2 cm . long, with numerous short internodes. Stems tufted or solitary, usually cymosely branched below or above the middle and bearing 2-5 (-12 or even more) heads, but often simple and monocephalous, the stems striate, somewhat angled and glabrous or glabrate below, becoming more distinctly sulcate and pubescent near the middle and on the branches, pale green to olivaceous in color, becoming stramineous in age. Peduncles (3-)5-$20(-30) \mathrm{cm}$. long, sulcate, pubescent below, often becoming copiously so beneath the phyllaries, naked or often leafy-bracted at the base. Leaves glabrous, entire, more or less 3-nerved, sometimes apparently 1 -nerved, the radical $4-10(-20) \mathrm{mm}$. wide, (2-) $4-8(-16) \mathrm{cm}$. long with obovate, spatulate or oblanceolate, obtuse blades, contracted below into broad, sheathing, petiole-like bases. The lower cauline leaves usually crowded at the base, $2-10(-12) \mathrm{mm}$. wide, (2-) $5-15(-18) \mathrm{cm}$. long, with linear-attenuate, linear-oblong or linear-oblong or linearlanceolate, obtuse, rarely acutish, blades, narrowed below into sheathing petiole-like bases about $1 / 2$ as long as the blades. Middle and upper cauline leaves similar to the latter in outline, becoming 1 -nerved and sessile above, gradually reduced in size upwards, extending at least to the middle of the stem and usually well up on the branches as reduced leaf-bracts at the bases of the peduncles. Involucres broadly campanulate or hemispherical, (10-) $15-25(-32) \mathrm{mm}$. wide, $5-15 \mathrm{~mm}$. high including the pales, often subtended by a remote, linear leaf-bract. Phyllaries glabrous, entire, herbaceous, green in color, except for the white-hyaline borders to the middle and above, thin in texture at anthesis, firm and somewhat rigid in age, subequal in about 2 series, the outer linear, linear-lanceolate or lanceolate in outline, $1-2(-3) \mathrm{mm}$. wide, ( $5-$ ) $7-12(-1.5) \mathrm{mm}$. long, usually imbricate at the base but sometimes merely approximate, scarcely at all imbricate. Receptacle domeshaped, conical in age. Pales of the receptacle linear, acute, $6-8 \mathrm{~mm}$. long, persistent bevond the shedding of the achenes. Florets white or cream-colored, rarely pale lavender. Dried corollas $10-12 \mathrm{~mm}$. long, the tube $5-7 \mathrm{~mm}$. long, sometimes slightly dilated above into a shallow throat. Pappus scales ( $1.5-) 2-3(-4) \mathrm{mm}$. long, white, tawny or ferru-
gineous in color, imbricate at the base, regularly serrulate or lacerate, acuminate, acute to scarcely acute, minutely scabrous, usually shorter than the mature achene. Achene $3-4 \mathrm{~mm}$. long, obconic or obpyramidal, 10 -ribbed, the ribs hairy with minutely bifurcate trichomes, achene-surface between the ribs concave, beset with minute resin atoms. Flowering in April and May, occasionally into June; fruiting in May and June. (Plate 10.)
distribution. Sandy prairies, limestone bluffs, dry hillsides; a common and characteristic plant of chalk and limestone outcrops and calcareous soils throughout central Texas; occurring locally in Ozark County, Missouri, on rocky ground of the "bald knobs." (Map 3.)
representative specimens. From cultivation: Harvard University Botanic Garden, 1884 (GH). Missouri. Ozark Co.-Tecumseh, Palmer 34811 (мо, PH, us). Texas. Without definite locality: Wright (GH); Lindheimer, April 1842 (PH), 1849-1851 (NY, POM). Rocky soil on the upper Guadalupe, Lindheimer 53 ( $\mathbf{G H}, \mathbf{M O}$ ), Pierdenales, Lindheimer, distributed under 647, Fasc. IV (GH, K-photograph, MO, PH) ; Phantom Hill, Hayes 494 (F, G, ny); Oak Cliff, Reverchon 532 (mo). Bell Co.-Crawford, Browning, 9 April 1947 (baylu); Normand, 21 April 1928 (mo, ny, taes, tex). Bexar Co.-19 mi. n. of San Antonio, Metz 635 (LCU, LlC, POM), 3000 (Ny, pOM). Blanco Co--Blanco, Palmer 12153 (mo, us). Bosque Co.-Clifton, Albers 47014 (tex). Burnet Co.-Schaupp, Aug. 1892 (ny, us). Collin Co.-White Rock School, McCort 1672 (ntsc, tex). Comal Co.-Comanche Spring [?], Lindheimer 948 (ariz, F, GH, MO, Ny, OKL, PENN, Ph, TEX, US). Cooke Co. -4.5 mi . n. of Gainesville, Shinners 12456 (smu). Corvell Co.6.4 mi. e. of Evant, Parks \& Cory 13079 (taes); Gatesville, Whitley 502 (nTsc). Dallas Co.-Dallas: Biltmore Herbarium (Collectors) $9301^{\text {a }}$ (Min, NY, RM, US) ; Bush 676 (Min, NCU, NY, us); Lundell d Lundell 9134 (GH, Lundell, NCSC); Reverchon, distributed under Curtiss' 1525 (F, GH, MIN, NY, PH, UARK, US), 532 (F, MO, PENN, US). Denton Co.-Harris, spring 1926 (tex). De Witt Co.-Yorktown, Riedel, 20 April 1942 (mo, smu). Ellis Co.-Waxahachie, Turrell, 11 May 1898 (ariz). Erath Co.-Dublin, Maxwell 41 (F); Gough 6512 (TEX, NA). Gillespie Co.-Fredericksburg, Bray $269 a$ (us); Otto Mt., Jermy 306 ( $\mathbf{F}$, mo). Gravson Co.-Whitewright, Gentry 51-1777 (tex). Hamilton Co.-13.4 mi. s. of Hamilton, Cory 53782 (GH, nCsc). Hays Co.-San Marcos, Stanfield (Ny). Hill Co.-Itasca, Smith 22 (tex); 4.25 mi . s.w. of Milford, Cory 23411 (Na). Hood Co.-Granbury, Bogusch 46248 (taes); Center Mills, Blackwell 29 (ntsc, ny). Johnson Co. - 13.5 mi. s.w. of Cleburne, Shinners 112.59 (ncsc). Kendall Co.-Boerne, Palmer 9850 (min, us); Lindendale, Palmer 9906 (mo); Waring, Parks \& Cory 12981 (Gh, taes). Kerr Co.-Kerrville, Heller 1618 (us-Type; Ariz, bKl, CU, F, GH, ill, MiN, MO, NY, Ph, pom, Rm, us-Isotypes). McLennan Co.-Crawford-Valley Mills Road, Smith 546 (tex, uark, us). Menard Co.-Menard: Palmer 11873
(MO, RM) ; McVaugh \& Harvill 8286 (GH, NA, TEX). Parker Co.-5.5 mi. e. of Weatherford, McVaugh 8369 (Gh, Na, tex). Real Co.Thousand Springs, Parks d Cory 8573, 12660 (taes). Sansaba CoNealley, collector not indicated, 1890 (F). Sutton Co. -29 mi . s.e. of Sonora, Cory, 2 June 1931 (GH). Tarrant Co.-Fort Worth, Eggert, 4 May 1900 (MO); Ruth 475, variously dated (CU, F, GH, iLL, NTSC, ny, Ph, ray, us), 983 (ny). Taylor Co.-Sayles, Parks \& Cory 8792 (taes); near Camp Barkeley on north rocky slope of Edwards Escarpment, Tolstead 7182 (mo, Tex). Travis Co.-Austin: Berlandier 1566 (bM, Fi, G, GH, K, P) ; Hall 366 (bkl, F, ill, MO, Ny, pom, us); Tharp 44061 (CU, DUKE, IND, LLC, MIN, NCU, NY, NTSC, OKL, OKLA, RM, TEX, UARK, Vdb, WVa), 46036 (CU, duke, GH, ind, Min, missa, mo, ntsc, OKL, OKLA, RM, TAES, TENN, TEX, UARK, VDB) ; York 460.37 (DUKE, ILL, min, mo, ncsc, ntsc, okl, taes, tex, uark). Val Verde Co.-Devil's River, Orcuff 6207 (mo). Wise Co.-Fouts' Ranch, McCart 1698 ( ntsc, Ny). Walker Co.-Hempstead, Hall, 1872 (us).

Although Marshallia caespitosa var. signata was first described by Beadle and Boynton in 1901, it had been previously recognized taxonomically by Lindheimer. Lindheimer collections dated as early as 1846, for example, carry such inscriptions as "M. caespitosa Var. caule folioso," "Variety" and "caule folioso!" These specimens were collected in Texas from rocky soil on the Upper Guadaloupe and were distributed under number 647. According to Gray's "Plantae Lindheimerianae" (Boston Journal Nat. Hist. 6: 231. 1850), those specimens distributed under number 647, Fasc. IV 7 , belong to Lindheimer's collection of $1847^{7}-$ 1848. Prior to the description of var. signata, the caulescent or branched specimens for the most part passed as Marshallia caespitosa Nutt.

The two varieties of Marshallia caespitosa appear to bear the same relationship to one another as far as growth habit is concerned as the varieties of M. obovata. Marshallia caespitosa var. caespitosa (Plate 9), which is scapose or subscapose in growth habit, may be considered to have been derived from its caulescent counterpart, var. signata (Plate 10). The differences in growth habit, which admittedly are no more absolute in this case than emphasized for M. obocata, represent the only means thus far discovered for distinguishing the varieties of $\mathbf{M}$. calspitosa morphologically. Only by classifying the relatively small percentage of subscapose individuals with the strictly scapose, however, will the distributions of the varieties correspond to that of Map 3 which roughly reflects the geologic picture of the area covered.

The vast majority of the specimens examined could easily be


Plate: 10. Marshallia caespitosa var. signata: Heller, 19-25 April 189-Isotype. Kerr County, Texas.
placed without question in either the caulescent or scapose category, only a relatively small proportion of individuals representing intermediates. Inadequate or obviously depauperate individuals were not taken into account unless they could with certainty be categorized on the basis of the morphological characters they exhibited, apart from any knowledge of the source of such specimens. By assembling all of the duplicates of a particular collection, a better picture of the local range in variation was presented and by this procedure, the distinction between the two varieties was established as precisely stated in the key.

Shinners (Field and Laboratory 17: 174, 175. 1949), seeking to differentiate between the two varieties on a local basis, utilized the relative difference in the number of cauline leaves below the first branch and the number of heads, even though in the original description of M. caespitosa the plant is patently ". . . caespitosa, caule simplici aphyllo 1-cephalo . . ." While this highly arbitrary, artificial system correctly resulted in the concentration of the range of var. signata in the "Hill Country" of central Texas, a dissected portion of the Edwards Peateau and one of the most notable areas of plant endemism in Texas, the procedure is nevertheless untenable. According to Shinners' approach a considerable proportion of var. signata would be classified with var. caespitosa, with the result that the range of the former is unduly restricted. More natural geographical varieties may be segregated on the basis of distinctions used in the present treatment, distinctions in large part corresponding to those of the original circumscriptions.

Precise habitat data are not available for all of the various collections of Marshallia caespitosa examined but the existing data suggest that the respective distributions of the two varieties may be explained on the basis of edaphic adaptation. Marshallia caespitosa var. signata (Map 3), according to Shinners (Field and Laboratory 17: 174. 1949, as M. caespitosa), is a common and characteristic plant of chalk and limestone outcrops and calcareous soils throughout central Texas. Marshallia caespitosa var. caespitosa (Map 3) occurs on apparently noncalcareous, sandy soils in southeastern Texas, Louisiana and Oklahoma. Although southeastern Texas is mostly sandy, there are rather narrow belts of calcareous clay and also small, scattered outcrops of such soil. This may permit plants of the caulescent variety to appear within the range of the scapose variety. This may be the explanation for the more or less isolated record of M. caespitosa
var. signata in Walker County Texas, within the range of var. caespitosa. Other examples of this same sort of interfingering of ranges are likely to be discovered with more extensive collecting of the varieties.

According to Shinners (personal communication), limestone beds often overlie sandstone in northern Texas and Oklahoma and in eroded country there may be mesas topped by limestone in a predominantly sandy area. The sand, however, is more calcareous than where limestone caps have been entirely removed. This would apparently permit Marshallia caespitosa var. signata to occur within the range of var. caespitosa in Oklahoma. Additional collections may substantiate this view also. The disjunct occurrence of M. caespitosa var. signata in Ozark County, southern Missouri suggests a relict population. The specimens upon which this record is based were originally identified as M. obovata var. platyphylla (var. obovata of this treatment). The specimens, as stated elsewhere, are exceptionally broadleaved, exhibiting an even closer resemblance in habit and appearance to certain phases of M. Mohrii than to M. obovata. The disjunction between $M$. caespitosa var. signata populations in Texas and Missouri is very similar to that of the calciphile Juniperus Ashei (J. mexicana of Gray's Manual).

It should be emphasized in connection with the results of the analysis of variation within this complex that the Oklahoma population of Marshallia caespitosa var. caespitosa contains a larger proportion of subscapose (as opposed to strictly scapose) individuals than the populations of southeastern Texas, at least as indicated by herbarium collections. The explanation for this is not known. It is a matter of conjecture as to whether or not and, if so, to what extent an established growth habit is conditioned by the influence of the concentration of alkali in the soil. Marshallia caespitosa is particularly adaptable to transplant experiments by reason of its perennial nature and cespitose habit. Reciprocal transplant studies would help to clarify the genetical and environmental relationships which may exist.

It would appear from these considerations that there is a definite correlation between the geologic history of the areas and the present distribution of the two varieties, respectively. The fact that Marshallia caespitosa var. caespitosa in general occupies the geologically more recent area lends support to the supposition that the scapose variety may have been derived from the caulescent. Marshallia caespitosa appears to have had an

Ozarkian origin but may at the same time be related to the Appalachian, broad-leaved species in that prior to the Mississippi Embayment a continuous distribution pattern of the genus may have existed between these two regions.

Marshallia caespitosa var. signata survives under ordinary greenhouse conditions on a non-calcareous, garden-type soil mixture and flowers satisfactorily. Individual specimens, however, fail to set fertile achenes. The caudices of plants persisting in the greenhouse over a two-year period become quite thickened and evidently rhizomatous. Greenhouse growth of M. caespitosa var. caespitosa was never well established and the specimens did not constitute a sample.

## 7. Marshallia graminifolia (Walt.) Small

Athanasia graminifolia Walt. Fl. Carol. 200. 1788. (bм-Type, on page 16 Herb. Walt.; GH -photograph of type examined.) South Carolina, Walter.

Persoonia angustifolia Michx. Fl. Bor.-Am. 2: 106. 1803. "Hab. in territorio Tennessee." (p-Type, Herb. Michx., subsequently labeled "Phyteumopsis angustifolia"; GH-photograph of type examined.)

Trattenikia angustifolia (Michx.) Pers. Syn. PI. 2: 403. 1807.
Marshallia angustifolia (Michx.) Pursh, Fl. Amer. Sept. 2: 520. 1814. "In swamps, near Wilmington, North Carolina . . v. v."

Marshallia angustifolia (Michx.) Tratt. Arch. Gew. 1: 109. 1814.
Phyteumopsis angustifolia (Michx.) Poir. Encycl. Suppl. 4: 406. 1816.

Marshallia graminifolia (Walt.) Small, Bull. Torr. Bot. Club 25: 482. 1898. As to basionym only, the binomial at least in part misapplied.

Marshallia lacinarioides Small, Bull. Torr. Bot. Club 25: 482.1898. "The original specimens were collected at Macon, Georgia, by Mr. [H. B.] Croom, and in North Carolina (eastern) by Mr. M. A. Curtis." (ny-Syntypes, ex Torrey Herbarium.) The single sheet carries two specimens both of which were originally labeled Marshallia angustifolia. One is marked "(N. Carol. Rev. M. A. Curtis)"; the other originally carried only the collector's name-"Croom," to which "Macon, Georgia" (thought to be erroneous) was subsequently added in a different hand, with different ink.

Marshallia graminifolia (Walt.) Small var. lacinarioides (Small) Beadle \& F. E. Boynt. Bilt. Bot. Stud. 1: 5, pl. 11. 1901.

Marshallia Williamsonii Small, Fl. Southeastern U. S. 1284, 1340. 1903. (NY-Type, collected by C. S. Williamson at Wilmington, North Carolina, September 2, 1900.) The sheet is marked "(Type) Marshallia Williamsonii Small."

Leafy-stemmed perennial herb, (1.5-) 4-8(-10) dm. tall, the stem
from a short crown or caudex, with coarse fibrous roots more or less clustered at the base and usually bearing conspicuous, coarse vascular fiber of decaving leaf bases, the elongated basal leaves firm-textured and more or less erect. Plants propagating by basal offsets, these usually not present at flowering time. Stem sometimes simple but usually treel c cimoselv branched near the middle, the slender, erect, somewhat spreading branches each terminated by a single, long-pedunculate head, the lower portion of the stem glabrous, longitudinally striate, more or less angled, reddish in color near the base, the upper stem and branches glabrate, becoming scabrous-pubescent with reddish, appressed-ascending, incurving, moniliform trichomes, terete, becoming strongly sulcate on the peduncles, stems leafy, the leaves gradually reduced upwards. Peduncles long and slender, (8-) $10-20(-30) \mathrm{cm}$. long, sulcate, scabrous-pubescent, usually becoming more densely so upwards, leafy-bracted by the gradually reduced leaves of the upper stem and branches. Leaves numerous, linear, linear-attenuate or linearlanceolate in outline, entire, glabrous, the basal and lower cauline leaves erect, $1-2 \mathrm{dm}$. in length, $1-1.5 \mathrm{dm}$. broad, prominently 3 -nerved, attenuate at the apices, with obtuse or acutish tips, gradually narrowed below into broad-margined, petiole-like bases, the cauline leaves sessile, gradually and successively reduced in size upwards to the mere linear, acute, leaf-bracts of the inflorescence branches and peduncles, finally becoming only 1 -nerved, the upper reduced leaves sometimes with a few moniliform hairs. Involucres hemispherical or broadly campanulate, ( $10-$ ) $15-25(-40) \mathrm{mm}$. wide, ( $8-$ ) $10-15(-20) \mathrm{mm}$. high including the pales. Receptacle dome-shaped, conical in age. Phyllaries herbaceous, often reddish in color especially at the apices, sparingly pubescent, thick in texture, rigid at least in age, frequently with scattered resin glands, (4-) $6-8(-10) \mathrm{mm}$. long, ( $1-$ ) $1.5-2.5(-3) \mathrm{mm}$. wide, rhomboidal in outline, broadest above or near the middle, with attenu-ate-subulate apices, the bases broadly winged from above or near the middle, with white-hyaline (sometimes reddish-tinged) or scarious borders or wings, the midrib thickened, raised above the surface of the adjacent tissue. Pales of the receptacle linear, conspicuously subulate-attenuate-tipped, (4-) $5-7(-9) \mathrm{mm}$. long, as long or longer than the phyllaries, green in color, often with reddish tips, frequently with scattered resin glands, persistent bevond the shedding of the achenes. Florets purple or pale lavender in color, rarely whitish. Dried corollas $8-10(-15) \mathrm{mm}$. long, the tube (4-).5-6(-8) mm. long, usually dilated above into a shallow throat. Stigmas divergent, recurved in age, exserted bevond the anther-column. Anthers purple or pale lavender, (2-) 2.5-3(-4) mm. long, the column and also the filaments exserted berond the corolla-throat. Pappus scales (1-) $1.5-2 \mathrm{~mm}$. long, ovate, acuminate, regularly serrulate, white-hvaline in color, sometimes tawny: Achenes $2.5-3(-4) \mathrm{mm}$. in length, turbinate, truncate at the suminit, 10 -ribbed, the ribs pubescent, the achene-surface between


Plate 11. Marshallia gramanifola: Channell 1:83, Pender County, North Carolina.
the ribs beset with minute resin atoms. Flowering from July through mid October; fruiting from August into October. (Plate 11.)
distribution. Low pine barrens, pitcher plant bogs, edges of shrub bogs, wet savannas, pocosins, sandy ditches and road shoulders, sphagnous bogs; distributed throughout the Coastal Plain of North and South Carolina, reaching the Piedmont only in very local Coastal Plain-like habitats. (Map 4.)
representative specimens. North Carolina. Without definite locality: McCarthy 112 ( $\mathrm{F}, \mathrm{US}$ ) , 1884 ( $\mathrm{F}, \mathrm{NY}$, US), 1885 (ARIZ, F, ILL, missa, ncu, us); McCarthy \& Schuette (min). County uncertain: Rebel Retreat, Hyams, June 1880 ( F ); near Kirkland, Rhoades, Aug. 1932 (Gн); Pineway, Schallert, 4 Aug. 1933 (Ny). Beaufort Co.-14 mi. s.e. of Chocowinity, Fox 3186 (GH, ind, nCsc, Smu); Washington. Freeman, 18 Oct. 1930 ( NA ). Bladen Co.-n. of White Lake, Correll d Blomquist 2569 (DUKE) ; 2.1 mi. n.e. of Columbus, Fox \& Whitford 1869 ( NCSC ). Brunswick Co. -2.5 mi . s. of Crissettown, Godfrey \& Fox 49735 (duke, GA, GH, MiN, NCSC, SMU); Southport, Godfrey 48456 (duke, GA, GH, nCSC, NCu, SMU); Seagate, Channell 1747 (to be distributed); near Supply, Channell 1758, 1780 (to be distributed). Carteret Co.-Newport, Godfrey \& Blomquist 49795 (GH, NA, NCSC); between Beaufort and Atlantic, Blomquist 11299 (duke, mo); Smyma. Channell 1668 (to be distributed); Beaufort-Moorehead City Airport, Channell 169.3 (to be distributed); Newport, Channell 1898, 1899 (to be distributed). Bladen Co.-Rt. 211, 2.1 mi . n.e. of Columbus Co. line, Fox \& Whitford 1869 (Flas, smu). Columbus Co.-Delco, Godfrey \& Fox 49755 (Duke, min, ncsc); Nakina, Schallert, 26 Aug. 1934 (nd, ny). Craven Co.-Newbern, Croom (GH); Newbern Airport, Blomquist 16429 (duke). Cumberland Co.-Favetteville, Biltmore Herbarium (Collectors) 14848 (us); 3 mi . w. of Stedman, Fox 1785 (NCSC). Duplin Co. -8 mi . w. of Richland, Godfrey 5864 (GH, us); between Wallace and Warsaw, Channell 1793, 1794 (to be distributed); between Bunnlevel and Richland, Channell 1796 (to be distributed). Guilford Co.-High Point, Shave, 1886 [?] (GH). Harnett Co.-between Erwin and Dumn, Correll \& Blomquist 25.55 (duke); Pineview, Channell 286.3 (to be distributed). Iredell Co.-Statesville [?], Hyams (ром, min). Martin Co.-Jamesville, Fisher. 26 Aug. 1890-1898 (PH). Moore Co. -3 mi . n.e. of Southern Pines, Woods $d$ Woods (NCSC); Pinehurst, Herb. Katzenstein, Aug. 1897 (GH). Nash Co.-Middlesex, Blomquist 7576 (Duke). New Hanover Co.-Wilmington: McCarthy 84 (us); Curtis (Dwe); Williamson, Aug. 1900 (CONN, PENN, PH); Channell 1737, 1757F, 1782, 2696, 2707 (to be distributed). Onslow Co.-Folkstone, Alexander, 25 July 1923 (NCU); 12 mi . n. of Jacksonville, Godfrey 5747 (GH, us); Deppe, Collins 171 (NA) ; 5 mi . n.w. of Richland, Blomquist 15357 (duke, penn). Pender Co.-Burgaw, Hyams, Aug. 1879 (min, mo, Ny, penn, us); Rt. 421, 1 mi from Sampson Co. line, Godfrcy id Fox 48715 (flas, ga, ncsc,
ncu, smu) ; 10 mi . s. of Holly Ridge, Channell 1722 (to be distributed); between Burgaw and Wallace, Channell 178.3 (to be distributed). Pitt Co.-3 mi. e. of Grimesland, Fox 3181 (GH, min, ncsc, smu). Richmond Co.-Smith, 30 July 1933 (duke). Sampson Co.Roseboro, Godfrey 5710 (duke, GH). South Carolina. Without definite locality: Curtis (mo). Allendale Co.-Ulmers, Bell 5190 (GH, ncu, duplicates to be distributed). Berkeley Co.-Cooper River, Wallace (charl); Santee Canal, Ravenel, Aug. 1??? (charl); 6 mi. n.e. of Summerville, Wilbur \& Webster 2848 (ncsc, smu); Monks Corner, Godfrey \& Tryon 142.3 (GH, NY, us). Charleston Co.-McClellanville, Schallert, 2 Sept. 1940 (GH, ND, MO); 6 mi. n.w. of McClellanville. Godfrey \& Tryon 11.36 (GH, NY, us). Chesterfield Co.-Cheraw, Hood 2470 (flas). Darlington Co.-Society Hill, Curtis (GH); Hartsville, Norton, 15 Sept. 1921 (NCU). Dorchester Co.-Summerville: Biltmore Herbarium (Collectors) B 2900 (us); Brownfield, Aug. 1893 (us). Georgetown Co. $-12 \mathrm{mi} . \mathrm{n}$. of Georgetown, Godfrey \& Tryon 1051 (Cu, duke, F, GH, Mo, Ny, tenn, us). Horry Co.-Conway, Schallert, 1 Aug. 1940 (UARK); Coker \& Coker, 25 July 1946 (nCU). Lexington Co.-Gaston, Wherry, 19 July 1932 (us); 5 mi. s. of Columbia, Godfrey \& Tryon 1267 (Cu, duke, F, GH, MO, NY, PENN, TENN, us). Orangeburg Co.-Orangeburg, Hitchcock, Aug. 1905 (ill). Richland Co.-Columbia, Harbemock [?] (charl-Herb. Ell.).

This species was first described from South Carolina by Walter in 1788 as Athanasia graminifolia. Historically, the epithet was almost completely displaced for over a century. From the brief original description, supplemented by a photograph of the type. it has been possible to confirm the identity of the species. It is, so far as the present study indicates, the only narrow-leaved Marshallia occurring in South Carolina. Moreover, the present study has shown this species to be restricted in distribution to the Carolinas, where it is confined largely to the Coastal Plain proper, but occurs also in the Piedmont in very localized, Coastal Plain-like habitats.

In 1803, Persoonia angustifolia was described by Michaux from Tennessee, an area in which no narrow-leaved Marshallia has subsequently been found. Insofar as the photograph of the type reveals, it is clearly the same at Athanasia graminifolia of Walter. (The type sheet, incidentally, did not originally carry the Michaux binomial but was subsequently labeled "Phyteumopsis angustifolia.") Moreover, the original description of Persoonia angustifolia compares very closely with that of A. graminifolia and could apply to no other species. In equating the names, it is suggested that the apparent discrepancy "Territorio Tennessee,"
given by Michaux as the "habitat" of P. angustifolia, may have resulted through an error in labeling. The original collection upon which P. angustifolia was based probably came from North Carolina where the species is well represented and where Michaux is known to have collected.

The adoption of the Michaux epithet for the species up to 1898 is of considerable importance, for its application was not confined to the narrow-leaved species of the Carolinas. It came to apply also to the coastal, narrow-leaved plant farther southward, a species recognized here as Marshallia tenuifolia Raf. At this point Small (1898) made the correct nomenclatural combination. M. graminifolia, erroneously applying it, however, to a more southern species with obovate basal leaves, the range of which was reputed at that time to extend northward into the Carolinas.

At the same time (1898) Small described Marshallia lacinarioides as new. This species was based on the two syntypes indicated in the synonymy above. One of the specimens was collected by Curtis in North Carolina; the other by Croom at Macon, Georgia. Apparently on the basis of these two specimens alone, Small gave the range of the species as extending from North Carolina. along the middle country, to Georgia. The species was reputed to differ from M. graminifolia on the basis of the smaller heads and a growth habit suggestive of certain "Lacinaria" species of Liatris, whence the specific name. The erect, elongate, basal leaves, with their prominently 3-nerved blades emphasized by Small, while imparting a distinctive aspect to certain individual specimens, represents a character which has not been found to segregate this so-called species, nor, indeed, has the smaller sized heads. In fact, all intergradations of the "graminifolia" and "lacinarioides" types were found to exist in each of several different populations. Marshallia lacinarioides is thus considered to be taxonomically inseparable from M. graminifolia, a species already shown to be confined to the Carolinas. This casts serious doubt. therefore, upon the validity of the collection data "Macon, Georgia" included on the label of the Croom specimen. In fact. this information appears to have been added to the label at a time subsequent to the collector's name, for these data appear in distinctly different handwritings and in different inks. In view of the fact that Croom is known to have collected the same species at New Bern, North Carolina, it seems much more likely that this syntype specimen was itself collected in North Carolina and subsequently mislabeled. especially since no other such
specimens have been reported from Georgia. This view is supported by an authentic Croom specimen in the Gray Herbarium labeled "New Bern" and by the inclusion of the species in "A Catalogue of the Plants of New-Bern, North Carolina" (with remarks and synonyms) by H. B. Croom (John Torrey, Editor), New York, 1831.

In the only revision of the genus, Beadle and Boynton (1901) upheld Marshallia lacinarioides but reduced it to varietal status under M. graminifolia. This change illustrated the type of confusion which has surrounded M. lacinarioides since its description and which has persisted up to the time of the present treatment. It illustrates further that Beadle and Boynton did not have the correct concept of Walter's Athanasia graminifolia, for they erroneously applied that epithet to a species not even represented in the Carolinas.

In 1903, Small described still another species, Marshallia Williamsonii, from Wilmington, North Carolina. The range of this species was given by Small as eastern North and South Carolina, the very area of the range of M. graminifolia. The minor quantitative characters by which the author distinguished this new species from $M$. lacinarioides are not considered to be of sufficient magnitude to warrant taxonomic recognition in any status. The present study has shown, especially in the areas near and around Wilmington, that specimens of M. graminifolia are oftentimes considerably taller, more branched and larger-leaved. This is particularly true of specimens growing in sphagnous situations in the edges of shrub bogs. Such specimens usually possess more heads and floral parts of correspondingly larger size, the very characters used by Small to distinguish his M. lacinarioides from M. Williamsonii. The shape of the pappus scales used by Small to distinguish these species has proved too variable in this complex for any taxonomic reliance.

Thus, Persoonia angustifolia, Marshallia lacinarioides and M. Williamsonii are treated as synonyms of Athanasia graminifolia. The combination M. graminifolia (Walt.) Small is in no way applicable to the species M. tenuifolia Raf. of this treatment. It is therefore restored in the present treatment to the taxon upon which the epithet was originally based. Finally, it is not surprising that practical difficulties have arisen in attempting to apply three names to the component variation of a single species exhibiting a more or less random assortment of quantitative variation.

It will be noted upon referring to Maps 1-4 that most of the
species of Marshallia exhibit allopatric distributional patterns. In North and South Carolina, however, M. graminifolia (Map 4) occurs over the same general geographical area as M. obovata (Map 2). Well-defined species both morphologically and in season of flowering, they occupy distinctly different ecological habitats within the area in question.

The source of two specimens of Marshallia graminifolia (pom, min) collected by M. E. Hyams and labeled "Statesville" has been questioned. Statesville, Iredell County, in the Piedmont of North Carolina, was Hyams' home and place of business as a seedsman and druggist and served as headquarters for rather extensive plant collecting. Although the locality notation may have been intended to indicate merely the collector's address, it suggests that the specimens were collected in that vicinity. If accepted as authentic, these records indicate the disjunct occurrence of the species outside its normal range on the Coastal Plain, well within the Piedmont, a distribution which is not entirely unlikely. As a matter of fact, pockets of Coastal Plain vegetation, including species of other genera as disjuncts, are known to persist in the vicinity of Statesville at the present time. On the basis of other collections, these habitats were known to Hyams, doubtless in what may be assumed to have been a less ravaged or disturbed state. Judging from the more or less isolated existence of M. graminifolia in other such areas, as, for example, Nash County, North Carolina, it is not inconceivable that the species at one time existed as disjunct colonies around Statesville also, but subsequently disappeared. In the absence of other collections or data to substantiate it, the Statesville record has not. however, been included as a part of the geographical range of the species. It is nevertheless intriguing and should not be completely ignored. It is unfortunate that the specimens were not accompanied by additional data.

Marshallia graminifolia grows well and flowers profusely under humid greenhouse conditions in sandy soil of a high organic content, when supplied with plenty of moisture. One of the most handsome species because of the purple or lavender heads. it grows naturally under moist acid conditions in pineland savannas as well as in the partial shade at the edges of shrub-bogs and pocosins. Variation in the size of leaves, heads and other parts of the plant is evidently controlled to a large extent by ecological factors. Neither narrow-leaved forms nor those with relatively small heads could be segregated satisfactorily as geo-
graphical varieties. The perennial duration of these plants may account for a certain amount of the quantitative variation prevailing. Older plants are often very robust while seedlings or relatively young plants are correspondingly smaller in size.

## 8. Marshallia tenuifolia Raf.

Marshallia angustifolia (Michx.) Pursh var. cyananthera Ell. Sk. 2: 317. 1823. ". . . collected by Dr. Baldwin, near St. Mary's, Georgia." (charl-Type, Herb. Ell. $)$

Marshallia tenuifolia Raf. New Fl. 4: 77, 78. 1838. "-found by Baldwin on the sea shore of Florida and Georgia . . ." (nwc-Lectotype, labeled "Georgia, Dr. Baldwin".) ${ }^{18}$

Leafy-stemmed herb, strict in habit, (2-)4-10(-12) dm. in height, the stem from a perennial crown or caudex with coarse fibrous roots and spreading, thin-textured, obovate or spatulate, obtuse radical leaves. Plants solitary or propagating by basal offsets and thus often somewhat clustered in disposition. Stem sometimes simple but usually branched near the middle, the branches erect and scarcely at all spreading, each terminated by a single long-pedunculate head, primary stem furrowed with longitudinal channels or grooves, somewhat angled, glabrous, reddish at the base, greenish or olivaceous above in drying. sulcate and sparingly pubescent with jointed (moniliform), incurved, purple-colored hairs, stems leafy throughout, the leaves numerous, gradually reduced upwards. Peduncles erect, long and slender, (1-) 1.5-2.5 (-4) cm. long, sulcate, sparingly pubescent below, becoming densely pubescent upwards, leafy-bracted by the gradually reduced, linear-subulate leaves of the upper stem and branches. Leaves numerous, glabrous, entire, the radical (2-) $3-10(-12) \mathrm{cm}$. long, (0.4-) 0.5-1 (-1.3) cm. wide, mostly 3 -nerved with the midrib prominent, spatulate, obovate or oblong-obovate in outline with obtuse, sometimes emarginate blades, gradually narrowed below into broadwinged, petiole-like bases usually shorter than the blades. Lower cauline leaves elongate, linear, linear-oblong or linear-lanceolate, attenuate, (2-) 0.4-2(-2.2) dm. in length, (1-)2-13(-14) mm. in width, broadest near the middle, gradually tapering to obtuse or acutish apices and more or less sessile, somewhat clasping bases, prominently 1-3-nerved, the laterals sometimes obscure. Upper cauline leaves narrowly linear, attenuate, acute, gradually reduced in size upwards to the mere linear-subulate leaf-bracts of the peduncles. Involucres hemispherical or broadly campanulate, globose in age, (0.5-) 1.5-2.0(-2.5) cm . wide, ( $0.5-$ ) $1-1.5(-2) \mathrm{cm}$. high including the pales. Receptacle dome-shaped, strongly conical in age. Phyllaries herbaceous, subequal in about two series, often reddish in color especially at the apices.

[^23]sparsely pubescent, frequently with scattered resin glands over the outer surtace, rigid, usually winged below the middle with whitehyaline or somewhat scarious margins, these sometimes remotely toothed or erose and occasionally with a few marginal trichomes, linearlanceolate, lanceolate or somewhat rhomboidal in outline, with strongly subulate apices, (2-) 4-5 (-6) mm . long, (1-) $1.5-2(-2.5) \mathrm{mm}$. wide. Pales of the receptacle linear-attenuate, strongly subulate-tipped, (4-) $5-6(-7) \mathrm{mm}$. long, longer than the phyllaries, green in color, often with reddish apices, frequently with scattered resin glands on the outer surfaces, persistent beyond the shedding of the achenes. Florets usually purple or pale lavender in color. Dried corollas (6-) 8-12(-14) mm . long, the tubes (3-) 4-5 (-6) mm. long, sometimes dilated upwards into a shallow throat. Stigmas divergent, recurved, exserted beyond the anther-column; the style usually included. Anthers purple, "blue" or pale lavender in color, $2-2.5 \mathrm{~mm}$. long, exserted bevond the corollatube. Pappus scales ( $0.7-) 1-2(-2.5) \mathrm{mm}$. long, shorter than the achene, ovate-acuminate or merely acuminate from a broad base, regularly serrulate, occasionally lacerate, white-hyaline in color, sometimes tawny in age. Achenes (1.5-) $2-2.5(-3) \mathrm{mm}$. long, turbinate, truncate at the summit, 10 -ribbed, the ribs pubescent with hairs shorter than the distance between adjacent ribs, the achene-surface between the ribs beset with minute resin atoms, sometimes copiously so. Flowering from July through September, occasionally in January and June; fruiting from August into October. (Plate 12.)
disthibetion. Wire grass-longleaf pine savannas, moist pine barrens, flatwoods, edges of barheads and shrub bogs, low swampy areas and pitcher plant bogs; occurring in southern Georgia and Florida, extending westward along the Culf Coast into eastern Texas. (Map 4.)
representative specimens. Georgia. Without definite locality: Balduin (DWC); Cleveland (flas); Harris, 5 Sept. 1930 ( NtSC ); Le Conte (PH); Nuttall (PH). Appling Co--Baxler, Biltmore Herbariam (Collectors) $2807^{\text {h }}$ (us, нм). Bullock Co.-Statesboro. Jones, summer 1923 (cu). Camden Co.-St. Marys, Baldwin (charl-Type of Marshallia angustifolia var. cyananthera Ell.). Charleston Co.Trader's Hill, Small, 24-26 July 1895 (NY, us). Clinch Co.-Homerville. McVaugh 5288 ( NA ). Colquitt Co.-Moultrie: Svenson 6941 (ND, bкi.) ; Channell 3276 (to be distributed). Glynn Co. -3 mi . n. of Brookman. W'iegand du Manning 3448 (cu, gh, pom). Irwin Co.Oscilla, Harper 1416 ( $\mathbf{F}, \mathrm{gh}, \mathrm{mo}, \mathrm{NY}, \mathrm{us}$ ) . Coffee Co.-Harper-photograph. mounted on Irwin Co. collection 1416 ( GH ). Lowndes Co.Valdosta, Small, 22-24 July 1895 (f, NY); 1.5 mi. e. of Hahira, Quarterman 145 (duke, Na). McIntosh Co--Darien, Stuckey, 20 Aug. 1933 (Cu). Telfair Co.-McRae, Biltmore Herbarium (Collectors) $2807^{\circ}$ (us). Thomas Co--Harper 1180 ( $\mathrm{GH}, \mathrm{mo}, \mathrm{NY}$, us). Tift Co. -15 mi . e. of Tifton. Sargent 641.5 (okla, okl). Ware Co--5 mi. s.e. of Waycross. Wilhur ${ }^{む}$ Webster 27.30 (GH, NCSC, sme); Waycross. Eggleston

5100 (ny), 5095 (Gh, mo, ny). Wayne Co.-Gessup, Biltmore Herbarium (Collectors) $2807^{i}$ (Ny, us). Worth Co.-8 mi. s. of Sylvester, Svenson 7268 (bkl, nd); Poulan, Pollard \& Maxon 550 (GH, ny, us). Florida. Without definite locality: Baldwin (charl), Chapman (f, GH, MO, NY, OKL, US); Buckley (GH, MO); Torrey ( PH ), 3119 ( $\mathbf{G H}$ ); Curtiss (F), 1875 (us). County uncertain: Fort Craine, Rugel 244 (f, mo, ny, us). Alachua Co.-Gainesville, Murrill 136 (us, mo); Alachua-Putnam Co. line, Channell 2098, 2099 (to be distributed). Baker Co.-5 mi. n. of McClenny, O'Neill, 12 Aug. 1929 (us, LCU). Bay Co.-Panama City Beach, Godfrey \& Kral 55056 (GH, duplicates to be distributed). Bradford Co-LLawtev, Murrill, 9 Sept. 1940 (flas). Brevard Co.-Okeechobee region, Fredholm 5878 (GH, mo, us). Calhoun Co.-Altha, West, 9 Aug. 1931 (flas, tex). Clay Co.Doctors Inlet, Murrill 302 (mo, us). Columbia Co.-Lake City: Rolfs 370 (Flas, F, ill, MO), 406 (F), 973 (Flas); Nash 2221 (CONN, PH, us) ; Hitchcook, June-July 1898 (F, mo). Duval Co.-Jacksonville: Drummond, Jan. 1835 (GH); Curtiss, Aug. 1876 (PAC), 1525 (bKL, CU, F, FLAS, GH, LCU, MiN, MiSSA, MO, NY, PH, SMU, US, YU), 4493 (mO, ny, US), 5109 (CU, F, GH, MIN, NY, US). Baldwin: Mohr, 29 July 1880 (PH, US) ; Nash 2318 (F, FLAS, GH, MIN, MO, NY, PH, POM, US). Escambia Co. -5 mi . w. of Pensacola, Morgan, 12 Aug. 1941 (GH, LCU, us); near Fla.-Ala. state line, Channell 3262 (to be distributed). Flagler Co.-St. John's Park, West \& Arnold, 10 Oct. 1940 (flas, pac). Franklin Co.-Apalachicola, Biltmore Herbarium (Collectors) 2807 " (GH, MO, ny, us), $2807^{\circ}$ (Gh, min, mo, Ny, us). Gadsden Co. -10 mi. w. of Quincy, Arnold, 20 Aug. 1940 (flas). Highlands Co.-4 mi. s.w. of Childs, Correll 6189 (Duke, GH, ind, Na); Highlands Hammock. Channell 2031, 20.35 (to be distributed). Indian River Co. -8 mi . w. of Vero Beach, Channell 2077 (to be distributed); 8 mi . e. of Yeehaw Junction, Channell 2082, 208.3 (to be distributed). Jackson Co.-Marianna: Weigand \& Manning 3450 ( $\mathrm{CU}, \mathrm{GH}$ ) ; Channell 327.3 (to be distributed). 11 mi . w. of Chattahoochee, Thorne 5962 ( $\mathrm{Cu}, \mathrm{GA}, \mathrm{GH}$ ). Liberty Co.-Bristol, Biltmore Herbarium (Collectors) $2807^{\circ}$ (min, us). Nassau Co.-Callahan, Knight, 28 July 1941 (flas). Okaloosa Co.Crestview, Hood 3138 (flas). Osceola Co.-Kissimmee: Singeltary 496 (Duke); Schallert 120 (flas). Vicinity of Yeehaw Junction, Channell 2085, 2089 (to be distributed). Putman Co.-between Palatka and Interlaken, Correll 6425 (duke, NA, NCSC); Palatka, Channell 2094 (to be distributed). Santa Rosa Co.-Milton, Ford 4071 (Gн). St. Lucie Co.-between Okeechobee City and Fort Pierce, Brass 20569 (GH). Union Co.-Lake Butler, O'Neill, 2 Aug. 1929 (flas). Volusia Co.National Gardens, Butts, 22 July 1943 (сн). Walton Co.-Argvle. Curtiss 5932 (bKL, CONN, CU, F, FLAS, GH, iLL, MIN, MO, NY, PAC, US). Washington Co.-Rock Hill, Kral 3532 ( GH ). Alabama. Baldwin Co.Southport, Webster \& Wilbur 3555 (GH, NCSC, SMU); 8 mi . west of Ala.-Fla. state line, Rt. 90, Channell 2111 (to be distributed). Coving-
ton Co.-McRae, Pennell 4610 (penn). Escambia Co.-Flomaton, Biltmore Herbarium (Collectors), 15 Aug. 1899 (us). Houston Co.Dothan, Blanton 58 (GH, LCU, Na, nd, NY, Rm). Mobile Co.-Mohr, Aug. 1870 (siu); Mobile, Mohr, 15 July 1875 (alu), 1879 (us), 1880 (PH); Williams, 28 Aug. 1951 (uala). Mississippi. Jackson Co.-4 mi. e. of Moss Point, Webster \& Wilbur 3464 (GH, NCSC, smu); Channell $2142,2258,2286,2314,2432,2437,2444,3260$ (to be distributed). Louisiana. Without definite locality: Hale (GH); Mead (F). Beauregard Parish.-10 mi. s. of De Ridder, Correll \& Correll 9670 (duke). Calcasieu Parish.-Lake Charles, Cocks, Sept. 1914 (nv). Natchitoches Parish.-Kisatchie, Correll \& Correll 9787 (duke, gh. Na). Rapides Parish.-Alexandria, Hale (no), 1840 (us). St. Tammany Parish.-St. Tammany, Cocks, Sept. 1900 (no). Texas. Anderson Co.-Grapeland Bog, Le Sueur \& Smith, 7 July 1935 (tex). Hardin Co.-Kountze-Saratoga Road, Tharp, Follansbee \& Thompson 51-1502 (min, penn, taes, tex); 2.2 mi. w. of Silsbee, Cory 4989.5 (Gh. smu, us). Jefferson Co.-Beaumont, Smith, 23 Oct. 1922 (tex). Newton Co. -5 mi . e. of Kirbyville, Cory 49802 ( $\mathrm{GH}, \mathrm{rar}, \mathrm{smu}, \mathrm{us}$ ). Orange Co. -Vidor, Tharp 2592 (tex, us). Trinity Co--Trinity, Tharp 937 (us). Tyler Co. -17 mi s. of Woodville, Cory 49.959 (GH, us).

This species was first described by Elliott in 1823 as Marshallia angustifolia (Michx.) Pursh var. cyananthera. The original description was based upon material collected by Baldwin near St. Marys, Georgia and, in an appended note, Elliott states that the new variety may represent a distinct species. The leaves of the plant are described as linear-lanceolate and conspicuously 3nerved. The type (charl), however, has cauline leaves which are linear and l-nerved, with only the basal leaves conspicuously 3 -nerved.

In 1836 Rafinesque described Marshallia tenuifolia. This species, like var. cyananthera above, was based upon material collected by Baldwin on the coast of Florida and Georgia. According to Rafinesque, it is more closely related to M. cyananthera [M. angustifolia (Michx.) Pursh var. cyananthera] than to M. angustifolia [M. graminifolia (Walt.) Small of this treatment]. Although no Baldwin specimen has been located which Rafinesque is definitely known to have examined, it seems safe on the basis of the close similarity of the original descriptions to conclude that the Baldwin specimens examined respectively by Elliott and Rafinesque were either duplicates of the same collection or otherwise very similar. The avowed close relationship of Rafinesque's M. tenuifolia to M. cyananthera suggests that this interpretation is correct. The close similarity of two other

Baldwin specimens to the Elliott type, marked "Georgia" (Dwc) and "Florida" (Charl), further supports this conclusion. In any case, the two descriptions do not differ in essential details. The only character of M. tenuifolia which Rafinesque considered to be diagnostic is "leaves quite slender uninerve," a feature which is shared as shown above by the Elliott type. The two names, var. cyananthera and M. tenuifolia, are thus treated as synonyms.
The taxon in question is recognized in the present study as a species, highly variable as to quantitative characters, distinct from Marshallia graminifolia. As indicated in the discussion of the later species, the names M. angustifolia and M. graminifolia were erroneously employed up to the time of the present study to the species in question. It is clear, however, that that name has no application outside of the Carolinas so far as present distributional records indicate.
The selection of the correct name for this species presents certain problems which are not clearly covered by the International Code. Specifically, the present case is complicated in that Rafinesque, in the original description of Marshallia tenuifolia, acknowledged the Elliott epithet cyananthera in the following phrase in pointing out the affinities of the new species: " . . nearer to $M$. cyananthera than $M$. angustifolia." It is impossible from this statement to determine whether or not Rafinesque intended to introduce the new combination Marshallia cyananthera, although one might assume that he did not. The problem is not clarified by Article 33 which states that "A name is not validly published when it is merely mentioned incidentally." According to this article, "By 'incidental mention' of a new name or combination is meant mention by an author who does not intend to introduce the new name or combination concerned." It is hardly possible, therefore, to determine whether the combination "M. cyananthera" as used by Rafinesque is validly published or not. If this reference constitutes valid publication, the two specific epithets date simultaneously from the same published article and the matter is thus one of choice by the author first uniting the taxa; if it does not, then tenuifolia, being the earliest available epithet in the rank of species, automatically becomes the correct name.
The present recourse has been the more or less arbitrary selection of Marshallia tenuifolia Raf. for the species. Although difficult to typify, this name, in the opinion of the present writer, is to be preferred because it has not been confused through erroneous application to any other taxon. This is not true of the epithet
cyananthera, however, as the following paragraph illustrates.
Marshallia angustifolia (Michx.) Pursh var. cyananthera Ell., as erroneously interpreted by Fernald (Bot. Gaz. 24: 435. 1897) and various subsequent authors, including Beadle and Boynton, refers only to a portion of the species treated here as M. tenuifolia Raf. The name was inadvertently applied to the very slender plants of the species first found by A. H. Curtiss (no. 5932) in "seepy pitcher-plant bogs" in Liberty and Walton Counties, west Florida, which are not typified by any Baldwin specimen. This was a very logical mistake in view of the fact that Elliott's description of var. cyananthera was naturally restricted, evidently based solely upon the Baldwin material, and did not circumseribe the species as such. It is an even more logical mistake when one recalls from the discussion of the preceding species that the name M. angustifolia for many years erroneously included the larger portion of the species under consideration here ( $M$. tenuifolia Raf.). It is not surprising, therefore, that the slender, bog Marshallia discovered by Curtiss completely usurped the name and description of Elliott's var. cyananthera to the present time. Nomenclaturally, it is clear that if the unit of variation exemplified by Curtiss' collections is ever recognized taxonomically, the epithet cyananthera cannot be employed for it.

The Marshallias with attenuate or subulate-tipped phyllaries and grass-like leaves form a complex distributed over the outer Coastal Plain from North Carolina southward into Florida and westward into Texas. Considerable confusion has resulted from the taxonomic interpretation of the component elements. Taxonomists have perhaps been unduly impressed by morphological variation as expressed by local populations. Disregarding minor quantitative variation, however, the complex, when viewed gengraphically from north to south, is seen to consist of only two, but highly variable species. Marshallia graminifolia is the northernmost species, restricted, so far as is known, to the Carolinas. Marshallia tenuifolia comprises the remainder of the complex.

Herbarium specimens of these two species are sometimes difficult to distinguish, especially when they do not provide evidence as to the form of the basal leaves or are otherwise inadequate. In nature, however, Marshallia tenuifolia (Plate 12) consistently possesses spreading basal leaves with obovate, spatulate or oblong, obtuse blades, distinctly unlike those of the stem proper. Such leaves are never produced by M. graminifolia (Plate 11), all the leaves of which have blades of an elongate,


Plate 12. Marshallia tenuifolia: Fig. 1, Channell 2098, Alachua County, Florida: Fig. 2, Channell 3273, Jackson County, Florida; Fig. 3, the so-called "cyananthera" variant, Channell 2111, Baldwin Counts, Alabama.
linear-attenuate type. It is largely because of the absolute nature of this morphological discontinuity that the two taxa are recognized here as distinct species. Insofar as the present distributional records indicate, the Savannah River forms a sharp line of demarcation between the ranges of the two species. It remains to be seen, however, if the ranges actually overlap in that area and whether or not the Savannah River serves as an effective barrier. Whether or not the history of the Savannah River watershed is in any way to be considered correlated with or the effective cause of the successful differentiation of the two species as they now exist, is purely speculative.

Of the two species, Marshallia tenuifolia exhibits considerably more diversity in growth-habit. Local variation of this sort, the nature and range of which are shown in part in Plate 12, is not surprising for a species distributed more or less continuously from Georgia southward into Florida and westward into eastern Texas.

The so-called "cyananthera" type of variant, collected in Baldwin County, Alabama (Channell 2111), is represented by the two specimens of Plate 12. Figure 3. These represent the same identical type of specimens as those collected by Curtiss in Walton County (Curtiss 5932) and Liberty County, Florida, reported by Fernald. This extreme form is evidently restricted to open, bog-like terraces and slopes in the pinelands of southern Alabama, extreme southern Georgia and western Florida, where the seepy coarse sandy soil conditions produce habitats which support Sarracenias, Droseras, Tofieldias, Xyris species, etc. Although local, these distinctive habitats are oftentimes quite extensive, in some cases covering several acres. As may be expected, therefore, the Marshallia in question occurs within these areas as relatively uniform populations of hundreds of individuals.

Thus, the extreme "cyananthera" type of variation is morphologically and ecologically distinct from the more widespread, sympatric element illustrated in Figure 1. Despite this, however, it has been impossible on a morphological basis to delimit the element satisfactorily as a separate taxonomic unit. Taking all of the available herbarium material into account, the "cyananthera" variant loses its identity as such. It appears to be connected to the remainder of the species by individuals such as that shown in Figure 2, to form a more or less complete intergradation series, no segment of which can be delimited taxonomically or segregated geographically.

Greenhouse studies involving the growth of sample specimens of two contrasting elements of the complex, although inadequate for establishment of general conclusions, indicate that the two elements tested are at least to some extent genetically adapted to their respective habitats. Specimens of the "cyananthera" element (Channell 2111) were collected from an open pitcherplant bog in Baldwin County, Alabama. Tall, robust specimens, representing the other, more widespread element (Channell 2031), were collected in the moist, shrubby flatwoods of Highlands Hammock, Highlands County, Florida. Transplanted on sods to the greenhouse and grown under moist, humid conditions of partial shade, favoring the Highlands type habitat, marked differences in the shape, size and quality of the basal leaves soon became evident, differences which persisted over the three-year period they were observed. The Highlands specimens produced spreading basal leaves of an oblong-spatulate shape and of such thin texture as to render them subiect to prompt wilting under conditions of low water supply. The "cyananthera" specimens produced basal leaves of a shorter, more ovate-spatulate shape, and of a distinctly firm, glossy texture, features apparently related to the resistance of comparatively long periods of low water supply without wilting. The spindly, single-stemmed, monocephalous habit, typical of "cyananthera" specimens in nature, was lost by the specimens tested during the period under which they were grown and observed. At the end of the period they had assumed essentially the same status and general appearance of the specimen shown in Plate 12, Figure 2, but with the production of a branched stem and two to four heads instead of only one. The heads were considerably larger than those shown in Figure 3, but did not attain the size of the larger heads of the specimen shown in Figure 1. The Highlands specimens retained in the greenhouse the more or less strict, typically monocephalous habit of growth as produced under natural conditions, but they did not attain maximum field height.
It is safe to conclude from these observations that the majority of the "cyananthera" specimens, occurring as more or less uniform populations under field conditions, do not attain their potential maximum size. This would appear to be due to environmental conditions imposed by the local habitats to which the "cyananthera" variant is apparently restricted. It is possible. therefore, that individuals dispersed as seeds to different habitats could become considerably larger, branched and several-headed.

Essentially no field data are available which would indicate the nature of variation encountered over the area between the typical "cyananthera" habitats, usually occurring as terraces on gentle slopes, and the low areas near streams, in relatively close proximity, where considerably larger, much-branched specimens occur. Nor are field data available on the variation encountered between these and still other habitats supporting the plants, such as moist, wire-grass savannas, moist, shrubby drainage draws within turkey-oak sand-hills, well-drained road-shoulders, etc.

Collectively, however, the herbarium material indicates that there is no sharp line of distinction on any basis between the typical "cyananthera" element and the remainder of the complex. Qualitative features observable in the living "cyananthera" specimens are obscured in herbarium material and are of little or no assistance as distinguishing criteria. No quantitative or qualitative floral or vegetative characters have been found to segregate the "cyananthera" element or any other element of the species as a taxonomic unit. Despite this, however, the "cyananthera" element exists, as stated previously, in distinctive habitats as relatively uniform populations, recognizable in the field. Further study of this problem would most likely clarify the relationship of these plants to Marshallia tenuifolia proper as ecotypic. The best recourse, with the information available at the present time, seems to be that of grouping all the variation together as a single species.

It is interesting to note that, for certain years, herbarium records indicate two flowering periods, annually, for the populations of Marshallia growing in the moist flatwoods of Highlands Hammock State Park, Highlands County, Florida. The flowering of these plants around the first of January as well as around the first of August was verified by the park naturalist, Miss Carol Beck. The significance of this is not known. Persisting over the colder months as rosettes, however, it would not be surprising, especially after a relatively warm winter, for such specimens to respond to favorable conditions by flowering. The ability of certain populations of this species to flower at a time other than in the fall is probably restricted to those populations of the warmer parts of Florida. It is mentioned here because of its bearing upon the problem of a possible means of contact with M. ramosa, a spring-flowering species of Georgia, with which it is believed to have hybridized. If vernal flowering of M. tenuifolia ever occurs as far north as south-central Georgia, where M. ramosa grows, it
is probably later than the first of January and may thus coincide with the flowering of M. ramosa. Putative hybrids of M. ramosa and M. tenuifolia are discussed under the former species.

## Doubtful and Excluded Species

Marshallia Lagunae (Scop.) Gmel. Syst. Nat. 2: 836. 1791.=Homalium Jacq. See (Kew) Bulletin Misc. Information, Nos. 6, 7, 8 \& 9, page $432,1935$.
Marshallia bulbosa Raf. Fl. Ludov. 61. 1817=Sarrette bulbeuse Robin, Vog. Louis. 3: 430. 1807. Collected in Louisiana. De Candolle (Prod. 5: 680. 1836) equates the Rafinesque name with Liatris (spec.?) which appears correct except for the scaly pappus which is unknown in that genus. Definitely not Marshallia.
Therolepta pumila Raf. Neogenyton 3: 1825. Collected in Kentucky by Rafinesque. The only clue to the identity of this binomial is that given by Rafinesque (New Fl. N. Amer. 4: 77. 1836) himself, to the effect that it may be Marshallia pumila (Raf.) Raf.
Marshallia aliena Spreng. Syst. Veg. 3: 446. 1826. Collected in Monte Video by Sello. De Candolle (Prod. 5: 680. 1836) equates the name with Heterothalamus brunioides Less.
Marshallia australis Spreng.! in h. Bald. 1822 sed in ejus oper. desid. Valde affinis Calea prunifoliae. (v.s.) This reference is included under Calea Berteriana DC. (Prod. 5: 680. 1836). Definitely not Marshallia.
Marshallia dentata Bertol. (Misc. Bot. 15) Mem. Accad. Sc. Instit. Bologna 5: 422, tab. 21. 1854 (collected in Alabama)=rayless plants of Gaillardia aestivalis (Walt.) H. Rock.

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$58,62,63,65,67,78,82$, $83,85,89,90,94,95,111$ var. platyphylla $48,78,82$, $83,88,90,111$
var. scaposa $50,55,56,58$,
$62,63,68,83,90,92,94,95$
pumila 130
ramosa $50,52,53,54,55,56$, $58,59,62,63,64,68,96,97$, $98,99,100,129,130$
Schreberi 46, 69, 73
spiralis 100,105
tenuifolia 52, 53, 54, 55, 58,
$59,62,63,64,68,99,100$, $117,118,120,123,124,125$, $126,127,129,130$
trinervia $50,51,52,54,55,56$, $57,58,59,61,62,63,67,68$, $69,70,72,73,74,78,82$
Williamsonii 112, 118
Mutisieae 60
Persoonia 46, 47, 65
angustifolia 46, 47, 112, 116,
117, 118
lanceolata 46, 65, 83, 87
latifolia 46, 68, 73
Phyteumopsis 47, 65
angustifolia 112, 116
lanceolata 65, 83
latifolia 69
Proteaceae 46
Racoubea 65
Railliardia 60
Sabazia 60
Sarrette bulbeuse 130
Therolepta 47, 48
pumila 47, 130
Trattenikia 46, 47, 65
angustifolia 112
lanceolata 65, 83
latifolia 69
Tridax 59
Verbesineae 59, 60
Vernonieae 60
Xyris 127

# CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY 

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NO. CLXXXII

THE GENUS PEDILANTHUS (EUPHORBIACEAE)<br>BY<br>Robert L. Dressler

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## PART I. GENERAL

## INTRODUCTION

Pedilanthus, a Mexican and circum-Caribbean genus of Euphorbiaceae-Euphorbieae, has long attracted the attention of botanists because of its strangely formed inflorescence, and the curious, succulent plants are often cultivated in greenhouses and tropical gardens. Nevertheless, the genus is botanically poorly known; identification by the use of herbarium material or published keys has been nearly impossible, and most of the morphological studies have been both superficial and obscure. The present study was initiated at the University of Southern California, after brief field acquaintance with the genus in western Mexico, and continued at the Gray Herbarium, with short periods of field work in other areas of Mexico. The taxonomy of the genus is herein revised, studies of several aspects of the morphology are given, and the probable evolution and relationships of the genus are treated.

The tribe Euphorbieae, of which this genus is a member, is characterized by its inflorescence, the "cyathium." This inflorescence, with its central (terminal) pistillate flower, surrounded by clusters of small staminate flowers, which, in turn, are subtended by a calyx-like whorl of bracts, is in many cases one of the most flower-like "pseudanthia" known. The tribe is especially interesting to students of phylogeny. It is very well defined, and the reduction and modification of the inflorescence seem to provide evidence of clear evolutionary trends. There is rarely need to resort to hypothesis or the fossil record for unsatisfactory "missing links" of a major sort. This is emphasized by the fact that the genus Euphorbia, which includes over a thousand diverse species, has so long resisted rational "splitting" on a worldwide basis. Pedilanthus is distinctive, within this tribe, by the possession of a zygomorphic, spurred involucre. Several other Euphorbieae (Cubanthus, Monadenium, Euphorbia subgenus Poinsettia) have developed some degree of zygomorphy, but only in Pedilanthus are the glands concealed in a spur.

While it is hoped that the taxonomy of the genus has been clarified by the present study, and although certain morpho-
logical features are treated here in some detail, Pedilanthus still deserves careful study in several aspects. We have, within a single, relatively small genus, a series of species with widely varying degrees of xeric adaptation. This genus would be appropriate for an intensive comparative study of anatomical and physiological adaptation to xeric conditions. The cytology of Pedilanthus is very inadequately treated in the present work. Slow-growing perennials are poor material for cytogenetic studies, but the group is one which appears to be undergoing rapid, radiative evolution, and may warrant careful cytological study for this reason. A careful field study of variation in P. macrocarpus should be rewarding, and the Antillean taxa need extensive field and laboratory study. The natural history of this interesting group, and especially the pollinating agents (presumably hummingbirds), remains essentially unknown.

## Acknowledgements

The author is deeply indebted to the many persons whose aid has made the present work possible. Dr. Reed C. Rollins has kindly guided and advised the author through the greater part of the research, and generously gave of his time in personally searching for critical material in European herbaria. Dr. Louis C. Wheeler first sparked the author's interest in the Euphorbieae (and, indeed, in botany); his nomenclatorial work, published and manuscript, has contributed much to the present study. Professor I. W. Bailey has greatly aided in the morphological studies by his interest and suggestions. Professor Ernst Mayr and Dr. Ernest E. Williams have read the manuscript and given valuable suggestions. Dr. Sherwin Carlquist has shown a sincere interest in the work, and his wide knowledge of techniques for anatomical and cytological study has been an invaluable source of help. Dr. Grady L. Webster, too, has taken an encouraging interest nearly throughout the present study. Living plants and other special materials have been contributed by a number of persons, including Dr. Lucas Calpouzos, Mr. Ladislaus Cutak, Dr. Charles DuQuesnay, Dr. Howard S. Gentry, Dr. Richard A. Howard, Mrs. Ruth Oberg, Dr. George R. Proctor and Dr. Grady L. Webster. Valuable photographs have been contributed by Dr. J. W.

Carmichael, Dr. Carl Partanen and Mrs. Anstis H. Wagner. Dr. Robert E. McLaughlin and Mr. Donald R. Whitehead have kindly prepared a number of pollen samples by acetolysis. The diagnostic drawings of involucres in Plates XVI to XXI were prepared by Miss Joan Ericksen; her patience and skill are deeply appreciated. Dr. Ding Hou helped greatly in preparing the habit sketches of the new species. Most of the distribution maps are based on Goode's Series of Base Maps, which are used by permission of the University of Chicago Press. The outline map on which Map 6 is based was made available through the kindness of Dr. Ira L. Wiggins. Drs. W. L. Brown, Jr., and E. O. Wilson have identified some of the ants which were found on plants of Pedilanthus, and the thrips were identified by Dr. Lewis J. Stannard. Much of the field work was made possible by grants from the Fernald Fund, for which I am indebted to Mr. F. W. Hunnewell. National Science Foundation predoctoral grants have given generous support during the later portion of this study.

The author is indebted to the curators who have kindly lent material for study, as well as to those who have searched their herbaria for critical specimens. Material from the following herbaria has been studied:

[^24]
## History

Pedilanthus was known to the pre-Columbian botanists of Mexico, and used there as a medicinal plant. A species, apparently $P$. tithymaloides, is described by Francisco Hernandez (1651) as chapolxochitl, or grasshopper flower, and its reputed medicinal uses and native synonymy are given. Cuttings of $P$. tithymaloides were early carried to Europe, and the plant was known to several pre-Linnaean writers. Linnaeus described this plant as Euphorbia tithymaloides in his Species Plantarum (1753), and two varieties were assigned to the species. Miller, in 1754, and Gomez Ortega, in 1783, considered this plant and its varieties to form a distinct genus, for which they took up pre-Linnaean names. The first, Tithymalus, is a homonym of the contemporaneous Tithymalus of Trew, used for a different segregate of the Linnaean Euphorbia; and the second, Tithymaloides, has remained in nearly total disuse. The now well-known name, Pedilanthus, was proposed by Necker (1790) and taken up by Poiteau (1812), who recognized three species (all here treated as subspecies of $P$. tithymaloides). Necker's generic name became a nomen genericum conservandum at the most recent International Botanical Congress (1954).

All of the earlier "species" which were described are very similar to Euphorbia tithymaloides L. in the inflorescence, and they are here considered to be conspecific with that taxon. The first clearly distinct species was described by Jacquin as Euphorbia bracteata (1798). Klotszch and Garcke, in their hasty and superficial revision of the Euphorbieae (1859), recognized three quite unnatural genera within Pedilanthus, and named several supposedly new species, with inadequate descriptions. Boissier revised the group for DeCandolle's "Prodromus" (1866), but accepted most earlier species and descriptions uncritically. At this time he created the subgenus Cubanthus, for $P$. linearifolius, described by Grisebach in 1860. Millspaugh (1913) presented a "revision" of Pedilanthus, with a number of putative new species, and raised Cubanthus to generic rank. The change in status for this group proves to be correct, but his paper otherwise contains numerous errors and is based on an entirely uncritical species concept. In all, about 57 epithets have been ascribed to the genus, and only a few are referable
to other genera (three to Cubanthus, two to Euphorbia). Most of these species have been described without the study of previous type specimens, and the descriptions are often diagnostic only for the striking generic characters. It is largely because of this sort of confusion that Pedilanthus has been known as a "difficult" genus.

## Economic Value

Aside from widespread cultivation as a somewhat ornamental and indestructible hedge plants in tropical and sub-tropical gardens, Pedilanthus is of little economic importance. Nearly everywhere, the latex is reputed to have drastically purgative action, and other medicinal qualities are sometimes ascribed to the plants, but their medicinal uses are now limited to folk-medicine. The stems of Pedilanthus, especially of $P$. cymbiferus, bear a wax similar to that of Euphorbia antisyphilitica, and the latices appear to have some rubber content, but neither of these has been exploited commercially. References to the commercial extraction of wax from "Pedilanthus Pavonis" stem from an early writer's confusion between Pedilanthus and the above-mentioned Euphorbia (both being called candelilla).

Pedilanthus tithymaloides is widely cultivated in tropical areas. It is readily propagated by cuttings, drought-resistant, and relatively unpalatable to animals, and the stem and leaves remain green and presentable, if not attractive, even after considerable mistreatment. During the winter months, the leaves are often shed, but the bright red involucres are then borne in abundance. This species and $P$. macrocarpus are frequently found in greenhouse culture in temperate latitudes. Other species which might prove useful as greenhouse or garden plants are P. Palmeri, P. Finkii, P. pulchellus, $P$. cymbiferus and $P$. bracteatus (especially the form from Iguala, Guerrero).

Common names are listed for each taxon, but a few of the names are, as with a majority of common names, generic rather than specific, and merit brief comment here. Ditamo real, from some fancied resemblance to the European Dictamnus, is widely used in Caribbean America, usually for the different forms of $P$. tithymaloides. Candelilla is applied to various Mexican species (especially the succulent ones)
as well as to Euphorbia. The colorful and oddly formed involucres of the genus may be compared to birds or shoes and have resulted in numerous names such as pie de niño (child's foot), zapato del diablo (devil's shoe), pericos (parrots), gallitos (little chickens), redbird cactus, slipper spurge, etc.

## PART II. MORPHOLOGY

## Materials and Methods

The specimens used in the morphological studies have been largely from the author's own collections, either collected in the field, or taken from plants grown in the greenhouse. In a few cases, samples (especially of stems) have been removed from herbarium specimens. Table I lists the collections used (materials used in pollen and chromosome studies are listed separately).

Materials were preserved in Formalin-Acetic acid-Alcohol (specimens from herbarium collections were softened in hot water and stored in FAA, with a little glycerine added). Samples of roots, stems, leaves and inflorescence parts were imbedded in paraffin, sectioned with a rotary microtome and stained with safranin and fast green (when not otherwise specified, the techniques are those given by Johansen, 1940). Older stems and wood samples were cut with a sliding microtome, without imbedding, and similarly stained. Wood macerations were prepared using Jeffrey's method.

Involucres and other parts were cleared, for study of the vascularization, in $85 \%$ lactic acid. The parts used were generally de-colored in hot $6 \%$ sodium hydroxide (in a paraffin oven) until translucent, washed in water, and then heated in lactic acid for ten minutes in a boiling water bath. Very small structures clear adequately without de-coloring. Materials containing tannins and similar substances do not de-color well with sodium hydroxide. Too long a period in sodium hydroxide results in very clear material, but this is too fragile for dissection. When stored in lactic acid, the samples become clearer and tougher with time, but only very slowly. Parts cleared by this technique may be conveniently mounted in Hoyer's medium (Beeks, 1955). Since pollen cannot be stored indefinitely in lactic acid mounts, a modification of the lactic acid treatment was developed;

Table 1. Materials used in morphological studies. When an herbarium specimen is not now available to document the study, the locality of origin is given for the collection. Data on the remaining collections will be found in the specimen citations in Part IV. The initial "D" refers to the author's collections.

Part Studied

Species and Collection
P. Palmeri, D 1064

Palmer 1995
P. Finkii, Thompson, s.n.
P. calcaratus, D 1067

D 1380, ca. Tuxtla
Gutiérrez, Chiapas
D 1766
P. gracilis, Hinton 10973
P. pulchellus, Conzatti, Reko and Makrinius 3106
12685
P. coalcomanensis, Hinton 12685

P. tithymaloides
ssp. tithymaloides, D 1376,
Cuicatlán, Oaxaca

| x | x | x | x | x |
| :--- | :--- | :--- | :--- | :--- |
| x | x | x |  |  |
| x |  |  |  |  |

ssp. parasiticus, D 1364
Maricao Mts., P. R., cult. at M. B. G. x
sp. angustifolius, Cutak, s.n., ssp. jamaicensis, R. A. Howard,
$\begin{array}{clllll}\text { Four Mile Wood, Jamaica } & \text { x } & & & \text { x }\end{array}$
this is given in full in the section on pollen morphology. Pollen samples were also prepared by acetolysis (Erdtmann, 1952).

All chromosome counts were obtained by using smears of young staminate flowers. Material collected late in the after-
noon of a sunny day generally proved most satisfactory. The involucres were opened and removed from the flowers under a dissecting microscope and the flowers placed in ferric propionate fixative (Hyde and Gardella, 1953) for about 24 hours. The anthers were then crushed and heated in aceto-carmine. These slides were later made permanent, without removing the cover slips, by washing out the acetocarmine with $40 \%$ acetic acid (applying the acid to one side of the cover slip and blotting up the stain on the other), leaving the slides overnight in a moist chamber with absolute alchohol, and then ringing with Diaphane. The slides may be counterstained by adding a drop of Fast Green ( $0.1 \%$ in $40 \%$ acetic acid) when removing the aceto-carmine.

## Vegetative Morphology

Habit. - The range in habit found within Pedilanthus is unusual in so small a genus. Pedilanthus calcaratus and $P$. coalcomanensis are usually small trees, with distinct trunk and extensive wood formation, sometimes reaching seven meters in height. Both are deciduous and bear large leaves (some ecotypes of $P$. calcaratus are only facultatively deciduous and may retain their leaves through the winter in moist sites). Pedilanthus Palmeri is distinctly woody and often reaches two meters in height, but branches extensively from the base. Pedilanthus bracteatus and P. tithymaloides and their immediate allies are distinctly shrubby, generally ranging from one to two meters in height and branching from the base. These plants often have a roughly obconic form when undisturbed. Pedilanthus cymbiferus and $P$. macrocarpus are clump-forming desert shrubs with no trace of a trunk or main stem (see Plate XVI). The former produces numerous rush-like stems from the ground and forms modified underground stems which serve to spread the colonies over short distances. Pedilanthus macrocarpus is larger and markedly succulent; a habit resembling that of $P$. cymbiferus is achieved by the formation of adventitious buds on the roots, giving rise to extensive clonal colonies. Pedilanthus Finkii, P. gracilis, P. pulchellus and P. tehuacanus are all species for which exact information concerning the habit is unavailable; the first is apparently less woody than $P$. Palmeri (its closest ally), the second and third are woody
and perhaps small trees, and P. tehuacanus appears to be a succulent plant similar to $P$. bracteatus or of smaller stature.

Although $P$. cymbiferus is a desert plant, it is scarcely more succulent than Ephedra, some species of which it resembles in growth form. Some populations of $P$. calcaratus have rather thick twigs, but true succulence is limited to $P$. bracteatus and $P$. tithymaloides and their allies (spp. 8-13). These species are predominantly stem succulents. The leaves of $P$. macrocarpus and $P$. nodiflorus may be somewhat fleshy, but they are small and soon shed. Pedilanthus tithymaloides subsp. parasiticus, on the other hand, includes some populations with quite fleshy leaves that are retained for some time.

Roots. - The roots of Pedilanthus are generally woody and much branched. In P. calcaratus, and possibly in some other species, the primary root and later some secondary roots form characteristic thickened storage organs. In these roots the pattern of the primary xylem is completely obscured, and the greater portion of the xylem consists of large, starch-bearing parenchyma cells, with irregularly scattered vessels, usually in small groups. The parenchyma cells near the vessel groups are smaller than the ground parenchyma cells and may occasionally be lignified or be accompanied by a few gelatinous fibers. The storage xylem of these roots increases in girth by cambial activity, and the cells in the outer portions are in more clearly radial alignment. In one storage root of Dressler 1380, the outermost mature xylem forms a lignified band $0.2-0.5 \mathrm{~mm}$. thick. In this band some fibers have weakly lignified gelatinous secondary walls, but the majority are septate, without gelatinous walls, and include starch grains. The longer parenchyma cells are also occasionally septate, making the distinction between fiber and parenchyma difficult. The septae often remain non-lignified, but it is apparent that these late-formed septae may become lignified, and often tend to be formed at the same level in adjacent cells; the series of cells from a single cambial initial thus simulating, at times, series of cells from separate initials.

Storage roots similar to those here described are found in Cubanthus Brittonii (in this species the parenchyma has a much more regular geometrical arrangement, but the
structure is otherwise very similar) and in Euphorbia radians (Reiche, 1923). Structures which may be similar are found in many other species of Euphorbia, Manihot, Cnidoscolus, and Jatropha, and in seedlings of Hevea and Joannesia.

Older roots form a homogeneous cork of thin walled cells. The root cortex consists of relatively large, isodiametric parenchyma cells, which often contain starch grains, and frequent laticifers (very young roots have not been examined). In the cortex of P. macrocarpus, there are found, in addition to starch grains, numerous spheroid bodies of varying size, which stain dull red with safranin. In the cortex of the storage roots of $P$. calcaratus there may be occasional gelatinous fibers. In large roots, and especially in storage roots, the outer cortical parenchyma includes tangential series of cells within the outlines of their mother cells, indicating that series of anticlinal divisions have taken place in the growth of the root.

The primary vascular system varies from triarch to pentarch, with a conspicuous pith remaining in the center. With secondary growth, broad, large-celled rays (1-)2-5 cells wide (wider near branch roots) are formed at the protoxylem points, and weakly lignified wood develops between these. This xylem contains numerous rays which are homogeneous (upright) and largely uniseriate; two- and three-seriate rays also occur, especially in older roots. The rays may be somewhat lignified. The vessels, which are in scattered radial groups, are scalariformly or occasionally (in $P$. calcaratus, often) alternately pitted. Wood parenchyma is mostly paratracheal. There are numerous fibers, which in smaller roots are scarcely or not at all lignified and have a markedly gelatinous secondary wall. In P. macrocarpus and $P$. nodiflorus the gelatinous fibers are very thick walled and stand out strongly in cross section; in the first species they are found in the primary body as well as in the secondary xylem. In $P$. tithymaloides and $P$. calcaratus the fibers are usually (in the material examined) thinner walled and less conspicuous, but still markedly gelatinous. Narrow bands of well-lignified wood may be found in the central portion of the root, and, in larger roots, the outer portion is largely well-lignified. The fibers in such areas have thinner walls and may occasionally be septate.

Stems. - The stems of Pedilanthus show an interesting range of variation. The stems of the arboreous species are woody and may produce extensive xylem, the trunk of $P$. calcaratus, for example, reaching $6-8 \mathrm{~cm}$. in diameter. In the nearly leafless extreme xerophytes, such as $P$. macrocarpus and $P$. cymbiferus, the stem may be thick and fleshy or thin and woody, but has very limited secondary growth. In intermediate types, such as $P$. bracteatus, there is no distinct trunk, but old stems develop a good deal of secondary xylem and may reach $2-3 \mathrm{~cm}$. in diameter at the base.

The stem epidermis is moderately to heavily cutinized, with the cutin extending between the epidermal cells for about half their thickness. In the markedly xerophytic species, and especially in P. cymbiferus, there is a conspicuous wax on the older stems. This wax, like that of Euphorbia antisyphilitica, may be removed by boiling water. The stem of $P$. cymbiferus is irregularly pitted, with the trichomes occurring on the ridges and tubercles, and the stomata in the pits. A tendency toward this pattern is seen in other more or less xerophytic types, but it is much less marked. The stomata are more or less flush with the stem surface in $P$. pulchellus and a collection of $P$. calcaratus from a relatively moist habitat (Dressler 1380), but they are slightly to markedly sunken below the surface in the other plants examined, including a more xerophytic form of $P$. calcaratus (Dressler 1067). The cutin is thin over the stomatal guard and accessory cells, but in some cases an especially thick cutin surrounds these (see fig. 9). The basal cell of each trichome is heavily cutinized on the basal and lateral walls. The stomata and trichomes will be described in greater detail under leaf structure.

When much secondary growth occurs, a smooth, grey, homogeneous bark of thin-walled cells is formed. Bark formation takes place immediately beneath the epidermis. On $P$. calcaratus, at least, small, reddish lenticels are formed.

The cortex consists of relatively spongy parenchyma and numerous branching laticifers. No cortical collenchyma has been observed, though this is reported for $P$. tithymaloides by Assailly (1954). Chloroplasts are found in the cortex of all species examined (not certain for $P$. pulchellus and $P$. coalcomanensis, where only herbarium material was available). In the large-leaved types only the outer one half to
two thirds of the cortex is photosynthetic, but most of the cortex in $P$. macrocarpus and $P$. nodiflorus and nearly all the cortical cells of $P$. cymbiferus bear chloroplasts. In these species the outer half of the cortical parenchyma has a distinctly "palisade" arrangement. The same arrangement is present in P. bracteatus, P. tithymaloides ssp. angustifolius and P.t. ssp. jamaicensis, and (but less marked) in P. tithymaloides ssp. parasiticus. Substomatal chambers are usually distinct in the stems of Pedilanthus, so that the stomata are macroscopically visible as pale flecks. In $P$. cymbiferus and forms of $P$. macrocarpus (Dressler 1090) the substomatal chambers are quite large. In another collection of $P$. macrocarpus (Gentry 7677a), however, the substomatal chambers are relatively small, and some of them are actually cutinized within. Starch grains are frequent in the cortical parenchyma, and small spheroidal bodies which stain dark red with safranin are frequent, especially in the chlorenchyma.

The laticifers are best developed in the cortex. Several to many laticifers are found in the pith, and laticifers occasionally extend through the secondary wood by way of small multiseriate rays. The most conspicuous concentration of laticifers is found in the inner cortex, where they are mostly longitudinal and of large diameter. These large laticifers are often thick-walled, and on one specimen of $P$. tithymaloides ssp. tithymaloides the walls of some laticifers seemed to be weakly lignified. In this same species (Dressler 1376 ), a few markedly constricted laticifers were noted, perhaps supporting Milanez, suggestion that the "nonarticulated" laticifers of the Euphorbieae actually develop by the fusion of distinct cells (1952). Laticifers of medium size are frequently seen to extend across the cortex more or less radially, and a network of very tiny laticifers is found immediately beneath the epidermis. These subepidermal laticifers, which are so small as to pass unnoticed or to be mistaken for intercellular spaces under low magnification, account for the ready "bleeding" of the stems at the slightest scratch. The laticifers are multinucleate (but the nuclei are difficult to distinguish except under very favorable circumstances) and contain numerous very elongate starch grains (fig. 5). Short or isodiametric starch grains are infrequent in the laticifers.

The primary vascular tissues of the stem are eustelic, with numerous protoxylem points surrounding the pith, and a similar number of groups of non-lignified primary phloem fibers. These phloem fibers are well developed in the woody species, including $P$. cymbiferus, moderately developed in $P$. bracteatus, $P$. tomentellus and $P$. nodiflorus, moderately to poorly developed in P. tithymaloides, and very poorly developed in P. macrocarpus.

The pith is largely composed of relatively isodiametric parenchyma cells, which often include starch grains. In $P$. calcaratus, one or two tubes which appear to be laticifers are found in the outer pith and are distinctive in being surrounded by a layer of small non-lignified cells, and a partial layer of two to three rows of lignified or partly lignified cells ; these latter are partly gelatinous fibers, in which only the primary wall is lignified (see fig. 8). Similar structures are found in the pith of $P$. coalcomanensis and $P$. pulchellus, but have been seen in no other species. The pith cells of $P$. coalcomanensis each contain a single dark-centered, manypointed druse, and smaller, more irregular crystals are found in the pith of P. Finkii. Pedilanthus cymbiferus is interesting for the occurrence of lignified parenchyma cells in the outer pith, touching and near the protoxylem.

Pedilanthus cymbiferus spreads locally by thick underground stems. The aerial stems of this species are 2.5-3.5 mm . in diameter, with strongly lignified xylem. The underground stems are about 5 mm . in diameter, produce cork externally, and have abundantly starch-bearing parenchyma in the cortex and pith (without chloroplasts, palisade arrangement, or lignified pith cells). The phloem fibers are well developed, as in the aerial stem. The secondary xylem of the "stolon" is weakly lignified, and, except for an incomplete (in the material seen) band of lignification, the fibers are moderately thin-walled and gelatinous. Some of the ray parenchyma is lignified in the band of lignification, and some of the fibers are septate.

Wood Structure. - The secondary xylem of Pedilanthus has been relatively well sampled, and the major trends of variation can be indicated, but better sampling of each species is needed for a detailed treatment.

No growth rings are present. The pores are commonly aggregated into radial multiples. This trend is much less
Table 2. Vessel features in Pedilanthus. Numbers represent averages of 50-60 measurements: all dimensions "D 1380, outer trunk."
VESSEL- VESSEL-
VESSEL PARENCHYMA , except in

" x "-present, " $x$ "-predominant, " $(\mathrm{x})$ "-present, but very infrequent
marked in the $P$. bracteatus and $P$. tithymaloides groups and $P$. Palmeri than in the other species (see Table 2). In $P$. Finkii and P. pulchellus the vessels tend to be in radial multiples, but the multiples are not so clearly delineated as in the species with larger vessels. The number of vessels per square millimeter is highly variable and, with the vessel diameter, seems to correlate to some degree with the habitat and the relative need for rapid water conduction. This relationship is better shown by the vessel diameters. The smallest diameters are found in the most mesophytic species, $P$. Finkii and P. pulchellus, and in some markedly xerophytic ones, $P$. cymbiferus and $P$. tehuacanus. In both the shaded mesophytes and the leafless xerophytes the stress of heavy transpiration, with the resultant need for rapid water transport, would be unlikely or infrequent, though for different reasons. The largest vessel diameters are found in those species which are large leaved deciduous trees of the tropical deciduous forest ; $P$. calcaratus and $P$. coalcomanensis. It is reasonable to assume that these trees are frequently subjected to heavy transpiration and that selection for efficient water conduction has been correspondingly effective. It is interesting that Dressler 1067 and Dressler 1766, collections of $P$. calcaratus from relatively xeric tropical deciduous forest, have very large vessels (av. 61-63 microns) in their inner wood, while Dressler 1380 , from a much wetter site, has markedly smaller vessels (av. 46-49 microns). Wood from the outer trunk of the last collection has, however, much larger vessels. A similar increase in vessel size with ontogeny would doubtless be found in the other species, if they were adequately sampled (Bailey and Tupper, 1918). The discrepancy between vessel diameter as measured in section and as measured from macerated wood, in this collection, is probably due to the presence of elements from one or two exceptionally large vessels in the sample chosen for maceration. One vessel element in that preparation showed an extreme diameter of 162 microns. The moderately succulent xerophytic species, such as $P$. tithymaloides and $P$. bracteatus, and the moderately mesophytic types, such as $P$. Palmeri and P.gracilis, tend to have vessel diameters intermediate between the extremes given above. The pattern of vessel element length is less clear; the relatively primitive, mesophytic $P$. pulchellus shows the longest vessel elements


Plate I. Wood Structure. Fig. 1. Pedilanthus t. ssp. tithymaloides, Dresster 1s76, cross section of old stem, showing small, scattered vessels, magnification ca. 155. Fig. 2. P. coalcomanensis, cross section of twig, magnification ca. 155.


Plate II. Wood Structure. Fig. 3. Pedilanthus $t$. ssp. tithymaloides, Dressler 1376, tangential section of old stem, note the biseriate rays, magnification ca. 155. Fig. 4. P. calcaratus, Dressler 1067, tangential section of small stem (ca. 1.5 cm . diam.) note the rays are uniseriate and scarcely distinguishable from the surrounding cells, magnification ca. 155.

 in longitudinal section, note the bone-shaped starch grains with elongate hila, magnifi-
 showing circular boralereal pit., in alternate artangement, magnification ca, 230. Fix. i. P. tomentellus, vessel, from tangential section, showing satariform and some transitional pitting. magnification ca. 230. Fig. S. P. calcuratus. Dressler lutiz, cross section of laticifer in outer pith, showing sheath of lignified cells, magnification ca. 230. Fig. 9. P. calcaratus, Dressler 1880, cross section of stoma on twig, magnification ca. 230.
and the extreme xerophyte, $P$. cymbiferus, the shortest, but the other species depart widely from this seeming tendency. Better sampling is needed of this feature, with careful selection of wood from comparable regions of the stem. Perforation plates are always simple. The end wall inclination is quite variable, but tends to be greater in narrow vessels. The "tails" projecting beyond the perforation plate are also quite variable in length.

Interesting trends are to be found in the pitting of the vessels. The pitting is quite variable within the individual sample; but the range of variation and the dominant type of pitting, so far as has been observed, are characteristic for species, and often for species groups. These ranges and trends, subjectively determined, are shown in Table 2. Though "transitional" customarily refers to the transition between scalariform and opposite, a second transition is shown between opposite and alternate; this should not cause confusion in the graphic presentation. The pitting tends to be spiral, even in scalariformly pitted vessels, so that the opposite pattern almost always tends to be transitional to alternate pitting. In the P. Palmeri and P. calcaratus alliances the intervascular pitting includes the alternate pattern and the predominant type is opposite and/or transitional between opposite and alternate. Pedilanthus coalcomanensis shows a slightly less advanced state, with scalariform pitting present, and opposite and scalariformopposite transition predominating. Pedilanthus pulchellus and $P$. cymbiferus show a smaller range of variability, and lack both scalariform and completely alternate pitting. The $P$. bracteatus and $P$. tithymaloides groups, with the exception of the always anomalous $P$. tehuacanus, have predominately scalariform pitting. The vessel-parenchyma pitting shows similar trends, but tends to lag behind the intervascular pitting in the phylogenetic series, scalariform pitting here being present in all species. Intervascular pitting is bordered, and the circular bordered pits often have elliptical apertures. Vessel-parenchyma pitting is wider and has reduced or no borders. Tyloses are commonly found in the vessels, but are not lignified.

The imperforate tracheary elements consist largely of cells with only moderately thickened walls and very small pits. In $P$. pulchellus and $P$. rymbiferus, these fiber-tracheids
have thicker walls than in the other species, and the pits are distinctly bordered, with narrow, crossed apertures. Crossed apertures are apparently present in some other species, but the borders are somewhat reduced, and the pits are so tiny that it is difficult to distinguish fiber-tracheids and libriform fibers, though both may be technically present. Gelatinous fibers are common and often form wide bands. They have been observed in all species, but are absent from the aerial stems of $P$. cymbiferus and from some stems of $P$. macrocarpus. Septate fibers, with thin, non-lignified cross walls, have been observed in P. Palmeri, P. Finkii, P. calcaratus and $P$. tithymaloides, and may be present in other species. Ray and wood parenchyma cells with such nonlignified cross walls have been observed in the above species and in $P$. macrocarpus.

The rays in most species of Pedilanthus are uniseriate and composed entirely of erect cells. In any species, an occasional multiseriate ray will be found containing a transverse laticifer. In P. bracteatus and P. tithymaloides there is a distinct tendency to multiseriate, slightly heterogeneous rays (see Plate II). In these species the body of the ray is often 2-3 cells in width, and, though the cells are not truly "procumbent," they are more nearly isodiametric than the erect cells of the "wings." In P. macrocarmus and P. tomentellus, the rays are predominately uniseriate, but the cells of the middle portion are often shorter than those of the extensions.
Both apotracheal and paratracheal wood parenchyma are found in Pedilanthus. Apotracheal parenchyma is diffuse, scanty, and very inconspicuous except in the bands of thickwalled gelatinous fibers. Paratracheal parenchyma is similarly quite scanty.

In summary, the vessel diameter is rather well correlated with the habitat and the relative need for efficient water transport; and the moderately succulent groups, such as $P$. bracteatus and $P$. tithymaloides, seem to have retained the most primitive features in their wood structure: many solitary vessels, scalariform intervascular pitting and slightly heterogeneous rays. Pedilanthus mulchellus, a mesophyte with narrow, very long vessel elements and indistinct radial multiples, may show the most primitive features among the truly woody species. While the evolutionary trends in wood structure are well established and, in major features, ir-
reversible (Bailey, 1944), it is possible that these trends are reversible in finer details; that is, within the framework of ontogenetic variability.

Leaf Structure. - The nodal anatomy of Pedilanthus is simply trilacunar, the three traces remaining distinct through the petiole and for some distance in the midrib. A small amount of collenchyma (of the "lacunar pattern," with intercellular spaces) is sometimes found in the petiole and midrib, especially if these are keeled. The stipules, which are borne on the stem, adjacent to the petiole base, vary from rudimentary or absent, as in $P$. macrocarpus, to nearly a millimeter in length, as in $P$. tomentellus and some forms of $P$. tithymaloides. They may be rounded and hemispheric in form, but are more commonly conic or spur-like. In P. tomentellus, which has been sectioned and examined microscopically, the stipules are definitely associated with the petiole base (though not shed with it) and are lacking in vascular tissue. The epidermis of the stipule is of the narrow palisade type, very similar to that of the inflorescence glands.
In those species of Pedilanthus with large foliage leaves, the leaves are bifacial, with 2-3 layers of palisade parenchyma beneath the upper epidermis, occupying $1 / 4$ to $1 / 3$ of the leaf thickness. The remainder of the leaf is made up of spongy parenchyma. In $P$. macrocarpus, the very small leaves are scarcely thicker than those of the mesophytic species, but there is no clearly defined palisade layer, the entire leaf chlorenchyma being made up of an open spongy tissue, the cells of which are somewhat perpendicular to the epidermis.

Only a single type of trichome is to be found in the genus. All trichomes are compound and uniseriate; the basal cell of each is very thick-walled and heavily cutinized throughout. The protoplasts of the trichome cells are thus cut off from the epidermal cells, and they die at an early stage. The second cell of the trichome is also frequently thick-walled, but less so than the basal cell.
The stomata of Pedilanthus are of the "Rubiaceous" pattern, with the subsidiary cells paralleling the guard cells. Stomata are found on both upper and lower leaf surfaces, but are more numerous on the lower surface. They are also numerous on the stems, which, in many species, take over
the photosynthetic role of the plant. The subsidiary cells are commonly deeper than either the guard cells or the surrounding epidermal cells (see fig. 9), and often partially enclose the guard cells above and beneath. The guard cells have both inner and outer ledges well developed. The stomata of the leaves which have been examined are only slightly sunken beneath the leaf surface, but the stem stomata of the more xerophytic species are markedly sunken.

In the stem of one collection of $P$. macrocarpus (Gentry ${ }^{7} 677 a$ ), a number of stomata were observed in which the substomatal chambers were partially filled by proliferation of the cortical cells, and the reduced chambers heavily cutinized within over nearly or quite the entire surface. Such stomata are apparently non-functional.

Markowski (1912) describes rudimentary stomata from the leaf of Pedilanthus (either P. cymbiferus or P. tithymaloides ssp. parasiticus?). Such non-functional stomata have, in the present study, been found to be frequent on the leaf of $P$. Palmeri, but very few have been found on the examined material of $P$. tithymaloides (all grown in the greenhouse). The subsidiary cells of the rudimentary stomata appear to be normal, but the guard cells are very narrow and shrunken in appearance. The opening between the guard cells is greatly reduced or, more frequently, absent. In some cases, two distinct cells cannot be recognized. These peculiar structures would appear to be the result of atrophy at an early stage of development, but more study is needed.

Abscission Layers. - The efficient removal of nonfunctional parts can be of some adaptive value to xerophytes, and mechanisms of abscission are well developed in Pedilanthus. The leaves are cut off by an abscission layer, very early in the extreme xerophytes, much later in the mesophytes. If the pistillate flower of a cyathium is not pollinated, the cyathium soon abscisses at the base of the peduncle. If pollination does occur, a ring of corky tissue is formed about the base of the involucre, cutting off the staminate flowers and the involucral bracts, which soon dry, but do not normally fall off. When the cyathia and fruits have all dried, the entire inflorescence is cut off by an abscission layer formed above the uppermost functional axillary bud. Of greater interest is the formation of such supra-axillary abscission layers anywhere in the plant, in the event of injury or un-
favorable conditions. Yellowing and death set in promptly just above the abscission layer, though the terminal portion of an internode may remain alive and green for some time after the onset of abscission. If little secondary growth has occurred, the stem falls off unaided, leaving a clean, corky layer on the living portion. If the stem is woody, the dead portion persists, but is very sharply delimited. The abscission layer is often not horizontal, but slanted or curved from a point above the axillary bud to a point nearly opposite the bud. This suggests that its formation is governed by growth substances formed in the axillary buds. Abscission layers were not observed on stems which still bore leaves. Occasionally one may find a moribund stem in which there is an abscission layer above each node and each internode is dying from the base upwards.

The abscission of the axillary bud, as reported by Markowski (1912), has not been observed in the present study. It is possible that the bud of the specimen sectioned by Markowski had started growth before collection, and that abscission of the young shoot started after the material was gathered and before it was preserved.

## Reproductive Morphology

Inflorescence. - The complete inflorescence of Pedilanthus is a compound dichasium of flower-like involucres. These compound dichasia may be either terminal or axillary, or both. The basic unit in this inflorescence is a terminal involucre subtended by two bracts and their axillary buds, each of which can develop into a similar unit (see fig. 31). Occasionally ( $P$. coalcomanensis and $P$. tehuacanus) the inflorescence may, by abortion, be monochasial for several successive nodes. The subtending bracts, which are sessile and clasping, conceal the developing involucre for a greater or lesser period (very briefly in $P$. macrocarpus and $P$. nodiflorus; nearly until anthesis in P.coalcomanensis and $P$. bracteatus). The three vascular traces which supply each bract branch before passing through the abscission layer, so that several to many veins enter the broad base of the bract.
As noted by Markowski (1912), the bracts of P. tithymaloides (and $P$. nodiflorus) are not quite opposite, but
nearly so, the abaxial angle (ventral, relative to the involucre) being a little less than 180 degrees, so that, as the dichotomous, axillary cluster of cyathia increases in size, none of the involucres faces back upon the main stem. This divergence may occur in other species, as well, but it is inconspicuous and not readily determined from herbarium material. In P. bracteatus, P. tomentellus, P. tehuacanus, and apparently in $P$. coalcomanensis, all species with very large bracts, the bracts are opposite, or, if anything, the lower (abaxial, in axillary dichasia) angle is a bit the larger. In these species, however, each successive pair of bracts is borne in the same plane as the preceding pair, so that the successive dichotomies are in the same plane, and the cyathia are all oriented more or less side by side, facing outward from the main stem (in axillary dichasia).

The Involucre of Euphorbia. - Before attempting to discuss the involucre of Pedilanthus, a brief discussion of the inflorescence of the related and better known genus Euphorbia is required. Lamarck first suggested (1788) that the "flower," with its central pistil, clusters of simple, jointed stamens and subtending "perianth," might possibly be an inflorescence, a condensed cluster of many tiny flowers. Since then, many conflicting interpretations have been given for this remarkable structure, the "cyathium," but there is now general agreement on most of the main features (a more complete summary of the literature may be found in the works of Schoute, 1937; Haber, 1925; and Schmidt, 1907). The Euphorbia cyathium normally consists of a terminal pistillate flower, which is naked or very nearly so, subtended by five condensed clusters of quite naked, one-anthered staminate flowers. The whole structure is enclosed by a more or less campanulate involucre of five bracts which closely subtend the staminate flower clusters. Each of these bracts shows a normal three-trace foliar vascularization pattern (see Plate IV).

From one to five (commonly four or five) nectariferous glands are borne in the sinuses between the involucral lobes. Each gland is a double structure, receiving half of its vascular supply from the lateral trace of the involucral bract on each side, and occasionally developing as two discrete glands, in mildly teratological cases. Since the glandular tissue is much more heavily vascularized than the


Plate IV. Vascularization of Euphorbia involucre. Fig. 10. Euphorhia Tirucalli (from cultivated plant), involucre cleared, split between involucral bracts and spread open, magnification ca. 10. Fig. 11. Euphorbia Nantii, Carter \&f Ferris 3376, two cleared involucral bracts, magnification ca. 10. A. petaloid appendage of gland: B. involucral lobe (not evident in E. Xantii); C. gland.
intervening foliar structure, the entire lateral trace of the involucral bract, and commonly a few branches from the median trace, go into the vascular supply of the gland. In Euphorbia, subgenera Agaloma and Chamaesyce (which are apparently related) and in the section Medusea of the subgenus Euphorbia (here, apparently developed quite independently), and in the genus Pedilanthus, the glands are differentiated into a basal, glandular portion and a flattened, distal, non-glandular portion, which is commonly white or red, and, in Euphorbia, is quite petal-like in appearance. These "petaloid appendages" account for the most startlingly flower-like cyathia, notably those of Euphorbia fulgens and E. Xantii. In the subgenus Agaloma (and in Chamaesyce, as well), a common pattern involves the development of only four glands and their appendages, the pistillate flower, after anthesis, recurving through the gap where no gland develops. It is from this slight asymmetry that the highly zygomorphic pattern of the genus Pedilanthus appears to have developed (see fig. 28).

The structures commonly referred to as "bracteoles" are found between the clusters of staminate flowers. These are continuous basally, and often abaxially, with the involucre, and may occur as irregular rows of trichome-like structures, as solid partitions separating or surrounding the clusters of staminate flowers, or, commonly, as somewhat intermediate structures; partitions which are laciniate above. Since these bracteoles are usually completely without vascular tissue, their exact morphological nature and relationship to the other parts of the inflorescence are often difficult to determine. It appears that two distinct structures may have been involved in the evolution of the bracteoles. (1) The infolded and connate margins of the involucral bracts. The structure of Anthostema, Dichostemma, and, apparently, of Neoguillauminia, as well as the course of the lateral bract traces in some species of Euphorbia (especially E. pulcherrima) suggest that the involucral bracts primitively enfolded their respective staminate flower clusters. A portion of the bracteole-partition may, thus, be derived from the involucral bracts. This suggestion is supported by the developmental patterns described by Schmidt (1907). (2) The bracts which accompany the condensed branchings of the staminate flower cluster. The bracteoles are customarily interpreted as rep-


Fig. 12. Terminology of Pedilanthus Involucre. On the left. schematic dorsal views of $P$. cymbiferus involucres, showing parts, the upper showing the interior of the spur; on the right lateral outlines of $P$. calcaratus.


Fig. 13. Longitudinal section of $P$. cymbiferus involucre, with the style and all staminate flowers but one removed. Abbreviations: bract., bracteoles; part., spur partition; lat., lateral; med., median or medial; gl., gland; inv.. involucral lobe; sp., spur lobe; pist., pistillate; stam., staminate; fl., flower.

Fig. 14. Diagrammatic sections through base of cyathium. A. peduncle, showing five larger vascular bundles to bracts and staminate flower clusters and five (often only three) smaller, inner traces, which supply the pistillate flower. B. The outer bundles branch, each giving rise to three bract traces and a trace to the staminate flower cluster. C. The three bract traces and the trace to the staminate flower cluster are distinct. D. The traces to the staminate flower cluster each form two branches and a small trace which supplies the central flower. E. The traces to each staminate flower are shown. F. section through cyathium of Euphorbia. 1. gland: 2. involucral lobe; 3. bracteole-partition; 4. staminate flower cluster; 5. pistillate pedicel. This last section is highly schematic, as little free space is actually found in the involucre, and the glands and bracteole-partitions are not actually found at the same level.
resenting such bracts, and part or most of the bracteolar structure is surely of this nature (see the developmental studies by Schmidt, 1907, and Michaelis, 1924). It is probable that the bracts subtending the first two branchings of the staminate flower cluster primitively form the greater part of the bracteoles (see the structure of Anthostema, Michaelis 1924; Calycopeplus and Euphorbia Tessmannii, Mansfeld 1929; and Neoguillauminia, Croizat 1938). The nature of the staminate flower cluster is still a subject of some controversy, and will be discussed at greater length under the morphology of Pedilanthus.

Terminology of the Involucre in Pedilanthus. - In some earlier descriptions of Pedilanthus, where the inflorescence is discussed in terms of inner and outer sepals or upper and lower lip, and even in some more recent descriptions, the discussion is almost impossible of interpretation, even with the plant in hand, because of difficulties in terminology. For the description of so complex a structure as the cyathium of Pedilanthus, a clear and exact terminology is necessary, yet, for so small a portion of the plant kingdom, a highly specialized and esoteric nomenclature is not justified. It is hoped that the accompanying illustrations, especially figures 12 and 13 , will aid in understanding the terms used herein. The terminology of Millspaugh (1913) has been followed, where practicable.

The bilateral symmetry of the Pedilanthus cyathium is so marked, and the normal position of the involucre so characteristic, that the relative terms dorsal, ventral, anterior, posterior, median and lateral are all useful, and, indeed, necessary. Their usage, which is straightforward, is indicated in fig. 12. The most characteristic feature of Pedilanthus is the hood-like or pocket-like structure in which the glands are concealed. This has often been termed the "appendix," but the older and more descriptive term, "spur," is here taken up. The German Drüsentasche (Markowski, 1912) is also appropriate and readily intelligible. This structure is, in effect, an involucral spur, and is usually markedly spur-like in form. The term appendix is awkward when the homologies with Euphorbia, with its petaloid appendages, are considered, and is not so evident in meaning as spur. "Apex of the spur," as here used, refers to the tip of the spur, not to the tip or tips of the spur lobes. The
"base" of the spur is less easily defined, and, for that reason, alternative measurements are given (see dotted and solid brackets in fig. 12, and discussion under measurement, p. 94). The number of spur lobes is always considered to be four, homologous with four petaloid appendages of Euphorbia, though the lateral lobes are always adnate to the involucral tube, and the two medial lobes may be completely connate. The glands within the spur are conveniently designated as lateral and medial, with the medial glands sometimes split into "gland-pairs." The spur may be partially divided into three chambers within; the parenchymatous dividing walls being "spur partitions." The two large and conspicuous involucral lobes are simply known as the "main" involucral lobes, and the three smaller, dorsal lobes are collectively termed the "accessory" lobes, being further designated as lateral or median. There is sometimes a "chin" developed on the underside of the involucral tube, which, analogous to that in some flowers, may be called the mentum. When the bracteolar structures form partitions between the groups of staminate flowers, they are referred to as bracteole-partitions, and when these are continued dorsally or anteriorly in the involucral tube as distinct ridges, these are the "bracteole-ridges." Small projections between and beneath the accessory involucral lobes are referred to as "roof lobules." The terms used here in discussion of the flowers, pedicel, filament, calyx, etc., are used in their usual senses; special terms such as androphore and calyculus being thought superfluous where the homologies are clear. "Peduncle," in the Euphorbieae, is used to refer to the stem bearing the individual involucre. Where confusion may occur between the involucral bracts and the opposite, free bracts subtending the involucre (and peduncle), the latter may be distinguished as "cyme bracts."

The Involucre of Pedilanthus. - The involucral homologies between Euphorbia and Pedilanthus have been correctly interpreted, on the basis of external form, by Ridola (1903) and Troll (1928), and well indicated by Michaelis' work on development (1924), yet the morphology of Pedilanthus has remained poorly known, and a detailed comparison with Euphorbia is quite lacking. The five involucral lobes of Pedilanthus correspond to those of Euphorbia, and the spur lobes (including the adnate, lateral lobes) correspond to four
petaloid appendages of the subgenus Agaloma. The striking differences between Pedilanthus and Euphorbia result from the very unequal size of the involucral lobes, above the level of the glands, and the great anterior-posterior and dorsoventral developmental deformation which places the four glands on one side of the involucre and forms the characteris-


Plate V. Vascularization of Pedilanthus calcaratus involucre. A. a bract of the lower pair; B. upper lateral bract; C. dorsal (median) bract; c. lateral view of dorsal bract in natural position; inset. outline of involucre, showing relationship of the involucral bracts. 1. accessory involucral lobe; 2. spur lobe; 3. gland. In C only the half-gland vascularized from this bract is shown on the right, but the complete gland, half of which is vascularized from the upper lateral bract ( $B$ ), is shown on the left. Magnification ca. 6.
tic spur, and a greater degree of adnation of parts than is usual in Euphorbia. This deformation and adnation of parts makes the interpretation of the involucre from external features, or from microtome sections, very difficult, but clearing and partial dissection show the relationships, at least of the vascularized parts, very well (Plates V and VI). The basal part of the involucre shows a radial symmetry (or nearly so) and agrees closely with the basal structure


Plate VI. Vascularization of Pedilanthas nodiflorus involucre. A. a bract of the lower pair; B. upper lateral bract; C. dorsal (median) bract; c. lateral view of dorsal bract in natural position; inset, outline of involucre, showing relationship of the involucral bracts (dorsal bract scarcely visible from side). 1. accessory involucral lobe; 2. spur lobe; 3. gland. Magnification ca. 7.
of the Euphorbia cyathium. Each of the five bracts has three main vascular traces, and, in the basal portions, the five bracts are of about equal width. In the material examined of $P$. calcaratus, a curious crimp or zig-zag is usually found at the base of each bract trace (Plate V). This may be related to the abscission layer which forms in that region after anthesis (if pollination occurs). The base of the bract trace is often a weak point, and breakage during dissection is all too easy, especially in the more weakly vascularized lower bracts.

The involucral bracts of Pedilanthus fall into three types: (1) two lower bracts, which include the main involucral lobes (A in Plates V and VI) ; (2) two upper lateral bracts, which bear the lateral accessory lobes ( B in Plates V and VI) ; and (3) a single, median dorsal bract, which bears the median accessory lobe and is bilaterally symmetrical (C in Plates V and Vi). These three types are described in greater detail below.
(1) The lower pair of bracts are the least complicated in structure. In those species with a scarcely elongate spur, such as $P$. tithyma!oides or $P$. nodiflorus, the lower in racts show a quite simple, three-trace, foliar pattern of vascularization. In those involucres with elongate spurs, however, the upper trace, or a large part of it, bends back and up into the spur, before bending sharply forward to vascularize part of the lateral spur lobe, which is not readily distinguished from the main involucral lobe. This upper trace may occasionally mibute to the lateral gland (when present) or, if this is small, as in $P$. nodiflorus, may even form the entire vascular supply for the gland. More commonly, however, no glandular tissue is directly connected with the lower bracts. There are frequently weak crossconnections between the lower bracts and the adjacent, upper lateral bracts in the spur, possibly representing, in $P$. calcaratus, the area of the non-developed lateral gland. Similarly, cross-connections may occur ventrally between the lower bracts.
(2) The upper lateral bracts are involved to a much greater extent in the formation of the spur, and are consequently more complicated. The lower vascular trace mostly goes into the lateral gland, when this is present, the remainder of the trace supplying the upper part of the lateral
spur lobes. The central trace of the bract extends to a point near the glands, where a single, central branch (rarely two small branches) bends more or less sharply forward to supply the lateral accessory involucral lobe. The branches on each side of this small, central branch continue to the apex of the spur and forward into the spur lobes. The upper trace of this bract follows a pattern similar to that of the lower trace, supplying the outer half of a medial gland, with small branches often continuing into the corresponding medial spur lobe.
(3) The median, dorsal bract resembles the upper portions of the adjacent bracts, but is bilaterally symmetrical. The lateral traces supply the inner halves of the medial glands, with small branches usually contributing to the inner halves of the medial spur lobes. The median trace produces a small central branch to the median accessory involucral lobe, and the remaining branches go to the medial spur lobes. Cross-connections between this and the adjacent bract-systems are absent, except at and just below the glands.

Interesting variation is to be found in the form and structure of the accessory involucral lobes. In P. bracteatus and its immediate allies, $P$. tehuacanus and $P$. tomentellus, and in $P$. nodiflorus, the accessory lobes are markedly thickened above near the base, and the thickening has the appearance of representing the up-folded and connate margins of widened lobes. In $P$. nodiflorus this appearance is found in the vascular pattern (Plate VI; here the two margins are separated and spread apart). The central part of the vascular supply runs forward near the ceiling of the involucral tube and lateral branches bend upward to supply the upturned margins. In $P$. bracteatus, which presents a similar external appearance, the dorsal portions of the lobes are without vascularization, only small lateral branches, if any, extending upward. In $P$. tithymaloides, the accessory lobes are greatly thickened basally, but there is much less appearance of folding. The vascular supply in this species curves abruptly upward and follows the upper surface, leaving the lower part of the thickened area without vascularization. Small lateral branches, which resemble the larger ones of $P$. nodiflorus, are sometimes seen. Pedilanthus cymbiferus also has thickened accessory lobes, but the curvature of the vascular traces, which are similar to those of $P$.
tithymaloides, is much less pronounced. Pedilanthus pulchellus and $P$. coalcomanensis are externally similar in this feature. In the other species which have been examined, the accessory lobes curve smoothly forward and downward from their origin in the spur.

The spur, it is evident, is a compound structure, involving all five involucral bracts, though not in equal degree. The spur, in any measurable sense, is not exactly homologous with the petaloid appendages of Euphorbia subgenus Agaloma. Only the spur lobes, including their usually connate bases, correspond to these appendages. The dotted line in fig. 11 is intended to indicate the approximate portion of the involucre which is homologous with the petaloid appendages. A considerable portion of the spur (where this is elongate) represents a lateral extension of the involucral tube. This extension is always solid and parenchymatous, though Millspaugh (1913) was led to consider the peduncle of P. macrocarpus as "centrally affixed to the tube;" an impression clearly obtained from dried material in which the parenchymatous core of the tube extension had been crushed. The lobing of the spur apex in some species corresponds, not to the number of petaloid appendages involved in its structure, but to the number of involucral bracts (three) involved at that point.

Glands. - The double nature of the glands, already clearly indicated for Euphorbia, is reflected in the vascular pattern of the involucre, and, in some species, the medial glands have, phylogenetically, each split again into two parts (that is, the primordia remain distinct). In other species, the primordia occasionally remain distinct as a slight anomaly. In Pedilanthus, none of the lateral branches of the median bract trace supplies the glands themselves, reflecting the proportionate increase in the gland appendages (spur lobes) and, at least in proportion to the involucre, a decrease in the amount of nectariferous tissue. The glands show a typical palisade epidermis, with thickened cuticle, which appears to slough off at maturity. The cuticle shows knoblike thickenings on the lower surface, which follow the lateral contacts between epidermal cells. The cells immediately beneath the epidermis may themselves be radially elongate and somewhat palisade-like, but the remainder of the cells are relatively small and isodiametric, with densely
staining cytoplasm. The gland structure of $P$. tithymaloides has been illustrated by Banerji (1951) and Sperlich (1939). Millspaugh described the glands of some species as "stipitate"; since, however, the "stipes" (spur partitions) are never free, the term is inappropriate. The glands produce an abundant supply of sweet nectar. In greenhouses, where no animals can remove the nectar, the gland chamber is soon filled to overflowing (see fig. 31).

The glands of the Euphorbieat have often been interpreted as stipular. Their lateral position and vascularization are such that they could be of stipular origin. As indicated by Warming (1879), however, the occur'ence of clearly nonstipular, lateral glands on foliar structures is very widespread in the Euphorbiaceae, so that the glands of the Euphorbieae cannot be considered as definitely stipular. Croizat (1938) has referred to the glands of Anthostema. Dichostemma and Neoguillauminia as occurring on the "enlarged apex of the floral axis." Such, indeed, is their external appearance. Serial sections show, for the first two genera, that the vascular pattern is basically that of Euphorbia. The glands are between the clusters of staminate flowers, but the vascularization is entirely from the lateral traces of the adjacent involucral bracts. In these genera, and probably in Neoguillouminia as well, the glands are lateral on the involucral bracts, which basally enfold the staminate flower clusters, so that the marginal glands are between these clusters, and even adjacent to the central pistillate flower.

The spur lobes are so formed as to enclose the gland chamber above and laterally, leaving an opening or groove between the median spur lobes and the accessory involucral lobes, where a slender beak or tongue may be inserted $(P$. tehuacanus is exceptional in this respect; the spur lobes do not always fit closely together). The spur lobes are, thus, elongate and thickened, as compared with the petaloid appendages of Euphorbia. The medial lobes are frequently thickened near their apices. In $P$. calcaratus and $P$. gracilis the medial lobes are each folded upon themselves, and the folded edges coalesced, the terminal portion forming a recurved thickened point, reminiscent of a plow blade in form (see Plate XVI). In several species of Pedilanthus, the color differences between the spur lobes (petaloid ap-
pendages) and the involucral lobes, which are usual in Euphorbia, are maintained, even though the structural boundaries are much blurred. In other species, the red color of the spur lobes may extend over part or all of the involucral tube, while the red color is quite lacking in the involucres of $P$. bracteatus and $P$. tomentellus, and nearly so in $P$. tehuacanus.

Partitions and Bracteoles. - The spur partitions form interesting and curious structures, whose exact significance is difficult to determine. In $P$. coalcomanensis and $P$. macrocarpus these partitions are especially well developed and divide the gland chamber into three compartments terminally. In other species the spur is not so greatly lengthened beyond the glands, and the spur partitions are conspicuous only as ridges running down and forward from the medial glands to insert between the accessory involucral lobes. Other species, such as $P$. calcaratus and $P$. nodiflorus, have three terminal compartments in the gland chamber, but the lateral ones are so small as to escape notice except in section. The glands, in $P$. macrocarpus at least, are partially vascularized through the spur partitions. Part of the vascular supply goes nearly to the tip of the spur and enters the glands from the dorsal side, as is shown for $P$. calcaratus (Plate V). The remainder of the vascular supply, particularly that of the medial glands, enters more directly from behind and beneath the glands, through the spur partition. The indirect route of the vascular traces in $P$. calcaratus and partly in $P$. macrocarpus suggests that the portion of the spur distal to the glands represents an "everted" portion of the involucral tube, with the spur partitions representing the bracteole-partitions. Position alone suggests that there may be a genetic and developmental relationship between the two sets of partitions. Since the partitions are largely parenchymatous, their exact structural relationships are not easily determined. However, the ridge descending from the medial gland and inserting between the accessory involucral lobes does sometimes have a weak vascular system of its own. In $P$. bracteatus, a branch may run forward from just beneath the gland; this passes between the accessory involucral lobes, spreading out somewhat laterally beneath the vascular systems of the accessory lobes (fig. 15). In that species, this weak vascular trace runs about half the length of the accessory lobes. A similar


Plate Vil. Fig. 1.j. I'edilanthus bracteatus, Dressler 180.3 , portion of cleared involucre, showing vascular supply to the tissues between and beneath the accessory involucral lobes (A); B. gland; C. lateral accessory lobe; D. median accessory lobe. The accessory lobes are separated, and the photograph is slightly retouched to show perspective, magnification ca. 10. Fig. 16. P. Palmeri, base of staminate flower cluster, cleared and with the pedicels separated abaxially and spread apart. The central flower is indicated above by no. 1, the arrows indicate the order of flowering. The older, central flowers have already formed a corky abscission layer near the base. The bract traces are shown below: L. lateral bract trace; M. median bract trace. Magnification ca. 17. Fig. 17. P. Palmeri, the central staminate flower and one branch, seen from the side, bract traces below, labelled as in Fig. 16. Magnification ca. 17.
branch is sometimes seen in $P$. macrocarpus, coming either from beneath the gland or from an adjacent branch of the lateral bract trace (which continues into the spur lobe). Much weaker branches of the same sort are seen in $P$. nodiflorus. None was observed in P. cymbiferus, $P$. calcaratus or $P$. tithymaloides. If the spur partitions are of bracteolar nature, as suggested, this vascular pattern may represent a nearly complete fusion of the bracteolar traces with the lateral bract traces. Patterns found in Euphorbia pulcherrima suggest that such a fusion has taken place.

The bracteolar tissues within the involucral tube typically form partitions which partially separate the clusters of staminate flowers basally. These partitions are more or less laciniate above into slender, filamentous, or occasionally ligulate, segments, which are tangled among the staminate flowers when well developed. These partitions are connate with the involucral tube basally, and, even in those species without bracteoles, basal ridges are present within the involucral tube. Such a ridge commonly continues upward beyond the point at which the bracteoles become free from the involucral wall, especially in the two dorsal bracteole groups (see fig. 13). In P. coalcomanensis a distinct ridge or keel runs the length of the involucral tube and terminates in small lobules ("roof lobules") in the sulci between the accessory involucral lobes. These lobules are frequently found in other species, where the dorsal ridges are indistinct, such as $P$. macrocarpus, $P$. bracteatus and $P$. nodiflorus. The parenchymatous ceiling of the involucral tube may be partly bracteolar in all species.

A single collection of $P$. macrocarpus (Wiggins 5345) has been seen in which some of the bracteoles contain vascular tissue. An involucre from this collection was carefully cleared and dissected, only to show that the vascular tissue did not connect with either the vascular system of the involucre or that of the staminate flowers. One vascularized bracteole occurred between each two adjacent staminate flower groups. One of these bracteoles had only about a millimeter of vascular tissue in the mid-portion; the other four were vascularized throughout their lengths, but the strands ended blindly at the bases.

Development of the Involucre. - The development of the cyathium of Pedilanthus has been investigated by Baillon
(1858), Beille (1902), Markowski (1912) and Michaelis (1924), in all cases using $P$. tithymaloides ssp. tithymaloides. The development of Euphorbia has been the subject of many


Plate VIII. Early development of the cyathium, unper row fresh material of $l^{\prime}$. calcaratus, lower row preserved specimens of $P$. cymbiferus. A. early primordium showing the central pistillate primordium and the five staminate flower cluster primordia, with the involucral bract primordia differentiating about these. The order of development for the staminate primordia is: lower left, upper, lower right, upper left, upper right (a 2 -5 spiral), magnification ca. 50. B. the staminate primordia are dividing within the involucre. and the gland primordia (3) are just beginning to differentiate, magnification ca. 33. C. the involucre has overtopped the staminate flowers: the gland primordia (3) are differentiated and the medial ones are differentiating into gland and spur lobe mrimordia the lateral ones form only spur lobes in this species); the main (1) and the nccessory (2) involucral lobes are already markedly different: the distinction between lateral spur lote and main involucral lobe is clear at this stage; the three carpels of the pistillate flower are seen in the center, magnification ca. 35. D. lateral view of the same abex. E. an ofder involucre, in which the adult form is approached, maxnification ca. 30. F. the same involucre as in E, lateral view: note the cyme primordium at the base: magnification ca. 20. 1. main involucral lobe; 2. accessory involucral lobe: 3. gland (or spur lobe) primordium.


Plate IX. Fig. 18. I'dilanthus c!mbiffrus, later stages, showing the development of the spur and involucral tube, scale 10 mm . Fig. 19. Developmental anomalies in I'. c!mbliferus. A and B. involucres with all bracts develoned on the "accessory lobe battern," the second with a slight degree of zygomorphy. C. an involucre with four accessory lobes (three free spur lobes) and only one main lobe. D. an involucre with only one accessory lobe (no free spur lobes) and four main lobes. Scale 10 mm .
investigations, those of Schmidt (1907) and Michaelis (1924) being especially useful. The early developmental stages in these genera agree closely. The dichasial primordium differentiates the two protecting cyme bracts at an early stage, and the developing cyathium is completely concealed by these bracts during the earlier stages. The first steps of the external differentiation of the young cyathium are the formation of five smaller primordia around the central portion which becomes the pistillate flower. Those five primordia, which represent the staminate flower clusters and their subtending involucral bracts, develop in a $2 / 5$ phyllotactic order, numbers 1 and 3 being abaxial (ventral), number 2 being adaxial (dorsal) and numbers 4 and 5 developing into the lateral bracts. These primordia differentiate into distinct upper portions, the primordia of the staminate flower clusters, and a lower 5-lobed ring, the united primordia of the gamophyllous involucre (Plate VIII A). This involucral ring soon overtops the developing staminate flowers, but before these latter are completely concealed, the first signs of marked zygomorphy appear. Large parts of the dorsal and lateral lobe primordia are differentiated as the gland primordia, leaving the corresponding involucral lobe primordia much smaller than the still enlarging ventral lobe primordia. The distinction between the gland primordia and the spur lobe primordia is soon evident. The spur lobes and the ventral (main) involucral lobes soon overtop the remaining structures (not quite concealing the accessory involucral lobes), giving a structure like that shown in Plate VIII E and F.

At this stage, though the glands and their appendages (spur lobes) are displaced dorsally and the ventral involucral lobes are disproportionately large, the involucre is readily comparable with that of many species of Euphorbia. It is the intercalary growth of later stages which brings about the bizarre forms of the mature involucre. In $P$. cymbiferus (fig. 18) and similar forms, this is seen to involve disproportionate growth in two areas: (1) the two ventral (main) involucral lobes, which elongate and make up the greater part of the involucral tube above the base; and (2) the involucral tube and the spur lobes in the immediate vicinity of the glands, which undergo great differential growth to form the spur. In $P$. macrocarpus and P. Palmeri, the spur
growth greatly exceeds the enlargement of the involucral lobes, so that the spur forms the greater and most conspicuous part of the mature cyathium. In $P$. tehuacanus, $P$. tithymaloides and $P$. nodiflorus, on the contrary, spur elongation is quite limited. Pedilanthus tithymaloides (and, doubtless, $P$. coalcomanensis) differs in its earlier stages from the development outlined above, in that the two medial spur lobes are connate throughout.

Developmental Anomalies. - In many species of Euphorbia, the occurrence of abnormal cyathia is frequent, especially involving the cyathium terminating a main stem, the first and central cyathium of a pleiochasium ( $E$. capitulata Reichb. is noteworthy in that the normal axillary cyathia abort and the single, terminal cyathium is regularly "abnormal," Schmidt, 1907). Similar phenomena are to be found in Pedilanthus, chiefly involving imbalance among the different patterns of bract development. The most common pattern of abnormal development is that in which all five bracts of an involucre develop along the accessory lobe pattern (fig. 19, A and B). In this case, the spur cannot elongate, but the gland chamber develops as a ring about the involucre. The five connate accessory involucral lobes leave such a small opening that only the pistillate flower is exserted, most of the staminate flowers remaining packed in the base of the involucre. The opposite case, in which all five bracts develop on the main lobe pattern, has only been seen once, on a small cutting of P.bracteatus. This involucre, essentially that of a Euphorbia without glands, failed to reach maturity, doubtless because of the small size of the plant. Intermediate patterns of abnormal growth are occasionally found, two of which are shown in fig. 19. In both of these cases, the normal number of five bracts is found, but in one case, four of the bracts form "main" involucral lobes, the fifth being a bilaterally symmetrical "lateral accessory lobe" (each half forming part of a lateral spur lobe) ; in the other, only one "main" lobe is formed, there being two "median accessory lobes." Since the photograph was taken, the remaining combination, an involucre with 2 accessory lobes and 3 main lobes, has been observed. There may be, basically, two patterns of development involved: the spur pattern and the non-spur (main lobe) pattern. If this is the case, the upper lateral bracts normally represent
intermediates, with the upper portions developing on the spur pattern and the lower portions approaching the main lobe pattern.

These abnormalities serve to emphasize the essential homology of the different sorts of involucral bracts and to indicate the importance and balance of the normal developmental pattern. The occurrence of such abnormal patterns in the central, terminal cyathium may possibly indicate that gravity (which might act equally on all sides of a terminal primordium) plays a part in the developmental pattern. In any case, later-formed cyathia are axillary and have adand ab-axial regions, which would be quite impossible for the terminal involucre.

Staminate Inflorescence. - The five clusters of staminate flowers borne within the cyathium remain the most controversial feature of the inflorescence; their exact nature is obscured by extreme condensation. The naked, monandrous, staminate flowers are, within each group, arranged in two tightly packed rows, the flowers in the two rows alternating with each other. The first of the flowers to mature is the innermost (adaxial), and development proceeds outward in a zig-zag manner. It is thus not surprising that Wydler (1845) and many subsequent students have regarded each cluster of staminate flowers as a simple cincinnus or scorpioid cyme. This view has been defended more recently by Schoute (1937). Schmidt (1907), on the basis of development and vascular pattern, considered each staminate flower cluster to represent a dichasium, with each branch of the dichasium forming condensed and compacted cincinni (presumably, these would technically be drepania, since each is compressed into one plane). Haber (1925), studying the vascular anatomy of the cyathium, supports this view and briefly mentions cases in Euphorbia clusiaefolia where continued dichasial branching occurs (p. 691). Either the simple or the double monochasium could be derived from the sort of dichasium found in the primitive genera Anthostema and Dichostemma, as diagrammatically shown in fig. 20.

Schmidt (1907) has reported that the primordia of both the second and third flowers of a cluster originate from the primordium of the first flower, and that the fourth is derived from the second, the fifth from the third, the sixth from the fourth, etc. This is the primary basis for his
hypothesis that the cluster represents a dichasium. Michaelis (1924) examined Pedilanthus tithymaloides and several species of Euphorbia, and reports that these do not show the order of development reported by Schmidt, but that the third primordium is derived from the second, the fourth from the third, etc. In my own work, I have examined a number of early stages of Pedilanthus (several species) and must report that the staminate flower primordia are so compacted that, on the basis of external features, at least, neither pattern of development can be proven to the exclusion of the other.

The vascularization of the staminate flower cluster is basically two-parted (in Euphorbia Xantii the two-parted nature is so marked that the two halves are independently inserted on the lateral bract traces; the primary staminate flower is aborted, or, at least, not centrally located, as in most Euphorbieae). The first staminate flower of each cluster is most commonly between the two halves, as illustrated by Schmidt (1907) and by Haber (1925), though it is often a


1


2
3
(1)


Fll. 20. The two hypothetical derivations of the staminate flower cluster. Circles represent staminate flowers, with size indicating order of flowering. The crescents represent bracteoles. A. central axis (b)istillate medicel): B. involucral hract. 1 . dichasial cluster such as found in Inthostema and Dichostemma: 2. the patterns of reduction involved in each hypothesis, dotted circles indicate suppressed flowers; 3. diagrams of the monochasial (above) and dichasial (below) hypotheses.
little more closely associated with one half or the other (as the primary flower in fig. 16 is markedly associated with the half on the left side of the illustration). The two branches from this primary staminate flower form, or closely simulate, much condensed monochasia. It is possible, as Schoute (1937) suggests, that the two separate sympodia of floral traces are merely the result of extreme condensation of a simple cincinnus. The vascular pattern alone, however, strongly supports the hypothesis of a dichasial nature for the staminate flower cluster of Euphorbia and Pedilanthus. Studies of Neoguillauminia, Calycopeplus and primitive species of Euphorbia will probably serve to clarify this controversy.

As Markowski (1912) has observed, the zygomorphy of Pedilanthus extends even to the staminate flower clusters, in that each of the two ventral clusters frequently has one less flower than does each of the three dorsal clusters. This tendency is especially striking in $P$. nodiflorus, in which the pistillate flower is markedly excentric and the ventral clusters of staminate flowers often have 2-3 less flowers each than the dorsal clusters. The staminate pedicels elongate greatly in development, so that the staminate flowers are exserted from the orifice of the involucral tube, as the anthers mature. The pedicels of the lower clusters curve and twist in such a way that each flower emerges from the top of the orifice, under the accessory involucral lobes, just before anthesis, pushing down the older flowers and being displaced itself after the pollen is shed. All anthers are oriented with the locules opening dorsally (with respect to the involucre). The pedicels are separated from the filaments by a transverse articulation and abscission layer, without trace of perianth, and with only slight thickening. The filaments are often differentiated from the pedicels by pubescence or color, but are structurally similar. It should be noted that the articulation in Anthostema and Dichostemma is directly beneath the rudimentary calyx, unlike the structure described by Nozeran (1953) for Dalechampia and some members of the Hippomaneae. There is surely no " pericladium" involved in the Euphorbieae, which do not fit well into the evolutionary (?) scheme offered by Nozeran (p. 114). The vascular trace of the filament ends with a clublike thickening in the connective, between the two halves
of the anther. The anther is of a normal four-locular type, becoming two-celled at maturity. Dehiscence is longitudinal and abaxial. The development of the anther in P. tithymaloides has been investigated by Banerji (1951). The tapetum is glandular, and the tapetal cells largely become binucleate, though quadrinucleate, and rarely trinucleate, cells are found. Meiosis is normal, the tetrads show a tetrahedral arrangement, and cytokinesis takes place by furrowing. The pollen grains are reportedly binucleate when shed.

Pollen Structure. - While Erdtman (1952) has devoted special attention to the pollen of the Euphorbiaceae, this large and interesting family is still imperfectly sampled, and the tribe Euphorbieae, in particular, has received only cursory attention from pollen students. The great interest in the identification of fossil pollen has led to the frequent adoption of methods designed to make pollen samples from living plants as much like the fossil pollen grains as possible. While this is necessary for the paleontologist, such methods obscure or destroy features of great interest to the botanist studying recent plants. In the present study, methods have been developed, largely by accident, which have proven quite satisfactory for Euphorbiaceous pollen. Details of exine structure are well shown by grains which are rendered transparent and expanded by treatment with sodium hydroxide and lactic acid. Since the latter has not proven satisfactory for permanent slides, Hoyer's mounting medium (Beeks, 1955) has been used. Raphide-like crystals are often formed in this medium, if it is improperly prepared, but pollen mounts are usable even when this occurs. The protoplast and intine are destroyed by sodium hydroxide, but their features may be seen in pollen preserved in FAA and treated with lactic acid. The protoplasts of fresh or dry pollen, or of pollen freshly killed in FAA, tend to swell excessively and obscure the features of the intine. Moderately good restoration of pollen from herbarium specimens may be obtained by storing the anthers in FAA.

In practice, the following schedule has given good results: 1. Two or more, usually six to ten, mature but unopened anthers are removed from preserved material and half of the sample set aside in a small vial of FAA. 2. The remaining anthers are placed in $6 \% \mathrm{NaOH}$ and heated in a paraffin oven for about six hours (a little longer may be required
for any inaperturate pollen types, and the large, inaperturate, "croton pattern" grains of Jatropha require about eight hours) . 3. The material from NaOH is washed in water, and the two portions of the sample combined and heated in $85 \%$ lactic acid in a boiling water bath for about ten minutes. 4. All the anthers are broken open on a slide in a large drop of Hoyer's medium. The larger fragments of the anthers may be removed under a dissecting microscope, if desired, before the coverslip is applied. The slide should be placed on the microscope lamp or other heat source for a few minutes, until the mounting medium has spread evenly under the coverslip.

The size of a pollen grain depends to a very great degree on the treatment which it has received. For this reason, measurements were taken from samples of pollen of $P$. Palmeri (all from one plant of Dressler 1064) which had been given a number of the different treatments used in the present study (Table 3). Similarly, at least one sample from each species, treated with NaOH and lactic acid, has been measured, and the average dimensions given in Table 4. Even though all samples were given similar treatment, some of the size differences may be due to differences in degree of expansion, and the size measurements, from so few samples, should only be taken to indicate the major trends in pollen grain size. In both tables, the averages represent thirty measurements where possible, and obviously shrunken or abnormal grains were not measured.

The pollen grains of most of the species are very much of the same type, though differing in details of wall thickness, coarseness of sculpturing and dimensions of furrows, furrow margins and pores. The predominant pollen type will be described first, and then the few markedly divergent species ( $P$. Finkii, P. tehuacanus and P. tomentellus) will be discussed. The terminology used is that of Faegri and Iverson (1950).

The grains are tricolporate (three furrows, each containing a pore) and, when shed, the three furrows are strongly plicate and folded inward, so that the grain is a footballshaped ellipsoid (Plate X-F), strongly three-lobed in equatorial section. In this form, very little of the structure can be observed. When the grain contacts an aqueous medium. the entire structure swells strongly, expanding the wall and

Table 3. Measurements of pollen from Pedilanthus Palmeri (Dressler 1064) after various methods of preparation. All measurements in microns.

TREATMENT POLAR AXIS EQUATORIAL DIAMETER

|  | range | average | range | average |
| :--- | :---: | :---: | :---: | :---: |
| NaOH and lactic acid | $72.5-89.8$ | 79.3 | $89.8-100.1$ | 94.4 |
| Lactic acid | $69.1-76.0$ | 73.3 | $85.2-93.2$ | 89.7 |
| NaOH | $71.4-80.6$ | 75.1 | $86.3-99.0$ | 91.6 |
| Mounted in Hoyer's | $68.0-73.7$ | 70.5 | $81.7-87.5$ | 85.3 |
| $\quad$from FAA (no treatment) |  |  |  |  |
| Acetylated, dry <br> Freshly shed pollen <br> $\quad$ mounted in oil | $66.8-81.7$ | 76.1 | $57.6-74.8$ | 66.4 |
| $\quad$ | $74.8-81.7$ | 79.1 | $51.8-61.0$ | 57.6 |

Table 4. Average dimensions (in microns) of pollen grains treated with NaOH and lactic acid. The measurement for $P$. Finkii represents the distance from furrow to opposite angle; the distance between angles averages 104 microns. In the inaperturate grain of $P$. tehuacanus poles and equator cannot be distinguished.

| SPECIES AND COLLECTION | Polar | equatorial |
| :---: | :---: | :---: |
|  | AXIS | diamete |
| P. Palmeri, D 1064 | 79.3 | 94.4 |
| P. Finkii, Thompson, s. n. | 64.7 | 96.6 |
| P. calcaratus, D 1067 | 59.6 | 71.5 |
| P. gracilis, Hinton 10973 | 60.1 | 68.1 |
| P. pulchellus, Conzatti, Reko \& Makrinius 3106 | 72.6 | 88.9 |
| P. coalcomanensis, Hinton 12685 | 68.7 | 79.8 |
| $P$.cymbiferus, D 1368 ca. | 92.0 | 105.1 |
| P. macrooarpus, D 1090 | 63.7 | 78.7 |
| Gentry 7677a | 65.2 | 73.5 |
| P. bractentus, D 978, northern Sinaloa | 79.1 | 96.7 |
| D 979 | 74.9 | 95.6 |
| D 1803 | 97.0 | 112.3 |
| $P$. tomentellus, Pringle 4912 | 73.3 | 82.7 |
| P. tehuacanus, D 1795 |  |  |
| P. nodiflorus, D 1362 | 72.8 | 91.4 |
| $P$. tithymaloides | 77.6 | 87.5 |
| SS1). tithymalordes, D 1376, Cuicatian, Oaxaca | 79.1 | 94.8 |
| Cutak, Isthmus of Tehuanteree | 82.6 | 103.8 |
| ssp. parasiticus, D 1807, <br> San Andrés Tuxtla, Veracruz | 71.0 | 82.4 |
| ssp. jamaicensis, Howard, <br> Four Mile Wood, Jamaica | 67.0 | 77.7 |
| ssp. angustifolius, Britton, <br> Cowell \& Brown 4607 | 55.0 | 67.6 |



Plate: X. Pollen structure. A. Pedilanthes c!mbijerus, cleared pollen grain: B $P$. rymbiferus, non cleared grain, which is broken open, showing the form of the jrotoplast: C. $I$. cllmbiferus, intact, non-cleared grain, showing the six hyaline intine thickenings; D. $P$. tehuacanus, cleared grain; E. $P$. Finkii, cleared grain; F. $P$. bracteatus, Dressler 979. freshly shed grain mounted in oil, showing the unexpanded condition: G. I'. calcaratus, cleared grain, sub-polar view, showing ends of the furrow and the pore; H. $I^{\prime}$. bracteatus, Dressler 979 , a thin section of the exine, showing the columellae in section and (especially below) the surface reticulum of the tectum, photographed by phase contrast. A - G magnification ca. i25, H. magnification ca. 1300 .
exposing the furrows and pores. In the fully expanded state the equatorial diameter of the pollen grain somewhat exceeds the polar axis, giving the grain a more or less flattened or oblate form. The expanded grains vary from large to very large (see Table 4). Each furrow (colpus) is fusiform in outline, tapering abruptly at each end of the pore, and attenuate to the blunt, or occasionally slightly bifid apex (Plate $\mathrm{X}-\mathrm{G}$ ). The furrows have distinct, narrow margins which are thinner than the remainder of the exine and have little or no sculpturing. These margins fold inward in the dry grain. The pores are distinct, large and oblong, occupying about one third to one half the length of the furrow, parallel to, and completely contained within, the furrow. Small irregular bits of exinous material or "opercula" sometimes occur on the pore, especially near the ends (usually absent after NaOH treatment).

The exine varies from about $3-3.5$ microns in thickness ( $P$. calcaratus) to about 5 microns ( $P$.cymbiferus), or even 6-7 microns ( $P$. bracteatus, Dressler 1803), in the thickest portion, midway between the furrows. The exine thins gradually and then abruptly to the finely or scarcely sculptured furrow margin. The inner,non-sculptured portion of the exine (endexine) is quite thin and inconspicuous. Thin sections (Plate X-H) show the sculptured portion (ektexine) to be composed of narrow, radial rods (columellae), whose uppermost portions are fused into a perforate reticulum (tectum), which gives the grains their characteristic surface texture.

The intine of Pedilanthus pollen shows distinct longitudinal thickenings, which, though characteristic of many Euphorbieae, seem never to have been described. These thickenings occur in three pairs which alternate with (or flank) the pores. The thickenings parallel the furrows, and are of about the same length as the furrows. In material treated with lactic acid, the thickenings are visible as hyaline depressions in the protoplast (Plate X-C). The protoplasts of grains treated as above retain their form when the exine is broken away; such a protoplast is shown in Plate X-B (this rigidity of the protoplast may only be the result of thorough fixation in FAA). The thickenings stain with fast green (as does the entire intine) and, in fresh material, stain rapidly and strongly with ruthenium red, probably
indicating that pectins or pectin-like compounds are present. When grains are broken and partly dissociated in microtoming, the intine thickenings usually separate from the protoplast, with the exine. These intine thickenings are different in location from those described by Hyde (1955, as "onci"), Bailey (1956) and others, in that they occur between, rather than beneath, the pores. It is possible that this pattern is derived, phylogenetically, from the more widespread condition of subporal thickenings. The thickenings are probably hygroscopic structures which aid in expanding the grain and opening the pores, when the grain is moistened. Intine thickenings of this general type (which may conveniently be termed "Euphorbioid intine thickenings") have been observed in Dichostemma, Anthostema, Elaeophorbia and Cubanthus, and in a number of species of Euphorbia (mostly woody or succulent) of the subgenera Esula, Euphorbia and Agaloma. Such a distribution strongly suggests that the pattern is primitive for the tribe. An apparently derivative pattern, in which two small latitudinal thickenings cross each furrow, one at each end of the pore, is found in some members of the subgenera Agaloma and Chamaesyce. Single, wider, interporal thickenings occur in some members of the Hippomaneae. A detailed study of pollen features, including intine thickenings, may greatly aid in an understanding and classification of the complex genus Euphorbia. The pattern of intine thickening in Pedilanthus differs from that in most Euphorbieae in that the two thickenings on each side of a pore are more widely separated from each other than the two between adjacent pores; that is, the sub-poral protrusions of the protoplast are wider than the inter-poral protrusions. The inter-poral protrusions sometimes fail to reach the pollen wall (especially when immature grains are prepared?), but the intine thickenings remain distinct in such cases. In Pedilanthus, the protoplast protrusions beneath the pores have slight "shoulders" on which the furrow margins rest when the grain is intact and expanded (Plate $\mathrm{X}-\mathrm{B})$.

The most aberrant pollen type within Pedilanthus is that of P. Finkii (Plate X-E). This is markedly triangular in equatorial outline, even when fully expanded, the furrows occurring on the sides of the triangle, between the blunt angles. The distance between adjacent angles (average

104 microns) is nearly a tenth greater than the distance between an angle and the opposite pore (average 96.6 mi crons). The grains are very markedly flattened in the polar dimension. The furrows of P. Finkii are narrowly elliptic, with no trace of a pore, and bear distinct, though irregular. "opercula" similar to those of other species, but better developed. The furrow margins, in strong contrast to those of the other species, are markedly thickened. These thick margins, unlike the "costa colpi" described by Faegri and Iversen (1950, p. 22) and Erdtman (1952, "crassimarginate grains"), are largely composed of ektexine and show distinct sculpturing similar to that of the remainder of the grain, though the endexine, too, appears to be thickened about the furrow. From the structure of these grains, it appears unlikely that any great volume changes could occur, such as regularly take place in the porate grains of other species. Intine thickenings occur, but are small and inconspicuous.

The pollen grains of $P$. tehuacanus are very strikingly different, in that they are completely inaperturate (Plate X-D). There are slight irregularities in the thickness of the exine, but no pores or furrows. Distinct intine thickenings occur, but these appear to follow no set pattern in their distribution. In texture and size, the grains of $P$. tehuacamus resemble those of $P$. tomentellus, which, also, are somewhat aberrant. A large percentage of the grains examined of this last species are shriveled, and evidently nonviable. Of those grains which expand normally, however, a large number lack pores, the furrows in these grains remaining narrow and unbroken. The appearance of the pollen strongly suggests that $P$. tomentellus is an abnormal, and perhaps hybrid, population.

Pistillate Flower. - The pistillate flower, which terminates the axis of the cyathium, is similar to that of Euphorbia. In several species, the terete pedicel elongates markedly and curves downward between the main involucral lobes, after anthesis, so that the ovary and styles are beneath the involucre and directed toward the peduncle when the staminate flowers mature. Self-pollination of a cyathium is thus effectively prevented. This does not occur, however, in $P$. pulchellus or $P$. coalcomanensis (and is variable in $P$. tithymaloides) ; in these two species the fruit develops within the involucral tube. A ring-like or very slightly lobed
"disk" occurs at the base of the ovary. This structure, totally lacking vascular tissue, is the only trace of a "calyx" to be found in the genus. Such a well-developed rudimentary perianth as that illustrated by Baillon (1858) or Michaelis (1924) has never been observed in the present study. Their drawings suggest material distorted by drying or rather crudely drawn. References to a distinct calyx in generic descriptions appear to stem from the inclusion in the genus Pedilanthus of Cubanthus, which does have a small but distinct calyx.

The ovary is of the structure typical for most of the Euphorbiaceae: a three-locular, three-carpellate syncarp with axile placentae, restricted to the upper part of the ovary. The three to five small central traces of the peduncle divide so as to form nine traces in the upper pedicel, three outer single strands and three alternating, inner pairs. The outer traces form the dorsal carpel traces, which are continuous through the style. These traces bear small lateral branches which anastomose through the carpel wall and converge between the dorsal traces at about the level of the placentae, where they pass inward through the septae to join with the ventral carpel traces. These lateral branches form a network which becomes more prominent as the fruit enlarges. The paired ventral traces from adjacent carpels pass upward through the axis of the ovary to just below the level of the placentae, where the pairs diverge. The diverging ventral trace pairs each fuse and terminate in the upper septae, where they merge with the lateral branches from the dorsal traces. One or two small strands may (but often do not) arise from each such plexus and pass through the style, alternating with the dorsal carpel traces, and usually closer to the center of the style. A small vascular strand arises from each ventral trace of a carpel, shortly above the point where the trace pairs diverge and the two fuse to form the vascular supply of the anatropous, pendulous ovule. This strand terminates in a radiating, spoke-like disk at the chalaza. The styles are elongate and nearly completely connate, and the three stigmas are each bifid. The dorsal carpel traces each divide into two to vascularize the stigmas, and this division may, in some cases, occur near the base of the style. The compound style is solid, with a central core or dense, collenchyma-like "stigmatoid tissue." Irregular
vascular bundles are often formed about this central core. These bundles may connect with the outer traces below or may end blindly.

The embryology of $P$. tithymaloides has been studied by Arnoldi (1912), Markowski (1912) and Banerji (1951). The ovules are bitegmic, the inner integument being formed first; the outer integument is formed soon after the inner and grows rapidly, covering the nucellus by the megaspore mother-cell stage. The outer integument is about four cells thick, except about the micropyle, where it is thicker. The inner integument is relatively thick, being about $8-10$ cell layers in thickness. Both integuments take part in the formation of the micropyle, which is relatively wide. The nucellus is relatively massive and more or less pointed; the beak projects into, but not through, the micropyle. The outermost layer of beak cells is somewhat elongated (markedly so in $P$. tithymaloides and $P$. nodiflorus, less so in $P$. cymbiferus and $P$. calcaratus). There is a single archesporial cell, which cuts off a parietal cell before functioning as megaspore mother-cell. Reduction division is normal, resulting in a linear tetrad (only three cells are formed, according to Markowski). The embryo-sac development follows the normal or "Polygonum" pattern. The antipodals are small and ephemeral, as in a number of Euphorbiaceae. The development of the embryo has not been studied. The early development of the endosperm follows the "nuclear" pattern.

Obturator and Caruncle. - The obturator, a characteristic feature of the family, arises from the placenta, above the ovule, at an early stage in ovule development. At the time of pollination, it forms a prominent mass of matted, elongate, almost mycelium-like cells which cap the micropylar end of the ovule. The cells of the obturator penetrate the micropyle and contact the beak of the nucellus. The obturator is continuous above with the stigmatoid tissue of the style and is thought to provide a pathway to the nucellus for the pollen tube. The obturator is representative of the type " $I$ " described by Schweiger (1905, p. 375), thus agreeing with Euphorbia. The cells of the obturator often contain starch grains. Soon after pollination, the obturator declines and is supplanted from beneath by a proliferation of the funiculus, the caruncle. This parenchymatous structure caps the seed (much as the obturator caps the ovule) until very late in
seed development. In Pedilanthus the caruncle remains firmly associated with the placental region, and, at maturity, shrivels and remains on the columella when the seed is shed. Here, the caruncle appears to have a nutritive function in seed development. In those species of Euphorbia with a well developed caruncle on the mature seed, the caruncle is reported to develop from the outer integument, rather than the funiculus (Schweiger, 1905) ; in Pedilanthus, the outer rim of the integument, at least, makes at most a negligible contribution to the caruncle, if the structure here described may be included under that term. It is interesting to note that the caruncle is often (perhaps always) well developed in all three locules, even when one ovule aborts from nonfertilization or other reason.

Fruit and Seed. - The fruit of most species of Pedilanthus is a capsule of the sort characteristic for the family: a septicidal and loculicidal capsule which dehisces explosively, throwing the seeds with surprising force, and leaving a three-angled or three-winged, more or less clavate, central axis, the columella. The endocarp of the fruit wall becomes woody with age and is so constructed that strong, twisting tensions are set up in drying. At maturity the largely parenchymatous exocarp shrinks and finally ruptures along the lines of dehiscence. The carpels split dorsally along the mid-vein and ventrally near the lateral traces, which remain in the columella. The septae split down to the columella. The columella is basally slender and slightly three-winged or angled (from the ventral portions of the three septae), and distally abruptly expanded (paralleling the diverging ventral carpel traces), where the three septal wings alternate with the persistent funicular "caruncles." A careful study of the anatomy and mechanism of dehiscence in the Euphorbia fruit would be of very great interest. Pedilanthus macrocarpus is anomalous in that the fruit is corky and indehiscent. The endocarp is thin and papery and the exocarp thick and spongy. What the function of this structure may be - to float during flash-floods, to hold moisture during germination, or some other - is not known.

The seeds of Pedilanthus are more or less ovoid in form. The hilum is subterminal and roughly elliptical. The raphe, extending ventrally from the hilum to the chalaza, is quite prominent. No caruncle is present on the mature seed. The
seed coat, whose structure has not been investigated, is either smooth or finely tuberculate. Endosperm is abundant and the embryo is straight, with plane cotyledons which are somewhat fleshy.

Cytology. - The meiotic chromosomes of several taxa have been examined, and the haploid chromosome number determined. The chromosomes are relatively small (see Perry, 194:3, for comparison with other Euphorbiucene), but can often be counted with some confidence at diakinesis or metaphase I. At other stages they are much more difficult to count. The chromosome numbers, so far as determined, are given in Table 5.

## TAble 5. Chromosome Numbers in Pedilintutes.

Species and collection
P. Palmeri, D 1064
P. calcaratus, D 1067
P. macrocarpus, D 1090
P. bracteatus, D 978
P. nodiflome D) 979
P. nodiflorus, D 1809

Haploid number
16 16
$P$ 17?
17
$P$. tithymaloides
ssp. tithymuloides, Cutak, Isthmus of Tehuantepeec
17
D 1366, cult., San Andrés Tuxtla, Veracruz 17
D 1378, Tomellín Canyon, Oaxaca 17
ssp. Smullii, cult., Harvard Biolngical Laboratories 17
"P. tithymaloides." cult., We
(Banerji, 19.).1)
"P. tithymuloides." cult., Florida (Perry, 194:3)

$$
\begin{equation*}
2 \mathrm{~N}=36 \tag{18}
\end{equation*}
$$

The data in the above table indicate that there is an aneuploid series within Pedilanthus. Perry (1943) has shown that the subgenera Agaloma, Chamaesyce and Poinsettia, of Euphorbia, all have a basic chromosome number of seven (without aneuploidy, though this is clearly found in the subgenus Esula). It may be suggested that Pedilanthus was derived from a tetraploid member of Euphorbia, subgenus Agaloma, with $n=14$, but more counts are needed in both genera, especially from the woody members. Whatever the primitive base number, there is clearly no basis for considering it to be 9 , as did Darlington and Wylie (19.5), on the basis of the counts of Perry and Banerji. There appears to be variation within $P$. tithymaloides, and it is unfortunate that the exact origin and nature of the plants studied by Perry
and Banerji are not known (they might be P.t. ssp. Smallii, or possibly P.t. ssp. parasiticus). In one preparation of $P . t$. ssp. tithymaloides (Dressler 1366) a single telophase II was found in which the chromosomes of all four daughter cells were easily counted. In this instance, unequal division had occurred, and while two of the cells each contained 17 chromosomes, the remaining cells showed 16 and 18 , respectively.


Fig. 21. Chromosomes of Pedilanthus. A. P. t. subsp. tith?/maloides (Cutak, Isthmus of Tehuantepec), diakinesis, showing 17 pairs of chromosomes; $n$ : nucleolus; B. P. bracteatus, Dressler 979, at metaphase 1, note that in each case one chromosome pair is markedly larger than all others, magnification ca. 1440.
This isolated case of imbalance may, however, be without great significance, as it is thought that simple reduplication of a chromosome pair is unlikely to result in a stable, increased basic number (Stebbins, 1950). No mitotic chromosomes have been examined in the present study, and little can be said concerning chromosome morphology. In the meiotic preparations, however, there appears to be some size variation and one chromosome pair usually appears much larger than the others, in all the species studied.

## PART III. DISTRIBUTION AND EVOLUTION

## Local Distribution

Most populations of Pedilanthus are characteristically local and discontinuous. Though the plants are numerous, where found, they are rarely frequent over an extensive area.

The only exception, which I have observed, is the extensive occurrence of $P$. tithymaloides in the Isthmus of Tehuantepec, Oaxaca, Mexico. There the plants are frequent along the highway for many kilometers, in arid tropical scrub. Elsewhere, Pedilanthus appears to be local in distribution, even when the vegetation type is relatively constant over a large area. While an adequate explanation of this tendency to local distribution is not available, the significance of such a discontinuous and localized population structure for evolutionary processes is generally recognized.

Soil type may be important in determining the occurrence of Pedilanthus. Several of the species, at least, are markedly calciphilous. Pedilanthus cymbiferus, $P$. nodiflorus and probably P. tehuacanus, seem to be restricted to calcareous regions; $P$. calcaratus, $P$. bracteatus and $P$. tithymaloides have all been observed on limestone outcroppings, but are not clearly limited to such areas. The last species (P.t. ssp. angustifolius) has been reported on serpentine soil in Puerto Rico (Wheeler, Cutak and White, 1944). Observations are lacking or inconclusive for the remaining species.

The different species of Pedilanthus are to be found in rather diverse habitats, as might be expected from the varied vegetative features. A few species are mesophytic or include mesophytic populations. Several are more or less markedly xerophytic. The degree of xeric adaptation rather closely parallels the environment or environments in which a species is to be found. In Table 6 the vegetation types in which Pedilanthus is found are considered as a spectrum, ranging from tropical evergreen forest to cactus desert. The terminology is that of Leopold (1950), though in the present paper applied to broad vegetation types, rather than to geographic zones. These vegetation types do, in fact, intergrade, and the distinctions may at times be difficult or meaningless. It will be seen that the species do have characteristic ranges in habitat, the more widespread and variable species often ranging into two vegetation types, and the very widespread $P$. tithymaloides occurring in a wide range of habitats. Pedilanthus calcaratus occurs on rocky, well-drained sites when in the more mesic forest types ; $P$. macrocarpus is to be found only in the drier, more open types of thorn scrub; and $P$. bracteatus in those types which approach thorn forest. Some of the habitats are shown in Plates XI and XII.


Plate XI. Habitats of Pedilanthus. Fig. :3!. Tropical deciduous forest on the road to El Sumidero, Tuxtla Gutiérrez, Chiapas, September, Elev. ca. $1,000 \mathrm{~m}$. Both $I^{\prime}$. calcaratus and $I$. t. ssp. tithymaloides occur at this site, the former ranging upward into wetter sites at about $1,300 \mathrm{~m}$, elevation. Fig. 23. Tomellin Canyon, near Tomellín, Oaxaca, July; arid thorn forest, approaching cactus desert. Pedilanthus t. ssp. tithymaloides is locally abundant.


Plate XII. Habitats of Pedilanthus. Fig. 24. Thorn forest near Sisal, Yucatan, Sentember, near sea level; the habitat of $P$. nodiflorus. Fig. 2.5. Desert near Tehuacán, Puebla, September; P. cymbiferus forms extensive colonies in the foreground (arrow).

Table 6. Habitats occupied by different species of Pedilanthus. Information is scanty or circumstantial for those species marked with a query.

| [ | Tropical evergreen forest | Tropical deciduous forest | Thorn forest | Arid tropical scrub | Desert |
| :---: | :---: | :---: | :---: | :---: | :---: |
| P. Palmeri |  |  |  |  |  |
| P. Finkii | - |  |  |  |  |
| P. calcaratus |  | - |  |  |  |
| P. gracilis |  | -?- |  |  |  |
| P. coalcomanensis |  | -?- |  |  |  |
| P. pulchellus | -?- |  |  |  |  |
| $P$. cymbiferus |  |  |  |  |  |
| P. macrocarpus |  |  |  | - |  |
| $P$. bracteatus |  |  |  |  |  |
| $P$. tomentellus |  |  | -?- |  |  |
| P. tehuacanus |  |  |  | -?- |  |
| $P$. nodiflorus |  |  |  |  |  |
| P. tithymaloides |  |  |  |  |  |
|  |  | I |  |  |  |

## Photoperiod

Most species of Pedilanthus flower in the winter and are markedly "short-day" plants, but there are several exceptions to this generality. As far as known, $P$. cymbiferus, $P$. tehuacanus and $P$. nodiflorus are all summer flowering species. Some populations of $P$. bracteatus are summer flowering (Taxco, Guerrero, but not the nearby Iguala collection),
and plants from other areas (northern Sinaloa) flower irregularly in cultivation. Pedilanthus macrocarpus appears to be largely winter flowering in nature, but flowers in spring and summer when cultivated in Massachusetts. The northernmost and westernmost Mexican populations of $P$. tithymaloides flower in summer, and the plants in Tomellín Canyon, Oaxaca, flower sporadically during August (but much less, apparently, than in the winter). This species is also variable as to flowering season in other areas. There seems to be a tendency for the plants of more arid habitats (as $P$. cymbiferus, etc.) to flower in the summer. Pedilanthus macrocarpus is an exception to this trend. The areas in which summer flowering is predominant may be those in which hummingbirds are of seasonal occurrence.

The photoperiodic response of Pedilanthus was unexpectedly demonstrated in the winter of $1955-56$, when cultivated plants of P. Palmeri, P. calcaratus and P. tithymaloides were beginning to flower. The lighting system in the greenhouse was (anonymously and apparently inadvertently) reset for long-day. This was first evidenced by a complete cessation of flowering in the first two species and continued abortion of young cyathia of the last. When the condition was discovered and corrected, P. tithymaloides proceeded to flower normally, but no flower primordia remained on the other species, and the expected cytological material was not available. In September when plants on an adjoining bench were given a lengthened day, $P$. nodiflorus reacted in the same manner as had $P$. tithymaloides; involucre primordia continued to differentiate, but the young cyathia aborted.

## Geographic Distribution

Pedilanthus is characteristically a Mexican genus. Only one species, the problematical $P$. Millspaughii, is found entirely outside of Mexico; two species, $P$. calcaratus and $P$. nodiflorus, range south to Guatemala and Honduras, respectively; and $P$. tithymaloides ranges widely in Caribbean America (with one poorly known form in the Amazon basin). Several species appear to have very restricted ranges, but this is by no means always the case. Pedilanthus tithymaloides is, as noted above, very wide-ranging; $P$. calcaratus and
$P$. bracteatus have wide ranges and $P$. Palmeri and $P$. macrocarpus also occur over relatively large areas. Pedilanthus Finkii, P. cymbiferus, P. tomentellus and $P$. nodiflorus, on the other hand, seem to have rather restricted ranges, and the remaining species are known only from the type localities. It is probable that further collecting will show all of the species to be less local than present knowledge implies. Note, for example, the wide range of P. Palmeri, which was described as recently as 1913. Its range is largely known through the collections of George B. Hinton.

Though the species of Pedilanthus are usually quite distinctive, sympatric species are unusual and seem to occur only very rarely within the species groups. Pedilanthus calcaratus and P. tithymaloides, which are in quite different species groups, have been found together in tropical deciduous forest in Chiapas (see fig. 22). Pedilanthus Palmeri and $P$. calcaratus, $P$. Finkii and $P$. calcaratus, $P$. calcaratus and $F$. pulchellus (found together, to judge from the mixture in Conzatti, Reko and Makrinius 3106), P. cymbiferus and $P$. tehuacanus; P. bracteatus and $P$. tithymaloides, and (if $P$. tithymaloides is native in coastal Yucatan) P. nodiflorus and $P$. tithymaloides are all pairs of species that occur in the same regions, but are not known to share the same habitats. Similarly, the ends of the $P$. tithymaloides circle of subspecies overlap in the West Indies, but there is no evidence that these broadly sympatric taxa actually occur together in the same habitat.

As noted above, the genus is essentially Mexican. There is no reason to doubt that the genus evolved in tropical Mexico, its present center of diversity. While its "center of origin" cannot be more exactly determined, it is interesting that the greatest number of species is to be found in western Mexico. Furthermore, in four of the five species groups, the least specialized species are to be found in western Mexico: P. Palmeri, P. gracilis, P. coalcomanensis, $P$. pulchellus and $P$. bracteatus. In the remaining species group, both species are rather specialized. These two species, $P$. nodiflorus and $P$. tithymaloides, seem to be more markedly Central American in distribution, though the latter is widespread in Mexico, as well. Pedilanthus is probably a recent invader in South America, having arrived in the late Tertiary, with the reestablishment of land connections with

North America. The development of the semi-arid corridor across northern South America probably facilitated the spread of P. tithymaloides in that continent. The dispersal and evolution of this species will be discussed in greater detail in later paragraphs.

## Biotic Relationships

The ecological relationships between Pedilanthus and other organisms are scarcely known, though one phase of these relationships, the pollination pattern, is probably of basic importance to the evolution of the genus. Several cases have been observed of arthropods living on or in Pedilanthus. The population of P. bracteatus near Taxco, Guerrero, is extensively affected by a lepidopteran whose larvae feed in the cyathia and developing fruit. When a larva infests an involucre, the staminate flowers, and sometimes the glands of the spur, are eaten. Many involucres are thus emasculated; nevertheless, a large proportion of the capsules develop. The damage caused by destroying the developing seed is probably more directly deleterious to the Pedilanthus population. Damage from similar infestations of the involucre has been noted occasionally in herbarium material of $P$. macrocarpus and rather frequently in $P$. tithymaloides ssp. padifolius. In P. nodiflorus one case was observed in which a lepidopteran larva (Phycitidae) had bound several involucres together with a web and was feeding on these involucres.

Smaller organisms, notably thrips (Thysanura) and mites (Acarina), often find the involucres both a secure haven and an abundant source of food. Both are occasionally found as dried and broken bodies in herbarium specimens, and they are probably to be expected in all or most species. They are usually in the involucral tube, among the staminate flowers and bracteoles, and only rarely in the spur. Thrips of the genus Frankliniella (in the tritici-cephalica complex) were found to be abundant in $P$. cymbiferus (Dressler 1368), $P$. bracteatus (Dressler 1803) and P. tithymaloides (Dressler 1378), while mites (Phytoseiidae) were recovered from $P$. bracteatus (Dressler 1803), P. nodiflorus (Dressler 1362) and $P$. tithymaloides (Dressler 1378). Ants visit the involucres of Pedilanthus, apparently seeking the nectar exuding
from the spurs. In a few cases dried ants (Monomorium and Solenopsis) have been found in the spurs of herbarium specimens of $P$. calcaratus and $P$. tithymaloides. Two or more genera of ants were observed on the involucres of $P$. cymbiferus at Tehuacán (Dressler 1368; unfortunately the collected specimens found their way into the museum without their identity having been recorded). Pedilanthus nodiflorus, with its exposed lateral glands, seems especially attractive to ants. Specimens of Campanotus (subgenus Myrmobrachys), Monomorium, Crematogaster, and Ectotoma tuberculatum Olivier were collected on the involucres of this species near Progreso, Yucatan (on Dressler 1362), and a fifth ant, seen but not collected, appeared to be a Pseudomyr$m e x$. The involucres, especially of $P$. calcaratus, are frequently chewed between and at the bases of the spur lobes or at the spur apex, indicating that short-tongued and chewing insects often seek the protected nectar.

An infectious disease of Pedilanthus has appeared in the author's greenhouse collections. This is manifested as a localized stem-rot in P. tithymaloides ssp. Smallii and causes severe damage to plants of that taxon. Similar but less severe symptoms occur in other forms of $P$. tithymaloides, $P$. bracteatus and $P$. macrocarpus. A deformation of young leaves, which may be due to the same infection, has been noted in $P$. calcaratus and $P$. bracteatus. Nothing is known of the origin or causative agent of this infection.

## Pollination

Although direct evidence is scanty, Pedilanthus is generally considered to be a hummingbird "flower." Porsch (1923) discusses this at some length, and cites the observation by Cammerloher of an Old World honeybird visiting cultivated $P$. bracteatus. Porsch gives the color (red in either bract or involucre, of nearly all species), lack of scent, abundance of nectar, lack of "Sitzfläche" or landing surface for insects, and the strength of the spur lobes (only a relatively large animal could insert its mouthparts into the spur), as evidence that Pedilanthus is adapted for bird pollination. It has, in recent years, been shown that hummingbirds seem to have no "preference" for red over other colors (Wagner, 1946 ; Bené, 1947), in spite of the observations of Porsch,

Pickens (1951) and others that red is the predominant color among bird flowers. The two groups of data are by no means in conflict. Red is complementary to green, contrasts strongly with the green background of vegetation, and should give a strong selective advantage in a species pollinated by an organism capable of detecting the red wave lengths, even though the pollinating agent may have no true color preference.

There are now available two records of hummingbirds visiting Pedilanthus under natural conditions. George R. Proctor has noted (Proctor 3418, in collection data) that $P$. tithymaloides is visited by hummingbirds on Isla de Providencia (in the Caribbean, ca. 270 km . east of Nicaragua). The only hummingbird reported from this island is Anthracothorax prevostii hendersoni (Cory), and is said to be common there (Bond, 1950). Ivan M. Johnston has observed hummingbirds visiting $P$. macrocarpus in Baja California (personal communication). Even with these two records, the greater part of the evidence is morphological and circumstantial. Pedilanthus fails to set seed in greenhouse culture unless hand pollinated, and it is difficult to see how any organisms other than birds (or possibly hawk moths) could account for the high percentage of seed-set in nature. Bees and other fairly large insects might profitably visit the involucres when the gland-chambers overflow, or bite into the spur, but pollination would only occasionally be effected. Hummingbirds, on the other hand, would have to approach the involucre from the front to insert their beaks into the gland-chamber, thus assuring that either the chin or the lower mandible would touch the stigmas or anthers, which successively occupy the same position relative to the involucre. For most species of the genus it is a reasonable, if not inescapable, hypothesis that they are pollinated by birds and that this relationship has strongly oriented the evolution of the genus.

The poorly known P. tehuacanus is an exception to the generalities of size, color and form which hold for the remainder of the genus. The bracts and involucre are green, the spur lobes do not snugly enclose the gland-chamber, the style is short and bent back toward the gland-chamber, and the staminate flowers are only shortly exserted. It seems most likely that it is pollinated by short-tongued insects.

The structure of $P$. nodiflorus is somewhat puzzling as to its adaptive significance. Its form is such that it could be quite efficiently pollinated by hummingbirds, but the small, exposed lateral glands would seem to have no direct part in this relationship. They might possible serve to attract shorttongued insects, such as bees and flies (or to keep them from biting through the spur), that could provide a secondary and less dependable means of pollination, which might nevertheless have some selective advantage. The small ants that have been observed on the cyathia are not likely to be effective in pollination. It would seem that such small insects could scarcely serve any function for the plant species.

## Generic Relationships

From its first botanical recognition, Pedilanthus has been considered a close ally, if not a member, of the Linnaean genus Euphorbia, but its relationships within that large and complex assemblage have received little consideration. There is no evidence to support the imaginative hypothesis of Croizat (1940-1942), which would derive the Euphorbieae from Dalechampia or a similar type, through Pedilanthus. Since a convenient summary of the Euphorbieae is not available, it may be useful to present such a summary here, in so far as this is presently possible.

## Synopsis of the Euphorbieae

1. Dichostemma Pierre: West Africa, 1 sp.; woody, involucre 4merous, glands large, between the staminate flower clusters, bracts within the involucre well developed and distinct, both staminate and pistillate flowers calyculate, cyathia often unisexual.
2. Anthostema A. Jussieu: West Africa and Madagascar, ca. 3 spp.; similar to no. 1, but involucre open on one side (through a gland), and bisexual.
3. Neoguillauminia Croizat: New Caledonia, 1 sp.; woody, involucre 5 -merous, involucral lobes enlarged and petaloid, glands large, in pairs between the staminate flower clusters, bracts within involucre well developed and distinct, pistillate flower calyculate.
4. Calycopeplus Planchon: Australia, 3-4 sp.; ephedroid shrubs with small, caducous leaves, involucre small, mostly 4 -merous, glands between and slightly within involucral lobes, bracts within involucre moderately well developed, pistillate flower calyculate.
5. Euphorbia L.: Cosmopolitan, but poorly developed in cooler regions, over 1,000 species; woody, succulent or herbaceous, involucre usually 5 -merous, glands between involucral lobes, usually distinct,
bracts within involucre (bracteoles) reduced, pistillate calyx small or absent. The numbers of species given for the subgenera (which follow Wheeler, 1943) are only crude approximations. Some obvious revision is needed, but would be out of place in the present work.

5a. subgenus Esula Pers.: largely Old World, ca. 375 spp.; diverse woody and herbaceous species without petaloid appendages on the glands, pistillate calyx sometimes present; includes the most primitive members of the genus (section Balsamis Webb. and Berthelot and § Laurifoliae Boiss.)

5b. subgenus Lyciopsis (Boiss.) L. C. Wheeler: African shrubs, ca. 10 spp .

5c. subgenus Eremophyton (Boiss.) L. C. Wheeler: Old World shrubs or herbs, ca. 10 spp.

5d. subgenus Euphorbia: Old World succulents, ca. 275 spp., a polyphyletic groun of at least four component phyla.

5e. subgenus Agaloma (Raf.) House: American, ca. 130 spp. ; woody, herbaceous, and a few succulent spp., glands with petaloid appendages, these sometimes reduced, pistillate calyx sometimes present.

5f. subgenus Chamaesyce Raf.: Cosmopolitan, probably of American origin, ca. 220 spp. ; a characteristic sympodial habit of growth in most species, glands with petaloid appendages, or these reduced; closely related to subgenus Agaloma.

5g. subgenus Poinsettia (Grah.) House: American, 8-10 spp.; woody or herbaceous, glands cup-like, often only one on each involucre; related to subgenus Agaloma.
6. Elaeophorbia Stapf: Africa, ca. 4 spp.; woody or semi-succulent trees, ovary sessile and fruit a drupe; similar to some members of Euphorbia, subgenus Euphorbia (sensu stricto).
7. Synadenium Boissier: Africa, ca. 15 spp.; woody or semi-succulent shrubs, involucral glands united into a ring.
8. Monadenium Pax: Africa, ca. 30 spp.; succulent or subherbaceous, glands united into an incomplete ring, which overtops the involucral lobes; apparently related to Synadenium.
9. Cubanthus (Boiss.) Millsp.: West Indies, 5 spp.; woody, glands two, united into a shield-like structure, pistillate flower calyculate.
10. Pedilanthus Necker: American, 14 spp .; woody or succulent, glands appendaged, the appendages forming a spur, involucral lobes unequal.

The petaloid appendages of the glands (spur lobes) of Pedilanthus, alone, clearly indicate that the Euphorbia ancestor of the genus would, if living, be assigned to the subgenus Agaloma. The woody habit of Pedilanthus, glandlike stipules, ecarunculate seeds (when mature), and small chromosomes are further characters shared with Euphorbia subgenus Agaloma. These features are also shared, in part, with the subgenera Poinsettia and Chamaesyce, but these subgenera could not, on morphological grounds, be as closely related or ancestral to Pedilanthus. The features which are clearly primitive or universal in Pedilanthus and might be
expected in its immediate ancestors are: woody habit; alternate, and possibly distichous, leaves ; small, conic, glandlike stipules; dichotomous, terminal or upper axillary, inflorescence; four red petaloid appendages on the involucre; primitive pollen with "euphorbioid" pattern of intine thickenings and moderately thick, reticulate exine. These features are not to be found in combination in any living Euphorbia, but all may be found in different species of the subgenus Agaloma.

> Table 7. A comparison of Pedilanthus and Cubanthus.

## Pedilanthus

1. Vessels never strictly scalariform pitted with slit-like pits.
2. Leaves distichous and distant.
3. Stipules small, gland-like.
4. Cymes dichotomous, terminal or axillary.
5. Involucral lobes unequal, partly free.
6. Glands two to six, free, appendaged and concealed by the appendages (spur).
7. Pollen: Intine thickenings closer between furrows than beneath furrows; furrows opening widely when grains are expanded, exposing pores.
8. Pistillate flower naked.
9. Haploid chromosome numbers 16, 17, 18.

## Cubanthus

1. Vessels strictly scalariform pitted with slit-like pits.
2. Leaves closely spiraled.
3. Stipules none.
4. Cymes pseudo-umbellate, densely crowded at stem apex.
5. Involucral lobes equal, completely connate.
6. Glands two, completely connate into a shield-like structure, without appendages.
7. Intine thickenings closer beneath furrows than between furrows: furrows narrow, not opening widely when grains are expanded.
8. Pistillate flower with a small calyx.
9. Haploid chromosome number 20.

Certain infrequently collected West Indian plants with spiral leaves, urn-shaped involucres, shield-like glands, and other distinctive features have been placed in Pedilanthus, as members of the section Cubanthus Boissier. Millspaugh elevated this group to generic rank in 1913, and a careful examination of the material shows this action to be well justified. The members of Cubanthus are not directly related to Pedilanthus, but have been derived from Euphorbia subgenus Esula (§ Laurifoliae), mainly through the connation of the non-appendaged glands. Relatively closely related species of Euphorbia, especially E. gymnonota Ur-
ban, are to be found in the West Indies. A partial comparison of Pedilanthus and Cubanthus is given in Table 7. In most of the features enumerated, Cubanthus agrees closely with the woody Antillean members of Euphorbia subgenus Esula.

## Species Relationships

The species of Pedilanthus fall into five fairly discrete species groups. These groups and their affinities are diagrammatically shown in figure 26. Some of the characters that vary within the genus and their specific distribution are shown in Table 8.

1. P. Palmeri group (species 1-2). These two species are closely allied by habit, inflorescence, prominent lateral spurlobes, and involucral texture. They are very similar in most


Fig. 26. Species relationships in Pedilanthus. The reticulate relationships between the species groups are shown by dotted lines.
features, but strikingly different in spur form. The group seems to be allied with the next group, because of broad spur lobes, habital and seed resemblances, and some degree of interfertility (see under Hybridization), but shows no close resemblances to the other groups.
2. P. calcaratus group (species $3-4$ ). These species are obviously quite closely related, and, as now known, differ mainly in proportion and aspect. They are related to the above group and to the $P$.cymbiferus group on the basis of seed and internal indument of the involucre. The keeled spur lobe suture, the thickened spur lobes and the aspect of the involucre suggest a less close relationship to the $P$. bracteatus group, especially to P. macrocarpus.
3. P. cymbiferus group (species 5-7). The form and structure of the involucre, as well as the non-elongating pistillate pedicel (of 2 species), and anatomical features tie these species into a very "natural" group. Aside from the resemblances to the $P$. calcaratus group (above), this assemblage shows affinity with the $P$. bracteatus group (especially through $P$. coalcomanensis) and to the $P$. tithymaloides group (especially through P. pulchellus). Features indicating an alliance with the first group are: wide cyme bracts, the branching of the cymes (nearly in one plane), the pilose staminate flowers, the texture and indument of the plant (these features approach $P$. bracteatus especially), and the spur partitions (like those of $P$. macrocarpus). The non-elongating pistillate pedicel, partial spur partitions, and truncate spurs sometimes found in $P$. tithymaloides, the indument (external and internal) of the $P$. nodiflorus involucre, as well as less definable textural resemblances, seem to indicate a relationship between the $P$. cymbiferus and $P$. tithymaloides groups.
4. P. bracteatus group (species 8-11). Pedilanthus bracteatus, $P$. tomentellus and $P$. tehuacanus are closely allied by resemblances of the plant, cyme, involucre and seed, as well as the unique yellow latex. If only the Sonoran and Sinaloan populations of $P$. macrocarpus were known, it probably would be placed in a separate species "group" of puzzling affinity. The peripheral, and presumably primitive, populations of Baja California closely resemble P. bracteatus in nearly all features. The apparent interfertility between the two species (see Hybridization) confirms this relationship.

Table 8. The distribution of certain features in Pedilanthus. $x$, present throughout the species; -, present in part of the species.
P. Palmeri
P. Finkii
P. colcaratus
P. gracilis
P. pulchellus
P. coalcomanensis
$P$. cymbiferis
P. macrocarpus
P. bracteatus
P. tomentellus
P. tehwacanus
P. nodiflomes
P. tithymaloides


The moderate resemblance between $P$. tehuacanus and $P$. nodiflorus is thought to be superficial, resulting from the parallel development of very short spurs and reduced leaves; in most characters they are quite different. There seems, however, to be a distinct affinity between the two species groups, especially because of the similarly formed accessory involucral lobes. These two species groups also share stem succulence, similar anatomical features (especially in the wood) and the same chromosome number.
5. P. tithymaloides group (species 12-13). This group is apparently related to groups 3 and 4 , as discussed above. It cannot be definitely shown that these two species are properly placed together. The involucres, however, are very similar in form, and anatomical, cytological and other observed features do not contradict this relationship.

## Hybridization

Only a limited number of cross-pollinations have been attempted with the greenhouse cultures of Pedilanthus. Dif-
ferences in flowering time and the small number of cyathia produced have limited the possibilities. The genus is further unsatisfactory for experimental hybridization in that only three ovules can develop from one pollination. Self-pollination and cross-pollination within a species usually meet with easy success. Pedilanthus tithymaloides has given somewhat erratic results and little can be said concerning its fertility relationships without more material and further tests. At present, one successful cross within a species group and one cross between closely allied species groups have been made in the greenhouse, and a putative hybrid between the same two species groups is represented by very poor herbarium material. Crosses which have been attempted without success are: P. Palmeri x bracteatus, P. calcaratus x bracteatus, $P$. calcaratus x tithymaloides, and $P$. nodiflorus x tithymaloides. In each case, only very few pollinations have been attempted (with reciprocal pollination, when possible), and these negative results cannot be given much weight. Known and putative hybrids are discussed below.

1. P. Palmeri x calcaratus. Pedilanthus Palmeri (Dressler 1064 ) set seed readily when pollinated with pollen of $P$. calcaratus (Dressler 1067), though the reciprocal failed. The seeds germinated well and four seedlings have now completed two seasons of normal growth. The leaves of the seedlings have a soft pubescence on the underside, which is lacking in the maternal parent, but are not otherwise markedly different from those of either parent. Two of the seedlings have recently flowered, and the proportions of the involucres are quite intermediate between those of the parent types, leaving no doubt of their hybrid nature. Even the position of the cyathium is intermediate: the peduncles twist about $90^{\circ}$ so that the spur projects horizontally. Microscopic examination shows about 45 percent of the pollen to be abortive. No crosses involving these hybrids have yet been attempted.
2. $P$. macrocarpus $\times$ bracteatus. A single cyathium of $P$. macrocarpus (Dressler 1090) was pollinated with pollen of P. bracteatus (Dressler 978). All three ovules developed and the seed germinated normally, the cotyledons being intermediate in width between the parent types. Two of the seedlings were lost through damping-off and slug damage. The remaining plant has grown for five years, and showed signs of flower initiation in the fall of 1956, though the
primordia all aborted. Its features are clearly intermediate between the parent species. The plant is of much slower growth than $P$. bracteatus, but has far outgrown $P$. macrocarpus seedlings of greater age. The leaves are flat and narrowly ovate, about $1-1.8 \mathrm{~cm}$. wide and $2-3.5 \mathrm{~cm}$. long; even the stem color is intermediate between the parent types. Several leaves beneath each developing inflorescence are small and bract-like, about 1 cm . long.
3. P. calcaratus x Finkii? Among the several sheets of Liebmann 5721 (all at C), all badly decomposed and damaged by insects, there are numerous leaves (mostly unattached) and a few involucres of typical $P$. calcaratus. In a packet of one of the sheets, however, there is an involucre that differs markedly from the known species of Pedilanthus and suggests either an interspecific hybrid or an undescribed species. It is tentatively considered a hybrid between $P$. calcaratus and P. Finkii. A description, as far as one can be written for such a damaged specimen, is given herewith:

Involucre glabrate without, thick in texture like that of $P$. calcaratus, tube ca. 11 mm . long, tomentulose within, main lobes obtuse, accessory lobes ca. 1.2 mm . wide, obtuse; spur arising ca. 1.5 mm . from peduncle, bending abruptly forward at ca. 2 mm . from tube and sub-parallel with the tube, terminal (sub-parallel) portion flattened, 5.5 mm . long, 7 mm . wide, broadly rounded, spur lobes arising beneath the flattened portion, lance-ligulate, ca. 3 and 4 mm . long (unequal), ca. 2 mm . wide basally and $0.7-0.8 \mathrm{~mm}$. wide terminally, obliquely truncate and somewhat folded and thickened terminally, glands four, 2 lateral and 2 folded about short terminal partitions; anther lobes slightly convergent ter-


Fig. 27. An involucre from Liebmann $5 \gamma 21$, which is thought to represent a hybrid between $P$. calcaratus and $P$. Finkii (the remainder of the collection is $r$. calcaratus). This involucre has been badly damaged by insects, and the sketch is a reconstruction. Note the long, free spur lobes (arrow). Magnification ca. 4.
minally (similar to P. Finkii), pollen averaging 76.6 microns in polar dimension and 93.8 in equatorial diameter ; pistillate pedicel glabrous, ca. 8 mm . long, ovary ovoid, ca. 2 mm . long, style 5.5 mm . long, branches 1 mm . long, spreading, subentire.

The bent and flattened spur, as well as the appearance of the anthers and style, point strongly to the distinctive $P$. Finkii, while the texture, the folding and thickening of the spur lobes, and the associated materials suggest $P$. calcaratus. These and the very different $P$. tithymaloides are the only species known from Veracruz. The pollen from the two half-eaten anthers does not show the distinctive thickened furrow-margins of P. Finkii, but does have relatively narrow pores and a sub-triangular equatorial outline suggestive of that species. The pollen neither confirms nor contradicts its hybrid nature, but there is not a high percentage of abortive pollen. The elongate, narrow spur lobes of this involucre are of special interest, since free, narrow spur lobes are not a feature of either putative parent. It is not impossible that these species are descended from types with narrow spur lobes like those of the $P$. cymbiferus group, and that hybridization in this case has broken down the modifying and inhibiting systems present in each parent species. Until material of $P$. Finkii is again available in cultivation, the nature of this interesting fragment cannot be experimentally checked.

The putative inter-subspecific hybrids of $P$. tithymaloides, which have been observed, are described with that species. There is some evidence of hybridization between $P$. t. ssp. tithymaloides and the subspp. Smallii and parasiticus, where cultivation has brought them together. Intermediates between P.t. ssp. angustifolius and P.t. ssp. padifolius are also known, but there is no indication of hybridization between $P$. t. ssp. angustifolius or its immediate allies and subspp. tithymaloides or parasiticus.

## Origin of the Genus

The genus Pedilanthus probably arose in tropical Mexico, possibly on the Pacific slopes. It clearly developed from a member of Euphorbia subgenus Agaloma, a woody plant whose involucres bore four appendaged glands, the appendages probably red. The differentiation of the distinctive
features of the genus must not have commenced until there were hummingbirds in tropical North America. This, unfortunately, cannot be dated. These distinctive South American birds have probably occupied their present ecological niche nearly or quite throughout the Tertiary. Wagner (1946) has suggested that the hummingbirds did not reach North America until the late Tertiary, but the Central American water gap can scarcely have confined them (Mayr, 1946), and we cannot agree that all the ornithophilous plants of Mexico are, without exception, recent immigrants from South America. More suggestive is the distribution of the Euphorbieae. The truly primitive genera of this tribe, with markedly calyculate flowers, are all found in the Old World, where they occur largely in peripheral areas: New Caledonia, Australia, Madagascar and western tropical Africa. The most primitive groups of the genus Euphorbia, the woody members of the subgenus Esula, also show relict, discontinuous distribution. There are in the New World several species in the West Indies and Middle America, but the few South American species are strictly Andean and rather closely related to the Middle American species, suggesting that they are recent invaders of South America (a few more advanced types of Euphorbia doubtless reached South America in the Tertiary, by "island hopping" from North America, and perhaps elsewhere). As a whole, the genus is poorly developed in South America. This distributional pattern is taken to indicate that the Euphorbieae invaded North America in the early Tertiary, when North and South America were already isolated. These two lines of evidence serve only to suggest that Pedilanthus has developed since the beginning of the Tertiary. One cannot be more exact.

The ancestral Eupliorbia was probably a local, not too successful sort, as a Euphorbia. Its closest approach, as an adaptive type (but taxonomically very distinct), E. fulgens, appears to be quite local, and no other close counterpart is found in the modern flora. The pattern by which this Euphorbia became a Pedilanthus can be rather readily visual'zed; the author's ideas of this pattern are sketched in fig. 28. The cyathia of Euphorbia are often slightly zygomorphic, in the lack of a fifth gland and the recurving of the pistillate pedicel to one side, through the gap between the petaloid appendages. This slight degree of zygomorphy is
apparently the basis from which the spurred, bent involucre of Pedilanthus has developed. The stigmas are receptive to pollen and fertilization is still possible while the pistillate pedicel recurves. A tendency for the pistillate flower to remain partly deflexed, coupled with a tendency for the gland appendages to remain partly folded (fig. 28b), as they do in E. lancifolia and some of its allies, would be enough to convert an appropriate Euphorbia into a hummingbird "flower," though an inefficient one. Once this stage was reached, it is easy to see that selection pressure toward the further stages shown in fig. 28 would be high. A further folding (or rather an inhibition of the unfolding) of the gland appendages would narrow the possible approach of the pollinating agent, and a lateral deformation leading to a spur and a bent, elongated involucral tube would require the bird to probe more deeply, both greatly improving the efficiency of the now zygomorphic flower cluster. This hypothetical pattern of evolution would lead to a type with an involucre of much the same general proportions as $P$. bracteatus, and all of the modern involucres could be readily derived from such a type. The intermediate types shown in


Fig. 28. Hypothetical derivation of Pedilanthus from Euphorbia subgenus Agaloma: above, top view; below, lateral view; concealed parts shown by dotted lines, connation by dashes. A. Euphorbia subgenus Agaloma, in which one gland is lacking; the other four glands, which alternate with the five involucral lobes, bear large, petaloid appendages. B. Same, in which the petaloid appendages do not spread. C. A hypothetical intermediate in which bilateral deformation has started to form an involucral tube anteriorly and a spur posteriorly. D. A generalized Pedilanthus.
fig. 28 b and c would seem to be in an "adaptive valley" (Simpson, 1953) : inefficient either as insect or hummingbird "flowers." As soon, however, as a moderate degree of zygomorphy was achieved, the species would be on the slope of a new "adaptive peak," and selection pressure would be especially great, with a correspondingly rapid change toward the new peak.

## Primitive and Advanced Features

No one species can be picked out as the primitive species of the genus. Pedilanthus has almost certainly arisen from Euphorbia subgenus Agaloma; the unique inflorescence of the tribe can only be derived through reduction from a certain type, and the evolutionary pattern of certain anatomical features is especially well known (Bailey, 1944). For these reasons, we can, with some certainty, enumerate primitive and advanced features for the genus (Table 9), but these

Table 9. Some primitive and advanced features in the genus Pedilanthus. Some of the primitive features are also primitive for the ancestral genus, Euphorbia.

## Primitive

1. Tree or large shrub, woody.
2. Vessels narrow.
3. Many solitary vessels.
4. Vessels mostly scalariform pitted.
5. Rays multiseriate, heterogeneous.
6. Latex white.
7. Leaves relatively large (possibly evergreen).
8. Cyme bracts of moderate or small size.
9. Cyathia green, with red spur lobes.
10. Numerous staminate flowers.
11. Well developed bracteoles.
12. Spur and involucral tube both moderately elongated.
13. Free medial spur lobes.
14. Glands 4.
15. Pollen colporate.

## Advanced

1. Small shrub, succulent or subherbaceous.
2. Vessels wide.
3. Most vessels in distinct radial multiples.
4. Vessels with opposite or alternate pitting.
5. Rays uniseriate, homogeneous.
6. Latex yellow.
7. Leaves small, caducous.
8. Cyme bracts large.
9. Cyathia solid red or solid green.
10. Few staminate flowers.
11. Bracteoles small or few.
12. Spur sessile or very elongate, or involucral tube greatly elongate.
13. Medial spur lobes connate.
14. Glands 2 or 6.
15. Pollen colpate or inaperturate.
features show a checker-board distribution among the species (Table 10). Pedilanthus tehuacanus deviates most widely from the hypothetical primitive type; $P$. tithymaloides, in spite of its involucral specializations, has a large number of primitive features, especially in wood structure. Most of the features in Table 9 are self-explanatory. In keeping with the evolutionary pattern given above for the genus, an involucre with both spur and involucral tube moderately elongated is taken as the primitive type. It would be possible to think of the primary differentiation of the genus as effecting only one of these structures, but such a pattern is less easily visualized and is not supported by the modern variation pattern of the genus. Wide, blunt spur lobes and proportionately wide accessory involucral lobes should both be primitive features for the genus. There is doubt, however, that they are primitive where now found. The species with wide spur lobes may very well be secondarily derived from ancestors with more narrow ones ( see P. Finkii x calcaratus?, under Hybridization). The proportionately wide accessory involucral lobes, in some species of the P. bracteatus and $P$. tithymaloides species groups, are thought to be the result of a certain degree of neoteny.

Table 10. The distribution of some primitive features in Pedilanthus. The numbering of features follows that in Table 9. An asterisk indicates that the feature checked is present in the species, but not necessarily in all plants.

|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| P. Palmeri | * |  | * |  |  | * | * | * |  | * |  |  | * | * | * | 10 |
| P. Finkii |  | * |  |  |  | * | * | * | * |  |  |  |  | * |  | 6 |
| P. calcaratus | * |  |  |  |  | * | * | * | * |  | * | * | * |  | * | 9 |
| P. gracilis | * |  |  |  |  | * | * | * | * |  | * | * | * |  | * | 9 |
| $P$. pulchellus | * | * |  |  |  | * | * | * |  |  | * | * | * | * | * | 10 |
| P. coalcomanensis | * |  |  |  |  | * | * |  |  | * | * | * |  | * | * | 8 |
| $P$. cymbiferus |  | * | * |  |  | * |  | * |  | * | * |  | \% | * | * | 9 |
| P. macrocarpus |  | * | * | * |  | * |  | * |  | * | * |  | * |  | * | 9 |
| P. bracteatus |  |  | * | * | * |  | * |  |  |  |  | * | * |  | * | 7 |
| $P$. tomentellus |  |  | * | \% |  |  | * |  |  |  |  | * | * | * | * | 7 |
| $P$. tehuacanus |  | * | * | * |  |  |  |  |  |  |  |  | * | * |  | 5 |
| $P$. nodiflorus |  | * | * | * |  | * |  | * |  |  | * |  | * | * | * | 10 |
| $P$. tithymaloides |  | * | * | * | * | * | 1 | * | * |  |  |  |  | * | * | 10 |

## Trends in the Involucre

The distinctive features of the genus are to be found in the involucre, and in this structure are to be found some of the most interesting modifications of the genus, if not of the tribe. Striking variation is to be seen in the relative development of the spur and involucral tube. In P. macrocarpus and P. Palmeri the involucral tube is relatively short, while the spur forms the greater part of the inflorescence. Similarly, the spur of P. Finkii overtops the involucral tube in size, though its form is very different. In $P$. nodiflorus and $P$. tithymaloides, on the other hand, the spur elongates only slightly and the involucral tube comprises the greater part of the cyathium. Pedilanthus tehuacanus has a very short spur, but here the development of the involucral tube is also arrested.
One of the themes of the adaptation of the involucre, or rather of the entire inflorescence, has been that of "Schauapparat," or the device to heighten the visibility of the inflorescence. This has been accomplished in various ways. Pedilanthus coalcomanensis, P. bracteatus and P. tomentellus have large, colored cyme bracts; in the last two species, indeed, the involucre itself is green. In most species the involucre, and especially the spur, is the most conspicuous feature. In $P$. macrocarpus and $P$. cymbiferus, leafless smallbracted desert species, the spur is widened and flattened to provide a more efficient "sign-board." That this is the main adaptive significance is especially evident in $P$. macrocarpus, for the flattened terminal part of the spur is solid and parenchymatous. Pedilanthus nodiflorus and P. tithymaloides have short spurs and relatively small involucres, as well as small inconspicuous cyme bracts. In these species, however, numerous cyathia are produced and these are borne in relatively compact clusters, so that the total inflorescence may be quite as showy as a few larger cyathia. Quite aside from size and flattening of the spur, there is great diversity in the form of the spur, the spur lobes and the glands. Without better information on the pollinating agents it would be futile to speculate further on the adaptive significance of these variations.

While the primary features of the genus result from an elaboration of the later stages of inflorescence ontogeny, the opposite trend also occurs. At least two groups of popula-
tions seem to owe their distinctive features largely to "paedomorphosis," or neoteny (see deBeer, 1954), of the cyathium. Pedilanthus tehuacanus and P. tithymaloides ssp. angustifolius differ from their respective allies by features which are best explained as arrested development of the entire involucre, coupled with normal maturation of the anthers, ovules and stigmatic tissues. The aspect of the $P$. tehuacanus involucre is sometimes approximated by involucres borne on cuttings of $P$. bracteatus when these fail to develop normally. The partial connation of the cyme bracts and the sessile involucre of this species also are best explained as arrested development. The pistillate flower, with its short, blunt style, looks distinctly "immature" in both P. tehuacanus and $P$. tithymaloides ssp. angustifolius. The short spurs of $P$. nodiflorus and $P$. tithymaloides, too, may be explained as a paedomorphic, or partly allometric, pattern. The young involucre of $P$. calcaratus, $P$. cymbiferus (see the first stages in fig. 18) and similar species is quite similar to the mature involucre of $P$. tithymaloides. If spur development be greatly arrested, relative to the development of the involucral tube, in any of the moderately long-spurred species, something very similar in proportion to P. tithymaloides would result.

## Xeric Adaptation

One of the striking features of Pedilanthus, as of the entire tribe Euphorbieae, is the adaptation of several lines for survival in dry habitats. The ancestral "proto-Pedilanthus" may have been adapted to a seasonally dry habitat, or it may have occupied a rather mesic niche. In any case, it possessed the morphological and physiological features which predispose the Euphorbieae to successful evolution as desert plants. The woody $P$. cymbiferus seems to have adapted to a truly desert habitat quite independently of the other xerophytes of the genus. The $P$. bracteatus and $P$. tithymaloides species groups both show true stem succulence, and this feature may have arisen only once within the genus. Essentially leafless xerophytes, however, have evolved several times among these few species. Both $P$. macrocarpus and $P$. tehuacanus appear to have evolved from a largeleaved ancestor similar to $P$. bracteatus. There are largeleaved populations of $P$. tithymaloides, which suggests that
its ally, $P$. nodiflorus, has taken up the microphyllous habit quite independently. Small or caducous leaved populations are to be found in $P$. tithymaloides in Oaxaca, Mexico, in Venezuela, and in the Greater Antilles.

The patterns of variation within the genus suggest that there may have been two or more ways in which the smallleaved xerophytic habit was achieved. In Pedilanthus nodiflorus and $P$. tithymaloides subsp. angustifolius and its close allies, leaf reduction has involved primarily reduction in width, resulting in a narrow, more or less lanceolate leaf form. In some other populations of $P$. tithymaloides, however, there is a certain degree of foliar dimorphism, suggesting a different pattern for the evolution of reduced leaf size.

In $P$. tithymaloides ssp. parasiticus and some populations of $P$. $t$. ssp. tithymaloides (Tomellín Canyon, see Plate XXI) there is a strong tendency for the upper branches to develop several to many small bract-like leaves, especially beneath the inflorescence. Such a pattern is not unusual among plants with distinctive bracts, and may suggest a pattern for the evolution of microphylly in a number of different xerophytes. These populations with a tendency towards dimorphic leaves are thought to represent a change in the threshold for some of the features of bract development, so that the upper leaves develop along a pattern intermediate between bracts and foliage leaves. In an isolated arid habitat selection for smallleaved variants might shift this threshold so that a greater proportion of the leaves develop on the "semi-bract" pattern, and with continued selection the normal foliage pattern might be entirely lost. Partial support for this interpretation is provided by the hybrid between P. macrocarpus and $P$. bracteatus; the first parent is a plant with only very small bract-like leaves, and the second a large-leaved plant with little or no reduction in the size of the upper leaves. The hybrid has several small ovate, bract-like leaves beneath the inflorescence; leaves very like the wide leaves of primitive $P$. macrocarpus (the parent plant of this species is an advanced type from Sinaloa, with nearly linear leaves). Pedilanthus cymbiferus and $P$. macrocarpus are species which may have evolved through such a pattern of foliar dimorphism. The populations of $P$. tithymaloides which show foliar dimorphism are probably prevented from further progress in this line by gene exchange with populations of
less xeric habitats. Isolation would seem to be necessary for successful adaptation to an extreme habitat.

A certain degree of genetic correlation between leaf and bract is evident. All of the truly microphyllous xerophytes have very small bracts. Pedilanthus tehuacanus is a partial exception in having relatively large bracts and relatively small leaves, but its leaves are markedly larger than those of the other xerophytes. With the involucres tightly enclosed by the bracts at anthesis, a further reduction in the bracts would be quite impossible. Selection for smaller leaves and selection for the same or larger bract size may be an uneasy balance in this species. Further reduction in leaf size will require mutations which do not affect bract size or ones which increase bract size relative to leaf size.

## Adaptive Radiation

Once the new adaptive type of a relatively efficient hummingbird "flower" was achieved by the ancestral Pedilanthus, something very like adaptive radiation occurred, and seems still to be occurring. This pattern, the relatively rapid ("tachytelic") evolution of a population (probably small) into a new adaptive type, followed by adaptive radiation in the new niche, is a well recognized phenomenon among animal groups, and is often connected with the origin of new families and other higher categories (Simpson, 1953). It may be argued that, as to pollination relationships, Pedilanthus (except for $P$. tehuacanus) occupies only one niche, and the scarcity of truly sympatric species pairs tends to support this. Nevertheless, the genus has adapted to that niche in diverse ways (see above, under Trends in the Involucre).

Simpson and others have rightly emphasized the primary role of environment and selection in adaptive radiation. Certain features of the genetic systems may, however, contribute to the rapid radiation of "new" groups. It sometimes appears that a new structure or developmental pattern is especially subject to variation in its phylogenetic youth, and such may, to a degree, be true. A strong selection pressure is required to develop a new adaptive type from a gene complex already well balanced about a different adaptive peak. With time the new pattern will become strongly "buffered" by the development of polygenic systems which affect its
ontogeny, but, until this buffering has occurred, mutations affecting the new structure will have a high degree of penetrance. According to this concept, a structure or developmental pattern might, indeed, have a stage of "youth," when it is not more mutable than in later stages, but when individual mutations may have a more pronounced effect and be more readily acted upon by selection.

The occurrence of Pedilanthus in a variety of habitats may also be considered a sort of adaptive radiation. This, however, has largely involved the evolution of similar xerophytic adaptations in several lines. Such parallelism involves no mystic "orthogenesis." When a species is already adapted to withstand some degree of drought, it will usually be found in a habitat where selection favors the evolution of further xeric adaptation.

## Parallelism

The interaction of similar environments and similar gene complexes often results in parallel patterns of evolution. This has been the case in several instances in the present genus. Probably the most striking case of parallelism is to be found in $P$. cymbiferus and $P$. macrocarpus. Both are grey-green, essentially leafless, clump-forming desert shrubs with small, caducous bracts and large, bright red involucres with wide conspicuous spurs. They are strikingly similar in aspect, yet they do not seem to be closely related: one is woody, the other succulent; one spreads by underground stems, the other by forming adventitious buds on the roots; the details of wood structure, leaf, involucre, fruit and seed are all markedly different. Their similarities seem clearly to result from the development of parallel features in similar habitats. Pedilanthus nodiflorus and P. tithymaloides ssp. angustifolius provide a less striking case of parallelism. The two species are thought to be closely related, yet the narrow leaves and proportional similarities of the involucre seem to have been derived quite independently in the two taxa. A more general case of parallelism is the development of small or caducous leaves in dry habitats in about seven separate populations within the genus (three different centers of xeric adaptation being counted for $P$. tithymaloides).

## Some Specific Patterns of Evolution

Having considered some of the general aspects of evolution in Pedilanthus, we will now consider three of the species in greater detail.

1. Pedilanthus macrocarpus. This Sonoran Desert species has apparently evolved from an ancestor very like the present day $P$. bracteatus. The common ancestor of these two species must have had white latex and retained red spur lobes, as well as the full complement of four glands, but in other features it may have differed very little from the modern $P$. bracteatus. The isolation of the ancestral $P$. macrocarpus population probably occurred somewhere on the present peninsula of Baja California. This isolation could have occurred as early as the middle Miocene, when the Gulf of California was being formed and the peninsula apparently became an archipelago (Gentry, 1949). This isolation could, of course, have occurred much more recently. In any case, the isolated population found itself in an arid or semi-arid habitat, and selection for reduced leaf and bract size and increased succulence was effective. In late Pliocene and Pleistocene the California Gulf region acquired its modern character, with some fluctuation in sea level during the Pleistocene, and large areas of arid coastal plain developed. In these geologically recent times, $P$. macrocarpus has occupied much of the peninsula and invaded the mainland of Sonora, where it is quite successful in the cactus desert of the coastal plain and has spread southward into northern Sinaloa. These mainland populations have a narrow, fleshy, almost sub-terete leaf very different from the ovate leaves of the peninsular populations (but leaves are known for very few collections from either area). In Sinaloa and southern Sonora there is clearly strong selection pressure for a larger, more readily visible spur and for more connate spur lobes. Whether this is due to a difference in pollinating agents or to other differences cannot be determined; the denser vegetation of the thorn scrub in this area might place a premium on larger, more visible spurs. There is a distinct cline in both involucre and fruit characters, from the highly specialized populations of the southern mainland, running north along the coast and then south on the peninsula to the primitive bracteatus-like populations of
the southern peninsula. The population of San Pedro Nolasco Island does not fit in the cline, but is very similar to the Cape population. It is not yet clear whether the cline represents a gradient of selection pressures (with some gene exchange, of course) or a relatively efficient dispersal and gene exchange between the northern populations across the gulf. The primitive nature of the San Pedro Nolasco population casts doubt on trans-gulf gene exchange. A relatively recent continuity about the northern end of the gulf is conceivable, but the gulf extended much further to the north in truly recent times. It should be noted that the bracteatuslike population is, geographically, the farthest removed from the range of $P$. bracteatus. There is no evidence that the ranges of $P$. bracteatus and $P$. macrocarpus actually overlap. Thus both introgression and character displacement seem to be excluded as causes of the variation in $P$. macrocarpus. Pedilanthus macrocarpus has the appearance of a population complex which is now undergoing rapid and obvious evolution. An intensive study of this species would undoubtedly be rewarding. At the very least, it shows us how strikingly different species, species as different as the five species groups of Pedilanthus, can and do arise from a common ancestry.
2. Pedilanthus tehuacanus. This species is known only from fragmentary material, yet its features are so striking that it well deserves special attention. Pedilanthus tehuacanus has arisen from the same ancestral stock as the preceding species, but not until this stock had acquired yellow latex and a tendency to reduce the red color of the involucre (perhaps also large cyme bracts, but the author is not prepared to state that the ancestor of $P$. macrocarpus did not also have large bracts like those of $P$. bracteatus). It is known only from the area of local aridity near Tehuacán, Puebla, a dry basin that may date, as such, from a late Tertiary orogeny. Whatever the original isolation, or its habitat, the population has become more markedly xerophytic than $P$. bracteatus, though this trend has not gone as far as in $P$. macrocarpus. It would appear that hummingbird pollination ceased to be adequate for the species; possibly because the birds were scarce in that habitat or because the trend to bract and leaf reduction had too greatly reduced the size of the bracts and the visibility of the inflorescence.

With a return to small insects as the major agents of pollination there was a very strong selection pressure for reduction in the size of the cyathium, so that the anthers and styles were closer to the nectaries. This was most easily achieved by neoteny, or a retardation of involucral development relative to the flowers. This same retardation further increased its efficiency as an insect "flower," by partial connation of the cyme bracts, which forces the insects to approach the involucre from one side, near the flowers. This effect has been further heightened by a shortening of the staminate flowers and a bending of the style so that both the stigma and the anthers are borne quite near the orifice of the bract hood. This one species, thus, has again left the adaptive type of its congeners and entered a new one. It is, to be sure, insect pollinated like most Euphorbias, but its structure is very different from that of any Euphorbia.
3. Pedilanthus tithymaloides. This species, the best known of the slipper spurges, occurs naturally over a wide area and in a variety of habitats. Its pattern of variation is especially interesting and informative, as to the origins and relationships of the West Indian populations. The exact geographic origin of such a widespread complex can rarely be determined, but distribution and occurrence of variability and primitive features suggest Central America as the center of dispersal for this species. The present discussion will deal largely with the Antillean populations, and little will be said of subspp. parasiticus and Smallii, except that they appear to have a common ancestry and to have reached the West Indies from Central America. The Floridian population of Smallii must be of very recent dispersal, as are most of the West Indian plants in the geologically recent tip of Florida. As noted previously, $P$. tithymaloides is thought to have reached South America in the late Pliocene, when the Tertiary water-gap between the divergent North and South American biotas was closed (Simpson, 1950; Mayr, 1946). Since the species can and does occasionally "island-hop," it may be argued that the water-gap would not be a serious barrier. If dispersal antedated the land connection, it probably did not occur until mid-Pliocene times, when the gap was being narrowed (had it occurred much earlier, one might expect specifically distinct populations). Once the species invaded South America, its dispersal along the
semi-arid north coast may have been relatively rapid. The history of $P$. tithymaloides in the West Indies, thus, would appear to concern the Pleistocene, the Recent and possibly the latest Pliocene. Since Pedilanthus has so successfully spread through the West Indies, one may inquire as to its means of dispersal. The seeds are moderately large (ovoid, $3-5 \mathrm{~mm}$. long) and without evident special means of dispersal other than the elastic dehiscence of the capsule, which could, at most, throw the seed only two or three meters. The island-hopping of this species is probably to be explained by the dispersal of parts of the plant itself in times of storm. The xeromorphic stems could probably survive brief immersion in salt water, and, if swept beyond the strand line, become established, even under relatively unfavorable conditions.

The population that invaded the West Indies, or soon evolved there, probably had a moderately large involucre with projecting, slightly three-lobed spur (such as is found in the Grenadines, western Jamaica and the western Bahamas), glabrous staminate flowers, and blunt, obovate leaves. Such a plant is very closely approached, in all its features, by the peripheral western population of $P$. tithymaloides ssp. jamaicensis. The principal trend in the Greater Antilles has been the development of a population complex with narrow leaves and very small involucres, probably the result of paedomorphic retardation of involucral development relative to the maturation of the flowers. The trend to narrower leaves is probably an adaptation to relatively dry habitats. This trend may have fluctuated markedly throughout the Pleistocene. The selective basis for reduction in involucre size is not clear. It is to be noted, though, that, except for Anthracothorax, the hummingbirds of the Greater Antilles are all quite small or tiny, which may be related to the size reduction in Pedilanthus. That there has been a selective basis for this trend in supported by the parellel size reduction of $P$. $t$. ssp. parasiticus involucres on Isle de la Gonave, Haiti. The populations of the Lesser Antilles were affected to some degree by these trends, especially in involucral form; but these populations have been isolated from those of the Greater Antilles for some time, and later gene exchange from the continent, as evidenced by pilose staminate pedicels, and probably wider leaves, has
not gone beyond St. Croix (where it is probably very recent).
The populations of the Bahamas and Jamaica are very closely related, and were probably derived from a Hispaniolan common ancester. The eastern Jamaican $j a-$ maicensis is somewhat closer to the modern angustifolius in involucral form and indument, suggesting that the last Jamaican invasion was relatively recent. Invasion of the eastern Bahamas has, however, apparently continued, the involucres of plants in this area closely resembling those of


Map 1. The probable routes of dispersal and gene exchange in Pedilanthus tithymalordes subsp, angustifolius and its immediate allies in the West Indies. Solid line: routes of primary dispersal, dashed lines: gene exchange, dotted lines: major barriers to gene exchange. A. the center of dispersal for the angustifolius type with narrow leaves and short involucres. B. the dispersal of genes for pilose staminate flowers into the Lesser Antilles. C. the dispersal of the coriaceous, obtuse leaf type of subsp. parlifolius into Trinidad. D. the center of dispersal of the small, pilose involucres and other features of the " $I$ '. Fondleri" type. Barriers: 1. Isolation of Andros, which preserves a primitive, long involucre type in the Bahamas. 2. the water gap between Hispaniola and Jamaica. 3. the water gap between Hispaniola and the Bahamas. 4. the water gap between the Greater and Leesser Antilles, which has apparently permitted limited gene flow from angustifolius to padifolius, but little if any in reverse. $\overline{0}$. the water gap between the Lesser Antilles and South America, which has permitted limited gene flow each way.
the Greater Antilles in size and form (or, again, this may be a matter of varying selection pressures). The Bahamas were not available for colonization until sometime in the Pleistocene (Clench, 1938), but their origin is not yet more exactly dated. Plants with quite narrow leaves are found in Puerto Rico, but the modern populations of Hispaniola and Cuba have moderately wide, oblanceolate leaves, suggesting that selection pressures may have changed in this area, if bahamensis and the eastern population of $j a$ maicensis were derived from a similar Hispaniolan ancestor. Both angustifolius and padifolius, as well as plants intermediate between the two, have been collected on St. Croix. One may suspect that padifolius has recently invaded this island, probably as an escape from cultivation, but field study is needed to clarify the matter.

The Pleistocene fluctuations of sea level in the West Indies have undoubtedly affected the evolution of the biota by uniting some island groups and facilitating dispersal between others. The present distribution and variation of Pedilanthus apparently reflects the last major lowering of the sea in the area, when the Bahamas, the Greater Antilles (except Jamaica?) and the lesser Antilles each formed a more closely interconnected archipelago. How else could the existence of distinctive population complexes in each island group be explained? The somewhat clinal variation in the Bahamas may possibly represent fragments of an actual cline which existed when the Bahamas were partially united in the late Pleistocene. The present distribution and variation of $P$. tithymaloides may best be shown by mapping centers for certain characters and character complexes, routes of gene exchange, and partial barriers to gene exchange (Map 1).

## PART IV. TAXONOMY

## Measurement

The terminology used in the taxonomic descriptions and discussion is that given under Morphology (p. 29), but some of the procedures used in measurement need explanation, as it is not always feasible to follow strict morphological boundaries for descriptive purposes. The involucral tube is measured from the top of the peduncle (a fairly definable point) to the apex of the main lobes, as shown in fig. 12.

The shapes given for the main lobes, however, refer to the anterior portions thereof, and, even then, are rather arbitrary, because the main lobes grade imperceptibly into the spur parts dorsally and posteriorly. The accessory involucral lobes, strictly speaking, should be measured from the glands, or, in some species, from fairly definable bases anterior to the glands. This procedure, is, in most forms, difficult to follow without demolishing the involucre. This difficulty is here avoided by measuring the differences in length between the main lobes and the accessory lobes (which are shorter) and giving the distances for which the lateral accessory lobes are free laterally and medially. The spur offers similar difficulties in measurement; the external boundary between involucral tube and spur is often obscure (and in P. Palmeri, its appearance varies with the condition of the involucre), so the length is given both from the peduncle (dotted bracket in fig. 12) and from the involucral tube (solid bracket in fig. 12). In those forms where the spur is scarcely elongate, its thickness is given and the distance between the peduncle and the base of the spur (in these forms this is clearly definable). The lateral spur lobes are difficult to measure, for much the same reasons which cause trouble with the main involucral lobes, and little attempt has been made to measure these structures, except where they are especially conspicuous. The measurements and descriptions given for the medial spur lobes refer only to the free portions. Where these lobes are markedly connate with each other and with the lateral spur lobes, the distance between the apex of the spur and the free portion of the spur lobes is given ("spur lobes arising at"). Where the lateral and medial (free) margins are markedly different, this is indicated. Bracteole-ridge refers to a marked keel on the inner wall of the involucre, which appears to represent bracteolar tissue completely adnate to the involucral wall. The measurements given for seeds refer to the length and the greatest diameter.

## Taxonomic Concepts

In the present work, the number of species recognized is less than half that listed by the last revision, that of Millspaugh (1913). In such a case the reader may reasonably
wish to examine critically the concepts used. A number of the changes in the present revision are due not to any unusual species concept, but merely to the great need for revision, and are changes which would have been made by any botanist with adequate material.

In recent years, much has been accomplished in the attempt to reach relatively objective species criteria which reflect accurately and conveniently the "natural" situation, as nearly as this can be done. The cornerstone of the most adequate species concepts has been the sympatric coexistence of distinct populations which retain their individuality. In spite of the complications of apomixis and polyploidy, these concepts are as usefully applicable to botany as to zoology. This "biological species concept" is used in the present paper. A species is considered to be a population or group of populations which share a common pool of genetic and morphological characters, which are interconnected by actual or potential gene exchange, and are separated from other such populations by barriers to gene exchange and by resultant gaps in morphological features. The barriers to gene exchange may be entirely "intrinsic" or may result from interactions between the intrinsic features of the organism and the "extrinsic" environmental factors. Some may object to the emphasis on the gaps between species, yet this is the one approach which allows a high degree of objectivity in the treatment of species, and the highest possible degree of objectivity should be sought at all levels of taxonomy. It has been well demonstrated that strong barriers to interbreeding do not always curtail all gene exchange (introgression), especially where the environment has been drastically altered. Nevertheless, the presence of any appreciable amount of hybridization places the burden of proof upon those who would recognize distinct species. The magic word, "introgression," is not enough ; it must be shown, by careful and critical analysis, that there are barriers, other than purely geographic factors, which separate the taxa. The demonstration of such gaps does not necessarily require genetic or embryological data, which cannot be obtained without lengthy experimental work. Critical taxonomy, based entirely on morphological features, was practiced before any alliance between genetics, evolution and taxonomy had been considered.

The biological species concept is most directly applicable when one is dealing with sympatric species. An arbitrary and subjective element is almost inevitable in the treatment of disjunct groups. Even extensive evidence of genetic compatibility cannot indicate what would occur if the populations were naturally sympatric, for they are not. When dealing with disjunct groups one must use a certain degree of "taxonomic judgment," and this is best acquired by the study of related, sympatric groups. The "species standard" concept (Rollins, 1952), devised primarily to deal with the complexities of apomixis and polyploidy, can be applied equally well to allopatric populations. A note of caution has recently been brought out by Brown and Wilson (1956), in their re-emphasis of character displacement. Where the features used to distinguish species are those affected by competition, or those involved in any way in the interspecific barriers, related species will be more sharply differentiated where they are sympatric. It is to be hoped, however, that this concept will not be used to justify the naming of many disjunct, putative species, merely because some of the populations might be distinct species.

Subspecies are used in the almost universal sense of geographic groups which are taxonomically recognizable, but which intergrade where their ranges are in contact. The term, "subspecies," is taken up in preference to "varietas" with considerable reluctance, for the latter term has been used in this same sense by many botanists, and simple "name-changing" should be kept at a minimum. There has been little uniformity and a good deal of chaos in the botanical usage of infra-specific taxa, and it is hoped that greater clarity may be achieved by the growing use of the more clearly defined term, "subspecies." However, this term, too, can easily be thrown into disrepute by careless usage. The existence of broadly sympatric populations which are partially isolated by ecological factors and quite correctly treated as subspecies is, in theory, possible. However, "sympatric subspecies" is something of a contradiction in terms, and they must not be proposed without critical study. Similarly, the description as subspecies of segments in a cline, populations which can only be recognized on a statistical basis, or (worst of all) phenotypes without population status, can only serve to devalue the concept.

While these concepts associated with the biological species concept and developed through the study of evolution can lead to a high degree of objectivity and a much greater uniformity in taxonomic treatments, most revisions must fall short of the ideal goal. This is not due to inadequate concepts or methods, or to inability of the taxonomist, but to inadequate sampling of the plants. By far the greater part of the world's vegetation is quite inadequately represented in the herbaria. With poorly known plants we must simply do the best we can and admit that our treatments may be modified when more material and information are available. Another source of inconsistency, the inconsistency of biological nature, is, of course, always with us, and cautions against overly narrow or rigid concepts. Borderline cases between subspecies and species, between species groups and genera, are to be expected, and must be recognized and studied as such. Indeed, our whole structure of evolutionary thought demands that such borderline cases occur.

## Pedilanthus Necker, Elem. Bot. 2:354. 1790.

Nomen conservandum. Type: Euphorbia tithymaloides L.
Tithymalus Mill., Gard. Dict. ed. 4, vol. 3. 1754. Type: T. my $[r] t i-$ folius Mill., not Tithymalus Trew, nomen conservandum.

Tithymaloides Ortega, Tab. Bot. ed. 2. 28. 1783. Type: Tithymalus myrtifolius Mill.

Ventenatia Tratt., Gen. Pl. 86. 1802. Type: Euphorbia bracteata Jacq.

Crepidaria Haw., Syn. Pl. Succ. 136. 1812. Type: Tithymalus myrtifolius Mill.

Tirucalia Raf., Fl. Tell. 4th part, 112. 1838. Based in part on Pedilanthus.

Diadenaria Kl. and Gke., Monatsb. Akad. Berl. 1859:254. 1859. Type: D. Pavonis Kl. and Gke.

Hexadenia Kl. and Gke., Monatsb. Akad. Berl. 1859:253. Type: Pedilanthus macrocarpus Benth.

For a detailed treatment of the generic and infra-generic synonyms of Pedilanthus and their typification, see Wheeler $(1939,1943)$.

Trees or shrubs, woody or succulent; leaves entire, alternate, distichous, stipules small, blunt or spur-like; cymes terminal or axillary, dichasial or partly monochasial by abortion, cyme bracts opposite, large or small, involucral bracts partly connate, of three sorts: a ventral pair, sometimes bearing glands an the dorsal edges, forming wide lobes (the main involucral lobes) above the level of the glands; 2 lateral bracts, basally asymmetric, bearing glands at least on the dorsal edges, and forming inconspicuous more or less ligulate lobes
(lateral accessory involucral lobes) above the glands; and a dorsal bract, bilaterally symmetrical, bearing glands on each edge and forming an inconspicuous, more or less ligulate lobe (median accessory involucral lobe) above the glands; the involucral tube distorted, with the glands all on the dorsal side, and often borne on a more or less elongate, solid, spur-like, dorsal extension of the tube; glands 2,4 or (by division of the medial glands) 6, appendiculate, the appendages (spur lobes) partly connate with each other and with the main involucral lobes, forming a more or less elongate spur, the lateral spur lobes completely adnate to the involucral tube, the medial spur lobes between the lateral lobes and (anteriorly) over the accessory involucral lobes; bracteoles absent to numerous, filamentous; staminate flowers numerous, monandrous, naked; pistillate flower naked, ovary 3 -celled, styles 3, bifid, largely connate; fruit capsular or indehiscent; mature seed ecarunculate, smooth or tuberculate.

## Key

Note that $P$. Millspaughii (species no. 14), of Costa Rica, is not included in the key because of inadequate description and lack of material.
A. Spur elongate, projecting obliquely from the involucral tube for more than 4 mm . or, if shorter, the bracts mostly more than 15 mm . long and partially concealing the involucre at anthesis .......... B
A. Spur short, cucullate, projecting less than 3 mm . from the involucral tube, bracts usually less than 15 mm . long, never concealing the involucre at anthesis L
B. Lateral spur lobes well developed, enfolding and partially concealing the medial lobes or completely connate with the medial lobes

B. Lateral spur lobes relatively small, not enfolding nor connate with the medial lobes
C. Medial spur lobes free, enfolded by the lateral lobes; spur projecting obliquely from the involucral tube (western Mexico)

1. P. Palmeri.
C. Medial spur lobes completely connate with each other and with the lateral lobes, leaving a small semi-circular orifice over the accessory involucral lobes; spur inflated and flattened parallel to the involucral tube (Veracruz)
2. P. Finkii.
D. Spur lobes obtuse, with a thickened, recurved point beneath, not attenuate E
D. Spur lobes attenuate, truncate, thickened beneath, but without a recurved point

E. Cymes congested; internodes mostly less than 4 mm . long; bracts usually pubescent without; glands ovate or oblong; leaves obtuse or broadly acute (Sinaloa to Guatemala) .................. 3. P. calcaratus.
E. Cymes lax, internodes ca. 10 mm . long; bracts glabrous without, glands orbicular or nearly so; leaves acuminate (coastal Guerrero) 4. P. gracilis.
F. Tip of spur truncate, sometimes 2 -notched and thus 3 -lobulate
F. Tip of spur rounded, if 3-lobulate then central lobe projecting beyond lateral lobes
G. Bracts large (ca. 2 cm . long), persistent, medial spur lobes completely connate (Michoacán)
3. P. coalcomanensis.
G. Bracts small (less than 1 cm . long), caducous, medial spur lobes not connate H
H. Tree or large shrub with large leaves (more than 4 cm . long), pistillate pedicel not elongating, capsule developing within the involucral tube (Oaxaca)
4. P. pulchellus.
H. Low desert shrub, leaves less than 1.5 cm . long, caducous; pistillate pedicel elongating and exposing the developing capsule (Puebla and adjacent Oaxaca)
5. P. cymbiferus.
I. Glands 6 , spur flattened terminally, strongly partitioned within, fruit turbinate, cornuate, indehiscent; latex white (Sonoran Desert)
6. P. macrocarpus.
I. Glands 2 or 4 , spur not terminally flattened or partitioned; fruit capsular, dehiscent; latex yellow

J
J. Cyathia pedunculate; style more than 6 mm . long, style branches usually spreading

K
J. Cyathia sessile; style ca. 4 mm . long, style branches connivent (Puebla)
11. P. tehuacanus.
K. Ovary densely puberulent; peduncles and petiole........................................... rufescenttomentose (Oaxaca) ............................................. 10. P. tomentellus.
K. Ovary glabrous; peduncles and petioles not rufescent-tomentose (Sonora to Oaxaca)
9. P. bracteatus.
L. Medial spur lobes free, attenuate, each with a pronounced tooth on the inner margin; lateral glands exposed (Yucatan and Honduras)
12. $P$. nodifloms.
L. Medial spur lobes truncate, usually connate, without later.............................................ent lateral glands concealed (widespread) .............. 13. P. tithymaloides.

## 1. Pedilanthus Palmeri Millspaugh

## Plate XVI, Map 2

P. Palmeri Millsp., Field Mus. Nat. Hist. Pub. Bot. 2: 364. 1913. Type: Tepic, Mexico, Jan. 5 to Feb. 6, 1892. Edward Palmer 1995 (NY! a poor specimen, but cited as type by Millspaugh, isotypes: A!, F!, GH!, S!, UC!, US!). -- Tithymalus koilopremnos Croiz., Am. Jour. Bot. 24: 704. 1937. based on P. Palmeri Millsp., not T. Palmeri (Engelm.) Abrams.
P. peritropoides Millsp., Field Mus. Nat. Hist. Pub. Bot. 2: 369. 1913. Type: Hacienda Coahuayula, Michoacán, Mexico, Nov. 1906, G. M. Emrick 80 (F no. 200, 416!). - Tithymalus peritropoides (Millsp.) Croizr, Am. Jour. Bot. 24:704. 1937.
Evergreen shrub $1-2 \mathrm{~m}$. tall; tending to branch from the base, stems woody, glabrous; leaves thin, glabrous, elliptic-oblong to oblanceolateobovate or oblong-obovate, $4-9 \mathrm{~cm}$. wide, $12-20 \mathrm{~cm}$. long, base cuneate to obtuse, often tapering to apex, this acute to obtuse, midrib carinate beneath, petiole $6-12 \mathrm{~mm}$. long; stipules small, spur-like, dark, 0.2 mm . long or less; infloresence terminal, of a terminal cyme and few (1-3) subterminal, axillary, pedunculate cymes, internodes (3-) $\overline{5}-13 \mathrm{~mm}$. long, puberulent; bracts pink to red, puberulent (often densely so), ovate to orbicular-obovate, acute, clasping basally, $10-20 \mathrm{~mm}$. long,
$8-15 \mathrm{~mm}$. wide; peduncle slender, puberulent, (12-) $20-30$ (-45) mm . long, apex expanded into an oblique receptacle; involucral tube green, glabrate to densely puberulent throughout, usually basally glabrate within, $8-12 \mathrm{~mm}$. long, ventrally indented at base, main lobes thin, ovate-orbicular, ventral margins free terminally for ca. 3-6 mm., apex obtuse, accessory lobes linear-ligulate, 1-1.4 mm. wide, obtuse, lateral involucral lobes free for $0.5-1 \mathrm{~mm}$. laterally and $1.5-2.5 \mathrm{~mm}$. medially, not clearly distinct from lateral spur lobes basally; median accessory lobe $0.5-1 \mathrm{~mm}$. shorter than lateral lobes; spur pink to scarlet, puberulent throughout, projecting posteriorly, 13-17 mm. long (from peduncle), indented posteriorly ca. 1 mm . from base in fresh material, incurved ca. 5 mm . from base in dried specimens, tip of spur broad, 6-9 mm. wide; lateral spur lobes well developed, narrowly rhombic-elliptic, extending from near tip of spur to tip of involucral tube, $13-18 \mathrm{~mm}$. long, 3-4.5 mm . wide, the free margin forming an obtuse angle at the widest point, the lobes incurved at and above this point, thus arching over and partially concealing the medial lobes and the accessory involucral lobes; the medial spur lobes arising at or near the apex of the spur, rectangular-deltoid, $5-8 \mathrm{~mm}$. long, 3-4 mm . wide at base, tapering evenly to truncate apex $1.5-2 \mathrm{~mm}$. wide, lobes slightly concave-folded above, this much accentuated in pressed material, the basal portions (up tc 2 mm .) of lobes connected to the posterior wall of the spur by small spur partitions scarcely developed anterior to the glands; glands smooth, orbicular-oblong, lateral glands $1-1.5 \mathrm{~mm}$. wide, $1.5-2 \mathrm{~mm}$. long, sometimes auricular twisted, medial glands in pairs, each pair placed back to back on the partition and touching at the margin of the partition, somewhat curved and sometimes subquadrate, $0.8-1.5 \mathrm{~mm}$. wide, $1.2-2 \mathrm{~mm}$. long; bracteoles absent or poorly developed, bracteole-ridges up to 8 mm . long and few filamentous bracteoles $4-5 \mathrm{~mm}$. long sometimes present; staminate flowers $35-52$, pedicels glabrous or apically hispidulous-puberulent, $9-14 \mathrm{~mm}$. long, filaments $2.5-3 \mathrm{~mm}$. long, glabrous to hispidulous-puberulent (especially terminally), anther ca. 1 mm . long, usually glabrous but occasionally sparsely puberulent; pistillate pedicel puberulent or densely puberulent, ovary trigonous-conic, ca. 2 mm . long, style 6-9 mm . long, trifid, style branches puberulent, ca. 1 mm . long, sub-entire to distinctly bifid; capsule deeply trilobed in cross section, subquadrate in outline, $7-10 \mathrm{~mm}$. long; seeds grey-tan mottled, turgid, subquadrate in outline, base obtuse, terminally apiculate, raphe dark and flanked by lighter bands, seeds $4.5-5.5 \mathrm{~mm}$. long, 4-4.25 mm . wide.

Specimens seen: Mexico. Nayarit: 7 mi . E. of San Blas, Dressler 1082 (GH); 29 mi . So. of Compostela, Dressler 1064 (GH). Jalisco. vicinity of San Sebastián, 3850-5000 ft., E.W. Nelson 4090 (GH, US) ; Santa Cruz de Vallarta, 300 m., Mexía 1255 (A, f, gh, mich, mo, NY, UC, US) ; upper slopes of barranca above summit of pass 9 mi . S. W. of Autlán, toward Manzanillo, McVaugh 10235 (GH, MICH) ; mountain summits $9-10 \mathrm{mi}$. S. W. of Autlán, 1300-1600 m., McVaugh 14199 ( MICH) ; along highway $15-18 \mathrm{mi}$. S. W. of Autlán, $900-1200 \mathrm{~m}$., McVaugh 119.38 (GH, MICH). Michoacán. Huizontla, Coalcomán, 600 m., G. B. Hinton et al. 15793 (AhFH, F, NY, U, UC, US). Guerrero. Guayameo-Santa Teresa, Mina, 1040 m., G. B. Hinton 9955 (AhFH,

F, G, K, NY, U, US) ; by the trail to Cundan-Grande, San Antonio, Montes de Oca, G. B. Hinton et al. 11678 (AHFH, F, GH, K, NY, U, UC) ; San Antonio,Montes de Oca, G. B. Hinton et al. 14004 (AhFH, F, GH, NY, U, UC, US) ; El Plato, Galeana, G. B. Hinton et al. 14379 (AHFH, GH, NY, US) ; Plato, Galeana, 1250 m., G. B. Hinton et al. 14991 (US) ; Puente del Rey, Galeana, 1000 m., G. B. Hinton et al. 11187 (AHFH, ARIZ, GH, K, NY, US) ; Plan de Carrizo, Galeana, 900 m., G. B. Hinton et al. 11058 (A, GH, K, NY, US) ; Sierra Madre, 1500 m., E. Langlassé 808 (GH, K). Without exact locality. Nueva España, Sessé, Mociño, Castillo and Maldonado 1768 (F).


Distribution and habitat. (Map 2) From near sea level to $1,500 \mathrm{~m}$. alt. along the western edge of the Sierra de Volcanes and the Sierra Madre del Sur, from Nayarit to north-central Guerrero. In Nayarit, this species was found along small streams in Orbignya palm forest (the palm forest is broken by scattered dicot trees along the streams) and in tall mixed forest. Data on collectors' labels, "dense shade," "forest by the river," "moist woods," "cañon bottom," "ravines," etc., indicate that these habitats may be fairly characteristic for the species. Flowering in winter, November to April.

Common names. Jumete, western Jalisco.
Variation. Leaf shape varies from narrowly elliptic (cuneate base and acute apex) to larger and broadly obovate
(obtuse base and apex) and is fairly constant for a given collection, but shows no clear-cut geographic pattern. Size of cyathium also seems to show no distinct geographic pattern, but this is obscured by differences in season of collection, the first formed cyathia usually being the largest on a given plant. The fruits and seeds (though these are poorly sampled) are apparently larger in southern plants than in the northern ones. The bracteoles tend to be better developed and the glands to be more nearly terminal in the spur (the spur partitions less well developed) in the southern collections. Langlassé 808 is distinctive in its relatively small leaves and its compact inflorescence (short internodes and peduncles) with relatively large bracts. It probably represents a population which has not been sampled by more recent collectors. Cultivated material of Dressler 1064 (Nayarit) consistently bears the cyathia upside-down as compared with all other species of Pedilanthus (in Plate XVI the cyathia are drawn in the upright position for better comparison with other species) ; the long peduncles, in effect, undergo resupination, and the large spurs are borne beneath the involucral tube, which, like the peduncle, is horizontal. The spur would seemingly serve its normal function quite well in this position, the anthers and stigma lobes touching the visiting hummingbird on the forehead rather than the chin. It is difficult to determine the posture of the cyathia from herbarium material ; the cyathia of the Langlassé collection discussed above, at least, seem not to be resupinate, and it seems improbable that its relatively short peduncles could twist in the same manner as the longer ones more characteristic of the species. This resupination, thus, may not be universal in P. Palmeri.

Relationship. Pedilanthus Palmeri is very distinctive in the position and great development of the lateral spur lobes and in the origin of the medial spur lobes near the apex of the spur. The unusual posture of the cyathia of at least some plants (discussed under Variation) is also unique. In aspect of the plant and structure of the cyathium, $P$. Palmeri resembles $P$. Finkii, and the two are doubtless closely related. They do not seem to be very close, in morphology, to any other species. The well developed and distinct spur lobes, the many staminate flowers, the short involucral tube,
and the evergreen habit may be interpreted as primitive features in P. Palmeri.

Notes. The only material seen of Emrick 80 the type of $P$. peritropoides, is badly moulded and quite lacking in cyathia or complete bracts. The lateral view of the cyathium as sketched by Millspaugh (in herb. F) is distinctly that of $P$. Palmeri, and the available foliar scraps do not differ in any way from that species. The other drawing made by Millspaugh shows the spur lobes and indicates that he dissected out the median accessory lobe of the involucral tube and interpreted this as a third spur lobe. The other species described by Millspaugh as having a "tripartite appendix lobe" is discussed under $P$. tithymaloides ssp. parasiticus, and here, too, the cyathium was apparently discarded after being sketched and described.

## 2. Pedilanthus Finkii Boissier

## Plates XIII \& XVI, Map 2

P. Finkii Boiss., DC. Prod. $15(2)$ : 1261. 1866. Type: Found in a single spot at the source of the Atoyac River in a very damp situation, from D. Hanbury IV/1865, from H. Finck, Córdova, Mexico (K!). Tithymalo[i]des Finkii (Boiss.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891.

Evergreen shrub (?), young stems sub-herbaceous, glabrous; leaves glabrous, oblanceolate to obovate-oblanceolate or oblong-oblanceolate, $11-14 \mathrm{~cm}$. long, $2.8-5.8 \mathrm{~cm}$. Wide, base cuneate, apex acute to obtuse, apiculate, midrib carinate beneath, petiole $7-12 \mathrm{~mm}$. long, stipules brown, spur-like, ca. 0.5 mm . long; inflorescence terminal, of one terminal and often 1 or 2 pedunculate, upper-axillary cymes, internodes (3-) $5-30 \mathrm{~mm}$. long, puberulent; bracts elliptic-oblong to ellipticcbovate, acute or obtuse, $6-9 \mathrm{~mm}$. long, $2.5-5 \mathrm{~mm}$. Wide, glabrate or sparsely puberulent, semi-persistent, green or pale pink (apparently); peduncles $7-10 \mathrm{~mm}$. long, puberulent; cyathium cuneate at base, involucral tube green, $9-10 \mathrm{~mm}$. long, glabrous or glabrate without excent near puberulent margins, puberulent within, lobes thin, main lobes ovate-oblong to oblong, obtuse, ventral margins free ca. 3.5-4 mm ., accessory lobes ligulate, densely appressed-puberulent, obtuse, $0.8-1.5 \mathrm{~mm}$. wide, lateral lobes slightly shorter (to 0.5 mm .) than main lobes, free $1.5-2 \mathrm{~mm}$. lateraliy, $2-3 \mathrm{~mm}$. medially, median lobe slightly shorter (to 0.5 mm .) than lateral lobes; spur pink, glabrous without, glabrate or puberulent within, arising near the peduncle and diverging nearly perpendicular to the axis of the involucral tube, at ca. $3 . \overline{5}-4 \mathrm{~mm}$. from the tube ( 7 mm . from peduncle) the spur bending abruptly forward and expanding into an inflated, semicircular hood flattened parallel to the involucral tube, this hood $7-8 \mathrm{~mm}$. in width and $8-12 \mathrm{~mm}$. long, the anterior edge reaching or surpassing the tip of the involucral tube; the medial and lateral spur lobes completely
connate, leaving a semicircular orifice ca. 1.5 mm . wide over the accessory involucral lobes at ca. 4 mm . from the apex of the involucral tube, the apices of the spur lobes (margin of orifice) thickened and densely puberulent within; glands sessile or slightly stipitate, flattened or somewhat folded, at the posterior curve of the spur or on the roof of the spur anterior to the curve, the medial glands anterior to the lateral glands; lateral glands semi-orbicular, $1-1.2 \mathrm{~mm}$. in diameter, medial glands each single, sub-rectangular, ca. $0.8 \times 1.2 \mathrm{~mm}$. ; partition none; bracteoles 1 -several in a cluster, filamentous, $3-6 \mathrm{~mm}$. long, cluster united basally; staminate flowers $30-37$, glabrous, pedicels $8-10 \mathrm{~mm}$. long, slender, filaments ca. $3-3.5 \mathrm{~mm}$. long, pistillate flower glabrous, pedicel $7-8 \mathrm{~mm}$. long, ovary spheric-ovoid, ca. 1.5 mm . long, style slender, ca. $7-10 \mathrm{~mm}$. long, trifid, branches attenuate, ca. 1.5-2 mm . long, entire or slightly bifid; fruit $6-7 \mathrm{~mm}$. long, sub-orbicular in outline, deeply trilobed in cross section; mature seed unknown.

Specimens seen: Mexico. Veracruz. Potrero, Vallée de Córdova, E. Bourgeau 1802 (F, P) ; Córdoba, Galeotti 875 (F, G). Cultivated at the Missouri Botanical Garden, from the Mexican Commission of the Louisiana Purchase Exposition, 1904, geographic source unknown, Jan. 21, 1907, C. H. Thompson (A, F, Mо, photos of living plant F, mo).

Distribution and habitat. (Map 2) Known only from the vicinity of Córdoba, Veracruz. The data accompanying the type collection indicate a rather moist habitat, as does the presence of epiphyllous bryophytes on the same collection, and a fragment of Peperomia (P. Deppeana or P. quadrifolia) pressed with Bourgeau 1802. From the scanty data, the locality and the texture of the plant, this may occupy the most mesic habitat of the genus.

Variation. There is little variation in the small sample available. The leaves of the plant cultivated at Missouri Botanical Garden are narrower and more acute than most leaves of the other collections, and the glands of Bourgeau 1802 are much further forward in the saccate spur than are those of the other collections. The type collection has quite large involucres.

RELATIONSHIP. This species is remarkable for the complete connation of the spur lobes and the hood-like, saccate spur parallel with the involucral tube. It is too similar to $P$. Palmeri to warrant the maintenance of section Calceolastrum.

## 3. Pedilanthus calcaratus Schlechtendal

## Plates XIII \& XVI, Map 3

P. calcaratus Schlecht., Linnaea 19: 255. 1847. Neotype (here chosen): Mexico, Veracruz, Barranca near Corral de Piedras,

Zacuapán, March, 1916, C. A. Purpus 7544 (UC 185411:, isotypes: A!, GH!, mo!, NY!, us!). - Tithymalus calcaratus (Schlecht.) Croiz., Am. Jour. Bot. 24: 704. 1937.
P. Ghiesbreghtianus Baill., Adansonia 1: 340. 1861. Type: A plant grown in Paris from material collected by Ghiesbreght in Mexico, no herbarium material has been located. - Tithymalo[i]des Ghiesbreghtianum (Baill.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891.
P. macradenius Donnell Smith, Bot. Gaz. 19: 263. 1894. Type: Guatemala, Canibal, Dept. Huehuetenango, alt. 3,180 ft., Dec., 1891, W. C. Shannon 412 (US 931112!). - Tithymalus macradenius (Donn. Sm.) Croiz., Am. Jour. Bot. 24: 704. 1937.
P. Purpusii Brandegee, Univ. Calif. Pub. Bot. 4: 377. 1913. Type: Mexico, Veracruz, Barranca de Santa María y Ternera, Zacuapán, Feb., 1912. C. A. Purpus 5759 (UC 155224!, isotypes: A!, GH!, mo!). - Tithymalus Purpusii (Brgee.) Croiz., Am. Jour. Bot. 24: 704. 1937.

Shrub or slender tree, generally deciduous, 1.5-7 m. tall; several of the roots thickened and farinaceous, to 2.5 or 3 cm . in diameter; stem glabrous, green when young, forming grey bark with age; leaves obovate or oblong-obovate, occasionally elliptic or oblong, 12-22 cm. long, $4.5-9.5 \mathrm{~cm}$. wide, obtuse to acute or sub-acuminate, mucronulate, base obtuse to cuneate, upper surface glabrous to sparsely sericeouspuberulent, lower surface glabrous to densely sericeous-puberulent, midrib carinate beneath, petiole $4-5(-7) \mathrm{mm}$. long, stipules dark brown, pulvinate or conic, ca. 0.5 mm . in height and diameter; inflorescence of congested cymes, upper axillary and terminal or occasionally terminal only, internodes $1-3(-4) \mathrm{mm}$. long, very densely hispid-pilose; bracts red or green, broadly obovate, or occasionally oblong-ovate, acuminate, densely pilose within, glabrate to densely pilose without, 6-11 mm . long, $4-7 \mathrm{~mm}$. wide; peduncle $7-11 \mathrm{~mm}$. long, hispid-pilose; involucral tube green beneath, pink to red above, glabrous or sparsely to densely hispidulous, densely sericeous-pilose within, 9-13 mm. long; main lobes oblong or cuneate-oblong, obtuse, free beneath for 3-7 mm ., sometimes forming a slight mentum at ca. $3.5-6 \mathrm{~mm}$. from the peduncle; accessory lobes ligulate to spatulate-ligulate, 1-1.1 mm. wide, hispidulous above, ciliate, lateral lobes $0.8-2 \mathrm{~mm}$. shorter than main lobes, free $1.5-2.5 \mathrm{~mm}$. laterally and $2-4 \mathrm{~mm}$. medially, median lobe sub-equal; spur pink to red, projecting obliquely, subterete, blunt, $7-13 \mathrm{~mm}$. long ( $5.5-10 \mathrm{~mm}$. from involucral tube), glabrous or glabrate to hispidulous, lateral spur lobes tapering evenly (rarely abruptly) from ca. 2 mm . anterior to the apices of the medial lobes, pinched together at ca. $3-4 \mathrm{~mm}$. anterior to the apices of the medial lobes, medial lobes arising (medially) at ca. $2-5 \mathrm{~mm}$. from apex of spur, $3.5-5 \mathrm{~mm}$. long, $2-3 \mathrm{~mm}$. wide, free laterally $2-3 \mathrm{~mm}$., median and lateral sutures salient as low keels, lobes ovate or deltoid-ovate, terminally slightly folded above, obtuse or shallowly retuse, with a thickening beneath for $1-2 \mathrm{~mm}$. projecting backward as a hispidulous point; glands 2 (rarely 4), sub-terminal, lateral (morphologically the medial glands), ovate to oblong, often auriculate twisted, $1.2-2.5 \mathrm{~mm}$. long, 1-1.5 mm. wide, the anterior portion often twisted slightly laterally about the small partition (in one collection, Hinton 18772, the partitions relatively well developed and the glands folded equally
about them), rarely (in some cyathia of Palmer 1328) the lateral glands developed, these small, ca. $0.5-1 \mathrm{~mm}$. in diameter and ca. 1 mm . directly anterior to the medial glands, spur partitions small, 0.5 mm . or less in height, the lateral chambers completely concealed beneath the glands; bracteoles numerous, filamentous, $5-14 \mathrm{~mm}$. long, twisted among the staminate pedicels, sometimes ligulate and/or sparsely pilose basally, united basally into partitions and connate with wall of involucral tube for $2-3 \mathrm{~mm}$.; staminate flowers 20-38, glabrous, pedicels $10-15 \mathrm{~mm}$. lang, filaments $2.5-4 \mathrm{~mm}$. long; pistillate flower glabrous, pedicel $7-13 \mathrm{~mm}$. long, ovary ovoid, trigonous, ca. 2 mm . long, style $5.5-9 \mathrm{~mm}$. long, trifid, the branches $0.5-1.5 \mathrm{~mm}$. long, bifid, connivent, upturned; capsule sub-quadrate, deeply 3 -lobed, ca. $6-7 \mathrm{~mm}$. in diameter; seeds ovoid to sub-rectangular in outline, grey-tan to reddish grey-brown, $4.5-5 \mathrm{~mm}$. lang, $3-4 \mathrm{~mm}$. wide, faintly pebbled at each end, weakly keeled dorsally and laterally, more or less flattened on radial surfaces, obtuse basally, broadly acute apically, hilum in concavity.

Representative specimens seen: Mexico. Sinaloa: Sierra de Chabarría, 1921, J. González Ortega 4066 (US). Nayarit: 10 mi . south of Compostela, Dressler $106 \mathrm{i}^{2}$ (GH) ; María Madre, Tres Marías Is'ands, Ferris 5700 (DS, Mo, us). Jalisco. Los Reyes to San Felipe de Hijar, alt. 1,425 m., Mexía 1922 (A, F, GH, NY, US). Michoacán: Chacalapa, Distr. Coalcomán, G. B. Hinton 13772 (GH, NY, uS) ; San José, Distr. Coalcomán, 700 m., G. B. Hinton 15892 (A, NY, U, US). Guerrero. Between km .335 and km. 340 on old highway Mexico-Acapulco (ca. $35-40 \mathrm{~km}$. beyond Chilpancingo), Nov., 1954, R. Oberg s. n. (GH). Veracruz: Zacuapán, leaves only, Purpus 7676 (GH, MO, NY, UC, US) ; barranca near Rancho Remudadero, Purpus 14279 (A, F) ; Barranca de Consoquitla, Mirador (there are 8 sheets with this data, labeled Liebmann 5721 and collected at different dates in 1841-1843, all at C) ; Los Baños, 18 mailen von Vera-Cruz, 100', C. Heller 192 (w); barranca near Camerón [Camarón?], Purpus 8912 (UC). Oaxaca: Cafetal Nueva Esperanza, 950 m., Reko 3574 (US) ; Cerro Concordia, 650-800 m., Morton and Makrinius 3678 (US). Chiapas: Encañada camino La Chacona a San Fernando cerca Tuxtla Gutiérrez, 1,100 m., Miranda 5121 (MEXU); Encañada entre La Chacona y El Aguacate N. O. Tuxtla Gutiérrez, 800 m., Miranda 6125 (mexu); Cerros Don Ventura 10 km . N.N.O. Tuxtla Gutiérrez, $1,200 \mathrm{~m}$., Miranda 5094 (MEXU); El Real, ca. 30 km . E. of Ocosingo, Dressler 1766 (GH) ; San Juan del Río - Zapaluta, 1,300 m., Quarles van Ufford 364 (U). Guatemala. Huehuetenango, between La Libertad and Paso del Boquerón, along Río Trapichillo, 1,200-1,800 m., Steyermark 5110.3 (A, F).

Distribution and habitat. (Map 3). On the western escarpment of Mexico from southern Sinaloa to northern Michoacán, on the eastern escarpment in central Veracruz, in the Sierra Madre del Sur of Guerrero and Oaxaca, in Chiapas and the adjacent Dept. of Huehuetenango, Guatemala; at elevations of 200 to $1,300 \mathrm{~m}$. In Nayarit, this species is a constituent of tropical deciduous forest (the Short-tree

Forest of Gentry, 1942). In northeastern Chiapas, it is found in local low tropical deciduous forest. Near El Sumidero, Tuxtla Gutiérrez, Chiapas, it is found in tropical deciduous forest on rocky limestone slopes at about $1,000 \mathrm{~m}$. elevation (see fig. 22). At higher altitudes in this same area, $P$. calcaratus ranges into a more mesic vegetation, transitional to the Selva alta subdecidua of Miranda (1953) ; on these higher, moister slopes the land is suitable for coffee cultivation. As far as is known, this species is found in

tropical deciduous forest or in rocky sites in more mesic vegetation. It is probably not nearly so rare as the known localities would seem to indicate. Flowering in winter and spring (November to May).

Professor Miranda states (personal communication) that, at El Sumidero, the deciduous habit is somewhat facultative, plants in slightly moister sites often retaining their leaves during the winter, but the leaves usually inrolling to some degree.

I am unable to locate the Sierra de Chabarría in Sinaloa, and have mapped the González Ortega collection as being inland from Mazatlán, near the Durangan town of Chabarría.

Common names. Zapato del diablo (Sinaloa), candelilla (Michoacán), suelda consuelda (Chiapas), Pie de niño (Guatemala), Tetlatil (Veracruz; Nahuatl, te-tlatia, "[that which] burns one").
Variation. This species is relatively uniform in its distinctive characters, but, as would be expected from its wide range, varies in several features. The thickness of the twigs varies considerably and is probably to be correlated with the dryness of the habitat, the thicker stemmed plants being found in drier areas. At the site near Tuxtla Gutiérrez, Chiapas, it was noted that the plants at lower (and drier) elevations had larger leaves and thicker stems than those on higher slopes in the same area. Leaf size and shape vary somewhat; the Veracruz collections show membranous, cuneate, sub-acuminate leaves, and the Oaxacan collections tend to be thicker and more glossy than most. Dressler 1766 (eastern Chiapas) has unusually narrow and puberulent leaves. The leaf pubescence varies, but seems to show the full range of variation at every locality that has been well sampled. The size of the cyathia varies from very small forms (involucral tube ca. 9 mm . long, spur 5.5-6.5 mm . long) in Michoacán to the very large types (involucral tube $11-13 \mathrm{~mm}$., spur $10-12 \mathrm{~mm}$.) from Jalisco to Sinaloa; plants of other areas have cyathia which tend to be intermediate in size. In the material from Veracruz the involucral tube and, usually, the spur are sparsely to rather densely hispidulous; the involucres are glabrous without at all other localities.

The one collection from the Tres Marias Island (Ferris 5700 ) is especially interesting, and adequate material might show that the insular population should be recognized as a distinct entity. The material available was collected at the start of the flowering season, and only two mature cyathia have been seen. The cymes are all terminal and the leaves are notable for being oblong and very glossy in appearance. It is possible that this plant is evergreen.

Relationship. In habit this species resembles $P$. coalcomanensis and $P$. pulchellus, especially the latter, and the internal pilosity of the involucre indicates the same relationship. The reduced number of glands does not necessarily indicate a relationship to $P$. bracteatus, since both species
sometimes show the primitive condition of 4 glands. The obtuse (rather than truncate) spur and the wide spur lobes with keeled sutures and thickened apices, however, would seem to indicate a distinct relationship to $P$. macrocarpus and $P$. bracteatus.

Notes. Though this species was described in "Plantae Lieboldianae," no Liebold collection number was given, as with the other species described there, and Schlechtendal comments on the lack of leaves, "da Schiede sagt, dass sie ohne blätter blüht, . . " On this basis, it is probable that he had at hand a Schiede collection from Veracruz. Though no probable type specimen has been found (the type presumably was destroyed at Berlin), there is little doubt that this is the species described by Schlechtendal. The wide, semi-circular leaf scars, the short cymes with close-set bract scars, the pubescent peduncle and involucre, and the size of bract and cyathium all point not only to this species but to material from Veracruz. Purpus 7544 is chosen as neotype, because it is well distributed, relatively well preserved, and from the region of the type locality; the specimen at the University of California is much the best. Liebmann's collections (all of which had been correctly determined as P. calcaratus) are in very poor condition.

Pedilanthus Ghiesbreghtianus, described from cultivated material, also applies to this species, as indicated by the large leaves, the number of glands, the internal tomentum of the involucre and the "plumose" accessory involucral lobes.

At El Real, Chiapas, the writer was informed that the latex of this plant was used to remove the "comoyote," a skin parasite.

## 4. Pedilanthus gracilis sp. nov.

## Plate XVII, Map 3

Shrub or small tree, ca. 2 m . tall; stem woody, moderately slender, glabrous; leaves glabrous, broadly oblanceolate, elliptic-obovate or elliptic, 9.5-17.5 cm. long, 3.8-6 cm. wide, apex acuminate, basally narrowly obtuse or cuneate, midrib moderately keeled, petiole $2-5 \mathrm{~mm}$. long, stipules low, blunt, ca. 0.4 mm . across; cymes terminal and upper axillary, lax, leafy lanceolate bracts ca. $3-3.5 \mathrm{~cm}$. long and $0.8-1 \mathrm{~cm}$. wide, sometimes persisting beneath the cymes at anthesis, internodes $3-11 \mathrm{~mm}$. long, hispidulous about base, bracts oblonglanceolate or elliptic-oblong, long-acuminate, glabrous without, pilose-
sericeous within, $9-11.5 \mathrm{~mm}$. long, $2.5-5 \mathrm{~mm}$. wide, peduncle slender, $8-12 \mathrm{~mm}$. long, basally $1 / 2-2 / 3$ hispidulous; involucre red, at least above, glabrous without, involucral tube sericeous-pilose within, ca. 10 mm . long, main lobes cuneate-ovoid, obtuse, free beneath for 3.5-4 mm ., accessory lobes ligulate, ca. $0.7-0.8 \mathrm{~mm}$. wide, hispidulous above, ciliate, obtuse, lateral lobes ca. 1 mm . shorter than main lobes, free ca. 1.5 mm . laterally and $2.5-3 \mathrm{~mm}$. medially, median lobe subequal; spur projecting obliquely, tapering, blunt, ca. 10 mm . long ( 7 mm . from involucral tube), glabrous without, hispidulous within, medial lobes arising (medially) at ca. $3-3.5 \mathrm{~mm}$. from apex of spur, ca. 4 mm . long, 2 mm . wide, free laterally ca. 3.5 mm ., more or less ovate, obtuse, terminally folded, but with only a slightly recurved point; glands two, ca. 1 mm . from apex of spur, lateral, suborbicular to oblong-orbicular, somewhat folded, $1.2-1.3 \mathrm{~mm}$. long, $1-1.2 \mathrm{~mm}$. wide, spur partition small, ca. 0.5 mm . high, the lateral chambers concealed beneath the glands; bracteoles numerous, filamentous, $6-10 \mathrm{~mm}$. long, twisted among the staminate pedicels; staminate flowers ca. 30-35, glabrous, pedicels $10-11.5 \mathrm{~mm}$. long, filaments $1.2-2 \mathrm{~mm}$. long; pistillate flower glabrous, pedicel $10-12 \mathrm{~mm}$. long, ovary ovoid, trigonous, ca. 2 mm . long, style slender, $7-8 \mathrm{~mm}$. long, trifid, the branches ca. 0.4 mm . long, bifid, connivent, upturned; fruit and seed unknown.

Frutex vel arbuscula, ca. 2 m . alta; foliis glabris, oblanceolatis, elliptico-obovatis vel ellipticis, $9.5-17.5 \mathrm{~cm}$. longis, $2.8-6 \mathrm{~cm}$. !atis, acuminatis, cymis terminalibus et axillaribus, laxis, internodiis 3-11 mm . longis, bracteis oblongo-lanceolatis vel elliptico-oblongis, longe acuminatis, extus glabris, 9-11.5 mm. longis, 2.5-5 mm. latis; pedunculis tenuibus, $8-12 \mathrm{~mm}$. longis; involucris extus glabris, intus sericeopilosis, ca. 10 mm . longis, calcaribus ca. 10 mm . longis, 2 mm . latis, ovatis, obtusis, glandulis 2 , suborbicularibus; floribus masculis $30-35$, glabris, pedicellis $10-11.5 \mathrm{~mm}$. longis; floribus foemineis glabris, pedicellis $10-12 \mathrm{~mm}$. longis, ovario ovoideo, ca. 2 mm . longo, stylis tenuibus, $7-8 \mathrm{~mm}$. longis; fructus seminaque ignota.

Mexico. Guerrero, Dist. Galeana, Atoyac, 240 m., Nov. 25, 1937, wooded hill, tree 2 m ., fl. red, sap milky, (feo. B. Hinton et al 10973 (type: GH!, isotypes: AhFH!, к!, mich!, NY!, UC!).

Distribution and Habitat (Map 3). Known only from the type locality, which is near the coast north of Acapulco. The area immediately about Atoyac is thorn forest, but at slightly higher elevations, as at "la Mina," the vegetation is tropical deciduous forest. Inquiry among the residents, in the summer of 1954 , disclosed that the plant sought was probably "gallitos," which might be found in "la Sierra" beyond the mine and on a different road. Limited time prevented another trip in search of the plant.

Relationship. Closely related to $P$. calcaratus, from which it is distinguished by a number of details. It is possible that this will prove not to be specifically distinct from that species, but the nearest collection, geographically (which,
however, is from the other side of the coastal mountain range), is quite distinct.

## 5. Pedilanthus pulchellus sp . nov.

## Plate XVIII, Map 4

Shrub or small tree (?), evergreen; stem woody, slender, glabrous; leaves glabrous, glossy, $5.5-10.5 \mathrm{~cm}$. long, 2.2-3.5 cm. wide, oblong to elliptic, obtuse or broadly acute, apiculate, basally obtuse or cuneateobtuse, midrib weak!y keeled, petiole $2-3 \mathrm{~mm}$. long, stipules small, conic, brown, caducous, ca. 0.3 mm . long and 0.2 mm . in width; cymes terminal and upper axillary, congested, internodes ca. $0.5-1 \mathrm{~mm}$. long, sparsely puberulent, bracts broadly ovate, acute, ca. 6 mm . long, 4-4.5 mm . wide, glabrate within, puberulent without along margin and midvein, peduncle finely puberulent, ca. 5 mm . long; involucre red throughout, sparsely and finely crisped-puberulent without, involucral tube ca. 10 mm . long, sericeous within, main lobes oblong, obtuse, free beneath for ca. 4 mm ., accessory lobes puberulent, ligulate, ca. 0.7-0.8 mm . wide, ca. $1.7-2 \mathrm{~mm}$. shorter than main lobes, subequal, lateral lobes free ca. 1 mm . laterally and 2 mm . medially; spur projecting obliquely, ca. 6 mm . long (from peduncle), flattened, truncate, ca. 5 mm . wide terminally, glabrous within gland chamber, otherwise puberulent within, lateral lobes very narrow, medial lobes arising at ca. 2.5 mm . from apex of spur, lance-ligulate, obtuse, ca. 4 mm . long, $1.5-2 \mathrm{~mm}$. wide basally, ca. 0.8 mm . wide terminally, lateral glands subterminal, oblong, ca. 1 mm . long and $0.7-0.8 \mathrm{~mm}$. wide, medial glands entire or divided, curved about short terminal partitions, $0.5-0.8 \mathrm{~mm}$. wide, ca. 2 mm . long if entire, or each half ca. 1 mm . long, spur partitions small; bracteoles filamentous, ca. 6 mm . long, roof lobules present and conspicuous; staminate flowers ca. 27-30, pedicels ca. 8 mm . long, terminally sparsely puberulent, filaments glabrous, ca. 1.5 mm . long, anthers glabrous; pistillate pedicel sericeous-puberulent, ca. 5 mm . long, not elongating, ovary ovoid, glabrous, style sparsely puberulent, ca. 7 mm . long, branches ca. 0.5 mm . long, bifid; fruit and seed unknown.
Frutex vel arbuscula; foliis glabris, nitidis, $5.5-10.5 \mathrm{~cm}$. longis, 2.2-3.5 cm. latis, oblongis vel ellipticis; cymis terminalibus et axillaribus, condensatis, internodiis ca. $0.5-1 \mathrm{~mm}$. longis, bracteis late ovatis, ca. 6 mm . longis, $4-4.5 \mathrm{~mm}$. latis, pedunculis ca. 5 mm . longis; involucris extus minute crispato-puberulentis, intus sericeis, ca. 10 mm . longis, calcaribus ca. 6 mm . longis, planis, truncatis, lobis centralibus lanceclato-ligulatis, obtusis, ca. 4 mm . longis, $1.5-2 \mathrm{~mm}$. latis, glandulis $4-6$, glandulis lateralibus oblongis, ca. 1 mm . longis, glandulis centralibus integris vel divisis, ca. 1 vel 2 mm . longis; floribus masculis ca. $27-30$, pedicellis ca. 8 mm . longis, apice sparse puberulentis, filamentis glabris; pedicellis foemineis sericeo-puberulentis, ca. 5 mm . longis, non elongatis, ovario glabro, ovoideo, stylis puberulentis, ca. 7 mm . longis; fructus seminaque ignota.

Mexico. Oaxaca. Distrito de Pochutla, Cerro Espino, 1,200 m., April 12, 1917, C. Conzatti, Reko and Makrinius 3106 (type: us 763840!, isotype: MEXU!).

Distribution and Habitat (Map 4). This distinct new species is known only from the type locality, which is apparently north of Pochutla, Oaxaca. The altitude in this region is moderately high, and the area is one in which coffee is a principal crop, so this evergreen, non-succulent species probably occurs in a relatively mesic habitat.

Relationship. This species is clearly related to $P$. coalcomanensis, as indicated by the non-exserted ovary, the form of the involucre, and habit. It is less specialized than that species in the free spur lobes and the smaller, caducous bracts. Pedilanthus pulchellus resembles P. calcaratus in habit and the form of the cymes, but it does not approach that species in the features of the involucre. The major phylogenetic interest of this new species is in providing a better link between the $P$. tithymaloides species group and the remainder of the genus. Pedilanthus pulchellus resembles the $P$. tithymaloides group in the basally thickened accessory involucral lobes, the form of the cymes and bracts, and in textural features. The non-elongating pistillate pedicel of this species and $P$. coalcomanensis is also found in some populations of $P$. tithymaloides.

Notes. With the type specimen are two branches of $P$. calcaratus; this same mixture occurs in the isotype. These are in advanced flowering condition, with dried involucres, young capsules and young leaves developing. They are somewhat discolored, and suggest that they may not have been collected and dried with the material of $P$. pulchellus, which is very well dried and not at all discolored. There must thus remain some doubt as to whether they were collected together and as to the correctness of the data.

## 6. Pedilanthus coalcomanensis Croizat

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\text { Plate XIX, Map } 4
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P. coalcomanensis Croiz, Jour. Wash. Acad. Sci. 33: 19. 1943. Type: Sierra Naranjillo, 1,550 m., Distr. Coalcomán, Michoacán, Mexico, March 11, 1941, woods, tree 5 m., bract red, fl. green, stamens red, "candelilla," George B. Hinton, et al 15765 (us 1808071!, isotypes: AhFH!, F !, NY!, UC!, Us!).

Deciduous tree $3-7 \mathrm{~m}$. tall, stem finely pilose-tomentose when young, glabrate the second year, soon forming a smooth brown-grey bark; leaves oblong-elliptic, $10.5-17.5 \mathrm{~cm}$. long, 5-7 cm. wide, base obtuse, apex obtuse or very broadly acute, leaves sparsely and minutely pilose above, finely puberulent-tomentose beneath, especially along midrib
and veins, midrib prominent beneath, but not carinate, petiole $3-7 \mathrm{~mm}$. long, densely pilose-tomentose; stipules ca. 0.7 mm . long, dark, pilose; inflorescence a terminal or a terminal and an upper axillary cyme, of few cyathia, cyme branching once or twice dichasially, or monochasial throughout, internodes $5-10 \mathrm{~mm}$. long, densely pilose; bracts persistent, scarlet, sparsely pilose-tomentose, ovate, subcordate, acute to acuminate, $23-30 \mathrm{~mm}$. long, $14-20 \mathrm{~mm}$. wide; peduncle $10-16 \mathrm{~mm}$. long, densely pilose; cyathium glabrous without, apparently completely red in color; involucral tube $14-18 \mathrm{~mm}$. long, finely pilose-tomentose within; main lobes asymetrically rhombic-oblong to nearly rectangular (anteriorly), tapering at an acute or nearly $90^{\circ}$ angle to the obtuse apex, forming a distinct mentum beneath (at ca. 10 mm . from the peduncle), fused to or beyond the mentum; accessory lobes ligulate-spatulate, carinate above, the apices obtuse or acute, ca. $1.5-2.5 \mathrm{~mm}$. shorter than the main lobes, median lobe subequal, lateral lobes free ca. 4-4.5 mm . laterally, 5-6 mm . medially; spur projecting obliquely, 12-15 mm . long (ca. 7 mm . from involucral tube), flattened, ca. $6-7 \mathrm{~mm}$. broad terminally, truncate, slightly 3 -lobed apically; spur glabrous within terminal gland chambers, otherwise pilose-tomentose within; lateral spur lobes lance-ligulate, tapering evenly forward to a point ca. 1.5 mm . beyond the end of the medial lobes, there each forming an obtuse angle and tapering more abruptly down to the involucral tube; medial lobes completely connate or occasionally free for ca. 0.5 mm ., together oblong-lanceolate, arising ca. $4-5 \mathrm{~mm}$. from apex of spur, $5-7.5 \mathrm{~mm}$. long, $3-5 \mathrm{~mm}$. wide basally, $1.5-2.5 \mathrm{~mm}$. wide at truncate apex, lobe deeply grooved medially beneath, terminally thickened beneath; glands flattened, sparsely pilose; lateral glands borne on lateral walls of spur, ovate-oblong or suborbicular, 1.7-2 mm. long, ca. 1.5 mm . wide, medial glands $1.7-2 \mathrm{~mm}$. wide, ca. 2 mm . long, ovate-deltoid (apex anterior), on inner walls of partitions, reaching or occasionally extending slightly around the margin of the partition (in one cyathium with short partitions, the glands oblong and equally folded about the partition margins); spur partitions completely dividing the spur apically for ca. $1.5-3 \mathrm{~mm}$., inserting above into the base of the median spur lobe and below between the accessory involucral lobes; bracteolepartitions well formed, lateral and dorsal bracteole-partitions bipartite, each with a medial, linguiform lobe ca. 5-7 mm. long, free for $1.5-3 \mathrm{~mm}$. from the remainder of the partition, the outer portion of the partition tapering upward and forward, the lateral pair inserting on the main lobes of the involucral tube, the dorsal pair running into ridges between the median and lateral accessory lobes, these ridges each terminating in a lobule (roof lobules) at the point where the accessory lobes become free; staminate flowers $35-40$, pedicels $18-22 \mathrm{~mm}$. long, pilose at least terminally; filaments $2.5-4 \mathrm{~mm}$. long, pilose; anthers sparsely pilose, ca. 1 mm . long; pistillate pedicels $5-7 \mathrm{~mm}$. long, pilose basally, not elongating, but recurving somewhat and sometimes straightening or curving upwards when the fruit matures; ovary glabrous, ovoid, trigonous, ca. 2.5 mm . long; style glabrous, ca. $7-11$ mm . lang, trifid, branches ca. 1.5 mm . long, minutely bifid; capsule subquadrate in outline; deeply 3 -lobed in cross-section, $9-10 \mathrm{~mm}$. in length and diameter; seed turgid subquadrate in outline, obtuse basally,
apiculate terminally, weakly carinate dorsally and at the base laterally; concave near the hilum, seed dark brown, with a raised, dark raphe which is flanked by lighter bands.

Specimens seen: There are four other collections by Geo. B. Hinton, all from the type locality (Sierra Naranjillo, Distr. Coalcomán, Michoacán, Mex.co) as follows: 1,440 m., Nov. 26, 1938, Hinton, et al 12685 (AHFH, GH, NY, S, UC, USS) ; 1,600 m., May 4, 1939, Hinton, et al 13733 (AHFH, GH) ; 1,580 m., May 4, 1939, Hinton, et al 1.37 .34 (AhFH, GH) ; Aug. 22, 1939, Hinton, et al 15130 (AHFH, GH).

Distribution and habitat (Map 4). Known only from the Sierra Naranjillo in northwestern Michoacán. The area is not well known, and further collection may extend its known range. No specific data are available concerning the habitat except "woods," 1,440-1,600 m. elev. From


Peters' brief description of the Coalcomán area (1954), this might be in the zone of oak forest or possibly below this, in what is probably tropical deciduous forest. Flowering in the winter (November to April). Collections made in May have only dried cyathia and fruits remaining, and the new foliage is starting. Some leaves remain on the November collection which is commencing to flower.

Common name. candelilla.
Variation. The sample is too small to show individual variation in plants at the same stage of development. Varia-
tion in the details of the spur, origin of median lobe, form of glands and development of spur partition, was observed within a single collection (Hinton 13733).

Relationsinips. The relationships of this species are with $P$. cymbiferus, $P$. macrocarpus and $P$. calcaratus, and will be discussed under those species.

Notes. One of the two truly arboreous species in the genus, this apparently narrow endemic shows the distinctive combination of connate medial spur lobes and large persistent bracts. Since the female pedicels do not elongate after anthesis, the fruit develops within and ruptures the involucral tube, exposing the wiry staminate pedicels. This feature, together with the conspicuous bracts, gives the specimens an unusual aspect. The flowering tree should be quite showy.

The specimen designated as type by Croizat (US 1808071) has the same aspect as Hinton's numbers 13733 and 13734, which were collected in May when flowering had nearly or quite ceased; and does not closely resemble the other sheets of Hinton 15765 . It is possible that mis-labeling has occurred, but no serious confusion can result in this case.

## 7. Pedilanthus cymbiferus Schlechtendal

## Plates XV \& XIX, Map 4

P. cymbiferus Schlecht., Linnaea 19: 253. 1847. Type: Tropisches Mexico, 1839 (?), E. Liebold 213 (HaL!). - Tithymalus cymbiferus (Schlechi.) Croiz., Am. Jour. Bot. 24: 704. 1937.
P. aphyllus Boiss. ex Kl. and Gke., Abh. Akad. Ber., Phys. 1859: 106. 1860. Type: Nueva España, Herb. Pavón (G!, Sessé, Mociño, Castillo and Maldonado 1741 (F!) is probably an isotype). - Tithymalo[ $i$ ] des aphyllum (Boiss.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891.

Shrub, $3-5(7.5) \mathrm{dm}$. tall, forming low, dense elumps, spreading by underground stems, these brown and ca. 5 mm . in diameter ( 30 cm . long in one specimen) ; stems slender, $2-3 \mathrm{~mm}$. in diameter, greygreen, crisp-puberulent when young, becoming heavily waxy-cutinized with age; leaves caducous, coriaceous, glabrous above, sparsely crisppuberulent beneath; 3-7 mm . wide, $3.5-11 \mathrm{~mm}$. long, rhombic-ovate to ovate, somewhat recurved, acute, basally cuneate to obtuse, midrib thickened but not conspicunus, subsessile, petiole ca. 1 mm . long, 2.5 mm . Wide, stipules brown, spur-like, ca. $0.7-0.8 \mathrm{~mm}$. long, inflorescence terminal, commonly of a terminal and then 2 lateral cyathia, internodes $3-15 \mathrm{~mm}$. long, crisp-tomentulose; bracts oblong to oblongobovate, acute, $6-8 \mathrm{~mm}$. long, $4-6 \mathrm{~mm}$. wide, crisp-puberulent without, glabrous within, peduncle $6-12 \mathrm{~mm}$. long, puberulent-tomentose basally; cyathia pinkish red, basally greenish, glabrous without, involucral tube $11-16 \mathrm{~mm}$. long, inner surface terminally tomentose, basally
glabrous, main lobes cuneate-ovate to oblong, obtuse, free beneath for 5-7 mm ., often forming a mentum at ca. $4-5 \mathrm{~mm}$. from the peduncle, accessory lobes tomentulose, ligulate, ca. 1.3 mm . wide, obtuse, carinate above, the medial lobes terminally partially concealed by the lateral lobes; lateral lobes ca. $0.7-1 \mathrm{~mm}$. shorter than the main lobes, free (2-) 3-4 mm . laterally, $3.5-5 \mathrm{~mm}$. medially; median lobe scarcely shorter (ca. 0.5 mm .) than lateral lobes; spur projecting obliquely, (9-) 11-13 mm. long ( $8-10 \mathrm{~mm}$. from involucral tube), somewhat flattened or thickened terminally, $6-8 \mathrm{~mm}$. wide, hispidulous within except near the glands; lateral lobes narrow, often narrowing abruptly ca. 0.5 mm . anterior to the apex of the medial lobes or forming a small, erect tooth or lobule there; medial lobes ligulate-lanceolate, arising ca. $3-6 \mathrm{~mm}$. from apex of spur, $6-8 \mathrm{~mm}$. long, ca. 1.7 mm . wide basally, ca. $0.8-0.9 \mathrm{~mm}$. wide terminally, truncate or obliquely concave-retuse, tomentose beneath, glands sub-terminal, lateral glands deltoid-oblong to ovate, ca. 1.5-1.7 mm . long, 1-1.2 mm. wide; medial glands laterally oblong, strongly folded about partitions, $1-1.2 \mathrm{~mm}$. wide and 2.3-3 mm. long, in some cases (Rose and Rose 11408 and Karwinski s. n.) truncately divided into gland pairs, and then each gland ca. 1.1-1.5 mm . long; partitions thick, but not dividing the spur terminally into chambers, variably well developed as ridges (0.8-1.3 $\mathrm{mm} . \mathrm{high}, 4-6 \mathrm{~mm}$. long) on the posterior wall of the spur, inserting anteriorly between the bases of the accessory involucral lobes; bracteoles well developed, numerous, filamentous, $5-12 \mathrm{~mm}$. long, basally united into a partition nearly or quite reaching the pistillate pedicel or uniting with an adjacent partition to surround the staminate cluster, roof lobules present but obscure; staminate flowers 30-42, glabrous, pedicels $13-15 \mathrm{~mm}$. long, filaments ca. 2 mm . long; pistillate flower glabrous, pedicel $12-14 \mathrm{~mm}$. long, ovary ovoid, weakly trigonous, ca. 3.5 mm . long, style $9-13 \mathrm{~mm}$. long, trifid, branches ca. 1.2 mm . long, shallowly to deeply bifid; capsule ca. $8-9 \mathrm{~mm}$. long, subquadrate, trigonous, seeds grey, minutely pebbled (tuberculate), oblong-ovoid to sub-rectangular in outline, basally truncate, terminally acute, hilum sub-terminal in a concave-flattened area, raphe dark, seed weakly keeled dorsally and somewhat angled laterally and ventrally, ca. $4.5-5.5 \mathrm{~mm}$. long and $2.5-3 \mathrm{~mm}$. in diameter.

Representative specimens seen: Mexico. Fuebla. Sept. 15, 1953, R. L. Dressler 1368 (GH); limestone hills W. of Tehuacán, Gentry 6993 (AHFH); Tehuacán, Liebmarn 5720 (C); Tehuacán, $5,500 \mathrm{ft}$., Pringle 6291 (F, G, Gif, MO, NY, P, PH, S, UC, US, W) ; near Tehuacán, J. N. and J. S. Rose 11408 (F, NY, US) ; near El Riego, Tehuacán, Sept., 1905, Rose, Painter and Rose 10022 (F, GH, US). Oaxaca. Trapiche de Aragón, 1830, L. B. de Karwinski s. n. (HAL, P, N).

Distribution and habitat (Map 4). Near Tehuacán, Puebla and apparently somewhere in Oaxaca. The habitat near Tehuacán is open desert scrub on limestone. The species is locally abundant and conspicuous when in flower. Apparently flowering over a long period in summer and early winter (coll. in May, and August to December).

There are many collections from about Tehuacán, Puebla; the only other collections with specific locality data are the Karwinski specimen from Oaxaca, and Botteri 968, which bears a form label reading "Orizaba, Mexico." It is possible that this latter is correctly labeled, but I suspect that it is not. The distance from Tehuacán to Orizaba is not great, but the towns are in very different habitats. Botteri lived in Orizaba, and it is quite likely that some collections from nearby areas were distributed with the same form label as those from Orizaba. Gates' (Cact. and Succ. Jour. $25: 176$ ) reference to a dwarf Pedilanthus at Zapotitlán de las Salinas (ca. 18 km . SW of Tehuacán, at a similar altitude) doubtless refers to this species.


Plate XV. Fig. 34. Pedilanthus c!mbiferus, a small clump in flower, near Tehuacán, Puebla, September. Fig. 35. P. macrocarpus, a small plant, near Yavaros, Sonora, December. The knife handle is about 9 cm . long.

Common name. gallitos.
Variation. The cyathia of this species vary rather strikingly. The degree of variation is not well indicated by the measurements, since (at least in Dressler 1368) the smallest cyathia often have the widest spurs. The variation may be correlated, with a large cyathium type tending to have a long spur, deltoid-ovate main lobes and a distinct
mentum beneath; and a smaller type with (proportionately) shorter spur, oblong main lobes, no mentum, and, in some, a wider spur. This impression may possibly result from a large sampling of few clones. A field study of the variation within and between clumps might prove of great interest. It is interesting that two collections with the medial glands divided (with 6 glands) were found. A single cyathium (from Purpus 3419) was seen in which the lateral halves of the medial glands were poorly developed. The Karwinski collection from Oaxaca, which is scanty and mostly badly damaged by insects, seems to fall within the range of variation of the Tehuacán material in most characters; it differs in being tomentose along the ventral midline within the involucral tube (along the line of connation of the main lobes), in having wider, more nearly orbicular, lateral glands and perhaps in less well developed bracteoles.

Relationship. This species seems most closely related to $P$. coalcomanensis, which it resembles in the form of the cyathium and the distribution of pubescence. While much more specialized than that species in its vegetative features, its cyathium is less specialized (medial spur lobes free, pistillate pedicel elongating normally and bracteoles well developed) than is that of $P$. coalcomanensis. Pedilanthus cymbiferus resembles the Sonoran Desert $P$. macrocarpus to some degree (large red cyathia, leafless grey-green stems), but these resemblances may not indicate a close relationship. There are also some resemblances (form and pubescence of cyathium) to $P$. calcaratus.

Notes. Though the smallest plant in the genus, this species has striking, large, brightly colored cyathia, and might prove to be a useful ornamental for desert gardens.

The involucral tubes (and occasionally the spurs) of Dressler 1368 were inhabited by numerous thrips of the genus Frankliniella. Some other collections contain a few mites (Phytoseiidae). Ants of several genera were observed on the involucres.

The type collection consists of an older and a younger twig and a single cyathium, which are easily recognizable as this species. Thus, $P$. cymbiferus of Schlechtendal is the correct name for the plant which has been known (in this hemisphere) as $P$. aphyllus Boiss. The name $P$. calcaratus

Schlecht. is clearly not applicable to the plants of this species.

An excellent photograph of the cyathia of this species is published in White, Dyer and Sloane, "The Succulent Euphorbieae" (Vol. 1, p. 25) as P. calcaratus.

## 8. Pedilanthus macrocarpus Bentham

Plates XV \& XIX, Map 5

P. macrocarpus Benth., Bot. Voy. Sulphur, 49, Pl. 23A. 1844. Type: Magdalena Island, Lower California, shrub 2 ft ., no foliage, fls. scarlet, George Barclay 3114 (bm, fragment F!). - Hexadenia macrocarpa (Benth.) Kl. and Gke., Abh. Akad. Berl., Phys. 1859: 107. 1860. - Tithymalo[i]des macrocarpum (Benth.) O. Kuntze, Rev. Jour. Bot. 24: 704. 1937.

Shrub, $0.5-1.5 \mathrm{~m}$. tall, branching from the base; stems thick, $5-10$ Gen. Pl. 2: 620. 1891. - Tithymalus macrocarpus (Benth.) Croiz., Am. mm . in diameter, fleshy, glabrate, the young stems puberulenttomentulose, especially in peninsular material, axillary buds densely tomentulose; leaves caducous, spatulate to ovate or obovate, the blade inrolled and fleshy in some plants. $3-10 \mathrm{~mm}$. long, $1.5-4 \mathrm{~mm}$. wide, acute or obtuse, basally obtuse or cuneate, petiole indistinct, $1-3 \mathrm{~mm}$. long; stipules absent; inflorescence terminal, of few cyathia, often on short axillary branches; internodes puberulent to tomentulose, to 3.5 mm . long, bracts tomentulose, red, elliptic-obovate to oblanceolate or nearly ligulate, acute, $5-11 \mathrm{~mm}$. long, $2-4 \mathrm{~mm}$. wide, peduncle puberulent to densely puberulent, $7-13 \mathrm{~mm}$. long; cyathia puberulent (densely tomentulose when small), red, tube $11-14 \mathrm{~mm}$. long, inner surface basally glabrous and terminally tomentulose, main lobes deltoid-ovate to oblong, obtuse or acute, free beneath for 4-7 mm., occasionally forming a slight mentum, accessory lobes tomentulose, ligulate, obtuse, ca. 1 mm . wide, the lateral lobes $1.5-2 \mathrm{~mm}$. shorter than the main lobes, free laterally for $0.5-3 \mathrm{~mm}$., medially for $0.5-5 \mathrm{~mm}$., terminally somewhat falcate (curving laterally with the margins of the main lobes), median lobe $1-2 \mathrm{~mm}$. shorter than the laterals, spur projecting obliquely, highly variable, $10-23 \mathrm{~mm}$. long ( $7-20 \mathrm{~mm}$. from involucral tube), more or less flattened and attenuate terminally, usually somewhat 3-lobed, 5-7 mm . wide at the level of the glands, solid (parenchymatous) terminally for $1-8 \mathrm{~mm}$., lateral spur lobes narrowing abruptly to the involucral tube for ca. 2 mm . beyond apex of medial lobes, medial lobes highly variable in degree of connation, deltoid-ovate, $3-4 \mathrm{~mm}$. wide basally, attenuate into a ligulate apex ca. 1 mm . wide, $3-4 \mathrm{~mm}$. long, truncate, thickened and puberulent beneath, somewhat triangular in cross section (the two apices fitting into the groove formed by the accessory involucral lobes and the lateral spur lobes), the lobes arising 3-10 $(-14) \mathrm{mm}$. from apex of spur, (3-) 5-8 mm. long, in material from Sinaloa and southern Sonora the basal portions of the lobes almost completely connate with each other and the lateral lobes, the terminal portion being free $3-5 \mathrm{~mm}$. laterally and $2-4 \mathrm{~mm}$. medially, the sutures between the basal portions of the lobes, and these and the
lateral lobes, tomentulose, raised as 3 low keels; glands 6, suborbicular to oblong, the lateral pair somewhat anterior to the medial glands, $0.7-2 \mathrm{~mm}$. long, $0.7-1.5 \mathrm{~mm}$. wide, medial glands 4 , paired on the partitions, usually well back of the partition margin, sub-terminal to ca. 9 mm . from apex of spur, $2-3 \mathrm{~mm}$. long, ca. 1.5 mm . wide (rarely, outer gland of each pair missing or an individual gland, either inner or outer, doubled), the spur divided into 3 chambers for $2-7 \mathrm{~mm}$. by 2 partitions connecting the basal portions of the medial lobes to the posterior wall of the spur, bracteoles variable, from nearly absent to several in each cluster, $3-11 \mathrm{~mm}$. long, filamentous (rarely ligulate, puberulent and vascularized), outermost connate with the involucral tube for $2-3 \mathrm{~mm}$., roof lobules present but obscure; staminate flowers glabrous, $24-45$, pedicels $12-14 \mathrm{~mm}$. long, filaments $2-4 \mathrm{~mm}$. long, anthers ca. 1 mm . long; pistillate pedicel glabrous or tomentulose, 8-13 mm. long, ovary ca. 2 mm . long, ovoid, style $6-14 \mathrm{~mm}$. long, basally thickened (ca. 1.5 mm . in diameter) so as to merge gradually with the ovary, trifid, the branches $0.5-1.5 \mathrm{~mm}$. long, entire to deeply bifid, connivent to widely spreading; fruit red, indehiscent or very tardily dehiscent, turbinate, $12-20 \mathrm{~mm}$. wide, $7-15 \mathrm{~mm}$. long, each carpel bearing 2 basal spur-like horns $1.5-4 \mathrm{~mm}$. long, the carpel wall thin and with visible lines of dehiscence in southern Baja California, elsewhere thick and parenchymatous-corky, without distinct lines of dehiscence; seeds grey to brown with a dark ventral line, sub-spheric to broadly conic-ovoid, obtuse or acute terminally, slightly flattened ventrally or on radial surfaces, $6-9 \mathrm{~mm}$. long, $5.5-8 \mathrm{~mm}$. wide.

Representative specimens seen: Mexico. Sinaloa. 70 mi . So. of Agiabampo (Sonora), ca. 50 ft. , Dressler 973 (GH). Sonora. Agiabampo, Gentry 7039 (AHFH, MICH); Agiabampo, E. Palmer 802 (F, GH, NY, US) ; Bicam, Rio Yaqui, Gentry 2192 (мо); Vicam, 200 ft ., Studhalter 1564 (US) ; 18 mi . W. of Los Arrieros on the road to Tastiota, Wiggins and Rollins 249 (A, MICH, MO, NY, US) ; San Pedro Nolasco Island, Gulf of California, Johnston 3124 (GH, UC, US). Baja California. Calamahué, alt. 950-1,000 ft., Nelson and Goldman 7136 (F, US) ; El Llano de Santana, May 10, 1889, T. S. Brandegee s. n. (F, UC) ; 3.5 mi . So. of Laguna Seca Chapala on the road to Punta Prieta, first observed here, Ferris 8678 (ny, US) ; 34 mi . No. of Punta Prieta, between Laguna Seca Chapala and Punta Prieta, $2,200 \mathrm{ft}$., Wiggins 5345 (GH, MICH, NY, UC, US) ; 24 mi . No. of Punta Prieta, Gentry $7677 a$ (AHFH) ; 29 km . No. of Punta Prieta, Carter, Alexander and Kellogg 1893 (UC, Us); Playa María, Aug., 1836, A. W. Anthony (UC) ; Los Ángeles Bay, Gulf of California, E. Palmer 605 (C, GH, us) ; 7 mi . E. of Rancho Mesquital, Shreve 6483 (ARIZ); San Borja, $28^{\circ} 47^{\prime}$ N., $113^{\circ} 57^{\prime}$ W., alt. $1,500 \mathrm{ft}$., Moran 1989 (UC) ; from Santo Domingo to Matancita, alt. 50-100 ft., Nelson and Goldman 7288 (F, US) ; Magdalena Island, Feb. 25, 1889, T. S. Brandegee (A, F); Magdalena Bay, Mason 1891 (F, GH, US) ; Estero Salinas, arm of Almejas Bay, south of Magdalena Bay, Wiggins 11494 (AHFH, UC); Santa Margarita Island, Rose 16294 (US); Espíritu Santo Island, Collins, Kearney and Kempton 135 (US) ; Cape region, 1901, C. Grabendorffer (UC) ; San José del Cabo, Sept. 2, 1893, T. S. Brandegee (UC); San José del Cabo, Rose 16458 (US).

Distribution and habitat (Map 5). In the southern Sonoran Desert (south of Lat. $30^{\circ} \mathrm{N}$. ) and south along the coastal plain into northern Sinaloa, apparently absent from the dry Vizcaíno Desert area. The species is so distinctive that I have not hesitated to map the localities listed by Johnston (1924) and Shreve (1951). Pedilanthus macrocar-

pus is found in desert shrub and, to the south, in open, marginal thorn forest. In Baja California it is apparently widespread and occurs either in sandy or loam soils or in rocky areas. On San Pedro Nolasco Island the plant is found on rocky slopes (Johnston 1924; Gentry 1949, Pl. 11), but on the mainland of Sonora and Sinaloa it has only been found on the coastal plain, often on old beaches. This distribution might suggest that $P$. macrocarpus had only recently invaded the mainland from the peninsula. Flowering in the winter (September to May).

References to this species occurring in Colima are erroneous. One specimen of Palmer 802 (1890) was mounted with a form label intended for Palmer's 1891 collections
from Colima, but reference to Palmer's list of collections for these years (Rose, 1895) shows that the 1890 collection numbers were not repeated in 1891, and that $P$. calcaratus was the only species of the genus collected by Palmer in Colima.

## Common names. Candelilla, gallito.

Variation. This striking species, being common in an area often visited by naturalists, has been, for a Pedilanthus, well collected. The available material is sufficient to show a very interesting pattern of variation. Collections from the Cape and Magdalena Bay areas show a relatively short spur which is only slightly tapering and flattened terminally, whereas plants from southern Sonora and adjacent Sinaloa produce cyathia with very long, flattened, tapering spurs (see Plate XIX). On tabulating the average spur length for each locality (Map 6), one finds a remarkably clear "hairpin" cline about the Gulf of California. It will be noted that the small sample (3 cyathia) from San Pedro Nolasco Island does not fit in the cline, having very short spurs. One cyathium from this collection is quite blunt, with no terminal flattening. The data for Map 6 were obtained by measuring the spurs of all available well-developed cyathia, in the dry state, and adding the measurements of those cyathia which were softened and expanded by boiling (or preserved in liquid) for dissection. This doubtless skews the data somewhat toward the larger cyathia; but the measurement of dried cyathia is skewed in the opposite way, since the larger spurs with greater proportion of parenchymatous tissue shrink greatly in drying.

Those features which are essentially functions of spur length, such as length of solid, parenchymatous portion of spur and relative position of glands, vary in the same manner as spur length. The degree to which the spur lobes are connate is, as noted, quite variable, especially in the northern part of the range (which is the area best sampled). In Dressler 1090, from Sinaloa, and some of the material from southern Sonora, the spur lobes are very highly connate, little more than the ligulate apices being free (and these sometimes partially connate with each other). Dressler 1090 also shows very deeply bifid style branches, the styles being nearly equally 6 -parted. The variation of the fruit parallels the spur-length pattern, the fruits from the main-


Map 6. Variation in spur length in Pedilanthus macrocarpus. The average spur length, to the nearest half mm . is given for each locality from which flowering material is available. The ranges of variability at representative points are northern Sinaloa (20.5) : $17-23 \mathrm{~mm}$., Laguna Seca Chapala (14.5): $13-17 \mathrm{~mm}$., Bahía de Magdalena (11): $8-25 \mathrm{~mm}$., Cape region (12.5) 10.15 mm .
land and northern part of the range are thick-walled, corky (punky) and indehiscent, with no trace of dehiscence lines, the largest and thickest walled type apparently being found in Sinaloa. Fruits from the Magdalena Bay region are smaller and thinner walled and show faint lines of dehiscence. The collections from the Cape region show yet smaller fruit types, thinner carpel walls and distinct lines of dehiscence; these appear to be tardily dehiscent. Seeds from
the Cape region are the smallest measured and those from southern Sonora the largest (larger than in Sinaloan material). Bracteole development is quite variable, but the largest bracteoles were found in peninsular material. In none of the above features is there a sharp break between peninsular and mainland populations. Sonoran and Sinaloan plants, as far as sampled, have narrow, very fleshy, inrolled leaves, whereas peninsular plants have wider, flat leaves (Plate XIX - C, 4 and $4^{\prime}$ ). The peninsular collections tend to be more puberulent or tomentulose than the mainland plants, and, when living, are darker in color. While these vegetative features may form slight constant differences between peninsular and mainland plants, they cannot be adequately determined from herbarium material. The variation of $P$. macrocarpus offers fascinating possibilities for careful field work.

Two collections, Wiggins and Rollins 249 and Palmer 605 , show unusually small cyathia (involucral tube 10-11 mm . long, spur $8-9 \mathrm{~mm}$. long) with cyathia of normal size. These small cyathia have much the aspect of those developed by cultivated plants when in poor condition or under unfavorable environment. The flowers are normally developed in these small cyathia (in such cyathia from cultivated plants the staminate flowers often abort). More troublesome are four unattached cyathia with very short spurs and the aspect of Cape-region material, accompanying Palmer 802 (US and F, one cyathium each, the latter doubtless removed from the US sheet) and the Brandegee, Llano de Santana collection (F, 2 cyathia). While the measurements of these cyathia were included in the survey of spur variation, they may well be viewed with suspicion, as indicated by the presence of unmistakable cyathia of $P$. calcaratus and $P$. bracteatus in packets accompanying other collections of $P$. macrocarpus. Carelessness on the part of Millspaugh is suspected.

Relationship. Pedilanthus macrocarpus is clearly related to $P$. coalcomanensis, $P$. cymbiferus and $P$. calcaratus, but is not especially close to any of the three; it resembles $P$. coalcomanensis in the partitions of the spur, $P$. cymbiferus in aspect, and all three in general form, color and pubescence of cyathium. Though quite different in aspect from $P$. bracteatus, P. macrocarpus, especially the more primitive type
from the Cape region, does resemble that species, especially in the form and pubescence of the spur. It seems probable that these two species (and thus $P$. tomentellus and $P$. tehuacanus, as well) share a common ancestry.

Notes. This species is occasionally grown in succulent collections as a novelty, both for its fleshy stems and for the bizarre inflorescences. Fasciated forms have been found.

## 9. Pedilanthus bracteatus (Jacq.) Boiss.

## Plate XX, Map 5

Euphorbia bracteata Jacq., Hort. Schoenbr. 3: 14, t. 276. 1798. Type: the plate in Hortus Schoenbrunnensis; material from the Schoenbrun gardens, in the Naturhistorisches Museum at Vienna, is probably from the type plant. - Ventenatia bracteatus (Jacq.) Tratt., Gen. Pl. Disp., 87. 1802. - Tithymalus [Trew]? bracteatus (Jacq.) Haw., Synopsis Pl. Succ. 138. 1812. - Pedilanthus bracteatus (Jacq.) Boiss., DC. Prod. 15(2):6. 1862. - Tithymalo [i]des bracteatum (Jacq.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891 - Tithymalus [Mill.] bracteatus (Jacq.) Croiz,, Am. Jour. Bot. 24: 704. 1937.
Diadenaria articulata Kl. and Gke., Abh. Akad. Berl., Phys. 1859: 109. 1860. Type: Herb. Pavón (without data) (G!, photo: F!). Pedilanthus articulatus (Kl. and Gke.) Boiss., IDC. Prod. 15(2): 6. 1862. - Tithymalo [i] des articulatum (Kl. and Gke.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891. - Tithymalus subpavonianus Croiz., Am. Jour. Bot. 24: 703. 1937. Based on D. articulata, "not T. articulatus Kl. and Gke."

Diadenaria involucrata Kl. and Gke., Abh. Akad. Berl., Phys. 1859: 108. 1860. Type: destroyed in Berlin (photo: F!). - Pedilanthus involucratus (Kl. and Gke.) Boiss., DC. Prod. 15(2): 6. 1862. Tithymalo $[i]$ des involucratum (K1. and Gke.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891. - Tithymalus aztecus Croiz., Am. Jour. Bot. 24: 703. 1937. Based on D. involucrata, not T. involucratus (E. Meyer) Kl. and Gke.
Diadenaria Pavonis Kl. and Gke., Abh. Akad. Berl., Phys. 1859: 108. 1860. Type: Nueva España, Herb. Pavón (G!, photo and tracing: F!). - Tithymalo [i]des Pavonis (Kl. and Gke.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891. - Pedilanthus Pavonis (K1. and Gke.) Boiss., DC. Prod. 15 (2): 6. 1862.

Pedilanthus rubescens Brandegee, Zoe 5: 209. 1905. Type: Culiacán, Sinaloa, Oct. 12, 1904, T. S. Brandegee s. n. (UC!). - Tithymalus eochlorus Croiz., Am. Jour. Bot. 24: 704. 1937. Based on P. rubescens, not T. erubescens (Boiss.) Kl. and Gke.
Perilanthus spectabilis Robins., Proc. Am. Acad. 43: 23. 1908. Type: limestone ledges, Iguala Cañon, 2,500 ft., ca. Iguala, Guerrero, Dec. 28, 1906, C. G. Pringle 13914 (GH!, isotypes: A!, F!, UC!). - Tithymalus spectabilis (Robins.) Croiz., Am. Jour. Bot. 24: 704. 1937.
Perilanthus Greggii Millsp., Field Mus. Pub. Bot. 2: 363. 1913. Type: Mexico, 1848-1849, J. Gregg 2511 (M0!, isotype: F!). - Tithymalus Greggii (Millsp.) Croiz., Am. Jour. Bot. 24: 704. 1937.

Pedilanthus Olsson-Sefferi Millsp., Field Mus. Pub. Bot. 2: 363. 1913. Type: Tomellín, Mexico, Aug., 1910, P. Olsson-Seffer s. n. (мо!, fragment: F!). - Tithymalus Olsson-Sefferi (Millsp.) Croiz., Am. Jour. Bot. 24: 704. 1937.

Shrub, branching from base, 1-3 m. tall, stems semi-succulent or thick and succulent, glabrous to sparsely puberulent (sometimes densely puberulent when young) ; leaves glabrous to sparsely puberulent, usually puberulent at least beneath, ovate to ovate-oblong or obovate, or occasionally oblanceolate-obovate, 4.5-10 (-17) cm. long, 2.5-6(-7.5) cm . wide, base obtuse to subcuneate or to subcordate, apex obtuse, mucronulate, occasionally broadly acute, midrib keeled beneath, petiole puberulent, $3-4 \mathrm{~mm}$. long, stipules brown, blunt, ca. $0.5-1 \mathrm{~mm}$. in diameter and height; inflorescence terminal, internodes puberulent to densely crisp-puberulent, $10-30 \mathrm{~mm}$. long; bracts broadly ovate or obovate to suborbicular, subcordate, acute to long-acuminate, red where exposed to sun, sparsely puberulent, or glabrate within, somewhat persistent, 1.8-4.5 cm. long, 1.5-3.5 cm. wide; peduncle puberulent, $4-8 \mathrm{~mm}$. long, cyathium fleshy, green or pale green, involucral tube glabrous to sparsely puberulent without, puberulent within, 10-16 mm . long, the main lobes ovate-oblong to ovate-lanceolate, obtuse, free beneath for 7-12 mm ., accessory lobes ligulate to ligulate-spatulate or sub-flabellate, 1-1.7 mm . wide, puberulent throughout, the lobes somewhat thickened basally (folded and connate with themselves), the median, especially, forming a dorsal keel terminating abruptly $1.5-3 \mathrm{~mm}$. anterior to the glands, the lateral lobes ca. $1-3 \mathrm{~mm}$. shorter than the main lobes, free laterally for $2.5-5 \mathrm{~mm}$. and medially for 5-7 mm ., median lobe subequal to 1 mm . shorter than the lateral lobes, partly concealed by the lateral lobes; spur blunt, projecting obliquely or posteriorly, the apex shallowly 3 -lobed, $10-15 \mathrm{~mm}$. long (ca. 5-8 mm . long from the tube, transition of ten obscure), the spur often constricted laterally just above the involucral tube, puberulent along sutures and puberulent within except near the glands, lateral spur lobes tapering abruptly at or just beyond the apex of the medial lobes, or forming an erect tooth there (to ca. 0.5 mm . high), medial spur lobes arising near apex of spur (1-5 mm. from apex), 5-8(-10) mm . long, basally $3-4 \mathrm{~mm}$. wide, apically ca. 1.5 mm . wide, from cuneate-deltoid and tapering evenly to ovate-deltoid and attenuate, terminally thickened beneath for ca. 3 mm . (the attenuate portion), truncate to retuse; glands 2 (rarely 3 or 4 ), thick, smooth, reniformoblong, the upper margin concave, $2-3.5 \mathrm{~mm}$. long and $1.5-1.7 \mathrm{~mm}$. wide, bent about the partitions, rarely split into gland-pairs, the lateral glands, if developed, smaller, hemispheric to oblong, 1-2 mm. long, $0.5-1 \mathrm{~mm}$. wide, $0-2.5 \mathrm{~mm}$. anterior and slightly lateral to the medial glands; partitions slight, $1-2.5 \mathrm{~mm}$. terminally, sometimes puberulent anterior to the glands; bracteoles poorly developed, from puberulent basal ridges ca. 1 mm . long to clusters of few filamentous bracteoles to 7 mm . long, roof of involucral tube with faint lobules; staminate flowers $28-38$, pedicels glabrous, $11-14 \mathrm{~mm}$. long, filaments puberulent (rarely glabrous), $1.5-3 \mathrm{~mm}$. long; anthers glabrous to sparsely puberulent; pistillate pedicel glabrous or puberulent, $7-12 \mathrm{~mm}$. long,
ovary glabrous, conic-ovoid, faintly trigonous, $2.5-3 \mathrm{~mm}$. in diameter and length, style glabrous or glabrate, $7-12 \mathrm{~mm}$. long, trifid, the branches $0.5-2 \mathrm{~mm}$. long, shallowly or deeply bifid, usually spreading; fruit conic-subquadrate, ca. $10-13 \mathrm{~mm}$. in diameter, shallowly 3 -lobed in cross section, the lines of dehiscence red; seed grey-brown to brown, ovoid to subquadrate or to conic-ovoid, strongly keeled dorsally and laterally, basally truncate, terminally acute, $5-7 \mathrm{~mm}$. long, $4-5 \mathrm{~mm}$. wide, hilum in a rhomboid, flattened area.

Representative specimens seen: Mexico. Sonora. Cañon Estrella, Dist. Álamos, Gentry 385 (ARIz, MICH). Sinaloa. Mocorito, Collins and Kempton 73 (US); 7 mi . So. of Guamúchil. Dressler 979 (GH) ; Culiacán, Gentry 6791 (AHFH, F, GH, MICH, US. There is an herbarium admixture of $P$. macrocarpus on the sheets at F and US); Culiacán, E. Palmer 176 r $^{\prime}$ (C, F, GH, NY, S, US) ; between Culiacán and Alcoyonque, Shreve 7795 (ariz, Mo); Mazatlán, Rose, Standley and Russell 13838 (A, F, NY, US) ; Mazatlán, J. González Ortega 7382 (F, US); Mazatlán, 10 m ., J. González Ortega 6476 (GH, PH, US) ; along road from Mazatlán to Villa Unión, MacDaniels 4 (F) ; Rancho el Huizache, Concordia, Sindicatura de Aguacaliente, 57 m ., Trejo 111.5 (US); vicinity of Labradas, Ferris and Mexia 5245 (A); trail from Los Labrados to Marisma, 5 m ., Mexía 969 (A, F, GH, Mich, Mo, Ny, UC, US). Zacatacas. near San Juan Capistrano, on the road to Huajuquilla, Rose 2941 (GH, US). Jalisco. on road between Bolaños and Guadalajara, Rose 302.3 (GH, us). Guerrero. 12 km . from Taxco on road to Cuernavaca (km. 149), Dressler 180.3 (GH) ; north of Taxco, Kenoyer C209 (F). Without exact locality. Nueva España, 1787-1795-1804, Sessé, Mociño, Castillo and Maldonado 1768 (F).

Distribution and habitat (Map 5). In southeastern Sonora, the coastal plain in northern and southern Sinaloa, southwestern Zacatecas and the northern extension of Jalisco, in northeastern Guerrero, and in Tomellín Canyon, Oaxaca. To be expected in many intermediate areas. A Pedilanthus of this type is reported to occur in Aguascalientes (Prof. Martínez, personal communication).

The Sonoran collection is reported as growing in "heavy bottom land growth with Taxodium mucronatum in canyon; Short-tree Forest" (Gentry 1942). In Sinaloa the plant seems characteristically to be an element in the thorn forest. At Taxco, Guervero, $P$. bracteatus occurs in an open monte bajo of a different sort, comparable to the cuajiotal of Miranda (1941). In Guerrero and at some places in Sinaloa (at least) it occurs on calcareous soil. Blooming in summer and early winter (April, August-December).

Common name. Candelilla (Sinaloa).
Variation. This relatively widespread species, as might be expected, is rather variable, but not enough so to justify
the long synonymy. The lack of data on some of the specimens, the poor condition of others, and the lack of material from some areas, make a treatment of the variation difficult and a rational and consistent infra-specific classification impossible, at least for the present. The variation which can be observed is summarized in the following outline, in which the outstanding features of each population or collection are given.

1. Northern Sinaloa (Culiacán and vicinity) : stems often quite succulent, glabrate; leaves sparsely puberulent, variable in shape, but generally ovate and obtuse both basally and apically, small to medium size (3.5-9.5 cm. long) ; inflorescence internodes puberulent, bracts small $(2-2.8 \mathrm{~cm}$. long), acute to somewhat acuminate, moderately persistent; cyathia glabrous without, fairly small ( $10-12 \mathrm{~mm}$. long), the main lobes broad, stamen filaments puberulent.
2. Sonora: similar to Culiacán population, but bracts (2.8-3.7 cm. long) and cyathia (13-15 mm. long) larger, main lobes of involucre more attenuate.
3. Southern Sinaloa (Mazatlán and vicinity) : similar to Culiacán population, but stems less succulent, bracts somewhat more persistent.
4. Zacatecas and Jalisco: stems puberulent; leaves puberulent, ovate, generally obtuse basally and apically, medium size ( $5-7.5 \mathrm{~cm}$. long) ; internodes puberulent; bracts large (2.5-4.5 cm. long), acuminate and persistent; involucres sparsely puberulent, medium size ( $12-13 \mathrm{~mm}$. long), main lobes broad, filaments puberulent.
5. Guerrero: stems glabrate, leaves medium size to large ( $5.5-10.5 \mathrm{~cm}$. long), puberulent, subcordate and obtuse, internodes puberulent, bracts large ( $3.5-5 \mathrm{~cm}$. long) persistent and acuminate to caudate-attenuate; cyathia glabrous, large ( $13-16 \mathrm{~mm}$. long), the main lobes attenuate; spur slightly flattened and projecting posteriorly so that the dorsal outline of involucre is plane and not concave as in other forms, filaments puberulent.
6. Tomellín, Oaxaca: stems puberulent, leaves puberulent, ovate, subcuneate, obtuse, $4-5 \mathrm{~cm}$. long, bracts acuminate, 2-2.8 cm. long, internodes densely puberulent, involucral tube sparsely puberulent basally, filaments and anthers puberulent.
7. Type of Diadenaria Pavonis: stems glabrate, leaves large ( $10-17 \mathrm{~cm}$. long), obovate, subcordate and broadly acute, glabrous, internodes densely crisped-puberulent, bracts small (2.2-2.5 cm. long), attenuate, somewhat persistent, cyathia sparsely puberulent, medium size (ca. 13 mm . long), filaments glabrous.
8. Sessé, Mociño, et al. collection: similar to type of $D$. Pavonis, but leaves puberulent, ovate, subcordate, obtuse, $8-8.5 \mathrm{~cm}$. long, filaments not known.

It is quite probable that some major discontinuities do occur in the distribution of P. bracteatus, as in central Sinaloa, where the coastal plain is narrow and the tropical deciduous forest meets the mangrove swamps (this, however, does not represent a marked gap in the variation of the species), and that a meaningful subspecific classification may eventually be possible.

Relationship. Closely related to $P$. tomentellus and $P$. tehuacanus, and more distantly to $P$. macrocarpus. This species probably represents the ancestral type of the first two species, and may be close to the ancestral type for $P$. macrocarpus. It shows some resemblance to $P$. coalcomanensis and $P$. calcaratus.

Notes. The plate taken as type agrees well with material of this species from southern Sinaloa, considering that it represents a cultivated plant, except in the 4 -glandular spur (developed lateral glands). The development of the lateral glands is sporadic, however, in material from northern Sinaloa and Guerrero, and may be expected in other areas. An herbarium specimen in the Naturhistorisches Museum, Vienna, bears a reference to Jacquin's publication and the notation: "Ex. h. Schoenbrunn. 1811." This is almost certainly from the type plant and agrees well with the plate, except that the development of the lateral glands is not consistent. A second sheet from the same herbarium is probably from this plant, but was badly damaged by insects while in the "Herb. Portenschlag."

The types of Diadenaria articulata, D. involucrata (photo only) and Pedilanthus Greggii (very poor specimen) all agree well with Sinaloan material of the species. The types of Diadenaria Paronis and P. spectabilis differ from the Sinaloan population in the ways enumerated under Variation. It will be of considerable interest to re-collect plants
of the D. Pavonis and Sessé, Mociño, et al. collection sorts and determine their distribution and variation. More and better material is also needed from the area of southern Zacatecas and from Oaxaca.

The type of $P$. Olsson-Sefferi is a very poor specimen and bears only immature cyathia (these are in the portion kept at F by Millspaugh), but clearly falls within P. bracteatus and differs from the nearby $P$. tomentellus as it is now known.

There are surely few cases in the history of nomenclature in which the same species and epithet have been assigned to two different, homonymous genera, but this has occurred with "Tithymalus bracteatus." The combinations of Haworth and Croizat cannot be considered homonyms, for they involve the same basionym; but there is hardly need for special rules to cover such anomalous instances as this.

## 10. Pedilanthus tomentellus Robins. and Greenm.

Plate XX, Map 5

P. tomentellus Robins. and Greenm., Am. Jour. Sci. 50: 164. 1896. Type: hedgerows near Oaxaca, $5,500 \mathrm{ft}$., Sept. 6, 1894, $5-8 \mathrm{ft}$., C. G. Pringle 4912 (GH!, isotypes: F!, MO!, PH!, S!, UC!, US!). - Tithymalus tomentellus (Robins. and Greenm.) Croiz., Am. Jour. Bot. 24: 704. 1937.

Shrub 2-4 m. tall, stems somewhat succulent, densely rufescentpuberulent when young, becoming sparsely puberulent with age; leaves somewhat fleshy, sparsely puberulent above, sparsely to densely puberulent beneath, ovate to ovate-elliptic, 3.8-7.5 cm. long, 1.5-4.5 cm . wide, decreasing in size upwards to the inflorescence, base cuneate to obtuse, apex acute to obtuse, mucronulate, midrib weakly keeled, petiole densely rufescent-puberulent, $2-6 \mathrm{~mm}$. long, stipules dark brown, spur-like, 0.7-1.2 mm . long; inflorescence terminal, dichotomous, the internodes densely rufescent-puberulent, $8-2 \overline{5} \mathrm{~mm}$. long, bracts red, sparsely puberulent, ovate to suborbicular, acuminate, $2.2-3.5 \mathrm{~cm}$. long, 2.2-2.6 cm . wide; peduncle densely puberulent, $3-6 \mathrm{~mm}$. long, involucre puberulent throughout, apparently green, involucral tube 11-13 mm. long, the main lobes cuneate-ovate to oblong-ovate, obtuse, free beneath for $8-10 \mathrm{~mm}$., often forming a slight mentum at ca. 2.5 mm . from the peduncle, accessory lobes ligulate, obtuse, ca. 1 mm . wide, each forming a deltoid tooth ca. 0.7 mm . high on the dorsal surface at ca. 2.5 mm . from the medial glands, lateral lobes ca. 1-2 mm . shorter than main lobes, free laterally for $2.5-3 \mathrm{~mm}$. and medially for ca. $4.5-5 \mathrm{~mm}$., median lobe ca. 0.5 mm . shorter than lateral; spur short, blunt, $6-7 \mathrm{~mm}$. long ( $3-4 \mathrm{~mm}$. from tube), the lateral lobes tapering abruptly near the apex of the medial lobes, the medial lobes arising at the apex of the spur, ca. $7-8 \mathrm{~mm}$. long, basally $2.5-4 \mathrm{~mm}$.
wide, terminally $1-1.5 \mathrm{~mm}$. wide, lanceolate to cuneate-lanceolate, truncate, terminally slightly folded above, and thickened beneath for ca. 2.5-3 mm., the thickening not sharply defined posteriorly; the glands 2 , or often 4 , the medial glands sub-terminal, reniform-oblong, bent about the partitions, $2-3 \mathrm{~mm}$. long and 1-1.5 mm . wide, lateral glands, if present, lateral and anterior to the medial glands, ovateoblong, the apex anterior, $1-2.5 \mathrm{~mm}$. long, $0.5-1 \mathrm{~mm}$. wide, partition slight, ca. 1 mm . terminally; bracteoles few, filamentous, $4-6 \mathrm{~mm}$. long, dorsal and lateral bracteole-ridges often well developed for ca. 5 mm .; roof lobules present but obscured by the indument; staminate flowers $26-37$, the pedicels $9-11 \mathrm{~mm}$. long, sparsely puberulent terminally, filaments puberulent, $2.5-3 \mathrm{~mm}$. long, anthers pilose-puberulent; pistillate pedicel densely pilose-puberulent, $6-9 \mathrm{~mm}$. long, ovary conicspheroid, ca. 2.5-3 mm. in diameter, densely puberulent, style glabrate, ca. 10 mm . long, the branches ca. 2 mm . long, deeply bifid, slender, spreading; fruit sub-spheroid, ca. 12 mm . in diameter, puberulent; seeds not known.

Specimens seen: Mexico. Oaxaca. 40 mi . N.E. of Oaxaca City, E.W. Nelson 1201 (US) ; Oaxaca, Seler 1402 (A, GH) ; Oaxaca Valley, 5,000 ft., C. L. Smith 1182 (some sheets " 216 and 1182") (F, MICH, MO, NY, US) ; Oaxaca, G. Andrieux 106 (к, w).

Distribution and habitat (Map 5). Known only from the Oaxaca Valley, where some of the collections, at least, are from plants growing in hedgerows. Flowering in fall and early winter (Sept. - Nov.).

Common name. Cordobán.
Variation. The few and rather poor collections available seem to be fairly uniform.

Relationship. This species is clearly related to $P$. bracteatus. It should perhaps be considered a subspecies of that taxon, but it differs in aspect and a number of details. The available material does not justify the reduction. Pedilanthus tomentellus is not especially close to the Guerreran collections of P. bracteatus but is approached by the Zacatecan (and Jaliscan) material, and, apparently, by the material from northern Oaxaca (a very poor specimen). Pedilanthus tehuacanus is also clearly related to the present species. The local nature of $P$. tomentellus and the frequent occurrence of aborted staminate flowers and pollen suggest that it may be a hybrid population, involving a cross between $P$. bracteatus and $P$. tehuacanus or a similar plant.

Notes. In Oaxaca, in the summer of 1954, inquiries concerning "cordobán" brought in a number of cuttings of this plant from the garden of an Indian cook; it was referred to as a "bejuco," and said to be medicinal. While the stems
might be somewhat weak and wand-like in cultivation, it is not likely that it is a vine. The plant is notable for the large stipules and the reddish indument. The cuttings, unfortunately, were lost, and fresh cyathia have not been seen.

A number of the involucres in the herbarium material at hand are thin in texture and seem poorly developed; these often have some or all of the staminate flowers aborted.

## 11. Pedilanthus tehuacanus Brandegee

Plate XX, Map 5

P. tehuacanus Brdgee., Univ. Calif. Pub. Bot. 6: 55. 1914. Type: Tehuacán, Puebla, dry rocky soil, May, 1913, C. A. Purpus 7065 (UC!, isotypes: A!, F!, GH!, mo!). - Tithymalus tehuacanus (Brdgee.) Croiz., Am. Jour. Bot. 24: 704. 1937.

Shrub, stems thick, succulent, sparsely puberulent (densely so when young), axillary buds densely tomentose-puberulent; leaves puberulent to densely puberulent throughout, fleshy, probably caducous, oblanceolate to lanceolate, $18-32 \mathrm{~mm}$. long, $6-8 \mathrm{~mm}$. wide, acute, base narrowly cuneate, midrib thick but not carinate, petiole broad (ca. 3 mm . wide), $1-3 \mathrm{~mm}$. long (if distinct), stipules spur-like, ca. 0.5 mm . long, obscured by the dense indument; inflorescence terminal, often branching monochasially for several nodes at any point after the first dichotomy, internodes densely puberulent-tomentose, $7-15 \mathrm{~mm}$. long, bracts ovate to orbicular-ovate, acute, strongly cucullate, puberulent within and densely puberulent without, $12-20 \mathrm{~mm}$. long, $11-15 \mathrm{~mm}$. wide, the apices and posterior margins of the bracts often (or usually) remaining connate during anthesis, separated by the development of the axillary cyathia and then soon shed, cyathia sessile, puberulent throughout, green or the spur more or less pink, involucral tube 8-9 mm . long, main lobes oblong, free beneath for $4.5-5 \mathrm{~mm}$., glabrate within, accessory lobes oblong-ligulate, obtuse, ca. 1-1.2 mm . wide, thickened basally, the thickening terminating in a sub-trigonous tooth ca. 0.5 mm . high, with the anterior face concave, at ca. $1.5-2 \mathrm{~mm}$. from the medial glands, the lobes bending markedly downward anterior to these, the lateral lobes $1.5-2 \mathrm{~mm}$. shorter than the main lobes, free laterally for $1 . \bar{\delta}-2 \mathrm{~mm}$., medially for $2-2.5 \mathrm{~mm}$., the median lobe ca. 0.5 mm . shorter than lateral lobes; spur not elongate, sessile on the involucral tube at ca. $4-5 \mathrm{~mm}$. from the peduncle, ca. 1.5 mm . thick, lateral spur lobes narrowing abruptly at ca. $4-5 \mathrm{~mm}$. from base, the terminal portion ( $1.5-2 \mathrm{~mm}$.) somewhat to strongly folded over laterally, lobes somewhat pinched in at ca. 2 mm . from base, in front of lateral gland-sites (especially if lateral glands developed), medial spur lobes oblong-lanceolate, arising ca. base of spur, $4.5-6 \mathrm{~mm}$. long, basally $2.5-3 \mathrm{~mm}$. wide, obtuse, apices slightly folded and thickened beneath for ca. 1.5 mm . (this thickening fitting in front of the thickened portions of the accessory involucral lobes); glands 2-4, flattened, the medial glands oblong, irregular in outline, bent about the partition, $2.5-3 \mathrm{~mm}$. long, $0.5-0.7 \mathrm{~mm}$. wide, tending to be dis-
placed dorsally and partly on the spur lobe, rather than between the lobe and the floor of gland chamber; lateral glands ovoid, $0.8-1.2 \mathrm{~mm}$. long, $0.5-0.8$ wide; partition small, developed only under the glands, ca. $1-1.5 \mathrm{~mm}$.; bracteoles few to several, filamentous, to ca. 3 mm . long, dorsal and lateral bracteole-ridges extending for $5-6 \mathrm{~mm}$.; staminate flowers ca. $30-35$, pedicels $7-8 \mathrm{~mm}$. long, glabrous, filaments ca. 1.5 mm . long, puberulent, anthers pilose-puberulent; pistillate pedicel $7-8 \mathrm{~mm}$. long, terminally puberulent, ovary puberulent to densely puberulent, conic-spheroid, ca. 2.5 mm . in diameter, style ca. 4 mm . long, bent upwards (especially at anthesis), branches ca. 1.2 mm . long, deeply bifid, connivent; capsule conic-spheroid, ca. 10-12 mm. in diameter, the carpel walls thick; seed grey, ovoid, ca. 7 mm . long and 6 mm . wide, obtuse basally, apex acute, weakly keeled dorsally and very weakly keeled ventrally at ca. 1.5 mm . to each side of raphe, which is dark, circum-hilar area concave, not angular.

Known only from the type and material brought from Tehuacán to the Instituto de Biología in Mexico for identification, in the summer of 1954. Part of this last was pressed and retained at the Instituto; the remainder is represented by alcoholic material in the author's collection (as Dressler 1795). From the appearance of the plant, and from the plants which were brought in with it, Prof. Miranda believed that it came from the hills well above Tehuacán. Its habitat may thus be less extreme than the desert immediately about Tehuacán (see fig. 25), but the plant is distinctly a xerophyte. Flowering material has been collected in May and late August.

VARIATION. In the small and rather poor sample available, the only variation notable (aside from developmental variation within a single plant) is that the medial spur lobes of Dressler 1795 are narrowly cuneate, with the lateral margins straight, while those of the type are more properly lanceolate, and the margins convex. On one specimen of the type collection, it appeared that the medial spur lobes had been pink in life.

Relationship. This bizarre species is clearly related to P.tomentellus and P. bracteatus, with which it shares yellow latex, large bracts, green involucres, similar glands, etc. It is remarkable for the inaperturate pollen, sessile cyathia, short involucral tube, non-elongate spur and the partially connate bracts. Its form is such that it could scarcely be pollinated by humming-birds. At anthesis the style bends up and back sharply, so that the stigmatic branches are near the small opening between the bracts and in front of the
spur opening. The form and arrangement of the parts suggest that the plant might be pollinated by short-tongued flies and bees.

While the proportions of the involucre are suggestive of an early stage in the evolution of the genus, all of its features point to a specialized nature as an offshoot of a bracteatus-like ancestor. The form of the involucre, the connation of the bracts, and the form of the short style are all, it is believed, derived through an "organ-neoteny." These features resemble early stages in the development of the other species and appear to represent an arrested development of these parts with normal maturation of the ovules, stigmatic surfaces and staminate flowers.

## 12. Pedilanthus nodiflorus Millspaugh

Plate XXI, Map 4

P. nodiflorus Millsp., Field Mus. Pub. Bot. 1: 305, pl. 17. 1896. Type: Mexico, Yucatan, Silam, abundant about the port, April, 1895, G. F. Gaumer 649 (F 36,452!, isotypes: A!, GH!, mo!, NY!). - Tithymalus nodiflorus (Millsp.) Croiz., Am. Jour. Bot. 24: 704. 1937.
P. personatus Croiz., Jour. Wash. Acad. Sci. 33: 20. 1943. Type: Comayagua, Honduras, semi-arid country, alt. 1,800 ft., Feb. 25, 1933, shrub 10 ft . tall, flowers salmon pink, "dítamo real," J. P. Edwards $P-581$ (A!, isotypes: F !, UC!, US).

Shrub 0.8-2 (-3) m. tall; stems slender, dark green, semi-herbaceous and sparsely puberulent when young, becoming woody and glabrate; leaves linear-lanceolate, caducous, somewhat fleshy, sparsely puberulent above and crisped-puberulent beneath, $8-60 \mathrm{~mm}$. long, 2-10 mm . wide, broadly cuneate at base, acute and apiculate terminally, midrib thickened or weakly keeled beneath, petiole indistinct, ca. 1-2 mm . long, stipules brown, spur-like, blunt, $0.5-0.7 \mathrm{~mm}$. long; inflorescence terminal and/or on short axillary branches, condensed, internodes $1.5-3 \mathrm{~mm}$. long, turgid, puberulent, bracts broadly deltoidovate to oblong-ovate, $3.5-6 \mathrm{~mm}$. long, $3-4 \mathrm{~mm}$. wide, puberulent on both surfaces, broadly acute, peduncle puberulent, $4-7 \mathrm{~mm}$. long; involucral tube 9-11.5 mm. long, green beneath or red throughout, glabrate to densely crisped-puberulent without, sericeous-puberulent to densely pilose-sericeous within, main lobes cuneate-oblong to oblong, obtuse or subtruncate, free beneath for $3.5-4 \mathrm{~mm}$., accessory lobes somewhat lanceolate, puberulent throughout, arising posteriorly near the medial glands and ascending for $1-1.5 \mathrm{~mm}$. and then abruptly bending forward and expanding into a flattened surface ca. 1.5 mm . in width, carinate (especially the median lobe) and the margins rimmed, with grooves between the lobes, the medial lobe sometimes with a low, trigonous tooth posteriorly, the lateral lobes each bent laterally, the posterior portions laterally concave about the lateral glands, the terminal portions of the accessory lobes ligulate to sub-
spatulate, obtuse or sub-truncate, the lateral lobes sub-equal to 1.5 mm . shorter than main lobes, free $0.5-2.3 \mathrm{~mm}$. laterally and $1-3 \mathrm{~mm}$. medially, the median lobe subequal, partially concealed terminally; spur cucullate, pink-red to red, puberulent within, glabrous without, $4-5 \mathrm{~mm}$. from peduncle to apex of spur, spur $3.5-4 \mathrm{~mm}$. thick, lateral spur lobes very narrow, with a shallow notch at the lateral gland (ca. 1-2 mm. from base), folded in over the accessory involucral lobes terminally, medial spur lobes $5-7 \mathrm{~mm}$. long, basally $3.5-4 \mathrm{~mm}$. wide and deltoid, tapering to a ligulate portion ca. $1.5-2.5 \mathrm{~mm}$. long and 1-1.2 mm. wide, this somewhat concave dorsally, bearing terminally on the inner margin a blunt, erect tooth or lobule $1-2.5 \mathrm{~mm}$. from apex of lobe, another similar but less marked tooth often borne on the outer margin and slightly anterior to the inner tooth, terminal lobule (beyond and between the teeth) more or less ligulate, sometimes laterally flattened and curved downward (especially in Honduran material), medial glands at the base of the spur, oblong-reniform to elliptic-oblong, $1.5-2 \mathrm{~mm}$. long, $0.8-1 \mathrm{~mm}$. wide, lateral glands ca. 2 mm . anterior to the medial glands, externally visible between the lateral and medial spur lobes, oblong-elliptic to elliptic-ovoid, 0.8-1.5 mm . long, $0.4-1 \mathrm{~mm}$. wide, spur partitions not developed; bracteoles several to numerous, ca. $8-10 \mathrm{~mm}$. long, filamentous, twisted (occasionally a few ligulate and pilose), basally connate, adnate to the involucral tube for ca. $3-4 \mathrm{~mm}$., the dorsal bracteole-ridge occasionally terminating in a pilose, linguiform lobe ca. 1 mm . long; roof lobules inconspicuous, or prominent lobes and ligules ca. $1-1.5 \mathrm{~mm}$. long beneath and between the accessory involucral lobes; ; staminate flowers glabrous, 20-34, the ventral clusters tending to have 2-3 fewer flowers than the lateral and dorsal clusters, pedicels $8-13 \mathrm{~mm}$. long, the filaments $2-3 \mathrm{~mm}$. long; pistillate pedicel glabrous or terminally puberulent, $7-11 \mathrm{~mm}$. long, ovary quadrate-ovoid, trigonous, ca. 3 mm . in diameter, glabrous to densely crisped-puberulent, style $7-10 \mathrm{~mm}$. long, usually puberulent basally, occasionally glabrous or sparsely puberulent throughout, style branches $0.5-1 \mathrm{~mm}$. long, bifid, connivent or spreading; fruit subquadrate, deeply 3 -lobed, ca. 6 mm . lone, glabrous to crisped-puberulent; seed ovate-subquadrate, truncate basally, broadly acute apically, very weakly keeled, ca. 3 mm . long, $2-2.5 \mathrm{~mm}$. wide, slate-grey or brownish grev, raphe dark, hilum flanked by 2 oblong dark areas, each about equal to the hilum in area.

Specimens seen: Mexico. Yucatan. About 6 km . from Sisal (Hunucmá road), Dressler 1810 (GH); km. 28, Mérida-Progreso road, C. L. and A. A. Lundell r978 (A, Us) ; km. 25, Mérida-Progreso road, Dressler 1.362 (GH) ; Progreso, Millspaugh $166 j^{7}$ (F) ; Mina de Oro, north coast, (i. F. Gutumer and sons 2.3.324 (A, F, GH, MO, NY, L'S) ; Silam, G. F. (rrumer $\therefore$. $n$. (F). Honduras. Dept. Comayagua, ca. 600 m ., Stundley avel J. Chacón P. 6034 (F) ; El Banco, Dept. Comayagua, 640 m ., Valerio Rodriguez 2:385 (F).

Distribution and habitat (Map 4). North coastal Yucatan and the Comayagua Valley in Honduras. In Yucatan this species is found in the open thorn scrub which is typical of the northern coast (see fig. 24). Near Sisal and Progreso,
the species occurs near the coastal swamps, in areas where the water table is very near the surface; at Progreso it is not limited to this narrow zone, but occurs for two or three kilometers along the Mérida-Progreso road. Like several other species of this genus, its local distribution is spotty and erratic, but it is quite abundant in some sites. Its habitat in Honduras is scarcely coastal, but appears to be an open thorn scrub similar to that of Yucatan. The distribution, as now known, is quite anomalous. Little is known of the phytogeography of the arid region of Honduras; it is clear, though, that the present distribution in Yucatan must be relatively recent, since the limestone which makes up the northern part of the peninsula is of late Pleistocene and Recent origin. Flowering in the spring and summer (Feb.Aug., flowering sparsely in September).

COMMON NAMES. Píe de niño, dítamo real (Honduras); Yaxhalalché (Yucatan, Mayan "green-stem-tree").

Variation. The Yucatan population of $P$. nodiflorus is variable in indument and color. The cyathia of the plants near Sisal and Progreso are all densely puberulent without and green beneath, the involucral tube being red only near the lateral spur lobes. The Silam collections vary from densely to rather sparsely puberulent, and the Mina de Oro collection from densely puberulent to nearly glabrous without. The indument of the ovaries varies correspondingly. Some of the cyathia from Mina de Oro, at least, are uniformly red (color cannot always be determined from dried material). Leaf size is highly variable, as is often the case with species which are essentially leafless. Honduran material differs somewhat from the Yucatan material in a number of details, but is, on the whole, very similar. The cyathia of Honduran plants average a little longer; the indument of the involucral tube is moderately dense without and somewhat shorter within than in Yucatan plants; the involucral lobes are wider terminally and the free portions of the accessory lobes longer; the medial spur lobes are a little more slender and the terminal lobules more strongly curved; the lateral glands tend to be smaller and less conspicuous; and the styles and staminate pedicels tend to be longer. The leaves, fruits and seeds of the Honduran plants are unknown.

Relationship. Reference to Miss Ericksen's accurate drawings (Plate XXI) will show that this, in the form of
its involucre, is one of the strangest of a bizarre genus. The eye-like, exposed lateral glands are unique and give the structure a quite animate appearance. Though $P$. nodiflorus superficially resembles $P$. tehuacanus in some respects, their juxtaposition is coincidental, and not meant to indicate close relationship. In the form of the involucral lobes and the shortness of the spur, the two species are similar, but they differ widely in most other characters, and their resemblances are probably largely parallel developments. In the cucullate spur, the "palate" at the base of the accessory involucral lobes, the reduction of the ventral clusters of staminate flowers, the folded lateral spur lobes, and the inflorescence, seed and fruit characters, $P$. nodiflorus resembles the $P$. tithymaloides complex, and they are thought to be close relatives. In inflorescence, indument, seed and involucral texture, this species somewhat resembles $P$. pulchellus, and, to a lesser degree, $P$. calcaratus. These resemblances are taken to represent a more distant common ancestry.

Notes. The Honduran plants of this species are, in general, very close to those from Yucatan; the gap in the known distribution is, itself, far more striking than the slight morphological differences which are apparent, and, at least until its range and variation are much better known, there is little advantage in subspecific recognition of the southern population.

## 13. Pedilanthus tithymaloides (L.) Poit.

This, the type species of the genus, is by far the most widely distributed and variable of the slipper spurges. It is the only species in which clear geographic populations of subspecific rank are found. The allopatric West Indian taxa have generally been treated as distinct species, but they are all very closely allied to $P$. tithymaloides, sensu strictiore. There is actual intergradation in some cases, and in others, the subspecies appear to hybridize freely, where their ranges have been changed by the influence of man. While angustifolius and parasiticus are broadly sympatric and appear to behave as distinct species (there is no evidence that they actually occur together, in the same habitat), each is closely tied in to the mainland population by a different chain of taxa. The best arrangement, at the present, is to
consider all of these geographically replacing populations as subspecies of the somewhat variable $P$. tithymaloides. It is interesting that there are no clear subspecies in the mainland population complex which ranges from northern Mexico to Surinam. Plants which appear to be hybrids between different subspecies are discussed on pages 167-170; such plants would be difficult to identify by the use of the following key.

## Key to the Subspecies of P. tithymaloides

A. Leaves wide, more than half as wide as long .................................. B
A. Leaves narrow, less than half as wide as long; staminate pedicels
B. Leaf apices acute, or, if obtuse, leaves ovate and somewhat attenuate to apex

C
B. Leaf apices obtuse or retuse, if obtuse, then leaves usually obovate

E
C. Leaf bases cuneate, leaves not markedly glossy ........................... D
C. Leaf bases obtuse to subcordate, leaves glabrate and glossy (Yucatan and Greater Antilles). 13b. P. t. ssp. parasiticus.
D. Stem straight or nearly so (Mexico to northern South America) 13a. P. t. ssp. tithymaloides.
D. Stem zig-zag, usually markedly so (Cuba and Florida).

13c. P. t. ssp. Smallii.
E. Leaves retuse, widest below the middle (Amazonia)

$$
13 \mathrm{~d} . P . t . \text { ssp. retusus. }
$$

E. Leaves obtuse, obovate or elliptic, widest above the middle (Lesser Antilles) 13e. P. t. ssp. padifolius.
F. Styles short, $3-5 \mathrm{~mm}$. long; involucral tube usually short, $6-9 \mathrm{~mm}$. long, glabrous without or sparsely pilose with stiffly erect hairs; ovary glabrous (Greater Antilles except Jamaica)

13g. P. t. ssp. angustifolius.
F. Styles longer, $5-10 \mathrm{~mm}$. long (if short, ovary densely tomentulose) ; involucral tube longer, $7.5-11.5 \mathrm{~mm}$. long, glabrous without or more or less puberulent

G. Involucres minutely crisped-puberulent without, the trichomes appressed (Bahamas) ............................. 13h. P. t. ssp. bahamensis.
G. Involucres glabrous or puberulent without, but not minutely crisped-puberulent (Jamaica) .................... 13f. P. t. ssp. jamaicensis.

## 13a. Pedilanthus tithymaloides subsp. tithymaloides

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\text { Plate XXI, Map } 7
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Euphorbia tithymaloides L., Sp. Pl. 453. 1753. Neotype (here designated) : Plate 92, Jacquin, Sel. Stirp. Amer. Hist., 1763. - Tithymalus tithymaloides (L.) Croiz., Am. Jour. Bot. 24: 704. 1937.

Euphorbia tithymaloides $[\alpha]$ myrtifolia L., Sp. Pl. 453. 1753. Type (here designated) : Plate 16, Commelin, Hort. Med. Amst. vol. 1,
1697. - Tithymalo[i]des myrtifolium (L.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891.

Tithymalus my $[r]$ tifolius. Mill., Gard. Dict. ed. 8, Tithymaius no. 1. 1768. Type: a plant sent from Cartagena by Robert Millar and cultivated by Miller. - Euphorbia myrtifolia (Mill.) Lam., Encyc. Meth. Bot. 2: 419. 1786 ( not E. myrtifolia L., Sp. Pl. ed. 2, 653. 1762. which is E. myrtillifolia L., Syst. Nat. ed. 10, 1948. 1759). - Crepidaria myrtifolia (Mill.) Haw., Syn. Pl. Succ., 136. 1812. - Pedilanthus myrtifolius (Mill.) Link, Enum. Hort. Berol. 2: 18. 1822.

Euphorbia canaliculata Lodd., Bot. Cab. 727. 1823. Type: Plate 727, Bot. Cab. - Pedilanthus canaliculatus (Lodd.) Sweet, Hort. Brit. ed. 1, 335. 1827.
P. Houlletii Baill., Adansonia 1: 431. 1861. Type: a plant grown in the garden of M. Houllet. in Paris; a sterile specimen at P ("cult. in hort. par., $1859^{\prime \prime}$ ) may be from this plant. - Tithymalo[i] des Houlletii (Baill.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891.
P. Fendleri Boiss., DC. Prod. 15 (2) : 5. 1866. Type: Venezuela, Fendler 1202 (G-DC, photo: F!, GH!). -Tithymalo[i]des Fendleri (Boiss.) O. Kuntze, Rev. Gen. PI. 2: 620. 1891. - Tithymilus Fendleri (Boiss.) Croiz., Am. Jour. Bot. 24: 704. 1937, not T. Fendleri Kl. and Gke.
P. Pringlei Robins., Proc. Am. Acad. 29: 322. 1894. Type: Mexico, San Luís Potosí, Limestone ledges, Las Palmas, July 25, 1891, C. G. Pringle 5107 (GH!, isotype: F!). - Tithymalus Pringlei (Robins.) Croiz., Am. Jour. Bot. 24: 704. 1937.
P. gritensis Zahlbr., Ann. K. K. Nat. Hofmus. Wien 12: 104. 1897. Type: Venezuela, La Grita, Mérida, Karsten s. n. (w! fragment and photo: F!).
P. Deamii Millsp., Field Mus. Pub. Bot. 2: 356. 1913. Type: Guatemala, Fiscai, elev. 3,700 ft., May 31, 1909, ravines, C. C. Deam 6081 (F 247,005!, isotypes: A!, GH!, MICH!, vs!). - Tithymalus Deamii (Millsp.) Croiz., Am. Jour. Bot. 24: 704. 1937.
P. campester Brdgee., Univ. Calif. Publ. Bot. 6: 56. 1914. Type: Mexico, Oaxaca, Picacho - San Gerónimo, Oct., 1913, dry, rocky plains, C. A. Purpus 6885 (UC 172,985!, isotypes: A!, F!, GH!, mo!, NY!, U'S!). - Tithymalus villicus Croiz., Am. Jour. Bot. 24: 704, based on P. campester, not T. campester (Cham. and Schlecht.) Kl. and Gke.
P. petrueus Brdgee., Univ. Calif. Publ. Bot. 10: 411. 1924. Type: Mexico, Veracruz, Comeso, April, 1923, on rocks, C. A. Purpus 8885 (UC 218,896!, fragment: A). - Tithymalus petraeus (Brdgee.) Croiz., Am. Jour. Bot. 24: 704. 1937.
P. ierensis Byitt., Buli. Torr. Bot. Cl. 53: 468. 1926. Type: Trinidad, B. W. I., Penal Rock Road, March 28, 1920, woodlands, 1.5 m . high, N. L. Britton, T. E. Hazen and W. Mendelson 1093 (NY!, isotype F!). - Tithymalus ierensis (Britt.) Croiz., Am. Jour. Bot. 24: 704. 1937. P. camporum, Standl. and Steyerm., Field Mus. Pub. Bot. 23: 124. Type: Guatemala, Dept. Retalhuleu, plains between Nueva Linda and Champerico, alt. 120 m . or less, Feb. 18, 1941, dry thickets, erect herb about 1 m . tall, stems dark green, involucre rose-red, common, P.C. Stundley 87781 (F 1,109,145!, fragment: A!).

Shrub 0.4-3 m. tall, deciduous or evergreen, stems slender and woody or thick and markedly succulent, puberulent when young, becoming glabrate with age; leaves ovate, elliptic or ovate-lanceolate, glabrous to puberulent above and glabrate to densely puberulent beneath, 1-16 cm . long and $0.8-10 \mathrm{~cm}$. wide, apex acute, narrowly obtuse or rarely retuse, usually somewhat attenuate, base cuneate, midrib keeled or strongly winged beneath, petiole $2-12 \mathrm{~mm}$. long, stipules brown or dark brown, spur-like, blunt, or depressed and transversely oblong, $0.3-1.2 \mathrm{~mm}$. in diameter; cymes terminal, axillary, and on lateral branches, condensed, internodes glabrate to puberulent, $1-3 \mathrm{~mm}$. long, bracts red, glabrate to crisped-puberulent without and sericeous within, 4-12 (-14) mm. long, 2-5 mm. wide, ovate, ovate-lanceolate or obovate, attenuate, acute or obtuse, peduncle glabrous to puberulent, $3-8 \mathrm{~mm}$. lang; involucral tube red above, basally green or greenish yellow, glabrous or pilosulous without, glabrous, pilosulous (especially dorsally), or sericeous within, $7-14.5 \mathrm{~mm}$. long, main lobes oblong or cuneate-oblong, obtuse, usually ciliolate or hispidulous-ciliolate on margins, free beneath for $2-4.5 \mathrm{~mm}$., accessory lobes ligulate or spatulate-ligulate, 0.9-1.5 mm. wide, basally thickened, glabrous or sparsely hispidulous above, usually hispidulous-ciliate on margins, lateral lobes $1-4 \mathrm{~mm}$. shorter than main lobes, free $1-2 \mathrm{~mm}$. laterally and $3.5-8 \mathrm{~mm}$. medially, median lobe $1-5 \mathrm{~mm}$. shorter than lateral lobes, 2-6 mm. long; spur red, glabrous or pilosulous without, glabrous or hispidulous within, cucullate, arising at $0.5-3.5 \mathrm{~mm}$. from peduncle, $2-4 \mathrm{~mm}$. thick, projecting $1-3 \mathrm{~mm}$. posteriorly, lateral spur lobes narrow, folded in over accessory involucral lobes, medial lobes connate, together narrowly deltoid, attenuate-deltoid or ligulate from a deltoid base, $3-6 \mathrm{~mm}$. long, $3-4.5 \mathrm{~mm}$. wide basally, $0.6-1.2 \mathrm{~mm}$. wide at truncate or retuse apex, often thickened beneath at apex or somewhat thickened for $2-2.5 \mathrm{~mm}$., usually hispidulous-ciliate on margins and sometimes hispidulous beneath apex; medial glands basal or (in markedly projecting spurs) sub-terminal, reniform-oblong, subdeltoid, oblong or quadrate-oblong, $0.8-1.6 \mathrm{~mm}$. long, $0.6-1 \mathrm{~mm}$. wide, somewhat bent about partitions, rarely more or less split into glandpairs, lateral glands $0.5-1.5 \mathrm{~mm}$. anterior to medial glands, oblong, ovate-oblong, elliptic-oblong or lanceolate, $0.3-2.5 \mathrm{~mm}$. long, $0.2-0.9$ mm . wide; partitions indistinct or strongly developed between medial glands and base of accessory involucral lobes, bracteoles none or few, filamentous, $6-9 \mathrm{~mm}$. long, adnate to the involucral tube for ca. 3 mm ., glabrous or puberulent; roof lobules inconspicuous; staminate flowers $20-34$, pedicels $7-14 \mathrm{~mm}$. long, glabrous, or terminally hispidulous to villous for $1-7 \mathrm{~mm}$., filaments glabrous or puberulent, $2.5-3 \mathrm{~mm}$. long, anthers glabrous or sparsely pilosulous; pistillate pedicel $4-14 \mathrm{~mm}$. long, glabrous to tomentulose, ovary oblong or oblong-obovate, trigonous, ca. $1.5-1.8 \mathrm{~mm}$. long and 1.2 mm . wide, glabrous, puberulent or tomentulose, style glabrous or sparsely pilosulous, $5-11 \mathrm{~mm}$. long, branches $0.5-1 \mathrm{~mm}$. long, sub-entire to $1 / 2$ bifid; capsule subquadrate, $5-6 \mathrm{~mm}$. in diameter, deeply 3 -lobed in cross section; seeds ovoid or subglobose to quadrate-oblong, faintly keeled or not at all, $3-4.5 \mathrm{~mm}$. long, $2.5-3.2 \mathrm{~mm}$. wide, ashen grey,
grey-brown or red-brown, usually mottled, base truncate or obtuse, apex acute but low.

Representative specimens seen: Mexico. Tamaulipas. 7 mi . So. of Padilla, June 25, 1951, C. M. Rowell 2350 (місн); Chamal Hacienda, June 25, 1919, E. O. Wooton s.n. (US). Veracruz: Km. 368, Jalapa to Veracruz, March 15, 1941, I. K. Langman 3403 (PH); Rancho Remudadero and Puente Nacional, March 1935, C. A. Purpus 1624 (c) ; Puente Nacional, 1928, C. A. Purpus 10981 (F). Guerrero. Petatlán, Montes de Oca, alt. O m., G. B. Hinton 10331 (A, AHFH, GH, K, MICH, NY, UC, US). Oaxaca. Vicinity of Cuicatlán, E. W. Nelson 1682 ( $\mathrm{F}, \mathrm{GH}$, US) ; dry hills bordering the valley of Cuicatlán, $2,000 \mathrm{ft}$. , Pringle 604.3 (A, GH, MO, NY, PH, S, UC, US) ; Tomellín Cañon, J. N. and J. S. Rose 11360 (NY, US) ; canyon above Tomellín, Gentry 6998 (ahfy) ; S. W. of Tomellín, Dressler 1378 (GH) ; San Bartolo Yauhtepec, Seler 1682 (GH) ; Salina Cruz, Deam 119 (GH, мich) ; Picacho, Purpus 7352 (UC). Chiapas. Copainalá, Wonderly 15 (MICH); PanAmerican highway 24 mi . S. E. of Comitán, Carlson 1942 (F); Trapichito, Comitán, $1,350 \mathrm{~m}$., Matuda 5670 (F). Guatemala. Retalhuleu. Plains between Nueva Linda and Champerico, 120 m . or less, Standley 87775 (F). Escuintla. Escuintla, 1,100 ft., J. Donnell Smith 2072 (US). Guatemala. Near Fiscal, about 1,100 m., Standley 80.399 (F) ; Concuá Bridge over Río Motagua between Guatemala and Rabinal, ca. 300 m. , Standley 59.338 (F). Chiquimula. Quebrada Shusho, above Chiquimula, ca. 480 m ., Standley $\mathbf{r} 4291$ (F); near divide on road from Zacapa to Chiquimula, ca. 660 m ., Standley 73 亿̃10 (F). Zacapa. Loma El Pichacho, above Santa Rosalía, Sierra de las Minas, 1,200-1,600 m., Steyermark 427.37 (F). Izabal. Between Bananera and "La Presa" in Montaña del Mico, 40-300 m., Steyermark 38141 (A, F). El Petén. Carmelita, in thicket bordering aviation field, Egler 42-284 (F) ; Uaxactun, Bartlett 12194 (F, GH, MICH, NY, US); San Andrés, Lake Petén, Lundell 3144 (MICH, US); Dos Arroyos, Bartlett 12117 (f, MiCh, US). British Honduras. El Cayo, Bartlett 11980 (MICH); El Cayo and vicinity, Chanek 70 ( $\mathbf{F}, \mathbf{M I C H}$ ). El Salvador. Vicinity of Metapan, Dept. Santa Ana, 370 m., Standley and Padilla V. 321.3 (F). Honduras. Near Progreso, Dept. Yoro, 30 m., Standley 55106 (A, F, US) ; valley near dam for water supply of Progreso, Atlantida, Bangham 350 (A, F); San Pedro Sula, Iept. Santa Bárbara, 350 m. , Thieme 5467 ( ('s) ; vicinity of Coyoles, Aguan River Valley, Dept. Yoro, Yuncker, Koepper and Wagner 86.39 (F, GH, MICH, MO, NY, S, US) ; Wispernini Camp, Guarunta region, Colón, $75-100 \mathrm{ft}$., C. and $W$. von Hagen 1.335 ( NY). Isla de Providencia (Colombia). Lat. $13^{\circ} 21^{\prime}$ N., Long. $81^{\circ} 23^{\prime}$ W., Proctor 3418 (PH, US). Costa Rica. Hacienda Animas, Prov. Guanacaste, 500 ft., Shannon 5011 (U'S) ; Ojo de Agua, Prov. Alajüela, Echeverría 461 (F) ; Río Torres, Prov. San José, $1,160 \mathrm{~m} ., J$. Donnell Smith $6 i 664$ ( C 's). Panama. Trail between Cañazas and the foot of the Cordillera Central, headwaters of the Río Cañazas, $300-600 \mathrm{~m}$., Prov., Veraguas, Allen 196 (F) ; Aguadulce, Prov. Coclé, Pittier 5000 (US); Penonomé and vicinity, Williams 229 (NY, us); Taboga Island, Macbride 2804 (F, US) ; near Madden Dam at Alahuela, 70 m. , Dodge, Steyermark and Allen 16824 (G, s) ; Tabernilla, Cowell 276 (NY). Colombia. Valle del Cauca. La Paila, 1853, I. F. Holton s. n. (Ny) ; El Valle, near Cali,
E. Dryander 2725 (US). Tolima. Altamira, Sprague 229 (K). Cundinamarca. Vicinity of Apulo, alt. about 455 m., Killip, Dugand and Jaramillo 38265 (US). Huila. Entre Gigante y Rioloro, $820-860 \mathrm{~m}$. Pérez Arbelaez and Cuatrecasas 8.339 (Us). Meta. Salinas de Macapay, H. García B. 5115 (vs). Bolívar. Tierrabomba Island, Cartagena Bay, Killip and Smith 14127 (GH, Ny, Us). Atlántico. Alrededores de Puerto Colombia, altura aproximada 200 m ., Barkley and Gutiérrez V. 1841 (GH, NY, US) ; entre Puerto Colombia y Salgar, Dugand and Jaramillo 322.3 (US) ; cerca de Ponedera, 5-10 m., Iugand and Jaramillo 2752 (us). Magdalena. Santa Marta, H. H. Smith 1295 (F, gH, MO, NY, PH, S, U, US) ; common on road from La Paz towards Manaure, ca. 200 m ., Haught 3871 (A, US). Goajira. 9 km . So. of Carraipía, 200 m., Haught 4262 ( $F$, US). Venezuela. Falcón. Cerro Santa Ana, Península de Paraguaná, 700-800 ft., Curran and Haman 717 (Gh, Ny). Carabobo. Hacienda Taborda near El Palito, 0-200 m., Pittier 7674 (GH, US); vicinity of Puerto Cabello, Rose and Rose 21862 (US). Aragua. Ocumare de la Costa, 0-15 m., Steyermark 54938 (F, NY). Distrito Federal. La Guaira, Robinson and Lyon s.n. (US); near Maiquet:a, Pittier 10297 (US). Sucre [?]. Alrededores de El Palmer, 300 m ., Guayana, Cardona 2117 (US). Isla de Margarita. El Valle, J. R. Johnston 59 (C, F, GH, Ny, US) ; El Valle, O. O. Miller and J. R. Johnston 31 (F, GH, mo, Ny, us). Curacao, D. W. I. South of the Hato plains, red flowers, Curran and Haman 204 (GH, NY). Trinidad. B. W. I. Western end of Monos Island, Britton, Britton and Broun 2737 (NY); Little Gasparee, Britton 2789 (GH, Ny, US); Manzanilla, N. L. and E. G. Britton 2194 (Gh, Ny, US) ; North Manzanilla, headland to E. of bay, $40 \mathrm{ft} .$, Baker and Simmonds (K); Trinidad, Fendler 699 ( $\mathbf{K}$ ). British Guiana. Waini River, Northwest Dist., lat. $8^{\circ} 20^{\prime}$ N., long. $59^{\circ} 40^{\prime} \mathrm{W} .$, De La Cruz 3771 (F, GH, MO, NY, PH, US, US). Surinam. Commewijne River near plant. Ma. Retraite, Soeprata 39 B (U).

Distribution and habitat (Map 7). From Tamaulipas and Guerrero in Mexico south through Central America (except Yucatan Peninsula) to southern Colombia, and along the northern coast of South America (including Curacao, Isla de Margarita and Trinidad) to Surinam.

In northern Oaxaca, this species is frequent in the open, arid thorn forest of Tomellin Canyon (see fig. 23) ; on the Isthmus of Tehuantepec, it is found in low thorn scrub, and, here too, it is quite frequent. Near Tuxtla Gutiérrez, Chiapas, $P$. tithymaloides is occasional and local in tropical deciduous forest on limestone (see fig. 22). On the Pacific slope of Guatemala the species is found in "brushy, rocky slopes," in Petén and Honduras, its habitats range from "semi-arid woodland" to "jungle," "logwood swamp," and "humid tropical forest." The vegetation of rocky sites (pedregal) occupied by this species at Uaxactun, Guatemala, is briefly described by Bartlett (1935, p. 20). In
northern South America, similarly, the sites in which this species is found range from "arid littoral scrub" to "cliffs in rather humid forest." It is evident that this species has


Maps 7 AND 8. The distribution of Pedilanthus tithymaloides. A single collection of subsp. tith!!maloides from Surinam is not shown in Map 7. but is shown in the inset of Map 8. Some or all of the localities for subsp. parasitieus outside of Hispaniola may represent escapes from cultivation.
a much wider range of habitats than any other in the genus, but that, in the wetter areas, it is usually to be found in rocky sites, and frequently on limestone. Flowering especially in the winter, but found in flower at all seasons of the year in different areas.

Common names. Candelilla (Tamaulipas, Mexico), saca espinas sin dolor (Puebla, Mexico, "remove spines without pain"), comalpahtli (central Mexico, Nahuatl: "griddle medicine," referring apparently to its preparation as medicine). The other Nahuatl names reported by Hernandez (1651), chapolxochitl (grasshopper flower), mincapahtli (arrow medicine), tenapalitl (live-forever), and pinipiniche (?, probably not Nahuatl), seem not to have been reported more recently, but some may still be in use. Suelda con suelda (Guatemala, referring to use in treating broken bones?), pie de niño (Central America), dítamo real and variants (bítamo, pitamo, ítamo, etc.) (Central and South America and West Indies), hierba ipecacuana (South America and West Indies, doubtless referring to its purgative qualities), espuela de gallo, clavo de Cristo (Colombia), pinopinita (Venezuela), Melksapblad (Surinam).

Variation. The vegetative features of Mexican $P$. $t$. ssp. tithymaloides reflect the relatively xeric habitat of these northern populations. The stems tend to be thick and succulent and the leaves to be puberulent and of moderate size ( $3-6 \mathrm{~cm}$. long) ; the leaves of Mexican plants are generally markedly elliptic. In northern Oaxaca, at least, the leaves on some shoots are quite small and there seems to be a distinct tendency toward foliar dimorphism (see Plate XXI). The cyathia of Mexican plants are of relatively large size (12-14 mm. long) and nearly or quite glabrous. The few collections from Veracruz bear cyathia which are sparsely hispidulous within and the cymes are mostly axillary.

In southern and western Guatemala (including Zacapa and Chiquimula), the plants bear foliage similar to that of the Mexican plants, but the stems are mostly very slender. The involucres are of moderate size ( $10-11 \mathrm{~mm}$. long) and nearly glabrous, except for the two collections from Retalhuleu, the basis of $P$. camporum. In these collections, the cyathia are pilosulous without (the hairs rather thin), the ovaries tomentulose and the anthers sparsely pilosulous, the staminate pedicels and filaments glabrous. The bracts of
these plants are small ( $4-5 \mathrm{~mm}$. long) and densely puberulent. No leaves are present in either collection; more material is needed from northwestern Guatemala. In Petén and Izabal, on the wetter Atlantic slopes of Guatemala, and in British Honduras, the plants of $P$. tithymaloides are mostly markedly different; they show the very slender stems of the other Guatemalan collections, while the leaves are larger (up to $8-12 \mathrm{~cm}$. long), glabrous or glabrate, more ovate (proportionally much wider near the base) and sometimes obtuse. The involucres of these plants are fairly large (ca. $11-12.5 \mathrm{~mm}$. long) and glabrous or nearly so.

Honduran collections are similar to those from Izabal and Petén in vegetative features, but some are remarkable for their large bracts and involucres and short, non-elongating pistillate pedicels; in Standley 55106, the bracts are 12-14 mm . long, attenuate and bright red, the involucres are 13.514.5 mm . long, and the pistillate pedicel $4-5 \mathrm{~mm}$. long. Most other Honduran collections are similar but less extreme in their features; Yuncker, Koepper and Wagner 1335 has only a few cyathia, but these have normally elongating pistillate pedicels. In the short pistillate pedicel, the Honduran $P$. tithymaloides resembles $P$. pulchellus and $P$. coalcomanensis. Proctor 3418, from Isla de Providencia, resembles the plants of eastern Guatemala, but has a more succulent stem. The rest of Central America is too poorly collected to permit any discussion of variation.

The plants from southern Colombia and some of the Panamanian collections (Cowell 276 and Williams 229) resemble the sort of plant which was described and figured as $P$. canaliculatus; these plants have widely lanceolate leaves which are strongly attenuate and have the midrib markedly winged beneath. The staminate pedicels of these plants are puberulent. This sort of plant is often cultivated in the West Indies and could well have been introduced from Panama.

South American collections of $P$. tithymaloides are quite variable as to leaf shape (probably to be correlated in large part with dryness of habitat), but show a very interesting pattern of variation in the features of the involucre. In western Colombia, the involucres are of medium size (10-12 mm . long) and glabrous or somewhat pilosulous, the staminate pedicels are puberulent or pilosulous, and the spurs
are similar to that figured in Plate XXI (a Mexican plant), rounded and somewhat projecting, with the median spur lobe partially connate to the lateral spur lobes. In eastern Venezuela, and especially on the islands of Margarita and Curacao, the involucres are much smaller ( $7-9 \mathrm{~mm}$. long) and markedly pilosulous without, the staminate pedicels are villous, the spurs are only slightly projecting, and the median spur lobes are free (from the lateral lobes) nearly or quite to the base. This last feature permits the spur to gape widely when lateral pressure is applied, as in pressed specimens (in this, the specimens have somewhat the aspect of subspp. bahamensis or angustifolius). It should not be thought that these two types are distinct populations; they are merely the two ends of a complex series of clines. The plants of eastern Colombia and western Venezuela bridge the gap as nearly as can be expected of the available collections (see Map 7). The type of $P$. gritensis is such an intermediate plant as to size and form of the involucre, but has an unusually dense indument in all parts, and proportionately very wide leaves.

Pedilanthus tithymaloides from Trinidad does not greatly resemble the Venezuelan plants (there is a considerable geographic gap, bridged only by one sterile collection), but the Trinidad populations are rather variable, and some plants show a marked resemblance to subsp. padifolius of the Lesser Antilles. Britton and Britton 2194, Britton 2789. and Baker and Simmonds $s n$. are especially similar to padifolius in leaf shape and texture. Fendler 699 and Britton, Hazen and Mendelson 1093 (the type of $P$. ierensis) have thin ovate leaves quite unlike those of padifolius; the type of $P$. ierensis has unusually large leaves (up to 16 cm . long).

The single collection from British Guiana is unusual in its sub-lanceolate leaves, which give it a quite distinctive aspect. The cyathia of this collection are similar to those of Mexican and Central American collections; they are medium large (11-11.5 mm. long) glabrous or nearly so, and have spurs which project posteriorly and arise quite near the peduncle (at ca. $0.5-0.7 \mathrm{~mm}$.). The staminate pedicels of this collection are apically puberulent, but not strongly so. The single collection seen from Surinam is without flowers,
and the leaves are badly broken, but it resembles the above collection vegetatively.

The above discussion is manifestly incomplete and subjective. An adequate treatment of this taxon would require many different measurements in the cyathium alone and careful statistical treatment. Even then, the major gaps in material from Central and South America and the rather poor material from some North American localities would make such a study only preliminary. Nevertheless, a study of this sort would be of great value, especially if augmented by field work in South America.

Relationship. Within the species, the subspecies is closely allied to subspp. Smallii, parasiticus, padifolius and retusus; all of these are probably derived from subsp. tithymaloides, or ancestral types which would fall within its rather wide range of variability. Pedilanthus tithymaloides seems clearly allied to $P$. nodiflorus in a number of features, and the two show some resemblances to the $P$. pulchellus alliance.

Notes. The typification of Euphorbia tithymaloides L. is a troublesome matter, since there are no specimens of this plant in the Linnean Herbarium and no plates are cited by Linnaeus under typical E. tithymaloides. Croizat (1943) has taken Poiteau's Plate 19 (1812) as neotype for the species. Unfortunately, this choice must be reconsidered. Pedilanthus tithymaloides has been traditionally applied to a plant with more or less cuneate leaf bases and puberulent staminate pedicels; the sort of plant which may be found in Central America or Colombia. From Dr. Croizat's discussion of Dugand and Jaramillo 2752 (Colombia), it would appear that he had no intention of changing the customary concept of $P$. tithymaloides. Poiteau's figure rather clearly represents the plant which has been variously known as $P$. parasiticus, P. ramosissimus, $P$. itzaeus and P. latifolius (here treated as $P$. tithymaloides subsp. parasiticus). The subcordate leaf bases, the small bract-like leaves below the inflorescence, the shortly exserted styles with widely spreading stigmas, and the locality, Cap Francais, St.-Domingue, all point strongly to this conclusion. Rather than take this poorly known (though easily recognizable) entity as type, I have chosen Jacquin's plate 92 (1763), which is, historically, a good choice, and which clearly rapresents the sort of
plant which has been consistently considered to be $P$. tithymaloides. To state that the Euphorbia tithymaloides of Linnaeus represented "a mixture of all the species in this group known to Linnaeus and his predecessors" (Croizat 1943) is to color the issue somewhat; there is no evidence that any Pedilanthus other than P. tithymaloides, including subsp. padifolius, were known to Linnaeus or the earlier European writers.

This plant is widely cultivated as a hedge and medicinal plant in tropical and sub-tropical America. It is the subspecies most commonly encountered in botanical gardens and greenhouses. Several forms in which the leaves are variegated with white or white and pink are widely grown. The physiological or genetic basis for this pattern is not known. The leaves of variegated plants are unusually narrow, but branches of these plants occasionally "sport" to the normal green-leaved sorts, and these normal branches (in those which have been seen to "sport") bear wider leaves which are typical of subsp. tithymaloides.

## 13b. Pedilanthus tithymaloides subsp. parasiticus (Kl. and Gke.) comb. nov.

P. parasiticus Kl. and Gke., Abh. Akad. Berl., Phys. 1859: 105. 1860. Type: Nueva España, Herb. Pavón (G!, photo and tracing: F!, Sessé, Mociño, Castillo and Maldonado 1773, F! is probably an isotype). P. ramosissimus Boiss., DC. Prod. 15 (2) : 5. 1866. - Tithymalo [i] des parasiticum (Kl. and Gke.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891. Tithymalus parasiticus (Kl. and Gke.) Croiz., Amer. Jour. Bot. 24: 704. 1937.
P. itzaeus Millsp., Field Mus. Pub. Bot. 1: 305, Pl. 18. 1896. Type: Mexico, Yucatan, on cultivated lands, port of Silam, March to June, 1895, G. F. Gaumer 452 (F 36255!). - Tithymalus itzaeus (Millsp.) Croiz., Amer. Jour. Bot. 24: 704. 1937.
P. latifolius Millsp. and Britton, Ann. Mo. Bot. Gard. 2: 43. 1915. Type: Bermuda, Castle Point, waste grounds, Aug. 27 - Sept. 21, 1912, 2 m . high, midrib not winged beneath, flowers salmon, S. Brown and N. L. Britton 820 (Ny!, isotypes: F!, PH!). - Tithymalus petanophyllus Croiz., Amer. Jour. Bot. 24: 704. 1937. Based on P. latifolius, not T. latifolius (C. A. Meyer) Kl. and Gke.

Shrub $0.8-2 \mathrm{~m}$. tall, succulent; stem thick, sparsely crisped-puberulent when young, becoming glabrate, straight or slightly zig-zag; leaves glabrous or glabrate above, sparsely puberulent beneath when young, becoming glabrate, succulent and glossy, deltoid-ovate or broadly ovate, rarely elliptic-ovate, apex acute or narrowly obtuse, usually acuminate, base truncate or subcordate, 3-9 cm . long, 2.5-6.5
cm . wide, branches with small bract-like leaves $0.7-2 \mathrm{~cm}$. long and $0.5-1 \mathrm{~cm}$. wide often occur, midrib weakly keeled, petiole $2-4 \mathrm{~mm}$. long, sparsely puberulent, stipules brown, blunt and spur-like or depressed, ca. 0.5 mm . wide and $0.2-0.5 \mathrm{~mm}$. high; inflorescence terminal or axillary, branches often partly monochasial by abortion, internodes $1-2.5 \mathrm{~mm}$. long, glabrate or sparsely puberulent, bracts red, oblong or ovate, acute or acuminate, $4-7 \mathrm{~mm}$. long, $3-4 \mathrm{~mm}$. wide, glabrous or sparsely puberulent within and usually sparsely puberulent without, especially along midvein and margins, peduncle $3-4 \mathrm{~mm}$. long, glabrous; involucre pink, entirely glabrous except on margins, involucral tube $7.5-11 \mathrm{~mm}$. long, main lobes oblong, obtuse, free for $2.5-3 \mathrm{~mm}$. beneath, ciliolate on margins, accessory lobes ligulate, $0.6-1.1 \mathrm{~mm}$. wide, obtuse, margins ciliolate, lateral lobes 1-2.5 mm. shorter than main lobes, free 1-2 mm. laterally and 3-5 mm. medially, median lobe $0.5-2 \mathrm{~mm}$. shorter than lateral lobes; spur cucullate, arising posteriorly at $2-3 \mathrm{~mm}$. from peduncle, $1.5-2 \mathrm{~mm}$. thick, projecting $1-2 \mathrm{~mm}$. posteriorly and sometimes faintly 3 -lobulate near base, lateral lobes narrow, folded over accessory involucral lobes, medial lobes usually completely connate, together attenuate-deltoid, $2-4 \mathrm{~mm}$. long, $2-5 \mathrm{~mm}$. wide at base, $0.9-1.2 \mathrm{~mm}$. wide at retuse apex, the attenuate portion slightly thickened, if medial lobes free, then only $1 / 2$ as wide and each lobe asymmetrically retuse; medial glands basal, oblong, markedly bent, 1-1.5 mm. long, $0.5-0.8 \mathrm{~mm}$. wide, lateral glands ca. 0.5 mm . anterior, ovate or oblong, $0.8-1.2 \mathrm{~mm}$. long, $0.5-0.8$ mm . wide; partition short ( $0.6-1 \mathrm{~mm}$. long), but distinct between medial glands and bases of accessory involucral lobes, ca. 0.4 mm . high; bracteoles absent or very few, filamentous, to 3 mm . long, dorsal and lateral bracteole-ridges $1.5-2 \mathrm{~mm}$. long, terminating in short linguiform lobes, roof lobules absent; staminate flowers $14-22$, pedicels glabrous, $8-12 \mathrm{~mm}$. long, filaments $1-2 \mathrm{~mm}$. long, glabrous or sparsely pilosulous, anthers glabrous; pistillate flower glabrous, pedicel 4.5-11 mm. long, apparently not elongating after anthesis, ovary ovoid, trigonous, ca. 1.5 mm . in diameter, style thick, $5.5-7 \mathrm{~mm}$. long, branches $0.7-1 \mathrm{~mm}$. long, shallowly bifid, usually spreading; fruit and seed unknown.

Representative specimens seen. Mexico. Yucatan. Mérida, Schott 552 (F) ; Yucatan, Valdez 85 (F). Veracruz. San Andrés Tuxtla, cultivated as hedge, I)ressler 1807 (GH). British Honduras. Corozal Dist., Gentle 360 (MICH). Jamaica. Parish of St. Thomas, Bank near Bath, Britton 3491 (NY). Haiti. Arid mountains northwest of Bombardopolis, 610 m., E. C. and (F. M. Leonard 13456 (USS) ; La Source, vicinity of Pikmi, Gonave Island, Leonard 5196 (ny, US) ; Dept. de l'Artibonite, Puilboreau road, vicinity of Ennery, $325-900$ m., Leonard 9711 (GH, US) ; Massif de la Hotte, western group, Jérémie, at Testas, escaped, Ekman 10787 (S). Santo Domingo. Sánchez, Rose, Fitch and Russell 4397 (US); Feb. 6, 1891, Wright, Parry and Brummel s. n. (Us). Puerto Rico. Local near Luquillo (Rio Grande to Fajardo), Britton, Britton and Brown $\gamma 040$ (Ny); near house, Ubero, Mona Island, Britton, Cowell and Ness 1786 (NY) ; St. Croix. Midland, Mrs. J. J. Ricksecker 287 (F).

Distribution and habitat (Map 7). Cultivated and perhaps native in the Yucatan Peninsula, apparently native in the Greater Antilles, in Jamaica and Hispaniola, and perhaps in Puerto Rico and St. Croix. Widely cultivated in Mexico and apparently cultivated in Bermuda and China as well as in the Greater Antilles. If native in Yucatan, the plant occurs in coastal thorn scrub similar to that occupied by $P$. nodiflorus (see fig. 24). The scant data from the Antilles indicate dry, and in some cases rocky, sites. Apparently flowering mainly in winter (Dec.-April), but flowering sporadically in summer (July - Sept.) as well.

Common names. Mayorga, zapatito de la reina (Sierra de Tuxtla, Mexico, the second name, "the queen's slipper," is clearly a poetic name and not the "common name" in the area) ; zapatito de la Virgen, "the Virgin's slipper," vela de sebo, "tallow candle," in reference to the thick, glossy, greyish stems (Guerrero, Mexico) ; yaxhalalché, Mayan: "green stem tree" (Yucatan peninsula) ; pie de niño, monkey fiddle (British Honduras) ; ipecacuana and variants (Hispaniola).

Variation. The variation pattern of this mysterious entity cannot yet be satisfactorily handled. The features of the involucre are relatively uniform except in size; the collection from Ile de la Gonave, Haiti, has very small involucres ( $7.5-8 \mathrm{~mm}$. long), suggesting a size reduction parallel to that of subsp. angustifolius and its allies in the Greater Antilles. Faintly three-lobed spurs were most clearly noted in the material from Bermuda (where it is doubtless introduced); the same feature is present, but less marked, in the specimens from Veracruz. Subspecies parasiticus is interesting for the frequent occurrence of free medial spur lobes, presumably, like the lobed spur apex, a primitive character within the species. This feature is of little taxonomic value, however, since it varies on a single plant. Plants of this subspecies are readily recognized not so much from leaf shape as from the succulent, glossy or almost glaucous leaves and stems. As cultivated in Veracruz and Yucatan, the plants show two very different aspects, the Veracruz plants having dark green, nearly plane leaves and the Yucatan plants bearing leaves which are much lighter in color and somewhat ruffled or crisped. When plants from these two sources are grown together in the
greenhouse, they are vegetatively indistinguishable. The tendency to produce branches with small bract-like leaves has been noted only in cultivated material in the mainland of Mexico and in some specimens from Hispaniola. Whether or not other populations have this potentiality is not known.

Relationship. This subspecies is closely related to subsp. Smallii, and both are notable for being nearly glabrous in most parts. This feature appears to point to the Atlantic slope of northern Central America. The non-elongating pistillate pedicel of parasiticus finds a parallel in Honduran material of $P$. t. ssp. tithymaloides. It is quite possible that parasiticus and Smallii were derived from plants which reached the West Indies from Honduras or Nicaragua and that parasiticus has only recently been introduced into the Yucatan Peninsula by man.

Notes. Though three times described as a new species, this plant has not been collected often, and adequate flowering specimens are few, indeed. Pedilanthus latifolius was clearly based on cyathia with free medial spur lobes, but this character is not constant, even for the type collection. The basis of $P$. itzaeus is less clear; if a normal plant were found which fit the description given by Millspaugh, it would well merit the "§ Anomalus" which Millspaugh used and later discarded. The type specimen is completely without cyathia, though the confusing description and even more confusing sketches were apparently based on this collection. It is suspected that these sketches were based upon the first involucre of a cyme (which is often abnormal), in which most of the involucral bracts had developed on the accessory lobe pattern.

The subspecific epithet is apparently that applied by Pavón as an herbarium annotation. It was wrongly credited, by Klotzsch and Garcke, to Boissier, who later re-named the species, commenting: "Nomen specificum Pavonii probabilissime improprium."

In the isolated Sierra de los Tuxtlas of southern Veracruz, this Pedilanthus is widely cultivated as a hedge and ornamental, the subsp. tithymaloides being seen only in its variegated form or an occasional green "sport." The variegated Pedilanthus was referred to by one housewife as mayorga de lucir, or "fancy mayorga," as contrasted with the ordinary mayorga of hedges. The common hedge plant
of $\operatorname{los}$ Tuxtlas agrees well with the type specimen of $P$. parasiticus, as far as can be determined; it is quite possible that the type was collected there by Mociño, in 1793 or 1794, when he visited the then active volcano near San Andrés Tuxtla and spent some time in the town. Pedilanthus tithymaloides ssp . parasiticus has been seen in cultivation in Cuernavaca, Morelos and Iguala and Atoyac in Guerrero; cuttings from these areas failed to survive in the greenhouse.

The collection from British Honduras is assigned to this taxon with some reservations; the plant, which is sterile, was rather damaged before collection, and the leaves were much crumpled in drying.

## 13c. Pedilanthus tithymaloides subsp. Smallii (Millsp.)

 comb. nov.P. Smallii Millsp., Field Mus. Pub. Bot. 2: 358. 1913. Type: Florida, in pinelands, Miami, Nov. 1-30, 1904, J. K. Small 2286 (NY!, photo and fragment: F!). - Tithymalus Smallii (Millsp.) Small, Man. S. E. Flora, 804. 1933.

Shrub $0.7-2 \mathrm{~m}$. tall, stems puberulent when young, becoming glabrate with age, each node usually bent sharply in an obtuse angle, so that the stem is conspicuously zig-zag; leaves sparsely pilose-puberulent beneath and glabrate or very sparsely puberulent above, generally $2.5-7 \mathrm{~cm}$. long and $1.3-3.2 \mathrm{~cm}$. wide, but branches with small bractlike leaves, mostly $0.8-1.5 \mathrm{~cm}$. long and $0.35-0.5 \mathrm{~cm}$. wide often formed, blades elliptic-ovate or lance-ovate, base cuneate, apex acuminate, acute or narrowly obtuse, midrib keeled or winged, petiole puberulent, $1.5-5 \mathrm{~mm}$. long, stipules dark brown, spur-like, blunt, ca. 0.5-0.6 mm. in diameter and height; cymes terminal and axillary, congested, internodes puberulent, $1-2 \mathrm{~mm}$. long, bracts red, oblong-lanceolate to oblong-ovate, acute or acuminate, puberulent without and more or less sericeous within, $5-7 \mathrm{~mm}$. long, $2-3 \mathrm{~mm}$. wide, peduncle glabrous, $6-9 \mathrm{~mm}$. long; cyathia pink or red, involucral tube glabrous throughout, $8.5-12 \mathrm{~mm}$. long, main lobes oblong or lance-oblong, obtuse, sparsely ciliolate on margins, free beneath for ca. 2.5 mm ., accessory lobes ligulate or subspatulate, obtuse, sparsely ciliolate, margins sparsely hispidulous above near base, $0.8-1 \mathrm{~mm}$. wide, lateral lobe ca. 2-3 mm . shorter than main lobe, free $1-1.5 \mathrm{~mm}$. laterally, $5-6 \mathrm{~mm}$. medially, medial lobe $1.5-2 \mathrm{~mm}$. shorter than lateral lobes; spur cucullate, arising at ca. 1.5 mm . from peduncle, ca. $2.5-3 \mathrm{~mm}$. thick, projecting $1-2 \mathrm{~mm}$. posteriorly, glabrous without, lobes basally hispidulous on and near margins within, lateral lobes folded in over accessory involucral lobes, medial lobes connate, together $3.5-5 \mathrm{~mm}$. long, basally $3.5-4.5 \mathrm{~mm}$. wide, subligulate from a broadly deltoid base, the ligulate portion $2-3 \mathrm{~mm}$. long, slightly thickened, $0.8-1.1 \mathrm{~mm}$. wide at the retuse apex, medial glands basal, thick, slightly bent, subquadrate to
oblang, $0.8-1.2 \mathrm{~mm}$. long, $0.7-0.8 \mathrm{~mm}$. wide, usually obliquely truncate where pressed together and to lateral glands in development, lateral glands ca. 0.5 mm . anterior, irregularly ovate or oblong, $1-1.2 \mathrm{~mm}$. long, $0.6-1 \mathrm{~mm}$. wide, partitions very slight; bracteoles absent or very few, filamentous, to 5 mm . long; roof lobules absent; staminate flowers ca. 20-30, glabrous, pedicels $9-11 \mathrm{~mm}$. long, filaments $1.7-2.5 \mathrm{~mm}$. long; pistillate flower glabrous, pedicel $6-10 \mathrm{~mm}$. long, protruding scarcely or not at all from the involucral tube, ovary oblong-ovoid, trigonous, ca. 1.5 mm . in diameter, style thick, $5-6 \mathrm{~mm}$. long, branches $0.7-1 \mathrm{~mm}$. long, ca. $1 / 3$ bifid, spreading or connivent; fruit unknown; seed grey, ovoid-subglobose, apiculate, base rounded, faintly keeled dorsally, 3.3 mm . long, 2.7 mm . wide, raphe dark brown.

Representative specimens seen. Florida. Eastern shore of Lake Okeechobee, Small, DeWinkeler and Mosier 11157 (GH, NY, s) ; Brickell Hammock, Miami, Dade Co., J. K. and G. K. Small 6826 (NY) ; at edge of Cox Hammock, west of Goulds, Dade Co., Moldenke 645 ( mo, NY, S) ; Meigs Key, Monroe Co., Small 7369 (Ny, S, us). Cuba. Vicinity of Matanzas, playa, Britton, Britton and Shafer 156 (F, NY) ; Santiago de las Vegas, Prov. Havana, cultivated in gardens, van Hermann 507 (F, NY) ; Antilla, Oriente, hotel garden, Britton, Britton and Cowell 12512 ( $\mathrm{F}, \mathrm{NY}$ ).

Distribution and habitat (Map 7). Southern Florida, from near Lake Okeechobee south to Meigs Key, and northern Cuba (Matanzas). Widely cultivated; specimens have been seen from Florida, Cuba, Mexico, El Salvador, Costa Rica, the Philippines, Java and China. The plants were probably carried from Cuba at an early date by Spanish ships. The habitat in Florida is given as pinelands and hammocks. Flowering in winter (Dec. - March).

COMMON NAMES. "Jacob's ladder" (Florida), pie de niño, bitamo real, zapatillo, lechilla (Central America).

Variation. As now sampled, this subspecies is relatively uniform in all its features. The stems are sometimes nearly straight and the leaves vary in size, but no conspicuous variation has been noted in other characters.

Relationship. Though this subspecies is very different in aspect from parasiticus, these two entities are closely related and differ mainly in leaf shape and texture, and in the more markedly zig-zag stems of Smallii. The involucral characters of the two are very similar except for the long-attenuate spur lobe of Smallii. This feature is also found in subsp. tithymaloides (Von Hagen and Von Hagen 1335) from Honduras, which further suggests that the ancestor of Smallii and parasiticus had its origin in Central America.

Notes. Plants of cultivated origin were transplanted to the greenhouse for further study, but all were destroyed by an infectious stem-rot, which also attacked some plants of parasiticus.

The type specimen has suffered serious attrition since the photograph at Chicago Natural History Museum was taken; the specimen is now without cyathia and nearly leafless.

Some of the variegated forms of $P$. tithymaloides which are cultivated are referable to this taxon, but, since the variegation distorts the leaves to some degree, it is often difficult to assign these forms to a subspecies.

## 13d. Pedilanthus tithymaloides subsp. retusus (Benth.) comb. nov.

P. retusus Benth., Hook. Jour. Bot. and Kew Misc. 6: 321. 1854. Type: Brazil, prope Barra [Manaos], Prov. Rio Negro, April, 1851, $R$. Spruce 1469 (Herb. Benth. at к, isotypes Herb. Hook. at K, G!, NY!, P!, fragment F!). - Tithymalo[i]des retusum (Benth.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891. - Tithymalus melanopotamicus Croiz., Ain. Jour. Bot. 24: 703. 1937, based on P. retusus, not T. retusus (Cav.) Kl. and Gke.

Shrub $0.7-1.7 \mathrm{~m}$. tall; stem glabrate, apparently sparsely puberulent when young; leaves glabrous above, glabrate or sparsely puberulent beneath, ovate, oblong-ovate or broadly elliptic, 3.2-7.3 cm . long, $1.5-4.8 \mathrm{~cm}$. wide, obtuse and usually retuse, base cuneate, midrib carinate, petiole $3-5 \mathrm{~mm}$. long, stipules dark, low, sub-hemispheric or transversely oblong, $1-1.7 \mathrm{~mm}$. long, $0 . \overline{5}-1 \mathrm{~mm}$. wide; inflorescence terminal, on lateral branches or axillary, internodes $3-5 \mathrm{~mm}$. long, sparsely puberulent, bracts oblong-ovate, glabrate within, puberulent without, especially along margins and mid-vein, $5-9 \mathrm{~mm}$. long, $2.5-3$ mm . wide, acute, peduncle $4-7 \mathrm{~mm}$. long, puberulent; involucre glabrous without, tube $8-9.5 \mathrm{~mm}$. long, pilosulous within, especially dorsally, main lobes oblong, obtuse, ciliolate, free beneath for ca. 2 mm ., accessory lobes thickened at ca. 2 mm , from medial glands, glabrous above except for hispidulous margins, ligulate or ligulate-spatulate, $1-1.2 \mathrm{~mm}$. wide, obtuse, ciliate, lateral lobes $1-2 \mathrm{~mm}$. shorter than main lobes, free ca. 1 mm . laterally, $2-4 \mathrm{~mm}$. medially, medial lobe $1.4-1.5 \mathrm{~mm}$. shorter than lateral lobes, free portion $2-3 \mathrm{~mm}$. long; spur cucullate, arising at $1.5-2 \mathrm{~mm}$. from peduncle, ca. 2 mm . thick, slightly projecting posteriorly, but rounded, lobes hispidulous along margins and within, lateral lobes folded in over accessory involucral lobes, medial lobes usually completely connate (free nearly to glands in Bento Pickel 2129, and then half as wide as the wider of the measurements given), together deltoid, truncate, $3.5-4.5 \mathrm{~mm}$. long, $3-5 \mathrm{~mm}$. wide basally, $1.2-1.4 \mathrm{~mm}$. wide at apex, slightly thickened apically, sericeous-puberulent or hispidulous-puberulent beneath,
somewhat grooved medially on underside, medial glands basal, oblong or reniform-oblong, straight or slightly bent, 1-1.3 mm . long, $0.6-0.8$ mm . wide, lateral glands $0.5-0.7 \mathrm{~mm}$. anterior to medial glands, lanceovate, attenuate, $1-1.5 \mathrm{~mm}$. long, $0.6-0.7 \mathrm{~mm}$. wide; partitions very slight; bracteoles none or few, filamentous, glabrous, $2-3 \mathrm{~mm}$. long; roof lobules absent; staminate flowers 19-24, pedicels $9-11 \mathrm{~mm}$. long, pilose terminally for $2-4 \mathrm{~mm}$., filaments ca. 1.5 mm . long, glabrous; pistillate pedicel $7-9 \mathrm{~mm}$. long, puberulent, ovary glabrous, oblongovoid, ca. 2 mm . long and 1.5 mm . wide, trigonous, style glabrate, $5-5.5$ mm . long, branches $0.5-1 \mathrm{~mm}$. long, shallowly bifid; capsule subquadrate, deeply 3 -lobed, ca. 6 mm . long; seed ashen grey, oblong-ovoid scarcely keeled, basally truncate, apically acute but low, apex brown, raphe light brown on dark brown band, seeds ca. 4 mm . long and 2.5-3 mm . wide.

Specimens seen. Peru. Río Mazán near Iquitos, Dept. Loreto, 125 m., L. Williams 81.33 (F) ; Iquitos, Dept. Loreto, 120 m ., L. Williams 3567 (F). Brazil. Rio Negro, Martius s. n. (M) ; Para, sylvis fl. Amazon. conterminis, Maio, Martius s. n. (M) ; Para, ad Breves in ins. Marajo, Aug., Martius 2654 (M) ; Pernambuco (Tapera), cult., D. Bento Pickel 2129 (US).

Distribution and habitat (Map 8). Known only from scattered localities in Amazonian South America where it may be cultivated. Ducke (1946) says of this plant (trans. from Portuguese) : "Sapatinho: . . plant with caustic latex, sometimes used in folk medicine, not infrequent on farms [quintais], in Para and Amazonas. Origin not known with certainty, possibly from the northern part of tropical America." Apparently flowering in autumn and spring (Sept., Oct., and April).

COMMON NAMES. Sapatinho, sapatinho do diabo (Brazil) ; zapatito del niño (Peru).

Variation. Little variation has been noted aside from the unusual, free medial spur lobes of Bento Pickel 2129. In this collection the spur lobes are uniformly free nearly to the base. This same condition occurs sporadically in subsp. parasiticus, but is rarely consistent throughout a collection. Bento Pickel 2129 also has somewhat more oblong leaves than do the other collections seen. The type collection, which is brittle and perhaps shrunken, seems to have slightly smaller involucres than do the other specimens at hand.

Relationship. In some respects this taxon is similar to subsp. padifolius. It is not certain that the leaf shape indicates actual relationship, and the other features are also shared with Venezuelan populations of subsp. tithymaloides. The geographically closer (as the ranges are now known)
subsp. tithymaloides of Colombia and of the Guianas do not approach retusus so closely as do the Venezuelan plants, either in indument of the involucre or in leaf shape.

## 13e. Pedilanthus tithymaloides subsp. padifolius (L.) comb. nov.

Euphorbia tithymaloides $\beta$. padifolius L., Sp. Pl. 1: 453. 1753. Type: A specimen in the Dillenian Herbarium (oxf, photo GH!). Tithymalus laurocerasifolius Mill., Gard. Dict. ed. 8. 1768. - $P$. padifolius (L.) Poit., An. Mus. Paris 19: 393. 1812. - Crepidaria padifolia (L.) Haw., Syn. Pl. Succ. 136. 1812. Tithymalo[i]des padifolium (L.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891. - P. tithymaloides var. padifolius (L.) Griseb., Fl. Br. W. I. 52. 1859. - Tithymalus padifolius (L.) Croiz., Am. Jour. Bot. 24: 703. 1937 - $P$. laurocerasifolius (Mill.) L. C. Wheeler, Contr. Gray Herb. No. 124:42. 1939.

Euphorbia anacampseroides Lam., Encyc. Meth. Bot. 2:420. 1786. Type: An unpublished plate of Tithymaloides frutescens, folio anacampserotis, of Martinique, by Plumier. - Pedilanthus anacampseroides (Lam.) Kl. and Gke., Abh. Akad. Berlin, Phys. 1859: 106. 1860.

Shrub 1-3 m. tall, stems glabrous, slender to moderately succulent; leaves glabrous, obovate, oblanceolate-obovate or elliptic. $6.5-12.5 \mathrm{~cm}$. long, 2.5-7.5 cm. wide, obtuse, infrequently retuse or acute, cuneate to a petiole $5-10 \mathrm{~mm}$. long, midrib thickened and often carinate, stipules spur-like, blunt, sometimes transversely oblong, $0.3-0.8 \mathrm{~mm}$. in diameter; inflorescence terminal and upper axillary, occasionally on lateral branches, becoming rather large (to 6 or 7 cm . across), internodes glabrate or sparsely puberulent, $4-10 \mathrm{~mm}$. long, bracts red, often tending to persist, glabrous or glabrate except on margins (and sometimes mid-veins) which are puberulent, ovate, oblong-ovate or obovate, obtuse, broadly acute or occasionally acute, sometimes apiculate, $8-15 \mathrm{~mm}$. long, $4.5-8 \mathrm{~mm}$. wide; peduncle sparsely puberulent, $8-11 \mathrm{~mm}$. long, involucral tube yellow-green beneath or red throughout, glabrous without except on margins, internally sparsely pilose above and otherwise glabrous or (rarely) sparsely hispidulouspilose, $9.5-12 \mathrm{~mm}$. long, main lobes oblong or deltoid-oblong, obtuse, ciliate or hispid-ciliate on margins, free beneath for $2.5-5 \mathrm{~mm}$., accessory lobes ligulate, lance-ligulate or sub-spatulate, $0.5-1 \mathrm{~mm}$. wide, glabrous or basally sparsely puberulent above except along margins, these hispidulous, somewhat thickened at ca. 2 mm . from the medial glands, terminally obtuse, ciliate or ciliolate, lateral lobes $1-2 \mathrm{~mm}$. shorter than main lobes, free laterally for $0.7-1.5 \mathrm{~mm}$. and medially for $3-4 \mathrm{~mm}$., median lobe partly concealed by lateral lobes, often narrower than lateral lobes, $1.2-2 \mathrm{~mm}$. shorter than lateral lobes; spur cucullate, red, arising at ca. 3 mm . from the peduncle, $2-3.5$ mm . thick, rounded or (in the Grenadines) attenuate and projecting $1-1.5 \mathrm{~mm}$. posteriorly, spur lobes glabrous except near margins within, where more or less hispidulous-puberulent, lateral lobes folded in over accessory involucral lobes, medial lobes completely connate, together attenuate-deltoid or deltoid, $3-5 \mathrm{~mm}$. long, (3-) $4-5 \mathrm{~mm}$. wide,
apex truncate or slightly retuse, $0.9-1.2 \mathrm{~mm}$. wide, thickened beneath for $1.5-2 \mathrm{~mm}$., occasionally sparsely hispidulous beneath behind the thickening, medial glands sub-basal, oblong, subquadrate or reniform, more or less bent about the partitions, $1-1.3 \mathrm{~mm}$. long, $0.7-1 \mathrm{~mm}$. wide, lateral glands sub-basal to ca. 0.5 mm . anterior to the medial glands, ovate to deltoid-ovate or oblong, 1-1.2 mm. long, $0.4-1.1 \mathrm{~mm}$. wide, spur partitions slight between glands and base of accessory involucral lobes, in some plants (from Grenadines) well developed for ca. 1 mm . posterior to the medial glands; bracteoles few, filamentous or occasionally ligulate, glabrous or pilose, 4-8 mm. long, adnate to the involucral tube for ca. $1.5-3 \mathrm{~mm}$. basally; roof lobules obscure or occasionally small seta-like lobules; staminate flowers 14-28, pedicels glabrate basally, terminally villous for $1 / 3-2 / 3$ of their length, $11-13 \mathrm{~mm}$. long, filaments glabrous, puberulent or somewhat pilose, ca. 2 mm . long, anthers glabrous; pistillate pedicel $10-13 \mathrm{~mm}$. long, puberulent or glabrate except for a puberulent collar about the base of the ovary, ovary glabrous or very sparsely pilosulous, ca. 2 mm . long and 1.5 mm . wide, oblong-ovoid, style $5-9 \mathrm{~mm}$. long, the branches $0.3-1 \mathrm{~mm}$. long, shallowly or deeply bifid; capsule subquadrate, ca. 7 mm . long; seed ashen grey to mottled dark brown, sometimes darker about apex, $4-5 \mathrm{~mm}$. long, $2.5-3.2 \mathrm{~mm}$. wide, ovoid-oblong to oblong, truncate basally, acute but low apically, weakly keeled, the keels sometimes terminating basally in low tubercles, raphe brown.

Representative specimens seen. Lesser Antilles. At. Croix. Big Princess, Mrs. J. J. Ricksecker 165 (F, M0); Signal Hill, A. E. Ricksecker 181 (F, Gir, MO, NY, US) ; East End, April 24, 1896, A. E. Richsecker s. n. (F, MO) ; Frederiksfort, Jan., 1874 Eggers s. n. (C). St. Martin. Marigot, A. Plée s. n. (P) ; from Belvedere to Oysterpont, Boldingh 2092 (U). St. Barthélemy. St. Jean, Questel $80 \mathrm{r}^{(N Y) . ~ S t . ~}$ Eustatius. Road along the lower part of Signalhill, Boldingh 92.3 (U); Gut near Fort de Wind, 50 m ., Boldingh 842 (U). St. Kitts. Basse Terre, Rose, Fitch and Russell 32.34 (Ny, US). Antigua. Crab Hill, Box 1366 (UC, US) ; near St. John, Rose, Fitch and Russell 324.3 (NY, US). Guadeloupe. Basse region, Père lluss 27.33 ( NY). Martinique. Case-Pilate, Marigo, Trois-Ilets, Père Ihuss 1988 (NY). Barbados. St. John, Moncrieffe, (fooding 61.3 (NY). Bequia. 500-1,000 ft. above sealevel, J. Dalton (for H. H. Smith) B. 122 (NY). Cannouan. On ridge from medium altitudes to summit of Mt. Royal, Howard 11076 (GH). Union Island. Western range of hills near Chattam Bay, Howard 1100.3 (GH). Isle of Ronde. Howard 10720 (GH).

Distribution and habitat (Map 8). The Lesser Antilles, including St. Croix, south to the Isle of Ronde and probably Grenada. Collections from Jamaica and St. Thomas are apparently cultivated or escapes from cultivation. An inhabitant of xeric and often rocky scrub and thorn forest. Howard (1952) writes, of its occurrence in the Grenadines: "Occasional . . . on the Isle of Ronde and Union where they grew in the Opuntia thickets or on rocky outcrops. These
plants were less than 3 ft . tall. On Cannouan, however, this was a very common plant in the dry woodlands on the slopes of Mt. Royal. Here the plants reached ten feet in height. The "flowers" were usually red and yellow although occasionally pure red stands were observed. The leaves are succulent when fresh and commonly a bright red color." Flowering mostly from mid-winter through mid-summer (Dec. - July).

Common names. Lady's slipper, dumb-cane (Barbados) ; Bois damoiselle (Martinique).

Variation. Relatively uniform except for intergradation with angustifolius in the north (see fig. 29). and subsp. tithymaloides in the south. The variation in pubescence of the pistillate pedicel seems to show no geographic pattern, but there is a slight increase in indument of most parts of the involucre and flowers from north to south. Style length and seed size show increases from north to south. Of special interest are the projecting spurs of the collections from the Grenadines (slightly projecting on Union and markedly so on Cannouan and Ronde). Distinctly projecting spurs are found also in jamaicensis and bahamensis, suggesting a primitive character for this phyletic group, which has persisted only on the periphery of the Antilles. Here it might also be interpreted as gene flow from subsp. tithymaloides of Trinidad.

Relationship. It is intermediate in most features between subspp. tithymaloides and angustifolius, with which it intergrades to a surprising degree (considering the insular distribution) ; related also to jamaicensis.

Notes. The specimen taken as type is annotated by Dillenius (as Tithymaloides laurocerasifolio non crenato [sic] H. Elth.), so that it may reasonably be considered the type for Tithymaloides laurocerasifolio non serrato, the preLinnaean basis for Euphorbia tithymaloides $\beta$ padifolia L. and Tithymalus laurocerasifolius Mill.

I have not seen the plate of Plumier which is the type of Euphorbia anacampseroides, but the locality, description and synonymy indicate that it is this plant.

This is apparently a rather attractive shrub, but little cultivated outside of its native area.

## 13f. Pedilanthus tithymaloides subsp. jamaicensis (Millsp. and Britt.) comb. nov.

P. jamaicensis Millsp. and Britt., Field Mus. Pub. Bot. 2: 356. 1913. Type: Jamaica, Negril and vicinity, March 9-12, 1908, rocky woods, 4 dm. high, N. L. Britton and A. Hollick 2067 ( NY!, isotype F!). - Tithymalus jamaicensis (Millsp. and Britt.) Croiz., Am. Jour. Bot. 24: 704. 1937.
P. Grisebachii Millsp. and Britt., Field Mus. Pub. Bot. 2: 361. 1913. Type: Jamaica, Kingston to Bath, Bull Bay, Sept. 14, 1908, bank, shoots 1 m., N. L. Britton $36 \mathrm{~F}^{7}$ (ny!). - Tithymalus Grisebachii (Millsp. and Britt.) Croiz., Am. Jour. Bot. 24: 704. 1937.
Shrub 0.4-2 (-4) m. tall; stems slender, puberulent when young, becoming glabrate; leaves sparsely and finely puberulent, highly variable in size and form, narrowly lanceolate to elliptic or oblanceolate, rarely narrowly obovate, $1-9.7 \mathrm{~cm}$. long, $0.2-3.9 \mathrm{~cm}$. wide, acute or obtuse, cuneate to the petiole, which is $1.5-5 \mathrm{~mm}$. long, midrib moderately to strongly keeled, stipules blunt, $0.3-1 \mathrm{~mm}$. in diameter; cymes congested, terminal and axillary, internodes glabrate to sparsely puberulent, $1-2 \mathrm{~mm}$. long, bracts ovate to lanceolate-oblong, obtuse or acute, $2.5-11 \mathrm{~mm}$. long, $1.5-3.5 \mathrm{~mm}$. wide, glabrate to sparsely puberulent, margins always puberulent, peduncle puberulent, 4-6 mm . long; involucres red, glabrous to pilose-puberulent without, tube $7.5-11.5 \mathrm{~mm}$. long, glabrate within, main lobes oblong or ovate-oblong, obtuse, margins hispid-ciliate, free beneath for ca. 2-2.7 mm., accessory lobes ligulate-spatulate, obtuse, ciliate, glabrous to puberulent above, thickened at about $2-3 \mathrm{~mm}$. from the medial glands, lateral lobes $0.5-1.5 \mathrm{~mm}$. shorter than the main lobes, free $1-1.2 \mathrm{~mm}$. laterally, $2.5-4 \mathrm{~mm}$. medially, median lobe $1-2 \mathrm{~mm}$, shorter than lateral lobes; spur cucullate, sometimes distinctly projecting posteriorly for ca. $1.7-2 \mathrm{~mm}$., arising at $1.7-2.5 \mathrm{~mm}$. from peduncle, $1.7-3 \mathrm{~mm}$. in thickness, hispid-puberulent within near margins, lateral lobes folded in over accessory involucral lobes, medial lobes completely connate, together attenuate-deltoid, 2.7-4 mm. long, $2.5-3 \mathrm{~mm}$. wide, apex sub-ligulate, ca. $0.7-1 \mathrm{~mm}$. wide, thickened and densely puberulent beneath for ca. 2 mm ., apex truncate or retuse, sometimes upturned, medial glands basal or ca. 1 mm . from base, oblong or oblong-ovoid, 1-1.1 mm. long, $0.6-0.9 \mathrm{~mm}$. wide, lateral glands ca. $0.5-1 \mathrm{~mm}$. anterior to the medial glands, ovoid or orbicular-ovoid, $0.6-0.8 \mathrm{~mm}$. long, $0.5-0.7 \mathrm{~mm}$. wide, partition small but distinct between glands and bases of accessory involucral lobes, sometimes developed for ca. 1 mm . posterior to the glands; bracteoles none or few, filamentous, ca. $3-5 \mathrm{~mm}$. long, basally adnate to involucral tube for up to 4 mm .. roof lobules slight or none; staminate flowers 17-24, pedicels $8-10 \mathrm{~mm}$. long, glabrous, filaments $1.5-2 \mathrm{~mm}$. long, glabrous or very sparsely pilose, anthers glabrous or very sparsely pilose; pistillate pedicel $8-11 \mathrm{~mm}$. long, sparsely pilosulous to puberulent, ovary glabrous to tomentulose, ca. 2 mm . long, oblong, trigonous, style glabrous to sparsely puberulent, $4-8.7 \mathrm{~mm}$. long, the branches $0.5-1 \mathrm{~mm}$. long, bifid, connivent; capsule glabrous or sparsely puberulent, ca. 6 mm . long; seed unknown.

Specimens seen. Jamaica. Negril, woods near lighthouse, March 11, 1908, W. Harris 10,238 (F, NY, US) ; Negril, March 24, 1955, M. L.

Farr s. n. (Institute of Jamaica) ; Manchester Parish, near Great Bay, 3 miles southeast of Alligator Pond, Proctor 11,957 (GH, Institute of Jamaica) ; Manchester Parish, 1 mile E.S.E. of Gods Well, north side of Round Hill, Proctor 11,940 (Gh, Institute of Jamaica); near Bull Bay, Harris 9,645 (Ny); near Bull Bay, Harris 12,117 (Ny) ; without exact data, Distin s. n. (K).

Distribution and habitat (Map 8). This plant is found along the south coast of Jamaica in rocky, arid thickets in areas of limestone outcrop. Flowering in spring and summer (March, April, June and Sept.).

Variation. The Jamaican populations of Pedilanthus tithymaloides show striking variation in several features. When only the Negril and Bull Bay populations were sampled (nearly the opposite ends of the island), there appeared to be two very distinct and isolated populations in Jamaica. Recent collections from intermediate localities indicate that there is a single, more or less continuous population, with strong clinal variation. The Bull Bay collections have very small, narrowly lanceolate leaves, which are 10 25 mm . long, and $2-3.5 \mathrm{~mm}$. wide, and apparently caducous. The leaves of Proctor 11,940, from Manchester Parish, are similar but somewhat larger, ranging from $15-30 \mathrm{~mm}$. long and $3.5-7 \mathrm{~mm}$. wide. The plants from Negril have very much larger leaves, which are obtuse and broadly oblanceolate or sometimes nearly obovate; these are mostly 5-9 cm . long and $1-4 \mathrm{~cm}$. wide. The smallest leaves from these collections tend to be more nearly lanceolate. Farr s. n. has somewhat narrower leaves than the other collections from Negril (mostly about 2 cm . wide), and Distin s. n. also has relatively narrow leaves ( $1-2.5 \mathrm{~cm}$. wide) which are mostly oblanceolate. The leaves of these western collections are relatively fleshy and persistent.

The involucral tubes and styles of the Bull Bay population are somewhat shortened as in subsp. angustifolius (involucral tube $7.5-9 \mathrm{~mm}$. long, style $4-6 \mathrm{~mm}$. long) ; the pistillate flowers are markedly puberulent, the ovaries densely so; and the involucres are puberulent externally. The indument of the involucres is intermediate in character between that of angustifolius and bahamensis, being neither stiffly erect nor strongly crisped and appressed. The other collections of this subspecies have larger involucres and styles (involucral tube $9.5-11.5 \mathrm{~mm}$. long, styles $6-8.5 \mathrm{~mm}$.
long) ; the pistillate flowers of these are glabrous and the involucre externally glabrous or nearly so. In these features Farr s.n. (western end of the island) approaches the eastern samples a little more closely than do collections from the middle of the south coast. The involucres of this collection are sparsely puberulent without and the styles $6-6.5 \mathrm{~mm}$. in length. It is evident that the clinal variation in leaf form is primarily found in the western end of the range, while the variation in involucral features is much the greatest in the eastern end. A much larger sample of this plant is needed.

Relationship. This interesting and variable subspecies shows close relationship to subspp. padifolius, bahamensis and angustifolius. The westernmost population (Negril) resembles padifolius in its vegetative features. These plants may well be peripheral relicts which retain many features of the population ancestral to all four subspecies. In subsp. jamaicensis the indument of the involucre is intermediate in character between angustifolius and bahamensis, but in other features it is closer to bahamensis. The parallel eastwest variation in involucre size in the Jamaican and Bahaman plants is striking.

Notes. As noted by Wheeler, Cutak and White (1944), the original description of $P$. Grisebachii was drawn in large part from Puerto Rican material of angustifolius.

## 13 g . Pedilanthus tithymaloides subsp. angustifolius (Poiteau) comb. nov.

## Plates XIV \& XXI, Map 8

P. angustifolius Poit., Ann. Mus. Paris 19: 393, t. 19. 1812. Type: Santo Domingo, "J'ai observé cette espèce dans le jardin de l'hôpital des Pères, au cap français," Poiteau s. $n$. ( P !, fragment: F!). - $P$. tithymaloides var. angustifolius (Poit.) Griseb., Fl. Br. W. I. 52. 1859. - Tithymalo[i]des angustifolium (Poit.) O. Kuntze, Rev. Gen. Pl. 2: 620. 1891. - Tithymetus sarissophyllus Croiz., Am. Jour. Bot. 24: 703. 1937, based on $P$. angustifolius, not T. angustifolius Gilib.

Shrub $0.8-3 \mathrm{~m}$. tall; stems slender to relatively thick and succulent, sparsely puberulent to puberulent when young, becoming glabrate with age; leaves persistent or deciduous, glabrate to sparsely puberulent above and sparsely to densely pilose-puberulent beneath, linearligulate or narrowly lanceolate to oblanceolate, $20-90 \mathrm{~mm}$. long, $2.5-$ 16 mm . wide, obtuse or broadly acute, basally cuneate, midrib keeled beneath, petiole $1-5 \mathrm{~mm}$. long, crisped-puberulent, stipules brown or
dark brown, sub-hemispheric, ca. 0.5 mm . wide; cymes terminal and on short axillary branches, internodes $1.3-8(-15) \mathrm{mm}$. long, glabrate to puberulent, bracts puberulent or sparsely puberulent without, glabrate within, elliptic-ovate to oblong, acute to obtuse, $5-10 \mathrm{~mm}$. long, 2-6 mm . wide, peduncle appressed pilose-puberulent, $4-7 \mathrm{~mm}$. long, involucral tube green beneath, $6-9 \mathrm{~mm}$. long, pilose-puberulent (rarely glabrate) within, glabrous or sparsely pilose-puberulent with erect hairs without, main lobes oblong or ovate-oblong, obtuse, free beneath for 2-2.5 mm., accessory lobes puberulent to glabrous above, oblong-ligulate or sub-spatulate, $0.7-0.9 \mathrm{~mm}$. wide, obtuse, the lateral lobes $0.5-1 \mathrm{~mm}$. shorter than main lobes, free $0.5-0.8 \mathrm{~mm}$. laterally and $1-1.7 \mathrm{~mm}$. medially, medial lobe ca. 1 mm . shorter than lateral lobes (rarely subequal) ; spur red, cucullate, at ca. $2.5-4 \mathrm{~mm}$. from the peduncle, $1.5-2 \mathrm{~mm}$. thick, glabrous or glabrate without, usually hispid-puberulent within, at least along lobe margins, lateral lobes folded in over accessory involucral lobes, medial lobes completely connate, together attenuate-deltoid, $3-4 \mathrm{~mm}$. long, basally $2.8-4 \mathrm{~mm}$. wide, apex truncate or shallowly retuse, $0.9-1.3 \mathrm{~mm}$. wide, somewhat thickened, medial glands basal, oblong to subquadrate, slightly bent, $0.8-1 \mathrm{~mm}$. long, $0.5-0.8 \mathrm{~mm}$. wide, occasionally split into gland-pairs, lateral glands deltoid-ovate, ca. $0.5-1 \mathrm{~mm}$. in diameter, near the medial glands or 1-1.3 mm. anterior, partition none or very slight; bracteoles few or none, filamentous, $3-5 \mathrm{~mm}$. long, adnate to the involucral tube for $1.5-2 \mathrm{~mm}$. ; roof lobules minute, sometimes seta-like; staminate flowers 20-27, glabrous, pedicels $6-8 \mathrm{~mm}$. long, filaments ca. 2 mm . long; pistillate pedicels sparsely to densely appressed pilose-puberulent, $8-10 \mathrm{~mm}$. long, 2 mm . wide, glabrous, style thick, $3.2-5 \mathrm{~mm}$. long, the branches $0.35-0.5 \mathrm{~mm}$. long, $1 / 3$ to completely bifid; capsule subquadrate, 3 -lobed in cross section, 6-7 mm . in diameter; seed oblongovoid to conic-ovoid, $3.5-5 \mathrm{~mm}$. long, $2.5-3 \mathrm{~mm}$. wide, weakly keeled dorsally and laterally, basally truncate, apically acute but low, mottled brown-tan to grey-brown (ashen), raphe brown.

Representative specimens seen. Cuba. La Perla, Oriente, Aug. 6, 1913, (flowered in Vedado in April), Hno. León 5025 (Ny); Maisí, Oriente, valley of Yumurí River, (coll. P. Matos) Hno. León 17935 (NY) ; La Laja, C. Wright s. n. (GH). Hispaniola. Haiti. Presqu'île du Nord-Ouest, Mole St.-Nicolas, Morne Rouge, fifth terrace, Ekman 4477 (S) ; arid west banks of Mole River, 2 mi. So. of Mole St. Nicolas, E. C. and G. M. Leonard 1309.3 (Ny, us) ; Presquîle du NordOuest, road Port-de-Paix to Jean Rabel, Morne Palmiste, Ekman 3556 (s, US) ; Aguin [Aquin?], Arndt 1.3 (PH) ; Port-au-Prince, Ekman 2108 (S). Dominican Republic. Mao, Prov. de Santiago, alt. 100-300 m., Abbott 10.31 (ny, us); La Romana, Prov. of Seibo, Taylor 525 (Ny); La Romana, Prov. Seibo, llano costero, La Caleta, Ekman 12080 ( $\mathrm{s}, \mathrm{u}$ ). Puerto Rico. Salinas de Boquerón, Britton, Cowell and Brown 4607 (F, MO, NY, US) ; prope Salinas de Cabo Rojo, P. Sintenis 769 (GH, K, US) ; Buena Vista, Carolina, Johnston and Stevenson. 1397 (NY) ; Guánica and vicinity, Britton and Shafer 1865 (F, NY); Yauco, Underwood and Griggs 6.37 (US) ; prope Peñuelas, Stahl 1084 (US) ; 2 mi . E. of Ponce, Heller 6192 (A, F, GH, MO, NY, PH, US) ; El Fuerto, Coamo River, Britton, Britton and Brown 6001 (F, NY);

Aguirre, Underwood and Griggs 407 (US) ; Manatí to Vega Baja, Underwood and Griggs 9.37 (NY); Vieques Island, vicinity of Isabel Segunda, Shafer 2410 (F, NY, US) ; Culebra Island, Britton and Wheeler 121 (NY, US). St. John. Lamosure, Britton and Shafer 619 (NY, US), St. Croix. Sandy Point, Paulsen 322 (c); Borgesen 1.33 (C) ; Raunkiaer 2578 (C).

Distribution and habitat. From eastern Cuba through the Greater Antilles to St. John and St. Croix, largely coastal. Collector's labels, "dry jungle," "dense scrub," "coastal thicket," "rocky woods," etc., suggest a dry scrub forest as the usual habitat for this subspecies; the Cuban localities are in relatively wetter parts of the Oriente, and may be less arid sites than those of most other collections. Though frequently reported from limestone soils, angustifolius apparently occurs in volcanic sites near Coamo Springs, P. R., ("eruptive rocks") and is found in lateritic soil in western Puerto Rico. For a photograph of the last habitat, see Wheeler, Cutak and White (1944). Flowering in late winter and spring (Dec.-June).

Common name. ipecacuana (Puerto Rico).
Variation. Subspecies angustifolius is a relatively uniform entity, in spite of its necessarily discontinuous range. Leaf shape varies considerably, being generally oblanceolate in Cuba and Hispaniola, but tending to be narrowly lanceolate in Puerto Rico and to the east. The degree of pubescence is variable in most parts, but shows no clear-cut pattern, though the involucres of the eastern populations tend to be more nearly glabrous without. The only Cuban collection with seed (León 17935) shows seed about a millimeter longer than any other collection (ca. 5 mm . long as compared to 3.5-4 mm. long). The Cuban material is otherwise quite comparable to that from Hispaniola.

Relationship. Closely related to bahamensis and jamaicensis, as discussed under those taxa. The relationship of this entity to padifolius is especially interesting and critical to any classification of this alliance. In two features, leaf shape and pubescence of staminate flowers, there is a sharp break between these two taxa (discounting the two collections which are so exactly intermediate as to suggest $F_{1}$ hybrids). In involucral shape, these populations approach each other rather closely, and there seems to be a geographic trend within each one, suggesting gene flow or continuing
differentiation. In angustifolius, the most striking features of the involucre are the small size and the proportionately long spur lobe. This plant strongly suggests a sort of "organneoteny," like that described for $P$. tehuacanus, in which the development of the involucral tube, especially, is arrested. In order to compare the involucral forms of different populations in a mathematical manner, measurements were made of main involucral lobes and spur lobes, both measurements being made from the apex of the spur (in retrospect, the base of the spur would provide a less subjective point). These measurements were made on 1-3 involucres from each herbarium sheet, depending on the material available. The ratios between these two measurements and the leaf length/ width ratios were averaged for each collection, and these ratios are graphed against distribution in fig. 29. The geographic trend in involucral proportion is seen rather clearly,


Fig. 29. Correlation of some characters of $P$. tithymaloides with distribution in the West Indies. The abscissa represents geographic occurrence, which is roughly linear. The ordinates represent ratios as indicated. Each collection is shown above and below its locality by symbols: diamonds, P. t. ssp. angustifolius; dots, P. t. ssp. padifolius; X. putative hybrids between angustifolius and parifolius; T, P.t. subsp. tithymaloides.
and the intermediate nature of the two collections discussed on p. 169 is shown.

## 13h. Pedilanthus tithymaloides subsp. bahamensis (Millsp.)

## comb. nov.

P. bahamensis Millsp., Field Mus. Pub. Bot. 2: 359. 1913. Type: Bahama Islands, Grand Turk Island, Waterloo and vicinity, rocky plain (pitted rock) south of town, where it is one of the common shrubs, C. F. and C. M. Millspaugh 9030 (F 287, 782!, isotypes: GH!, ny!). - Tithymalus bahamensis (Millsp.) Croiz., Am. Jour. Bot. 24: 704. 1937.

Erect shrub $0.7-1.5 \mathrm{~m}$. tall, branching from the base, the branches somewhat arching; stems succulent, glabrate; leaves glabrate or sparsely and finely puberulent above, sparsely crisped-puberulent beneath, caducous, lanceolate to ligulate-oblanceolate, $15-30 \mathrm{~mm}$. long, $3.5-6.5 \mathrm{~mm}$. wide, obtuse or acute (?), cuneate to an indistinct petiole ca. 1-1.5 mm . long, midrib strongly keeled (winged), stipules dark brown, sub-hemispheric, ca. 0.3 mm . in diameter; cymes terminal and on short axillary branches, internodes glabrate or sparsely crisped-puberulent, bracts ovate or deltoid-ovate, obtuse or acute, glabrate or finely puberulent on both surfaces, 2.5-3 mm. long, 1.8-2 mm . wide; peduncle glabrate or finely puberulent, $6-9 \mathrm{~mm}$. long, involucre minutely crisped-puberulent without, red (apparently throughout), tube $7.5-12 \mathrm{~mm}$. long, glabrous within or sparsely pilosulous (especially dorsally), main lobes oblong, obtuse or truncate-obtuse, free beneath for ca. $1.5-2 \mathrm{~mm}$., accessory lobes ligulate to ligulatespatulate or (median) sub-flabellate, finely and densely puberulent above, somewhat thickened at ca. 3 mm . from medial glands, apices obtuse and ciliate or ciliolate, lateral lobes 0.6 mm . shorter than main lobes to subequal, free laterally $0.7-1.7 \mathrm{~mm}$., medially $2-3.5 \mathrm{~mm}$., median lobe $0.3-1.2 \mathrm{~mm}$. shorter than lateral lobes; spur cucullate, rounded or shallowly 3 -lobed posteriorly, arising at ca. $2.5-4 \mathrm{~mm}$. from peduncle, $2-2.5 \mathrm{~mm}$. thick, finely puberulent within, lateral lobes completely connate, together attenuate-deltoid to oblong-deltoid, 2.5-4 mm . wide basally, usually tapering to a ligulate portion $1-1.2 \mathrm{~mm}$. wide and $1.5-2 \mathrm{~mm}$. long, this thickened and densely puberulent beneath, apex truncate and shallowly retuse to bilobulate, medial glands basal, oblong to subquadrate, more or less bent about partitions, $0.8-1 \mathrm{~mm}$. long, $0.6-1 \mathrm{~mm}$. wide, occasionally split into gland pairs, lateral glands ca. $0.5-1 \mathrm{~mm}$. anterior to medial glands, oblong to oblong-ovate or deltoid-ovate, $0.8-1.2 \mathrm{~mm}$. long, $0.6-0.8 \mathrm{~mm}$. 'wide, partitions variable, absent to ca. 0.7 mm . posterior to glands; bracteoles none or few, filamentous, $3-6 \mathrm{~mm}$. long, distinct bracteole-ridges ca. 5 mm . long dorsally in some (Andros), roof lobules none or inconspicuous; staminate flowers glabrous, $18-27$, pedicels $8-14 \mathrm{~mm}$. long, filaments ca. 2 mm . long; pistillate pedicel $9-12 \mathrm{~mm}$. long, glabrate to puberulent, ovary glabrous to puberulent, oblong-ovoid, ca. 2 mm . long and 1.5 mm . wide, trigonous, style glabrous or sparsely puberulent, $6.5-9.5 \mathrm{~mm}$. long, branches $0.7-1 \mathrm{~mm}$. long, shallowly to deeply bifid; capsule subquadrate, ca. 6 mm . long; seed grey-brown to red-
dish brown, turgid sub-spheric to ovoid, obtuse basally, apex acute but low, weakly 3 -keeled, raphe brown.

Specimens seen. Bahama Islands. Deep Creek, Andros Island, Brace 5145 (F, NY) ; Deep Creek, Andros, I. J. and A. R. Northrop 693 (F, G, GH) ; Spring Point, Acklin's Island, Brace 4244 (F, NY) ; Atwood [Samana] Cay, Wilson 7410 (F, NY) ; Salt Cay, Turk's Islands, C. F. and C. M. Millspaugh 9392 (F); Grand Turk Island, Nash and Taylor 3761 (F, NY) ; Grand Turk Island, Waterloo and vicin:ty, C. F. and C. M. Millspaugh 9390 (F, NY).

Distribution and habitat (Map 8). The Bahama Islands, collected or reported from southern Andros Island, Acklin's Island, Samana Cay, South Caicos Island, and the Turks Islands. The habitat of this subspecies in the Turks Islands is described as "rocky plain;" a photograph taken by Millspaugh (in Herb. F and NY) shows the plant to be locally abundant in open, xeric scrub with Opuntia and other low shrubs. On Andros, bahamensis was collected in "coppet," a hardwood thicket or low forest. In both areas Pedilanthus evidently occurs on the eroded limestone which is typical of the Bahamas. Flowering in both winter and summer (Dec.March, July and August).

Common name. "Monkey-fiddle," the stems being rubbed together by children to produce a high squeak, according to Millspaugh.

Variation. This subspecies shows a very interesting pattern of variation ; the plants from Turks Islands and Acklin's Island bear small involucres with very short tubes, very like angustifolius in form, while the Andros Island collections show large involucres with long involucral tubes, the form being comparable to that of subsp. tithymaloides or jamaicensis. The collection from Samana Cay is intermediate. The Andros collections have relatively slender stems, more evenly tapering spur lobes, ligulate accessory involucral lobes, and, correlated with the larger involucres, longer staminate flowers and styles. Turks Island collections have abruptly attenuate spur lobes and sub-spatulate accessory involucral lobes. Average involucre lengths for the small samples from each island, from east to west, follow: Grand Turk - 8.3 mm ., Salt Cay - 9 mm ., Samana Cay - 10 mm ., Acklin's - 8.5 mm ., Andros - 11.5 mm .

Relationship. In leaf size and shape (as far as known) this subspecies is similar to jamaicensis (eastern popula-
tion), which it also resembles in the characters of the involucre; it is also quite close to angustifolius (especially the eastern populations). The Andros Island form closely approximates western jamaicensis or subspecies tithymaloides in involucral size and shape. Both this subspecies and the western population of jamaicensis probably represent the peripheral persistence of primitive characters within the West Indian complex related to angustifolius.

Notes. As described by Millspaugh, this would be a most remarkable plant. No evidence can be found, however, of the "siliceous transverse ridges" of the stem (the waxy cutin might well cause a high pitched squeak when the stems are rubbed together), the glands are 4 as in all the $P$. tithymaloides complex, and small caducous leaves are clearly produced by normal growth, as shown by the fragments accompanying Brace 4244 and Brace 5145, and Brace's partly illegible notes (with Brace 5145).

## Pedilanthus tithymaloides, subsp. tithymaloides $\times$ subsp. Smallii

Two collections have been seen, whose characters suggest that the plants are the result of hybridization between Smallii and different forms of subsp. tithymaloides (cultivated or escaped). Each collection is briefly described below.
A. Stem straight, succulent, glabrate; leaves glabrous above, puberulent beneath, ovate, long-attenuate, basally obtuse, $\overline{5}-6.8 \mathrm{~cm}$. long, $2.5-3.8 \mathrm{~cm}$. wide, midrib strongly keeled beneath; cymes terminal and axillary; involucral tube ca. $12-13 \mathrm{~mm}$. long, glabrous within and without, median spur lobe attenuate-deltoid, ca. 5 mm . long, 4.5 mm . wide, spur lobes and upper surface of accessory involucral lobes markedly hispidulous basally and marginally; staminate pedicels glabrate, with a few hairs apically, filaments sparsely pilosulous; bracteoles few, filamentous, ca. $5-6 \mathrm{~mm}$. long ; pistillate flower glabrous, style 9 mm . long.

Cuba, Havana, inter Marianao et la Lisa, May 4, 1914, in fruticetum (ad domum), Ekman 713 (s).

While the glabrate involucres with attenuate spur lobes suggest Smallii, the straight stem, wide leaves, and the slightly greater indument within the involucre indicate that this plant may include subsp. tithymaloides in its ancestry, probably the " $P$. canaliculatus" form, widely cultivated in the Antilles.
B. Stem moderately zig-zag, sparsely puberulent, leaves ellipticovate, puberulent above and beneath, 3-4.5 cm. long, 1.5-2.3 cm. wide, broadly cuneate basally, acute but not attenuate apically, midrib strongly keeled or winged; cymes terminal, peduncles sparsely puberulent, involucral tube ca. 11 mm . long, glabrous without and sparsely pilose within, spur lobe attenuate-deltoid, $3.5-4 \mathrm{~mm}$. long, 3-3.5 mm. wide, apex thickened and hispidulous beneath, margins of spur lobes and accessory involucral lobes markedly hispidulous within spur; bracteoles few, ca. 6 mm . long, pilosulous; staminate pedicels sparsely pilose apically, filaments glabrate; pistillate pedicel pilosulous-puberulent, style ca. 7 mm . long.

Cuba, Santa Clara Prov., Milpa, Cienfuegos Bay, July 1941, Howard 5441 (GH, NY).

In vegetative features this collection diverges from Smallii less than the first, except for the too strongly puberulent leaves and less tangible textural features. The hispidulous spur lobe, the puberulent pedicels, and the pilose involucral tube all indicate the influence of subsp. tithymaloides.

These plants were collected in cultivated or disturbed areas, and a hybrid nature for both of them seems probable. Nothing is known, however, of the Pedilanthus which is probably native to the eastern two thirds of Cuba. It is reasonable to expect that this area should be the home of Smallii or of forms intermediate between that and parasiticus. As the greater part of lowland Cuba has been much disturbed over a long period, it is possible that unquestionably native Pedilanthus will never be found there.

Pedilanthus tithymaloides, subsp. tithymaloides $\times$ subsp. parasiticus
Though no herbarium specimens showing this parentage have been seen, there are some indications that hybridization between these subspecies may have occurred in the West Indies, since the introduction of subsp. tithymaloides. Some plants sent from Jamaica by Dr. DuQuesnay resembled the " $P$. canaliculatus" form of subsp. tithymaloides, but had shorter, broader leaves. The first few cyathia formed in each cyme of these plants bore free medial spur lobes, as are frequently found in parasiticus; cyathia formed later had connate medial spur lobes. Truncate spur lobes, hispidulous both above and beneath, hispid-pilose staminate pedicels and sparse pilosity within the involucral tube are
all features of subsp. tithymaloides, which were shown by these plants. Unfortunately, all of the plants were severely attacked by the stem-rot which killed the plants of Smallii in greenhouse culture (in itself evidence of parasiticus influence) before herbarium specimens had been made, and no vegetative material has been saved.

The plant illustrated in León's "Flora de Cuba" (3:126) resembles the plants discussed above; its leaf shape is nearly that of subsp. tithymaloides (" $P$. canaliculatus" form), but the bract-like upper leaves strongly indicate the influence of parasiticus.

## Pedilanthus tithymaloides, subsp. padifolius $\times$ subsp. angustifolius

The description of two similar specimens from St. Croix, which are evidently intermediate between subsp. padifolius and angustifolius, follows. Features which are similar or identical in both putative parents may be omitted.

Stem glabbrate (apparently sparsely crisped-puberulent when young) ; leaves sparsely crisped-puberulent beneath and very sparsely puberulent above, narrowly elliptic to broadly oblanceolate, $5.5-9 \mathrm{~cm}$. long, stipules spur-like, brown, ca. 0.8 mm . long; inflorescence terminal, internodes $3-25 \mathrm{~mm}$. long, sparsely crisped-puberulent, bracts red, semi-persistent, oblong or obovate-oblong, obtuse, apiculate, 8-24 mm . long, $5-9 \mathrm{~mm}$. wide; peduncle $12-14 \mathrm{~mm}$. long, sparsely crispedpuberulent, involucral tube $9-10 \mathrm{~mm}$. long, glabrous without, sparsely pilosulous to sericeous within, accessory involucral lobes hispidulous above near base, median lobe ca. 1.5 mm . long, spur at ca. 3 mm . from peduncle, ca. 3 mm . thick, median lobe attenuate-deltoid, 4-4.5 mm . long, ca. 4 mm . wide, $0.6-0.7 \mathrm{~mm}$. wide terminally, truncate, slightly retuse, thickened for ca. 2 mm . terminally, hispidulous beneath (behind the thickened portion); bracteoles filamentous, pilosulous, $3.5-7 \mathrm{~mm}$. long, staminate flowers ca. 24 , pedicels $8-10 \mathrm{~mm}$. long, pilosulous terminally for ca. 3 mm ., filaments pilosulous, but less densely so than pedicels; pistillate pedicel ca. 10 mm . long, puberulent, ovary glabrous, style $6.5-7 \mathrm{~mm}$. long, branches ca. 0.3 mm . long; capsule ca. 6 mm . long; seed oblong-ovoid, grey, brown about apiculate tip, ca. 4.5 mm . long and 2.8 mm . wide.

These intermediate collections are: St. Croix. Near East End, May, 1896, A. E. Richsecker s. n. (F) ; Bassin, May, 1896, A. E. Richsecker 8.n. (мо).

The East End collection has somewhat larger leaves than the other and markedly larger bracts; the accompanying packet contains two nearly mature seeds, and the plant had
clearly produced a number of capsules. The Bassin collection is in a younger stage, but shows one young capsule and a quantity of apparently normal pollen. Both plants are intermediate between the supposed parent types in nearly every character. The bracts in the East End collection are unusually large for either subspecies.

## 14. Pedilanthus Millspaughii Pax and K. Hoffm.

P. Millspaughii Pax and K. Hoffm., Fedde Rep. Spec. Nov. 19: 174. 1923. Type: Costa Rica, Miravalles, Brade 2302 (apparently destroyed by war at Berlin). - Tithymalus Millspaughii (Pax and K. Hoffm.) Croiz., Am. Jour. Bot. 24: 704. 1937.
"Stem thick, fleshy; leaves thin (when dry), glabrous, ovate, acute, $9-11 \mathrm{~cm}$. long, $4-7 \mathrm{~cm}$. wide, attenuate to the petiole; cymes short, apical, bracts small, shorter than the peduncles, peduncles ca. 5 mm . lang, glabrous; cyathium $10-12 \mathrm{~mm}$. long, tube glabrous without, pubescent within, long fissured; spur $1 / 4$ the length of the tube, spur lobes lightly tridentate, the lateral teeth larger; glands 2; staminate and pistillate pedicels pilose."

No material of Brade 2302 has been located, nor has any other collection which might be referable to this species been seen. It is probable that it is a distinct species, but it cannot be placed with any assurance without specimens. Most of the features, as described by Pax and Hoffmann, are strongly reminiscent of $P$. calcaratus; this species, however, has pilose peduncles and glabrous staminate pedicels. Whether or not the median spur lobes are connate is not stated, and what is meant by "lightly tridentate" spur lobe is unclear. Perhaps the spur lobes are similar to those of $P$. nodiflorus, but with larger lateral teeth; or possibly there are two completely connate, retuse lobes. The authors indicate that this species may be related to $P$. Oerstedii, but the basis for this cannot now be determined; there may have been authentic material of that species at Berlin.

## Excluded or Dubious Species

Diadenaria psilocarpa Kl. and Gke., Monatsb. Akad. Berl. 1859: 254. 1859 , nomen nudum.

Pedilanthus Brittonii (Millsp.) Pax and K. Hoffm., Engl. and Prantl, Nat. Pflanzenfam. 2, 19c: 223. 1931. = Cubanthus Brittonii Millsp., Field Mus. Pub. Bot. 2: 372. 1913.

Pedilanthus cordatus Sprengel, Linn. Syst. Veg. ed. 16, 3: 802. 1826. Based on the following.

Pedilanthus cordellatus (Haw.) Steud., Nomenclator Botanicus ed. 2, 2: 282. - Euphorbia cordellata Haw., Misc. Nat. 185. 1803. -

Crepidaria? cordellata Haw., Syn. Pl. Succ. 136. 1812. Assigned to Crepidaria with a query by Haworth; there is nothing in the description to indicate that it is a Pedilanthus.

Pedilanthus linearifolius Griseb., Mem. Am. Acad. n. s. 8: 161. 1861. $=$ Cubanthus linearifolius (Griseb.) Millsp., Field Mus. Pub. Bot. 2: 372. 1913.

Perilanthus ? lycioides Baker, Jour. Linn. Soc. Bot. 22: 516. 1887. $=$ Euphorbia pedilanthoides Denis, Euph. Iles Austr. Afrique 76. 1921. The latter is a somewhat unfortunate choice of epithet, since the plant does not resemble Pedilanthus.

Pedilanthus Oerstedii Kl. and Gke., Abh. Akad. Berlin, Phys. 1859: 106. 1860. Supposedly based on an Oersted collection from "prope Segovia, America centrali" (Nicaragua ?), no type can be located and the description is hopelessly inadequate. The plant illustrated by Markowski (1912) is P. cymbiferus and, though the geographic origin is not given, was probably collected by Karsten at Tehuacán. The status of $P$. Oerstedii cannot be decided until authentic or topotypic material is at hand.

Pedilanthus pectinatus Baker, Jour. Linn. Soc. Bot. 25: 343. 1890. Doubtless a Euphorbia; the type could not be found by Denis, Euph. Iles Austr. Afrique 120. 1921.

Pedilanthus subcarinatus Haw. ex Steudel, Nomenclator Botanicus ed. 2, 2: 282. 1841, nomen nudum.

## SUMMARY

Pedilanthus differs from Euphorbia by the strongly bilateral symmetry of the involucre. Fourteen species are recognized in the genus, including the questionable $P$. Millspaughii, of which no specimens are available. The most widely known species, $P$. tithymaloides, is widespread and variable, with a number of geographic populations distinguishable as subspecies, especially in the West Indies. In the Greater Antilles two of these subspecies (angustifolius and parasiticus) seem to form the two ends of an overlapping circle of subspecies and interact as distinct species, but there is no evidence that the two are narrowly sympatric. The thirteen species which are represented by herbarium specimens are arranged in five interrelated species groups. Sympatric species pairs are few, even between species groups. The West Indian plants of the "section Cubanthus" are to be excluded from Pedilanthus, being derived from a different ancestral group (Euphorbia subgenus Esula).

All species (except Pedilanthus Millspaughii, of Costa Rica) are Mexican or Mexican and Central American, and $P$. tithymaloides ranges into peninsular Florida, the West Indies and South America. The plants are usually local and
discontinuous in distribution and often occur on areas of limestone outcrop. While a few species are mesophytic trees with large foliage leaves, there is a wide range of habitat and vegetative specialization, some species being low, succulent desert shrubs with small caducous leaves.

Morphological features indicate that Pedilanthus is derived from a member of Euphorbia subgenus Agaloma, which is characterized by petal-like appendages on the involucral glands. The spur, largely formed of these gland appendages, is the most distinctive feature of Pedilanthus. This structure is thought to have developed as an adaptation to hummingbird pollination, and its possible evolution is sketched on p. 80.

The distribution of primitive Euphorbieae and the probable geologic occurrence of hummingbirds suggest that the evolution of Pedilanthus has largely occurred during the Tertiary, probably in Mexico. The dispersal of the genus into South America and the West Indies is thought to be not older than late Pliocene. The relatively few species of Pedilanthus are highly diverse in involucral structure, and it is suggested that a relatively rapid adaptive radiation has occurred since the development of a spurred involucre. In certain cases it appears that the evolution of the involucre has occurred through neoteny, or the developmental retardation of certain characters. Adaptation to xeric environment has occurred in several lines within the genus, and a mechanism is suggested through which relatively rapid reduction in leaf size might be accomplished. An aneuploid series of chromosome numbers is found in the genus, involving haploid numbers of 16,17 and 18 . It is suggested that this genus evolved from a Euphorbia with a haploid number of 14 (a base number of 7 is characteristic of Euphorbia subgenus Agaloma).

The wide range in habit shown by Pedilanthus is paralleled by its anatomical features. The more marked xerophytes, especially, possess a number of the structural adaptations which are usual in desert plants: small, caducous leaves; heavy cutin; a waxy coating over the cutin; sunken stomata; thick chlorenchyma in the stem cortex, often with a palisade arrangement; and, in one species, a thickened storage root. A system of abscission layers at the nodes


Plate Xill. Fig. 30. Pedilanthus Finkii. a plant cultivated at Missouri Botanical Garden. cyathia, showing the inflated spur and small orifice without free spur lobes, twice life size, photo by C. H. Thompson, January, 1907, courtesy of Missouri Botanical Garden. Fig. 31. P. calcaratus, Dressler 1067, in cultivation, cyathium ca. 2.5 times life size, note the drop of nectar exuding from the spur orifice (two drops have also flowed down to the base of the staminate flowers), photo by J. W. Carmichael.


Plate XIV. Foig. 32. I'edilanthus tithymuloides subsp. angmstifolius, near Villa Isabel, Monte Cristi Prov., Dominican Republic, March 1!5, slightly enlarged, from a kodachrome by Mrs. Antis H. Wagner. Fig. 33. P. t. subsp. jamaicensis (eastern population). Four Mile Wood, Jamaica, January 1956, about 2.5 times life size, from a kodachrome by Dr. R. A. Howard.
permits ready shedding of injured or non-functional parts. The wood structure is especially interesting and has been relatively well sampled. Extensive secondary xylem is formed by some species, but wood formation is markedly limited in the extreme xerophytes. The number of vessels per unit area and, especially, the vessel diameter are closely related to the habitat and the presumed water loss through transpiration. The large-leaved trees of tropical deciduous forest possess many large vessels, while both the true mesophytes and the xerophytes with reduced leaf area show smaller and usually fewer vessels. The moderately succulent plants, such as $P$. bracteatus and $P$. tithymaloides, appear to retain the most primitive features in wood structure: many solitary vessels, scalariform intervascular pitting and slightly heterogeneous rays. Pedilanthus pulchellus, a mesophyte with narrow, very long vessel elements and indistinct radial multiples may show the most primitive features among the truly woody species. The anatomical features, as far as observed, do not contradict the classification offered, and often support the relationships hypothesized. Since many of the anatomical features are markedly adaptive, anatomical similarities between plants of similar habit and habitat, as between $P$. bracteatus and $P$. tithymaloides, are not necessarily indicative of close phylogenetic relationship.

The inflorescence of Pedilanthus, as of most Euphorbieae, is a compound dichasium of involucres. The involucre has the same basic structure as that of Euphorbia. There are five involucral bracts, each subtending a cluster of staminate flowers. Each bract shows a normal foliar three-trace pattern of vascularization, with the lateral traces vascularizing the glands, when these are present. The glands are double structures, and occasionally develop as separate gland-halves. The glands bear petaloid appendages which. in Pedilanthus, are highly modified to form part of the dorsal spur. The strong zygomorphy of the genus involves the development of three types of involucral bracts: two ventral "main lobe" bracts which form the greater part of the involucral tube above the level of the glands, and three "accessory lobe" bracts, of which the median member is bilaterally symmetrical and the two lateral ones are not. The "acces-
sory lobe" bracts contribute largely to the formation of the spur and form inconspicuous ligulate lobes above the level of the glands. Within the involucre, the five clusters of staminate flowers are usually separated by more or less laciniate bracteoles. These bracteoles are thought to be derived from two types of structure: the bracts which subtend the branchings of the staminate flower cluster and the incurved and connate margins of the involucral bracts. These bracteoles often form solid partitions basally, and the partitions which divide the gland chamber of the spur in some species are thought to be developmentally related to those of the involucral tube. The clusters of staminate flowers are extremely condensed, and there is still controversy concerning the branching of these structures. The vascular pattern strongly suggests that each cluster is basically dichasial with each branch forming a monochasium throughout. The primitive type of inflorescence for the Euphorbieae was probably that still found in a few relict genera: one in which the involucral bracts strongly enfold their respective dichasial clusters of staminate flowers and the pairs of marginal glands are borne between these clusters. The development of the involucre of Pedilanthus agrees closely with that of Euphorbia in its earlier stages.

The pollen of most species of Pedilanthus is three-colpate, with large oblong pores and reticulate exine. The pollen of $P$. tehuacanus is completely inaperturate, while that of $P$. Finkii has no pores, and narrow furrows with greatly thickened margins. A pattern of six longitudinal intine thickenings is found in Pedilanthus and appears to be characteristic of most woody Euphorbieae.

While no caruncle is present on the mature seed of Pedilanthus, a caruncle or caruncle-like structure develops from the funiculus and appears to serve a nutritive function during seed development. This structure withers and stays on the columella when the seed matures.

## Plates XVI-XXI

The drawings are uniformly numbered as follows. 1. cyathium, lateral view; 2. cyathium, dorsal view; 3. dorsal view of spur, cut open to show gland chamber; 4. leaf outline ; 5. bract outline; 6 . as indicated.


Plate XVI. A. P. Palmeri, based on Dressler 1064, living material. B. P. Finkii, based on C. H. Thompson s. n. C. P. calcaratus, based on Dressler 1067, living material, 6. longitudinal section of spur.


Plate XVII. P. gracilis, based on Hinton 1097s, 6. habit sketch.


Plate XVIII. P. pulchellus, based on Conzatti, Reko \& Makrinius 3106, 6. habit sketch.


Plate XIX. A. P coalcomanensis, 1-3 \& 5 based on Hinton 12685, 4 on Hinton 15130. B. P. cymbiferus, based on Dressler 1368, material preserved in liquid. C. $P$. macrocarpus, based on Dressler 1090, living material and specimens preserved in liquid. 4', a leaf from Gentry $7767 a ; 6$, cross section of leaf.


Plate XX. A. P.brarteatus, based on Dressler 979, living material. B. P. tomentellus, 1-3 \& 5 based on Pringle 4912, 4 based on Dressler 1375. C. P. tehuacanus, 1-3, 5 \& 6 based on Dressler 1795, preserved in liquid, 4 based on Purpus 7065. 6, lateral view of cyathium, with cyme bracts in place.


Plate XXI. A. P. nodiflorus, based on Dressler 1362, living material. B. P. t. ssp. tithymaloides, based on Dressler 1376, preserved in liquid, 4' a small, bract-like leaf from the same plant. C. P.t. ssp. angustifolius, 1-3 \& 5 based on Britton, Cowell \& Brown 4607, 4 based on León 5025.

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# CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY 

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXIII

## THE SYSTEMATICS AND EVOLUTION OF TOWNSENDIA (COMPOSITAE)

By<br>John H. Beaman

## PUBLTSHED BY <br> THE GRAY HERBARIUM OF HARVARD UNIVERSITY CAMBRIDGE, MASS., U.S.A.

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## ABSTRACT

The genus Townsendia (tribe Astereae) consists of perennial, biennial, and annual herbs that occur in the western United States, Mexico, and southwestern Canada. Twenty-one species are now recognized in the genus; two new species and one new variety have been described in this paper.

Reproduction in several species of the genus has received cytogenetic and embryological study. Meiosis in both micro- and megasporogenesis in diploid, sexual plants ( $n=9$ ) is regular with the formation of tetrads of micro- and megaspores. At anthesis the pollen grains are 3-nucleate, and the percentage of aborted grains is very low. Development of the female gametophyte from the megaspore tetrad is sometimes trisporic and sometimes tetrasporic. The mature female gametophyte in sexual plants usually consists of from 12 to 16 nuclei. Apomixis has been detected in 12 species. Meiosis in both micro- and megasporogenesis in polyploid, apomictic plants ( $2 n=27-36$ ) is irregular with many or all of the chromosomes occurring as univalents at metaphase I. When some bivalents are present in microsporogenesis, a tetrad usually is produced, but a wall often encloses the whole tetrad, and a giant, several-nucleate pollen grain results; at anthesis the percentage of aborted grains is high. When no bivalents are present in microsporogenesis, a restitution nucleus (chromosome clump) is formed at metaphase I; the following anaphase is equivalent to anaphase II of normal meiosis, and a dyad with unreduced nuclei results. The two halves of the dyad develop separately into 3-nucleate pollen grains that are conspicuously larger than those produced by diploid, sexual plants; at anthesis the percentage of aborted grains is high. It is suggested that the unreduced dyads resulting after apomictic megasporogenesis are produced in the same manner as those in apomictic microsporogenesis. The megaspore dyad develops directly into a 2 -nucleate embryo sac, and after two series of mitotic divisions the female gametophyte in apomictic plants matures at the 8 -nucleate level. Division of the unreduced egg nucleus is initiated slightly before that of the two fused polar nuclei. The female gametophyte escapes reduction by diplospory; apomixis is obligate, and pollination is not required to initiate development of the embryo or endosperm. No diploid plants are known to be apomictic; similarly, no polyploid plants are known to be sexual.

The apomicts have not been given special taxonomic recognition. They have been referred to species known also from one or more sexual populations. Apomictic plants are concentrated at the higher elevations and higher latitudes relative to the whole range of the species in which thev occur. Apomixis is found most commonly in species with the perennial habit; however, it occurs also in some biennials.

Hybridization apparently has been extensive in the genus. Intermediate populations involving 15 species have been found. Certain apomictic races in six species exhibit morphological evidence of hybridity, but other apomicts are clearly of non-hybrid origin.

The species of Townsendia are considered to be mostly of recent derivation. The most primitive species, T. formosa, has many characters in common with three other genera, Dichaetophora, Astranthium, and Boltonia. Geographic isolation may have been the principal factor governing speciation in Townsendia. Experimental crosses and putative natural hybrids suggest that genetic isolating barriers are not involved in initial evolutionary
divergence. Polyploidy apparently has not been a mechanism of evolution, as it seems to be closely associated with obligate apomixis. Several examples of parallel or convergent evolution have been discussed.

## Introduction

A cytotaxonomic study begun with several seed collections was the forerunner of the present paper. Early in the study it became evident that apomixis might be present in Townsendia. In the limited herbarium material then examined, several of the specimens seemed difficult to determine. Thus, it appeared that Townsendia was deserving of a full-scale systematic investigation, even though it had been revised by Larsen (1927).

From several standpoints Townsendia has proved to be an ideal genus in which to employ some of the more recently developed taxonomic techniques. The western North American distribution of its 21 species offers certain practical advantages for a biosystematic investigation. Field studies within the ranges of all the species have been made. Some of these have been necessarily brief, but the plants are within a convenient distance for further population studies of a more detailed nature. The concentration of herbarium material of Townsendia is in American herbaria and a large percentage of this has been examined. With the recent interest in collecting in the western United States, most of the species have become well represented by herbarium specimens. A knowledge of intraspecific variation is therefore possible, and, where feasible in the present systematic treatment, an attempt has been made to note the type of population diversity that has been encountered. The small size of the plants of most of the species frequently has permitted collectors to include several plants on a single herbarium sheet. Some herbarium specimens approach being "mass" collections. Abundant plants in single collections have facilitated the understanding of intrapopulation variation.

The position of Tounsendia in the Astereae is a fortunate one from the comparative cytological standpoint. Relatively few investigations of a cytological nature have been made in this tribe of the Compositae. Erigeron and Aster are the only genera of the tribe other than Townsendia that have received more than cursory cytological attention, while genera in some of the other tribes of the Compositae, especially in the Cichoricae, have been the subjects of considerable cytotaxonomic and cytogenetic interest. The chromosomes of Townsendia are large and easily prepared for observation. Although chromosome morphology has proved of
little systematic or evolutionary interest in the present study, more intensive future investigations may reveal its importance.

As an experimental subject, Townsendia may have potentialities which are now completely unexploited. However, it will probably be necessary to grow most of the species under outdoor conditions in the western portion of the United States. Few of the species exhibit entirely normal growth in the greenhouse or in the garden at Cambridge, Massachusetts. But in the garden at Pullman, Washington and probably in other areas of the West with continuously cold winters and slightly basic soils, entirely satisfactory growth of the plants may be obtained.

Most of the species appear not to have strong genetic isolating mechanisms. However, growing hybrids to more than the first or second filial generations may show up isolating barriers of the genetic type which are not expressed in first-generation hybrids. If it were possible to demonstrate why species which appear to be cross-compatible with other species can maintain clear or only slightly blurred specific boundaries when they grow side by side, information on a problem of wide biological significance would be obtained. The possibility for such a study is present in Townsendia.

In Townsendia, studies on the evolutionary significance of polyploidy appear to have little promise because of the strong correlation of polyploidy with obligate apomixis. However, the opportunities in Townsendia for research on the causal aspects of polyploidy and apomixis have not been exhausted.

The present investigation embodies an attempt to bring together as much information about Townsendia as is now available. It is hoped that the systematic treatment will provide a solid foundation upon which future investigations may be built. Obviously, all of the problems associated with Townsendia have not been solved. But if this study can serve as a reference point from which problems in plant migration, population variability, and phylogenetic modification can be attacked, then a primary aim will have been fulfilled.

## Acknowledgments

The inspiration from Dr. Reed C. Rollins has contributed much to this study. He provided numerous suggestions and facts which aided in the research and writing of the paper, and his help in obtaining funds, facilities, and material for the investigation has been invaluable. Appreciation is extended also to Dr. Marion Ownbey for his advice when the study was in its early stages.

I wish to thank the curators of the herbaria from which specimens have been used. These herbaria are listed at the beginning of the systematic treatment.

Most of the field investigations were financed by a generous grant from the Fernald Fund of Harvard University. To Mr. F. W. Hunnewell of Wellesley, Massachusetts, a large measure of appreciation is due for providing the Fernald Fund. I am indebted to Mr. Irwin Lane and Mr. Henry Andreozzi for handling the collections of living plants which were sent to them while the field studies were in progress.

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The devoted assistance of my sister, Mary Lou Beaman, in the summer of 1956 made possible a timely completion of the study.

## Historical Account

Some details in the history of the genus Townsendia have been recorded in the revision by Larsen (1927). In addition to two new species in the present treatment, three species ( $T$. dejecta, T. minima, and T. anomala) have been described since the time of Larsen's treatment. One of these, T. minima, is recognized as T. montana var. minima in this study. The other two are placed in synonymy.

Botanists who have done the most work with Tounsendia have generally considered the genus a difficult one. Thus Gray (1880) stated: "Ever since the discovery of a considerable number of species, this very characteristic genus of the Rocky Mountain region has been particularly difficult." And Marcus Jones (1893) in his Notes on Townsendia stated: "This genus has always been
a trying one to me because the descriptions have not fitted the plants as they grow." Heiser (1948) noted that "A number of problems in the genus Townsendia call for extensive field work and experimental studies." The recognition of apomixis and its effects in the genus has been a great aid in solving problems which confronted and to some extent confounded previous investigators.

The taxonomic treatment of the present paper corresponds more closely to that by Gray than to the revision of Larsen. Improvements on Gray's treatment have been possible mainly because many more specimens are now available. The present study indicates that only three of the 17 species recognized by Gray cannot be maintained. Generally, the varieties he described are not recognized in this treatment, but one of his varieties, T. sericea var. leptotes, was elevated to specific rank by Osterhout and is here recognized as such. The revision by Larsen, although based on more specimens than were available to Gray, shows a lack of understanding of Townsendia. Larsen's confusion of T. mensana with T. Hookeri (T. sericea in her treatment), of T. condensata with T. spathulata, and of T. Fendleri and T. annua with T. strigosa has caused considerable difficulty for botanists working with the flora of the western United States. Furthermore, her key is not satisfactory for determining many of the species.

One helpful contribution of Larsen's (1927) study of Townsendia was her demonstration that Hooker's "species," T. sericea, was based on two specifically distinct elements. She indicated that plants collected in the "Rocky Mountains" by Drummond accord with Hooker's description of T. sericea in his "Flora Boreali-Americana," and that those collected by Richardson (which are the type of Aster? exscapus = T. exscapa [Richards.] Porter) present some discrepancies with Hooker's description, particularly in the character of the leaf, pubescence, and pappus. She consequently interpreted the Drummond plants as the type of T. sericea Hook. and the type of the genus.

Two specifically distinct elements were represented in the plants collected by Richardson and Drummond. However, T. exscapa must be taken as the type of the genus because its type was included in the original species of Townsendia. Furthermore, Hooker's species, T. sericea, cannot be maintained to include the element of the original material which is not T. exscapa because it included the type of the earlier Aster? exscapus. This other element is referred to a newly described species, T. Hookeri.

## The Localities of Nuttall's Townsendia Collections

The largest number of species recognized in this study which has been described by a single botanist is four. Both Asa Gray and Thomas Nuttall described that number. The specimens upon which Gray's species are based were obtained by several collectors and their data are fairly precise. The specimens upon which Nuttall's species are based were collected by himself during his journey with the Wyeth expedition from St. Louis, Missouri, to Fort Vancouver, Oregon, in 1834. In general the localities Nuttall listed for his specimens are almost impossibly vague. The localities for his specimens of Townsendia are no exception. No journal made by Nuttall during this trip is known (Graustein, 1951), so most of the information about his localities must come from his published account ( 1840,1841 ) and the label data on his specimens.

In addition to the papers of Jepson (1934) and Pennell (1936) which consider Nuttall's journey across the West, the problem has recently been approached by Goodman (1943), Barneby (1947), and Rollins (1950) in regard to Parthenium alpinum. One of the species of Townsendia which Nuttall described ( $T$. spathulata) has range limitations somewhat similar to Parthenium alpinum. The other species of Townsendia which Nuttall described also have relatively small and well-defined ranges. Therefore, it has been considered worthwhile to bring together the available data on Nuttall's Townsendia collections and make a critical analysis of them. For recording the label information on the specimens in the British Museum, I am indebted to Dr. Rollins.

The four species Nuttall described and the one additional species he collected are listed below with the data which Nuttall published and the data which accompany his specimens.

## Townsendia grandiflora.

Published locality: "Hab. With the preceding, . . ." [the preceding is $T$. strigosa].

Label localities: Hills of the Platte and into the R. Mts. (bм). Black Hills of the Platte (bм). Plains of Platte, June (pH). Platte ( ch, ex Herb. John A. Lowell). Platte (Ny, not in Nuttall's handwriting). Platte, Hills (GH, in Gray's handwriting). Plains of the Platte ( GH , in Gray's handwriting).
Townsendia Hookeri Beaman (the determination by Nuttall was $T$. sericea Hook.).

Published locality: "Hab. On the Black Hills, (an alpine chain
toward the sources of the Platte). Flowering probably in April." None of Nuttall's collection of this species is in American herbaria and through an oversight of mine the data of the specimen in the British Museum were not recorded by Dr. Rollins.

## Townsendia incana.

Published locality: "Hab. With the above [T. Hookeri]. Flowering in June."

Label localities: Black Hills of the Platte, June (вм). Black Hills of the Platte, grassy plains (вм). Black Hills of the Platte ( $\mathbf{P H}$ ). Platte plains (GH, ex Herb. John A. Lowell). Rocky Mts. lat. $42^{\circ}$ ( $\mathrm{GH}, \mathrm{in}$ Gray's handwriting).

## Townsendia spathulata.

Published locality: "Hab. With the above." [T. Hookeri and T. incana].

Label localities: Black Hills of the Platte, June (bм). Black Hills of the Platte in "[?, nearly illegible] campis etato rocky" (BM). Black Hills of Platte (PH). Black Hills [of, illegible] Platte (GH, ex Elias Durand).

Townsendia strigosa.
Published locality: "Hab. On the Black Hills, (or eastern chain of the Rocky Mountains,) near the banks of the Platte.-Flowering in June."

Label localities: Black Hills of the Platte (bм). Black Hills of the Platte, June (bм). Black Hills (GH, in Gray's handwriting). R. Mts. Platte ( $\mathbf{P H}$ ).

The most confused and inconsistent of the sets of data above is associated with $T$. grandiflora. It seems unlikely that Nuttall could have collected $T$. strigosa and $T$. grandiflora together as he stated. The well-defined ranges of the two species are not known to be less than 100 miles apart at their closest points. Townsendia grandiflora is probably the eastern-most species of the genus collected by Nuttall. It appears likely that the locality "Plains of Platte" as is on the Philadelphia Academy specimen is more accurate than the published locality or that on the specimens of the British Museum. It is possible that Nuttall obtained the species more than once, which may account for some of the diversity of his label information. Evidence is presented in the systematic treatment under the discussion of T. spathulata which suggests that Nuttall obtained this species from more than one locality.

Nuttall's inference that he obtained T. Hookeri, T. incana, and $T$. spathulata together seems likely. I have obtained these
three species from a single locality near Alcova, Natrona County, Wyoming (T. Hookeri, Beaman 877, T. incana, Beaman 875, and T. spathulata, Beaman 878). Townsendia incana and T. spathulata have been obtained at this locality by other collectors also. It is interesting that Parthenium alpinum has recently been obtained by Ripley and Barneby and by Porter at this same locality after being known only from the type collection for more than 100 years. Ironically, Nuttall's locality data for Parthenium and those for the Townsendia species are entirely different.

It seems probable that Nuttall's term "Black Hills of the Platte" embraces a rather large area in central and western Wyoming. His "Black Hills" are possibly the Wind River Mountains. These mountains are an alpine chain and are at one source of the Platte (actually Sweetwater) River. They would have been the highest mountains which Nuttall saw in Wyoming, as he followed the Oregon Trail. Aside from his Townsendia collections, the "Black Hills" locality was not frequently used by Nuttall. He used it for Gnaphalium dimorphum ( $=$ Antennaria dimorpha), for Antennaria plantaginea $(=$ ?, I have not seen specimens of this Nuttall collection), and for A. parvifolia. Neither Antennaria dimorpha nor A. parvifolia has a very limited range as do the Townsendia species, and therefore are of little value for locating the "Black Hills." One feature about Nuttall's locality data throughout his paper $(1840,1841)$ is that he frequently used the same or similar locality information for each species or most of the species of a genus. This makes one wonder if the similarity always resulted from a coincidence of collecting several species of a genus in one locality, or if some other factor accounts for the similarity. In Townsendia, with the possible exception of T. grandiflora, Nuttall's locality data are vague enough to escape being classed as incorrect.

## Geographical Distribution, Climatic and

## Edaphic Requitements

Townsendia is primarily a genus of the Rocky Mountains of the United States. The ranges of apomictic populations of three species extend into Canada. One of these species, T. exscapa, is found also in Mexico. Only one other species, a Mexican endemic, is now known from that country. The easternmost range of a member of the genus is that of T. exscapa, which occurs as far east on the Great Plains as northeastern Nebraska. The western limit of the genus is on the Columbia River plateau in central

Oregon where T. florifer occurs. Townsendia is mostly found above 3500 to 4000 ft ., but along the Columbia River in Oregon and Washington T. florifer is at less than 1000 ft . The upper elevational limit of the genus is marked by apomictic populations of T. Rothrockii and T. leptotes which occur at least as high as $13,000 \mathrm{ft}$. in Colorado.

Ten species have been collected in both Colorado and Wyoming; nine occur in Utah and seven are found in New Mexico. Idaho and Nevada each have six; Montana has five, and Arizona has four species. Several of the western states have two or three species each. It is unusual for a species of Townsendia to be found in more than four states, and ten of the 21 species occupy only small areas in one or two states. Narrow endemism may be regarded as a common feature of the genus.

It may be inferred from the distributions outlined above that both latitudinal and altitudinal climatic influences are important in governing the distribution of the species of Townsendia. Townsendia exscapa, T. Hookeri, and T. leptotes are the only species which do not occur within a relatively narrow climatic province. Even in the latter two of these species, the sexual forms are restricted to small areas with nearly uniform climatic conditions. Thus it seems probable that climate has had an important role in the evolution of the members of the genus.

In many instances edaphic factors appear to be even more important than climatic factors in regulating the distribution of the species of Townsendia. Especially within the range of a species, the occurrence of plants on very localized edaphic situations is frequently striking. As a generalization, with not too many exceptions, it may be stated that the acaulescent, rosulate forms require more highly specialized edaphic situations than do the caulescent types. The former mostly require open, finely divided limestone, sandstone, or shale rubble with a sparse vegetation. Edaphic sites of this type are illustrated by the habitat photographs in Plate XV, figs. 1 and 2 and in Plate XVI, fig. 2. These edaphic conditions might be characterized as stable in a short-time sense and unstable in a longer- (geological) time sense. Even though the caulescent forms are less strictly limited edaphically, their requirements are somewhat parallel to those of the acaulescent types.

Soil samples have been collected at habitats of all the species, but time limitations have not permitted an analysis of these. A pH analysis is planned as a future study. Tentatively it may be inferred from the general character of the soils of the western

United States that the species in the more arid habitats occur in soils on the basic side of the pH range, while those in the moister habitats are probably in neutral or only slightly acid soils.

## Generic Relationships

In a genus with species as closely related to one another as are those of Townsendia, it would seem that relationships of the genus to other genera might also be evident. However, few investigators have committed themselves on the generic relationships of Townsendia. The limits of the genus never have been questioned. There has been but a single species placed in Townsendia which belongs in a different genus, and this was first excluded by Gray, its author. Likewise, there have been no species transferred from other genera into Townsendia (with the exceptions of T. exscapa and T. florifer which were described originally with doubt as to their generic position). Consequently, the generic relatives of Townsendia are not revealed by its nomenclatorial history.

The genera conventionally assigned close to Townsendia have not had a similarly tranquil history. The many changes in Aster are well known. Astranthium has been with Bellis; Dichaetophora has been with Boltonia; and Keerlia is now in Chaetopappa. These examples by no means exhaust the list of changes, but the reader is referred to Shinners (1946a) for further details.

Although the uncomplicated nomenclatorial history of Townsendia suggests for it a distinct phyletic position, its features were not considered unique by Bentham (1873). In his comprehensive "Notes on the Compositae" he wrote (p. 408): "Thus we have the Asiatic and North-American Boltonia, the Asiatic Heteropappus, and the N.-American Townsendia, Monoptilon, and Psilactis differing from the typical Asters of the same regions in scarcely any thing but the pappus." Gray (1888) in his "Synoptical Flora" in the section Megalastrum of Aster tersely wrote: "related to subsection Xylorrhiza and to Townsendia." And Larsen (1927) noted that "the heads [of Townsendia] resemble those of the closely related genus Aster." Otherwise, ideas of the generic relationship of Townsendia have been indicated only by its systematic position in works by such authors as Gray (1888) and Hoffmann (1897). The rationale of the statement by Gray (quoted above) is evident. Section Megalastrum includes Aster Wrightii which Gray had once put in Townsendia. From the present study, it appears that Aster Wrightii could be considered to have
only a rather distant relationship with Townsendia. Species of several other genera have a considerably closer relationship.

In Shinners' (1946b) study of some of the Astereae he noted that in the American genera of the heterochromous Astereae an arrangement on the basis of the form of the receptacle was better than that based on the pappus. Those conical-receptacled genera which he treated are Egletes, Erigeron (in part), Aphanostephus, Astranthium, Dichaetophora, and Boltonia. In his key to separate the above genera, Astranthium, Dichaetophora, and Boltonia fall into one group. An examination I have made of these three genera indicates that they have a number of morphological similarities. Also, they have characteristics in common with Townsendia, which was not included in Shinners' treatment because it was not at that time known to have a conical receptacle. In the present study, Townsendia formosa has been found to have a conical receptacle. Through this species it is possible to recognize the relationship of Townsendia with Dichaetophora, Astranthium, and Boltonia. Another feature which indicates their relationship is the stem pubescence, which is consistently of simple, strigose trichomes. The leaves, especially of Dichaetophora and some of the Astranthium species, are very similar in shape, texture, and pubescence to those of T. formosa. The pappus of T. formosa is very similar to that of Astranthium, while the pappus of Boltonia and Dichaetophora is somewhat similar to that of T. eximia. The achenes, which are compressed, ovate in shape, and with two conspicuous margins (extended into wings in Dichaetophora), are very similar in all four genera. Dichaetophora also has duplex, glochidiate achenial hairs ("peculiar glandtipped hairs" according to Shinners) on the central portion and margins of the achenes. These hairs are indistinguishable from those of several species of Townsendia. The achenes of Dichaetophora also are papillose in a manner very similar to those of some of the members of Townsendia.

The four genera also have a close phytogeographic relationship. The center of diversity of Townsendia is in the southern cordillera of the United States. The centers of Dichaetophora and Astranthium are not far to the south, and that of Boltonia is to the east.

Townsendia and Dichaetophora are probably the two closest members of this four-genus alliance, but Astranthium is not too distantly related. Boltonia seems somewhat more widely set apart.

Within Townsendia, the characters I regard as primitive are:
a perennial, fibrous-rooted, rhizomatous and stoloniferous habit; erect, monocephalous stems; large, thin, glabrate, spatulate leaves; lightly pubescent stems; large heads; a conical receptacle; several rows of broad phyllaries with narrowly scarious and minutely ciliate margins; large, obovate achenes; and a small, unelaborated pappus. With the exception of the phyllaries, about which I am not sure, these characters may be considered to be primitive (when present) also in the three other genera under discussion. Townsendia formosa appears to be a more unspecialized form than the other Townsendia species, and also the members of the other three genera.

The concept of a small, squamellate, unelaborated pappus as a primitive character requires explanation. Under most circumstances it would be looked upon as a reduced feature. But in this case, $T$. formosa and three closely related genera have the small pappus. Within Townsendia, the species most closely related to T. formosa (T. eximia) has a larger but similar pappus. The derived relatives of T. eximia in turn have a pappus which is even more highly elaborated. It seems, therefore, that the evolutionary trend has been in the elaboration rather than the reduction of the pappus. The selective advantage of a large pappus as an agent of dispersal seems evident.

The alternative explanation, that the pappus of Townsendia formosa is a reduced feature, would require the postulate that the genera related to Townsendia have been more recently segregated from $T$. formosa stock than have the rest of the Townsendia species. This explanation seems improbable. Although many similarities between $T$. formosa and the three other genera have been indicated above, the latter still have greater differences from T. formosa than do the other species of Townsendia. For example, Dichaetophora, which seems to be the genus most closely related to Townsendia, is comprised of a single annual species. This lifeform is surely a long phylogenetic distance from the rhizomatous, long-lived T. formosa.

It is beyond the scope of the present work to consider the position of Townsendia and its close generic relatives in regard to their position with the rest of the Astereae. However, it should be noted that the embryological similarities between Townsendia and Erigeron (considered in the section on reproduction) do not necessarily suggest a close relationship for the two genera. These peculiar embryological features may eventually be found in still other members of the Astereae.

## Species Concept

It is hoped that the present systematic treatment approaches an ideal which has been expressed by Cain (1944). He stated (p. 7): "Taxonomy attains a logical basis when the data of comparative morphology can be arranged in a geographical pattern that coincides with the probable phylogeny of the group and the history of the floras . . . in which it has been involved." In this study an attempt has been made to designate the taxa by a system which applies insofar as possible a traditional nomenclature, yet emphasizes the morphologically recognizable units on a geographic basis.

There is a marked tendency in Townsendia for species with the same flowering periods to have allopatric ranges. A criterion of strict genetic isolation cannot be used in Townsendia. Such an approach would result in the "lumping" of most or all of the species into one. Geographic barriers are most important in isolating the species of Townsendia. If genetic barriers do exist in the genus, they are probably not strongly expressed in the first hybrid generation in most instances.

An understanding of the mechanism of reproduction in Townsendia has been a necessary basis for explaining peculiarities of geographic distribution of some of the species. Cytogenetic and embryological data have therefore been of value in facilitating an understanding of the comparative morphology of the group on a geographic basis. But these data have been of little value in the determination of specific boundaries.

Most of the species are nearly parallel in their degree of distinctness. However, T. formosa possesses a considerably larger set of unique characteristics than does any other species. Those taxa at the varietal level were placed there as geographic segregants with fewer characters distinguishing them from their nearest relatives than were usually available to distinguish species. No complete intergrading series is known between the varieties, in the two species where they were designated. The term "variety" rather than the term "subspecies" is used for the infraspecific units primarily because its use in this sense has long been accepted in botanical classification. According to the International Code of Botanical Nomenclature (Lanjouw et al., 1956, Article 4) either of the terms might have been used. In the present taxonomic interpretation of Townsendia, it would not have been possible to use both of these infraspecific categories.

## Reproduction

Apomixis in Townsendia previously was suggested by five indirect lines of evidence reported in a preliminary cytogenetic investigation in the genus (Beaman, 1954). In the present study the problem of apomixis was attacked directly by comparative embryological examinations of mega- and microsporogenesis and subsequent development in sexual and apomictic populations. Knowledge of the mechanism of apomixis in Townsendia has been considered indispensable to a formulation of taxonomic concepts in the genus. Different types of apomixis may have different effects on evolutionary trends. For example, pseudogamous apomicts are more dependent on environmental factors, such as pollinating agents, than are autogamous apomicts. Facultative apomicts may lack some of the efficiency in reproduction which characterizes obligate apomicts. But obligate apomicts may be less plastic under the action of selective forces than are facultative apomicts. Therefore, this study was designed to expose the morphological and cytological features of apomixis in Townsendia and to evaluate the significance of apomixis to evolution in the genus.

## MATERIALS AND METHODS

The plant material which has been used in this study is listed in Table 1. Voucher specimens are filed in either the Gray Herbarium of Harvard University or in the Herbarium of the State College of Washington. The plants were grown in the experimental gardens at Harvard University in Cambridge, Massachusetts or at the State College of Washington in Pullman, Washington. In some cases buds used in the study were taken from plants growing in their native habitat.

Studies of microsporogenesis and male gametophyte development were made from florets fixed and smeared according to a method previously outlined (Beaman, 1954). A few observations of microsporogenesis were made in embedded and sectioned anthers prepared along with the florets used in the study of megasporogenesis. However, this material was unsatisfactory for critical examinations.

Studies of pollen were made from unopened (i.e., preanthesis) florets from herbarium specimens. The corollas of these florets were macerated in a drop of aceto-carmine on a slide and observed immediately under the microscope. Pollen size and
degree of abortion are readily apparent by the use of this rapid technique, which was employed in the taxonomic study to determine whether the herbarium specimens represented sexual or apomictic populations. The pollen nuclei become darkly stained after being exposed to aceto-carmine for from one to ten minutes. Pollen may be satisfactorily photographed for about 45 minutes after being placed in aceto-carmine. If the staining period is longer, the cytoplasm becomes darkly stained, and a satisfactory contrast between the nuclei and the cytoplasm cannot be obtained.

Studies of megasporogenesis, female gametophyte development, and embryogeny were made from buds fixed either in Belling's modified Navashin's fluid or in a Carnoy's fluid ( 6 parts absolute alcohol: 3 parts chloroform: 1 part glacial acetic acid). When Carnoy's fluid was used, the buds were transferred to 70 per cent alcohol after being in the fixative for about one hour. With Navashin's fluid, aspiration was sometimes employed. The best fixation was obtained by removal of the top portion of the achene before fixation. Aspiration was unnecessary when ovaries were opened in this manner. The period of fixation lasted from a few days to over two years. As might be expected, the material used shortly after fixation yielded the best results. Also, material fixed in Navashin's fluid gave much better results with the paraffin-embedded technique than did that fixed in Carnoy's fluid. Material fixed in the latter was used only to supplement the material fixed in Navashin's fluid.

Material fixed in Navashin's fluid was washed in water and dehydrated in a tertiary butyl alcohol series. Material fixed in Carnoy's fluid was transferred directly from 70 per cent alcohol to the tertiary butyl alcohol series. The material was embedded in Fisher Tissuemat and sectioned at from 10 to 15 microns. Even in old florets, 10 microns proved to be the most satisfying thickness. A ferric ammonium sulphate-haematoxylin staining schedule, described by Esau (1944), gave good results. The slide preparations are in the personal collection of the author.

The photomicrographs were made with Bausch and Lomb photomicrographic equipment and a Zeiss microscope with apochromatic $20 \mathrm{X}, 40 \mathrm{X}$, and 90 X objectives. Ansco Isopan film was used.

## THE MALE REPRODUCTIVE PHASE

In a previous paper (Beaman, 1954) studies of microsporogenesis in ten species ( 13 according to the species delimitations
then used) of Townsendia were reported. At that time the basic chromosome number $x=9$ was postulated for the genus. In diploid, sexual plants almost no meiotic irregularities were found, but a high degree of meiotic irregularity was encountered in polyploid, apomictic plants. The specific names of some of the material used in the previous study (l.c.) should be emended as follows: T. anomala (culture 33) $=T$. condensata; T. arizonica (cultures 4 and 5) $=T$. incana; T. Hookeri (culture 38) was

TABLE I.
Material of Townsendia used in the embryological and cytological investigations. ${ }^{1,2}$

| Taxon | Collection | Culture <br> Chromosome <br> number | Place grown |
| :--- | :--- | ---: | ---: | ---: | :--- | :--- | | Date of |
| :--- |
| fixation |

[^26]misidentified as T. mensana; T. minima (culture 3) $=$ T. montana var. minima; T. condensata (culture 47) was misidentified as T. spathulata. The chromosome numbers of five species not included in the previous study are reported in Table I in the present paper.

## Microsporogenesis in diploid, sexual plants

In all but one collection of the diploid material examined in this study, microsporogenesis was regular and nine bivalents were observed at metaphase I. In the exceptional collection (Beaman 945 ) at least one plant was characterized by 10 bivalents. Apparently the pairing attraction of the tenth chromosome pair was not very strong, as some cells were found with nine bivalents and two univalents instead of ten bivalents. Other material collected from this same population is characterized by nine bivalents at metaphase I and no meiotic irregularities. It seems probable that the ten-chromosome material is a rare abnormality.

An examination of the meiotic karyotype of T. mexicana revealed meiotic chromosomes of a smaller size than has been found in any other species of Townsendia. A metaphase plate from a preparation of T. mexicana is shown in Plate I, fig. 3. This figure may be compared with Plate I, fig. 2, which illustrates larger metaphase chromosomes typical in the genus. The karotype of T. annua, the species morphologically most similar to T. mexicana, has not been examined.

## Microsporogenesis in polyploid, apomictic plants

In the present study no special attempts have been made to obtain additional chromosome counts in apomictic material. Instead, investigations have been concentrated on material from apomictic populations of two species. These were chosen particularly because one is triploid and the other tetraploid. Both bivalents and univalents are found at metaphase I in the triploid. This stage in the tetraploid is characterized by 36 univalent chromosomes. The triploid material is from a population (culture 6) of T. incana. This species, especially this population, has been used extensively also in the investigation of megasporogenesis. Thus, comparative data of the male and female reproductive phases in the same population have been obtained. The tetraploid material is from a population (culture 8) of T. Parryi. Megasporogenesis in this population also has received attention.

Townsendia incana (culture 6). Meiosis in the anthers of plants of this population is characterized by a considerable
amount of chromosome pairings, as may be seen from Plate I, fig. 4. The number of bivalents in relation to the number of univalents is not constant. Mostly there are between five to ten bivalents and six to 15 univalents. No pollen mother cells with all univalents have been observed. Meiosis in the ovules, on the other hand, frequently is characterized by all univalent chromosomes at late prophase and metaphase (see Table III). Some variation of the chromosome number occurs within the population. In addition to the chromosome count of $2 n=28$ which was previously reported (Beaman, 1954), the count $2 n=27$ also has been obtained. From some of the examinations of microsporogenesis it appears that the number $2 n=26$ might occur in the population, but chromosome counts from microsporogenesis are difficult to obtain and often are unreliable. A variable chromosome number could be expected in the population, however, as a result of meiotic irregularities in megasporogenesis. Micronuclei, which have been observed with dyads of megaspores, probably represent chromosomes or chromosome fragments excluded during megasporogenesis. In this triploid population the loss or gain of a small amount of chromosomal material might not be lethal.

At anaphase I in culture 6, lagging univalents are frequently seen (Plate II, fig. 1). The halves of the bivalents go directly to the poles during anaphase I, but univalents seem to be much less strongly attracted to the poles. Usually the univalents eventually reach one of the poles, but sometimes they are excluded from the main nuclei and form micronuclei. Chromosome counts at metaphase II indicate that in the first division the triploid number of chromosomes is reduced by about half in the two resulting nuclei. Usually 12 to 15 chromosomes are seen at metaphase II. The distribution of the univalents at the first anaphase is unequal, and the two poles do not receive exactly the same number of chromosomes.

Tetrads of microspores in culture 6 (Plate II, fig. 2) have a fairly normal appearance. Their subsequent development, however, is not normal. Cell walls usually do not form between the microspore nuclei, and all four nuclei are surrounded by a wall which develops the structural characteristics of an ordinary pollen wall (Plate II, fig. 3). The ultimate "male gametophyte" which results from this type of development is a giant, several-nucleate pollen grain (Plate IV, fig. 2). At anthesis, in addition to the large grains, there are many aborted grains of various sizes. The determination, from herbarium specimens, of plants from apomictic populations is an easy matter when the pollen has been
formed in the manner outlined above. A reference to this peculiar method of pollen development was made by Holmgren (1919) in his study of Erigeron. He noted, in sexual material, that pollen of florets in a transitional position on the head between pistillate ray-florets and hermaphroditic disk-florets developed by wall formation around the four nuclei of the tetrad. He stated that this abnormality was not infrequently encountered in apomicts and hybrids. A few other references to this type of pollen development occur in the embryological literature.

Microsporogenesis and pollen development in culture 6 are of interest in regard to the recognition of apomixis in populations from herbarium specimens. However, since reduction occurs in this material, little information is gained on the mechanism of meiosis on the female side where reduction must be avoided. Tetraploid culture 8 of T. Parryi differs in its microsporogenesis from culture 6 of T. incana and possibly may have similar processes in both the male and female phases.

Townsendia Parryi (culture 8). Gustafsson $(1934,1935)$ has reviewed and defined three processes by which chromosome reduction may be avoided in apomicts during the development of the archesporial cell to form a female gametophyte. These processes have been termed "semiheterotypic division" (restitution nucleus formation), "pseudohomeotypic division" (a single division of the univalent chromosomes to form a dyad, not involving restitution nucleus formation), and "mitotic division" (the archesporial cell divides to form a dyad and no features of meiosis are found in the process). The process by which unreduced dyads are formed in Townsendia has some resemblance to a normal meiosis; thus, either the semiheterotypic or the pseudohomeotypic division must occur, and the mitotic type will not be further considered.

No anaphase restitution nuclei have been positively identified in Townsendia in mega- or microsporogenesis. It might seem, therefore, that the pseudohomeotypic division occurs in the genus. The univalent chromosomes observed in megasporogenesis in the apomicts might also be suggestive that the pseudohomeotypic division occurs in Townsendia. Especially, the occurrence, at diakinesis or prometaphase in megasporogenesis, of univalents with visible chromatids (Plate I, fig. 5) might indicate this type of division.

Fagerlind recently has examined megasporogenesis in apomictic material of Rudbeckia (1946), Erigeron (1947a), and Taraxacum (1947c), and microsporogenesis in apomictic Hierac-


Plate I. Photomicographs of meiotic chromosomes in Tounsendia (all $\times 1200$ ). Fig. 1. Nine bivalents at diakinesis in microsporogenesis in sexual, diploid T. incana. Fig. 2. Nine bivalents at metaphase I in microsporogenesis in T. eximia. Fig. 3. Nine bivalents at metaphase I in microsporogenesis in T. mexicana. The chromosomes are smaller in $T$. mexicana than those known in any other species of the genus. Fig. 4. Bivalent and univalent chromosomes at metaphase I in microsporogenesis in apomictic, triploid T. incana. Fig. 5. Univalent chromosomes at diakinecis or prometaphase in megasporogenesis in apomictic, eriploid T. incana. The microtome blade bisected this cell, and the portion shown contains about half of the chromosomes. Fig. 6. Chromosomes at metaphase II in microsporogenesis in sexual, diploid $T$. incana.


Plate II. Some aspects of microsporogenesis in apomictic populations of Townsendia. Fig. 1. Anaphase I with lagging univalent chromosomes in triploid $T$. incana ( $\times 1200$ ). The halves of the bivalents go directly to the poles at anaphase I while the univalents lag. Usually the univalents reach one of the poles but sometimes they are incorporated into separate micronuclei. Fig 2. Tetrads in triploid $T$. incana $(\times 200)$. These have the appearance of normal tetrads, but the microspores do not separate, and all four nuclei are incorporated within a single pollen grain. Fig. 3. Young pollen grains of triploid $T$. incana formed by the inclusion of a tetrad of microspores within one wall $(\times 470)$. Fig. 4. Pollen mother cells with all univalent chromosomes in tetraploid T. Parryi ( $\times 200$ ). Fig. 5. A more highly magnified view than fig. 4 of 36 univalent chromosomes at metaphase I in T. Parryi ( $\times 1200$ ). Fig. 6. Anaphase I in tetraploid T. Parryi $(\times 1200)$. This is an extreme anaphase. Usually these univalent chromosomes do not have a strong tendency to migrate to the two poles.


Plate III. Some phases of microsporogenesis in apomictic populations of Townsendia (continued from Plate II). Fig. 1. A metaphase restitution or contraction nucleus composed of univalent chromosomes in tetraploid T. Parryi (X 1175). Fig. 2. A restitution or contraction nucleus in tetraploid $T$. Parryi at a slightly later stage than that in fig. 1, showing chromatids of some of the chromosomes ( $\times 1175$ ). Fig. 3. Polar view of metaphase II after the formation of the restitution or contraction nucleus in tetraploid T. Parryi ( $\times 1175$ ). It is evident from this photograph that the chromosome number has remained unreduced. Reduction is prevented when all the chromosomes clump at metaphase I instead of migrating to the two poles and remaining there at anaphase I. Fig. 4. Side view of metaphase II in tetraploid T. Parryi ( $\times 1175$ ). Fig. 5. Side view of anaphase II in tetraploid T. Parryi ( $\times 1175$ ). Reduction did not occur at anaphase I and thus a dyad is formed at anaphase II. Fig. 6. Dyads in apomictic polyploid T. condensata $(\times 200)$. The two microspores develop separately into pollen grains. Apomicts which have all or nearly all univalent chromosomes at metaphase I form dyads rather than tetrads of microspores.


Plate IV. Photomicrographs of pollen in sexual and apomictic populations of Townsendia (all $\times 330$ ). Fig. 1. Pollen of sexual, diploid T. incana. Fig. 2. Pollen of apomictic, triploid T. incana. These giant grains result from the incorporation of the four microspores of a tetrad into a single grain. Non-abortive grains contain more than three nuclei but these are so contorted that it is not possible to determine exactly how many are present. Fig. 3. Pollen of apomictic, tetraploid T. Parryi. These very large grains have developed from dyads similar to the ones shown in Plate III, fig. 6. The nuclei in these pollen grains have the unreduced, tetraploid chromosome number. Fig. 4. Pollen from a randomly selected herbarium specimen of $T$. incana (Walker 206). The percentage of aborted grains in apomicts is usually as high as or higher than that indicated here by the grains without nuclei.
ium (1947b). His observations in these genera have led him to doubt that the pseudohomeotypic division occurs frequently or that it even occurs at all. He emphasizes that restitution nuclei are not necessarily formed only at anaphase but may occur also at metaphase, prometaphase, diakinesis, or even earlier in prophase. Fagerlind especially stresses the fact that the "contraction nuclei" (a term coined by Rosenberg for the clumped meiotic chromosomes of Hieracium) he observed in Erigeron, Hieracium, Taraxacum, and Rudbeckia might be restitution nuclei which are formed at metaphase or earlier.

A clumping of meiotic chromosomes in several apomictic collections of Townsendia was reported in the previous cytogenetic study in this genus (Beaman, 1954). Clumped chromosomes in meiosis appear to be a regular feature in many apomictic forms. In Townsendia, the clumping in microsporogenesis is so prevalent in material from some populations that it defies analysis. In culture 8 of T. Parryi, however, it has been possible to analyze the various processes of the apomictic meiosis in microsporogenesis, and to determine the probable sequence of the meiotic stages. Smears have been used in this study in order to render visible as much as possible of the chromosomal detail. Fagerlind's studies apparently have all been made with sectioned material. Also, other investigators of the mechanism of the meiotic non-reduction phenomena have used mostly sectioned material. Sectioned microsporocytes of Townsendia are unsatisfactory for critical chromosomal analyses.

Bivalents have never been found in microsporogenesis in culture 8 of T. Parryi. When chromosomes become clearly evident in this material at diakinesis or prometaphase they are univalents. Whether the chromosomes were paired at an earlier stage and have come unpaired, or whether they were never paired, was not determined in this study. More refined cytological techniques will be required for the solution of that problem. Typical univalent chromosomes in this material are shown at two different magnifications in Plate II, figs. 4 and 5. Infrequently, a slight tendency is manifested for a migration of the univalents to the two poles (Plate II, fig. 6) at anaphase I. More frequently, a single clump of chromosomes is found at the center of the cell (Plate III, fig. 1). In some clumps, in cells which are apparently at slightly later stages (Plate III, fig. 2), the chromatids become evident. Seen in polar view at a still later stage, the clump is loosened and the chromatids are very conspicuous (Plate III, fig. 3). A count of the chromosomes at this stage indicates that
the number has not been reduced. After the anaphase that follows, the chromosomes in the resulting dyad have a telophase II or slightly mitotic aspect (Plate III, fig. 5). These are like telophase I chromosomes. A wall is formed after this division and an unreduced dyad results. Perhaps this dyad is homologous to those found after megasporogenesis! The "microspore dyads" which result after non-reductional meiosis soon separate into their component "microspores" and these may develop into normalappearing (except for their large size) pollen grains (Plate IV, fig. 3). At anthesis many aborted grains of various smaller sizes are present also. It is therefore possible to detect these apomictic forms by herbarium specimens.

It appears, according to the events outlined above, that the univalents at metaphase I may undergo a migration toward the poles. The migration is weak, however, and two nuclei and a corresponding reduction in the chromosome number do not occur. Rather, the chromosomes are oriented into a single clump (contraction nucleus). While thus clumped, chromatid separation becomes evident. By the time the clump loosens, the chromatids are nearly separated. Anaphase II begins immediately and two unreduced nuclei result.

Discussion of microsporogenesis in polyploid, apomictic plants.
Fagerlind has stressed the point that at the time of formation of the contraction nucleus, a nuclear membrane re-encloses the chromosomal mass. No evidence of a nuclear membrane around the chromosome clumps has been detected in the smears of Townsendia microsporocytes. In sectioned preparations, the nuclear material is rather diffuse at this stage, but such figures might be interpreted as having a nuclear membrane around the chromosome clump. No indications of twisted or variously contorted chromosomal masses have been observed in smears of anthers of Townsendia. However, misshapen nuclei were seen at corresponding stages in sectioned material. It is possible that some of the details of Fagerlind's description of the metaphase restitution nucleus (contraction nucleus) are based on artifacts in his sectioned material. Smears are most useful for chromosomal analysis, and sectioned material is mainly valuable as a check for determining the proper sequences in meiotic development which are more difficult to determine in smears.

The evidence from smears of material of Townsendia seems to corroborate Fagerlind's idea of the significance of the clumped meiotic chromosomes. It seems probable that the genetic controls
of the rhythm of meiosis are such that, even in apomicts, univalent meiotic chromosomes cannot behave as ordinary mitotic chromosomes. Some of the features of the two-step meiotic cycle necessarily are retained. The tendency of univalents not to divide at first division is emphasized by univalent behavior in culture 6 of T. incana. In that material, the univalents regularly lag at anaphase I, and the chromatids do not separate until anaphase II. The chromosome clump at metaphase I in material with all univalents is actually equivalent to telophase I in normal, sexual material. In some of the apomicts meiosis may be impossible to analyze because the contraction nucleus or chromosome clump is formed earlier than metaphase. It appears, therefore, that the apomicts of Townsendia have a specialized type of meiosis (the semiheterotypic division) which avoids reduction of the chromosomes during microsporogenesis. From the present studies of megasporogenesis it seems probable that the type of meiosis outlined above for the male reproductive phase of culture 8 of T. Parryi may occur also in the female phase of this and the other apomictic populations of the genus.

It should be noted that Avers (1954) has produced evidence for the occurrence of a functional tertiary split of meiotic univalents in the microsporogenesis of triploid Aster hybrids. In her material univalent division appears to occur frequently at anaphase I in addition to the normal anaphase II division. No similar mechanism has been observed in Townsendia.

The peculiar alterations of microsporogenesis in the polyploid apomicts of Townsendia suggest a lack of functionality of the pollen which results. Also, it is unusual in these plants for the percentage of nucleated pollen to run higher than 20 per cent. Frequently this percentage is lower than five per cent, and sometimes no pollen is produced. Thus, the evidence from the male reproductive phase in the apomicts argues strongly for obligate apomixis in this genus. Evidence from the female reproductive phases reinforces this conclusion.

## THE FEMALE REPRODUCTIVE PHASE

Investigations of the female reproductive phase in Townsendia have not been made previously. However, studies in other members of the Compositae, especially in Erigeron, are of significance to this study. Harling (1950, 1951a, and 1951b) recently has been making comparative embryological studies in certain tribes of the Compositae. His paper on embryology in the Astereae (1951b) includes investigations in 14 genera of this
tribe. Except for one genus, Harling found a single, constant type of embryo-sac development in the Astereae. This development is of the "normal," monosporic type with the production of an eight-nucleate embryo sac. The exceptional genus, Erigeron, has embryo-sac development of the normal type in some of its members, but also bisporic and tetrasporic developmental-types are found in the genus. Variation occurs both within and between species.

In the Astereae the only genus other than Townsendia now known to have apomictic forms is Erigeron. In the latter, asexual reproduction was known from embryo-sac studies as early as 1915 from a preliminary report by Tahara. Several investigators have made subsequent studies of apomixis in Erigeron. Fagerlind (1947a) has reviewed these investigations and given a new interpretation regarding the mechanism of non-reduction in the meiosis of apomicts of Erigeron. His ideas have been considered in detail in this paper under the section on microsporogenesis in apomictic plants.

The features of both sexual and apomictic reproduction in Townsendia are very similar to those in Erigeron. The processes in apomictic reproduction in these two genera are not known to be exactly duplicated in any other genus. Thus, the results of the investigations in Erigeron have significance in the interpretation of the embryological phenomena in Townsendia.

## The female reproductive phase in sexual plants

Material of Townsendia incana has been more extensively used that that of any other species in the investigation of sexual and apomictic reproduction in the genus. Several populations of both sexual and apomictic types have been available for study. Comparisons of the two types of reproduction are therefore possible within a single species. Sufficient material of other species also has been available to indicate that most of the reproductive phenomena encountered in T. incana occur in other members of the genus.

Townsendia incana (culture 971). This species, as is characteristic for the genus, has a single archesporial cell in each ovule. The early prophase stages of meiosis are morphologically similar in all the material thus far examined, including the apomicts. It does not seem possible with the present techniques to determine at early prophase whether the chromonematal strands are unpaired, pairing, or paired. Therefore, the terms leptotene, zygotene, and pachytene are not used. A frequently encountered fea-
ture at early prophase is the so-called synezesis which consists of clumped chromonematal material and an associated, distinct nucleolus. Synezesis generally is considered to be an artifact present at zygotene and pachytene. It occurs in the prophase stages of both sexual and apomictic types of Townsendia (Plate V, figs. 3 and 4). Diakinesis is characterized by bivalents with pairing configurations similar to diakinesis division-figures in microsporogenesis (cf. Plate I, fig. 1 and Beaman, 1954, p. 173). No metaphase stages were encountered in culture 971.

In the one dyad observed in culture 971 no cell plate was present. At the tetrad stage and at subsequent stages certain peculiarities become evident. Twenty-one ovules were observed in which no nuclei of the tetrad were separated by cell walls. These, with the exception of one tetrad which still possessed a phragmoplast between two of the nuclei and was thus too young for determination, may be considered as 4-nucleate coenomegaspores. The megaspore nuclei are arranged in a linear fashion, and, usually, the nucleus nearest the micropyle is separated by a considerable distance from the other three nuclei. Ten tetrads were observed which had cell walls between the micropylar and submicropylar megaspore nuclei (the micropylar megaspore nucleus is the one nearest the micropylar end of the ovule, etc.). Eight tetrads were found with a wall between the submicropylar and subchalazal megaspore nuclei. In one ovule the cell wall had formed on the micropylar side of the micropylar megaspore nucleus.

In Harling's (195lb) study of Erigeron, he noted variations in wall formation in tetrads. Some of his material was characterized by no walls; some had wall formation apparently after metaphase I, some apparently after metaphase II, and some by wall formation after both meiotic divisions. He inferred the time of wall formation from the position of the walls relative to the nuclei of the tetrad. In Erigeron glabellus he found all of these conditions in a single plant. In Townsendia incana the occurrence of a wall outside of the tetrad, separating none of its nuclei, suggests that wall formation between the nuclei of tetrads has no perfect synchronization with the meiotic divisions. Furthermore, in much of the sexual Townsendia material, the abundance of walls between only the micropylar and submicropylar megaspore nuclei, without corresponding walls between the chalazal and subchalazal megaspore nuclei, suggests some lack of correlation of wall formation with meiotic division.

In culture 971, tetrasporic embryo sac development is most
common, but also one of the megaspore nuclei may degenerate and the other three germinate to form a three-nucleate embryo sac. This fact is indicated by the observation of two threenucleate and two six-nucleate embryo sacs. However, tetrasporic development must be more frequent than other types in this population (cf. Table II). The embryo sac becomes morphologically organized after two series of mitotic divisions.

Sufficient observations in culture 971 have not yet been made to permit a full understanding of the great amount of variability in nuclear number in embryo sacs above the eight-nucleate level. This type of variability has been observed also in several other composite genera, particularly in Erigeron (cf. Harling, 1951b). In regard to several species of Erigeron, Harling states that in the development of the female gametophyte, one or more of the chalazal nuclei "strike" (i.e., cease dividing while others continue). Nuclear fusions in the embryo sacs of some plants, including Erigeron, have been noted. However, nothing which might indicate nuclear fusion has been observed in any of the material of Townsendia. Thus, it seems plausible that the variable number of nuclei in the embryo sac in culture 971 results from the "strike" of some of the chalazal nuclei at either or both of the postmeiotic divisions.

A statement is necessary in regard to the rather large amount of aborted and undetermined ovules of culture 971 (recorded in Table II). Some of this material was fixed after two or three nights with frosts, and it appears probable that freezing had adverse affects. Material from the same plant fixed before the frosts was not affected.

Townsendia incana (cultures 5 and 802). No material at a stage later than the beginning of female gametophyte development has been available from these populations. Fewer meiotic stages, also, were examined in these ovules than in those of culture 971, but no significant differences in meiosis in the three populations were noted. A difference is apparent at the tetrad stage. however. In cultures 5 and 802 a wall and a space regularly separate the micropylar nucleus from the other three members of the tetrad (Plate VI, fig. 4). A sufficient number of later stages has not been seen to permit conclusions regarding further development of the embryo sac in these two populations, but the female gametophyte is initially three-nucleate from the development of the three chalazal megaspore nuclei and the abortion of the micropylar nucleus.

A difference in genetic constitution probably is responsible

## TABLE II.

Comparative classification of ovule development in five sexually reproducing populations of three species of Townsendia. ${ }^{1}$


[^27]for the differences in tetrad-wall formation between culture 971 and the other two populations of T. incana. However, since the plants were grown in a different environment, and the buds were fixed at different seasons, environmental factors cannot be entirely disregarded as a possible influence. Positive conclusions about this type of variation will require further study.

Townsendia grandiflora (culture 39). One collection of this species was studied. The meiotic prophase is similar in all details to that described for culture 971 of T. incana. The tetrads, like those of cultures 5 and 802 of T. incana, are characterized by having a wall regularly formed between the micropylar and submicropylar megaspore nuclei. The micropylar megaspore nucleus also is separated by a considerable distance from the other three nuclei.

The series of developmental stages examined in T. grandiflora is complete enough to indicate that embryo sac development in this population is usually trisporic. Harling designated some of his Erigeron material as pseudotrisporic when, from the fournucleate coenomegaspore, only three of the tetrad nuclei gave rise to the embryo sac and the other nucleus degenerated. In addition to Erigeron, this condition has been recorded also by Harling in Chrysanthemum (1951a), Anthemis (1950), and Matricaria (1951a) and by Fagerlind (1941) in Chrysanthemum. Mauritzon (1933) has reported for the crassulaceous species Aldasorea (Aeonium) guttata (nom. nud.?) that sometimes a single megaspore nucleus was separated from the other three of the tetrad by a wall. Subsequent embryo sac development could therefore be monosporic or trisporic, and Mauritzon has illustrated a 12 -nucleate embryo sac (p. 28, fig. 9G) presumably of trisporic origin. Unfortunately his culture was lost before adequate developmental stages were obtained and before voucher specimens were prepared; thus, some doubt is left as to the identity of this material. In Townsendia grandiflora and in other populations of this genus which have a wall separating one nucleus of the tetrad from the other three, embryo sac development is trisporic. Thus, Townsendia may well be the first genus in which true trisporic embryo sac development is adequately documented.

In culture 39 of $T$. grandiflora, trisporic development is most frequent, but bisporic or pseudobisporic development may occur infrequently. Occasional two-nucleate embryo sacs have been observed. It seems probable that the initial development was
trisporic; then one of the three nuclei of the female gametophyte disintegrated at about the time the other two began enlarging previous to their first mitotic division. The nucleus nearest the chalazal end of the embryo sac frequently is weak (Plate IX, fig. 1). Thus, these two-nucleate embryo sacs probably are the result of pseudobisporic development because no tetrads were observed which exhibited wall formation anywhere but between the micropylar and submicropylar megaspore nuclei.

The occurrence of five-nucleate embryo sacs in T. grandiflora seems to be the result of a "strike" by the chalazal-most nucleus at the first post-meiotic division. An eight-nucleate embryo sac observed in this material had already reached the morphological organization stage; presumably it was produced by pseudobisporic development and two subsequent series of mitotic divisions.

The antipodal cells observed in T. grandiflora were onenucleate. Disintegration of these begins soon after morphological organization of the 12 -nucleate embryo sac. When disintegration has commenced, it becomes very difficult to determine the total nuclear number of the female gametophyte. Later stages are "sesignated according to the position of the polar nuclei. (The "unfused polars" stage is earlier than the "fusing polars" stage.)

Townsendia montana var. montana (culture 35). A considerable range of developmental stages in this population has been available in the present study. The stages of prophase differ in no visible manner from those described under T. incana (culture 971). The cell plate, an uncommonly seen feature in megasporogenesis, was observed in one dyad (Plate VII, fig. 1). This is the only instance in the examination of sexual material that a cell plate has been found in a dyad. Apparently this structure has a very short duration, and no wall formation follows its occurrence.

Tetrads with no walls between the nuclei (four-nucleate coenomegaspores) and tetrads with a cell wall between the micropylar and submicropylar megaspore nuclei were encountered in about equal numbers in this material. The micropylar nucleus is always separated by a considerable distance from the other three nuclei, whether or not a wall is present in this position. Since a larger number of four-nucleate than three-nucleate embryo sacs was found, it seems probable that all four megaspore nuclei may sometimes germinate to form the four-nucleate female gametophyte, even though a wall separates one nucleus from the
other three. A few cases were observed in which this wall between the micropylar and submicropylar nuclei appeared to be disintegrating.

Eight-nucleate embryo sacs observed in the preparations of T. montana are the result of one post-meiotic division of the four megaspore nuclei and are not ready for morphological organization until another mitotic division occurs. The preponderance of 12 -nucleate embryo sacs over those with 16 nuclei may indicate trisporic development or may result from a "strike" of the four nuclei at the chalazal end of the embryo sac at the second postmeiotic division. The 14 - and 15 -nucleate embryo sacs indicate a strike of one or two of these chalazal nuclei. The occurrence of 10 - and 11 -nucleate embryo sacs might be the result of the disintegration of some of the nuclei at the chalazal end of the embryo sac between the time of the first and second post-meiotic divisions.

In this population of T. montana the antipodal cells are better developed than in any other material of Townsendia yet examined. Ordinarily in T. montana there are three large antipodal cells (Plate XI, fig. 1) and four small ones at the extreme chalazal end of the embryo sac. All the antipodal cells are uninucleate.

Since conditions at or after anthesis in sexual material are important as a standard of comparison with the apomictic forms of Townsendia at corresponding developmental stages, a number of ovules of T. montana at these stages were examined. It should be noted that no stages later than embryo sacs with eggs and fusing polar nuclei have been found in pre-anthesis material from any of the sexual forms.

In material collected at and past anthesis only three instances of developmental stages earlier than the stage with polar nuclei beginning to fuse were encountered. One sure example of fused polar nuclei was found and six probable cases were noted. Apparently fusion is completed at about the time of fertilization since one embryo sac was observed in which the egg was still undivided but the primary endosperm nucleus was at telophase. In ovules from florets slightly past anthesis either an embryo and endosperm are present, or the interior of the ovule is in the process of disintegration. The latter condition probably results if fertilization does not occur.

## The female reproductive phase in apomictic plants

Most of the investigation of apomixis in Townsendia has been concentrated on T. incana. Culture 6 of this species, which has


Pran V. Photomacrographe of longitudimal sectoms of soung onule in Tonensendia. Fig. 1. An incompletely inverted ovale of apomatic, triploid $T$. incana $(\times 220)$. The nucellar epidermis surrounding the single archesporial cell has not been completels inclosed by osergrowth of the integument. Fig. 2. Barly prophase of meiosis in apomictic, triploid $T$. incana $(X f(1))$. This part of meiosis in the apomets differs in no visible way from the corresponding stage in sexual plants. It is not possible we determine in ths preparation whether ar not the chromaton thread are pared. Fig. 3. Early prophase of meiosis in sexual diploid T. incana ( $X$ foll ) Synezesis apparently results during fixation at this stage. Fig. H. Barly prophate of meiosis in apomictic, triploid T. incana $(X 400)$. Synezesis is a prophase feature in both sexual and apomictic material.


Plate VI. Photomicrographs of longitudinal sections of ovules in Tounsendia (all $\times 400$ ). Fig. 1. Metaphase I with clumped and scattered univalents in apomictic, triploid T. incana. Fig. 2. Anaphase II in apomictic, triploid T. incana with three extra groups of chromosomes excluded from the two main nuclei at anaphase I. Fig. 3. A tetrad of megaspore nuclei (t-nucleate conenomegaspore) in apomictic, triploid $T$. incana. Fig. 4. A tetrad of megaspore nuclei with the nucleus at the micropylar end of the tetrad separated by a space and a wall from the other three megaspore nuclei, in sexual, diploid T. incana. Embryo sac development is trisporic from tetrads of this type.


Plate VII. Photomicrographs of longitudinal sections of ovules and owaries in Townsendia. Fig. 1. Dyad of sexual, diploid T. montand var. montana, showing a cell plate $(\times 400)$. Fig. 2. 1)yad of sexual, diploid T. incana, without cell plate ( $\times 400$ ). This is the most frequently encountered type of dyad in sexual material. Fig. 3. Dyad of apomictic, polyploid $T$. Rothrockii $(\times 400)$. This is the only population of Townsendia known to have walls separating the dyad nuclei. Fig. 4. Ovule and ovary at the dyad stage in apomictic, triploid $T$. incana $(\times 185)$.


Plate VIII. Photomicrographs of longitudinal sections of ovules in apomictic, triploid T. incana (all $\times 400$ ). Fig. 1. Dyad. Fig. 2. A very young 2 -nucleate embryo sac which has developed from an unreduced dyad. At the time of fixation the nucellar epidermis was in the process of disintegration and the embryo sac was expanding, filling the cavity formed by the overgrowth of the integument. Fig. 3. A 2 -nucleate embryo sac with the nuclei at prophase. Fig. 4. A young 4 -nucleate embryo sac. This embryo sac is the result of tetrasporic development of a 4 -nucleate coenomegaspore.


Plate IX. Photomicrographs of longitudinal sections of ovules in Tounsendia (all $\times 400$ ). Fig. 1. A very young 3 -nucleate embryo sac, the result of trisporic development, in sexual, diploid $T$. grandiflora. At the time of fixation the nucellar epidermis was in the process of disintegration. The remnants of the fourth megaspore nucleus and part of the nucellar epidermis are evident at the micropylar end of this embryo sac. Fig. 2. A 3 -nucleate embryo sac which has resulted from trisporic development in sexual, diploid $T$. grandiflora. Fig. 3. A 4 -nucleate embryo sac which has resulted from tetrasporic development in sexual, diploid T. montana. Fig. 4. A 6 -nucleate embryo sac in sexual, diploid T. grandiflora. The six nuclei are the result of one mitotic division-series in a 3 -nucleate embryo sac of the type shown in fig. 2.


Plate X. Photomicrographs of longitudinal sections of embryo sacs in apomictic, triploid T. incana (all $\times 400$ ). Fig. 1. A 4 -nucleate embryo sac with all four nuclei at metaphase. Figs. 2-4. The egg cell (fig. 2), the unfused polars (fig. 3), and the synergids (fig. 4) in serial sections through a single embryo sac. At this stage the antipodals have already disintegrated.


Plate XI. Photomicrographs of longitudenal sections of embryo sace in Tounsendia (all $\times 400$ ). Fig. 1. A 12 -nucleate embryo sate in sexual, diploid $T$. montana var. montana. Three large antipental cells are shown in the upper portion of this figure; four smaller antipostal cells farther toward the chalazal end were excluded in this figure. Townsendia montand is the only species of the genus presently known to have well-developed antipodal cells. The egg cell was included in an adjacent section. The two conical-shaped synergid cells are immediately below the fusing polar nuclei in this figure. Fig. 2. The egg and fusing polar nuclei in apomictic, triploid $T$. incana. Portions of the synergids are at the bottom of the figure. Figs. 3-4. Adjacent sections of an embryo sac in apomictic, triploid T. incana. The 2-nucleate proembryo (fig. 3) is associated with fusing polar nuclei (fig. 4).


Plate XII. Photomicrographs of longitudinal sections of embryo sacs, with embryos, in apomictic, triploid Townsendia incana. Figs. 1-4 from florets at pre-anthesis stages. Fig. I. A 4 -celled embryo $(\times 350)$ accompanied (in another section) by fusing polar nuclei similar to those shown in Plate XI, fig. 4. One of the intact, conicalshaped synergid cells is at the lower right of the embryo. Figs. 2-3. Adjacent sections in an embryo sac showing an 8 -nucleate proembryo, accompanied by 4 -nucleate endosperm (three of the endosperm nuclei were not included in this section) ( $\times 350$ ). At the time of fixation, the three apical nuclei of this embryo had not been separated by walls. Fig. 4. A non-median section showing 3 of the 8 endosperm nuclei in this embryo sac at metaphase ( $\times 350$ ). Fig. 5. A portion of the ovary and its contents from a floret just past anthesis ( $\times 90$ ).
been used most extensively, was grouped into five series according to the stages selected for examination and the conditions under which it was grown. Series I-IV were grown in Cambridge, Massachusetts and fixed in November, 1955. Series V was grown in Pullman, Washington and fixed in the spring of 1955.

Townsendia incana (culture 6-I). The material of this series was taken from five plants. The developmental stages of the florets ranged from pre-meiotic to pre-anthesis. Early prophase of megasporogenesis is similar in appearance in sexual and apomictic forms (Plate V, figs. 2 and 4). Synezesis is as frequent in the early prophase stages in the apomicts as in the sexual material. Diakinesis is the earliest stage at which differences between the sexual and the apomictic types become apparent. At this stage both megaspore mother cells with all the chromosomes unpaired and those with some pairing have been observed. In sectioned material it is often difficult to determine how many chromosomes are present and whether or not they are paired. Accurate appraisals are possible only in very good preparations.

Metaphase configurations with all univalent chromosomes and those with some of the chromosomes paired have been found in this apomictic form. A metaphase figure with univalents scattered along the spindle is shown in Plate 6, fig. 1. Fagerlind (1946, 1947a, 1947b, 1947c), in his publications on the mechanism of apomictic megasporogenesis, has considered the scatteredunivalent configuration to be a stage just preceding formation of the metaphase restitution nucleus. Interpretation of this feature in megasporogenesis in Townsendia is not attempted at this time. Smears of anthers at the proper stages are more amenable to interpretation of the mechanism of the apomictic meiosis, and the problem is more fully considered under the section in this paper on the male reproductive phase.

Megaspore tetrads are rare in this apomictic population of T. incana (cf. Table IV). The most normal-appearing tetrad which has yet been found is shown in Plate VI, fig. 3. It should be noted that no walls separate the megaspore nuclei. When reduction occurs, embryo sac development is tetrasporic (Plate VIII, fig. 4). Tetrads indicate reduction in the chromosome number. This fact is evident from the study of microsporogenesis in Townsendia. In this triploid, apomictic material, nuclei with a reduced chromosome number probably cannot function in the production of new embryos. It appears improbable that the few eggs which might develop with the reduced chromosome number would be fertilized by functional sperms, especially since the

TABLE III.
Comparative classification of ovule development in six apomictically reproducing populations of three species of Townsendia. ${ }^{1}$

| Developmental stage in ovule | Numbers of ovules observed in the populations (cultures) |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $6-1 a^{2}$ | 6-II | 6-Va | 17-I | 875 | 8 | 27 | 798 |
| Archesporial cell | - | 11 | - | - | 2 | 2 | - | 6 |
| Early prophase | 14 | 53 | 10 | 28 | 5 | 5 | 2 | 22 |
| Diakinesis (all univalents) .... | 1 |  |  | 1 | - |  |  |  |
| Diakinesis (some pairing) ........ | - | 1 | - | - | - | - |  |  |
| Diakinesis (pairing not det.) | - | 3 | 6 | 9 | 4 | 1 | 3 | 3 |
| Prometaphase (all univalents) | 2 | - | - | - | 1 |  |  |  |
| Metaphase I (all univalents) ... |  | 1 | - | - | - | 2 | - |  |
| Metaphase I (some pairing) ... | 2 | 1 | - | - | - |  | - |  |
| Metaphase I (pairing not det.) | - | 1 | 3 | 4 | - | 1 | 2 | 1 |
| Anaphase I ............................. | - | - | 1 | 5 | 1 |  |  |  |
| Dyad | 96 | 47 | 23 | 69 | 32 | 64 | 8 | 9 |
| Dyad with micronuclei | 5 | , | 2 | - | - |  |  | - |
| Dyad ? .... | 3 | - | - | - | - | - | - | - |
| Metaphase II | 1 | - | - | - | - | - | - | - |
| Anaphase II | 1 | 1 | - | - | - | - | - |  |
| Tetrad | 4 | 5 | - | 2 | - | 4 | - | 11 |
| Tetrad with micronuclei | 2 | - | - | 1 | - |  | - |  |
| Double tetrad | 1 | - | - | - | - | 1 | - | - |
| Tetrad ? | 2 | 1 | - | - | - | - | - | - |
| 1 -nucleate embryo sac | 6 | - | - | - | - | - | - | - |
| 1 -nucleate " ? | 12 | - | - | - |  | - | - |  |
| 2-nucleate " " ........... | 110 | 30 | 7 | 12 | 55 | 1 | 14 | - |
| 2-nucleate " "............ (with micronuclei) |  | - | - | 1 |  | - | - | - |
| 2-nucleate embryo sac ? | 19 | 3 | - | - | - | - | - | - |
| 3 -nucleate " " | 1 | - | - | - | 1 | - | - | - |
| 4-nucleate " | 38 | 4 | - | - | 3 | - | 8 | - |
| 4-nucleate " " | 8 | $\cdots$ | - | - | - | - | 1 | - |
| 6 -nucleate " " | 1 | - | - | - | - | - | - | - |
| 8 -nucleate " " | 11 | - | - | - | - | - | - |  |
| 8 -nucleate " " ? | 2 | - | - | - | - | - | - | - |
| 9 -nucleate " " | 1 | - | - | - | - | - | - |  |
| Egg and unfused polars | 83 | - | - | - | - | - | 11 |  |
| Egg and unfused polars ? ........ | 11 | - | - | - | - | - | - |  |
| Egg and fusing polars . | 22 | - | - | - | - | - | - |  |
| Egg and fusing polars ? | 2 | - | - | - | - | - | 1 | - |
| Embryo and fusing polars | 1 | - | - | - | - | - | - |  |
| Embryo and endosperm | 2 | - | - | - | - | - | - |  |
| Embryo and endosperm ? ... | 1 |  |  | - | - | - | - | - |
| Abortive | 73 | 3 |  | 1 | - | 4 | 1 |  |
| Not determined | 100 | 8 | 4 | 2 | 2 | 17 | 2 | 8 |
| Total | 636 | 174 | 56 | 135 | 106 | 102 | 53 | 61 |

[^28]pollen develops in an anomalous manner by the formation of a wall around the four members of the microspore tetrad.

The consequence of much chromosomal pairing in apomictic megasporogenesis probably is sterility. Asexual reproduction is possible only when all or nearly all the chromosomes occur as univalents. One expression of apomictic "meiotic irregularity" as a result of pairing in an apomict is shown in Plate VI, fig. 2. In this photograph of anaphase II, three small groups of dividing chromosomes may be seen in addition to the two main dividing groups. Each of the five groups of chromosomes has its own spindle mechanism. The three small groups of chromosomes would probably have become micronuclei. Both dyads and tetrads with micronuclei have been observed. Such irregularities must often prevent the formation of viable seeds, but the variable chromosome number in this apomictic population suggests that slightly aberrant chromosome races may survive.

The great abundance of dyads in this apomictic form in contrast to their rarity in sexual material (cf. Table IV) is one criterion of apomixis. In addition to the difference in numerical ratio of dyads to tetrads between apomictic and sexual forms, there are considerable morphological differences in the dyads of the two types. The dyad stage of the apomicts is one of long duration during which nuclear-size increase, vacuolation, and a gradual breaking down of the nucellus occur. The dyad stage of the apomicts corresponds to the entire period in sexual forms from the dyad to the early female gametophyte.

The development of dyads directly into two-nucleate embryo sacs was demonstrated by Holmgren (1919) in apomictic forms of two species of Erigeron. Townsendia apparently is the only other genus in which unreduced female gametophytes are now known to develop regularly in the same manner. It should be noted that the process by which a dyad becomes a twonucleate embryo sac is a gradual one with no very sharply marked steps. Therefore, assignment of the material at intermediate stages to either the dyad or the two-nucleate categories is sometimes difficult. In this study an arbitrary distinction, based on the condition of the nucellar epidermis, has been made between the two stages. When this structure is intact the material is considered to be at the dyad stage. When the nucellar epidermis disintegrates, the two-nucleate embryo sac stage has been reached.

A few uninucleate embryo sacs have been found in this apomictic form of T. incana. They are rare, however, and the present
material is insufficient to permit an interpretation of their significance. Three- and six-nucleate embryo sacs present in this culture could be the result of trisporic embryo sac development. Most of the four-nucleate embryo sacs (Table III) are merely in intermediate stages between two- and eight-nucleate female gametophytes. However, a few are the direct result of tetrasporic development from the megaspore tetrad. A four-nucleate embryo sac of the former type is shown in Plate $\mathbf{X}$, fig. 1. One of the latter type is shown in Plate VIII, fig. 4.

The eight-nucleate stage of the embryo sac is short. The antipodal nuclei disintegrate almost as soon as they are formed. Hence, eight-nucleate embryo sacs are found only at the earliest stages of morphological organization of the female gametophyte.

When the eight-nucleate stage is reached and the antipodals disintegrate, further developmental processes can no longer be designated as the eight-nucleate stage. Only five nuclei, the egg, the two synergids, and the two polars, are involved in subsequent developmental processes. But two major phases are distinguishable during morphological organization of the female gametophyte. Before the polar nuclei have come together, a stage "unfused polars" may be designated (Plate X, figs. 2, 3, and 4 and Tables III and IV ). After they have come together, the stage "polars fusing" has been reached (Plate XI, fig. 2 and Tables III and V). Some less conspicuous changes of the egg and synergids occur during the migration and fusing process of the polar nuclei, but these changes are not obvious enough to use in designating developmental stages. In the apomicts the polar fusion process is not completed until after the first division of the egg or a few subsequent nuclear divisions in the proembryo (Plate XI, figs. 3 and 4 and Table VI).

The fairly large amount of abortive and undetermined material in culture 6-I should be noted. This material was fixed after three nights with frost. Freezing may have adverse affects on megasporogenesis and female gametophyte development in apomictic as well as in sexual plants of T. incana. Abortion in sexual material, probably caused by freezing weather, was noted previously.

Townsendia incana (culture 6-II). An examination of megasporogenesis in a single plant ( 6 HF ) of $T$. incana was made as a check against the other investigations which employed several plants. It is evident from this examination that both "normal" apomictic development and meiotic irregularities indicating features "abnormal" in apomictic reproduction may occur in a single

TABLE IV.
Megasporogenesis in sexual and apomictic populatons of Tou'nsendia.

| Taxon | Culture ${ }^{1}$ | Chromo some no., $2 n$ | No. of ovules examined | Percentages of ovules with sporogenous tissue at the fol lowing stages |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | Arche- <br> sporial cells | Dividin megaspo mother | dyads <br> $1 s$ | tetrads |
| Sexual |  |  |  |  |  |  |  |
| T. incana | 971 | 18 | 55 | 3.6 | 16.4 | 1.8 | 78.2 |
| T. incana | 5 | 18 | 97 | - | 7.2 | 2.1 | 90.7 |
| T. incana | 802 | 18 | 58 | 1.7 | 19.0 | 3.5 | 75.8 |
| T. montana | 35 | 18 | 55 | 1.8 | 30.9 | 10.9 | 56.4 |
| var. montana |  |  |  |  |  |  |  |
| T. grandiflora | 39 | 18 | 25 | - | 16.0 | 4.0 | 80.0 |
| Apomictic |  |  |  |  |  |  |  |
| $T$. incana | 6-Ia | 28 | 135 | - | 16.3 | 77.0 | 6.7 |
| T. incana | 6-1I | 28 | 126 | 8.7 | 48.5 | 38.1 | 4.7 |
| T. incana | 6-Va | 28 | 45 | - | 44.4 | 55.6 | - |
| T. incana | 17-I | ca. 30 | 119 | - | 39.5 | 58.0 | 2.5 |
| T. incana | 875 | 36 | 45 | 4.5 | 24.5 | 71.0 |  |
| T. Parryi | 8 | 36 | 80 | 2.5 | 11.3 | 80.0 | 7.2 |
| T. Parryi | 27 | 36 | 15 | - | 46.7 | 53.3 | - |
| T. Rothrockii | 798 | ? | 52 | 11.5 | 50.0 | 17.3 | 21.2 |

${ }^{1}$ Explanation of the culture-series symbels will be found in the text, pp. 28-50.
plant. Diakinesis and metaphase figures were found in which some of the chromosomes were paired, and one metaphase was observed in which all the chromosomes were unpaired. The dyadtetrad numerical ratio (Table IV) in this plant approximates that of the other plants from culture 6. Micronuclei were found associated with a dyad in one preparation of this material, and the same feature was observed several times in the plants of the mass collection. The study of a single plant suggests, therefore, that all the deviations from the usual apomictic reproductive cyele in the mass collection (culture 6-I) did not come from a single plant. Rather, in this apomictic population, various plants may have irregularities which result primarily from occasional (hromosome pairing. Total univalent formation, on the other hand, permits a regular apomictic "meiosis."

Townsendia incana (culture 6-III). The achenes used in this series were from florets in which the corollas had not opened. More advanced florets of the same heads had already reached anthesis. The use of heads with both open and unopen florets made it possible to obtain achenes from florets which would have very soon reached anthesis. The florets which had already opened on these heads were put in the next series to be discussed.

Culture 6-III provides strong direct evidence for apomixis in

Townsendia. A very high proportion of precociously developed embryos were found in the ovules of these florets with unopened corollas (Table V). Some details of early embryo development have been listed in Table VI. These data indicate that the division of the egg ordinarily precedes the completion of the fusion process of the polar nuclei. In angiosperms the division of the primary endosperm nucleus normally occurs before the division of the zygote. This is not true in apomictic T. incana. Holmgren (1919) indicated that as far as he could discern, embryo and endosperm development proceeded concurrently in apomictic Erigeron. It may be found, however, that the same division sequence, with embryo development before that of the endosperm, will be found to be similar in apomicts of Erigeron and Townsendia.

When the process of fusion of the polar nuclei is completed the first ensuing division apparently occurs immediately. In this material no completely fused polars, i.e., primary endosperm nuclei, were found. Wall formation in the endosperm probably occurs after the first or second mitotic division series. The nuclear number in the embryo at the earliest stages of development exceeds that of the endosperm, but at slightly later stages the nuclear number of the endosperm is greater than that of the embryo. Very little endosperm remains when the embryo has attained its maximum size. Embryo development appears to be in accordance with the asterad type. The early development of the embryo must be recorded by nuclear number rather than by cell number because wall formation does not always immediately follow mitosis (cf. Plate XII, fig. 3). Mitotic divisions in the young embryo are not synchronous, but those in the early development of the endosperm are. The latter feature is illustrated in Plate XII, fig. 4.

Townsendia incana (culture 6-IV). This series was made from opened florets on the same heads from which unopened florets for the last series were taken. In most of the material at this stage of development the embryos and endosperm had attained a fairly advanced degree of development (Plate XII, fig. 5). The few ovules without embryos and endosperm already developed may have resulted from megaspores with the reduced chromosome number and probably would have aborted at slightly later stages. The ovules with embryos without endosperm and those with endosperm without embryos were rare and abnormal.

Townsendia incana (culture 6-V). As a check on the reproductive behavior of this apomictic population of T. incana in a different environment, material grown in Pullman, Washington and fixed during spring rather than fall growing conditions has

TABLE V.
Classification of ovule development just before anthesis and at or just after anthesis in apomictic populations of two species of Townsendia.

| Taxon | Culture |  | Percentages of contents listed |  | embryo <br> below | sacs with the |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | No. of embryo sacs examined | Egg and fusing polars | Embryo and fusing polars | Embryo and endo sperm | Abortive | $\begin{aligned} & \text { Not } \\ & \text { deter- } \\ & \text { mined } \end{aligned}$ |
| Just before anthesis |  |  |  |  |  |  |  |
| T. incana | 6-III | 202 | 11.9 | 6.9 | 68.3 | 9.9 | 3.0 |
| T. incana | $6-\mathrm{Vb}$ | 15 | 26.6 | - | 46.8 |  | 26.6 |
| T. incana | 17-II | 8 | 12.5 | - | 25.0 | 12.5 | 50.0 |
| T. condensata | 47 | 32 | 6.3 | 3.1 | 59.3 | 6.3 | 25.0 |
| At or just after anthesis |  |  |  |  |  |  |  |
| T. incana | 6-IV | 144 | 2.1 | 1.4 | 82.6 | 10.4 | 3.5 |
| T. incana | 6 -Vc | 22 | - | - | 90.9 | 9.1 |  |

TABLE VI.
Comparative developmental stages of embryos and endosperm just before anthesis in apomictic Townsendia incana, Culture 6-1II. ${ }^{1}$

| Developmental stage ${ }^{3}$ | Number observed |
| :---: | :---: |
| 2-nucleate embryo and fusing polars | 11 |
| 4 -nucleate embryo and fusing polars | 3 |
| 2 -nucleate embryo and 2-nucleate endosperm | 1 |
| 4-nucleate embryo and 4-nucleate endosperm | 2 |
| 4-nucleate embryo and 16-nucleate endosperm | 1 |
| 5-nucleate embryo and 4-nucleate endosperm .. | . 1 |
| 7 -nucleate embryo and 4-nucleate endosperm | 1 |
| 8-nucleate embryo and 4-nucleate endosperm .. | 1 |
| Embryo and endosperm at various later stages | 131 |
| Total ......................................................................... | 152 |

[^29]been utilized. The series was divided into the subseries $a, b$, and c according to developmental stages. A comparison of the data regarding the material grown in the different environments (cul-ture-series 6-I, 6-II, 6-III, and 6-IV with 6-V in Tables III, IV, and V) suggests that environmental factors cause no significant differences in apomictic reproduction in a single biotype.

Townsendia incana (cultures 17 and 975 ). Apomictic populations from the northern portion, the southern portion, and about the middle of the range of the species were used in this study to determine what intraspecific variation occurs in apomictic reproduction. A comparison of the data (Tables III and IV) from these different populations of apomictic T. incana suggests
that no major and very few minor differences in the apomictic process occur between populations. Culture 17 was divided into two series, I and II, according to developmental stage, for convenience in tabulation.

Townsendia Parryi (cultures 8 and 27 ). Most of the study of apomixis in Townsendia has been made in material with a triploid or triploid-derived chromosome complement, but it was considered essential also to employ some material with the tetraploid chromosome number. Therefore, investigations have been made in two tetraploid populations of T. Parryi. The apomictic process in these plants is very similar to that observed in triploid and tetraploid populations of T. incana. In T. Parryi, as in T. incana, the number of univalent chromosomes at diakinesis or metaphase in megasporogenesis is difficult to determine, but numbers approaching 36 may be counted. A double tetrad in one ovule of this material may have resulted from the functioning of two archesporial cells instead of the usual single cell. Some of the integumentary cells in these ovules have a more sporogenous appearance than those in any other Townsendia species which has been examined.

Townsendia Rothrockii (culture 798). Microsporogenesis in this population is so irregular that no approximation of the chromosome number has been obtained (seeds for root-tip chromosome counts were not available). Most features of megasporogenesis in these plants are similar to those in apomicts of the other species. However, the dyads and tetrads are somewhat different from those encountered in other material. The dyads are characterized by a wall between the two nuclei. No other population of Townsendia is known which has wall formation between the dyad nuclei. Wall formation in the megaspore tetrads of this species also is peculiar. The nuclei of the tetrad have been numbered arbitrarily $1,2,3$, and 4 , in order, proceeding from the micropylar to the chalazal end of the ovule. A single wall has been found in some tetrads between nuclei 1 and 2, in some between 2 and 3, and in some between 3 and 4. In other instances two walls are present, between nuclei 1 and 2 and between 3 and 4. For an apomictic population, the percentage of tetrads formed by these plants is very high. It seems possible that the structures which appear to be tetrads actually are not. Instead, two adjacent archesporial cells may have given rise to dyads and these merely appear to be tetrads because of their adjacent position. More material must be examined before this problem can be satisfactorily solved.

Townsendia condensata (culture 47). A very limited amount of this material was available. The present investigation has demonstrated only that embryos and endosperm are formed in ovules before the corollas open, and evidence of apomixis in the population is thereby obtained.

## THE CAUSAL ASPECTS OF APOMIXIS IN TOWNSENDIA

No data on the genetic control of apomixis in Townsendia have been obtained. Therefore, the only information on the causes of apomixis in this genus must now come from inference.

The special conditions under which apomixis is expressed in Townsendia are suggested by the geographical distribution patterns of the sexual and apomictic forms. Without exception, the apomicts of Tounsendia are concentrated at the higher elevations and higher latitudes relative to the total range of the species in which they occur. It seems scarcely deniable that a cold, rigorous climate is a very important factor in permitting the expression of apomixis in Townsendia.

A correlation is found in Townsendia (as apparently in all groups with apomicts) of the perennial habit and apomixis. This correlation is shown in Chart 1. Gustafsson (1948) and Stebbins (1950) have reviewed the current ideas on the relationship of the perennial habit with polyploidy. Stebbins' interpretation from the available evidence is that the longer growth period of perennials, compared with annuals or biennials, permits a longer time during which a sterility "bottleneck" may be overcome after the initial polyploidization. No experimental attempts have been made to induce apomixis in plants of Townsendia by increasing the chromosome number, and it seems futile, therefore, to speculate on the importance of the increase in the chromosome number per se in permitting apomixis. However, the lack of correlation of apomixis with hybridization in the genus and the apparently frequent independent recurrence of apomixis in many populations suggest that little more than polyploidy may be required to release the potential apomictic mechanisms. If apomixis is immediately expressable when the polyploid state has been attained, the perennial habit would hardly be necessary for the prevention of a sterility "bottleneck."

It is generally recognized that the perennial habit, rather than the annual or biennial habit, is correlated with cold, rigorous climates. Apomixis in Townsendia also is associated with this type of climate. Perhaps the correlation of apomixis in Townsendia with the perennial habit is merely coincidental in that both
features are more or less independently correlated with a cold, rigorous environment. The two features cannot be entirely independent, of course, because apomixis must be of some adaptive advantage to the plants in which it occurs. However, its origin could be merely incidental to the perennial habit. The fact that apomixis occurs in some biennial plants of Townsendia as well as in perennial plants supports to some extent this view.

## Townsendia as an Agamic Complex

From the investigation of Babcock and Stebbins (1938), the agamic complex (a term defined by these authors) in the American species of Crepis has become well known. Their work may therefore serve as a standard of comparison for evaluation of the agamic complex in Townsendia. Stebbins (1950) has pointed out that from the systematic and phytogeographic points of view, Crepis is easier to understand than most of the other known agamic complexes. American Crepis is confined to one geographic and climatic zone, and is so recent that the diploid species which gave rise to the polyploids are still growing in the same area. These features are exactly duplicated in Townsendia, but similarities extend little farther.

The first difference apparent between the two genera is that their mechanism of apomixis is not the same. Reduction is avoided in Crepis by apospory. In Townsendia diplospory prevails.

A striking difference apparent between Crepis and Townsendia is in the role of hybridization with apomixis. In Crepis, Babcock and Stebbins (1938, p. 45) state: ". . . these diploids are completely distinct from one another in their morphological characteristics, and are completely isolated from one another genetically." The experimental and comparative morphological studies in Townsendia clearly indicate that diploid, sexual plants of several of the species of Townsendia will hybridize and possibly no great reduction in the fertility of the hybrids results.

In Townsendia it appears that hybridization may occur entirely independent of polyploidy. No polyploid system is necessary to permit the exchange of genes between the species. Likewise, in Townsendia hybridization seems to be an entirely unnecessary feature for setting in action apomictic reproduction. In spite of frequent hybridization between the diploid forms of the species of Townsendia there are as many, if not more, suspected populations of autoploid apomicts as alloploid apomicts. All of the presently known apomicts of T. Rothrockii, T. scapigera,
T. strigosa, and T. grandiflora are apparently autoploid. Townsendia Parryi and T. Hookeri have a very high percentage of autoploid apomicts, and even T. leptotes, T. exscapa, and T. montana seem to have numerous autoploid apomicts. In none of the species do all of the apomicts appear to be alloploid. Thus, apomixis in Townsendia, apparently unlike that in Crepis, can be viewed independently from hybridization. The only reason that hybridization appears to be involved in the apomicts of Townsendia is because some of the diploid, hybrid-derived types have become polyploid apomicts. Probably some of the gene recombinations which result from hybridization are more vigorous than the nonhybrid types, and when these are fixed by apomixis they have an advantage over the non-hybrid types and thus become widespread. Otherwise, hybrid apomicts in Townsendia might not even be known.

Another strongly contrasting feature between the apomicts of Crepis and those of Townsendia is that some of the sexual forms of Townsendia which have apomixis are definitely not relict types. Stebbins (1950, p. 400, in quoting Gustafsson's characterization of Hieracium and Taraxacum) has indicated that five of the seven species of Crepis are "depauperate and relict." In only four taxa of Townsendia, T. condensata, T. montana, var. montana, T. Parryi, and T. Rothrockii, do the sexual forms have a very limited and possibly relict distribution. Even T. Parryi probably should not be included in the above group because its sexual forms have both a considerabie geographic range and interpopulation variability. In the other species of Townsendia which have apomixis, the sexual forms have much morphological diversity and often are nearly as widespread as, or even more widespread than, the apomictic forms. Thus, even though the American species of Crepis are similar to the species of Townsendia in occupying a single geographic and climatic realm, and in having the sexual precursors of all the species known, the two agamic complexes have few other common features.

A limited evolutionary future for the apomicts of Townsendia may be postulated, as the embryological data indicate that apomixis is obligate in the genus. The statement by Stebbins ( 1950, p. 417) that agamic complexes are "blind alleys" is probably better applicable to the Townsendia apomicts than to the facultative apomicts of many other genera.

The best evidence that the apomicts of Townsendia have not given rise to any new apomictic forms lies in the fact that no species of the genus is represented only by apomictic types. Sex-
ual precursors of all the apomictic forms are known, which is positive evidence that the apomicts have undergone little if any evolution.

Although their evolutionary future may be limited, the success of the apomicts in colonizing wide areas is evident. Apomixis occurs in 12 of the 21 species of Townsendia; it occurs abundantly in nine species. The geographic range of the apomicts in some of these species exceeds considerably that of the sexual forms. Therefore, apomixis must have potent adaptive advantages.

## Trends of Evolution

## DIVERGENT EVOLUTION

The patterns of speciation in Townsendia seem explainable mainly on a geographic, climatic, and edaphic basis. A correlation of the morphological traits of the taxa of Townsendia with their geographic distributional-patterns makes possible a suggestion of their phylogenetic relationship. A tentative phylogenetic diagram is presented in Chart 1. The center of this diagram may be imagined as the time when diversification in Townsendia began.


APOMIXIS FREQUENT
apomiris infnequent
s APOMEXIS UMKNOWN
Chart 1. Phylogenetic relationships of the species of Townsendia and a summary of the habit and the presence of apomixis in the species.

The present time level is indicated by the terminations of the various lines at the species names. The length of separation of each line from the others is intended to suggest the relative amount of morphological divergence which each species has developed from the others. At the periphery of the diagram the species have been placed, in so far as feasible, closest to the species which their development parallels. The broken line through the center of the figure separates the caulescent from


[^30]the acaulescent types. The relative amount of apomixis in the various species has been indicated.

The phylogenetic relationships of the species on a geographic basis are suggested by Map 1. The arrow-points indicate derived species, and where there are no arrows terminating the lines, the possible derivations are not suggested. The broken lines indicate indistinct relationships between more primitive types.

The extensive climatic variations of the Pleistocene must be acknowledged as important factors in the phylogenetic history of Townsendia. It seems probable that some of the species as they are now known were not in existence during much of the Pleistocene. The high level of correlation of some species with specialized edaphic and climatic conditions suggests that climatic changes could have easily taken their toll of various evolutionary experiments. On the other hand, the relative abundance of Townsendia species now in habitats which were unavailable during the last glacial advance could indicate both the recent evolution of some new types and the ability for rapid migration of some of the older forms.

An understanding of the evolutionary trends in Townsendia requires an understanding of the primitive characteristics in the genus. Townsendia formosa seems to qualify in all respects as the most primitive member. The probable primitive generic characters are outlined in the section on generic relationships.

The species with the greatest morphological similarity to T. formosa is T. eximia. The latter species most conspicuously differs from the former in having a shorter life-span, in developing a branched stem, and in having a taproot rather than a fibrousroot system. These species occur allopatrically in adjacent mountain masses mostly in New Mexico. Townsendia eximia has close relatives on all geographic sides of its range. To the east and north, respectively, are the very close cognates $T$. texensis and T. grandiflora. Townsendia glabella, which occurs only a short distance to the northwest, is similarly closely related to T. eximia.

A continuation of the reduction trend which has produced T. glabella is found a short distance to the north in T. leptotes. These two species occur together in southwestern Colorado, but T. leptotes is more diversified to the north of the range of T. glabella. Differentiation through isolation probably occurred while the two populations were isolated from each other by the mountain masses in western Colorado, and the populations of $T$. leptotes within the range of $T$. glabella in southwestern Colorado are probably recent migrants there.

Populations of the T. leptotes type which migrated to the east side of the Rocky Mountains in Colorado have been geographically isolated there and the resulting evolutionary divergence has produced T. Hookeri. Both of these species are advanced types; one obvious feature indicating their advanced nature is the extreme reduction of the aerial portions of the plant body. It should be noted that the sexual forms of T. Hookeri and T. leptotes are entirely allopatric, but the apomicts of T. Hookeri occur in the range of the sexual forms of T. leptotes. The apomicts of both species have wide geographic ranges.

Speciation from the T. eximia-T. glabella stock can also be traced geographically to the west of the range of that evolutionary complex. Townsendia montana (both varieties) exhibits a fairly close morphological relationship to the T. eximia-T. glabella stock and probably has resulted after geographical isolation in the mountainous areas of central and north-central Utah. Differentiation may have occurred in isolated populations at both high and low elevations; the high-elevation type has become T. montana, while evolution in the populations at lower elevations has resulted in T. mensana.

The evolutionary trends in specialization from a more generalized T. eximia stock have occurred in the mountainous areas to the northeast, north, and northwest of the range of $T$. eximia. Such a pattern is probably attributable mostly to the fact that a large number of habitats suitable for occupancy by Townsendia populations occur in that area. Because of the mountainous terrain, the populations were easily isolated from each other, and climatic changes probably have facilitated the isolation. The divergences apparently have been recent enough that the morphological trends they followed are still evident. Many connecting "links" may not yet have become extinct in spite of numerous Pleistocene climatic fluctuations.

Speciation with a different geographic pattern from that outlined above has had an orientation from the northern rather than from the southern limits of the diversity of the genus. The most primitive member of the northern complex is T. Parryi. One clear trend of specialization away from that species involves $T$. florifer and T. scapigera. The stock which has given rise to T. florifer apparently became adapted to the arid conditions of the Snake River plains and spread from there to the south and west. Townsendia scapigera is apparently a recent segregant from plants in the western portion of the range of $T$. florifer. From the very different climatic conditions which must have prevailed during
the last ice advance in the area which $T$. florifer and $T$. scapigera now occupy, it must be inferred that these two species have had a recent origin. Townsendia Parryi, their closest relative, is in a geographic position which further indicates that this evolution must have been recent. The geographic trend in evolutionary specialization along this line is from the northeast in Montana to the southwest in Nevada. It can best be interpreted as a morphological reduction series which occurred only in one direction. The advanced forms probably have spread since the last glaciation into more arid regions from an area relatively near the present range of T. Parryi.

A different evolutionary trend from T. Parryi stock appears to have occurred in a southeastern direction from the present range of that species. Townsendia condensata and T. spathulata are the specialized members along this line of development. They appear to have become strongly adapted to some of the peculiar edaphic situations of western Wyoming. Townsendia condensata may be a relict type of a former colder and more moist period, and it is now represented mostly by alpine apomicts. Edaphically, T. spathulata is one of the most highly specialized species of Townsendia. Its unusual habitat requirements probably are a reflection of its reduced morphological features. Very likely it could not withstand the competition from larger plants on sites more than sparsely vegetated.

Part of the evolutionary line which may have diverged from a T. Parryi prototype is not so closely related to that complex as the two trends just outlined. However, the ancestral forms which gave rise to $T$. strigosa and $T$. incana probably occupied the Colorado Plateau and Green River basin area and may have been somewhat similar to T. Parryi. The T. strigosa-T. incana stock probably migrated into the central highlands of Mexico and, with isolation, T. mexicana has arisen. The separation of T. strigosa and T. annua into distinct taxa appears to have been a recent occurrence. Townsendia incana and T. Fendleri similarly are cognate species.

The clearest patterns of speciation in Townsendia indicate that geographic isolation has been of prime importance in the evolution of the members of the genus. A position of importance for polyploidy in the evolutional pattern seems to be ruled out, as no polyploid sexually reproducing species are known to exist. The role of hybridization in the development of new forms in Townsendia seems relatively unimportant, but the process does occur and cannot be entirely excluded as a possible evolutionary
agent. However, none of the present species is suspected to be of hybrid origin.

The importance of geographic isolation in speciation in Townsendia is further emphasized by the unique case of T.exscapa. It is pointed out in greater detail in the systematic treatment that this species occurs in an area where Pleistocene climatic fluctuations probably would not break up its range into geographically isolated populations. Townsendia exscapa has therefore not become differentiated into segregate species but rather is a single large species showing clinal variation.

From both the negative approach (with T. exscapa) and the positive approach (with the other species), the role of geographic isolation in the development of the species of Townsendia i striking. Other factors, such as polyploidy and hybridization, may be important evolutional factors after a group has become somewhat differentiated through geographic isolation. In the young and actively evolving species of Townsendia the primary importance of geographic isolation in permitting the fixation of independent gene mutations seems amply clear.

## CONVERGENT EVOLUTION

Convergent or parallel evolution is a feature of some of the species of Townsendia. This phenomenon is forcefully illustrated by mixed collections which are often unwittingly made by collectors when two species grow side by side. For example, the apomictic plants of T. montana var. montana and those of $T$. leptotes which occur in the high mountains of northern Utah and northcentral Idaho are so similar that they have been confused in the field by five collectors (including myself). A careful examination of the plants and a knowledge of the total range of variation to be expected in each of the species made it possible to show that two specific elements were involved.

Perhaps the instance of convergent evolution in Townsendia which has misled the most botanists is between T. exscapa and T. Hookeri. When Hooker established the genus he did not realize that his material included two species. Ninety-three years later Larsen (1927) first recognized that Hooker had based his "species" on two different specific elements. Specimens from the central portions of the ranges of the sexual forms of these species are easily distinguishable.

In the cases of parallel evolution in T. montana and T. leptotes and in T. exscapa and T. Hookeri, hybridization may have been the factor which permitted convergent evolution. Strong selec-
tive forces in the rigorous habitats these plants occupy probably permitted only a very limited number of morphological (and physiological) recombinants to survive. These happened to be nearly intermediate forms between the two species. Successful recombinations between the species are now fixed by apomixis.

An instance of convergent evolution which has probably involved hybridization but not apomixis is found between T. Fendleri and T. annua. These species were similar enough that Larsen was confused and treated them as a single species in her revision of the genus. A mixed collection of the two species has occurred at least once (cf. discussion of T. Fendleri in the systematic treatment).

Two cases of convergent evolution which appear not to have involved hybridization are between T. mensana var. Jonesii and T. scapigera on the one hand and T. mensana var. mensana and T. Hookeri on the other. In the former case, the populations of T. mensana var. Jonesii in the Charleston Mountains of Nevada are superficially very similar to some of the plants of T. scapigera in the Inyo Mountains of California. There is no evidence that these populations of the two species have ever hybridized. Rather, it seems probable that the very similar climatic regimes in the two areas have been responsible for the selection of lifeforms which have a considerable degree of morphological similarity. One is led to assume that the genetic complement of the genus is such that it will permit the expression of only a limited number of morphological types under a given set of environmental conditions.

In the case of the convergent evolution of T. mensana var. mensana and T. Hookeri, the possibility of hybridization seems to be very clearly ruled out. In the Uinta Basin of Utah where this convergence occurs, the population of T. Hookeri is apomictic. Sexual forms of T. Hookeri are known only on the eastern side of the Rocky Mountains and it seems probable that the population of this species in the Uinta Basin migrated there as an apomict (this postulate is given fuller consideration under the discussion of $T$. Hookeri in the systematic treatment). These apomictic plants have been able to survive because their basic genotype was already suited for the cold winters and dry summers and peculiar edaphic conditions which occur in the Uinta Basin. The narrowly endemic T. mensana var. mensana, in contrast, is a sexual form which apparently has developed under the influence of the factors of natural selection in the Uinta Basin. The similar-
ity of T. Hookeri and T. mensana is sufficient that Larsen (surely on a superficial basis) considered them to be a single species.

It seems unlikely that the convergent evolution which has been outlined above could be important in progressive speciation in Townsendia. However, its frequent occurrence gives a strong indication of the great genetic plasticity of the species of Townsendia under the action of diverse environmental forces. This plasticity must have made possible the rapid divergent evolution in Townsendia.

## Hybridization

Experimental $\mathrm{F}_{1}$ hybrids have been obtained between the seven species of Townsendia which are indicated on Chart 2. All crosses attempted were successful. One plant of the cross $T$. florifer $\times$ T. incana and one of the reciprocal were grown to maturity. These had neither meiotic irregularities nor a greatly reduced pollen fertility (cf. Beaman, 1954). Conditions at the time the $F_{1}$ plants were available did not permit securing the $F_{2}$ crosses, so none have been made. Plants of the other $F_{1}$ crosses were grown for some time under greenhouse conditions in Cambridge, Massachusetts, but growth of both hybrids and nonhybrids was unsatisfactory. From the few crosses which have been obtained, it appears that genetic barriers are lacking between those species involved, but further experimental evidence is needed.

Most of the crosses attempted were between relatively closely related species (compare experimental crosses, Chart 2, with phylogenetic relationships, Chart 1). A greater number of crossing attempts, with special emphasis on obtaining hybrids between the more distantly related species, is contemplated as a future project. Such crosses might provide evidence in addition to that of comparative morphology for inferring evolutionary relationships. Also, extensive crossing experiments could provide important data on the nature of genetic barriers between species. With a closely related series of species, such as those of Townsendia, it might be possible to correlate levels of morphological differentiation with the development of genetic isolating mechanisms. Thus a better insight might be gained on the nature of this important factor in speciation.

Evidence for natural interspecific hybridization has been outlined in the systematic treatment under the discussions of the species. The species between which natural hybridization is sus-

## HYBRIDIZATION IN TOWNSENDIA



Chart 2. Hybridization in Townsendia
pected are indicated on Chart 2. Putative hybrids from sexual populations are indicated by the symbol "sex." and those from apomictic populations by the symbol "ap.". Species in which hybridization seems frequent, based on examination of herbarium material, are connected by heavy lines, and those which appear to hybridize only infrequently are connected by narrow lines.

In a genus with 21 species it seems unusual that 15 of its mem-
bers should be involved in hybridization. To understand the basis of this peculiarity, it is natural to inquire why the other species are not involved also. Hybridization is not known in T. formosa, T. glabella, T. mexicana, T. Rothrockii, T. scapigera, and T. texensis. Most of these species are geographically isolated from all the other species. Townsendia glabella and T. scapigera are the only two members of this group which, on a geographic basis, might be suspected of being involved in hybridization with other species. Neither of these is well enough known to permit a sufficient understanding of its population diversity. The distribution of natural hybridization among the species suggests that the principal requirements for its occurrence are an overlapping or adjoining of ranges of the species and a coincidence of flowering time.

Sexual hybrids occur in a greater number of species than do hybrids in which apomixis is involved (Chart 2). From their distribution within the species, it appears that in Townsendia hybridization and apomixis are independent phenomena. Hybridization probably is not necessary to permit the expression of apomixis. However, certain hybrid derivatives which become apomictic probably have a greater survival value than some nonhybrid apomicts.

It seems probable that in Townsendia hybridization is not a function of intermediate edaphic conditions. Most of the species which occur together have similar, rather specialized, edaphic requirements. Thus it appears that soil conditions figure principally in permitting species to grow together where they can hybridize.

Although hybridization occurs in numerous species, there is little or no evidence to indicate that it is an important factor in speciation in Townsendia. It seems mainly to have increased the morphological diversity of certain species where it is coupled with apomixis. Sexual hybrids are most abundant between T. exscapa and T. Hookeri, and may be abundant between T. florifer and T. mensana var. Jonesii. Otherwise they are not frequently encountered. The diversity in the species as a result of hybridization seems slight in comparison to that which has resulted from geographic isolation.

## Morphology

Townsendia is similar to many other genera of the Compositae in that its members have considerable microscopic homogeneity. Gross morphology is more useful than minute structure in deter-
mining specific limits. Proper determination of the taxa usually must be based on several characters from various aspects of the plant.

One species of Townsendia has been the subject of an anatomical study by Bunton (1910). Her investigation was directed at determining in T. exscapa the anatomical adaptations to xerophytism.
habit. Two trends occur in the genus in the modification of the habit. Erect, monocephalous stems and a rhizomatous basal mat, a primitive and unspecialized habit, are found only in T. formosa. One reduction trend has resulted in low, densely rosulate, matted or tufted perennials, as in T. Hookeri. Another trend involves less shortening of the stem, but the life-span of the plant is reduced, as in T. annua.
roots. All but one of the species of Townsendia have taproots; the exception is T. formosa which has a fibrous root-system. The taproots of young plants are slender and light in color; in older plants they become thick and woody but never develop a thick, rough bark. A gradual transition zone is usually found between the root and stem, and leaf-scars best indicate the change from root to stem. The biennials are characterized by an enlarged root-stem junction which seems to develop during the rosette stage of the first year of growth; this swollen portion may be hollow or have a chambered pith.
stems. The perennial species usually have a branched, woody caudex which forms a crown at the ground surface. Herbaceous stems may develop from the caudex branches, as in T. glabella, or they may be terminated only by tufts of leaves and flowering heads, as in T. Hookeri. The caudex branches of the short-lived perennials are slender; those of the longer-lived species become correspondingly thicker. In most of the species, the stem is expanded just below its junction with the head. This condition is seen most clearly in T. Parryi. Some members of the genera closely related to Townsendia exhibit the same feature. A few of the species of Townsendia are characterized by peduncles, but this character is not prevalent in the genus. Usually the heads terminate more or less leafy stems.
leaves. External leaf morphology in Townsendia is remarkably uniform. Throughout the genus leaf modifications are minor ones in shape, pubescence, and texture. The insertion is alternate and there is no strong differentiation between blade and petiole. The leaves are expanded at the junction with the stem, narrowed into a petiole-like portion, and expanded again into the blade.

With but two minor exceptions, the margins are always entire. Two minute notches infrequently occur at the apices of the leaves of T. Parryi, and in T. mexicana one or two small lobes are sometimes found near the apices. In the acaulescent species all the leaves on a single plant are essentially the same size and shape. Caulescent plants have a basal rosette of leaves longer and broader than those of the upper portions of the stem. There is little differentiation between upper and lower leaf surfaces in any of the species. Thickened leaves are found mostly in plants growing at moderate to high altitudes, as in T. Rothrockii, but some species frequenting the higher elevations do not have thickened leaves. Involute leaves occur primarily in the narrow-leaved forms.
pubescence. Both the stems and foliage in the members of Townsendia are characterized by a strigose pubescence. The trichomes are usually few-celled (3-8) and have a somewhat enlarged basal portion and a sharp-pointed apex. Taxonomically, the most useful pubescence variation is in density. Excluding the achenial hairs, there are only two variations in trichomes in the genus which are not merely quantitative. Simple, multicellular trichomes, conspicuous because of their very short cells, are found on the upper portion of the stem in T. formosa. In T. condensata and $T$. spathulata the trichomes are very long, with elongate cells which have conspicuous end walls; these trichomes may be very abundant, giving the plant a woolly aspect.

The phyllaries may be strigose, pilose-strigose, or glabrous. In several species the trichomes of the phyllaries tend not to be appressed in a single, apical direction while stem and leaf trichomes almost invariably are apically appressed.
involucre and receptacle. Generally, the involucre in Townsendia is hemispheric or campanulate, but in T. montana and T. mensana it may be somewhat obconical.

Phyllary morphology comprises a useful set of taxonomic criteria in the genus. In addition to the number of series in which the phyllaries occur, overall phyllary shape, form of the apex, and nature of the margin are useful characters. In species with very broad phyllaries, the apices tend to be obtuse, while in those with narrower phyllaries, the apices are acute, but acuminate apices occur both in species with wide and with narrow phyllaries. Only two species, T. eximia and T. grandiflora, are characterized by conspicuously bristly phyllaries. The margins always are at least somewhat scarious and ciliate or lacerate-ciliate and may serve as a useful character to someone familiar with the group,
but characters of the margin are too intangible to be useful in the key.

Characteristics of the receptacle have proved useful primarily in the demonstration of the generic relationships of Townsendia. A conical receptacle is found only in T. formosa, the most primitive member of the genus; all the other species have nearly flat or slightly convex receptacles. The close generic relatives of Townsendia have conical receptacles.
flowers. The pistillate ray-florets occur in a single series. As is characteristic in the heterochromous members of the Astereae, the species of Townsendia have only cyanic pigments in the ray-corollas, and ray color is often a useful taxonomic character. Uniformly blue or bluish-purple rays occur in four species and in some populations of two others. In most of the members of the genus, the rays are white on the adaxial surface and have a darker abaxial surface, often with a median stripe which may be pinkish, lavender, or mauve-purple. In old or dried rays the color usually is darker. The adaxial surface of the ray-corollas is generally glabrous, but the abaxial surface in several species is beset with few to numerous gland-like hairs, which apparently are under the control of very few genes. Care must be observed in their taxonomic use, but they are a constant feature of a few species. The length of the ray-corollas is sometimes helpful in delimiting species. The width, on the other hand is of little use. In some of the apomicts the rays never fully expand.

The only character of the disk-corollas which has been used in this study is their length. A comparison of the length of the pappus to that of the disk-corollas has been helpful in several instances.

The style-branches of Townsendia are typical for a member of the Astereae. The disk-styles have the upper portion of the branches modified with projecting hairlike cells, while the raystyles have marginal stigmatic surfaces extending nearly to the apices of the branches. There are slight differences in shape of the style-branches between some of the species, but these are of no use for distinguishing closely related or nearly similar species.

Neither anther structure nor morphological characteristics of the pollen has been employed as taxonomic criteria in this investigation. However, pollen studies have been of great value in distinguishing specimens from sexual populations from those representing apomictic populations. The peculiarities of pollen formation in the apomicts are considered in the section on reproduction. Pollen of the sexual plants (see Plate IV, fig. 1) is
spherical, three-pored, and uniformly spinescent. It is threenucleate at anthesis. At maturity its mean diameter ranges between 23 and 30 microns.
achenes and pappus. There is considerable diversity in size and shape of the achenes of the species of Townsendia. Within the species the achenial morphology is relatively uniform, and in some instances provides useful taxonomic characters. Among the more problematical species the achenes are so similar that they are of little systematic value. Achene shape varies from narrowly oblanceolate to obovate, and the achenes are always somewhat compressed. They usually have ribbed or callousthickened margins.

Gray (1880) in his synopsis of the genus placed considerable reliance on the achenial hairs in delimiting species and groups of species. In the present study also the character of these hairs has been found useful. Macloskie (1883) examined the achenial hairs of all the species of Townsendia known at the time of his study, and the descriptive terms which he and Gray used have been employed in this paper. The achenial hairs are always duplex; two connate cells project from the surface of the achene. One cell originates at the surface of the achene, while the other joins an enlarged or unenlarged basal cell. A second basal cell might occasionally be present but apparently is mostly reduced or absent. The distal portions of the two principal cells may remain connate and be acutely terminated or one cell may exceed the other and have an acute apex. Hairs with acute apices are termed "entire" in this treatment. Hitchcock and Thompson (1945) noted that the hairs of T. condensata (called T. spathulata in their paper) are simple. However, the duplex condition is retained in the hairs of this species, and the term "simple" is misleading. In some species of Townsendia the achenial hairs are bifurcate or emarginate, but glochidiate hairs are commonest in the genus. In the latter type, the distal ends of the two elongate cells are separate and recurved. There is no evidence in Townsendia of a glandular nature of the achenial hairs.

The pappus has been a much-used taxonomic character, and within limits it has great value. It cannot be used, however, to the exclusion of other characters for distinguishing species. The pappus is always uniseriate and is made up of connate setae which are usually arranged in well-developed, rather stiff bristles. At frequent (sometimes very frequent) intervals along the bristles, individual setae project out as non-recurved or rarely recurved barbs or barbulae. In T. exscapa the bristles may reach a length
of 13 mm . while in $T$. formosa the longest never attain a length of 1.5 mm . The pappus of T. eximia usually consists of two bristles and a crown of squamellae, but as many as 50 bristles are found in T. exscapa. The ray-pappus of several species is much shorter than the disk-pappus; the former sometimes is so short that the connate setae merely form a ring of coroniform squamellae around the apex of the achene. The short ray-pappus is a constant feature in some species but mostly there are exceptions which make it an unreliable character. In T. mexicana the ray-pappus appears to have been reduced mostly to single, separate setae which frequently are somewhat glochidiate, resembling the achenial hairs.
measurements. In this study the measurements have been based on dried material. Boiling was employed only in the width measurements of the ray-corollas. Small objects, such as phyllaries, were measured under $9 \times$ magnification with a millimeter rule. Very small parts, such as ray-pappus squamellae, were measured with the same rule under $54 \times$ magnification. Pollen measurements were obtained with a compound microscope and a calibrated ocular micrometer.

## Systematic Treatment

In the citation of specimens, herbarium abbreviations in the third edition of "Index Herbariorum" (Lanjouw and Stafleu, 1956) have been used. These herbaria and their abbreviations are: National Museum of Canada (Can); California Academy of Sciences (cas); University of Colorado (COLO); Carnegie Museum (CM); Colorado A. and M. College (cs); Science Service, Department of Agriculture, Canada (dao); Dudley Herbarium of Stanford University (ds); Chicago Natural History Museum (f); Gray Herbarium (GH); University of Illinois (ill); Idaho State College (ids); Herbarium, Royal Botanic Gardens, Kew (k); Herbario Nacional del Instituto de Biologia de la Universidad Nacional de México (mexu); University of Michigan (MICH); Missouri Botanical Garden (мо); Montana State College (молt); Montana State University (montu); Michigan State University (MSC); United States National Arboretum ( NA ); University of Notre Dame (nd); New York Botanical Garden (Ny); Oberlin College (oc); Bebb Herbarium of the University of Oklahoma (okL); Philadelphia Academy of Natural Sciences (PH); Pomona College (ром); Rocky Mountain Herbarium, University of Wyoming (rm); Rancho Santa Ana Botanic Garden (rsA); Sul Ross State College (sRsc); University of California (UC); National Museum, Smithsonian Institution (Us); University of Utah (UT); Intermountain Herbarium of the Utah State University (UTc); University of Wisconsin (wis); State College of Washington (ws); University
of Washington (wTU); Yale University (yU). Approximately 4500 specimens were examined in this study.

The symbol "\$" before an herbarium abbreviation signifies that pollen from that specimen is characteristic for sexually reproducing, diploid plants; the symbol " $f$ " signifies that pollen from that specimen is characteristic for apomictic, polyploid plants (in some cases no pollen was produced). The symbol "o?" signifies that the specimen probably represents a sexual, diploid population, but the advanced flowering stage did not permit a positive determination.

Townsendia Hook. Fl. Bor.-Am. 2: 16. 1834.
Annual, or most frequently biennial or perennial, caulescent or acaulescent herbs with taproots (fibrous-rooted in one perennial species); erect, suberect, decumbent, or rosulate; leaves alternate, spatulate to linear, entire or rarely lobed or toothed, glabrate to densely pubescent; indument of simple, few- to many-celled, mostly appressed trichomes; heads pedunculate or terminal on stems or sessile and submerged in tufts of leaves, large or small and correspondingly few- to many-flowered; receptacle convex, rarely conical, areolate, minutely pubescent; phyllaries imbricate, in 2-7 series, obovate-ovate to linear-subulate, usually scarious-ciliate margined; rav-florets pistillate, fertile, uniseriate, ca. 10-100, mostly 20-40; raycorollas broadly linear to oblong-linear, uniformly blue, or whitish to pink (rarely dull red or lavender) on the adaxial surface and darker on the abaxial surface, often with a median pink to lavender stripe, inconspicuously 2-3-toothed, glabrous or glandular mostly on the abaxial surface; disk-florets hermaphroditic, more or less numerous; diskcorollas yellow and frequently pink- or purple-tipped or tinged, glabrous or lightly glandular; style-branches lanceolate, oblanceolate or oblong-linear, $0.8-2.5 \mathrm{~mm}$. long, the upper portion (shorter or absent in the rays) with elongate, hair-like cells, the lower stigmatic margins minutely and densely papillose; disk-styles elongating at anthesis, serving as pollen-disseminators; achenes oblanceolate to obovate, compressed, 2 -ribbed, those of the ray sometimes 3 -ribbed, glabrate or most frequently pubescent with duplex hairs, the hairs with glochidiate, bifurcate, emarginate or entire apices, achenes sometimes papillose; diskpappus uniseriate, of few to numerous subulate or acicular, terete or obcompressed, plurisetose, barbellate bristles (rarely of very short bristles and squamellae less than 1.5 mm . long) ; ray-pappus similar to that of the disk, or variously shortened, sometimes to a mere crown of connate or semi-connate, short bristles or squamellae (rarely reduced to glochidiate setae). Type-species (originally the only species): Townsendia exscapa (Richards.) Porter.

## ARTIFICIAL KEY TO THE SPECIES AND VARIETIES

A. Disk-pappus of very short bristles and squamellae less than 1.5 mm . long; plants fibrous-rooted and rhizomatous or stoloniferous; receptacle
A. Disk-pappus of bristles longer than 2 mm . (rarely with squamellae or short bristles also); plants taprooted, not rhizomatous or stoloniferous; receptacle merely convex or flat
B.
B. Disk-pappus of short squamellae or bristles and 2-4 (rarely up to 8) longer, coarse bristles

2. To eximia.
B. Disk-pappus of 12 or more plurisetose bristles ..... C.
C. Phyllaries bristly-stiff, apices attenuate-acuminate3. T. grandiflora.
C. Phyllaries not bristly-stiff, apices acuminate, acute, or obtuseD.D. Achenes at or near maturity with readily deciduous pappus;plants villous-woolly with long trichomes .................. E.
E. Phyllaries acuminate; involucres of largest heads more than 17 mm . wide . . ............................ 15. T. condensata.
E. Phyllaries acute; involucres of all heads less than 16 mm . wide
3. T. spathulata.
D. Achenes with persistent pappus; plants not villous-woolly ...F. F. Achenial hairs bifurcate or unevenly forked with one prong exceeding the other (sometimes appearing simple), not glochidiate by recurved prongs
G.
G. Plants rosulate or cespitose-acaulescent; heads pedunculate or sessile among the tufts of leaves
H. Ray-corollas glabrous or lightly glandular on the abaxial surface; achenes with delicate tangled hairs near the base ..................7b. T. montana var. minima.
H. Ray-corollas densely glandular on the abaxial surface; achenes pubescent from base to apex with straight or nearly straight hairs
I. Phyllaries in 3 (rarely 4) series, acute, pilose-strigose on the outer surface ................ 14. T. scapigera.
I. Phyllaries in 4 (rarely 5 ) series, obtuse or acute, nearly glabrous or the outer lightly pilose-strigose near the apex ....................8b. T. mensana var. Jonesii.
G. Plants with erect or spreading-suberect stems; heads terminating leafy stems
J.
J. Rays blue (rarely whitish or pinkish); phyllaries acuminate, in 4-7 (mostly 5) series ........ 12. T. Parryi.
J. Rays white or pinkish; phyllaries acute, in 3-4 (rarely 2) series
4. T. florifer.
F. Achenial hairs glochidiate or achenes glabrous
K.
K. Phyllaries linear to narrowly lanceolate (broader in some plants with the disk-corollas longer than 6 mm . and in some plants with very narrow, glabrous leaves), apices acuminate or acute, in 5-7 series
L.
L. Phyllaries with a tuft of tangled cilia at the apex, linear, acuminate
5. T. Hookeri.
L. Phyllaries without a tuft of tangled cilia at the apex, narrowly lanceolate, acute
M. Disk-pappus more than 6.5 mm . long; leaf mid-veins usually conspicuous 11. T. exscapa.
M. Disk-pappus less than 6.5 mm . long (if longer, the
ray-pappus less than half the length of the disk-pappus); leaf mid-veins not conspicuous .............N.
N. Leaf bases densely woolly-pubescent with long trichomes .........8a. T. mensana var. mensana.
N. Leaf bases glabrous or only lightly pubescent 9. T. leptotes.
K. Phyllaries broadly lanceolate to ovate or elliptic, apices obtuse or acute, in 2-5 series O.
O. Leaves or achenes or both glabrate .............. P.
P. Ray-pappus nearly as long as the disk-pappus

7a. T. montana var. montana.
P. Ray-pappus less than $1 / 3$ as long as the disk-pappus. Q.
Q. Leaves conspicuously thickened; heads nearly sessile or short-pedunculate; phyllaries obovate, ovate, or broadly oblanceolate, mostly obtuse
6. T. Rothrockii.
Q. Leaves not conspicuously thickened; heads longpedunculate; phyllaries lanceolate, acute

> 5. T. glabella.
O. Leaves and achenes conspicuously pubescent ........R.
R. Disk-pappus shorter than the disk-corollas ....... S.
S. Phyllaries in 2 series; plants of Mexico
21. T. mexicana.
S. Phyllaries in $3-4$ series; plants of the United States T.
T. Plants annual; phyllaries mostly in 3 series, the apices obtuse
20. T. annua.
T. Plants perennial; phyllaries mostly in 4 series, the apices acute
18. T. Fendleri.
R. Disk-pappus as long as or longer than the disk-corollas
U. Caulescent biennials or short-lived perennials V. V. Ray-corollas blue; plants of the Texas Panhandle and western Oklahoma 4. T. texensis. V. Ray-corollas whitish or pinkish; plants not of Texas or Oklahoma ........................
W. Stems gray-white with a dense pubescence (canescent) 17. T. incana.
W. Stems merely lightly to moderately strigose 19. T. strigosa. U. Acaulescent, rosulate, long-lived perennials X. X. Leaves linear, with dense tufts of long, simple trichomes at the base

8a. T. mensana var. mensana.
X. Leaves oblanceolate or spatulate Y.
Y. Leaves conspicuously thickened

7b. T. montana var. minima.
Y. Leaves not conspicuously thickened ....... Z.
Z. Phyllaries glabrous or the outer ones only lightly pubescent; ray-corollas densely glandular

8b. T. mensana var. Jonesii.
Z. Phyllaries conspicuously strigose; ray-corollas glabrous to lightly glandular .17. T. incana.

## 1. Townsendia formosa Greene

Townsendia formosa Greene, Leafl. Bot. Obs. \& Crit. 1: 213. 1906. Type: Metcalfe 1434, Sawyer's Peak, ca. 9000 ft . alt., Grant Co., New Mexico, 30 Sept. 1904 (CAs, lectotype; colo, mo, oc, isotypes).

Townsendia pinetorum Greene ex Nels. Coult. \& Nels. Man. Cent. Rocky Mts. 508. 1909 (in synonymy, nom. nud.).

Fibrous-rooted perennial, with a basal rhizomatous or stoloniferous mat, producing few to many erect, monocephalous (or very rarely weakly branched), leafy stems; aerial stems striate, lightly strigose, becoming more heavily so near the head with both few- and many-celled, simple trichomes, up to 7 dm . but mostly ca. 3.5 dm . high; basal leaves spatulate or broadly oblanceolate, rounded at the apex and sometimes emarginate, nearly glabrous except for the ciliate margin and sometimes pubescent midrib, 1.5-8 cm . long, $0.5-2 \mathrm{~cm}$. wide; lower cauline leaves similar, becoming more oblanceolate; middle and upper cauline leaves gradually becoming smaller upward, the uppermost often linear or lanceolate and sometimes with a slightly scarious margin; receptacle conical, involucres $1.5-3 \mathrm{~cm}$. wide, $1-1.5$ cm . high; phyllaries in 4-6 series, ovate, obovate or oval and the inner becoming lanceolate, apex acute, acuminate or obtuse, broadly scariousmargined and minutely ciliate, nearly glabrous or lightly pubescent along the midrib, $4-14 \mathrm{~mm}$. long, $1.5-5.6 \mathrm{~mm}$. wide; ray-florets ca. $20-35$; raycorollas white on the adaxial surface and blue-purple or mauve abaxially except for the white margins, inconspicuously glandular on the abaxial surface, $14-26 \mathrm{~mm}$. long, $2-3.5 \mathrm{~mm}$. wide; disk-corollas yellow, $3.5-5 \mathrm{~mm}$. long, lightly glandular outside; achenes broadly oblanceolate to broadly obovate, compressed, 2 -ribbed, those of the ray sometimes 3 -ribbed, glabrous or minutely glandular, $3-4.5 \mathrm{~mm}$. long, $2-2.5 \mathrm{~mm}$. wide; ray-pappus of minute coroniform squamellae, less than 0.5 mm . long; disk-pappus of one to few (mostly 2) short, stiff, plurisetose bristles usually less than 1 mm . long and of short squamellae similar to those of the ray-pappus. $2 n=18$. Reproduction sexual. Mountains of southern New Mexico and adjacent southeastern Arizona. Map 2. Plate XVIII, fig. 1.

Representative specimens. Arizona. Apache Co.: Riverside Ranger Station, Greer, Apache Forest, 2700 m. alt., Eggleston 17118 ( ${ }^{\circ} \mathrm{NY}$, us); 9 mi . east of McNary on road to Springerville (State Highway 73), White Mountains, Ferris 1011.3 (ds, uc); Thompson Ranch, Black River, White Mountains, Goodding 561 (COLO, GH, NY, ${ }^{\text {r RM, US) }}$ ) Phelps Botanical Area, White Mountains, 9500 ft . alt., Phillips \& Phillips 3169 (cas). New Mexico. Catron Co.: 0.3 mi . east of Willow Creek Camp Ground, 18 mi . northeast of Mogollon, Beaman 994 ( ${ }^{\circ} \mathrm{GH}$ ) ; Gilita Camp Ground, 20 mi . northeast of Mogollon, ca. 8000 ft . alt., Hitchcock et al. 4403 (CAS, GH, NA, UC, UTC, ws, wTU); Mogollon Mountains, on or near the West Fork of the Gila River, ca. 8500 ft . alt., Metcalfe 413 (DS, GH, "MO, NY, POM, RM, UC, US). Grant Co.: Sawyer's Peak, ca. 9000 ft . alt., Metcalfe 1434 (cas, Colo, mo, oc); Black Range, west flank of Sawyer's Peak, Silver Canyon, around Mitchell Gray's cabin, 7300 ft . alt., Pilsbry s.n., 20 Aug. 1915 (PH). Otero

Co.: Cloudcroft, Slater s.n., Aug. 1914 (us); Sacramento Mountains, Wooten s.n., 23 July 1899 (COLO, DS, OC, POM, ${ }^{\circ}$ RM, UC, US).

Townsendia formosa is the most sharply defined of the species of Townsendia. Its rhizomatous or stoloniferous, fibrous-rooted habit is unique in the genus. None of the taprooted species occupies as mesic a habitat as does this fibrous-rooted species (the evolutionary trend of the genus is toward drier conditions). Townsendia formosa is the only species with a conical receptacle. Monocephalous stems are found elsewhere only in T. Parryi. The peculiar small pappus also is not duplicated in any other species. All of the foregoing characteristics are interpreted to be primitive features in this genus. These are discussed in greater detail in the sections on generic relationships and trends of evolution.

The primitive characters of $T$. formosa do not obscure the fact that it is related to T. eximia. Some degree of similarity can be seen in almost every aspect of the two. Their habits are similar; they have a similar indument; their phyllaries are (slightly) similar; their achenes are very similar; and their pappus is similar. The edaphic requirements and geographical distribution of the two species fit a pattern which, when correlated with the morphological similarities, indicates a close relationship.

## 2. Townsendia eximia A. Gray

Townsendia eximia A. Gray, Mem. Am. Acad. 4 (Pl. Fendl.) : 70. 1849. Type: Fendler 353, sides of high mountains, Santa Fé Creek, Santa Fé Co., N. Mex., June 28, 1847 (GH, holotype; MO, Ph? [not numbered], yv, isotypes).

Townsendia Vreelandii Rydb., Bull. Torr. Bot. Club 28: 22. 1901. Type: Vreeland 639, side of Veta Mountain, 8500 ft . alt., Huerfano Co., Colo. (ny, holotype; Can, rm, isotypes).

Caulescent, taprooted, biennial or short-lived perennial, erect or nearly so; stems few to numerous, branching from the base or above or both basally and above, often red-purple, especially near the base, striate, sometimes swollen at junction with the head, lightly to heavily pubescent with pilose-strigose or villous, few-celled trichomes, up to 5 dm . high; basal leaves oblanceolate to slightly spatulate, entire, mucronate, sometimes slightly apiculate, nearly glabrous to lightly strigose especially along the median nerve, 2 lateral nerves frequently present but inconspicuons, up to 13 cm . long and 1.1 cm . wide; upper cauline leaves similar, becoming smaller and more apiculate near the head; involucre $1.2-4 \mathrm{~cm}$. wide; phyllaries in 4-6 series, lanceolate to ovate-lanceolate with bristly-stiff, acuminate apices, glabrous or very lightly strigose, ciliate and scarious-margined, 5-15 mm . long, $1.5-4.2 \mathrm{~mm}$. broad, those of the inner series longest and narrowest; ray-florets ca. $15-55$; ray-corollas blue, $8-20 \mathrm{~mm}$. long, $1.5-2.5 \mathrm{~mm}$. wide;
disk-corollas yellow, sometimes red-purple-tinged, $3.5-5 \mathrm{~mm}$. long; achenes obovate to broadly oblanceolate, truncate, compressed, those of the diskflorets 2 -ribbed, those of the ray-florets $2-3$-ribbed, sparsely pubescent with short, thick, duplex, glochidiate or bifurcate trichomes, slightly denser on the ray than the disk; achenes often papillose, $3.2-4.4 \mathrm{~mm}$. long; pappus of the ray-florets of stiff, coroniform, basally connate squamellae less than 0.5 mm . long; pappus of the disk-florets of similar or slightly longer squamellae, and also of 2 , or rarely more, coarse, stiff, plurisetose, barbellate bristles, as much as 4 mm . longer than the squamellae, not equalling the length of the disk-corollas. $2 n=18$. Reproduction sexual. Mountainous areas from south-central Colorado to north-central New Mexico. Map 2. Plate XVIII, fig. 2.

Representative specimens. Colorado. Conejos Co.: Cumbres, Ferril s.n., 2 Aug. 1902 (cs). Costilla Co.: east side of La Veta Pass, 9000 ft . alt., Hitchcock et al. 4160 (na, wtu). Huerfano Co.: south side of Mt. Mestas (formerly Veta Mountain), Beaman 745 ( ${ }^{(\mathrm{GH}) ; ~} 4 \mathrm{mi}$. northeast of Cucharas Pass, San Isabel National Forest, west of La Veta, $10,000 \mathrm{ft}$. alt., Rollins 1301 (GH, mo, NA, NX); side of Veta Mountain, 8500 ft . alt., Vreeland 639 (Can, NY, RM). Las Animas Co.: Stonewall, 8300-9000 ft. alt., Beckwith 233 ( ${ }^{* N y}$ ); near head of Berwind Canyon on road east of Delagua, 7500 ft alt., Robbins 518 (UC). New Mexico. Bernalillo Co.: crest of Sandia Mts., $10,670 \mathrm{ft}$. alt., Beaman 699 ( ${ }^{\circ} \mathrm{GH}$ ); hillsides, Balsam Park, Sandia Mts., 8200 ft . alt., Ellis 56 ( ${ }^{\circ} \mathrm{MO}$, NY, US) ; Albuquerque, Sandia Mts., Jones 4157 (CAS, F, GH, MSC, NY, OC, PH, POM, ${ }^{\circ}$ RM, US, UTC). Colfax Co.: Cimarron, Berg 3135 (cs); Colfax Co. (?) : Cimarron Pass in Raton Mts., McKelvey 2419 ( $\mathbf{\text { GH, }}$ Ром) ; vicinity of Ute Park, $2200-2900 \mathrm{~m}$. alt., Standley 14490 ( ${ }^{*} \mathrm{ny}$, us). Mora Co.: 10 mi . northwest of Mora, Beaman 719 ( ${ }^{\circ} \mathrm{GH}$ ). Sandoval Co.: 11 mi . northeast of Jemez Pueblo on U. S. Forest Service road, Beaman 704 ( ${ }^{\circ} \mathrm{GH}$ ) ; University Field School area, Jemez Springs, Nelson 11640 (ds, GH, ${ }^{\circ}$ MO, MONTU, NY, RM, uc, UTC); Sandia Mts., Wooton s.n., 4 Aug. 1910 (Us). San Miguel Co.: vicinity of Las Vegas, Anect 41 (CAS, GH, US) ; hillside along Pecos River, Drouet \& Richards 3316 (Ds, GH, MICH, ${ }^{\circ} \mathbf{M o}$ ). Santa Fé Co.: $1 / 2 \mathrm{mi}$. west of Glorieta in Glorieta Pass, Beaman 717 ( ${ }^{\circ} \mathrm{GH}$ ); sides of high mountains, Santa Fé Creek, Fendler 353 (GH, MO, PH? [not numbered], yU); Cañoncito, 7200 ft . alt., Heller \& Heller 3726 (daO, ds, GH, ill, © MO, MSC, ND, NY, OC, POM, RM, RSA, US, ws, wTU); canyon wall 20 mi . south of Golden, ca. 7000 ft . alt., Hitchock et al. 4229 (DS, NA, UC, wTU). Taos Co.: 18 mi . south of Taos, Beaman $723\left({ }^{\circ} \mathrm{GH}\right) ; 9 \mathrm{mi}$. east of Questa, Beaman 740, ( ${ }^{\circ} \mathrm{GH}$ ); 5 mi . south of Questa, ca. 7000 ft . alt., Hitchcock et al. 4175 (CAS, DS, GH, NA, UC, WTU).

Plants of the southernmost geographical segment of this species have only slightly bristly-acuminate phyllaries that have a very sharp demarcation between the ciliate margin and herbaceous inner portion. The rest of the species is characterized by strongly bristly-acuminate phyllaries with a transitional scarious


Maps 2-3. 2. Geographic distribution of Townsendia formosa and T. eximia. 3. Gergraphic distribution of Townsendia rexensis and sexual and apomictic $T$. grandiflora.
area between the ciliate margin and herbaceous inner portion. The southern populations of T. eximia tend to approach their more southern neighbor, $T$. formosa, but there is no evidence which suggests hybridization between the two. Possibly this resemblance is merely an indication of relatedness of the two species. Further evidence of their relationship was outlined in the discussion of T. formosa.

Under most conditions T. eximia is a biennial, but in highelevation populations, such as those near the crest of the Sandia Mountains and in the Raton Mountains, the perennial habit is well-developed. It appears that life-duration is not a stronglyfixed genetic character in the species. A parallel variation occurs in T. scapigera in eastern California where it occupies low- and high-elevation habitats. Likewise, several other members of the genus may be biennial or perennial, depending upon the habitat which they occupy.

In the southern portion of its range T. eximia is usually an erect, sparsely-branched plant; to the north, especially in southern Colorado, it is suberect and more abundantly branched. In this feature $T$. eximia approaches $T$. grandiflora. Two collections, Standley 13289 and Standley 6357, from the vicinity of Raton, New Mexico, strongly suggest hybridization between these species. The plants in question have the widely branched habit of T. grandiflora. The disk-pappus, of several bristles, is intermediate between the two. The very bristly-acuminate phyllaries are suggestive of T. grandiflora. Most of the other characters are typical of T. eximia, and these plants have been referred to that species. Field studies might reveal the relative importance of whatever gene interchange occurs between $T$. eximia and $T$. grandiflora.

## 3. Townsendia grandiflora Nutt.

Townsendia grandiflora Nutt. Trans. Am. Phil. Soc. VII: 306. 1840. Type: Nuttall s.n., "On the Black Hills, (or eastern chain of the Rocky Mountains,) near the banks of the Platte," 1834 (bm, holotype, examined by Dr. R. C. Rollins; Gh!, PH!, isotypes).

Caulescent, taprooted biennial; root-stem junction enlarged; stems branched at the base, few to numerous, less branched above, mostly spreading and suberect, striate-angled, with a moderate to dense strigose-pilose pubescence, ca. $1.5-30 \mathrm{~cm}$. long; basal leaves spatulate, entire, obtuse, sometimes slightly mucronate, lightly strigose above, nearly glabrous below, up to 5 cm . long and 1 cm . wide, mostly deciduous by flowering time; cauline leaves spatulate to oblanceolate, entire, acute or slightly acuminate or obtuse, mucronate, with a fairly conspicuous median nerve, lightly strigose especial-
ly along the nerve and margins, up to 9 cm . long (averaging ca. 4 cm .) and 1 cm . wide (averaging ca. 4 mm .); heads borne at the ends of the stems, often subtended by one or a few leaves; involucres $15-30 \mathrm{~mm}$. wide, 10-18 mm . high; phyllaries in 4-7 series, ovate-lanceolate or lanceolate with bristly-acuminate apices, ciliate and broadly scarious-margined, with a median green or rarely greenish-purple streak, glabrous or lightly strigose on the outer surface, $4-13 \mathrm{~mm}$. long, $1.5-4.5 \mathrm{~mm}$. wide, the next-to-inner series usually longest; ray-florets ca. 20-40; ray-corollas white above and usually with a median pink or purplish stripe below, $12-23 \mathrm{~mm}$. long, $1-2.5$ mm . wide; disk-corollas yellow, rarely pink-purplish tipped, $4-6 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 -ribbed, lightly to densely pubescent (denser on the disk than the ray) with rather short, thick, duplex, glochidiate or bifurcate hairs, $3.0-4.5 \mathrm{~mm}$. long, $1.1-1.8 \mathrm{~mm}$. wide; ray-pappus of short, coroniform squamellae or plurisetose bristles, not more than 2 mm . long; disk-pappus of ca. $15-30$ stiff, plurisetose, barbellate bristles, $3.8-6 \mathrm{~mm}$. long. $2 n=18$ in sexual plants, and $2 n=27-36$ ? in apomictic plants (the latter inferred from pollen measurements). Reproduction mostly sexual, rarely apomictic. Southwestern South Dakota south to northeastern New Mexico. Map 3. Plate XVIII, fig. 3.

Representative specimens. Colorado. Boulder Co.: southeast-facing slope near summit of Flagstaff Mtn., Beaman \& Preece 509 ( ${ }^{*}$ ws); Eldorado Springs, 5300 ft . alt., Clokey 2810 (Can, Cas, Ds, F, ${ }^{\circ} \mathrm{Ny}$, RM, uc, us). Custer Co.: southern slope, Hardscrabble Creek, above Wetmore, 6000 ft . alt., Klinger s.n., 1 Sept. 1951 (*cs). Douglas Co.: hillside 10 mi . north of Castle Rock, 6000 ft . alt., Ownbey 684 ( ${ }^{\circ} \mathrm{Rm}$, ws). El Paso Co.: mountain side, Manitou, Shear 3687 (ny, ${ }^{\circ}$ us). Fremont Co.: 11 mi. east of Canon City, Waterfall 11490 ( ${ }^{\circ} \mathrm{Uc}$ ). Jefferson Co.: Mount Morrison, southwest of Denver, 6100 ft . alt., Constance d Rollins 1932 (nA, UC, ${ }^{\circ}$ ws). Gilpin Co.: Central City, Scovell s.n., 1869 ( $\left.{ }^{\circ} \mathbf{~ m i c h}\right)$. Larimer Co.: hill 2 mi . west of Bellvue, Preece \& Turner 2858 ( ${ }^{\circ}$ ws) ; Owl Canvon, ca. 18 mi . northwest of Fort Collins, Weber 4873 ( ${ }^{\circ} \mathrm{COLO}$ ). Park Co.: 7 mi . south of Fairplay, 9000 ft . alt., Ripley \& Barneby 10371 (tcas). Pueblo Co.: $2^{1 / 2}$ mi. northwest of Rye, Beaman 744 ( ${ }^{\circ} \mathrm{GH}$ ). Weld Co.: Grover, Johnston 228 ( ${ }^{\circ} \mathrm{Rm}$ ). Nebraska. Banner Co.: hills south of Pumpkin Seed Valley, Rydberg 160 ( ${ }^{\circ} \mathrm{Ny}$, us). Dawes Co.: Bryan Canvon, Crawford, Hapeman s.n., June 1939 ( ${ }^{\circ} \mathrm{mo}$, Ny, UC). Sioux Co.: hilltop 5 mi . east of Harrison, 5100 ft . alt., Ripley \& Barneby 9106 ( ${ }^{\circ} \mathrm{Cas}$ ). Scotts Bluff Co.: Scotts Bluff, 5000 ft alt., Hapeman s.n., 13 July 1935 ( мо, ${ }^{\circ}$ UC). New Mexico. Colfax Co.: Raton Mountains, Bell s.n., Aug. 1867 ( ${ }^{( } \mathrm{PH}$ ); Goat Mountain, Raton, Cockerell $\&$ Cockerell s.n., 26 Aug. 1900 (us). Mora or Colfax Co.: prairie between Ocate Creek and Rio Colorado, Fendler 533 ( ${ }^{\circ} \mathbf{m o}$ ); Mora River prairie, Fendler 157 ( ${ }^{\circ} \mathbf{\text { mo }}$ ). South Dakota. Shannon Co.: Cedar Draw, 8 mi . northeast of Rocky Ford, McIntosh s.n., ( ${ }^{\circ} \mathrm{DAO}$ ); sandbars, White River, Over 2399 (Us). Washabaugh Co.: summit of Snake Butte, Over 2069 ( ${ }^{*}$ us). Wyoming. Albany Co.: South Sibvlee, Nelson 7373 (CM, COLO, ${ }^{\circ}$ GH, ill, MO, NY, POM, RM, us). Goshen Co.: Fort Laramie, Nelson 8312 ( ${ }^{\circ} \mathrm{GH}, \mathrm{Mo}, \mathrm{Rm}, \mathrm{us}$ ). Lar-
amie Co.: Cheyenne, 1850 m. alt., Eggleston 12563 ( ${ }^{\text {evs }) . ~ N i o b r a r a ~}$ Co.: Mexican Mines (Spanish Diggings), Nelson 578 (GH, ill, msc, nd, ${ }^{\circ}$ PH, RM, ws). Platte Co.: hillsides 6 mi . north of Chugwater, Porter 3391 (ds, GH, "mo, Ny, Rm, uc, us, wTu); slopes on the Oregon Trail near Warm Springs, 3 mi. west of Guernsey, 4400 ft . alt., Porter 4910 (COLO, DAO, ${ }^{\circ}$ GH, MONT, OKL, PH, RM, RSA, UC, US, UTC, WTU).

The bristly-acuminate phyllaries, erect or suberect, biennial habit, allopatric ranges, and same flowering times suggest a close relationship between T. grandiflora and T. eximia. ' Iownsendia grandiflora is adapted to the relatively arid foothills east of the Front Range in Colorado while T. eximia ocupies slightly more moist habitats at higher elevations in mountains to the south. A T. eximia stock may have migrated north along the foothills area and become isolated from the central concentration of T. eximia. During that isolation the two species as they are now known probably developed. Townsendia grandiflora is the more specialized of the two.

An interesting parallel in the occurrence of apomixis in $T$. grandiflora and in another biennial, T. scapigera, has been mentioned in the discussion of the latter species. Unlike apomictic $T$. scapigera, the apomicts of $T$. grandiflora appear to have retained the biennial nature of their sexual precursors (the apomicts of $T$. scapigera are short-lived perennials, although most plants of the species are biennial). It should be noted that the locality of Ripley \& Barneby 10371 is the highest-elevation station now known for this species, and is the only station from which the species is known to be apomictic.

## 4. Townsendia texensis Larsen

Townsendia texensis Larsen, Ann. Mo. Bot. Gard. 14: 15, pl. 3. 1927. Type: Eggert s.n., rocky bluffs of the Red River, Randall Co. (?), Texas, 13 Aug. 1900 (мо 121021, holotype, missing; GH!, POM!, isotypes).

Caulescent, taprooted biennial; root-stem junction enlarged or elongated; stems branched mostly at the base, few-branched above, the central stem erect and the laterals spreading-suberect, striate, with a moderate to dense strigose-pilose pubescence, ca. $0.5-2.5 \mathrm{~cm}$. long; basal leaves mostly deciduous by flowering time; cauline leaves oblanceolate, acute, mucronate, 1nerved, lightly strigose on both surfaces to nearly glabrous, up to 60 mm . long and 5 mm . wide; heads borne at the ends of the stems, often subtended and surpassed by a few leaves; involucres $1.3-2 \mathrm{~cm}$. wide, $0.7-1.1 \mathrm{~cm}$. high; phyllaries in 4-6 series, ovate-lanceolate or lanceolate, acute or slightly acuminate, ciliate and broadly scarious-margined, with a darker median streak, strigose on the outer surface or sometimes nearly glabrous, $3.5-10 \mathrm{~mm}$. long. $0.5-2.4 \mathrm{~mm}$. wide, the inner series usually longest; ray-florets ca. 25-40;
ray-corollas blue or very rarely white, sometimes pubescent on the abaxial surface, $0.9-1.8 \mathrm{~cm}$. long, $1.5-2.5 \mathrm{~mm}$. wide; disk-corollas yellow, $3.5-5 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 -ribbed, lightly to moderately pubescent with rather short, thick, duplex, glochidiate hairs, $3-3.8 \mathrm{~mm}$. long, $1.1-1.7 \mathrm{~mm}$. wide; ray-pappus of coroniform-concreted squamellae or short, plurisetose bristles, usually not more than 1 mm . long but rarely up to 2.5 mm . long; disk-pappus of ca. 16-25 plurisetose, barbellate bristles, equalling or shorter than the disk-corollas. $2 n=18$. Reproduction sexual. Texas Panhandle and adjacent western Oklahoma. Map 3. Plate XVIII, fig. 4.

Representative specimens. Oklahoma. Roger Mills Co.: side of one of the Antelope Hills, in northwestern part of county, Beaman 691 (ch); Antelope Hills, Goodman 2614 (GH, mo, ny, okl, RM, wTU). Texas. Briscoe Co.: 5.6 mi . northwest of Quitaque, Cory 17306 (na). Carson Co.: ca. 4 mi. south of Borger, Beaman 696 (GH). Hansford Co.: near Paloduro Creek, 6 mi . southeast of Gruver, Beaman 694 ( ${ }^{\circ} \mathrm{GH}$ ) ; 5 mi . southeast of Gruver, Shinners 8227 ( ${ }^{\circ} \mathrm{Rm}, \mathrm{UC}$ ). Hartley Co.: 13.6 mi . west of Channing, Cory 16458 (nA). Hemphill Co.: near the Canadian River, 5 mi . south of Canadian, Beaman 693 (GH). Hutchinson Co.: 10 mi . southeast of Stinnett, Cory 16352 (na). Motley Co.: hillside 3 mi . west of Matador, Waterfall 7839 (сн, ${ }^{\circ} \mathbf{~ м о ) . ~}$ Oldham Co.: 4 mi . north and $11 / 2 \mathrm{mi}$. east of Vega, 4000 ft . alt., Howard 159 (na). Randall Co.: bluffs, 1 mi . north of Canyon, Beaman 698 (GH).

In most of its morphological characters, $T$. texensis is intermediate between T. eximia and T. grandiflora. It is closely related to but distinct from both. Townsendia texensis and $T$. grandiflora probably are about equally derived species from a T. eximia ancestral stock. The non-cuspidate (rarely minutely cuspidate) phyllaries distinguish T. texensis from the other two species.

My field observations of T. texensis in Roger Mills County, Oklahoma and several counties in the Texas Panhandle indicate that it is abundant in that area. It grows on Cretaceous limestones exposed by stream erosion of the deep, black soils of the high plains.

## 5. Townsendia glabella A. Gray

Townsendia glabella A. Gray, Proc. Am. Acad. 16: 86. 1880. Type: Newberry s.n., La Pagosa (Pagosa Springs), Archuleta Co., Colo., July 29, 1859 (GH, holotype; Ny, yU, isotypes).

Townsendia Bakeri Greene, Pittonia 4: 157. 1900. Type: Baker 727, Los Pinos (Bavfield), La Plata Co., Colo. (nd, lectotype; F, GH, " MO, NY, POM, RM, UC, US, isotypes).

Long-lived, decumbent-cespitose, taprooted perennial; caudex widely branched, becoming woody and subterranean; young stems at ends of the
caudex branches leafy, more densely so near the tips, up to 5.5 cm . long, often with one or a few peduncles in the axils of the upper leaves; leaves spatulate to oblanceolate, entire, the apex sometimes apiculate and mucronate or sometimes rounded, blades dark green, shiny, glabrous or nearly so below, very lightly strigose above, up to 65 (averaging 45) mm. long, 4-11 mm . wide; peduncles up to 7 cm . long, sometimes expanded at junction with the head, naked or rarely with a small bract near the head, striate, with light pilose-strigose pubescence becoming denser near the head, involucres $8-24 \mathrm{~mm}$. wide, $7.8-12.3 \mathrm{~mm}$. high, often broadly expanded at maturity; phyllaries in 3-6, mostly 4, series, broadly lanceolate or oblanceolate, acute or rarely slightly acuminate, glabrous or nearly so, scarious-margined, ciliate, $3.5-10 \mathrm{~mm}$. long, $1.2-2.5 \mathrm{~mm}$. wide, the inner longest; ray-florets ca. $12-35$; ray-corollas white to light blue-pink (lavender-purple), glabrous, $8-14 \mathrm{~mm}$. long, $1.5-2.5 \mathrm{~mm}$. wide; disk-corollas yellow, sometimes greenish or pinkish purple-tipped, $3.6-5.3 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 -ribbed, those of the ray-florets rarely 3 -ribbed, sparsely pubescent with long, slender, duplex, glochidiate hairs; ray-achenes usually minutely papillose, disk-achenes smooth; ray-pappus of short, plurisetose, barbellate bristles, rarely exceeding 1.8 mm . in length; disk-pappus of ca. 15-35 plurisetose, barbellate bristles, 4-7 mm . long, mostly exceeding the length of the diskcorollas, rarely of the same length or shorter. $2 n=18$. Reproduction sexual. Southwestern Colorado. Map 5. Plate XIX, fig. 1.

Representative specimens. Colorado. Archuleta Co.: 9 mi . southeast of Pagosa Springs, Beaman 761 ( ${ }^{\circ} \mathrm{GH}$ ); hills, Pagosa Springs, 2160 m. alt., Bethel, Willey \& Clokey 4340 (CAN, CAS, COLO, DS, F, MICH, ${ }^{\circ}$ MO, MONTU, NY, PH, POM, RM, UC, US, UTC, WS, WTU) ; 1.5 mi . southeast of Pagosa Springs, Turner 2892 (ws) ; mesa slopes ca. 12 mi. north of Arboles, 6400 ft . alt., Weber \& Livingston 6238 (COLO, DAO, ${ }^{\circ} \mathrm{rm}$, rsa, ws, wtu). La Plata Co.: hillside near Dix, 8500 ft . alt., Baker, Earle \& Tracy 548 (См, F, GH, MICH, ${ }^{\circ}$ MO, NY, OC, РOM, RM, UC, US); 7.5 mi. east of the Montezuma Co. line, east of Mancos, Beaman 772 $\left({ }^{\circ} \mathrm{GH}\right) ; 15 \mathrm{mi}$. west of Durango, Waterfall 11716 ( ${ }^{\circ} \mathrm{UC}$ ). Montezuma Co.: Mesa Verde National Park, Nelson 10419 (Gh, ${ }^{\text {² }}$ mo, montu, NY, rm, UC).

This species is closely related to T. eximia. Such features as the similar involucral bracts, similar vesture, and similar habit ( of the high-elevation types of T. eximia and T. glahella) suggest the relationship. Townsendia glabella has the more specialized form of the two, and appears also to have much more specialized habitat requirements. It is abundant only on the Mancos shales of southwestern Colorado. Its endemism may be an expression of precise edaphic and climatic requirements that are satisfied only in that area.

Even though its range is restricted, T. glabella is somewhat variable. Phyllary variation is especially noticeable. For example, in Baker 727 some plants have slightly bristly-acuminate phyllaries; others have acute, and in one plant (POM) broadly obtuse,
phyllaries. The plants of this collection also have shorter peduncles than do plants of the other collections. It is perhaps the minor divergence of Baker 727 from typical T. glabella which led Greene to describe T. Bakeri.

One of the plants which Gray had at hand when he described T. glabella is a teratological form. Its ray-corollas, with long tubes and two conspicuous lateral lobes, are intermediate between ray- and disk-corollas. The ray-pappus is half as long as the diskpappus. I have not considered the abnormal features of this particular plant in the key.

## 6. Townsendia Rothrockii A. Gray ex Rothrock

Townsendia Rothrockii A. Gray ex Rothrock, Wheeler Rept. U. S. Geograph. Surv. 6 (Bot.) : 148. Pl. VII, A. 1878. Type: Rothrock 875, South Park, Park Co., Colorado, 13,500 ft. alt., July 1873 (F, holotype; GH, $\dagger_{\mathrm{Ny}}$, isotypes).

Rosulate perennial with taproot; caudex short-branched, with tufts of leaves at the ends, becoming woody, often subterranean; leaves spatulateoblanceolate, entire, acute or obtuse, sometimes mucronulate, conspicuously thickened, shiny, glabrous or very lightly strigose, $10-35 \mathrm{~mm}$. long and $2-7 \mathrm{~mm}$. wide; heads sometimes nearly sessile, but usually on short peduncles up to 2.7 cm . long; peduncles naked or with a phyllary-like bract near the involucre, striate, villous; involucres $12-28 \mathrm{~mm}$. wide, $8-12 \mathrm{~mm}$. high; phyllaries in 4-6 series, elliptical, ovate, obovate, broadly lanceolate, or oblanceolate, acute, sometimes rounded at the tip, glabrous, scariousmargined, ciliate, red-tinged near the apex, $6-9.5 \mathrm{~mm}$. long, 2-4 mm. wide; ray-florets ca. 18-40; ray-corollas blue, glabrous, $8-16 \mathrm{~mm}$. long, $2-3 \mathrm{~mm}$. wide; disk-corollas yellow, often slightly greenish tipped, $3.3-4.8 \mathrm{~mm}$. long; achenes broadly oblanceolate, compressed, 2 -ribbed, those of the ray-florets rarely 3 -ribbed; ray-achenes moderately pubescent with long, thin, duplex, glochidiate hairs, papillose; disk-achenes lightly pubescent with hairs similar to those of the ray, or nearly glabrous, not papillose; ray-pappus much reduced, of plurisetose, coroniform squamellae or bristles not over 1.5 mm . long; disk-pappus of ca. $15-30$ plurisetose, barbellate bristles, $3.2-6 \mathrm{~mm}$. long, usually about equal to or slightly exceeding the length of the disk corollas. $2 n=18$ ? in sexual plants (inferred from pollen measurements) and $2 n=36$ in apomictic plants. Mountains of southwestern Colorado. Map 6. Plate XIX, fig. 2.

Representative specimens. Colorado. Archuleta Co. (?) : mts. east of Bayfield, $10,000 \mathrm{ft}$. alt., Bequaert s.n., July 1929 ( ${ }^{\circ} \mathrm{GH}$ ). Gunnison Co.: crest of ridge between Avery Mtn. and Virginia Mtn., near Gothic, Beaman \& Barclay $798\left(\dagger_{\mathrm{GH}}\right)$; Taylor Pass, $12,400 \mathrm{ft}$. alt., Langenheim 442 ( $\dagger$ colo) ; foot of Matchless Mitn., $11,000 \mathrm{ft}$. alt., Langenheim 1310 ( $\dagger$ colo ) . Hinsdale Co.: Crystal Lake near Lake City, $11,000 \mathrm{ft}$. alt., Pease s.n., 28 June 1878 (†yu). Mesa Co.: 6 mi . above Taylor Ranch, between Gateway and Whitewater, 8000 ft . alt., Kelly 1643 ( ${ }^{\circ} \mathrm{CoLO}$ ). Park Co.: Hoosier Ridge, Beaman, Weber \& Preece 516 (tws); Hoo-


Maps 4-7. 4. Geographic distribution of Townsendia Fendleri. 5. Geographic distribution of T. glabella. 6. Geographic distribution of sexual and apomictic $T^{\prime}$. Rothrockii. 7. Geographic distribution of sexual and apomictic T. montana var. montana and T. montana var. minima.
sier Ridge, $12,000-13,000 \mathrm{ft}$. alt., Weber \& Rollins 7166 (cas, colo, dao, gh, †rm, rsa, ws, wtu) ; South Park, Wolf 417 (ny, us). San Juan Co.: Engineer's Peak, 12,000 ft. alt., Purpus s.n., 27 July 1893 ( $\mathbf{F}, \dagger_{\mathrm{f}} \mathrm{GH}, \mathbf{M I C H}, \mathrm{MSC}$ ).

Townsendia Rothrockii appears specialized for existence in a very cold climate. Its morphological specialization obscures its relationship with other species, but possibly its nearest, although not too close, relationship may be with $T$. glabella.

In Park and Gunnison Counties, Colorado, two apomictic populations of the species have very unusual habitats. At elevations over $12,000 \mathrm{ft}$. they grow in red sandstone fragments under snowbanks, flowering as the snow melts away. Such peculiar conditions perhaps are not required by the species but may be optimum, thus helping to explain the narrow endemism of T. Rothrockii.

## 7. Townsendia montana M. E. Jones

Rosulate-pulvinate, taprooted perennial; caudex becoming muchbranched, often partly subterranean, the old leaf-bases often persisting for several years, sometimes becoming much elongate in plants growing in talus, bearing the persistent scars of old leaves and developing adventitious roots; leaves spatulate, sometimes thickish, entire, obtuse, sometimes mucronate, rarely emarginate, nearly glabrous to moderately strigose, up to 40 mm . long and 8 mm . wide; heads pedunculate (rarely sessile); peduncles naked or nearly so, swollen at junction with the head, with pilose-strigose pubescence, up to ca. 6.5 cm . long; involucres obconical at base, $8-15 \mathrm{~mm}$. wide, $6-12 \mathrm{~mm}$. high; phyllaries in $3-6$, mostly 4 , series, oblong, obovate, oblanceolate to lanceolate, obtuse and rounded at the apex or rarely acute, red-scarious-margined, ciliate, glabrous or very lightly strigose on the abaxial surface, $2-8 \mathrm{~mm}$. long, $0.8-2.9 \mathrm{~mm}$. wide, the inner longest; ray-florets ca. 12-30; ray-corollas blue, white, or pink, sometimes glandular on the abaxial surface, $6-12 \mathrm{~mm}$. long, 1-3.5 wide; disk-corollas yellow, sometimes pink-greenish tipped, $3.3-5.2 \mathrm{~mm}$. long; achenes narrowly or broadly oblanceolate, compressed, 2 -ribbed, those of the ray-florets sometimes 3 -ribbed, glabrous or sparsely pubescent with rather long, duplex, bifurcate hairs, or with delicate, tangled, duplex, bifurcate or glochidiate hairs, sometimes papillose, $3.7-5.2 \mathrm{~mm}$. long, $1.0-1.6 \mathrm{~mm}$. wide; pappus of the rayand disk-florets similar, of ca. 15-35 plurisetose, barbellate bristles (rarely pappus of the ray-florets very short). Reproduction sexual and apomictic. Western Montana and Wyoming to central Idaho and south to southern Utah.

## KEY TO THE VARIETIES

Heads at least slightly pedunculate; rays blue or white; leaves not involute, not conspicuously thickened

7a. var. montana.
Heads sessile; rays pink; leaves involute, conspicuously thickened
7b. var. minima.

## 7a. Townsendia montana M. E. Jones var. montana

Townsendia montana M. E. Jones, Zoe 4: 262. 1893. Type: Jones s.n., above the Flagstaff Mine, Alta, 9500 ft . alt., Salt Lake Co., Utah, 7 August 1879 (ром 40755, holotype).

Townsendia alpigena Piper, Bull. Torr. Bot. Club 27: 394. 1900. Type: Cusick 2294, subalpine ridges of the Wallowa Mts., 7000 ft . alt., Wallowa Co., Oregon, July 31, 1899 ( $\dagger$ ws, lectotype; F, GH, mO, msC, uc, us, isotypes).

Tounsendia dejecta A. Nels. Bot. Gaz. 37: 267. 1904. Type: Goodding 1238, Dyer Mine, Uinta Mts., ca. 3000 m . alt., Uintah Co., Utah, July 3, 1902 ( ${ }^{*}$ ? Rm , holotype; mo, us, isotypes).
$2 n=18$ in sexual plants and $2 n=36$ in apomictic plants. Reproduction predominantly apomictic. Mountains of western Montana to eastern Oregon and south to central Utah. Map 7. Plate XIX, fig. 3.

Representative specimens. Idaho. Blaine Co.: Mt. Hyndman, Sawtooth Range, 8000 ft . alt., Thompson 13626 ( ch ; мо p.p., with 1 plant of T. leptotes; ny, ph, us, †ws, wtu). Custer Co.: southeast of Double Springs summit, 8 mi . northeast of Dickey, 8500 ft . alt., Cronquist 3197 (GH, $\dagger$ ids, mo, all p.p., with plants of T. leptotes); head of Mahogany Creek northwest of Borah, Hitchcock \& Muhlick 11039 ( $\dagger_{\text {Ny, w w }}$ ). Fremont Co.: east side of Mt. Jefferson, southwest of Henry's Lake, 9500 ft . alt., Cronquist 1924 (IDs, †mo, utc, wTU); mountains northeast of Henry Lake, 8700 ft . alt., Payson \& Payson 1986 (cas, †cm, GH, mo, ny, rm, uc). Lemhi Co.: Liberty Range, west of Gilmore, Christ \& Ward 14886 (†Ny p.p., with 5 plants of T. leptotes). Teton Co.: Teton Peaks, Davis s.n., July 1930 ( $\dagger \mathrm{ids}$ ). Montana. Beaverhead Co.: ridge connecting Sheep and Black Lion Mts., Pioneer Range, ca. 9300 ft . alt., Hitchcock \& Muhlick 13003 (ds, †mo, rm, rSA, Uc, ws, wTU). Gallatin Co.: without definite locality, 8500 ft . alt., Tweedy s.n., Aug. 1886 ( $\dagger \mathrm{Yu}$ ). Madison Co.: $1 / 2 \mathrm{mi}$. north of Kock Peak, Taylor Mts., Hitchcock \& Muhlick 15176 (†ny, wTU); head of Cottonwood Creek, Tobacco Root Range, 9000 ft . alt., Blankinship s.n., 10 Aug. 1902 ( $\dagger$ mont, utc, wtu). Oregon. Wallowa Co.: subalpine ridges of the Wallowa Mts., 7000 ft . alt., Cusick 2294 (F, GH, MO, MSC, UC, US, łws); source of Imnaha River, 2700 m . alt., Cusick 3702 (ws, wTU); summit, east side of Lostine Canyon, 18 mi . above Lostine, Peck 17866 ( $\mathrm{DS}, \nmid \mathrm{NY}$ ); slope above Ice Lake, 3000 m . alt., Peck 18546 ( $\mathrm{Ds}, \mathrm{NY}$ ). Utah. Cache Co.: trailside, saddle of Mt. Naomi, 9500 ft . alt., Maguire, Hobson, \& Maguire 14227 (can, †utc, wTu). Duchesne Co.: 14 mi . south of Theodore, 7000 ft . alt., Jones s.n., 18 May 1908 ( ${ }^{\circ}$ ? ром). Salt Lake Co.: crest of ridge above Flagstaff Mine at Alta, Beaman 843 ( $\dagger \mathrm{GH}$ ); headwaters of Little Cottonwood Creek, above Alta, Rydberg 6607 (can, $\mathrm{t}_{\mathrm{ny}}$, rm, us). San Pete Co.: side of Mt. Baldy, 2 mi. west of intersection of skyline drive and road from Mavfield, Beaman 806 $\left({ }^{\circ} \mathrm{GH}\right)$; ridges and slopes, Mayfield Canyon, $1 / 2 \mathrm{mi}$. above Ranger Station, $10,982 \mathrm{ft}$. alt., Maguire 19987 ( ${ }^{\circ} \mathrm{Ny}$, us, uTc). Summit Co.: ridge
east of East Fork of Bear River, Uinta Mts., 11,000 ft. alt., Goodman d Payson 452 (okl, $\dagger_{\text {rm }}$ ); divide between East Fork of Bear River and Black's Fork, $10,500 \mathrm{ft}$. alt., Goodman \& Hitchcock 1517 (F; GH p.p., with 4 plants of $T$. leptotes; †ny p.p., with 3 plants of $T$. leptotes). Uintah Co.: Dver Mine, Uinta Mts., Goodding 1238 ( $\mathbf{m}$, ${ }^{\text {©? } ? ~ R M, ~ u s) ; ~}$ rocky crest of east side of Whiterocks Canyon between Red Pine and Paradise Creeks, $10,000 \mathrm{ft}$. alt., Graham $10065\left({ }^{\circ} \mathrm{Cm}\right.$, $\left.{ }^{\circ} \mathrm{NA}\right)$. Wyoming. Big Horn or Sheridan Co.: summit of Big Horn Mts., Blankinship s.n., 1890 ( $\dagger_{\mathrm{Ny}}$ ). Fremont Co.: Indian Point, 8 mi . northeast of the Dennison Ranch above Wiggins Fork, 10,000 ft. alt., Porter 6625 ( fuc). Lincoln Co.: ridge near Cottonwood Lake, east of Smoot, $10,400 \mathrm{ft}$. alt., Payson \& Armstrong 3706 (GH, †mo, MSC, RM); Dead Man Peak, 9500 ft . alt., Williams 1301 (cas, †mo, rm, utc). Sublette Co.: summit, Piney Mtn., 25 mi . west of Big Piney, Payson \& Payson 2694 (GH, †мо, Ром, rm, UC, US); slopes in the vicinity of Green River Lakes, $10,300 \mathrm{ft}$. alt., Payson \& Payson 4542 ( $\mathrm{ch}, \dagger_{\mathrm{MO}}, \mathrm{MSC}, \mathrm{PH}, \mathrm{RM}$, ws); slopes in the vicinity of Green River Lakes, $10,300 \mathrm{ft}$. alt., Payson \& Payson 4549 ( $\dagger_{\text {rm }}$ ). Teton Co.: southeast facing slope on south side of Teton Pass, ca. 9000 ft . alt., Beaman \& Preece 505 ( ${ }^{\circ} \mathrm{ws}$ ); Teton Pass Mts., east of Victor, Idaho, 9200 ft . alt., Payson \& Payson 2078 (cas, cm, gh, mo ${ }^{*} \mathrm{Ny}, \mathrm{rm}$ ) ; Teton Pass, 9000 ft . alt., Ripley \& Barneby 8898 ( ${ }^{\circ} \mathrm{Cas}$ ); Sheep Mtn., alpine, $10,200 \mathrm{ft}$. alt., Tweedy 532 ( $\dagger_{\mathrm{Ny}}, \dagger_{\mathrm{yu}}$ ); vicinity of Teton Pass, 9500 ft . alt., Williams 786 ( ${ }^{\circ} \mathrm{Cas}$, gh, mo, ny, rm, utc). Yellowstone National Park: Mammoth Hot Springs, Oleson 116 (†rm).

7b. Townsendia montana M. E. Jones var. minima (Eastwood) Beaman, comb. nov.

Townsendia minima Eastwood, Leafl. West. Bot. 1: 206. 1936. Type: Eastwood d Howell 727, Bryce Canyon, Garfield Co., Utah, June 19, 1933 (cas, holotype).
$2 n=18$ ? in sexual plants (inferred from pollen measurements) and $2 n=27$ in apomictic plants. Southwestern Utah. Map 7. Plate XIX, fig. 4.

Representative specimens. Utah. Garfield Co.: Red Canyon near Bryce, 7000 ft alt., Cottam 9691 (†ut); Red Canyon, Eastuood 785 (cas); Red Canyon, 10 mi. from Bryce Park entrance, Hitchcock 2962 ( ${ }^{6}$ wtu) ; Red Canyon, 10 mi . west from Bryce Canyon, 7500 ft . alt., Harrison 9016 , ( $\left.{ }^{\circ} \mathrm{NA}\right)$; head of canvon above Tropic, 7000 ft . alt., Jones $5312 a r$ (ny, pom, us); Bryce Canyon, Maguire 5034 (can, ${ }^{*}$ utc, wTu) ; Pink Cliffs, 1 mi. east of Pine Lake, Table Cliff Plateau, Powell National Forest, 9000 ft . alt., Maguire 19120 (GH, NY, UTC). Kane Co.: near summit of Pink Cliffs, headwaters, left fork Virgin River, 15 mi . northwest of Orderville, Maguire 18807 (UTC); 5 mi . west of Long Valley Junction on Highways 14 and 89, Preece \& Turner 2462 ( $\dagger \mathrm{GH}, \mathrm{h}^{2} \mathrm{ws}$ ).

Townsendia montana appears to be a continuation of the T. eximia-T. glabella evolutionary line. Its relationship with this
group is indicated by the glabrate leaves, lightly pubescent or glabrous achenes, and broad, glabrate phyllaries. Townsendia montana may be the evolutionary result of isolation of this (T. eximia-T. glabella) stock in the mountains of Utah away from the central core of the genus in the Rocky Mountains.

Variety montana is mostly a high-elevation type, occurring at about timberline. Variety minima is found at somewhat lower elevations, but probably does not occur below the ponderosa pine belt. It has been collected at elevations as high as 9000 ft .

Although var. montana is known from very few collections that represent sexually reproducing populations, each of these is slightly different morphologically from the others. At the southern extremity of its range, the San Pete County population is a fairly close morphological approach to var. minima.

The most problematical portion of T. montana is in the Uinta Mountains. A collection (Goodding 1238) described by Nelson as $T$. dejecta is somewhat distinct from the other collections of T. montana var. montana. Variety montana usually has pedunculate heads, while the heads of this collection are sessile. Typical var. montana has glabrate, spatulate leaves, and this material has moderately pubescent, oblanceolate leaves. In these unusual features Goodding 1238 seems to approach T. leptotes. Another collection (Graham 10065) from the same area represents the only known population of T. montana with a short ray-pappus. It seems significant that T. leptotes in this area also has a short raypappus. Only apomictic T. leptotes is now known in the Uinta Mountains, but sexual material could be there now or recently may have been there. Sexual T. leptotes of the long ray-pappus form is nearby in western Moffatt County, Colorado (Wolf du Dever 5193). The type of variation in the collections Goodding 1238 and Graham 10065 seems most readily explainable on the basis that hybridization between T. montana var. montana and T. leptotes has occurred. It should be noted also in this connection that the collection Goodman \& Hitchcock 1517, from the Uinta Mountains, is a mixture of T. montana var. montana and T. leptotes. These specimens of the two species are very difficult to distinguish from each other and appear to be from apomictic populations of hybrid derivation.

The sexual population of T. montana var. montana in Wyoming at Teton Pass, Teton County, is of interest because of its considerable intra-population variation. Four collections, Beaman d Preece 505, Payson \& Payson 2078, Ripley \& Barneby 8898, and Williams 786, each consisting of a fairly large number of plants,
have been made at or near the same spot. Plant-to-plant variation in these collections is evident in at least three features. Some plants have nearly glabrous ray-corollas; in others the ray-corollas are moderately or densely glandular. Some plants have nearly glabrous phyllaries; in others the phyllaries, especially the outer ones, are moderately or densely strigose. The apex of the phyllaries likewise is variable. In some plants the apices are broadly obtuse; in others they are acute, and in still others they are intermediate. Variety montana is ordinarily characterized by glabrous ray-corollas, and nearly glabrous or only lightly pubescent, obtuse phyllaries. The unusual characters in this population probably belong to T. florifer. The latter species has densely glandular ray-corollas and moderately strigose, acute phyllaries. It seems possible that pollen occasionally has been carried up to the T. montana population by insects which have visited T. florifer plants in the lower areas of adjacent Idaho.

Apomixis in var. montana is concentrated in the high-elevation, northernmost populations. This pattern is no different from that of the other species in the genus with abundant apomixis. Variety minima is so restricted that the geographic and altitudinal pattern of the range of its apomictic forms is not at present demonstrable. It should be noted that in one area (Red Canyon) apomicts and sexual plants of var. minima occur together.

## 8. Townsendia mensana M. E. Jones

Rosulate-pulvinate perennial with well-developed taproot; caudex developing few to numerous short, often subterranean, branches; leaves spatulate, oblanceolate or linear, entire, acute or slightly acuminate, mucronate, gray-strigose pubescent, often involute, up to 35 mm . long and $1-5 \mathrm{~mm}$. wide; heads sessile or pedunculate; peduncles up to 3 cm . long, pilosestrigose; involucres often obconical at base, $6.5-17 \mathrm{~mm}$. wide, $8.0-13.5 \mathrm{~mm}$. high; phyllaries in 4-5 series, lanceolate to narrowly obovate, mostly acute, infrequently obtuse, with scarious or ciliate margins, glabrous to lightly strigose-pilose on the outer surface, $3.5-10 \mathrm{~mm}$. long, $1.3-3.0 \mathrm{~mm}$. wide; rayflorets ca. 12-30; ray-corollas whitish, pink or dull red, densely glandular on the abaxial surface, $7-12 \mathrm{~mm}$. long, 1-2.3 mm . wide; disk-corollas yellow, often pink-tinged, 4-6 mm . long; achenes oblanceolate, compressed, 2 -ribbed, those of the ray-florets sometimes 3 -ribbed, moderately to heavily pubescent with duplex, glochidiate or bifurcate hairs; pappus of the ray-and diskflorets similar, of $15-35$ plurisetose, barbellate bristles, $4.2-6.5 \mathrm{~mm}$. long, or pappus of the ray-florets variously shortened. Reproduction sexual. Northeastern Utah to southeastern Nevada.

## KEY TO THE VARIETIES

Leaves narrowly oblanceolate to linear, abaxial surface of leaf-bases densely woolly with long, white, multicellular trichomes; phyllaries lanceolate;
heads sessile, almost hidden in the tufts of leaves; plants of the Uinta Basin of Utah 8a. var. mensana. Leaves oblanceolate to spatulate; abaxial surface of leaf-bases merely strigose with short trichomes; phyllaries broadly lanceolate to narrowly obovate; heads usually short-pedunculate, or if appearing sessile, not obscured by dense tufts of leaves; plants of western Utah and southeastern Nevada

8b. var. Jonesii.

## 8a. Townsendia mensana M. E. Jones var. mensana

Townsendia mensana M. E. Jones, Contr. West. Bot. 13: 15. 1910. Type: Jones s.n., benches of the Uintas, Theodore (now Duchesne), $7,500 \mathrm{ft}$. alt., Duchesne Co., Utah, 14 May 1908 (pom, holotype). Uinta Basin, Utah. Map 8. Plate XX, fig. 1.

Representative specimens. Utah. Duchesne Co.: 26 mi . southwest of Myton, 7000 ft . alt., Barneby 12701 ( ${ }^{\text {c Cas) ; }} 15 \mathrm{mi}$. west of Duchesne, Beaman 865 (GH); "bench" of the Uintas, 11 mi. north of Duchesne, Beaman 868 (GH); 3 mi . west of Duchesne, 5500 ft . alt., Ripley \& Barneby 4677 (cas). Uintah Co.: between Hill Creek and Green River, ca. 20 mi . south of Ouray, Bartholomew \& Bartholomew s.n., June 1955 (GH).

8b. Townsendia mensana M. E. Jones var. Jonesii Beaman, var. nov.
Type: Jones s.n., Mammoth, 7000 ft. alt., Juab Co., Utah, 10 May 1910 (ром 39891, holotype).

Leaves oblanceolate or spatulate, acuminate, the bases strigose on the abaxial surface; heads mostly short-pedunculate. Western Utah and southeastern Nevada. Map 8. Plate XX, fig. 2.

Foliis oblanceolatis vel spathulatis, acuminatis, basi strigosis, capitulis plerumque breviter pedunculatis.

Representative specimens. Nevada. Clark Co.: Deer Creek, Charleston Mountain, 8250 ft . alt., Alexander 774 ( ${ }^{\circ} \mathrm{Uc}$ ); ridge south of Deer Creek, 2670 m . alt., Clokey 7772 (Uc); Lee Canyon, 2650 m . alt., Clokey 7773 (Uc); Hidden Forest Canyon, Sheep Range, 9500 ft . alt., Munz 16836 (pom, Uc). Lincoln Co.: Mt. Irish, 6000 ft . alt., Jaeger s.n., 19 June 1938 (ром). White Pine Co.: Schellbourne, Jones s.n., 13 July 1891 (ром). Utah. Juab Co.: McIntyre's Ranch, Jones s.n., 18 May 1891 (ром); Silver City, Jones s.n., 27 March 1896 (ром) ; Tintic Junction, 5500 ft . alt., Jones s.n., 9 May 1910 (ром). Millard Co.: Leamington, 5000 ft . alt., Jones s.n., 8 May 1911 (pom, atypical, hybrid with T. florifer?, ef. discussion); San Pete Co.: 2 mi . southeast of Ephraim, Beaman 820 (GH); Gunnison, 5000 ft . alt., Jones s.n., 18 April 1911 (ром). Sevier Co.: ridge between Cottonwood and Willow Creeks, 8000 ft . alt., Robinette 105 L. R. ( ${ }^{\circ} \mathrm{NA}$ ). Tooele Co.: Deep Creek, Jones s.n., 6 June 1891 (pom). Tooele or Utah Co.: Mercur, 5500 ft . alt., Jones s.n., 6 June 1896 ( ${ }^{\circ} \mathrm{mo}$, NY, pom, us, ${ }^{\circ}$ UTC). Wayne Co.: 10 mi . southeast of Teasdale, Beaman 822 ( ${ }^{\circ} \mathrm{GH}$ ).

This nearly unknown species has recently figured in a nomenclatorial confusion. It was placed in synonomy under T. sericea ( $=$ T. Hookeri) by Larsen (1927). Its resemblance to that species is superficial. ${ }^{1}$ Cronquist first recognized that $T$. sericea is invalid as it included the type of the earlier Aster? exscapus $[=$ Townsendia exscapa (Richards.) Porter]. With T. mensana residing in synonomy under T. sericea in Larsen's treatment, it appeared that the epithet "mensana" should be taken up for the latter species. Both Cronquist (1955, pp. 326-327) and I (Beaman, 1954, p. 172) fell into a trap by not having seen the type of T. mensana. Critical study of the type and other material indicates that $T$. mensana must be recognized as a species in its own right.

Townsendia mensana var. mensana is endemic to the Uinta Basin of Utah. From my field observations, it appears that the variety has its best development on the pinon- and junipercovered "benches" of the Uintas to the north and west of Duchesne. It occurs also at slightly lower elevations, with a host of other specialized little xerophytes, on the white shales of the Green River formation.

Townsendia mensana var. Jonesii occurs over a wider area and is represented by many more specimens than is var. mensana. Marcus E. Jones, however, has been the principal collector of var. Jonesii, and the variety is named in his honor.

The diversity of T. mensana var. Jonesii is considerable. The plants of Utah mostly have narrow, oblanceolate leaves, the heads are borne on conspicuous peduncles, and the phyllaries are usually acute. The Nevada plants, on the other hand, mostly have broader, nearly spatulate leaves, the heads are nearly sessile, and the phyllaries are usually slightly obtuse. The variation between plants of the two areas is continuous, however, and it seems best to consider the material as a single taxon.

The variation trend of the Utah material of var. Jonesii is in the direction of T. florifer. For the most part this variation is subtle, and the present material is not adequate to permit a good understanding of its cause. Only two collections, Jones s.n., 8 May 1911 (Millard Co., Utah) and Jones s.n., 6 June 1891 (Tooele Co., Utah), show strongly intermediate characters between T. florifer and T. mensana var. Jonesii. Unfortunately both collections are scanty, one consisting of one small plant, the other of two. In the Millard County collection ( 2 plants), one plant seems nearer

[^31]

Maps 8-9. 8. Geographic distribution of Townsendia mensana var. mensana and T. mensana var. Jonesii. 9. Geographic distribution of sexual and apomictic $T$.
leptotes.
T. florifer, the other nearer T. mensana var. Jonesii. One plant has mostly glochidiate achenial hairs; the other has mostly bifurcate hairs. The plant with the bifurcate hairs appears to be annual or biennial; the other could be perennial. The phyllaries of both plants are in three series and similar to those of T. florifer. In the Tooele County specimen the achenial hairs are bifurcate, the phyllaries are in four series and have a strigose pubescence intermediate between typical T. florifer and typical T. mensana var. Jonesii. In general aspect this plant seems closer to typical T. mensana var. Jonesii than do the two Millard County plants.

This evidence of hybridization between T. mensana var. Jonesii and T. florifer is meager. However, in view of the general situation in Townsendia as regards interspecific hybridization, it would be surprising if crossing did not occur between the two. They occur sympatrically over a fairly large area in the sagebrush lands of west-central Utah. They probably occupy the same or at least very similar habitats. Marcus Jones (1893, p. 262) states that T. mensana var. Jonesii (det. by him as T. scapigera) is rare. Very likely it is, since he is the only collector of it in the area of probable hybridization. But even though it is rare, an intensive field investigation might be expected to demonstrate considerable gene interchange between T. florifer and T. mensana var. Jonesii.

The closest relationship of T. mensana appears to be with T. montana. The ancestral stock in the Wasatch region may have differentiated into low-elevation T. mensana and high-elevation T. montana. Some relationship between the two species is shown by the similar habit, the similar involucral bracts (especially between T. montana and the southern Nevada populations of T. mensana var. Jonesii which have broad, obtuse phyllaries), and the similar light pubescence of the phyllaries.

The differences between the two varieties of T. mensana are minor, although constant. The two taxa have been placed at the varietal level to indicate their very close morphological relationship. Variety mensana has probably been isolated in the Uinta Basin for sufficient time to become somewhat differentiated from a more primitive var. Jonesii stock.

## 9. Townsendia leptotes (A. Gray) Osterhout

Townsendia leptotes (A. Gray) Osterhout, Muhlenbergia 4: 69. 1908. [lepotes apparently a typographical error by Osterhout of Gray's epithet leptotes]. T. sericea Hook. var. leptotes A. Gray, Proc. Am. Acad. 16: 85. 1880. Type: Parry s.n., Middle Park, Grand Co. (?),

Colorado, July-August 1864 ( ${ }^{\circ} \mathrm{GH}$, holotype; F, MO, NY, PH, UC, YU, isotypes; Us, probable isotype but dated 1862).

Rosulate-pulvinate perennial with well-developed taproot; caudex of few to numerous, short, subterranean branches terminated by tufts of leaves; leaves linear to oblanceolate or narrowly spatulate, entire, mucronate, thickish, usually involute, glabrous to rather heavily strigose-sericeons, up to 60 mm . long and 3.5 mm . wide; heads sessile or pedunculate, the peduncles not more than 2.8 cm . long; involucres campanulate, $0.8-2.3 \mathrm{~cm}$. wide, $0.5-1.5 \mathrm{~cm}$. high; phyllaries in 4-7 (rarely 3) series, linceolate to linear, acute or rarely slightly rounded, ciliate and scarious-margined, glabrous or very lightly strigose on the outer surface, $3.5-12 \mathrm{~mm}$. long, $0.5-2$ mm . wide; ray-florets ca. 15-40; ray-corollas whitish, cream, pink, or blue, glabrous or nearly so, $8-14 \mathrm{~mm}$. long, 1-2.5 mm . wide; disk-corollas yellow, sometimes pinkish-tinged, $3.2-7 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 -ribbed, those of the ray sometimes 3 -ribbed, lightly to moderately pubescent with long, thin, duplex, glochidiate hairs or glabrous with only a few basal hairs, sometimes papillose; pappus of the ray- and disk-florets similar, of plurisetose barbellate bristles, $3-8 \mathrm{~mm}$. long, or pappus of the ray-florets variously shortened or absent. $2 n=18$ in sexual plants, and $2 n=27-36$ ? in apomictic plants (inferred from pollen measurements). Western Montana to central Idaho and south to northwestern New Mexico, central Nevada and east-central California. Map 9. Plate XX, figs. 3 and 4.

Representative specimens. California. Mono Co.: R. 34 E, T. 5 S. Sect. 2, White Mountains U. S. G. S. Map, 11,500 ft. alt., Duran 1661 (†uc); north slopes of Sheep Mountain, White Mountains, 12,000 ft . alt., Maguire \& Holmgren 26109A (UC, †uTc). Colorado. Archuleta Co.: Pagosa Springs, Bethel s.n., 23 May 1917 ( ${ }^{\circ} \mathrm{Cs}$ ); hillsides, southeast of Pagosa Springs, 7200 ft . alt., Ripley \& Barneby 7589 ( ${ }^{\circ} \mathrm{Cas}$ ) ; Pagosa Springs, Smith s.n., 12 May 1894 (PH). Grand Co.: 4.5 mi . west of Kremmling, Beaman \& Preece 513 ( ${ }^{\circ}$ ws) ; Kremmling, Osterhout 5221 ( $\left.{ }^{\circ} \mathrm{OKL}, ~ Р О М, ~ R M\right) ~ ; ~ 1 ~ m i . ~ e a s t ~ o f ~ G r a n d b y, ~ 7800 ~ f t . ~ a l t ., ~$ Ripley \& Barneby 10586 ( ${ }^{\circ} \mathrm{Cas}$ ). Gunnison Co.: crest of ridge between Avery Mountain and Virginia Mountain, near Gothic, Beaman d Barclay 799 ( $\dagger \mathrm{GH}$ ); North Station Ridge near Gothic, 12,000 ft. alt., Langenheim 725 ( $\uparrow$ colo, cs); Fairview Peak, $13,200 \mathrm{ft}$. alt., Langenheim 1292 ( $\dagger$ colo); Matchless Mountain, $12,000 \mathrm{ft}$. alt., Langenheim 1309 (colo). Lake Co.: near Leadville, Schedin \& Schedin 478 ( ${ }^{\circ}$ Rм). La Plata Co.: 5 mi . northwest of Hesperus, Pennell 21464 ( ${ }^{\circ} \mathrm{Ny}, \mathrm{PH}$ ). Moffat Co.: saddle just west of fire lookout, summit of Roundtop Mountain, Dinosaur National Monument, 2800 m . alt., Wolf \& Dever 519.3 ( ${ }^{\circ}$ Colo). Montezuma Co.: Mancos, Eastwood s.n., June 1891 ( ${ }^{\circ} \mathrm{POM}$ ); Cortez, Nelson 10437 (GH, MO, NY, ${ }^{\circ}$ nm, UC). Park Co.: South Park, Wolf \& Rothrock 418 ( $\dagger$ GH, NY, tus). Saguache Co.: Marshall Pass., Ferrill s.n., 13 June 1903 ( ${ }^{\circ} \mathrm{Cs}$ ); Cochetopa Park, just south of summit of Cochetopa Pass, ca. 9600 ft. alt., Weber 9421 (colo, ©GH). Idaho. Blaine Co.: Mt. Hyndman,

Sawtooth Range, 8000 ft . alt., Thompson 13626 (mo p.p., with 3 plants of T. montana). Clark Co.: 3 mi . from head of Medicine Lodge Creek, Davis 3148 ( $\dagger_{\text {ids }} \dagger_{\text {na }}$ p.p., with 1 plant of T. Hookeri). Custer Co.: Mt. Borah, Chilly, Christ \& Ward 10424 (†NY); southeast of Double Springs Summit, 8 mi . northeast of Dickey, 8500 ft . alt., Cronquist 3197 ( $\dagger \mathrm{GH}$, ids, mo, all p.p., with plants of T. montana); pass in mts. 7 mi . north of Dickey, 8500 ft . alt., Hitchcock et al. 3790 ( $\dagger$ wTU) ; mouth of Rock Creek, north slope, Lost River Mountains, Hitchcock 15725 (†wtu). Lemhi Co.: Liberty Mountain, Lemhi Range, west of Gilmore, Christ \& Ward $1488 \dot{6}$ ( $\dagger_{\text {ny }}$ p.p., with 3 plants of T. montana); near head of Spring Canyon ca. 8 mi . southeast of Gilmore, Lemhi Mountains, Hitchcock \& Muhlick 9317 (ny, †wtu). Montana. Madison Co.: without definite locality, 9500 ft . alt., Tweedy 229 ( $\dagger_{\mathrm{Ny}}$ ). Nevada. Nye Co.: summit above Pine Creek Basin, Toquima Range, $11,300 \mathrm{ft}$. alt., Maguire \& Holmgren 25818 ( $\dagger_{\mathrm{NY}, \mathrm{UC}, \mathrm{UTC}) ;}$ summit extending northeast, 1 mi . from Toivabe Dome, $10,500 \mathrm{ft}$. alt., Maguire \& Holmgren 25944 (cas, †ny, vc, UTC). New Mexico. Rio Arriba Co.: hills south of village, Tierra Amarilla, 2300 m . alt., Eggleston 6444 (F, "GH, "MO, NY, US). Utah. San Pete Co.: Spring Hollow Drainage above Great Basin Experiment Station, Manti National Forest, 10,200 ft. alt., Holmgren \& Shaw 7640 ( $\dagger_{\text {Uc, utc }}$ ). Summit Co.: ridge east of East Fork of Bear River, Uinta Mountains, $11,400 \mathrm{ft}$. alt., Goodman \& Payson 450 (okl, †rm); divide between East Fork of Bear River and Black's Fork, Uinta Mountains, 10,500 ft. alt., Goodman \& Hitchcock 1517 (ds, F; GH p.p., with 1 plant of T. montana; mich, †mo, montu, $\dagger \mathrm{Ny}$ p.p., with 2 plants of T. montana; PH, RM, UC). Wyoming. Fremont Co. (?) : gravelly hills, Wind River Mts., Hayden s.n., 15 May 1860 ( $\dagger$ mo). Yellowstone National Park: Saddle Mountain, $10,000 \mathrm{ft}$. alt., Tweedy 697 (†GH, NY).

Townsendia leptotes exhibits the greatest interpopulation variation of any species in the genus. No two collections from sexual populations are entirely similar. Variation occurs even between populations which are only a short distance apart. The species is most diversified in western Colorado.

Sexual populations of T. leptotes appear to be confusing and difficult to determine, mostly as a result of hybridization with T. exscapa. The populations of southwestern Colorado and adjacent Rio Arriba County, New Mexico exhibit a polymorphy which seems attributable only to the influence of T. exscapa. In southwestern Colorado T. leptotes becomes a large plant with a much-branched caudex; it has relatively large, sessile heads with involucres averaging ca. $2.0-2.5 \mathrm{~cm}$. wide; the disk-corollas are unusually long, averaging $5.5-6 \mathrm{~mm}$., and the disk-pappus is
correspondingly long. These atypical features of T. leptotes are characteristic of T. exscapa.

An unusual character, not from T. exscapa, in the southwestern Colorado material of T. leptotes is the short ray-pappus. Townsendia glabella, which occurs in that area also, has a short raypappus. However, no other features definitely suggest gene exchange between these two species. This character could have had an independent development in the southwestern Colorado populations of T. leptotes. As the ray-pappus is a variable character in several other Townsendia species, such an explanation might apply here.

The polymorphy between populations of the apomicts of $T$. leptotes indicates that apomixis must have occurred independently in several different sexual populations. For this reason the apomicts are interesting from a phytogeographic point of view. Those of the Uinta Mountains (e.g., Goodman \& Hitchcock 1517) are very similar to the plants of southwestern Colorado. They have the short ray-pappus and the habit almost exactly duplicates that of the purer (relatively undiluted with T. exscapa) sexual plants of southwestern Colorado (e.g., Ripley \& Barneby 7589). The apomicts of Park County, Colorado (Wolf \& Rothrock 418) are very similar to sexual T. leptotes from Marshall Pass, Saguache County, Colorado (Ferril s.n., 13 June 1902). The apomicts of San Pete County, Utah, Nye County, Nevada, and Mono County, California (e.g., Holmgren \& Shaw 7640, Maguire \& Holmgren 25944 and Maguire \& Holmgren 26109A, respectively) are more difficult than the preceding examples to relate to a known sexual type but they are morphologically close to some of the alpine apomicts from Gunnison County, Colorado (e.g., Beaman \& Barclay 799). The Idaho apomicts are closest morphologically to the apomicts of the Uinta Mountains of Utah, but in the Idaho material (in contrast to the Uinta material with the short raypappus) the ray-pappus is about as long as that of the disk.

In Wyoming T. leptotes is known only from apomicts of two old collections (Tweedy 697 and Hayden s.n., 15 May 1860). These are perplexing because of their resemblance to $T$. spathulata. Their narrow phyllaries and glabrous achenes are characters of T. leptotes. Their pubescence is nearly as dense as that of T. spathulata, and their pappus is deciduous like that of T. spathulata. The oblanceolate leaves are about intermediate between the two species. These plants could be apomictic hybrid derivatives of T. leptotes and T. spathulata. Further field studies of the
populations in western Wyoming are needed to help clarify the relationship that seems to exist between these two species.

Putative hybridization between T. montana var. montana and T. leptotes in the Uinta Mountains has been considered in the discussion of the former species. It is possible that the Idaho apomicts of T. leptotes are hybrid derivatives of these two species. In Idaho the two are so similar that previously they both have been referred to T. montana. Their similarity is apparent from the mixed collections in which they occur (Christ \& Ward 14886, Cronquist 3197, and Thompson 13626).
10. Townsendia Hookeri Beaman, sp. nov.

Type: Clokey 4338, dry hills, Mt. Vernon Canon, 1730 m . alt., Jefferson Co., Colorado, 13 April 1920 ( ${ }^{\circ}$ colo 12061, holotype; can, CAS, dS, F, GH, MICH, MO, MONTU, NA, PH, POM, ${ }^{\circ}$ RM, UC, US, UTC, ws, wTU, isotypes).

Densely rosulate-pulvinate perennial with well-developed taproot; caudex of few to numerous short, subterranean branches, appearing smooth with the matted pubescence of the old, persistent leaf bases, the branches terminated by tufts of leaves and frequently by a flowering head; leaves linear to narrowly oblanceolate, entire, acute, mucronate, involute, thickish, densely strigose-sericeous, up to 45 mm . long and 2 mm . wide (rarely up to 3.5 mm . wide) ; heads sessile (rarely short-pedunculate on peduncles up to 1.3 cm . long ) at the ends of the caudex branches, embedded in and surpassed by the tufts of leaves; involucres obconical-campanulate, $8-18 \mathrm{~mm}$. wide, $9-15 \mathrm{~mm}$. high; phyllaries in 5-7 (rarely $3-4$ ) series, linear or nearly so, acute or acuminate, mostly terminated by a tuft of tangled cilia, ciliate and scarious-margined, the outer phyllaries sometimes glandular on the lower margin, nearly glabrous to pilose-strigose on the outer surface, purplish upward, $5-13 \mathrm{~mm}$. long, $0.6-1.8 \mathrm{~mm}$. wide; ray-florets ca. $15-30$; ray-corollas white on the adaxial surface, the abaxial surface cream or pinkish, glabrous or nearly so, $8.5-14 \mathrm{~mm}$. long, $1-2.5 \mathrm{~mm}$. wide; disk-corollas yellow, sometimes pinkish-tipped, $4.0-6.5 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2-ribbed, pubescent with long, thin, duplex, glochidiate hairs, sometimes papillose, $3.5-4.7 \mathrm{~mm}$. long, $1.0-1.4 \mathrm{~mm}$. wide; ray-pappus variable, of very short plurisetose bristles ca. 1 mm . long or of plurisetose, barbellate bristles up to 5.5 mm . long or with both long and short bristles on the same achene; disk-pappus of plurisetose, barbellate bristles $5-8.2 \mathrm{~mm}$. long, exceeding at least slightly the length of the disk-corollas. $2 n=18$ in sexual plants and $2 n=27-36$ ? in apomictic plants (the latter inferred from pollen measurements). Northeastern British Columbia south to southern Colorado and central Utah. Map 10. Plate XVII and Plate XX, figs. 5 and 6.

Herba perennis pulvinata; radix fusiformis; ramosis caudicis paucis vel numerosis; folia linearia ad suboblanceolata, integerrima, strigoso-sericea, ad 4.5 cm . longa et 2 mm . lata. Capituli in summo caudicis sessiles; involucrum $8-18 \mathrm{~mm}$. latum, $9-15 \mathrm{~mm}$. altum; involucri squamis plerumque 5-7 seriatis, lineari-subulatis, acutis vel acuminatis, $5-13 \mathrm{~mm}$. longis, $0.6-1.8 \mathrm{~mm}$. latis.

Corollae radiorum $8.5-14 \mathrm{~mm}$. longae, $1-2.5 \mathrm{~mm}$. latae; corollae disci 4.0-6.5 mm . longae. Achaenia oblanceolata, compressa, pubescentia cum pilis glochidiatis, $3.5-4.7 \mathrm{~mm}$. longa, $1.0-1.4 \mathrm{~mm}$. lata; radiorum pappo ca. 1 mm . longo vel usque 5.5 mm . longo; disci pappo plurisetoso, $5-8.2 \mathrm{~mm}$. longo.

Representative specimens. Canada. Alberta. Rocky Mountains, Drummond 573 ( $\dagger$ can); Sweet Grass Hills, Macoun 10897 (can, nd); Waterton Lakes National Park, hilltop near north park entrance, 4200 ft . alt., Breitung 17067 (Ny); Banff National Park, upper drainage of N. Saskatchewan River, Valley of Mistaya River, between Saskatchewan Crossing and Waterfowl Lakes, 4500 ft . alt., Porsild \& Breitung 14758 (CAN, GH); Medicine Hat, Spreadborough 5027 (can, †GH, mo, Ny, us). British Columbia. Fort McLeod, Cowdry 7709 (CAN). Saskatchewan. Cypress Hills, summit of hills east of Boyd's Ranch, Breitung 5357 (dao); Maple Creek, Campbell 129 ( $\ddagger$ dao p.p., with 1 plant of T. exscapa). united states. Colorado. Boulder Co.: near Boulder, Ramaley 654 (colo, ${ }^{\text {RMM) ; }} 1 / 2 \mathrm{mi}$. east of Hi-Way Mine, 3 mi . south of LaFayette, Weber 3713 (colo, p.p., with 1 plant of T. exscapa). Clear Creek Co.: Georgetown, Wolf d Rothrock 416 ( $\mathrm{F}, \mathrm{f}_{\mathrm{GH}}$; US p.p., with 1 plant of T. leptotes). Custer Co.: high mountain valley, Cusack s.n., 1888 (F); Denver Co.: Denver, 5000 ft . alt., Bethel s.n., 1 May 1894 ( ${ }^{*}$ Ny; us p.p., with 1 plant of T. exscapa). Fremont Co.: Canon City, Brandegee 41 (*? PH p.p., with 2 plants of T. exscapa). Gilpin Co.: Central City, Scovell s.n., 1869 ( $\left.{ }^{\circ} \mathbf{M I C H}\right)$. Gunnison Co.: Sapinero, Wheeler 598 (colo: $\dagger_{\text {rM }}$ p.p., with 2 plants of T. exscapa). Larimer Co.: Foothills (Fort Collins), Crandall 305 ( ${ }^{\circ}$ us p.p., with 3 plants of T. exscapa) ; Horsetooth Gulch, Crandall 3131 (Cs, ${ }^{\text {NY }}$, RM, yU). Mineral Co.: the "Mesa", Creede, Rio Grande National Forest, 8900 ft . alt., Murdock 4503 (DS, F, †MO, US). Idaho. Clark Co.: 3 mi . from head of Medicine Lodge Creek, Range 31 E., Twp. 13 N., Davis 3148 ( $\dagger_{\text {Na }}$ p.p., with 2 plants of T. leptotes). Montana. Cascade Co.: Great Falls, Anderson 203 ( $\dagger$ montu, yu). Dawson Co.: Glendive, Temple s.n., 30 April 1952 (†mont). Gallatin Co.: Bozeman, Tweedy s.n., May 1882 ( $\dagger_{\text {ny }}$ ). Granite Co.: east of Drummond, Rose 30 ( $\dagger_{\text {mo, montu, ws). }}$. Lewis \& Clark Co.: Helena, Kelsey s.n., April 1888 (ds, †pom, UC). Liberty Co.: Cottonwood Coulee, ca. 20 mi . southeast of Chester, Marks s.n., 4 May 1946 (†wis). Madison Co.: Silver Star, Fitch s.n., May 1893 ( $\dagger$ NY). Musselshell Co.: Musselshell City (or Roundup or Petroleum City) Wickland s.n., 28 May 1936 (N.Y.A. Project) ( $\dagger$ montu). Meagher Co.: 9 mi . south, 5 mi . west of White Sulphur Springs, Wright, Cash \& Booth 5469 ( $\dagger$ mont). Park Co.: 8 mi. west of Livingston, Booth s.n., 9 May 1948 (mont, montu, †rm). Powder River Co.: 6 mi . west of Boves, Anderson \& Scharff s.n., 23 April 1952 ( $\dagger$ Mont). Powell Co:: Deer Lodge, along Spencer Creek, Kirkwood 1360 ( $\dagger_{\mathrm{GH}}$, montu). Stillwater Co.: Absarokee, Hawkins s.n., 20 April 1919 ( $\dagger$ mont). Sweetgrass Co.: northeast corner of county, Anderson \& Scharff s.n., 21 April 1952 (†mont). Wibaux

Co.: Wibaux, Blankinship 1503 (†mont). Yellowstone Co.: 7 mi . south of Custer Station, Northern Pacific Railway, Big Horn River, Blankinship 147 ( $\dagger$ mo, mont, us). South Dakota. Custer Co.: Pringle, Black Hills National Forest, 4900 ft. alt., Murdock 3510 ( $\mathbf{F}, \mathbf{G H}, \dagger_{\mathrm{Ny}}$ ). Fall River Co.: 5 mi . southwest of Buffalo Gap, McIntosh 18 (†dao, Rm). Meade Co.: Black Hills, near Ft. Meade, Forwood 93 (tus). Utah. Carbon Co.: Scofield, Jones s.n., 24 June 1904 (ром). Duchesne Co.: Theodore (now Duchesne), benches of the Uintas, 8000 ft . alt., Jones s.n., 13 May 1908 ( $\dagger_{\text {POM) }}$ ). Wyoming. Albany Co.: ca. 12 mi . southeast of Laramie on U. S. Rt. 30, ca. 8800 ft . alt., Beaman \& Preece 508 ( ${ }^{*} \mathrm{ws}$ ); Laramie, Nelson 7055 (мо, Ny, Ром, ${ }^{\circ}$ rm, us). Crook Co.: hillsides near Hulett, 4000 ft . alt., Ownbey 526 (COLO, GH, ids, †MO, MONTU, NY, RM, UC, UTc, ws, wtu). Fremont Co.: 1 mi. south of Pacific Creek, Beaman 884 (GH). Fremont Co. (?): Pilot Knob, Hobbs 5 ( $\dagger_{\mathbf{P H}}$ ). Johnson Co.: hillsides about 8 mi . west of Buffalo, Rollins 408 (mo, ny, †ws). Laramie Co.: bluffs near Chevenne, Havard 10 ( ${ }^{\circ} \mathrm{Ny}$ ). Natrona Co.: 4 mi . west of Alcova, Beaman 877 (Gн). Natrona Co. (?): southwest end of Bate's Hole, Payson \& Payson 4738 ( $\dagger_{\mathrm{rm}}$ ). Park Co.: Shoshone Mountains, Hapeman s.n., May 1907 (†mo). Teton Co.: 11 mi . north of Jackson, ca. 6200 ft . alt., Beaman \& Preece 506 (ws); Black Tail Butte, Moose, Craighead s.n., 25 May 1947 ( $\dagger$ ids). Uinta Co.: near Lyman, 6500 ft . alt., Rollins 1619 ( $\mathrm{GH}, \dagger_{\mathrm{NY}}$ ). Yellowstone National Park: Hills near Mammoth Hot Springs, 6200 ft . alt., Burglehaus s.n., May 1893 (†US, wTU).

Larsen (1927) recognized that Hooker had included two specific elements in his species, Townsendia sericea, upon which he based the genus. She did not recognize, however, that T. sericea was invalid because it included the type of the earlier Aster? exscapus (cf. Beaman, 1954, Cronquist, 1955, and the discussion of T. mensana in the present paper). Thus, the element which was not Aster ? exscapus [Townsendia exscapa (Richards.) Porter] was not described by her. The "new" species, T. Hookeri, is named in honor of the founder of the genus Tounsendia.

To the layman, T. Hookeri is perhaps as well known as any species of Townsendia. In Colorado it is abundant at the base of the Front Range and is one of the first flowers of the year; hence, its name Easter Daisy (applied also to T. exscapa). The botanists' confusion of T. Hookeri and T. exscapa is a result of the great similarity of the two, which may have resulted from extensive hybridization. In addition, over most of their ranges from Wyoming and Nebraska northward, both species reproduce only apomictically. Some specimens are easy to distinguish, but others are more intermediate and may be distinguished only with difficulty.


Maps 10-11. 10. Geographic distribution of sexual and apomictic Townsendia Hookeri. 11. Geographic distribution of sexual and apomictic T. Parryi.

In southeastern Wyoming and the Front Range of Colorado sexual T. Hookeri and sexual T. exscapa occur together. I have not seen the two growing side by side, but several mixed collections such as Bethel s.n., 1 May 1894, Brandegee 41, Crandall 305, Rydberg \& Vreeland 5408, and Weber 3713, indicate that they must grow very close together. Their flowering periods at least partly coincide (both species of the plants of the mixed collections are in flower), and thus conditions to permit hybridization appear favorable. The nature of variation of plants of both species strongly suggests that hybridization has occurred. Field studies should be made to permit a better understanding of the frequency of hybridization and introgression, which, from herbarium material, appear to be important in these two species. As an aid to field population studies, the important characteristics of the pure T. Hookeri and T. exscapa populations are compared in the table below.

Although the dates of collection of the mixed collections of T. Hookeri and T. exscapa from the Front Range of Colorado indicate that the two do flower at the same time, they may be at least partly isolated by differences in flowering period. Dr. Marion Ownbey (in conversation) has indicated that he found T. Hookeri (Ownbey 526, apomictic) in flower on April 27 and noted that
T. Hookeri

Caudex branches very short, or in old plants becoming longer and thicker, appearing smooth to the unaided eye with the matted pubescence of old leaf bases.

Leaves linear or very narrowly oblanceolate, involute, sericeous-canescent.

Heads relatively small, sessile, the involucres ca. 1.5 cm . wide.

Phyllaries linear-subulate, with a tuft of tangled cilia at the apex.

Achenes moderately to densely pubescent.

Disk-corollas ca. 5 mm . long.
Disk-pappus barely exceeding the length of the disk-corollas.
T. exscapa

Caudex branches short, or becoming longer in old plants, but not conspicuously thickened, the leaf bases less pubescent and more completely deciduous than in $T$. Hookeri, thus the branches without the superficially smooth texture of T. Hookeri.

Leaves oblanceolate to narrowly spatulate, not involute, strigose.

Heads relatively large, frequently shortpedunculate, the involucres ca .2 .2 cm . wide.

Phyllaries mostly narrowly lanceolate, without a tuft of cilia at the apex.

Achenes moderately to densely pubescent.
Disk-corollas ca. 9-10 mm. long.
Disk-pappus conspicuously longer than the disk-corollas.
other rather similar plants at the same locality were still in bud. He returned to this locality on May 6 and collected the laterflowering plants which proved to be T. exscapa (Ownbey 534, apomictic). The behavior of these apomicts may indicate that the flowering periods of their sexual precursors are slightly different. Townsendia Hookeri is closely related to T. leptotes. This relationship is evident from a number of characters common to both species. Both have linear or at least very narrowly lanceolate leaves; in both, the phyllaries are very narrow. The habit of both is similar, and the two have a flowering period closely correlated with the beginning of spring. Townsendia Hookeri may have differentiated from a stock close to the present T. leptotes, as a result of isolation of populations on the two sides of the Front Range in Colorado.

The center of diversity of T. exscapa is to the south of Colorado. It probably was well-differentiated from T. Hookeri or the prototype of $T$. Hookeri before the two jointly occupied the area east of the Front Range in Colorado. It is possible, although entirely speculative, that the adaptation of T. exscapa to the Great Plains area has been coupled, through hybridization and apomixis, with the specialization of $T$. Hookeri to a colder environment. A combination of these two characteristics in the apomicts of both species may have permitted their migration far into the plains of Canada. It must be pointed out, of course, that some of the apomicts of the northern regions seem to have most of the characteristics of the pure species. This is particularly true of the apomicts of T. Hookeri in Montana. In that area they are more easily dis-
tinguished from T. exscapa than are some sexual T. Hookeri plants in Colorado. Of the two species, T. exscapa appears to be the one more markedly affected by hybridization.

Townsendia Hookeri is especially difficult to culture in the greenhouse as it merely develops buds which abort before they reach the meiotic stage. A cold treatment of at least two or three months is required to induce preformed buds to continue development and flower. When this species was first collected by Drummond he noted this characteristic. In so far as I know, it has never since been mentioned. Drummond stated (1829, p. 206): "It has a very singular habit, little like that of the genus Aster [he considered it to be Richardson's Aster ? exscapus]; the flower buds are formed in Autumn, and bear an exact similarity to those of Globularia vulgaris." Drummond was disappointed in the small, inconspicuous rays. Many apomicts, and his was one, have rays which do not fully expand.

The geographic pattern of sexual-apomictic distribution of T. Hookeri is a nearly diagrammatic one. The sexual forms occupy a limited area at the southern portion of the range. The apomicts, on the other hand, seem to be excluded from the immediate area where the sexual plants occur (except for highelevation apomicts) but are widely distributed to the north.

## 11. Townsendia exscapa (Richards.) Porter

Townsendia exscapa (Richards.) Porter, Mem. Torr. Bot. Club 5: 321. 1894. Aster? exscapus Richards. Frankl. Journ. Bot. App. 748. 1823. Townsendia sericea Hook. Fl. Bor.-Am. 2: 16. 1834. Type: Richardson s.n., Carleton House, Saskatchewan ( $\dagger_{\mathbf{k}}$, holotype).

Townsendia sericea Hook. $\beta$ papposa A. Gray, Mem. Am. Acad. 4 (Pl. Fend.) : 69. 1849. Type: Fendler 349, arid hillsides, less frequent in grassy places, Santa Fé, Santa Fé Co., N. Mex., April-May 1847 ( ${ }^{\circ} \mathrm{GH}$, holotype; NY, PH, UC, US, isotypes).

Townsendia Wilcoxiana Wood, Bull. Torr. Bot. Club 6: 163. 1877. Tounsendia exscapa Wilcoxiana (Wood) Nels. in Coult. \& Nels. Man. Bot. Rocky Mts. 510. 1909. Type: Wilcox s.n., Camp Supply, Indian Territory (Oklahoma, Woodward Co.), March 1877 (us, holotype).

Townsendia intermedia Rydb. in Britt. Man. 944. 1901. Type: Rich 718, Prairie, Trego Co., Kansas, 1896 ( ${ }^{\circ} \mathrm{Ny}$, holotype; $\mathbf{~ G H , ~ M O , ~}$ RM, US, isotypes).

Rosulate, taprooted perennial; caudex developing several short (or rarely elongated), often subterranean, branches, becoming woody; leaves oblanceolate, sometimes only narrowly so, entire, mucronate, strigose or strigose-sericeous, up to 8 cm . long, averaging ca. $3-3.5 \mathrm{~cm}$., and up to 0.6 cm . wide, rarely with the widest less than 2 mm . wide; heads sessile
or short-pedunculate (in the southern portion of the range), the peduncles rarely more than 3 cm . long; involucres $1.3-3.7 \mathrm{~cm}$. wide, $1-2.2 \mathrm{~cm}$. high; phyllaries in 4-7 series, lanceolate or linear, acute or rarely obtuse, scarious-ciliate-margined, glabrous or lightly strigose on the outer surface, $5-14 \mathrm{~mm}$. long, $1-3.9 \mathrm{~mm}$. wide; ray-florets ca. 20-40; ray-corollas white or pinkish, often with a darker pink, longitudinal stripe on the abaxial surface, glabrous, 1222 mm . long, $1-3 \mathrm{~mm}$. wide; disk-corollas yellow, often pink- or purple-tipped or tinged, $6-11 \mathrm{~mm}$. long; achenes oblanceolate or elliptic, compressed, 2 -ribbed, those of the ray rarely 3 -ribbed, moderately to heavily pubescent with long (or rarely short), duplex, glochidiate (or rarely only very slightly forked) hairs, if papillose only very inconspicuously so, $3.7-6.5 \mathrm{~mm}$. long, $1.0-2.2 \mathrm{~mm}$. wide; pappus of the disk and ray similar, of ca. 20-45 slender, plurisetose, barbellate bristles, $6-13 \mathrm{~mm}$. long, that of the ray usually slightly shorter than that of the disk. $2 n=18$ in sexual plants and $2 n=27-36$ ? in apomictic plants (the latter inferred from pollen measurements). Central Manitoba to southwestern British Columbia and south to northern Mexico and southern Arizona. Map 12. Plate XVII and Plate XXI, fig. 1.

Representative specimens. canada. Alberta. Briggs Creek, Elbow River, Macoun 22787 ( †CAN); Rosedale Coulee, $2200-2500 \mathrm{ft}$. alt., Moodie 839 ( $\mathrm{F}, \mathrm{łGH}_{\mathrm{GH}}$ us); Medicine Hat, Spreadborough 5026 (†Can). British Columbia. 3 mi. north of Athalmer, McCabe 6133 ( $\dagger \mathrm{UC})$. Manitoba. Aweme, Criddle 900 ( $\dagger \mathrm{daO}, \mathrm{mo}$ ); hills southwest of Routledge, 7 mi. east of Virden, Scoggan 11187 (Can). Saskatchewan. Maple Creek, Campbell 129 (†dao p.p., with one plant of $T$. Hookeri); Qu'Appelle Valley, Carmichael R-10 (†dao); 8 mi. south, 1 mi . west of Saskatoon, near Beaver Creek, Frankton 1132 (†DAO); $1 / 2 \mathrm{mi}$. north of North Saskatchewan River, on Highway 5 near Ceepee, Frankton 1300 (†dao); Langham, Fraser s.n., 24 Mav 1938 (†dao); Broadacres, Harrison s.n., 1919 (†dao). mexico. Chihuahua. vicinty of Madera, 2250 m . alt., Palmer 315 in 1908 ( ${ }^{\circ}$ Us); vicinity of Miñaca, Rose 11636 ( ${ }^{\circ}$ us) ; Puerta de St. Diego, 6500 ft . alt., Hartman 591 ( ${ }^{\circ} \mathrm{GH}, \mathrm{us}$ ) ; Puerta de St. Diego, 6500 ft . alt., Hartman $641\left({ }^{\circ} \mathrm{GH}\right)$. united states. Arizona. Apache Co.: near Roof Butte, north end of Tunicha Mts., 2800 m . alt., Goodman \& Payson 2912 (nA). Cochise Co.: west slopes, Burro Mts., Maguire 11575 (GH, ${ }^{\circ}$ NY, UTc, ws, wTU); Huachuca Mts., Orcutt 57 ( ${ }^{\circ}$ Uc) ; Chiricahua Mts., Price s.n., 8 April 1894 ( ${ }^{\circ}$ Ds). Coconino Co.: Jacob Lake, 7925 ft . alt., Barkley d Reed 4372 (GH, ${ }^{\text {montu, na) } ; 1 \mathrm{mi} \text {. south of camp-grounds at Park }}$ Headquarters, Grand Canyon National Park, Jones 800 ( ${ }^{\circ}$ ws); vicinity of Flagstaff, 7000 ft . alt., MacDougal 31 (F, GH, NY, PH, RM, uc, us). Gila Co.: near North Peak, Matzatzal Mts., 1200 m . alt., Collom 290 (GH, місн, ${ }^{\circ}$ мо) ; near Payson, Nelson \& Nelson 2004 (Rм); 12 mi north of Reynolds Creek, Sierra Ancha, 5600 ft . alt., Peebles 13269 (GH, Ny). Mohave Co.: Uinkaret Plateau in vicinity of Mt. Emma, Grand Canyon National Monument, Toroweap, 7200 7600 ft . alt., Cottam 13982 (cas, †ut). Navajo Co.: roadside near Showlow, Foster \& Arnold 285 ( $\dagger_{\mathrm{GH}}$ ); Fort Apache, Shuttleworth s.n., 1892 (us). Santa Cruz Co.: hills between Patagonia and Sonoita,

Nelson d Nelson 1582 (GH, PH, RM, Uc, US, UTC, ws); Sonoita, 4800 ft alt., Peebles \& Fulton 11473 (CAS, F, ${ }^{\circ} \mathrm{GH}, \mathrm{MiCH}$, ny, POM). Yavapai Co.: just north of Prescott, 5200 ft . alt., Barkley 4313 (nA): Prescott, Palmer 601 in 1876 ( ${ }^{\circ} \mathrm{GH}, \mathrm{MO}, \mathrm{yu}$ ). Colorado. Adams Co.: 9 mi . north of Denver, 5500 ft . alt., Gierisch 865 ( ${ }^{*}$ UTc). Alamosa Co.: Morris Gulch, Great Sand Dunes National Monument, 8350 ft . alt., Bean 51-7 ( ${ }^{*}$ Colo). Boulder Co.: $1 / 2 \mathrm{mi}$. east of Hi-Way Mine, 3 mi . south of LaFayette, Weber 3713 (colo p.p., with 3 plants of T. Hookeri). Chaffee Co.: 19 mi . south of Granite, Beattie 13 (*ws); Buena Vista, Harper (?) s.n., May 1886 ( ${ }^{\circ}$ Colo); 2 mi. south of Antero Junction, 9200 ft alt., Weber \& Livingston 6138 ( ${ }^{\circ} \mathrm{colo}$ ). Denver Co.: Denver, Eastwood s.n., May 1888 ( ${ }^{\circ}$ Pом); plains near Denver, 1500 m . alt., Rydberg \& Vreeland 5409 (cs, ${ }^{\circ} \mathrm{NY},{ }^{*} \mathrm{RM}$ ). Eagle Co.: Eagle, Osterhout 4704 (NY, †RM). Elbert Co.: 14 mi . east of Elbert, 6000 ft . alt., Weber 5980 ( ${ }^{*}$ Colo). El Paso Co.: plains, Colorado Springs, Jones 25 ( $\mathrm{NY},{ }^{\circ} \mathbf{P O M}, \mathrm{UTC}$ ); range pasture near Ramah, 6500 ft . alt., Lamm 19389 (Can, ${ }^{\circ}$ RM); near Colorado City, 6100 ft . alt., Moldenke 8192 ( $\dagger_{\mathrm{Ny}}$ ); mesas near Colorado Springs, Rydberg $d$ Vreeland 5408 ( ${ }^{\circ} \mathrm{Ny}$ p.p., with 2 plants of T. Hookeri). Fremont Co.: Canon City, Brandegee 41 ( ${ }^{*} \mathrm{NY}$; ${ }^{\circ} \mathrm{PH}$ p.p., with 1 plant of T. Hookeri). Gunnison Co.: near Gunnison, 7700 ft . alt., Langenheim 1227 ( $\dagger$ colo); Sapinero, Wheeler 598 ( $\dagger_{\text {rм }}$ p.p., with 2 plants of $T$. Hookeri). Hinsdale Co.: Lake City, Pease s.n., 16 May 1878 ( $\dagger_{\mathrm{Ny}}$, tus). Huerfano Co.: hills southeast of La Veta, 2200-2300 m. alt., Rydberg of Vreeland 5407 ( ${ }^{\circ} \mathrm{Ny}$, ${ }^{\circ} \mathrm{Rm}$ ). Lake Co.: Malta Station near Leadville, Osterhout 3197 ( ${ }^{*}$ RM). La Plata Co.: Los Pinos (Bayfield), Baker 730 (F, GH, MO, ND, NY, POM, †rm, us). Larimer Co.: foothills, (Ft. Collins), 6000 ft . alt., Crandall 305 ( ${ }^{\circ} \mathrm{us}$ p.p., with 3 plants of T. Hookeri); plains near foothills, Ft. Collins, Crandall 3132 (cs; *Montu p.p., with 1 plant of T. Hookeri; ny, RM, US, YU) ; foothills west of Ft. Collins, Preston s.n., 28 April 1921 ( ${ }^{\circ} \mathrm{Cs}$ ). Las Animas Co.: hillside about 1 mi . south of western end of Mesa de Maya, Rogers 5647 ( ${ }^{\circ}$ colo). Lincoln Co.: 17 mi . south of Limon, Highway 71, Middle Rush Creek, Maslin s.n., 28 April 1951
 ground, Spruce Canyon, Mesa Verde National Park, Mathias 668 ( ${ }^{\circ}$ мо, Ром). Montrose Co.: hillside, Naturita, 6000 ft . alt., Payson 326 (COL, GH, †mo, rm). Otero Co.: 5 mi . east of La Junta, 4100 ft . alt., Harrington 2494 ( ${ }^{\circ} \mathrm{CS}$ ). Park Co.: Glentivar, in basin, Christ 224 $\left({ }^{\circ} \mathrm{Cs}\right)$. Pueblo Co.: sides of gulches about Pueblo, Woodward s.n., 1883 (ch, ${ }^{\circ} \mathrm{Yu}$ ). Rio Grande Co.: hillside just south of Beaver Creek Campground, Rio Grande National Forest, west of South Fork, 8200 ft alt., Weber \& Livingston 6205 ( $\dagger$ colo). San Miguel Co.: Telluride, Eastwood 5259 (†cas). Sedgwick Co.: vicinity of Ovid, Weber 6037 ( ${ }^{\text {cholo) }}$. Weld Co.: Pawnee Buttes, Mattoon s.n., 3 April 1953 ( ${ }^{\circ} \mathrm{COLO}$ ) ; Windsor, Osterhout 932 ( $\mathrm{NY},{ }^{\circ} \mathrm{RM}$ ) ; vicinity of New Windsor, Osterhout s.n., 11 May 1899 (F, ny, ${ }^{\circ}$ Rm). Kansas. Clark Co.: with-
out definite locality, Curtis s.n., ( ${ }^{\circ}$ mo). Ellis Co.: $2^{1 / 2}$ mi. east of Hays, Bondy 513 (Can, F, ${ }^{\text {Mo, wTU }}$ ); hills 2 mi . west of Hays, Runyon 319 (CM, PH, "rm). Finney Co.: Garden City, Bennett 69 ( ${ }^{\circ} \mathrm{Rm}$ ). Ford Co.: Spearville, collector unknown, 27 April 1886 ( ${ }^{*}$ US). Meade Co.: Meade, Smyth 129 (US). Mitchell Co.: without definite locality, Carleton s.n., April 1888 (ill, ${ }^{\circ} \mathrm{Yu}$ ). Osborne Co.: hills within a radius of 5 mi . of Osborne City, Shear 2 (Gh, mo, ny, rm, "us). Pratt Co.: slope near Cullison, Norris s.n., 31 March 1888 ( ${ }^{*}$ mo). Trego Co.: prairie, Rich 718 (GH, mo, ${ }^{\text {a }} \mathrm{Ny}$, rm, us). Montana. Cascade Co.: Sand Coulee, Anderson s.n., May 1888 ( $\dagger$ montu). Custer Co.: U.S.R.L. Experiment Station, Wind Mill Creek near telephone line, 2300 ft . alt., E.J.W. (U.S. Forest Service collector) s.n., 15 May 1936 (†montu). Gallatin Co.: without definite locality, 5500 ft . alt., Tweedy 20 (mONT, ny; †yu p.p., with 1 plant of T. Hookeri). Nebraska. Brown Co.: Long Pine, Dudley s.n., 7 May 1893 ( ${ }^{\text {D Ds }}$ ). Cherry Co.: Valentine, Bates s.n., 15 April 1891 ( ${ }^{\circ} \mathrm{Ny}$ ). Knox Co. (?) : Fort Niobrara, Wilcox s.n., May 1888 ( ${ }^{\text {CCAN, Ny }}$ ). Lincoln Co.: range south of North Platte, 2900 ft. alt., Kiener 18713 ( ${ }^{\circ} \mathrm{GH}$ ) ; Hershey, Mell s.n., 20 April 1903 ( ${ }^{\circ} \mathrm{US}$ ). Red Willow Co.: McCook, Swezey (?) 59 ( $\dagger \mathrm{Ny}$ ). Sioux Co.: Harrison, Petersen s.n., May 1926 ( ${ }^{\circ} \mathrm{Ny}$ ). Thomas Co.: Halsey, Mell \& Knopf s.n., 1 May 1903 ( ${ }^{\circ}$ mo, oc). Nevada. Lincoln Co.: hillsides, Pioche, 6000 ft . alt., McMillan 436 ( ${ }^{\circ} \mathrm{RsA},{ }^{\circ} \mathrm{Ut}$ ). New Mexico. Bernalillo Co.: Sandia Mts., Albuquerque, 6500 ft . alt., Brooks 2819 ( ${ }^{\circ} \mathrm{CoLO}$ ). Colfax Co.: without definite locality, St. John s.n., May 1893 ( ${ }^{\circ} \mathrm{GH}$ ). Grant Co.: Silver City, Eastwood 8187 ( ${ }^{\circ} \mathrm{Cas}$, GH, mo, us). Hidalgo Co.: 1 mi . east of Monument 66, southeast of former site of Cloverdale, McVaugh d Harvill 8083 ( ${ }^{\circ}$ MICH). Lincoln Co.: Capitan Mtn., Huber s.n., 28 March 1929 ( ${ }^{\circ} \mathrm{PH}$ ). Mora Co.: Shoemaker, Nelson 168 ( ${ }^{\circ} \mathrm{Rm}$ ); Wagon-mound, Nelson 11302 ( ${ }^{\circ}$ RM, UC). Otero Co.: between Mescalero and Cloudcroft, Wiegand \& Wiegand 2665 ( ${ }^{\circ} \mathrm{GH}$ ); Guadalupe Mts. near "Box" triangulation station, Wilkens 1777 (PH). Quay Co.: Nara Visa, Fisher 103 ( ${ }^{\circ}$ us); 15 mi . southwest of Ima, near the QuayDeBaca county line, Norvell 1559 ( ${ }^{\circ}$ ds). San Juan Co.: Aztec, Baker 729 (tus p.p., with 6 plants of T. incana). San Miguel Co.: hill at railroad station, Las Vegas, Gray s.n., May $1885\left({ }^{\circ} \mathrm{GH}\right)$. Sandoval Co. (?): Sandia Mts., mesas and foothills near Madera, Ellis 234 ( ${ }^{\circ}$ Us). Santa Fé Co.: Chamisa Arroyo, 10 mi . southwest of Santa Fé, Goodman s.n., 23 April 1938 ( ${ }^{\circ} \mathrm{NY}$ ). Union Co.: just over line from Oklahoma panhandle, McFarland 68 ( ${ }^{*}$ okl). North Dakota. Billings Co.: Medora, Moran s.n., 22 May 1938 ( окц). Slope Co.: Bad Lands, Marmarth, Moyer 455 (†ny). Stark Co.: prairie, Dickinson, Reiche s.n., 18 May 1942 ( $\mathrm{fuc}_{\text {) }}$. Oklahoma. Beaver Co.: 15 mi . southwest of Beaver, Stevens $358 \frac{112}{\prime}(\mathrm{GH})$. Blaine Co.: on side of draw leading to the Canadian River, 1 mi . north, 1 mi . east, $2^{1 / 2} \mathrm{mi}$. north, and $11 / 2 \mathrm{mi}$. east of Hydro, Beaman 689 (ch). Cimarron Co.: top of Black Mesa, Okla-homa-New Mexico state line, 5000 ft . alt., Goodman 2419 ( OKL). Comanche Co.: Medicine Park, Myers s.n., 20 March 1926 ( ${ }^{\circ} \mathrm{GH}$,
© okl). Wichita Mts., Hopkins, Nelson d Nelson 979 ( ${ }^{\circ} \mathrm{rm}$ ). Custer Co.: hillside in prairie, 3 mi . south and 7 mi . west of Clinton on Highway 66, Waterfall 2554 ( $\mathrm{GH},{ }^{*}$ OKL). Greer Co.: 7 mi . southwest of Jester, Bull 70 ( ${ }^{\circ} \mathrm{OKL}$ ). Harper Co.: hills 10 mi . south of Buffalo, Goodman 2391 ( ${ }^{\circ}$ OKL); near Buffalo, Stevens 307/1/2 ( ${ }^{\circ} \mathrm{GH}$ ). Roger Mills Co.: Red Lands, Engleman 1681 (okl). Woods Co.: hillside near Alva, Stevens 216 (DS, GH, ill, mo, Ny, okl, us). Woodward Co.: vicinity of Camp Supply, Wilcox s.n., 5 April 1905 (CAN, F, ch, MO, NY, PH, "UC). South Dakota. Fall River Co.: slopes just north of Hot Springs, McIntosh 672 ( $\dagger_{\text {rm }}$ p.p., with 2 plants of T. Hookeri). Pennington Co.: prairie near Rapid City, Lee 529 ( ${ }^{\circ} \mathrm{Rm}$ ). Washabaugh Co.: hillsides, Bear Creek, Over 2068 ( † us). Texas. Armstrong Co.: 2 mi . southwest of Triassic Peak, Palo Duro Canyon State Park, 3400 ft . alt., Jespersen \& Jespersen 2653 (Ds, "UC). Bell Co.: Camp Hood, Bergseng s.n., 5 March 1945 (†wis). Brewster Co.: south slopes of hills in Paradise Canyon, 5 mi . west of Alpine, Brown B164 ( ${ }^{\circ}$ SRSC); main canyon east of Mt. Ord, Sierra del Norte, about 10 mi . southeast of Alpine, ca. 800 m . alt., McVaugh \& Harvill 7861 (Ds, mich, na, ${ }^{\circ}$ srsc). Culberson Co.: summits of Guadalupe Mts. above Frijole, 2400 m. alt., McVaugh \& Harvill 8155 (Ds, ${ }^{\circ} \mathrm{GH}, \mathrm{MICH}, \mathrm{NA}$, sRsc). Dickens Co.: hills in southeastern part of county, Engleman s.n., 20 May 1940 (okl). El Paso Co.: Hueco Mts., Thurber 141 ( ${ }^{*} \mathrm{GH}$ ). Hood Co. (?): bluffs, Falls Creek, Reverchon 1533 (ds, F, mo, us). Jeff Davis Co.: Davis Mts., Allen s.n., 14 March 1915 (mich, $\dagger_{\text {Ny }}$ ); hills nears Limpia Creek, Davis Mts., Allen s.n., 14 March 1915 ( ${ }^{\circ}$ mo) ; Davis Mts., HO Canyon, near Sawtooth Mtn., ca. 1900 m . alt., Hinkley s.n., 13 March $1937^{\circ}{ }^{\circ} \mathrm{GH}$ ). Johnson Co.: 15 mi . southwest of Cleburne, Cory 53967 ( ${ }^{\circ}$ ws). Lubbock Co.: Bolls Ranch, 10 mi . southeast of Lubbock, Demaree 7442 ( ${ }^{\circ} \mathrm{Ds}$ ). Presidio Co.: Gage estate, 7 mi . west of Alpine, Buechner s.n., 12 March 1947 ( ${ }^{\text {s SRSC). Randall }}$ Co.: Palo Duro Canyon, Glassman 2280 ( ${ }^{\circ} \mathrm{OKL}$ ). Terry Co.: Brownfield, Wooten s.n., 20 May 1925 (us). Utah. Garfield Co.: Bryce Canyon, Eastwond \& Howell 769-1 (†cas); Bryce Canyon, 6000 ft . alt., Stone $256\left(\dagger_{\mathrm{Ny}}\right)$. Salt Lake Co.: Salt Lake City (this locality incorrect?) Fletcher s.n., 1911 (†Gн). Wyoming. Crook Co.: 1 mi west of Hulett, 4000 ft . alt., Ownbey 534 (COLO, GH, ids, MONTU, Ny, uc, tutc, ws). Laramie Co.: Chevenne, Nelson s.n., June 1904 ( ${ }^{\circ} \mathrm{Rm}$ ).

Some difficulty is met with in an attempt to make entirely certain what material is the type of T. exscapa. The problem becomes apparent from study of the "type sheet" in Kew (Plate XVII). The plants on this sheet have no label which identifies their locality or collector except the words "Carleton House Drummond," in Hooker's handwriting (fide Dr. Rollins). This note at about the middle of the sheet was originally (before the paper was cut and the specimen removed) between two plants of T. Hookeri and two more were above this position on the sheet.


Map 12. Geographic distribution of sexual and apomictic Tou'nsendia exscapa.
One plant of T. exscapa, now cut out and removed (photographs of the two presently missing plants, the cutouts of which fit into the holes on this sheet, may be seen in Larsen's (1927) revision of Townsendia in Plate 7, figs. 29 and 32), was directly below the
note and two more are to the lower left of the sheet. Another plant of T. Hookeri is near the lower right of the sheet. A faint pencil line on the sheet divides the last five-mentioned plants from "Carleton House Drummond" and the top four plants of T. Hookeri. Recently (at the time of or subsequent to Larsen's study) the plants of T. exscapa on the sheet have been marked " 1 " and the note " 1 . Aster ? exscapus Richardson Type." has been placed near the bottom of the sheet. The plants of T. Hookeri are similarly marked " 2 " and in the upper left portion of the sheet identified with the note " 2 . Townsendia sericea Hook. Type." These notes were probably added under Larsen's direction or on the basis of her paper (1927) by Dr. A. W. Hill or Mr. T. A. Sprague of Kew. These are the two members of Kew given acknowledgment by Larsen for assistance.

The type-locality of Aster? exscapus (Townsendia exscapa) is "at Carleton House" (Richardson, 1823). Three recent collections of T. exscapa have been made near Carleton, Saskatchewan (Frankton 1132 and 1300, and Fraser s.n., 24 May 1938). No specimens of T. Hookeri are known from closer than about 240 miles (to the southwest) from Carleton. The plants of T. exscapa on the type sheet in Kew are very similar to those of Frankton 1300. Thus it seems probable that the plants of T. exscapa on this sheet were collected by Richardson at Carleton House. The plants marked "1" on the type sheet are therefore interpreted as the type of Townsendia exscapa (Richards.) Porter. After examining a photograph of this sheet, Dr. A. E. Porsild, whose experience with the collections of Richardson and Drummond is well known, has informed me (personal correspondence) that the interpretation outlined above is the most probable one.

Townsendia exscapa has the widest range and is the most polymorphic of the species of Townsendia. Its degree of diversity approaches that of the combined diversity of many of the other species of the genus. Although the form of T. exscapa sometimes strongly resembles that of T. leptotes and T. Hookeri in certain areas of its range, it is not closely related to these species. Its ancestral stock appears to have become separated from that of the other two at a relatively early time.

The geographic position of the range of T. exscapa is peculiarly and uniquely situated relative to the ranges of the other species of Townsendia. If one considers only the sexual plants of this species, then T. exscapa ranges mainly to the south and east of the other members of the genus. Also, it occurs at rather low elevations, and there are extensive and nearly contiguous areas
both lower and higher than those presently inhabited by the species. Thus, it probably has not had its range fragmented by climatic fluctuations (as may have happened to some of the more northern and higher elevation species). Rather, as a result of climatic changes, it probably has merely migrated to higher or lower elevations as a single interbreeding population. Consequently, it has undergone only regional differentiation, and no populations have had sufficient geographic isolation to permit the fixation of specific or even varietal distinctions.

In spite of its considerable polymorphy, sexual T. exscapa usually is not difficult to determine. The only perplexing specimens from sexual populations are from Chaffee, Lake, and Park counties in Colorado. Superficially these plants resemble T. Hookeri. Their actual morphological variation, however, is in the direction of T. leptotes. Their leaves are relatively short and narrow and their pubescence is light; the heads are small and the phyllaries narrow. In spite of their deviation away from T. exscapa, however, the basic affinity of these specimens seems to be with that species. Only one specimen, Schedin \& Schedin 478 (near Leadville, Colorado), seems almost wholly intermediate. I have referred it to T. leptotes. Field studies near Leadville are needed to amplify the understanding of T. exscapa and T. leptotes in that area.

Leadville is not the only area where T. exscapa and T. leptotes present a problem. West of the continental divide in Colorado, apomixis and hybridization apparently are coupled. Some apomictic collections, such as Baker 730 and Pease s.n., 16 May 1878, are fairly typical T. exscapa. Others, such as Eastwood 5259, Langenheim 1227, and Osterhout 4704, vary strongly toward T. leptotes. Nearly linear, involute, lightly pubescent leaves and narrowly lanceolate phyllaries are found in plants which otherwise have the characteristics of T. exscapa.

Except in the extreme southwest corner, sexual T. exscapa is not known from western Colorado. Apomictic material of this species is fairly widespread in that part of the state. Possibly certain "cold-climate" adaptations of T. leptotes have been fixed in T. exscapa by apomixis. The occurrence of the latter species over western Colorado may be a result of this fixation.

Sexual populations of T. leptotes in southwestern Colorado vary toward T. exscapa. This variation, which probably has resulted from hybridization, is considered in the discussion of the former species. Similarly, putative hybridization of T. exscapa and $T$. Hookeri is considered in the discussion of the latter.

## 12. Townsendia Parryi D. C. Eat. in Parry

Townsendia Parryi D. C. Eat. in Parry, Am. Nat. 8: 212. 1874. Type: Parry 144, Wind River Mts., Wyoming, 9000 ft. alt., July 1873 ([yU ?, holotype, missing] GH, MO, NY, isotypes).

Townsendia Parryi var. alpina A. Gray, Proc. Am. Acad. 16: 83. 1880. Townsendia alpina (A. Gray) Rydb. Mem. N. Y. Bot. Gard. 1: 390. 1900. Type: Parry 145, high divide between Stinking Water and the Yellowstone, Wyoming, 1873 ( $\dagger \mathrm{GH}$, holotype; F, MO, NY, isotypes).

Erect, taprooted biennial, or, infrequently, short-lived perennial; mostly few-stemmed, sometimes single-stemmed or rarely abundantly branched; branches from the base, if also from above, late and weak; stems up to 3.5 dm . high, striate, scape-like, usually conspicuously expanded at junction with the head, lightly to heavily pubescent with pilose-strigose, severalcelled trichomes; basal leaves spatulate, entire or 3 -toothed near the apex, apiculate or mucronate, 1 -nerved, thickish, dark green and shiny, nearly glabrous or pubescent along the veins or moderately strigose on both surfaces, up to 10 cm . long and 1.3 cm . wide; upper cauline leaves much reduced, becoming bract-like near the head, with partly scarious margins; heads large, the first-formed one usually conspicuously the largest; involucres up to 4 cm . wide and 1.8 cm . high; phyllaries in 4-7, mostly 5, series, lanceolate, acuminate or rarely acute, with broad, lacerate-ciliate, scarious margins, $4-16 \mathrm{~mm}$. long, $0.8-3 \mathrm{~mm}$. wide, the next-to-inner series usually longest, usually only the outer 2-3 series lightly strigose; ray-florets 20-70, mostly ca. 40; ray-corollas blue or very rarely white or pink, $12-25 \mathrm{~mm}$. long, $2-4 \mathrm{~mm}$. wide; disk-corollas yellow, $4.0-6.0 \mathrm{~mm}$. long; achenes oblanceolate to narrowly obovate, compressed, $2-3$-ribbed, with a longitudinal ridge frequently produced on one or both faces of the achene from growth pressure of the imbricate achenes against each other, rather densely pubescent with duplex, evenly or unevenly bifurcate hairs, papillose, $3.2-4.7 \mathrm{~mm}$. long, $1.0-2.2 \mathrm{~mm}$. wide; pappus of the ray- and disk-florets nearly equal, of ca. 15-40 plurisetose, barbellate bristles, $4-7.5 \mathrm{~mm}$. long, slightly exceeding the length of the disk-corollas. $2 n=18$ in sexual plants and $2 n=36$ in apomictic plants. lieproduction predominantly apomictic, sexual only in a small area in northwestern Wyoming and adjacent Montana. Southwestern Alberta and adjacent British Columbia south to central Idaho and northwestern Wyoming. Map 11. Plate XXI, fig. 2.

Representative specimens: canada. Alberta. River bar near Waterton townsite, 4100 ft . alt., Breitung 15647 ( $\dagger \mathrm{Ny}$ ); Morley District, mountainside, Dada (Dead?) mans Gulch, near Seebee, 6200 ft. alt., Brinkman 3554 (łus); Milk River, Dawson 7707 (†CAN); head of High River, Rocky Mts., Craig 7708 (łcan); 5 mi . west of Pincher Creek, Moss 804 ( $\ddagger \mathrm{daO}, \mathrm{GH}$, wis); alpine slopes, Upper Red Deer River, east of Scalp Creek, 7200-7600 ft. alt., Porsild 18325 (†Can, GH). British Columbia. Crow’s Nest Pass, 6000 ft . alt., Henry 7 ( $\left.\dagger_{\mathrm{Gh}}\right)$. united states. Idaho. Clark Co.: above basin at head of Webber Creek, west of Argora, 10,000 ft. alt., Cronquist 1979 (mo, futc). Custer Co.: 8 mi . northeast of Dickey, at Double Springs sum-
mit, on ridge rising north of pass, Christ \& Christ 17777 ( $\dagger_{\mathrm{Ny}}$ ) ; on upper slopes of Mt. Borah, Chilly, Christ \& Ward 10442 ( $\dagger_{\mathrm{Ny}}$ ); hillside in Willow Creek Canyon, 8 mi . northeast of Dickey, 8000 ft . alt., Cronquist 3151 (GH, †iDs, mo); Railroad Ridge, 9500 ft. alt., Davis 629 (CAS, †ids, mo, ws); mtn. tops near Challis, 8000 ft alt., Henderson 3680 (†us); meadow over ridge west of head of Mahogany Creek, Lost River Mts., vicinity of Mt. Borah, Hitchcock \& Muhlick 11046 (CAN, CAS, DS, F, GH, †ids, MO, NY, PH, RM, UC, US, UTC, WS, WTU); 7 mi. north of Dickey, Highway 93, Preece \& Turner 2412 (†ws). Fremont Co.: Henry Lake, 6000 ft . alt., Payson \& Payson 2026 (cas, cm, mo, †GH, ny, rm). Lemhi Co.: 9 mi . east of Leadore, Christ $d$ Ward $14823\left(\dagger_{\mathrm{NY}}\right)$; Liberty Mtn., in Lemhi Range west of Gilmore, Christ \& Ward 14872 (NY) ; ca. 4 mi. south of Lemhi, Hitchcock \& Muhlick 9223 (†wtu); knoll near head of Spring Canyon ca. 8 mi . southeast of Gilmore, Lemhi Mts., Hitchcock \& Muhlick 9318 (cas, ny, uc, utc, tws, wtu). Montana. Beaverhead Co.: slopes 10 mi. east of Monida, Nelson \& Nelson 5425 (см, †ds, GH, мо, NY, pom, Rм, uc, us, ws, wTu). Broadwater Co.: summit of grade between Townsend and White Sulphur Springs, Hitchcock \& Muhlick 11858 (can, cas, ds, GH, mo, Ph, fm, ${ }^{\circ}$ UC, utc, ws, wtu). Carbon Co.: meadow 17 mi . southwest of Red Lodge, Beartooth Mts., 8500 ft . alt., Rollins d Muñoz 2825 (Ds, GH, łus). Fergus Co.: meadow on high plateau to east of Half Moon Canyon, Big Snowy Mts., Hitchcock \& Muhlick 11918 (CAN, CAS, ds, Gh, MO, MONT, Ph, RM, UC, UTC, †ws, wTu). Gallatin Co.: Valley View, 1 mi. southwest of Bozeman, Booth 1512 ( ${ }^{\circ}$ mont, montu, utc, ws, wtu); above timberline on Mt. Baldy, near Bozeman, 8500 ft . alt., Brown 551 ( ${ }^{\circ} \mathrm{MiCH}$ ); Bridger Mts., 7000 ft. alt., Rydberg \& Bessey 5132 (Can, f, GH, mont, ${ }^{\circ}$ montu, ny, Ph, rm, us). Glacier Co.: bluffs, Midvale, Umbach 254 (colo, †ds, f, MSC, RM, Us, wis). Lewis and Clark Co.: high cliffs directly south of Gibson Lake, and ca. 3 mi . southwest of Gibson Dam, ca. 25 mi . northwest of Augusta, Lewis and Clark National Forest, Hitchoock 18041 (†rm, rsa, uc, ws, wtu). Liberty Co.: Cottonwood Coulee, 20 mi. south of Chester, Marks s.n., 10 July 1946 (łwis). Madison Co.: $1 / 2$ mile north of Kock Peak, Taylor Mts., Hitchoock \& Muhlick 15170 (Ds, мо, RM, $\dagger_{\text {rsA }}$, UC, ws). Meagher Co.: along Checkerboard Creek, northeast base of Castle Mts., Hitchcock \& Muhlick 12152 (CAN, CAS, DS, GH, MO, PH, ${ }^{\circ}$ RM, UC, UTC, ws, ${ }^{\circ}$ WTU); southwest slope of King's Hill, Little Belt Mts., 7900 ft . alt., Hitchcock \& Muhlick 12340 ( Ph, ws, †wTu). Park Co.: Gardiner, Hawkins 197-i ( $\dagger$ mont); Cooke Guard Station, near Cooke City, Ounbey s.n., 1948 (†ws); near top of hills along Yellowstone River, 19 mi . northeast of Livingston (just south of Springdale), Ownbey 3369 ( ${ }^{\circ}$ ws) ; meadows, Cooke Guard Station, 3 mi . east of Cooke City, 8000 ft . alt., Witt 1162 (rSA, †ws, wTU). Powell Co.: benches bordering Blackfoot River ca. 16 mi. west of Lincoln on Ovando Road, Hitchcock \& Muhlick 11578 (CAN, CAS, DS, GH, ILL, MO, MONT, PH, RM, UC, US, UTC, †WS, WTU).

Silver Bow Co.: hills, Melrose, Shear s.n., 5 July 1895 ( $\dagger_{\mathrm{Ny}}$ ). Stillwater Co.: bluff south of Yellowstone River, 30 mi . southeast of Big Timber (east of Reedpoint), Ownbey 3371 (*ws). Sweetgrass Co.: Wreck Creek, Greycliff, 1200 m . alt., Eggleston 7883 ( ${ }^{\circ} \mathrm{NY}$, us). Wheatland Co.: bench near Big Elk Creek, southwestern part of county, Hitchcock 2360 (cas, ${ }^{\text {M MONTU, pom). Oregon. Wallowa Co.: }}$ ridges of the Wallowa Mts., 7000 ft . alt., Cusick 2295 ( $\mathbf{F}, \mathrm{GH}, \dagger_{\mathrm{mo}}$, msc, nd, rm, uc, us, ws). Wyoming. Big Horn Co.: near Medicine Mtn., 8000 ft . alt., Williams \& Williams 3035 (GH, MO, Ny, hm, †ws, wtu). Fremont Co.: low hilltop, Dickenson Park, Wind River Mts., Rollins \& Costello 2048 ( $\dagger_{\mathbf{G H}, \mathrm{MO}}$ ). Lincoln Co.: ridge near Cottonwood Lake, east of Smoot, 10,300 ft. alt., Payson \& Armstrong 3693 (COLO, GH, ILL, $\dagger_{\text {MO, }}$ MSC, PH, POM, RM). Park Co.: meadow, summit of Clay Butte, west of Beartooth Butte, $10,000 \mathrm{ft}$. alt., Porter 5881 (COLO, DAO, DS, GH, PH, RM, $\dagger_{\text {RSA, }}$ UC, WTU). Sheridan Co.: knoll at top of Red Grade, west of Big Horn, Big Horn Mts., Rollins 511 (†os). Sublette Co.: Wyoming Range, 15 mi . west of Merna, Payson \& Payson 2762 (F, GH, MO, PH, POM, RM, †UC, US). Teton Co.: south slope of Sheep Mtn., 9000 ft . alt., Murie 2828 ( $\dagger_{\mathrm{NA}}$ ). Washakie Co.: upper Ten Sleep Canyon, ca. 7500 ft . alt., Ownbey 805 (rm, łws). Yellowstone National Park: hills near Mammoth Hot Springs, 6000 ft . alt., Burglehaus s.n., July 1893 (ill, Mich, †mo, MSC, Ny, OC, POM, us, UT, wru); hillside, Mammoth, Davis 5332 (†ids, uc); Mammoth Hot Springs, Tweedy 158 ( Ny , ${ }^{\circ} \mathrm{Yu}$ ).

Townsendia Parryi is a relatively unspecialized member of the genus and is most closely related to several morphologically more advanced species. Its relatives mostly occupy more arid habitats than does T. Parryi. The clearly marked features of this species are blurred only by hybridization with T. florifer. The putative hybrids occur in collections from apomictic populations.

The ranges of T. florifer and sexual T. Parryi do not overlap. They most closely adjoin in the corners of northeastern Idaho and northwestern Wyoming. Some of the intermediate plants are found in that area. In addition, a single sexual collection (Tweedy 158) of T. Parryi which shows faintly the influence of T. florifer is also from this area (Yellowstone National Park). In Idaho the probable hybrids are in an area of overlap of the ranges of T. florifer and apomictic T. Parryi in Custer County. The characters of pure T. Parryi and pure T. florifer and their putative hybrids are compared in tabular form below.

The following collections are putative apomictic hybrids of T. florifer and T. Parryi: Burglehaus s.n., July 1893 (місн, mo, NY, POM, US, UT, [wTU is a non-hybrid apomict]); Christ \& Christ 17777 ( NY, p.p., with non-hybrid apomicts) ; Christ \& Ward 14823 (NY); Cronquist 3151 (GH, ids, mO,ws); Hawkins 197-i (mONT);

| T. Parryi | T. florifer | putative hybrids |
| :---: | :---: | :---: |
| Plants few-stemmed. | Plants many-stemmed. | Plants few- to manystemmed. |
| Stems, at least the firstformed ones, thick. | Stems slender. | Stems slender. |
| Phyllaries acuminate, mostly in 5-7 series. | Phyllaries acute, in 2-4 series. | Phyllaries acute or acuminate, mostly in 5-6 series. |
| Ray-corollas blue, glabrous. | Ray-corollas whitishpink, glandular (in the area of the hybrids). | Ray-corollas mostly blue (difficult to determine from herbarium material), glandular. |

Henderson 3680 (us); Hitchcock \& Muhlick 9223 (wTu); Preece \& Turner 2412 (ws). Burglehaus s.n., Hawkins 197-i, and Henderson 3680 are strongly intermediate types, while the others are closer to pure T. Parryi. The fact that these obligate apomicts are not all intermediate between T. Parryi and T. florifer in the same degree suggests that more than one change from sexuality to apomixis after hybridization may have occurred.

The apomictic material (Parry 145) described by Gray as T. Parryi var. alpina also appears to be of hybrid derivation. These plants have pink, glandular ray-corollas and abundant pubescence of long trichomes. The presence of these characters suggests that hybridization has occurred between T. condensata and T. Parryi. Parry 145 was collected near the eastern boundary of Yellowstone National Park where the ranges of sexual T. condensata and sexual T. Parryi most closely approach each other. It should be noted that Larsen (1927) placed T. Parryi var. alpina in synonymy under T. spathulata. It is not that species. On two sheets which Larsen examined ( $\mathbf{M O}$, Рн) it was accompanied by plants of Parry 142 (T. spathulata). The superficial resemblance of these may have caused her misdetermination.

The abundance of apomixis in this primarily biennial species is surprising, but the distribution pattern of the apomictic types is not unusual. The success of the apomicts in populating higher elevations and higher latitudes not occupied by the sexual forms is evident in their geographic distribution (Map 11). However, it is peculiar that apomixis is nearly absent within the range of the sexual types. Within this area a sexual form (Brown 551) has been found even above timberline.

## 13. Townsendia florifer (Hook.) A. Gray

Townsendia florifer (Hook.) A. Grav, Proc. Am. Acad. 16: 84. 1880. Erigeron? florifer Hook. Fl. Bor.-Am. 2: 20. 1834. Aplopappus
florifer (Hook.) Hook. \& Arn. Bot. Beechey Voy. 351. 1840. Stenotus florifer (Hook.) T. \& G. Fl. N. Am. 2: 238. 1842. Type: Douglas s.n., Priest's Rapids of the Columbia ( $\kappa$, examined by Dr. R. C. Rollins).

Townsendia Watsoni A. Gray, op. cit. p. 84. T. florifer (Hook.) A. Gray var. Watsoni (A. Gray) Cronquist, Leafl. West. Bot. 6: 49. 1950. Type: Watson 520, Stansbury Island, Tooele Co., Utah (GH, holotype; us, yu, isotypes).

Townsendia scapigera D. C. Eat. in S. Wats. var. ambigua A. Gray, op. cit. p. 84. T. ambigua (A. Gray) Rydb. Fl. Rocky Mts. 874, 1067. 1917. Type: Ward 523, Rabbit Valley, Wayne Co., Utah, 6800 ft . alt. ( GH , holotype; us, isotype).

Townsendia florifer (Hook.) A. Gray var. communis M. E. Jones, Proc. Cal. Acad. Sci. 5: 697. 1895. Original material: Jones 5315b, 10 mi . south of Coyote, Garfield Co., Utah, 6500 ft . alt. (Us); Jones 5322 f , Kingston, Piute Co., Utah, 5300 ft . alt. (pom, us); Jones 5323, Marysvale, Piute Co., Utah, 6000 ft . alt. (F, мо, мSC, POM, US).

Caulescent, taprooted, winter annual or biennial; stems ascending-suberect, branched at the base and sometimes above, strigose-hirsute, up to 2.5 dm. high; basal leaves spatulate or infrequently oblanceolate, entire, obtuse or acute, sometimes mucronate, strigose, up to 60 mm . long and 12 mm . wide; cauline leaves oblanceolate, spatulate, or linear, strigose, up to 40 mm . long, $1.8-8 \mathrm{~mm}$. wide; heads terminating the stems; involucres campanulate, $15-35 \mathrm{~mm}$. wide (sometimes narrower in late-formed heads), $6.5-14 \mathrm{~mm}$. high; phyllaries in 3-4 (rarely 2) series, pliant in texture, lanceolate, acute, with ciliate or lacerate-ciliate, scarious margins, strigose on the outer surface, $4-12 \mathrm{~mm}$. long, $1-3 \mathrm{~mm}$. wide; ray-florets ca. $15-30$; ray-corollas white to pinkish, usually darker abaxially, frequently glandular on the abaxial surface ( rarely also glandular on the adaxial surface), $8-16 \mathrm{~mm}$. long, $1.5-2.5$ mm . wide; disk-corollas yellow, frequently tipped or tinged with pink, 3.36.3 mm . long; achenes oblanceolate to narrowly obovate, compressed, 2 ribbed, those of the ray-florets rarely 3 -ribbed, pubescent with duplex, bifureate or unequally forked hairs with the prongs not recurved, papillose, $3.5-5.6 \mathrm{~mm}$. long, $1.1-2.1 \mathrm{~mm}$. wide; disk-pappus of ca. 20-49 plurisetose, obcompressed, barbellate or ciliate bristles, 3.5-7.6 mm. long, usually slightly exceeding the length of the disk-corollas; ray-pappus of ca. 20-30 bristles, similar to but shorter than those of the disk-pappus, $2-6.7 \mathrm{~mm}$. long, or of short bristles or squamellae less than 2 mm . long. $2 n=18$. Reproduction sexual. Eastern Idaho to central Washington and south to sonthern Oregon, northeastern Nevada, and southern Utah. Map 13. Plate XXI, fig. 3.

Representative specimens. Idaho. Bannock Co.: Pocatello, Henderson 4105 (cs, GH, RM). Bingham Co.: Blackfoot, Moore (?) s.n., 28 May 1904 (сн). Bonneville Co.: Idaho Falls, Ayres 4460 (ny). Butte Co.: Arco, 5300 ft . alt., Machride \& Payson 3095 (см, GH, мо, ny, rm, us). Canyon Co.: Lowell Butte, near Caldwell, Cronquist 10.3-36 (UTC); near Nampa, Mulford s.n., 1 July 1892 (GH, mo, ${ }^{\circ} \mathbf{N Y}$ ). Clark Co.: Paddock No. 1, U. S. Sheep Experiment Station, S. 27, T. 11 N., R. 36 E., Lingenfelter 541 ( ${ }^{*} \mathrm{NY}$, RSA, ws, wTu). Custer Co.: near Willow Creek, 4 mi . northeast of Dickey, 7000 ft . alt., Cronquist

3147 (Gн, мо); ca. 15 mi . west of MacKay, Hitchcock \& Muhlick 8901 (Can, Cas, ds, Gh, ${ }^{\text {a }}$ NY, RM, UC, UtC, ws, wtu); Custer-Lemhi Co. line, Highway 93, Preece \& Turner 2389 ( ${ }^{*}$ ws). Elmore Co.: King Hill, 2580 ft . alt., Nelson \& Macbride 1129 (CAN, DS, F, GH, MO, MONT, ${ }^{*}$ ny, pom, rm, uc, us). Fremont Co.: hills near St. Anthony, Quayle 41 (DS, POM, RM, UC). Gooding Co.: 8 mi . south of Gooding, Christ \& Ward 7190 (Ny). Jefferson Co.: 10 mi . northwest of Terreton, Christ 12275 ( ${ }^{\circ} \mathrm{NY}$ ). Lemhi Co.: 25 mi . southwest of Salmon, Christ 12231 (ny) ; Birch Creek, R29E, T11N, Davis 3800 (ids, ${ }^{\text {and, }}$ UC, ws). Lincoln Co.: Shoshone, Palmer 562 (us). Minidoka Co.: 7 mi . southeast of Minidoka, Christ \& Ward 7896 (ny). Oneida Co.: 7 mi . west of Holbrook, Christ 12320 (ny). Owyhee Co.: 3 mi. north of Murphy, Christ 9563 (Ny) ; Bruneau, Jones s.n., 23 June 1930 (DS, ${ }^{\circ}$ MO, MONTU, pom, wtu); Reynolds Creek, 5000 ft . alt., Macbride 1017 (Ds, GH, мо, Rм) ; $1 / 2 \mathrm{mi}$. southeast of Grand View, Maguire d Holmgren 26214 (CAN, CAS, COLO, DS, idS, MO, NY, PH, POM, UC, US, UTC, wS, WTU). Payette Co.: New Plymouth, 2200 ft . alt., Macbride 90 (CM, ds, GH, hle, mo, ny, rm, uc, us, ws). Twin Falls Co.: Twin Falls, Bennitt 75 (rm). Nevada. Elko Co.: highway 40, 2 mi . west of Wendover, Cantelow s.n., 10 May 1942 (CAS); vic. Furguson Springs, 4500 ft . alt., Holmgren \& Lund 3 (UTC); 20 mi . west of Goldhill, Utah, 4900 ft . alt., Maguire \& Becraft 2828 (UTC); Silver Zone Pass, 5200 ft . alt., Ripley \& Barneby 4613 (cas). White Pine Co.: 8 mi . west of Baker, $5800-6100 \mathrm{ft}$. alt., Ripley \& Barneby 3569 (cas). Oregon. Baker Co.: Huntington, Sweetser (P) s.n., (UC). Crook Co.: just west of Prineville, Twp. 14 S., R. 15 E., S. 36, 2900 ft . alt., Cronquist 6960 ( ${ }^{\circ} \mathrm{GH}$, ws); Cline Falls, Nelson 815 (Cm, GH, mO, Ny, ${ }^{\circ} \mathrm{Rm}, \mathrm{UC}$ ). Deschutes Co.: 15 mi . north of Bend, ca. 3500 ft . alt., Hitchcock \& Martin 4906 (DS, NA, ${ }^{\circ}$ NY, POM, UC, UTC, ws, wTU). Gilliam Co.: west slope along John Day River, 1 mi . above the mouth of Rock Creek, Twp. 1 N., R. 19 E., Cronquist 6209 (ws). Harney Co.: western slopes north of Squaw Butte, Squaw Butte Experiment Station, Maguire \& Holmgren 26510 (ny, UC, UTC). Jefferson Co.: flats at Cove Palisades, 13 mi. southwest of Madras, Twp. 12 S., R. 12 E., S. 2., 1900 ft . alt., Cronquist 6946 (Cas, ds, ill, rSA, UC, UTC, ws). Lake Co.: hills west of Silver Creek, Cusick 2616 (F, GH, MO, MSC, ND, ${ }^{\circ} \mathrm{NY}$, POM, RM, UC, US, ws). Malheur Co.: near Vale, Leiberg 2067 (GH, MO, NY, PH, UC, US). Morrow Co.: slopes about 10 mi . north of Lexington, Twp. 1 N ., R. 26 E., Cronquist 6593 (ws, wTU) ; near Lexington, 420 m . alt., Leiberg 34 ( $\mathbf{F}, \mathbf{G H},{ }^{\text {© }}$ MO, NY, POM, UC, US). Umatilla Co.: about 20 mi . south of Umatilla, just east of Butter Creek, Twp. 2 N., R. 27 E., Cronquist 6589 (COLO, daO, okl, rSa, utc, ws, wTU). Wasco Co.: near Shaniko, Gale 101 (mo, Ph). Utah. Beaver Co.: Frisco Mine, on Highway 21, ca. 30 mi . west of Milford, 5000 ft . alt., Cottam 4636 (UC); Milford, Goodding 1046 (ch, rm). Box Elder Co.: 20 mi . north of Lucien, Maguire \& Maguire 21518 (Can, GH, ${ }^{\circ} \mathrm{mo}$, NY, Ph, UTC, ws, wTu). Garfield Co.: 10 mi . south of Coyote, 6500 ft . alt., Jones
$5315 b$ (us). Juab Co.: 2 mi . east of Troutcreek, 5000 ft . alt., Maguire \& Becraft 2829 (GH, uTc). Millard Co.: 37 mi . west of Delta, 5200 ft. alt., Maguire \& Becraft 2830 (Ром, "Rм, uc, uTc); Warm Point Ridge, west end Pine Valley, 5 mi. west Hdqts. Desert Range Experiment Station, Maguire 20880 ( $\mathrm{GH},{ }^{\text {o }} \mathrm{Ny}$, UTC). Piute Co.: Marysvale, 6000 ft alt., Jones 5323 (f, mo, msc, pom, us). Sevier Co.: Joseph City, 5500 ft . alt., Jones 6.379 ( ${ }^{\circ}$ мо, ром, us). Tooele Co.: Gold Hill, Jones s.n., 6 June 1917 (ром); Dugway, Jones s.n., 30 May 1891 (cs, GH, POM); Stansbury Island, Watson 520 (GH, US, YU). Tooele or Utah Co.: Mercur, 5500 ft . alt., Jones s.n., 6 June 1896 (ром). Utah Co.: Goshen, Garrett 3955 (ut). Wayne Co.: Rabbit Valley, 6800 ft . alt., Ward 523 ( $\mathrm{ch}, \mathrm{us}$ ). Washington. Adams Co.: Ritzville, 488 m . alt., Sandberg d Leiberg 169 (Can, Cas, F, GH, MO, Ny, PH, Uc, Us, ws). Benton Co.: Columbia River opposite Umatilla, Howell s.n., 29 April 1882 (CAN, CM, F, MO, PH, US). Chelan Co.: slopes near Wenatchee, Cantelow s.n., (wTU). Franklin Co.: hillside, Kahlotus, Cotton 1013 (us, ws). Grant Co.: slopes north of Soap Lake in Grand Coulee, Thompson 11498 (CAS, DAO, DS, ${ }^{\circ}$ GH, MO, MONT, MONTU, NA, NY, PH, pom, rsa, us, ws, wTu). Kittitas Co.: near Vantage, Thompson 13707 (f, GH, MO, NY, US). Klickitat Co.: Columbia River opposite Willows, Howell s.n., 18 April 1880 (GH). Lincoln Co.: slopes at Almira, Thompson 11666 (cas, ds, mo, ny, pom, wtu). Walla Walla Co.: hills, Wallula, Cotton 1034 (us, ws). Yakima Co.: ravine near Highway 97, on Logy Creek, Hitchcock \& Martin 3386 (Ds, NA, POM, RM, RSA, UC, ws, WTU).

Townsendia florifer is a sharply defined species and may be determined with ease. It has been taxonomically troublesome, however, when attempts have been made to distinguish T. Watsoni A. Gray from T. florifer. The type of T. Watsoni (Watson 520 ) is from near the center of the geographic range of T. florifer and is intermediate in the gamut of morphological variation of $T$. florifer. It cannot, therefore, be maintained at the specific or varietal level.

Townsendia florifer is closely related to T. Parryi. The two species occasionally have been confused, apparently because of hybridization between them. This is considered in the discussion of T. Parryi. The close phylogenetic relationship of T. florifer and T. scapigera is considered in the discussion of the latter species.

Townsendia florifer is common and has been abundantly collected along the Snake River Plains of Idaho and in central Oregon and western Utah. It flowers mostly in May and June. Between Hinkley, Utah and the Utah-Nevada boundary, I made arbitrary stops every 10 miles for 70 miles, during the summer of 1954. A plant or two of $T$. florifer was found at three of these stops. At two non-arbitrary stops plants were also found. It
appears that the species is ubiquitous in that area. It probably is abundant only in moist seasons.


Maps 13-14. 13. Geographic distribution of Townsendia florifer and sexual and apomictic T. scapigera. 14. Geographic distribution of sexual and apomictic T. incana.

## 14. Townsendia scapigera D. C. Eat. in S. Wats.

Townsendia scapigera D. C. Eat. in S. Wats. Bot. Expl. Fortieth Parallel, 145, pl. 17. 1871. Type: Watson 518, Trinity Mts., 5000 ft. alt., Pershing Co., Nevada, May 1868 (yu, holotype; us, isotype).

Townsendia scapigera var. caulescens D. C. Eat. in S. Wats. ibid. p. 145. Type: Watson 519, Monitor Valley, 5000 ft . alt., Nye Co., Nevada (yU, holotype; GH, NY, us, isotypes).

Cespitose, taprooted biennial or short-lived perennial; much-branched and densely leafy at the base, sometimes with a well-developed woody caudex with prominent leaf scars; leaves spatulate, entire, obtuse, sometimes mucronate, infrequently emarginate, strigose, up to 70 mm . long (averaging ca. 30 mm .) and 9 mm . wide (averaging ca. 5 mm .) ; peduncles from the ends of the stems, naked or infrequently with 1 or 2 reduced leaves, striate, strigose or pilose, more densely pubescent near the head, slightly expanded near the junction with the head, up to 1.2 dm . long; involucres obconicalcampanulate, $12-32 \mathrm{~mm}$. wide, $7-14 \mathrm{~mm}$. high; phyllaries in $3-4$ (rarely 5) series, pliant in texture, lanceolate, acute, with lacerate-ciliate, scarious margins, strigose or pilose-strigose on the outer surface, $3-13 \mathrm{~mm}$. long, $1-2.8 \mathrm{~mm}$. wide; ray-florets ca. 18-35; ray-corollas whitish, pinkish, or dull red, densely glandular on the abaxial surface, 6.5-16 mm. long, $1.5-2.4 \mathrm{~mm}$. wide; disk-corollas yellow, frequently pink-tipped or tinged, $3.6-5.4 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 -ribbed, those of the ray-florets rarely 3 -ribbed, pubescent with long, thin, duplex, bifurcate hairs, papillose,
3.8-5.6 mm. long, 1.1-2.0 mm. wide; pappus of ca. 20-30 plurisetose bristles, the bristles awl-shaped, obcompressed, densely barbellate or ciliate; raypappus $3.1-6.2 \mathrm{~mm}$. long; disk-pappus slightly longer than the ray-pappus, $5.0-7.2 \mathrm{~mm}$. long, slightly exceeding the length of the disk-corollas. Reproduction mostly sexual, rarely apomictic. Nevada and eastern California. Map 13. Plate XXI, fig. 4.

Representative specimens. California. Inyo Co.: Teufel Canyon, Inyo Mts., 25 mi. northwest of Darwin, 4600 ft . alt., Jaeger s.n., 28 May 1938 ( Ром); Teufel Canyon, southern Inyo Mts., 5200 ft . alt., Jaeger s.n., 27 May 1939 (ds); Seep Hole Spring, Invo Mts., Kerr s.n., May 1940 ( ${ }^{\circ} \mathrm{Cas}$ ); Reed Flat and 1 mi . south of Reed Flat, White Mts., $10,000 \mathrm{ft}$. alt., Roos \& Roos 5120 (Ds, *RSA, UC); Westgard Pass, 7000 ft . alt., Alexander \& Kellogg 2492 (uc, ws); Westgard Pass, summit of ridge above small canyon, 7300 ft . alt., Alexander d Kellogg $2492 a$ (DS, UC); Mazourka Canyon, 7800 ft . alt., Alexander \& Kellogg 2993 ( $\mathbf{m O}$, ${ }^{\text {r rm, uc, us, UTC) ; Cerro Gordo Peak, crest of }}$ divide above Cerro Gordo Mines, 8000 ft . alt., Alexander \& Kellogg 3020 (Uc). Modoc Co.: Ft. Bidwell, Austin s.n., April 1878 (GH); Buffalo Ravine, near Surprise Vallev, Lemmon 29 ( ${ }^{\circ} \mathrm{mo}$, yu); Warner's Ranch, Lemmon s.n., May 1879 (Uc). Mono Co.: western side of Sweetwater Canyon, 10,500 ft. alt., Alexander \& Kellogg 3959 ( $\dagger_{\mathrm{Uc}}$ ); top of divide east of Deep Creek, 11,200 ft. alt., Alexander dr Kellogg 4053 (Gh, mo, rm, tuc, utc, wtu); divide, 1 mi . north of Mt. Patterson, $11,000 \mathrm{ft}$. alt., Alexander \& Kellogg 4556 (мо, Uc) ; east of Swamp Meadows, 9500 ft . alt., Alexander \& Kellogg 4561 (Gн, " мо, ve, UTC); 15 mi . north of Mono Lake P. O., on Conway Grade (to Bridgeport), ca. 7500 ft . alt., Blake 11831 (ds). Plumas Co.: without definite locality, Austin s.n., 1880 (Ny). Nevada. Elko Co.: north of Deeth, upper Humboldt Vallev, 5350 ft. alt., Hall 10365 ( ${ }^{*} \mathrm{UC}$ ); Cobre, 6000 ft . alt., Jones s.n., 16 June 1906 (РОм); mesas and hills, near Cave Creek Post Office, Ruby Valley, Mason 4694 (uc). Esmeralda Co.: between Pinchot Creek and Pinon Hill on road to B. \& B. Mine, 6700 ft . alt., Duran 2758 ( ${ }^{*} \mathrm{UC}$ ); Magruder Mtn. south end of the Silver Peak Range, 8200 ft . alt., Maguire $d$ Holmgren 25640 (GH, Ny, uc, ${ }^{\circ}$ UTC). Eureka Co.: Palisade, Jones s.n., 14 June 1882 (ром). Humboldt Co.: 5 mi . north of Farnham Hot Springs, Quinn River Valley, 5000 ft . alt., Train TC4 (us). Lander Co.: Victory Highway, 20 mi . east of Battle Mountain, Eastwood \& Howell 175 (cas). Mineral Co.: top of ridge, north, overlooking Hawthorne, 9500 ft . alt., Alexander \& Kellogg 4440 ( ${ }^{\circ} \mathrm{Uc}$ ); Mount Grant, Wassuk Range, $10,000 \mathrm{ft}$. alt., Archer 7130 (vc); road west to Laphan Canyon rim along north basin, edge of Laphan Meadows, west slope of Mt. Grant, Wassuk Range, 9400 ft . alt., Train 4178 (rsa, vC). Nve Co.: 4 mi . south of Millett, 5500 ft . alt., Lindsdale \& Linsdale 690 (cas, utc); west slope, Toquima Range, mouth of Mariposa Canvon on Manhattan-Round Mountain road, 5700 ft . alt., Train 27.38 (Ny, uc, utc, wTu). Pershing Co.: Rochester,
mtn. slopes, 4000 ft . alt., Train R30 (us); Trinity Mts., 5500 ft . alt., Watson 518 (Ny); Pah-Ute Mts., 5500 ft . alt., Watson 518 (ch). White Pine Co.: Warm Springs, King s.n., May 1918 (cas).

Townsendia scapigera is morphologically closest to the central Oregon populations of $T$. florifer. In that area the stem leaves of T. florifer are few and the base of the plant is very leafy. Only a slight change from that condition would be required to produce T. scapigera. In northeastern Nevada, on the other hand, where the ranges of $T$. scapigera and $T$. florifer most closely adjoin, the two species are more distinct. The stems of T. florifer in that area are abundantly leafy upward and not very leafy at the base. This conspicuous difference between $T$. scapigera and T. florifer in that area is a further reason for maintaining a specific rather than a varietal distinction between them. More collecting in northern Nevada and southern Oregon will be required to elucidate completely the status of the two species.

Townsendia scapigera attains a considerable degree of diversity in the mountains of Inyo and Mono Counties in California. This diversity has already been noted by Heiser (1948). He suggested that apomixis might be involved. It is involved, but probably is not important in increasing the diversity of these populations. The large plants in the mountains of Mono County probably have become differentiated from the smaller plants in the mountains of Inyo County largely as a result of geographic semi-isolation.

In Inyo County especially, one might expect the development of different ecotypes. In that county, plants have been collected as low as 4600 ft . elev. (Jaeger s.n., 28 May 1938) and as high as $10,000 \mathrm{ft}$. (Roos \& Roos 5120 ). This is the greatest elevational range in a species of Townsendia. If ecotypes have developed, they are not very apparent in herbarium material, however. The only obvious feature is that the low-elevation plants are smaller and shorter-lived than those from higher elevations.

Apomixis in this primarily biennial species parallels the correspondingly small amount in another biennial, T. grandiflora. Apomixis in these species is rare, and occurs only in plants of high elevations. In the Sweetwater Mountains of California, plants from the summit or very near the summit of the mountains are apomicts. Morphologically very similar sexual plants (Alexander \& Kellogg 4561) occur on a protected knoll about 1000 ft . below the summit of the mountains. The apomicts must have some adaptational qualities, not present in the sexual plants, which better suit them to the tops of these mountains.

## 15. Townsendia condensata D. C. Eat. in Parry

Townsendia condensata D. C. Eat. in Parry, Am. Nat. 8: [106 nom. nud.] 213. 1874. Type: Putnam s.n., Washakies Needles, Owl Creek Range, Hot Springs Co., Wyoming, 1873 (yu, holotype; †GH, isotype).

Townsendia anomala Heiser, Madroño 9: 240. 1948. Type: von Schrenk s.n., Holm Lodge, about 40 mi . west of Cody, Park Co., Wyoming, 26 Aug. 1922 (mо, holotype).

Rosulate-pulvinate, taprooted, short-lived perennial; caudex becoming moderately branched, sometimes elongate, often subterranean; stems few and very short or sometimes nearly absent in alpine plants, or sometimes numerous and several-branched in lower-elevation plants; leaves spatulate with a short, abruptly expanded blade portion and a longer, narrow, petiolelike portion, obtuse or rarely acute, lightly to very densely villous-woolly with simple, several-celled trichomes with conspicuous end-walls, $12-35 \mathrm{~mm}$. long, $2-4 \mathrm{~mm}$. wide; heads in alpine plants mostly sessile and embedded in the tufts of leaves, in plants of lower elevations the first-formed head usually sessile, the later, lateral heads terminating the stems in a corymbose manner; involucres $10-40 \mathrm{~mm}$. wide, $8-18 \mathrm{~mm}$. high; phyllaries in $3-5$ series, lanceolate or sometimes linear, acuminate or less often acute, scarious- and long-ciliate-margined, abundantly pubescent with long, several-celled trichomes with conspicuous end-walls, $4-14 \mathrm{~mm}$. long, $0.5-2.8 \mathrm{~mm}$. wide; ray-florets ca. 12-100; ray-corollas whitish or pink to light lavender, glandular on the abaxial surface, $8-16 \mathrm{~mm}$. long, $1.5-3 \mathrm{~mm}$. wide; disk-corollas yellow, sometimes pink-tinged, $4-6.5 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 ribbed, those of the ray florets sometimes 3 -ribbed, moderately pubescent with bifurcate or entire, duplex hairs, papillose, 3.2-4.5 mm. long, 0.8-1.3 mm . wide; pappus of the ray- and disk-achenes similar, of ca. 20-35 plurisetose, barbellate bristles, deciduous in a ring around the apex of the achene, 4.4-8.0 mm. long. $2 n=18$ in sexual plants and $2 n=36$ ? in apomictic plants. Reproduction predominantly apomictic, rarely sexual. Mostly at high elevations, western Montana and Wyoming to east-central California. Map 15. Plate XXIII, figs. 2 and 3.

Representative specimens. California. Mono Co.: western side of Sweetwater Canyon, $10,500 \mathrm{ft}$. alt., Alexander \& Kellogg 3953 (fuc); top of divide east of Deep Creek, 11,200 ft. alt., Alexander \& Kellogg 4061 ( fuc$)$ ) ; R. 34 E., T. 5 S., Sec. 2, White Mt. U.S. G.S. $^{\text {S }}$ Map, $11,500 \mathrm{ft}$. alt., Duran 1662 (tuc); north slopes of Sheep Mt., White Mts., Maguire \& Holmgren 26109 (łutc). Idaho. Custer Co.: saddle near head of Rock Creek, ca. 1 mi . northwest of Mt. Borah, Beaman 89.3 ( $\dagger_{\mathrm{ch}}$ ); Lost River Mts., 1 mi . west of Borah, at summit of Saddle between Rock and Mahogany Creeks, $10,800 \mathrm{ft}$. alt., Hitchcock \& Muhlick 10977 (cas, ds, †ny, rm, uc, utc, ws, wtu). Montana. Glacier Co.: Aberkuny [Appekunny Mtn.], Glacier Nat. Park, 8000 ft alt., Evans s.n., 16-30 July 1924 ( $\mathrm{t}_{\mathrm{F})}$ ). Park Co.: Ram Pasture Mtn., on the Wyoming border, northeast of Cooke City, Witt 1884 (†ws). Wyoming. Fremont Co. (?): Wind River, Parry 143 (Gн). Hot Springs Co.: Washakies Needles, Owl Creek Range,

Putnam s.n., 1873 ( $\dagger_{\mathrm{GH}}$, yu). Park Co.: south-facing slope near Holm Lodge on Crossed-Sabre Ranch, 8 mi . east of the east entrance of Yellowstone National Park, 7000 ft . alt., Beaman \& Preece 503 (GH, ${ }^{*}$ ws); Holm Lodge, about 40 mi . west of Cody, von Schrenk s.n., 26 Aug. 1922 (mo).

This species has long been problematical to the few botanists who have seen it. Some of its peculiar characters are shared with the related and almost equally rare species, T. spathulata. This similarity led Larsen (1927) to consider T. condensata to be the same as T. spathulata. She stated (p.23) that the head size is of no value for specific demarcation between the two species. This notion was occasioned by her confusion of material of a third species, T. Parryi, with these two. She reduced T. condensata and T. Parryi var. alpina ( $=$ T. Parryi) to T. spathulata apparently because the head size of the plants of T. Parryi was intermediate between the other two species. Townsendia condensata and T. spathulata may be distinguished by head size and by several other characters as well. These are given in tabular form below.

Townsendia condensata
Short-lived perennial.
With or without conspicuous caudex and often with conspicuous lateral stems.

Phyllaries acuminate.
Primary heads large, involucres (of the primary heads, at least) more than 1.7 cm . wide.

Townsendia spathulata
Long-lived perennial.
With caudex densely matted with the old and new leaves.

> Phyllaries acute or only slightly acuminate.

> All heads small, the involucres less than 1.6 cm . wide.

Townsendia condensata is known almost entirely from alpine, apomictic material. Fortunately, attention was called to a sexual population of the species in Park County, Wyoming when Heiser (1948) described T. anomala. The material on which Heiser's species is based is a little different from the alpine apomicts of T. condensata. However, the differences are only in the degree of pubescence and length of stems, and both of these characters vary from population to population in the apomicts. If T. spathulata had not been confused with $T$. condensata at the time of Heiser's investigation, he probably would have been able to associate his material with the latter species.

Sexual material of $T$. condensata probably will be found also in Fremont County, Wyoming. Parry 143, from the Wind River


Maps 15-16. 15. Geographic distribution of sexual and apomictic Townsendia condensata and sexual and apomictic $T$. spathulata. 16. Geographic distribution of T. mexicana.

Valley, is a single dried-up plant, but it is much like the presentlyknown sexual population in Park County. The Wind River Valley has a number of habitats similar to that in Park County where the sexual population is now known to occur. Further collections in western Wyoming will be required to solve the problems of location and diversity of sexual plants of this peculiar little species.

A feature not apparent in sexual material of $T$. condensata grown in its native habitat becomes apparent in greenhouse cultures. Under these conditions it does not remain a pulvinate little mass, but instead develops a single, erect, leafy stem which later branches at the base. This habit reveals a close, but otherwise not too obvious, relationship with T. Parryi. Once the similarity in habit has been noted, other indications of this relationship become more evident. Additional features the two have in common include the long-acuminate phyllaries, large heads, and bifurcate achenial hairs.

## 16. Townsendia spathulata Nutt.

Townsendia spathulata Nutt. Trans. Am. Phil. Soc. 7: 305. 1840. Type: Nuttall s.n., "On the Black Hills, (an alpine chain toward the sources of the Platte.)", 1834. (bм, holotype, examined by Dr. R. C. Rollins; GH!, PH!, isotypes).

Densely rosulate-pulvinate, taprooted perennial; caudex becoming several-branched, obscured by the dense tufts of new leaves and the persistent dead leaves; leaves spatulate, entire, acute or obtuse, mucronulate (usually hidden by the pubescence), densely pubescent with a villouswoolly or sericeous pubescence of simple, multicellular trichomes with conspicuous end-walls, $7-20 \mathrm{~mm}$. long, $1.5-4 \mathrm{~mm}$. wide; heads embedded in the leaves and appearing sessile but usually on very short peduncles not over 10 mm . long; involucres $8-16 \mathrm{~mm}$. wide, $6.3-10 \mathrm{~mm}$. high; phyllaries in 3-4 series, mostly lanceolate, sometimes narrowly ovate or elliptical, acute or very slightly acuminate, scarions- and lacerate-ciliate-margined, the cilia sometimes long and tangled, lightly or densely pubescent with long, simple, multicellular trichomes, $3-9 \mathrm{~mm}$. long, 0.8-2.5 mm . wide; ray-florets ca. 12 30; ray-corollas pinkish, brownish orange, or lavender, often glandular on the abaxial surface, $2-3$-toothed, $6-12 \mathrm{~mm}$. long, $1.5-3 \mathrm{~mm}$. wide; diskcorollas yellow and usually pinkish or reddish tinged, $3.8-5.3 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 -ribbed, moderately pubescent with short, duplex, bifurcate or glochidiate hairs, densely papillose, $2.8-4.1 \mathrm{~mm}$. long, $1-1.5 \mathrm{~mm}$. wide; pappus of the ray- and disk-florets similar, of ca. 14-30 plurisetose, barbellate (sometimes with recurved barbs) bristles, deciduous in a ring around the apex of the achene, $4.5-6.2 \mathrm{~mm}$. long. Reproduction sexual and apomictic. Fremont, Natrona, and Sweetwater Counties, Wyoming. Map 15. Plate XXIII, fig. 4.

Representative specimens. Wyoming. Fremont Co.: Beaver Hill, 32.5 mi . southeast of Lander, Beaman 880 (cн); 1 mi . south of Pa-
cific Creek, Beaman 883 (GH); open ridges, 1 mi . south of Pacific Springs, Porter 4544 (†gh, †rm, rsa, wtu); South Pass, Wind River Mts., 7650 ft. alt., Ripley \& Barneby 7965 (* and fcas). Fremont Co. (?): Wind River, Parry 142 (F, GH, MO, NY, ${ }^{\text {PPH, yU }}$ ). Natrona Co.: 4 mi . west of Alcova, Beaman 878 (GH); on the Satanka Formation ca. 4 mi . west of Alcova, 5400 ft . alt., Porter 4428 ( ${ }^{\circ} \mathrm{DAO}, \mathrm{GH}$, ${ }^{\text {orm, rat }}$ wtu). Sweetwater Co.: Bush Ranch (near Steamboat Mtn.), Nelson 7094 (†rm).

Although T. spathulata and T. condensata are amply distinct species, they are closely related. The confused history of the two gives one indication of that relationship. The following similarities between the two give further indication: spatulate leaves, densely pubescent with long, simple, multicellular trichomes with conspicuous end-walls; bifurcate or entire achienial hairs (although some populations of T. spathulata have glochidiate hairs ); very deciduous pappus; conspicuously papillose achenes. Even though sexual $T$. condensata seems to be rarer than T. spathulata, the former species is the more generalized type. Townsendia spathulata appears to have become specialized to conditions on the relatively arid plains of central Wyoming.

The type-localities of this and the other Nuttall species have been considered with the history of the genus. An additional feature, which concerns only this species, was merely mentioned there. In the specimen Ripley \& Barneby 7956, from South Pass, Fremont County, Wyoming, two plants on the sheet differ in certain minor features from a third. A pollen examination revealed that the one represents apomictic and the other two sexual material. In examining the Nuttall type-material of this species in the British Museum, Dr. Rollins noted (on a slip of paper now with the Gray Herbarium material of T. spathulata): "I would say that there is the possibility of 3 of the 4 plants belonging to one thing and the other to another. The three are less dense, less wooly etc." In these same features the plants of Ripley d Barneby 7956 differ. The sexual plants are less dense and less woolly. In addition, the ray-corollas of the sexual plants are densely glandular and those of the apomicts are nearly glabrous. Also, the raycorollas of the sexual plants are more fully expanded than are those of the apomicts. Is it possible that Ripley and Barneby have sampled the same populations of sexual and apomictic plants which yielded Nuttall's type-collection of this species?

It seems likely that Nuttall collected this species in more than one locality. The plants of the type collection in the British Museum are in flower. Nuttall's specimens in the Gray and Phila-
delphia Academy Herbaria are well past flowering. Ripley d Barneby 7956 in flower was collected on June 14 and Porter 4428 in flower was collected on May 9. Dr. Porter's material from near Alcova, Natrona County, Wyoming, grew at an elevation about 2000 ft . lower than South Pass where Ripley and Barneby made their collection. Possibly Nuttall first collected T. spathulata at a low elevation after it had flowered. As he proceeded west he may have obtained flowering material from some higher station. This higher station could be South Pass, through which his expedition traveled.

## 17. Townsendia incana Nutt.

Townsendia incana Nutt., Trans. Am. Phil. Soc. 7: 305. 1840. Type: Nuttall s.n., "On the Black Hills, (an alpine chain toward the sources of the Platte.)", 1834 (bм, holotype, examined by Dr. R. C. Rollins; GH!, PH!, isotypes).

Townsendia Fremontii T. \& G., Bost. Journ. Nat. Hist. 5: 106. 1845. Original material: apparently collected in Wyoming by Fremont on his first expedition in 1842 (GH).

Townsendia arizonica A. Gray, Proc. Am. Acad. 16: 85. 1880. Type: Palmer 204 in 1877, Trumbull, Mohave Co., Arizona ( ${ }^{\circ} \mathrm{GH}$, lectotype; "MO, NY, US, syntypes).

Townsenda arizonica $X$ incana M. E. Jones, Zoe 2: 248. 1891. Type: Jones s.n., south Little Colorado, Navajo or Apache Co., Ariz., 9 June 1890 ("Ром, holotype).

Townsendia incana Nutt. var. ambigua M. E. Jones, Zoe 4: 264. 1893. A variety based on several vaguely designated collections.

Townsendia diversa Osterhout, Bull. Torr. Bot. Club 55: 75. 1928. Type: Osterhout 6116, hills south of Grand Junction, Mesa Co., Colo. ( ${ }^{\mathrm{rmm}}$, holotype).

Pulvinate or suberect, taprooted, perennial (rarely biennial); caudex becoming much-branched, sometimes subterranean; stems mostly conspicuously canescent, sometimes long and much-branched; leaves narrow spatulate or oblanceolate, entire, acute, mucronate, moderately to densely strigose, up to 45 mm . long and 5 mm . wide; heads mostly terminal on the stems, infrequently pedunculate; involucres campanulate, $8-19 \mathrm{~mm}$. wide, $7-14 \mathrm{~mm}$. high; phyllaries in $3-4$ (rarely 5) series, lanceolate, acute, scari-ous- and lacerate-ciliate-margined, strigose on the outer surface, $3-12 \mathrm{~mm}$. long, $1-3.6 \mathrm{~mm}$. wide; ray-florets ca. $10-30$; ray-corollas mostly white on the adaxial surface and often with an abaxial median pink stripe, $7-13 \mathrm{~mm}$. long, $1.5-3 \mathrm{~mm}$. wide; disk-corollas yellow and often pink-tinged, 3.7-6.5 mm . long; achenes oblanceolate, compressed, 2 -ribbed, pubescent with duplex, Elochidiate hairs, $3.0-4.7 \mathrm{~mm}$. long, $1.0-1.8 \mathrm{~mm}$. wide; ray-pappus of ca. 15-3. plurisetose, barbellate bristles, 0.3-6.3 mm. long, often of different lengths on the same achene, not as long as the disk-pappus; disk-pappus of ca. 15-35 plurisetose, barbellate bristles, slightly exceeding the length of the disk-corollas. $2 n=18$ in sexual plants and $2 n=27,28,29$, ca. 30 ,
and 36 in apomictic plants. Central Wyoming southwest to Nevada and central Arizona. Map 14. Plate XXII, fig. 1.

Representative specimens. Arizona. Apache Co.: Water Lily Canyon, 35 mi . northeast of Kayenta, Burton s.n., Aug. 1934 ( $\dagger_{\mathrm{NA}}$ ); 5 mi . west of Rock Point, Cutler 2196 (cas, GH, †mo, us); Navajo Indian Reservation, about the north end of the Carrizo Mts., Standley 7332 ( $\dagger_{\mathrm{Ny}}$, us). Coconino Co.: ca. 24 mi . north of Flagstaff, Beaman 971 ( ${ }^{*} \mathrm{GH}$ ) ; 6 mi . west of Grand Canyon Bridge, Marble Canyon, 3800 ft . alt., Benson 129 (†uc); Moqui Wash, 8 mi . west of Winslow, 5000 ft . alt., Darrow 2699 ( ${ }^{*}$ CAs) ; 6 mi. south of Kaibito, Navajo Indian Reservation, 6300 ft . alt., Darrow 2730 ( $\mathrm{f}_{\mathrm{CAS}}$ ) ; U. S. Highway 89 along Vermilion Cliffs about 19 mi. east of Jacob Lake, Ferris 10262 (†Ds); between Winslow and Flagstaff, McKelvey 4507 ( ${ }^{\circ} \mathrm{GH}$ ) ; 15 mi . northeast of Tuba City, 5450 ft . alt., Kearney \& Peebles 12889 ( $\dagger$ mich, Ром) ; 2 mi . east of Ashfork, Preece \& Turner 2617 ( ${ }^{*}$ ws). Mohave Co.: brink of Toroweap Fault, Kanab Plateau, Grand Canyon National Monument, Toroweap, 6300 ft . alt., Cottam 14026 ( ${ }^{\text {U }}$ UT); Hackberry, Jones 4516 (ds, "NY, POM, RM, uc, Us, UTC); Peach Springs, Lemmon \& Lemmon s.n., June 1884 ( ${ }^{*}$ and tuc, ${ }^{*}$ us). Navajo Co.: Betatakin, Howell 24451 ( ${ }^{\circ} \mathrm{CAS}$ ); south of Winslow, Peebles 9535 ( ${ }^{\circ} \mathrm{MICH}$ ); Monument Valley on the Utah-Arizona line, Howell 24731 ( $\dagger$ cas). Yavapai Co.: Clemenceau, W. W. Jones s.n., 10 July 1922 ( ${ }^{\text {UUC }}$ ); Smelter Grounds, W. W. Jones s.n., 19 July 1922 ( ${ }^{\circ}$ MO, UC, Us). Colorado. Delta Co.: Hotchkiss, 6000 ft . alt., Cowen 337 ( $\dagger \mathrm{yu}$ ). Eagle Co.: McCoy's, Osterhout 2761 ( ${ }^{*}$ RM) ; Eagle, Osterhout 4716 ( $\dagger_{\mathrm{RM}}$ ). Garfield Co.: mountain between Loma and junction to Varnal Highway, $6000-9000 \mathrm{ft}$. alt., Cottam 5997 (†ut); 3 mi . northwest of Carbondale, Langenheim 2020 ( †colo); west-facing slope, along Government Creek, 5 mi . north of Rifle, 1900 m . alt., Weber 3319 (cas, colo, cs, †rasa, utc, ws). Gunnison Co.: hillside 15.6 mi . west of Gunnison on Highway 50, Preece \&Turner 2795 ( $\dagger$ ws). Grand Co.: Kremmling, Osterhout 3497 ( ${ }^{*}$ RM). Mesa Co.: 1.4 mi . inside Colorado National Monument on road from Grand Junction, Beaman $801\left(\dagger_{\mathrm{GH}}\right) ; 1 \mathrm{mi}$. outside Colorado National Monument toward Glade Park, Beaman 802 ( ${ }^{\circ} \mathrm{GH}$ ) ; Grand Junction, Eastwood s.n., Mav 1891 (†pom, US); 5 mi. west of Gateway in southern part of county, 4300 ft alt., Harrington 4362 ( ${ }^{\circ} \mathrm{COLO}$ ); Grand Junction, Jones s.n., 15 April 1891 (†pom); 4 mi . south of Mesa, 7800 ft . alt., Rollins 2190 (DS, GH, ${ }^{\circ} \mathrm{NA},{ }^{\circ}$ US, UTC). Moffat Co.: Craig, Osterhout 5117 (†rm); canyon near confluence of Green and Yampa Rivers, ca. 7000 ft . alt., Porter 3620 ( $\dagger \mathrm{DS}$, GH, RM, uc, us, wtu). Montezuma Co.: McElmo Creek, Eastwood s.n., June 1892 (†ром); entrance of Mesa Verde National Park, Nelson 10419 a (Gh, MO, $\dagger_{\text {NY, }}$ rm, UC). Montrose Co.: Naturita, 5400 ft alt., Payson 242 (CM, COLO, GH, MO, MONT, †RM, ws); hills near Montrose, 5800 ft . alt., Payson 657 ( $\dagger_{\mathrm{rm}}$ ); Paradox, 5400 ft . alt., Walker 90 (DS, $\mathbf{~ c h}$, mo, ny, pom, †rm, us) ; bench above San Miguel River, 24 mi . northwest of Naturita, Weber 3566 (COLO, CS, DS, MONTU, OKL, PH, †RM, RSA, UC,
utc, ws). Rio Blanco Co.: south side of White River, 2 mi . southeast of mouth of Wolf Creek, 6000 ft . alt., Graham 9039 (cm, † fA ); bluff by White River, 23 mi . east of Rangely, 5500 ft . alt., Ripley \& Barneby 7783 (†cas). San Miguel Co.: Norwood Hill, 7000 ft. alt., Walker 448 (DS, GH, †mO, NY, ром, RM, US); ridgetops, Gypsum Valley, 4 mi. east of Gypsum Gap, T 44 N, R 16 W, east of Gladel, Weber 4725 ( $\dagger$ colo, hsa, uc, ws, wtu). Nevada. Lincoln Co.: Panaca, Jones s.n., 6 Sept. 1912 (†ром); Cathedral Gorge, north of Panaca, 5000 ft . alt., Ripley \& Barneby 6344 (tcas). Nye Co.: Tonopah, 6000 ft . alt., Shockley 103 ( $\dagger \mathrm{Uc}$ ). New Mexico. McKinley Co.: Gallup, Eastwood 5628 (†cas). Sandoval Co.: Jemez Biological Camp, Jemez Mts., Castetter 1170 (†rm). San Juan Co.: Aztec, Baker 729 (†mo, ny, pom, rm; us p.p., with 1 plant of T. exscapa). Utah. Beaver Co.: Frisco, Jones s.n., 1880 ( ${ }^{\circ} \mathrm{GH}$ ) ; Milford, 5000 ft . alt., Jones 1794 (CM, mo, "Ny, Ph, POM, us, UTC, "ws, yu ). Carbon Co.: Price, Flowers F1830 (*UT) ; Sunnyside, Jones s.n., 15 Nov. 1907 (†ром); 4 mi. north of Price, Maguire \& Maguire 18342 (CAN, †NY, uTC). Daggett Co.: base of cliff, Sheep Creek, 12 mi . south of Manila, 6000 ft . alt., Hitchcock et al. 3913 (DS, na, †wtu). Duchesne Co.: Myton, 5000 ft alt., Jones s.n., 20 May 1908 (†ром). Emery Co.: $1 / 2$ mi. north of the San Rafael River crossing along the Hanksville-Greenriver Road, Holmgren, Boyle, d Will 7768 (tuTc); Orangeville, 6000 ft . alt., Jones 5464 c (POM, fus); first fork of Calf Springs Canyon, San Rafael Swell, Maguire d Maguire 18.303 (GH, $\dagger_{\mathrm{NY}}$, us, utc, ws). Garfield Co.: wash east of Escalante, 5500 ft . alt., Cottam 4402 ( $\dagger \mathrm{uc}, \mathrm{ut}$ ); west slopes of Henry Mts., 5500 ft . alt., Cottam 5524 ( (tut); open forest, northwest rim of Bryce Canyon, 8000 ft . alt., Degener \& Peiler 16533 ( $\dagger$ мо) ; 7 mi . east of Escalante, Holmgren d Nielson 7736 ( $\dagger$ Uc, UTC); 25 mi. southeast of Hanksville, Colorado River Rim, Parry s.n., 6 June 1941 (ny, futc); 5 mi . north of Hatch, 7000 ft . alt., Ripley \& Barneby 8537 (†cas). Grand Co.: Thompson, Jones s.n., 7 May 1891 ( ${ }^{\circ}$ ром) ; Westwater, 4400 ft . alt., Jones s.n., 28 June 1898 (†fom); Moab and vicinity, $1200-1500 \mathrm{~m}$. alt., Rydberg d Garrett 8444 ( $\dagger_{\mathrm{NY}, \mathrm{RM}, \mathrm{UC}) \text {. Iron }}$ Co:. Cedar City, Parry 94 ( $\mathrm{GH}, \dagger_{\mathrm{mo}}$, yu). Kane Co.: 8 mi . north of Kanab, Eastwood \& Howell 9270 ( $\dagger \mathrm{Cas}$ ); 2 mi . east of Zion Park, east entrance, Highway 15, Preece \& Turner 2510 ( $\dagger \mathrm{ws}$ ). Piute Co.: Marysvale, 7000 ft . alt., Jones $5355 q$ (tus). San Juan Co.: at Natural Bridge north of Montecello, Clover \& Jotter 2007 ( $\dagger$ Mich); without definite locality, 4300 ft . alt., Cottam 5816 ( ${ }^{\circ} \mathrm{NA}$ ); along San Juan River, near Bluff, 1200-1500 m. alt., Rydberg \& Garrett 9962 (ny, RM, fut). Sevier Co.: near Belknap, 6000 ft . alt., Stokes s.n., 10 June 1900 (†Ds, NY, us); Richfield, 5500 ft . alt., Ward 176 (Gн, $\dagger_{\text {mo, }}$ PH, us). Uintah Co.: hills east of Dinosaur National Monument, 5000 ft alt., Graham 7563 ( $\mathrm{CM}, \nmid \mathrm{NA}$ ); ridge, east side of Green River, Island Park, 5000 ft . alt., Graham 9194 (CM, †mo, na). Wayne Co.: plains, edge of Green River Desert about 5 mi . northeast of Hanksville, ca. 1500 m . alt., McVaugh 14563 (cas, †ny); Fruita Arch Canyon, Ma-
guire \& Maguire 18123 (GH, NY, US, tutc). Wyoming. Fremont Co.: canyon side above Wind River, 16 mi . southeast of Dubois, Beaman $\&$ Preece 507 ( $\dagger \mathrm{ws}$ ); hillside near Black Buttes Mill Site, 20 mi . north of Shoshoni, 5200 ft . alt., Freytag 78 ( $\dagger_{\text {rim }}$ ); Badwater (probably Badwater Creek near Lysite), Nelson s.n., 26 June 1910 (†rm); Riverton, Nelson s.n., May 1920 (†rm). Natrona Co.: 4 mi . west of Alcova,
 water Co.: 6 mi north of McKinnon, Goodman 3105 ( $\dagger_{\mathrm{MO}}$, $\dagger_{\mathrm{Ny}}$ ); hills near Rock Springs, 6200 ft . alt., Larsen 17 (†rm); Granger, Nelson 4622 ( $\mathrm{ch}, \dagger_{\mathrm{Mo}}$ Ny, rm, us). Uinta Co.: Ft. Bridger, Nelson 4599 (CM, CS, MONT, $\dagger_{\text {NY, }}$ POM, RM).

Apomicts of T. incana usually are easy to determine as that species; sexual populations sometimes are more difficult. A most-ly-sexual geographic segment of this species which has long caused taxonomic difficulties is located in northern Arizona. Gray described these plants as $T$. arizonica and distinguished them from T. incana by their long ray-pappus. Subsequently, long-raypappus forms of T. incana from many parts of its range were referred to T. arizonica. It is evident from the material now available that the ray-pappus length is much too variable to be a useful taxonomic character in T. incana.

Larsen (1927) accepted T. arizonica and referred some of the western Colorado specimens of T. incana to T. arizonica. Her key was designed to separate the two by leaf length and shape. However, the vigor of the plant influences these characters which are not constant, even in obligate apomicts. In addition, Larsen did not distinguish T. annua and T. Fendleri from T. strigosa, and her key does not satisfactorily separate many specimens of T. strigosa (as she understood it) from T. incana.

The most atypical portion of T. incana is represented by three sexual collections, Rollins 2190 and Osterhout 2761 and 3474, from northwestern Colorado. The habit of these plants is unlike that of typical T. incana. The former have short, thick caudices, not unlike T. exscapa. The heads, borne on short peduncles, are somewhat embedded in the tufts of leaves. In their other features these plants are characteristic of T. incana. They are from relatively high elevations and possibly represent elevational and geographic polymorphy in T. incana.

Another sexual population which diverges from typical T. incana is Jones 1794 from Beaver County, Utah. These plants are distinctive because of their reduced size and very heavy, canescent pubescence. The apomicts in this area are morphologically more typical of T. incana.

A small amount of variation in T. incana is not attributable to geographic differentiation. In San Juan County, Utah two collections, Cottam 5816 and Holmgren 3183, are intermediate between T. annua and T. incana. Although these plants seem to be shortlived perennials, their general aspect is that of T. annua. The disk-pappus of Holmgren 3183 is shorter than the disk-corollas, a characteristic of T. annua. The stems are canescent, and the phyllaries are in 4-5 series, characteristic of T. incana. Hybridization of the two species in this area therefore seems probable.

The ranges of T. incana and T. annua overlap in an extensive area, and their flowering periods coincide. Probably they are at least partly interfertile. Herbarium material, however, suggests that hybridization is very rare. The great abundance of apomixis, or more directly, the rarity of sexual material of T. incana probably restricts the frequency of hybridization between these two species.

It is possible that some of the T. incana populations in Mesa County, Colorado and Grand County, Utah have been affected through hybridization with T. strigosa. Several collections from this area are of suberect plants, characteristic of $T$. strigosa but not of T. incana. However, since some of the best characters for distinguishing these two species involve the habit, it is very difficult, with as variable a species as T. incana, to be reasonably sure, on the basis of herbarium specimens, that hybridization has occurred. Jones s.n., 7 May 1891 (Grand Co., Utah) is an example of possible crossing. Five plants of this collection ( POM 39664) are fairly typical T. incana. A sixth plant has a swollen root-stem junction with persistent, broad basal leaves, resembling T. strigosa. This plant retains the canescent pubescence of $T$. incana.

Townsendia incana occurs at elevations from approximately 4000 to 8000 ft . It is especially abundant on the Colorado Plateau in sandy soils amidst junipers and piñons. It flowers in the spring and summer at times when sufficient moisture is available, usually in May and early June. Some flowering material, however, has been collected in April, July, August, and September. All material which has been available for greenhouse and garden cultures exhibits a more or less indeterminate flowering period. Some plants lived and flowered in the greenhouse for as long as two years.

Townsendia incana is most closely related to T. Fendleri. The latter was probably derived from ancestral stock nearly or quite like the former species. No other species are very closely related to these two.

## 18. Townsendia Fendleri A. Gray

Townsendia Fendleri A. Gray, Mem. Am. Acad. 4 (Pl. Fendl.): 70. 1849. Type: Fendler 350, gravelly hillsides, Santa Fé, Santa Fé Co., New Mexico, May-July 1847 (Gн, holotype; mo, Uc, isotypes).

Caulescent, decumbent or suberect, or infrequently rosulate, taprooted perennial (or sometimes biennial?); caudex becoming much-branched, often subterranean; stems much-branched, short or becoming elongate, strigose or pilose-strigose, sometimes canescent, up to 3 dm . long; leaves narrowly oblanceolate to nearly linear, entire, acute, mucronate, mostly involute, strigose, up to 35 mm . long and 3.5 mm . wide; heads terminal on the stems; involucres campanulate, $6.4-13 \mathrm{~mm}$. wide, $5.0-8.5 \mathrm{~mm}$. high; phyllaries in 4-5 series, lanceolate or ovate-lanceolate, acute, ciliate and broadly scarious-margined, strigose on the outer surface, $2.7-8 \mathrm{~mm}$. long, $1-3 \mathrm{~mm}$. wide; ray-florets ca. 10-25; ray-corollas white on the adaxial surface and with an abaxial pinkish or blue-purplish streak, 4.8-10 mm . long, $1-2.5 \mathrm{~mm}$. wide; disk-corollas yellow, infrequently pinkish-tinged, $2.0-3.5 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 -ribbed, 2.1-3.2 mm. long, $0.8-1.2 \mathrm{~mm}$. wide, pubescent with duplex, glochidiate hairs; ray-achenes more densely pubescent than those of the disk, papillose (the disk-achenes infrequently minutely papillose); ray-pappus of connate-coroniform squamellae or short, plurisetose bristles up to 1.5 mm . long; disk-pappus of ca. 15-25 plurisetose, barbellate bristles, $2.4-3.5 \mathrm{~mm}$. long, shorter than the disk-corollas. Reproduction sexual. South-central Colorado and north-central New Mexico. Map 4. Plate XXII, fig. 2.

Representative specimens. Colorado. County unknown: valley of the Arkansas, Wolf 517 (F, POM, us). Chaffee Co.: Salida, Baker, Earle \& Tracy 1016 (F, MO, NY, POM, US); Salida, Osterhout 3424 (DS, GH, NY, POM, "rm) ; Arkansas River near Poncha Pass, Jones 767 (CAS, CM, COLO, DS, GH, ${ }^{\circ}$ MO, NY, OC, POM, UTC); hills southeast of Buena Vista, lower end of Trout Creek Cn., Penland 4352 (colo); ridge along the Arkansas River, 8 mi . northwest of Salida, Waterfall 11511 (okl, rsa, "uc). Fremont Co.: Texas Creek, Brandegee 951 ( MO, PH, UC); sandbar, Canon City, 5280 ft . alt., Brandegee s.n., June 1876 ( ${ }^{\circ} \mathrm{UC}$ ). Huerfano Creek, Brandegee 1294 (GH, MO, UC). Pueblo Co.: Pueblo, Bethel s.n., 2 July 1897 ( ${ }^{\circ} \mathrm{Cs}$ ). New Mexico. Rio Arriba Co.: Ghost Ranch, Rio Chama drainage, Goodwin s.n., 24 Aug. 1932 ( ${ }^{\circ} \mathrm{GH}$ ) ; 13 mi . south of Cebolla, Ripley \& Barneby 10294 (cas); Ojo Caliente, 6000 ft . alt., Smith s.n., 27 Aug. 1894 (PH). Sandoval Co.: 6 mi . west of San Ysidro, 5500 ft . alt., Ripley \& Barneby 8344 ( ${ }^{\circ} \mathrm{Cas}$ ); San Ysidro, Nelson 11619 ( ${ }^{\circ}$ RM, uc). Santa Fé Co.: Santa Fé, Degener 4689 (Ny); near Española, 5600 ft . alt., Heller \& Heller 3547 (nd, ny; us p.p., with 1 plant of T. annua); 2 mi . north of Santa Fé, ca. 7000 ft . alt., Hitchcock et al. 4186 (na, ${ }^{\circ} \mathrm{wtu}$ ).

Since Larsen (1927) made no distinction between T. annиa and T. strigosa, and considered T. Fendleri a worthless taxon, she reduced the latter to T. strigosa. Her confusion, of course, was between T. annua and T. Fendleri. No modern material of these
species is difficult to determine. However, some of the specimens she had, especially Brandegee 951 and Jones 767 have considerably longer stems than is usual for T. Fendleri. In addition, on one sheet she examined ( mo 121087) Brandegee 951 was accompanied by the following undated scribbled note in Gray's handwriting: "951 fits much of my Townsendia strigosa well. I dare say Fendleri will not be very Im'pt.!" This note, and the poor specimens mentioned above, must have influenced Larsen to reduce T. Fendleri. In the confusion, Brandegee 1094 further complicates matters; mo 121070 with the number 1094 is clearly T. Fendleri. Brandegee 1094 in the New York Botanical Garden Herbarium and the Philadelphia Academy Herbarium is clearly T. аппиа. A Brandegee collection in the Gray Herbarium without a number but with essentially the same label data "Adobe plains, San Juan R." is also T. annua. Brandegee 1294 (GH, мо 121088, uc) Huerfano Creek, Huerfano Co., Colo., is T. Fendleri. It is probable that Brandegee 1094 is not actually a mixed collection of the two species. Very likely, because of the similarity of the numbers 1094 and 1294, the label 1094, with its accompanying data, was erroneously transferred to specimen mo 121070 which should be Brandegee 1294. The high degree of similarity of the two plants on this sheet to Brandegee 1294 supports this idea. Moreover, it is improbable that T. Fendleri occurs on the "adobe plains" of the San Juan River valley.

In most areas, and in most collections, T. Fendleri and T. annua are easily distinguishable. But around Santa Fé, New Mexico, where their ranges overlap, the two species closely resemble each other. Tounsendia Fendleri especially seems to approach T. annua. The mixed collection, Heller \& Heller 3547 from near Santa Fé, indicates a considerable similarity of the two. ${ }^{2}$ Townsendia Fendleri is probably not a perennial in that area, while it is in the other portions of its range. In northern New Mexico it may have obtained genes for a shorter life-cycle from T. annua. Except in that area the two species probably are fairly well isolated geographically. Tounsendia Fendleri occurs at moderate elevations mostly within the piñon-juniper belt while T. annua occurs at lower elevations below the piñons and junipers.

Although T. annua and T. Fendleri have been confused because of their similarity, the closest relationship of T. Fendleri seems to be with T. incana. These two species are allopatric (considering the range of the sexual forms of T. incana only)

[^32]and T. Fendleri probably is a specialized, reduced form from more generalized $T$. incana stock. The habit of the two species (at least of some forms of T. incana) is almost identical. The differences are mainly quantitative ones, paralleling those between T. strigosa and T. annua.

## 19. Townsendia strigosa Nutt.

Townsendia strigosa Nutt. Trans. Am. Phil. Soc. 7: 306. 1840. Type: Nuttall s.n., "On the Black Hills, (or eastern chain of the Rocky Mountains,) near the banks of the Platte.", 1834 (bм, holotype, examined by Dr. R. C. Rollins; GH!, pH!, isotypes).

Townsendia incana Nutt. var. prolixa M. E. Jones, Contrib. West. Bot. 13: 15. 1910. Type: Jones s.n., Chepeta Well, Uintah Co. (?), Utah, 6000 ft . alt., 23 May 1908 ( ${ }^{\text {POM, holotype). }}$

Caulescent, taprooted biennial; root-stem junction enlarged; stems branched at the base, few to moderately numerous, branched again just below the heads in a cymose manner, mostly spreading-suberect, usually red with cyanic pigments, striate, strigose-pilose, up to 2 dm . long; basal leaves persistent, oblanceolate or spatulate, entire, mucronate, obscurely 1-3-nerved, lightly to moderately strigose on both surfaces, up to 45 mm . long and 7.0 mm . wide; cauline leaves similar, smaller, often clustered immediately below and overtopping the fastigiate heads; involucres $5-20 \mathrm{~mm}$. wide, $5-10 \mathrm{~mm}$. high; phyllaries in 3-4 series, elliptic-ovate to lanceolate, acute or rarely slightly acuminate, with broad, scarions, lacerate-ciliate margins, $2.5-9 \mathrm{~mm}$. long, $1.5-3.0 \mathrm{~mm}$. wide, the inner longer than the outer, the outer moderately strigose on the abaxial surface, the inner only slightly if at all pubescent near the mid-axes and apices; ray-florets ca. 12-30; raycorollas white to pink, often darker near the base and with a darker longitudinal streak on the abaxial surface, $5-14 \mathrm{~mm}$. long, $1.5-2.8 \mathrm{~mm}$. wide; disk-corollas yellow or mottled with pink, 3.3-5.0 mm . long; achenes oblanceolate, compressed, 2 -ribbed, those of the ray-florets rarely 3 -ribbed, moderately pubescent with duplex, glochidiate hairs, those of the ray-florets generally slightly more pubescent than those of the disk-florets, both generally papillose, $3.0-4.0 \mathrm{~mm}$. long, $0.8-1.3 \mathrm{~mm}$. wide; pappus of the rayachenes of short, plurisetose, barbellate bristles mostly connate at the base, rarely exceeding 1.6 mm . in length; pappus of the disk-achenes of ca. 20-35 plurisetose, barbellate bristles, $3.3-5.5 \mathrm{~mm}$. long, mostly equalling or slightly exceeding the length of the disk-corollas, rarely shorter. Reproduction mostly sexual, rarely apomictic. Northeastern Utah and southwestern Wyoming, probably also in adjacent northwestern Colorado. Map 17. Plate XXII, fig. 3.

Representative specimens. Utah. Carbon Co.: 9-mile Canyon, 5000 ft . alt., Jones s.n., 22 May 1896 ( ${ }^{\circ} \mathrm{POM}$ ). . Duchesne Co.: north of Duchesne along the Victory Highwav, Osterhout 6196 ( ${ }^{\circ}$ RM). Uintah Co.: 5 mi . northwest of Dinosaur National Monument, 5500 ft . alt., Graham 7671 ( NA p.p., with 2 fragments of T. incana); bench west of Green River, south of mouth of Sand Wash, 5000 ft . alt., Graham 7946 (CM, ${ }^{\circ} \mathrm{NA}$ ) ; eastern slope of Big Pack Mountain, west of Willow

Creek, Thorne's Ranch, Uinta Basin, 5500 ft . alt., Rollins 1705 ( ${ }^{\circ} \mathrm{GH}$, ny). Wyoming. Carbon Co.: Solon, Williams s.n., July 1897 ( ${ }^{\circ}$ Rм) . Sublette Co.: roadside, Big Piney, Payson \& Payson 4350 ( $\dagger$ gh, мо, msc, ph, †rm, ws). Sweetwater Co.: Green River, Nelson 3031 ( ${ }^{\circ} \mathrm{GH}$, ill, mo, ny, ${ }^{\text {rm, us }}$ ) ; Green River, Nelson 4724 ( ${ }^{\text {chm, cs, mont, }}$ pom, ws); 21 mi . west of Green River, Payson \& Armstrong 3205 (GH, ill, MO, MSC, PH, POM, ${ }^{\text {r }}$ RM) ; desert about 40 mi . south of Rock Springs, on the Hiawatha road, Porter 457.3 (dao, gh, "rm, rsa, wtu). Uinta Co.: 6 mi . out of Mountainview toward Lonetree, Holmgren \& Tillett 9474 ( ${ }^{*}$ Uc, UTC); hillside near Lyman, 6500 ft . alt., Rollins 1636 (Ds, ${ }^{\text {a }} \mathrm{NA}$, us, ws).

Townsendia strigosa is not restricted to the Green River shales, but it occurs mostly within the bounds of the Green River formation in northeastern Utah and southwestern Wyoming. From the


Map 17. Geographic distribution of Townsendia annua and sexual and apomictic T. strigosa.
observations of Mr. and Mrs. W. L. Bartholomew (personal communication), residents of the Uinta Basin of Utah, I have learned that the species is abundant in that area. It flowers in May and early June, and often occurs in fairly dense, conspicuous stands. It sometimes is mixed among apomictic plants of T. incana and sometimes occurs in pure stands. Sheep browse the plants, and by the end of June scarcely any standing plants are to be found.

Some variation in this species, especially near Green River, Wyoming, suggests hybridization with T. annua. Most of the plants of Nelson 3031 and 4724 have the disk-pappus shorter than the disk-corollas. Some plants have ovate phyllaries, in others the phyllaries are merely broadly lanceolate. The short disk-pappus and ovate phyllaries are characters of T. annua. One other specimen, Jones s.n., 22 May 1896, from Carbon County, Utah, very close to the range of T. annua, also has ovate phyllaries. Although T. strigosa and T. annua are allopatric, hybridization could be expected between them. Their ranges adjoin and there is no geographic barrier. They are very similar and probably have no strong genetic barriers to interbreeding.

Townsendia strigosa is closely related to T. annua, which is an evolutionarily more advanced species. The two have no other very close relatives. Townsendia strigosa superficially resembles T. florifer but is readily distinguished from that species by its glochidiate rather than bifurcate achenial hairs. It has been confused with T. incana; however, these two species are distinct enough so that no confusion is necessary.

As might be expected in a biennial, apomixis is unimportant in T. strigosa. It is interesting, but of minor significance, that the only known apomictic collection is from the northernmost station in the range of the species.

## 20. Townsendia annua Beaman, sp. nov.

Type: Maguire 13509, sand bed of Cottonwood Wash, vicinity of Wayland's Ranch, $1 \frac{112}{2}$ mi. north of Bluff, San Juan Co., Utah, April 19, 1936 ( ${ }^{\circ} \mathrm{GH}$, holotype; CAN, PH, UC, UTC, wTU, isotypes).

Caulescent, taprooted annual; stems few to numerous, prostrate to ascending, branching at the base and above, minutely striate, strigose, $0.2-2.5 \mathrm{dm}$. long; basal leaves short-lived, oblanceolate or spatulate, entire, often mucronate, lightly strigose on both surfaces, up to 3 cm . long; cauline leaves similar to, but usually slightly smaller than, the largest basal leaves, longer-persistent, more or less evenly distributed on the stems, but appearing clustered on young branches below unexpanded heads, usually not surpassing expanded heads; heads terminating the leafy stems, or pedunculate on inconspicuous peduncles; involucres $8-16 \mathrm{~mm}$. wide, $4.5-7.5 \mathrm{~mm}$. high,
broadly expanded at maturity; phyllaries in 3, rarely 2-4, series, elliptical, obovate or ovate, obtuse, acute, or rarely slightly acuminate, the margins scarious and ciliate at least above, $2-6.7 \mathrm{~mm}$. long, $1-2.6 \mathrm{~mm}$. broad, the outer shorter than the inner, lightly or rarely moderately strigose-pilose on the outer surface, the inner series nearly or entirely glabrous; ray-florets ca. 12-30; ray-corollas white to pink or light lavender, often with a darker longitudinal streak on the abaxial surface, $5-9 \mathrm{~mm}$. long, $1.5-2.7 \mathrm{~mm}$. wide; disk-corollas yellow, sometimes pink- to purple-tipped, $2.3-3.7 \mathrm{~mm}$. long; achenes oblanceolate to obovate, compressed, 2 -ribbed, those of the ray-florets rarely 3 -ribbed, lightly to moderately pubescent with duplex, glochidiate hairs, those of the ray-florets often slightly more pubescent than those of the disk-florets, both, especially those of the ray-florets, often papillose, $2.0-2.8 \mathrm{~mm}$. long, $0.6-1.2 \mathrm{~mm}$. wide; pappus of the ray-achenes of short, plurisetose, barbellate bristles, rarely exceeding 1 mm . in length; pappus of the disk-achenes of ea. 15-28 plurisetose, barbellate bristles, 1.83.0 mm . long, very rarely equalling the length of the disk-corollas. Reproduction sexual. East-central Utah south to southern Arizona, New Mexico, and Texas, probably in adjacent northern Mexico. Map 17. Plate XXII, fig. 4.

Herba annua. Caules decumbentes, pauci ad numerosi, striati, strigosi, $0.2-2.5 \mathrm{dm}$. longi; foliis inferioribus oblanceolatis vel spathulatis, integerrimis, strigosis, fluxibus, superioribus similibus, minoribus et vivacioribus; pedunculis usque 5 cm . longis, strigosis. Involucrum $8-16 \mathrm{~mm}$. latum, 4.77.5 mm . altum, maturitate aperiens; involucri squamis plerumque 3 -seriatis, oblongis vel ovatis, $2-6.7 \mathrm{~mm}$. longis, $1-2.6 \mathrm{~mm}$. latis; achaeniis oblanceolatis vel obovatis, compressis, aliquanto pubescentibus cum pilis glochidiatis, $2.0-2.8 \mathrm{~mm}$. longis, $0.6-1.2 \mathrm{~mm}$. latis; radii pappo semper breve, squamellato (squamellis coroniformibus); disci pappo plurisetoso, quam disci corollae plerumque breviore.

Representative specimens. Arizona. Apache Co.: Four Corners, 5000 ft . alt., Deaver 40.37 (cas); low hills just north of Petrified Forest, near the Rio Puerco, Nelson \& Nelson 2144 ( ${ }^{\circ}$ нм ). Coconino Co.: 10 mi . south of Navajo Bridge across the Colorado River, 4000 ft . alt., Rollins \& Chambers 2432 (DS, GH, NA, UC, US, UTC); Cameron to Tuba City, 4700 ft . alt., Peebles \& Fulton 11827 (Cas, ${ }^{\circ} \mathrm{Ny}$, us). Graham Co.: Tanque, 1200 m. alt., Eggleston 19872 (GH, us); Diversion Works in Freeman flat, 5 mi . southwest of Safford, Maguire \& Maguire 10094 ( ${ }^{\circ} \mathrm{UTc}$ ). Navajo Co.: between Kaventa and Betatakin, Eastwood \& Howell 6575 (CAS); between Winslow and Holbrook, McKelvey 4561 (GH); Holbrook, Ward s.n., 15 June 1901 (NY, us). Pinal Co.: near Dudleyville, Griffiths 3673 (na). Yavapai Co.: Beaver Creek, Purpus 8300 (mo, uc, us). Colorado. Delta Co.: between Delta and Grand Junction, 4800 ft . alt., Penland 1763 (cas, rsa). Montezuma Co.: Mancos, southwestern Colo., Eastwood s.n., June 1890 (colo). Montrose Co.: Paradox, 5400 ft . alt., Walker 93 (Gh, ill, Mo, Ny, POM, ${ }^{\circ}$ RM, us, ws, wTu) ; Naturita, 5400 ft . alt., Payson 321 (cm, Colo, ds, F, MO, mont, ${ }^{\text {rm, ws }}$ ). New Mexico. Bernalillo Co.: plains near Albuquerque, Palmer 31206 (мо, рн). Dona Ana Co.: Mesilla Vallev, near Mesilla, Standley s.n., 23 May 1906 (* Us); Mesilla Valley, 3850 ft. alt.,

Wooton \& Standley s.n., 2 April 1907 (DS, F, MO, NY, *RM, us). Grant Co.: Mangas Springs, 18 mi. northwest of Silver City, 4300 ft . alt., Metcalfe 15 (CAS, DS, GH, LlL, MO, NY, POM, "RM, UC, US). Lincoln Co.: Carrizoza, Earle 607 (Ny). McKinley Co.: along Highway 66, 15 mi . east of Gallup, Nelson \& Nelson 2174 (mO, NY, ${ }^{*}$ RM, UTC). Otero Co.: desert, just outside entrance to White Sands National Monument, Goodman \& Waterfall 4987 (окц). San Juan Co.: Aztec, Baker 728 (F, GH, MO, ND, NY, POM, ${ }^{\text {RM, US }}$ ) ; 2 mi. northwest of Waterflow, Cutler 3331 ( ${ }^{*}$ mo, na, us). Sandoval Co.: Torreones arrovo, Keesecker 38 (okl). Santa Fé Co.: Santa Fé, Fendler 351 (GH, MO, PH); near Española; 5600 ft . alt., Heller \& Heller 3547 ( ${ }^{*}$ mo, msc; us p.p., with 2 plants of T. Fendleri). Sierra Co.: Hillsboro, north of Percha, 5500 ft . alt., Metcalfe 1510 ( Cas, f, GH, мо, Ny, pom, uc, us). Socorro Co.: Datil Forest, above Walter Medley's Ranch, ca. 9 mi. north of Magdalena, Eggleston 16197 (мо). Taos Co.: Taos, 6900 ft . alt., Castetter 1302 ( ${ }^{\circ} \mathrm{RM}$ ). Valencia Co.: Mount Taylor, between coal mine and Grants, 7000 ft . alt., Parker 2318 (rsA, uc). Texas. El Paso Co.: El Paso, 3700 ft . alt., Ripley \& Barneby 4211 (cas). Hudspeth Co.: in a basin between hills, 4 mi . east of Hueco, Waterfall 3867 (GH). Utah. Emery Co.: Green River, Jones s.n., 9 May 1890 ( ${ }^{*}$ mo, msC, pom, Uc, us); Mounds, Jones s.n., 5 Sept. $1901^{(\text {(pom) }}$; Red Knoll enclosure, vic. Buckhorn Reservoir, San Rafael Swell, Maguire 18493 (GH, NY, Us, UTC, ws; wTU p.p., with 1 plant of T. incana). Garfield Co.: Henry Mts., 5000 ft . alt., Stanton 1059 (ut). Grand Co.: 5 mi . south of Crescent Junction, Holmgren \& Hansen 3295 (CAN, GH, ids, ${ }^{\circ}$ mo, ny, UC, US, UTC, ws, wTU); Westwater, Jones, s.n., 20 May 1901 (Ром) ; Moab and vicinity, 1200-1500 m. alt., Rydberg \& Garrett 8441 (ny). San Juan Co.: Cottonwood Wash, vicinity of Wayland's Ranch, $11 / 2 \mathrm{mi}$. north of Bluff, Maguire 13509 (CAN, ${ }^{\text {a }} \mathrm{GH}, \mathrm{PH}, \mathrm{UC}, \mathrm{UTC}$, wTU).

Previously this species has been identified as T. strigosa. ${ }^{3}$ It is indeed closely related to that species. The present material, however, is separable into two clear-cut groups, each with its own range of variation which hardly overlaps that of the other. Townsendia annua and T. strigosa may be distinguished by the characters tabulated below.

In addition to the differences indicated in the table above, there are others which do not lend themselves to tabulation. Townsendia annua is more delicate in appearance and has very slender branches. On herbarium specimens it usually has no anthocyanin in the stems while T. strigosa usually does. The phyllaries of T. annua usually are shorter and broader with more conspicuously lacerate margins than are those of $T$. strigosa.

[^33]Townsendia annua
Townsendia strigosa

Annual.
Basal leaves soon deciduous.
Root-stem junction not enlarged.
Phyllaries mostly in 3, rarely 4, series.

Disk-corollas 2.3-3.7 mm . long.
Achenes 2.0-2.8 mm. long.
Disk-pappus 1.8-3.0 mm. long, usually shorter than the diskcorollas.

Biennial.
Basal leaves persistent.
Root-stem junction enlarged.
Phyllaries mostly in 4, rarely 3 , series.

Disk-corollas $3.3-5.0 \mathrm{~mm}$. long.
Achenes 3.0-4.0 mm. long.
Disk-pappus $3.3-5.5 \mathrm{~mm}$. long, about equal to or longer than the disk-corollas.

Aside from the purely morphological evidence for this species being a true annual, the flowering time also gives that indication. Specimens in flower collected in every month from February to October are included in the present material. May and June collections are most frequent.

Townsendia annua appears to be derived from a prototype nearly or entirely similar to T. strigosa. The distinguishing characteristics of T. annua are mostly quantitative, reduced features of $T$. strigosa. The comparative measurements in the table above suggest this fact. Townsendia annua probably has become specialized for a somewhat more xeric existence than that of T. strigosa. This adaptation has come about primarily by development of the annual habit and correlation of the flowering season with the availability of water.

Putative hybridization of T. annua with T. strigosa is considered in the discussion of the latter species; that with T. incana under the discussion of T. incana, and that with T. Fendleri under the discussion of that species.

## 21. Townsendia mexicana A. Gray

Townsendia mexicana A. Gray, Mem. Am. Acad. 4 (Pl. Fendl.): 70. 1849. Type: Gregg s.n., Saltillo, Coahuila, Mexico, March 1847 (GH, holotype; mo, NY, isotypes).

Low, caulescent, taprooted perennial; stems often slightly woody at the base, loosely branched from the base upward, usually decumbent, sometimes terminally ascending and suberect, strigose-sericeous, up to 2.0 dm . long; leaves more or less evenly distributed on the stems. linear to narrowly oblanceolate, acute, mucronate, entire, or with 1-2 small lateral lobes near the tip, strigose, $5-25 \mathrm{~mm}$. long, $0.4-2.5 \mathrm{~mm}$. wide; peduncles solitary or rarely $2-3$ at the ends of the branches, strigose, densely so near the head; involucres $6-12 \mathrm{~mm}$. wide, $3.5-7.0 \mathrm{~mm}$. high, broadly expanded at maturity; phyllaries in 2 (rarely 3) series, elliptic-obovate, scarious-margined, ciliate
near the obtuse-rounded (rarely acute) apices, the outer 2.5-4.5 mm. long, $0.5-2.2 \mathrm{~mm}$. wide, lightly to moderately strigose on the abaxial surface, the inner $3.5-6.0 \mathrm{~mm}$. long, $0.8-2.4 \mathrm{~mm}$. wide, lightly strigose to nearly glabrous; ray-florets ca. $15-35$; ray-corollas white on the adaxial surface and sometimes with a pink to purple median stripe on the abaxial surface, $5-10 \mathrm{~mm}$. long, $1-1.7 \mathrm{~mm}$. wide; disk-corollas yellow, the tips sometimes pink-purple, $1.8-3.4 \mathrm{~mm}$. long; achenes oblanceolate, compressed, 2 -ribbed, moderately to lightly pubescent with duplex, glochidiate hairs, ray-achenes more pubescent than those of the disk, both or only the ray-achenes papillose, 1.82.7 mm . long, $0.5-1.2 \mathrm{~mm}$. wide. $2 n=18$. Reproduction sexual. Southern Coahuila south to Mexico D. F., Mexico. Map 16. Plate XXIII, fig. 1.

Representative specimens. mexico. Coahuila. Ca. 3 mi. southwest of Saltillo, Beaman 1002 ( ${ }^{*} \mathrm{GH}$ ); Saltillo, Palmer 499 in 1880 ( ${ }^{*}$ мо, ny, us, yu) ; valley 15 kms . west (?) of Conception del Oro just within Coah. border, 2300 m . alt., Stanford, Retherford \& Northcraft 509 (dS, Gh, "mo, ny, uc, wtu). Distrito Federal. Vicinity of Rancho de Flores near San Pablo, 15 mi . south of Mexico City, $7350-7600 \mathrm{ft}$. alt., Happ 296 ( ${ }^{\text {mo }}$ ). Hidalgo. El Arenal, slopes at Km. 100 Pan American (Laredo) highway south of Actopan, 2500 m . alt., Moore 1395 ( ${ }^{*} \mathrm{GH}, \mathrm{UC}$ ) ; bluffs near Tula, 6800 ft . alt., Pringle 6573 (CAN, CAS, CM, F, GH, MEXU, MO, MSC, ND, *NY, PH, UC, US). Nuevo León. 17 mi . southeast of Galeana, Schneider 1115 (F). Querétaro. Near Higuerillas, Rose et al. 9791 (GH, us). San Luis Potosí. Estacion Catorce, Sierra Madre Oriental, 2000-2100 m. alt., Pennell 17575 (PH, us). Tamaulipas. Near reservoir of Miquihuana at base of hills, Stanford, Taylor \& Lauber 2384 ( uc, wtu). Zacatecas. Between La Honda and Santa Rita via Pinos, Johnston 7472 ( ${ }^{\circ} \mathrm{GH}, \mathrm{Us}$ ) ; near Concepcion del Oro, Palmer 252 in 1904 ( $\mathbf{F}, \mathrm{GH}, \mathrm{mo}$, Ny, us).

This Mexican endemic probably is the most highly evolved species of Townsendia. Its diminutive size, two series of phyllaries, very short ray- and disk-corollas, short pappus, and small achenes all are features of reduction. It is the only member of the genus with lobed leaves. All of its meiotic chromosomes are distinctly smaller than those known in any other species of Townsendia (cf. Plate I, fig. 3). ${ }^{4}$ Townsendia mexicana has no very close relatives but belongs with the group of species which include T. incana, T. Fendleri, T. strigosa, and T. annua. Townsendia Fendleri, T. annua, and T. mexicana exhibit a very strong parallel development.

The range of $T$. mexicana probably coincides with the occurrence of alkaline soils in central Mexico between the elevations of ca. $5000-8000 \mathrm{ft}$. It has been collected in flower from March to September.

[^34]
## Species Excluded from Townsendia

Townsendia Wrightii A. Gray, Bot. Mex. Bound. Surv. p. 78. 1859. = Aster Wrightii A. Gray, Smithson. Contrib. Knowl. 5 (Art. 6): 75. 1853.

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Peate XIII. Habitats of Tounsendia. Fig. 1. The Antelope Hills in Roger Mills County, Oklahoma. Tounsendia texensis is an endemic of this area, restricted to limestones exposed by stream erosion of the deep, black soils of the high plains. Fig. 2. Near Gothic, Gunnison County, Colorado. Apomicts of the endemic T. Rothrockii grow under snowbanks in red, sandstone soils at the tops of these mountains. They flower as the snow melts off. Apomicts of $T$. leptotes are found at the mountain crests also, but on drier sites.


Plate XIV. Habitats of Tou'nsendia. Fig. 1. In the Colorado National Monument near Grand Junction, Mesa County, Colorado. A typical locality for T. incana. Both sexual and apomictic plants are found here. Fig. 2. The type-locality of T. montana var. montana, above the Flagstaff Mine at Alta, Salt Lake County, Utah. The plants are restricted to the crest of this subalpine limestone ridge.


Plate XV. Habitats of Tounsendia. Fig. 1. A white shale outcrop of the Green River formation in the Uinta Basin of Utah. The endemic T. mensana var. mensana is found amidst the shale fragments. Fig. 2. Fairyland Canyon near Bryce Canyon in Garfield County, Utah. The endemic T. montana var minima grows in finelyfragmented limestones at the tops of these cliffs.


Plate XVI. Mt. Borah, the highest peak in Idaho. Apomicts of $T$. condensata, T. leptotes, T. montana var. montana and T. Parryi grow on the limestones of this mountain. Fig. 2. The Satanka formation, near Alcova, Natrona County, Wyoming. Nuttall may have first collected T. spathulata here in 1834. The densely rosulate little plants of this species are abundant in localized areas among the shale fragments.


Plate XVII. Photograph of the original collections of Tounsendio (see explanation in the discussion of T. exscapa).


Plate XVIII. Photographs of representative specimens of species of Townsendia. Fig. 1. The lectotype of $T$. formosa. Fig. 2. A representative specimen of $T$. eximia. Fig. 3. A representative specimen of $T$. grandiflora. Fig. F. A representative specimen of $T$. texensis.


Plate XIX. Photographs of representative specimens of species of Tounsendia. Fig. 1. Townsendia glabella (Turner 2892). Fig. 2. Townsendia Kothrockii (Beaman, Weber, © Preece 514). Fig. 3. Townsendia montana var. montana. Fig. 4. Townsendia montana var. minima (Hitchcock 2962).


Plate XX. Photographs of representative specimens of species of Townsendia. Fig. 1. The holotype of $T$. mensana var. mensana. Fig. 2. The holotype of $T$. mensana var. Jonesii. Fig. 3. A representative sexual specimen of T. leptotes (Ripley *ひ Burneby 7589). Fig. 4. A representative apomictic specimen of T. leptotes (Holmgren © Shaw 7640). Fig. 5. The holotype of T. Hookeri (Clokey 4338, colo 12061). Fig. 6. Part of Drummond's collection (Drummond 573) of T. Hookeri from the Rocky Mountains.


Plate XXI. Photugraphs of representatise specimens of species of Tounsendia. Fig. 1. Townsendia exscapa. Fig. 2. Townsendia Parryi. Fig. 3. Tounsendia florifer. Fig. 4. Townsendia scapigera.


Plate XXII. Photographs of representative specimens of species of Townsendia. Fig. 1. A representative specimen of T. incana. Fig. 2. A representative specimen of T. Fendleri. Fig. 3. A representative specimen of T. strigosa (Holmgren \&b Tillett 9474). Fig. 4. The holotype of T. annua (GH).


Platt XXIII. Photographs of representative specimens of species of Tounsendu. Fig. 1. Tounsendia mexicana. Fig. 2. Sexual T. condensata. Fig. 3. Apomictic T. condensata. Fig. 4. Townsendia spathulata.

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NO. CLXXXIV

# A CATALOGUE OF THE FERNS AND FLOWERING PLANTS OF BOLIVIA 

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## INTRODUCTORY NOTE

When I first began to work on Bolivian plants, I hoped to produce a Flora of Bolivia. Unfortunately, inevitable delays and the slowness with which the work has proceeded make the chance of its completion within my lifetime extremely doubtful. Consequently, it seems advisable to publish this catalogue of the ferns and flowering plants of Bolivia. Although a complete listing is too much to be hoped for, it is the most nearly complete catalogue of Bolivian plants yet to appear. Additional records are being accumulated and supplements will be published from time to time, whenever the number of additions makes this advisable.

Plant families are arranged in the Engler and Prantl sequence. Within families, genera are arranged alphabetically; within genera, species are cited alphabetically. Italics mean that the name is considered to be a synonym. A ? before a name indicates considerable doubt as to the correctness of the identification.

Some idea of the richness of the Bolivian flora can be gained from the fact that 196 families of pteridophytes and phanerogams are included in this list. Although quite conservative generic concepts have been followed (with few exceptions), 1874 genera are listed here. They are distributed as follows:

Pteridophytes
Gymnosperms
Monocotyledons
Dicotyledons

68 genera
3 genera

## 355 genera

1252 genera

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## PTERIDOPHYTA

## HYMENOPHYLLACEAE

Hymenophyllum apicale v. d. B. in Ned. Kr. Arch. 4: 397 (1859),
H. Buchtienii Rosenst. in Fedde, Repert. Spec. Nov. 5: 229 (1908) = H. elegantulum.
H. crispum HBK. Nov. Gen. \& Spec. 1: 26 (1816)
H. crispum var. brasilianum Fée, Crypt. Vasc. Brés. 1: 195, t. 71, fig. 2 (1869).
H. dendritis Rosenst. in Fedde, Repert. Spec. Nov. 6: 308 (1909).
H. elegans Spreng. Syst. Veg. 4: 133 (1827).
H. elegantulum v. d. B. in Ned. Kr. Arch. 4: 408 (1859)
H. fragile (Hedw.) Morton in Contrib. U. S. Nat. Herb. 29(3): 172 (1947).
H. fucoides Sw. in Schrad. Journ. 1800 (2): 99 (1801).
H. helicoideum Sod. Crypt. Vasc. Quit. 20 (1893).
H. Herzogii Rosenst. in Meded. Rijks Herbar. 19: 5 (1913).
H. hirsutum (L.) Sw. in Schrad. Journ. 1800 (2): 99 (1801).
H. interruptum Kunze in Linnaea, 9: 107 (1834).
H. microcarpum Desv. in Mém. Soc. Linn. Paris, 6: 333 (1827).
H. multiflorum Rosenst. in Meded. Rijks Herbar. 19: 3 (1913).
H. myriocarpum Hook. Sp. Fil. 1: 106, t. 37D (1844).
H. nigrescens var. gracile Rosenst. in Meded. Rijks Herbar. 19: 4 (1913).
H. Orbignianum v. d. B. in Ned. Kr. Arch. 5 (3) : 191 (1863) = H. crispum.
H. peltatum (Poir.) Desv. in Mém. Soc. Linn. Paris, 6: 333 (1827).
H. peruvianum Hook. \& Grev. Ic. Fil. 2: t. 208 (1831).
H. plumosum Kaulf. Enum. Fil. 267 (1824).
H. polyanthos Sw. in Schrad. Journ. 1800 (2): 102 (1801).
H. protrusum Hook. Sp. Fil. 1: 104, t. 37B (1844).
H. pyramidatum Desv. in Mém. Soc. Linn. Paris, 6: 332 (1827).
H. Ruizianum (Kl.) Kunze in Bot. Zeit. 5: 199 (1847).
H. speciosum v. d. B. in Ned. Kr. Arch. 5(3): 181 (1863).
H. spectabile Mett. in Linnaea, 35: $392(1867-1868)=$ H. speciosum.
H. tenerrimum v. d. B. in Ned. Kr. Arch. 5(3): 185 (1863).
H. Trianae Hieron. in Engler, Bot. Jahrb. 34: 429 (1904).
H. trichophyllum HBK. Nov. Gen. \& Spec. 1: 27 (1816).
H. undulatum var. regenerans C. Chr. in Ark. Bot. 20A (7): 8 (1926).
H. valvatum Hook. \& Grev. Ic. Fil. 2: t. 219 (1831).
H. verecundum Morton in Contrib. U. S. Nat. Herb. 29: 183 (1947).

Trichomanes angustatum Carm. in Trans. Linn. Soc. 12: 513 (1818).
T. angustatum var. subexsertum (v. d. B.) C. Chr. in Ark. Bot. 20A (7): 9 (1926).
T. Ankersii Parker ex Hook. \& Grev. Ic. Fil. 2: t. 201 (1831).
T. crispum L. Sp. Pl. 2: 1097 (1753).
T. cristatum Kaulf. Enum. Fil. 265 (1824).
T. delicatum v. d. B. in Ned. Kr. Arch. 5(2): 145 (1861).
T. diversifrons (Bory) Mett. ex Sadeb. in Engl. \& Prantl, Nat. Pflanzenfam. 1(4): 108 (1899).
T. Herzogii Rosenst. in Meded. Rijks Herbar. 19: 5 (1913).
T. Krausii Hook. \& Grev. Ic. Fil. 2: t. 149 (1830).
T. Kunzeanum Hook. Sp. Fil. 1: 127, t. 39D (1845).
T. membranaceum L. Sp. Pl. 2: 1097 (1753).
T. montanum Hook. Ic. Pl. 2: t. 187 (1837).
T. pinnatum Hedw. Fil. Gen. \& Spec. t. 4, fig. 1 (1799).
T. plumosum Kunze in Linnaea, 9: 104 (1834).
T. polypodioides L. Sp. Pl. 2: 1098 (1753).
T. pyxidiferum L. Sp. Pl. 2: 1098 (1753).
T. radicans Sw. in Schrad. Journ. 1800 (2): 97 (1801).
T. rigidum Sw. Prodr. 137 (1788).
T. rupestre (Raddi) v. d. B. in Ned. Kr. Arch. 4: 370 (1859).
T. Sellowianum Presl, Hym. 15, 37 (1843).
T. Trollii Bergdolt in Flora (N. S.) 127: 263 (1933).

## CYATHEACEAE

Alsophila armata (Sw.) Presl, Tent. 62 (1836).
A. bulligera Rosenst. in Fedde, Repert. Spec. Nov. 25: 57 (1928).
A. lasiosora Mett. ex Kuhn in Linnaea, 36: 157 (1869).
A. Lechleri Mett. Fil. Lechl. 2:28 (1859).
A. mapiriensis Rosenst. in Fedde, Repert. Spec. Nov. 25: 57 (1928).
A. pubescens Baker, Synop. Fil. (ed. 1) 449 (1868).
A. quadripinnata (Gmel.) C. Chr. Ind. Fil. 47 (1905).
A. rostrata (HBK.) Mart. Ic. Crypt. Bras. 64, t. 39 (1834).
A. rufa Fée, Crypt. Vasc. Brés. 166, t. 59, fig. 1 (1869).
A. villosa (Humb. \& Bonpl.) Desv. in Mém. Soc. Linn. Paris, 6: 319 (1827).

Cyathea castanea Baker, Synop. Fil. (ed. 2) 451 (1874).
C. cuspidata Kunze in Linnaea, 9: 101 (1834).
C. cuspidata var. rigida Rosenst. in Meded. Rijks Herbar. 19: 6 (1913).
C. furfuracea Baker, Synop. Fil. (ed. 2) 450 (1874).
C. Herzogii Rosenst. in Meded. Rijks Herbar. 19: 7 (1913).
C. mexicana var. boliviensis Rosenst. in Fedde, Repert. Spec. Nov. 25: 56 (1928).
? C. pilosa Baker, Synop. Fil. (ed. 2) 19 (1874).
C. Schanschin Mart. Ic. Crypt. Bras. 77, t. 29, fig. 3-4, t. 54 (1834).
C. vestita Mart. in Denkschr. Bot. Ges. Regensb. 2: 146 (1822).
C. yungensis C. Chr. in Ark. Bot. 20A (7): 10 (1926).

Hemitelia grandifolia (Willd.) Spreng. Syst. Veg. 4: 125 (1827).
H. subincisa Kunze in Bot. Zeit. 2: 296 (1844).

## POLYPODIACEAE

Adiantopsis radiata (L.) Fée, Gen. 145 (1850-1852).
A. ternata Prantl in Gartenfl. 32: 101 (1883).

Adiantum Baenitzii Rosenst. in Fedde, Repert. Spec. Nov. 5: 230 (1908).
A. boliviense Christ \& Rosenst. in Fedde, Repert. Spec. Nov. 5: 230 (1908).
A. chilense Kaulf. Enum. Fil. 207 (1824).
A. cuneatum Langsd. \& Fisch. Ic. Fil. 23, t 26 (1810).
A. decorum var. quadripinnatum Rosenst. in Meded. Rijks Herbar. 19: 8 (1913).
A. digitatum Presl ex Hook. Sp. Fil. 2: 38: (1851).
A. latifolium Lam. Encyc. 1: 43 (1783).
A. Lorentzii Hieron. in Engler, Bot. Jahrb. 22: 393 (1896).
A. macrophyllum Sw. Prodr. 135 (1788).
A. Moorei Baker in Gard. Chron. 1873: 811.
A. obliquum Willd. Sp. Pl. 5: 429 (1810).
A. Orbignyanum Mett. ex Kuhn in Linnaea, 36: 78 (1869).
A. peruvianum Kl. in Linnaea, 18: 555 (1844).
A. petiolatum Desv. in Ges. Naturforsch. Berl. Mag. 5: 326 (1811).
A. platyphyllum Sw. in Kgl. Vet. Akad. Handl. 1817: 74, t. 3, fig. 6.
A. Poiretii Wikstr. in Kgl. Vet. Akad. Handl. 1825: 443 (1826).
A. polyphyllum Willd. Sp. Pl. 5: 454 (1810).
A. pulverulentum L. Sp. Pl. 2: 1096 (1753).
A. serrato-dentatum Willd. Sp. Pl. 5: 445 (1810).
A. tinctum Moore in Gard. Chron. 1862: 932.

Anetium citrifolium (L.) Splitg. in Tijdschr. Nat. Gesch. 7: 395 (1840).
Antrophyum discoideum Kunze in Bot. Zeit. 6: 702 (1848).
A. lineatum (Sw.) Kaulf. Enum. Fil. 199 (1824).

Asplenium abscissum Willd. Sp. Pl. 5: 321 (1810).
A. abscissum var. subaequilaterale Rosenst. in Fedde, Repert. Spec. Nov. 12: 470 (1913).
A. alatum Humb. \& Bonpl. ex Willd. Sp. Pl. 5: 319 (1810).
A. auricularium var, acutidens Rosenst. in Fedde, Repert. Spec. Nov. 12: 469 (1913).
A. auricularium var. subintegerrimum (Hieron.) Rosenst. in Fedde, Repert. Spec. Nov. 12: 469 (1913).
A. auriculatum Sw. in Kgl. Vet. Akad. Handl. 1817: 68.
A. auritum Sw. in Schrad. Journ. 1800 (2): 52 (1801).
A. auritum var. davallioides Rosenst. in Fedde, Repert. Spec. Nov. 5: 232 (1908).
A. auritum var. davallioides forma diversifolium Rosenst. in Fedde, Repert. Spec. Nov. 5: 232 (1908).
A. Ballivianii Rosenst. in Fedde, Repert. Spec. Nov. 11: 55 (1912).
A. Bangii Hieron. in Hedwigia, 60: 245 (1918).
A. Bangii Gandoger in Bull. Soc. Bot. France, 66: 305 (1920).
A. castaneum Schlechtd. \& Cham. in Linnaea, 5: 611 (1830).
A. cirrhatum Richard ex Willd. Sp. Pl. 5: 321 (1810).
A. Claussenii Hieron. in Hedwigia, 60: 241 (1919).
A. cristatum Lam. Encyc. 2: 310 (1786).
A. debile Fée, Mém. 10: 28, t. 35, fig. 2 (1866).
A. depauperatum Fée, Mém. 7: 52, t. 15, fig. 3 (1857).
A. dimidiatum var. boliviense Rosenst. in Fedde. Repert. Spec. Nov. 12: 470 (1913).
A. discrepans Rosenst. in Fedde, Repert. Spec. Nov. 12: 469 (1913).
A. divergens Mett. ex Baker in Mart. Fl. Bras. 1(2): 445 (1870).
A. erosum L. Syst. (ed. 10) 2: 1324 (1759).
A. fluminense Hieron. in Hedwigia, 61: 17 (1919).
A. formosum Willd. Sp. Pl. 5: 329 (1810).
A. fragile Presl, Tent. 108 (1836).
A. fragrans Sw. Prodr. 130 (1788).
A. fragrans var. foeniculaceum (HBK.) Hook. Sp. Fil. 3: 181 (1860).
A. Gilliesii Hook. Exot. Fl. 3: ad t. 208 (1827).
A. harpeodes Kunze in Linnaea, 18: 329 (1844).
A. harpeodes var. incisum (Rosenst.) Hieron. in Hedwigia, 60: 238 (1918).
A. hastatum Kl. ex Kunze in Linnaea, 23: 235, 305 (1850).
A. Herzogii Rosenst. in Meded. Rijks Herbar. 19: 12 (1913).
A. integerrimum Spreng. in Nov. Act. Acad. Caes. Leop. 10: 231 (1821).
A. laetum Sw. Syn. 79, 271 (1806).
A. Lorentzii Hieron. in Engler, Bot. Jahrb. 22: 375 (1896).
A. lunulatum Sw. in Schrad. Journ. 1800 (2): 52 (1801).
A. monanthes L. Mant. 130 (1767).
A. monanthes var. yungense Rosenst. in Fedde, Repert. Spec. Nov. 11: 54 (1912).
A. obtusifolium L. Sp. Pl. 2: 1080 (1753).
A. partitum (K1.) C. Chr. Ind. Fil. 125 (1905).
A. poloënse Rosenst. in Fedde, Repert. Spec. Nov. 12: 469 (1913).
A. praemorsum Sw. Prodr. 130 (1788).
A. radicans L. Syst. (ed. 10) 2: 1323 (1759).
A. recumbens Gandoger in Bull. Soc. Bot. France; 66: 305 (1920).
A. resiliens Kunze in Linnaea, 18: 331 (1844).
A. rigidum Sw. in Kgl. Vet. Akad. Handl. 1817: 68.
A. Rusbyanum Domin, Pterid. Domin. 171 (1929).
A. rutaceum (Willd.) Mett. Aspl. 129, no. 98 (1859).
A. sanguinolentum Kunze ex Mett. Aspl. 98, no. 35, t. 4, fig. 10 (1859).
A. serra Langsd. \& Fisch. Ic. Fil. 16, t. 19 (1810).
A. serratum L. Sp. Pl. 2: 1079 (1753).
A. serratum var. caudatum Rosenst. in Fedde, Repert. Spec. Nov. 6: 310 (1909).
A. sessilifolium Desv. in Ges. Naturforsch. Berl. Mag. 5: 322 (1811).
A. sessilifolium var. minus Hieron. in Engler, Bot. Jahrb. 34: 461 (1904).
A. spinescens Mett. ex Kuhn in Linnaea, 36: 98 (1869).
A. squamosum L. Sp. Pl. 2: 1082 (1753).
A. tocoraniense Rosenst. in Meded. Rijks Herbar. 19: 11 (1913).
A. tricholepis Rosenst. in Fedde, Repert. Spec. Nov. 12: 468 (1913).
A. trilobatum C. Chr. in Ark. Bot. 20A(7): 15, fig. 1 (1926).
A. triphyllum Presl, Rel. Haenk. 1: 45 (1825).
A. triphyllum var. compactum Hook. Sp. Fil. 3: 203 (1860).
A. uniseriale Raddi, Opusc. Sci. Bologn. 3: 291 (1819).
? Athyrium Dombeyi Desv. in Mém. Soc. Linn. Paris, 6: 266 (1827).
Blechnum auriculatum Cav. Descr. 262 (1802).
B. blechnoides (Lag.) C. Chr. Ind. Fil. 151 (1905).
B. blechnoides var. gracilipes Rosenst. in Fedde, Repert. Spec. Nov. 9: 343 (1911).
B. brasiliense Desv. in Ges. Naturforsch. Berl. Mag. 5: 330 (1811).
B. Buchtienii Rosenst. in Fedde, Repert. Spec. Nov. 5: 231 (1908).
B. caudatum Cav. Descr. 262 (1802).
B. chilense (Kaulf.) Mett. Fil. Lechl. 1: 14 (1856).
B. delicatum Maxon \& Morton in Bull. Torr. Bot. Club, 66: 41 (1939).
B. fraxineum Willd. Sp. Pl. 5: 413 (1810).
B. glandulosum Link, Enum. Alt. 2: 462 (1822).
B. glandulosum var. distans (Presl) C. Chr. in Ark. Bot. 20A (7): 17 (1926).
B. gracile Kaulf. Enum. Fil. 158 (1824).
B. Kunthianum C. Chr. Ind. Fil. Suppl. 1906-1912: 16 (1913).
B. lanceola Sw. in Kgl. Vet. Akad. Handl. 1817: 71, t. 3, fig. 2.
B. lima Rosenst. in Fedde, Repert. Spec. Nov. 11: 53 (1912).
B. loxense Hook. ex Salomon, Nomencl. Gefässkr. 117 (1883).
B. malacothrix Maxon \& Morton in Bull. Torr. Bot. Club, 66: 40 (1939).
B. nigro-squamatum Gilbert in Bull. Torr. Bot. Club, 24: 258 (1897).
B. occidentale L. Sp. Pl. 2: 1077 (1753).
B. penna-marina (Poir.) Kuhn, Fil. Afr. 92 (1868).
B. penna-marina var. bolivianum Rosenst. ex Looser in Rev. Univ. Catol. Chile, 32: 77 (1948).
? B. Raddianum Rosenst. in Hedwigia, 46: 91 (1906).
B. Sprucei C. Chr. Ind. Fil. 160 (1905).
B. subtile Rosenst. in Fedde, Repert. Spec. Nov. 11: 54 (1912).
B. unilaterale Sw. in Ges. Naturforsch. Berl. Mag. 4: 79, t. 3, (1810).
B. volubile Kaulf. Enum. Fil. 159 (1824).

Bolbitis crenata (Presl) C. Chr. Ind. Fil. Suppl. 3: 47 (1934).
B. serratifolia (Martens) Schott, Gen. Fil. t. 13 (1834).
B. Stuebelii (Hieron.) C. Chr. Ind. Fil. Suppl. 3: 50 (1934).

Cheilanthes boliviana C. Chr. in Ark. Bot. 20A (7): 19 (1926).
C. elegans Desv. in Ges. Naturforsch. Berl. Mag. 5: 328 (1811).
C. Hieronymi Herter in Anal. Mus. Nac. Montevideo (ser. 2) 1: 360 (1925).
C. marginata HBK. Nov. Gen. \& Spec. 1: 22 (1816).
C. myriophylla Desv. in Ges. Naturforsch. Berl. Mag. 5: 328 (1811).
C. obducta Mett. ex Kuhn in Linnaea, 36: 83 (1869).
C. pilosa Goldm. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 455 (1843).
C. Poeppigiana Mett. ex Kuhn in Linnaea, 36: 84 (1869).
C. pruinata Kaulf. Enum. Fil. 210 (1824).
C. rufo-punctata Rosenst. in Meded. Rijks Herbar. 19: 9 (1913).

Cyclopeltis semicordata (Sw.) J. Sm. in Bot. Mag. 72: Comp. 36 (1846).
Cystopteris fragilis (L.) Bernh. in Schrad. Neu. Journ. 1(2): 27, t. 2, fig. 9 (1806).

Dennstaedtia adiantoides (Humb. \& Bonpl.) Moore, Ind. XCVII (1857).
D. bipinnata (Cav.) Maxon in Proc. Biol. Soc. Wash. 51: 39 (1938).
D. cornuta (Kaulf.) Mett. in Ann. Sci. Nat. (ser. 5) 2: 260 (1864).
D. D'Orbignyana Kuhn in Linnaea, 36: 146 (1869).
D. glauca (Cav.) C. Chr. ex Looser in Rev. Hist. Geog. Chile, 69: 184 (1932).
D. Mathewsii (Hook.) C. Chr. Ind. Fil. 218 (1905).
D. rubiginosa (Kaulf.) Moore, Ind. XCVII (1857).

Didymochlaena truncatula (Sw.) J. Sm. in Journ. Bot. 4: 196 (1841).
Diplazium ambiguum Raddi, Opusc. Sci. Bologn. 3: 292 (1819).
D. Ballivianii Rosenst. in Fedde, Repert. Spec. Nov. 6: 311 (1909).
D. Buchtienii Rosenst. in Fedde, Repert. Spec. Nov. 6: 312 (1909).
D. cristatum (Desr.) Alston in Journ. Bot. 74: 173 (1936).
D. cuneifolium Rosenst. in Fedde, Repert. Spec. Nov. 12: 470 (1913).
D. delitescens Maxon in Contrib. U. S. Nat. Herb. 10: 497 (1908).
D. divergens Rosenst. in Fedde, Repert. Spec. Nov. 12: 471 (1913).
D. Lindbergii (Mett.) Christ in Pittier, Primit. Fl. Costar. 3: 27 (1901).
D. mapiriense Rosenst. in Fedde, Repert. Spec. Nov. 6: 310 (1909).
D. marginatum (L.) Diels in Engl. \& Prantl, Nat. Pflanzenfam. 1(4): 229 (1899).
D. pinnatifidum Kunze in Linnaea, 9: 72 (1834).
D. plantaginifolium (L.) Urb. Symb. Ant. 4: 31 (1903).
D. yungense Christ \& Rosenst. in Fedde, Repert. Spec. Nov. 5: 233 (1908).

Doryopteris concolor (Langsd. \& Fisch.) Kuhn in v. Deck. Reis. 3(3): Bot. 19 (1879).
D. crenulans (Fée) Christ in Bull. Herb. Boiss. (ser. 2) 2: 549 (1902).
D. Lorentzii (Hieron.) Diels in Engl. \& Prantl, Nat. Pflanzenfam. 1(4): 270 (1899).
D. nobilis (Moore) Baker, Synop. Fil. (ed. 2) 167 (1874), in synon.
D. ornithopus (Mett.) J. Sm. Hist. Fil. 289 (1875).
D. pedata var. multipartita (Fée) Tryon in Contrib. Gray Herb. 143: 38 (1942).
D. pedata var. palmata (Willd.) Hicken in Rev. Mus. La Plata, 15: 253 (1908).

Dryopteris ampla (Humb. \& Bonpl.) O. Ktze. Rev. Gen. 2: 812 (1891).
D. amplissima (Presl) O. Ktze. Rev. Gen. 2: 812 (1891).
D. andina Morton in Journ. Wash. Acad. Sci. 28: 526 (1938).
D. angustifolia (Willd.) Urb. Symb. Ant. 4: 21 (1903).
D. argentina (Hieron.) C. Chr. Ind. Fil. 253 (1905).
D. aspidioides (Willd.) C. Chr. Ind. Fil. 253 (1905).
D. Bangii C. Chr. in Dansk. Vidensk. Selsk. Skr. (ser. 7) 4: 333 (1907).
D. boliviensis Morton in Journ. Wash. Acad. Sci. 28: 527 (1938).
D. Cañadasii (Sod.) C. Chr. Ind. Fil. 256 (1905).
D. catocarpa (Kunze) O. Ktze. Rev. Gen. 2: 812 (1891) = D. nemophila.
D. cheilanthoides (Fée) C. Chr. Ind. Fil. 257 (1905).
D. coarctata (Kunze) C. Chr. Ind. Fil. 258 (1905).
D. concinna (Willd.) O. Ktze. Rev. Gen. 2: 812 (1891).
D. contermina (Willd.) O. Ktze. Rev. Gen. 2: 812 (1891).
D. dentata (Forsk.) C. Chr. in Dansk. Vidensk. Selsk. Skr. (ser. 8) 6: 24 (1920).
D. denticulata forma boliviensis C. Chr. in Dansk. Vidensk. Selsk. Skr. (ser. 8) 6: 116 (1920).
D. Desvauxii Maxon \& Morton in Bull. Torr. Bot. Club, 65: 369 (1938).
D. Desvauxii forma glandulosa Maxon \& Morton in Bull. Torr. Bot. Club, 65: 372 (1938).
D. diplazioides (Desv.) Urb. Symb. Ant. 4: 21 (1903).
D. diplazioides var. chacoënsis C. Chr. in Ark. Bot. 20A (7): 12 (1926).
D. effusa (Sw.) Urb. Symb. Ant. 4: 16 (1903).
D. Guentheri Rosenst. in Fedde, Repert. Spec. Nov. 25: 59 (1928).
D. Herzogii Rosenst. in Meded. Rijks Herbar. 19: 15 (1913).
D. honesta (Kunze) C. Chr. Ind. Fil. 271 (1905).
D. Jurgensenii (Fée) Maxon \& Morton in Bull. Torr. Bot. Club, 65: 360 (1938).
D. Leprieuri (Hook.) O. Ktze. Rev. Gen. 2: 813 (1891).
D. leucothrix C. Chr. in Smithsonian Misc. Coll. (new series) 5: 377 (1909).
D. leucothrix var. glanduligera C. Chr. \& Rosenst. in Fedde, Repert. Spec. Nov. 12: 471 (1913).
D. macrotis var. nephrodioides Rosenst. in Fedde, Repert. Spec. Nov. 7: 298 (1909).
D. mapiriensis Rosenst. in Fedde, Repert. Spec. Nov. 6: 313 (1909).
D. meniscioides var. conferta (Kaulf.) Morton in Bull. Torr. Bot. Club, 66: 51 (1939).
D. nemophila (Kunze) C. Chr. in Dansk. Vidensk. Selsk. Skr. (Ser. 8) 6: 57 (1920).
D. nephrodioides var. glandulosa C. Chr. \& Rosenst. in Fedde, Repert. Spec. Nov. 12: 473 (1913).
D. nervosa (Kl.) C. Chr. Ind. Fil. 279 (1905).
D. oligocarpa (Humb. \& Bonpl.) O. Ktze. Rev. Gen. 3(2): 378 (1898).
D. oligophylla var. aequatorialis C. Chr. in Dansk. Vidensk. Selsk. Skr. (ser. 7) $10(2): 189$ (1913).
D. oligophylla var. pallescens C. Chr. in Dansk. Vidensk. Selsk. Skr. (ser. 7) $10(2): 188$ (1913).
D. opposita var. furcativenia Rosenst. in Fedde, Repert. Spec. Nov. 6: 313 (1909).
D. paleacea (Sw.) C. Chr. in Amer. Fern Journ. 1: 94 (1911).
D. patens (Sw.) O. Ktze. Rev. Gen. 2: 813 (1891).
D. patula (Sw.) Underw. Our Native Ferms (ed. 4), 117 (1893).
D. Pavoniana (Kl.) C. Chr. Ind. Fil. 283 (1905).
D. permollis Maxon \& Morton in Bull. Torr. Bot. Club, 65: 372 (1938).
D. phacelothrix C. Chr. \& Rosenst. in Fedde, Repert. Spec. Nov. 11: 56 (1912).
D. piloso-hispida (Hook.) C. Chr. in Dansk. Vidensk. Selsk. Skr. (ser. 7) 10 (2): 148 (1913).
D. ptarmiciformis C. Chr. \& Rosenst. in Fedde, Repert. Spec. Nov. 12: 472 (1913).
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E. angustissimum (Fée) C. Chr. in Ark. Bot. 20A(7): 25 (1926).
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E. Bangii Christ, Monog. Elaph. 99 (1899).
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E. Engelii var. subnudum Rosenst. in Fedde, Repert. Spec. Nov. 11: 59 (1912).
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E. Jamesonii (Hook. \& Grev.) Moore, Ind. 10 (1857).
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E. Lindbergii var. truncatum Rosenst. in Fedde, Repert. Spec. Nov. 25: 63 (1928).
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E. Mandonii (Mett.) Christ, Monog. Elaph. 128 (1899).
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E. unduaviense var. leptophylloides Rosenst. in Fedde, Repert. Spec. Nov. 11: 58 (1912).
E. Wacketii Rosenst. in Hedwigia, 46: 151 (1907).

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N. Fraseri (Mett.) Baker, Synop. Fil. (ed. 2) 514 (1874).
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P. bolivianum var. brevipes Rosenst. in Fedde, Repert. Spec. Nov. 12: 473 (1913).
? P. brevifolium Link, Hort. Berol. 2: 90 (1833).
P. bryopodum Maxon in Contrib. U. S. Nat. Herb. 17: 568 (1916).
P. Buchtienii C. Chr. \& Rosenst. in Fedde. Repert. Spec. Nov. 5: 237 (1908).
P. Caceresii Sod. Crypt. Vasc. Quit. 360 (1893).
P. choquetangense Rosenst. in Meded. Rijks Herbar. 19: 18 (1913).
P. chrysolepis Hook. Ic. Pl. 8: t. 721 (1848).
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P. ciliolepis C. Chr. in Ark. Bot. 20A (7): 21 (1926).
P. cinerascens Lindm. in Ark. Bot. 1: 238 (1903).
P. circinatum Sod. Crypt. Vasc. Quit. 333 (1893).
P. crassifolium L. Sp. P1. 2: 1083 (1753).
P. crassifolium var. longipes Rosenst. in Fedde, Repert. Spec. Nov. 11: 58 (1912).
P. crystalloneuron Rosenst. in Fedde, Repert. Spec. Nov. 11; 57 (1912).
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P. decumanum Willd. Sp. Pl. 5: 170 (1810).
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P. filicula Kaulf. Enum. Fil. 275 (1824).
P. fraxinifolium Jacq. Collect. 3: 187 (1789).
P. fulgens Hieron. in Hedwigia, 48: 268 (1909).
P. fuscopunctatum Hook. Sp. Fil. 5: 69, t. 285A (1864).
P. Gilliesii C. Chr. Ind, Fil. 529 (1906).
P. glaucophyllum Kunze ex Kl. in Linnaea, 20: 393 (1847).
P. Herzogii Rosenst. in Fedde, Repert. Spec. Nov. 6: 176 (1908).
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P. leucosticton Kunze ex Kl. in Linnaea, 20: 380 (1847).
P. longum C. Chr. Ind. Fil. 541 (1906).
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P. loriceum var. hirto-pubescens Hieron. in Hedwigia, 48: 263 (1909).
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P. paradiseae Langsd. \& Fisch. Ic. Fil. 11, t. 11 (1810).
P. pectinatum L. Sp. Pl. 2: 1085 (1753).
P. pendulum Sw. Prodr, 131 (1788).
P. pendulum var. boliviense Rosenst. in Fedde, Repert. Spec. Nov. 25: 60 (1928).
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P. sericeo-lanatum Hook. Sp. Fil. 4: 221 (1864).
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Gleichenia Bancroftii Hook. Sp. Fil. 1: 5, t. 4A (1844).
G. bifida (Willd.) Spreng. Syst. Veg. 4: 27 (1827).
G. Buchtienii Christ \& Rosenst. in Fedde, Repert. Spec. Nov. 5: 229 (1908).
G. flexuosa (Schrad.) Mett. in Ann. Lugd. Bat. 1: 50 (1863).
G. nervosa (Kaulf.) Spreng. Syst. Veg. 4: 25 (1827).
G. pectinata (Willd.) Presl, Rel. Haenk. 1: 71 (1825).
G. tomentosa (Sw.) Spreng. Syst. Veg. 4: 27 (1827).
G. velata (Kunze) Mett. Fil. Lips. 113 (1856).
G. yungensis Rosenst. in Fedde, Repert. Spec. Nov. 5: 228 (1908).

## SCHIZAEACEAE

Anemia anthriscifolia Schrad. in Gött. Gelehrt. Anz. 1824: 865.
A. anthriscifolia forma nana Lindm. in Ark. Bot. 1: 258 (1903).
A. flexuosa (Sav.) Sw. Syn. 156 (1806).
A. Herzogii Rosenst. in Meded. Rijks Herbar. 19: 24 (1913).
A. myriophylla Christ in Bull. Herb. Boiss. (ser. 2) 7: 793 (1907).
A. phyllitidis (L.) Sw. Syn. 155 (1806).
A. Presliana Prantl, Schiz。 104 (1881).
A. rotundifolia Schrad. in Gött. Gelehrt. Anz. 1824: 865.
A. tomentosa (Sav.) Sw. Syn. 157 (1806).
A. trichorhiza Gardn. in Hook. Ic. Pl. 9: t. 876 (1852).
A. Wettsteinii Christ in Denkschr. Akad. Wiss. Wien, 79: 54, t. 9 (1908).

Lygodium polymorphum (Cav.) HBK. Nov. Gen. \& Spec. 1: 31 (1816).
L. venustum Sw. in Schrad. Journ. 1801(2): 303 (1803).

## SALVINIACEAE

Azolla filiculoides Lam. Encyc. 1: 343 (1783).
A. microphylla Kaulf. Enum. Fil. 273 (1824).

Salvinia auriculata Aubl. Hist. Pl. Guian. 2: 969 t. 367 (1775).

## MARSILIACEAE

Pilularia Mandonii A. Br. in Monatsber. Akad. Berl. 1870: 752.

## MARATTIACEAE

Danaea Moritziana Presl in Abh. Böhm. Ges. Wiss. (ser. 5) 4: 295 (1847).
Marattia alata Sw. Prodr. 128 (1788).
M. Kaulfussii J. Sm. in Hook. Gen. sub t. 26 (1838).

## OPHIOGLOSSACEAE

Botrychium cicutarium (Sav.) Sw. Syn. 171 (1806).
B. Schaffneri Underw. in Bull. Torr. Bot. Club, 30: 51 (1903).

Ophioglossum coriaceum A. Cunn. in Hook. Compan. Bot. Mag. 2: 361 (1837).
O. crotalophoroides Walt. Fl. Carol. 256 (1788).
? O. ellipticum Hook. \& Grev. Ic. Fil. 1: t. 40A (1827).
O. nudicaule var. tenerum (Mett.) Clausen in Mem. Torr. Bot. Club, 19(2): 146 (1938).
O. reticulatum L. Sp. Pl. 2: 1063 (1753).
O. scariosum Clausen in Mem. Torr. Bot. Club, 19(2): 153 (1938).

## EQUISETACEAE

Equisetum bogotense HBK. Nov. Gen. \& Spec. 1: 42 (1816).
E. giganteum L. Sp. Pl. (ed. 2) 2: 1517 (1763).
E. pyramidale J. E. Goldm. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 469 (1843).

## LYCOPODIACEAE

Lycopodium andinum Rosenst. in Fedde, Repert. Spec. Nov. 5: 239 (1908).
L. aristatum Humb. \& Bonpl. ex Willd. Sp. Pl. 5: 17 (1810).
L. bolivianum Rosenst. in Fedde, Repert. Spec. Nov. 11: 59 (1912).
L. bolivianum var. teretiusculum Rosenst. in Fedde, Repert. Spec. Nov. 11: 60 (1912).
L. Brongniartii Spring, Monog. 1: 33 (1842).
L. carolinianum L. Sp. Pl. 2: 1104 (1753).
L. cernuum L. Sp. Pl. 2: 1103 (1753).
L. clavatum L. Sp. Pl. 2: 1101 (1753).
L. complanatum L. Sp. Pl. 2: 1104 (1753).
L. contiguum K1. in Linnaea, 18: 519 (1844).
L. dichotomum Jacq. Enum. Stirp. Vindob. 314 (1762).
L. Jussiaei Desv. ex Poir. in Lam. Encyc. Suppl. 3: 543 (1813).
L. Lechleri Hieron. in Engler, Bot. Jahrb. 34: 571 (1905).
L. linifolium L. Sp. Pl. 2: 1100 (1753).
I. longipes Hook. \& Grev. in Hook. Bot. Misc. 2: 372 (1831).
L. myrsinites Lam. Encyc. 3: 654 (1789).
L. nubigenum Herzog in Meded. Rijks Herbar. 27: 2 (1915).
L. paniculatum Desv. ex Poir. in Lam. Encyc. Suppl. 3: 543 (1813).
L. Pearcei Baker, Handbk. Fern-Allies, 14 (1887).
L. reflexum Lam. Encyc. 3: 653 (1789).
L. Saururus Lam. Encyc. 3: 653 (1789).
L. subulatum Desv. ex Poir. in Lam. Encyc. Suppl. 3: 544 (1813).
L. taxifolium Sw. Fl. Ind. Occ. 3: 1573 (1806).
? L. tetragonum Hook. \& Grev. Ic. Fil. 1: t. 109 (1828).
L. verticillatum L. f. Suppl. 448 (1781).
L. Williamsii Underw. \& Lloyd in Bull. Torr. Bot. Club, 33: 112 (1906).

Urostachys Pflanzii Nessel in Fedde, Repert Spec. Nov. 36: 181 (1934) = Lycopodium sp.

## PSILOTACEAE

Psilotum nudum (L.) Beauv. Prodr. Cinq. \& Six. Fam. L'Aethéogamie, etc. 112 (1805).

## SELAGINELLACEAE

Selaginella anceps Presl in Abh. Böhm. Ges. Wiss. (ser. 5) 3: 581 (1845).
S. Galeottii Spring in Bull. Acad. Roy. Bruxelles, 10 (3) : 230 (1843).
S. haematodes (Kunze) Spring in Mart. Fl. Bras. 1(1): 126 (1840).
S. leptoblepharis A. Br. in Planch. \& Triana in Ann. Sci. Nat. (ser. 5) 3: 279 (1865).
S. macrophylla A. Br. in Planch. \& Triana in Ann. Sci. Nat. (ser. 5) 3: 302 (1865).
S. microphylla (HBK.) Spring in Bull. Acad. Roy. Bruxelles, 10 (3): 234 (1843).
S. Mildei Hieron. in Engl. \& Prantl, Nat. Pflanzenfam. 1(4): 671 (1901).
S. peruviana (Milde) Hieron. in Hedwigia, 39: 307 (1900).
S. peruviana var. Dombeyana Hieron. in Hedwigia, 39: 308 (1900).
S. polycephala Baker in Journ. Bot. 21: 332 (1883).
S. radiata (Aubl.) Spring, Monog. 2: 120 (1849).
S. rubescens Hieron. in Hedwigia, 43: 236 (1904).
S. silvestris Asplund in Ark. Bot. 20A(7): 30, fig. 3-5 (1926).
S. trisulcata Asplund in Ark. Bot. 20A(7): 34, fig. 6 (1926).

## ISOËTACEAE

Isoëtes boliviensis Weber in Hedwigia, 63: 247 (1922).
I. glacialis Asplund in Ark. Bot. 20A(7): 35, fig. 7 (1926).
I. Herzogii Weber in Hedwigia, 63: 250 (1922).

## GYMNOSPERMAE

## CYCADACEAE

Zamia boliviana (Brongn.) A. DC. Prodr. 16(2): 540 (1868).

## PODOCARPACEAE

Podocarpus Cardenasii Buchholz \& Gray in Journ. Arnold Arb. 29: 142 (1948).
P. magnifolius Buchholz \& Gray in Journ. Arnold Arb. 29: 133 (1948).
P. montanus sensu Britton in Bull. Torr. Bot. Club, 16: 13 (1889) = P. utilior.
P. oleifolius Don in Lambert, Pinus, 2: 20 (1824).
P. Parlatorei Pilger in Engler, Pflanzenr. IV, 5: 86 (1903).
P. Rusbyi Buchholz \& Gray in Journ. Arnold Arb. 29: 134 (1948).
P. salicifolius sensu Britton in Bull. Torr. Bot. Club, 16: 13 (1889) = P. Rusbyi.
P. utilior Pilger in Fedde, Repert. Spec. Nov. 1: 189 (1905).

## GNETACEAE

Ephedra americana var. andina (Poepp.) Stapf in Denkschr. Akad. Wiss MathNaturw. K1. 56: 86 (1889).
E. americana var. Humboldtii Stapf in Denkschr. Akad. Wiss. Math.-Naturw. K1. 56: 85 (1889).
E. americana var. rupestris (Benth.) Stapf in Denkschr. Akad. Math.-Naturw. K1. 56: 86 (1889).
E. andina var. humilis (Wedd.) Parlatore in DC. Prodr. 16 (2): 353 (1868). $=\mathrm{E}$. americana var. rupestris.
E. breana Phil. in Anal. Univ. Chile, 91: 519 (1895).
E. triandra Tul. in Ann. Sci. Nat. ((ser. 4) 10: 125 (1858).

## ANGIOSPERMAE

## MONOCOTYLEDONEAE

TYPHACEAE
Typha domingensis Pers. Synops. Pl. 2: 532 (1807).

## POTAMOGETONACEAE

Potamogeton filiformis Pers. Synops. Pl. 1: 152 (1805).
P. pectinatus L. Sp. Pl. 127 (1753).
P. pectinatus var. striatus (R. \& P.) Hagstr. in Kgl. Sv. Vetensk. Akad. Handl. 55(5): 51 (1916).
Ruppia filifolia (Phil.) Skottsb. in Kgl. Sv. Vetensk. Akad. Handl. 56(5): 171 (1916).
Zannichellia palustris L. Sp. Pl. 969 (1753).

## NAJADACEAE

Najas guadalupensis (Spreng.) Morong in Mem. Torr. Bot. Club, 3(2): 60, t. 67 (1893).

## SCHEUCHZERIACEAE

Lilaea subulata Humb. \& Bonpl. Pl. Aequin. 1: 222, t. 63 (1808).
Triglochin concinna var. deserticola (Phil.) J. T. Howell in Leaff. West. Bot. 5(1): 19 (1947).

## ALISMACEAE

Alisma bolivianum Rusby in Mem. N. Y. Bot. Gard. 7: 208 (1927).
A. tenellum Mart. ex Schult. f. Syst. Veg. 7: 1600 (1830).

Echinodorus grandiflorus var. ovatus Micheli in DC Monog. Phan. 3: 58 (1881):
E. subulatus Engelm. in Gray, Man. (ed. 1) 460 (1848).
E. tenellus (Mart.) Buchenau in Abh. Naturw. Ver. Bremen, 2: 21 (1868).
E. tenellus var. latifolius (Seubert) Fassett in Rhodora, 57: 202 (1955).

Lophotocarpus guyanensis (HBK.) Dur. \& Schinz, Consp. Fl. Afr. 5: 487 (1894).
Sagittaria lancifolia L. Syst. (ed. 10) 2: 1270 (1759).
S. montevidensis Cham. \& Schlechtd. in Linnaea, 2: 156 (1827).

## BUTOMACEAE

Hydrocleis cryptopetala R. E. Fries in Ark. Bot. 8(8): 47, t. 2, fig. 1-3 (1908). H. nymphoides (Willd.) Buchenau in Bremen Abh. 2: 7 (1869).

## HYDROCHARITACEAE

Elodea chilensis (Planch.) Casp. in Monatsber. Berl. Akad. 1857: 47.

## GRAMINEAE

Aciachne pulvinata Benth. in Hook. Ic. Pl. 14: 44, t. 1362 (1881).
A. uniflora Baill. in Bull. Mens. Soc. Linn. Paris, 2: 1073 (1893).

Aegopogon bryophilus Doell in Mart. Fl. Bras. 2(3): 239 (1880).
Ae. cenchroides Humb. \& Bonpl. ex Willd. Sp. Pl. 4(2): 899 (1806).
Ae. Fiebrigii Mez in Fedde, Repert. Spec. Nov. 17: 145 (1921) = Ae. bryophilus.
Ae. geminiflorus var muticus Pilger in Engler, Bot. Jahrb. 27: 25 (1899) $=$ Ae. bryophilus.
Agenium villosum (Nees) Pilger in Fedde, Repert. Spec. Nov. 43: 82 (1938).
Agropyron attenuatum (HBK.) Roem. \& Schult. Syst. Veg. 2: 751 (1817).
A. boliviacum P. Cand. Tribu des Hordées, 25, 46 (1901).
A. breviaristatum Hitchc. in Contrib. U. S. Nat. Herb. 24: 353 (1927).

Agrostis araucana Phil. in Anal. Univ. Chile, 94: 14 (1896).
A. boliviana Mez in Fedde, Repert. Spec. Nov. 18: 1 (1922).
A. breviculmis Hitchc. in U. S. Dept. Agric. Bur. Pl. Ind. Bull. 68:36, t. 18 (1905).
A. exasperata Trin. in Mém. Acad. St. Pétersb. (ser. 6) 4(1): 352 (1841).
A. gelida Trin. in Mém. Acad. St. Pétersb. (ser. 6) 4(1): 343 (1841).
A. Haenkeana Hitchc. in Contrib. U. S. Nat. Herb. 24: 381 (1927).
A. montevidensis Spreng. ex Nees, Agrost. Bras. 403 (1829).
A. nana (Presl) Kunth, Rév. Gram. 3: 596 (1829) = A. breviculmis.
A. perennans (Walt.) Tuckerm. in Amer. Journ. Sci. 45: 44 (1843).
A. stolonifera L. Sp. Pl. 62 (1753).
A. tolucensis HBK. Nov. Gen. \& Spec. 1: 135 (1816).
A. verticillata Vill. Prosp. Pl. Dauph. 16 (1779).

Aira conferta (Pilg.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 361 (1927).
Alopecurus aequalis Sobol. Fl. Petrop. 16 (1799).
A. alpinus var. aristatus Hook. f. Fl. Antarct. 2: 370 (1847).
A. bracteatus Phil. in Anal. Univ. Chile, 94: 6 (1896).
A. Hitchcockii Parodi in Rev. Fac. Agron. Vet. Buenos Aires, 7: 366 (1931).

Andropogon altus Hitchc. in Contrib. U. S. Nat. Herb. 17: 208 (1913).
A. bicornis L. Sp. Pl. 1046 (1753).
A. cirratus Hack. in Flora, 68: 119 (1885).
A. condensatus HBK. Nov. Gen. \& Spec. 1: 188 (1816).
A. cordatus Swallen in Contrib. U. S. Nat. Herb. 29(6): 274 (1948).
A. Fabricii Thunb. ex Henr. in Meded. Rijks Herbar. 40: 44 (1921).
A. Hassleri Hack. in Bull. Herb. Boiss. (ser. 2) 4(3): 266 (1904).
A. hirtiflorus (Nees) Kunth, Rév. Gram. 2: 569 (1832).
A. lateralis Nees, Agrost. Bras. 329 (1829).
A. leptocladus Hack. in Flora, 68: 122 (1885).
A. leucostachyus HBK. Nov. Gen. \& Spec. 1: 187 (1816),
A. nutans var. agrostoides (Speg.) Hack. in DC. Monog. Phan. 6: 952 (1889).
A. nutans var. stipoides (HBK.) Hack. in DC. Monog. Phan. 6: 530 (1889).
A. Riedelii Trin. in Mém. Acad. St. Pétersb. (ser. 6) 2: 263 (1833).
A. saccharoides Sw. Prodr. 26 (1788).
A. saccharoides subsp. genuinus var. barbinodis (Lag.) Hack. in DC. Monog. Phan. 6: 494 (1889).
A. saccharoides var. laguroides (DC.) Hack. in Mart. Fl. Bras. 2(3):293 (1883).
A. saccharoides var. parvispiculus Hitchc. in Contrib. U. S. Nat. Herb. 24: 497 (1927).
A. saccharoides var. perforatus (Trin.) Hack. in DC. Monog. Phan. 6: 496 (1889).
A. Selloanus (Hack.) Hack. in Bull. Herb. Boiss. (ser. 2) 4: 266 (1904).
A. tener (Nees) Kunth, Rév. Gram. 2: 565 (1832).
A. tener var. genuinus subvar. hirtiglumis Henr. in Meded. Rijks Herbar. 40: 42 (1920).
A. ternatus subsp. macrothrix (Trin.) Hack. in Mart. Fl. Bras. 2(3): 287 (1883).
A. villosus (Nees) Ekman in Ark. Bot. 11(4): 9 (1912).
A. virgatus Desv. ex Hamilt. Prodr. Pl. Ind. Occ. 9 (1825).

Anthaenantia gigantea (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1): 329 (1900).
Anthaenantiopsis Fiebrigii Mez in Engler, Bot. Jahrb. 56, Beibl. 125: 11 (1921).
Anthochloa lepidula Nees \& Meyen in Meyen, Reise, 2: 14 (1835).
A. rupestris Remy in Ann. Sci. Nat. (ser. 3) 6:347 (1846) = A. lepidula.

Aphanelytrum procumbens Hack. in Oesterr. Bot. Zeitschr. 52: 13 (1902).
Aristida adscensionis L. Sp. Pl. 82 (1753).
A. adscensionis var. coerulescens subvar. condensata Hack. apud Stuckert, Contrib. Conoc. Gram. Argent. 91 (1904).
A. adscensionis var. humilis forma viridis O. Ktze. Rev. Gen. 3(2):339 (1898).
A. adscensionis var. normalis forma violascens O. Ktze. Rev. Gen. 3(2): 339 (1898).
A. Asplundii Henr. in Meded. Rijks Herbar. 54: 42 (1926).
A. capillacea Lam. Encyc. Tabl. 1: 156 (1791).
A. circinalis Lindm. in Kgl. Sv. Vet. Akad. Handl. 34 (6) : 13, t. 7 a (1900).
A. complanata Trin. in Mém. Acad. St. Pétersb. (ser. 6) 1: 853 (1830).
A. ecuadoriensis Henr. in Meded. Rijks Herbar. 58A: 307 (1932).
A. enodis Hack. in Fedde, Repert. Spec. Nov. 11: 21 (1912).
A. Friesii Hack. ex Henr. in Meded. Rijks Herbar. 54: 186 (1926).
A. implexa Trin. in Mém. Acad. St. Pétersb. (ser. 6) 2(1): 48 (1836).
A. inversa Hack. in Ark. Bot. 8(8) : 37 (1909) $=$ A. mendocina.
A. longiramea var. boliviana Henr. in Meded. Rijks Herbar. 40: 56 (1921) $=$ A. complanata.
A. longiseta var. robusta Merrill in Circ. U. S. Div. Agrost. 34: 5 (1901).
A. Mandoniana Henr. in Meded. Rijks Herbar. 40: 55 (1921) = A. adscensionis.
A. mendocina R. A. Phil. in Anal. Univ. Chile, 36: 205 (1870).
A. mendocina var. macrantha (Parodi) Henri, in Meded. Rijks Herbar. 54A: 267 (1927).
A. Pflanzii Mez in Fedde, Repert. Spec. Nov. 17: 151 (1921) = A. enodis.
A. riparia Trin. in Mém. Acad. St. Pétersb. (ser. 6) 2(1): 48 (1836).
A. riparia var. andina Henr. in Meded. Rijks Herbar. 58A: 185 (1932).

Arthrostylidium racemiflorum Steud. Syn. Pl. Gram. 336 (1854).
Arundinaria Herzogiana Henr. in Meded. Rijks Herbar. 40: 75 (1921).
Arundinella Berteroniana (Schult.) Hitchc. \& Chase in Contrib. U. S. Nat. Herb. 18: 290 (1917).
A. confinis (Schult.) Hitchc. \& Chase in Contrib. U. S. Nat. Herb. 18: 290 (1917).

Arundo donax L. Sp. PI. 81 (1753).
Avena barbata Brot. Fl. Lusit. 1: 108 (1804).
A. fatua L. Sp. Pl. 80 (1753).
A. scabrivalvis Trin. in Mém. Acad. St. Pétersb. (ser. 6) 2: 28 (1836).

Axonopus aureus Beauv. Ess. Agrost. 12 (1812).
A. barbigerus (Kunth) Hitchc. in Contrib. U. S. Nat. Herb. 24: 433 (1927).
A. capillaris (Lam.) Chase in Proc. Biol. Soc. Wash. 24: 133 (1911).
A. chrysoblepharis (Lag.) Chase in Proc. Biol. Soc. Wash. 24: 134 (1911).
A. compressus (Sw.) Beauv. ex Steud. Nomencl. (ed. 2) 1: 174 (1840).
A. elegantulus (Presl) Hitchc. in Contrib. U. S. Nat. Herb. 24: 433 (1927).
A. fissifolius (Raddi) Kuhlm. in Comm. Linkas Telegr. Matto Grosso, 67: 87 (1922).
A. Herzogii (Hack.) Hitch. in Contrib. U. S. Nat. Herb. 24: 431 (1927).
A. marginatus (Trin.) Chase in Contrib. U. S. Nat. Herb. 17: 226 (1913).
A. Purpusii (Mez) Chase in Journ. Wash. Acad. Sci. 17: 144 (1927).
A. siccus (Nees) Kuhlm. in Comm. Linkas Telegr. Matto Grosso, 67: 87 (1922).
A. scoparius (Flügge) Hitchc. in Contrib. U. S. Nat. Herb. 22: 471 (1922).

Bouteloua aristidoides (HBK.) Griseb. Fl. Brit. W. Ind. 537 (1864).
B. curtipendula Torr. in Emory, Milit. Reconn. 154 (1848), nomen provisorium.
B. megapotamica (Spreng.) O. Ktze. Rev. Gen. 3(2): 341 (1898).
B. prostrata Lag. in Varied. Cienc. 2(4): 141 (1805).
B. racemosa Lag. in Varied. Cienc. 2(4): 141 (1805).
B. simplex Lag. in Varied. Cienc. 2(4): 141 (1805).
B. simplex var. actinochloides Henr. in Meded. Rijks Herbar. 40: 65 (1921) = B. simplex.
Brachiaria plantaginea (Link) Hitchc. in Contrib. U. S. Nat Herb. 12: 212 (1909).

Brachypodium mexicanum (Lag.) Link, Hort. Berol. 1: 41 (1827).
Briza Mandoniana (Griseb.) Henr. in Meded. Rijks Herbar. 40: 70 (1921).
B. Mandoniana var. Herzogiana Henr. in Meded. Rijks Herbar. 40: 71 $(1921)=$ B. Mandoniana.
B. Mandoniana var. tuberculata Henr. in Meded. Rijks Herbar. 40: 71 (1921) = B. Mandoniana.
B. Mandoniana var. vallegrandensis Henr. in Meded. Rijks Herbar. 40: 71 $(1921)=$ B. Mandoniana.
B. spicigera (Presl) Steud. Nomencl. (ed. 2) 1: 225 (1840).
B. stricta (Hook. \& Arn.) Steud. Nomencl. (ed. 2) 1: 225 (1840).

Bromidium hygrometricum var. breviaristatum O. Ktze. Rev. Gen. 3(2): 342 (1898) $=$ Calamagrostis sp.?

Bromus angustatus Pilg. in Engler, Bot. Jahrb. 25: 719 (1898) = B. unioloides.
B. Buchtienii Hack. in Fedde, Repert. Spec. Nov. 11: 30 (1912) = B. pitensis.
B. lanatus HBK. Nov. Gen. \& Spec. 1: 150 (1816).
B. Mandonianus Henr. in Fedde, Repert. Spec. Nov. 23: 177 (1926) $=$ Dielsiochloa floribunda.
B. Pflanzii Pilg. in Engler, Bot. Jahrb. 49: 189 (1913) = B. lanatus.
B. pitensis HBK. Nov. Gen. \& Spec. 1: 152 (1816).
B. segetum HBK. Nov. Gen. \& Spec. 1: 151 (1816).
B. Trinii Desv. in Gay, Fl. Chile, 6: 441 (1853).
B. unioloides HBK. Nov. Gen. \& Spec. 1: 151 (1816).

Calamagrostis amoena (Pilg.) Pilg. in Engler, Bot. Jahrb. 42: 60 (1908).
C. Antoniana (Griseb.) Steud. ex Hitchc. in Contrib. U. S. Nat. Herb. 24: 378 (1927).
C. Beyrichiana Ness ex Doell in Mart. Fl. Bras. 2(3): 53, t. 16 (1878).
C. boliviensis Hack. in Fedde, Repert. Spec. Nov. 6: 156 (1908) = C. heterophylla.
C. brevifolia (Presl) Steud. Nomencl. (ed. 2) 1: 249 (1840).
C. calderillensis Pilg. in Engler, Bot. Jahrb. 42: 72 (1908).
C. cephalantha Pilg. in Engler, Bot. Jahrb. 42: 61 (1908).
C. chrysantha (Presl) Steud. Nomencl. (ed. 2) 1: 250 (1840).
C. curta (Wedd.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 376 (1927).
C. curvula (Wedd.) Pilg. in Engler, Bot. Jahrb. 42: 60 (1908).
C. elegans (Wedd.) Henr. in Meded. Rijks Herbar. 40: 61 (1921) = C. eminens.
C. eminens (Presl) Steud. Nomencl. (ed. 2) 1: 250 (1840).
C. eminems var. sordida O. Ktze. Rev. Gen. $3(2): 344$ (1898) = C. eminens.
C. eminens var. tunariensis O. Ktze. Rev. Gen. 3 (2). 344 (1898) = C. eminens.
C. Fiebrigii Pilg. in Engler, Bot. Jahrb. 42: 68 (1909).
C. filifolia (Wedd.) Henr. in Meded. Rijks Herbar. 40: 61 (1921) = C. amoena.
C. glacialis (Wedd.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 375 (1927).
C. gracilis (Wedd.) Henr. in Meded. Rijks Herbar. 50: 61 (1921).
C. heterophylla (Wedd.) Pilg. in Engler, Bot. Jahrb. 42: 64 (1908).
C. Humboldtiana Steud. Nomencl. (ed. 2) 1: 250 (1840).
C. Jamesonii Steud. Syn. Pl. Glum. 1: 191 (1854).
C. leiophylla (Wedd.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 367 (1927).
C. Lilloi Hack. in Stuckert in Anal. Mus. Nac. Buenos Aires, 13: 477 (1906).
C. longearistata (Wedd.) Hack. ex Sodiro in Anal. Univ. Quit. 3: 481 (1889).
C. montevidensis Nees, Agrost. Bras. 401 (1829).
C. montevidensis var. linearis Hack. in Fedde, Repert. Spec. Nov. 6: 15̄7 $(1908)=$ C. montevidensis.
C. nitidula var. elata Pilg. in Engler, Bot. Jahrb. 42: 70 (1908) = C. rigida.
C. nivalis (Wedd.) Hack. ex Buchtien, Contrib. Fl. Boliv. 1: 75 (1910).
C. Orbignyana (Wedd.) Pilg. in Perkins in Engler, Bot. Jahrb. 49: 184 (1913). (1913).
C. ovata (Presl) Steud. Nomencl. (ed. 2) 1: 251 (1840).
C. pentapogonoides O. Ktze. Rev. Gen. 3(2): 344 (1898) = C. vicunarum.
C. Pflanzii Pilg. in Perkins in Engler, Bot. Jahrb. 49: 184 (1913) = C. ovata.
C. Pflanzii var. major Pilg. in Perkins in Engler, Bot. Jahrb. 49: 185 $(1913=$ ?
C. recta (HBK.) Trin. ex Steud. Nomencl. (ed. 2) 1: 251 (1840).
C. rigescens (Presl) Scribn. in Rept. Missouri Bot. Gard. 10: 37, t. 32, fig. 3 (1899).
C. rosea var. macrochaeta Hack. in Ark. Bot. $8(8): 40$ (1908) $=$ C. tarmensis.
C. tarijensis Pilg. in Engler, Bot. Jahrb. 42: 71 (1908) = C. tarmensis.
C. tarmensis Pilg. in Engler, Bot. Jahrb. 42: 70 (1908).
C. toluccensis densiflora O. Ktze. Rev. Gen. 3(2): 345 (1898) [disposition uncertain, according to Hitchcock].
C. toluccensis var. laxiflora O. Ktze. Rev. Gen. $3(2): 345$ (1898) = C. leiophylla.
C. trichophylla Pilg. Engler, Bot. Jahrb. 42: 67 (1908).
C. vicunarum (Wedd.) Pilg. in Engler, Bot. Jahrb. 42: 62 (1908).
C. violacea (Wedd.) Hack. ex Buchtien, Contrib. Fl. Boliv. 1: 75 (1910).

Cenchrus echinatus L. Sp. Pl. 1050 (1753).
C. myosuroides HBK. Nov. Gen. \& Spec. 1: 115, t. 35 (1816).
C. nervosus var. ramosus O. Ktze. Rev. Gen. 3(2): 347 (1898).
C. pauciflorus Benth. Bot. Voy. Sulphur, 56 (1844).
C. viridis Spreng. Syst. Veg. 1: 301 (1825).

Chaetochloa argentina (Herrm.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 480 (1927).
C. barbinodis (Herrm.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 480 (1927).
C. geniculata (Lam.) Millsp. \& Chase in Field Mus. Publ. Bot. 3: 37 (1903).
C. oblongata (Griseb.) Hitch. in Contrib. U. S. Nat. Herb. 24: 480 (1927).
C. Poiretiana (Schult.) Hitchc. in Contrib. U. S. Nat. Herb. 22: 159 (1920).
C. scandens (Schrad.) Scribn. \& Merr. in U. S. Dept. Agric. Div. Agrost. Bull. 21: 17 (1900).
C. tenacissima (Schrad.) Hitchc. \& Chase in Contrib. U. S. Nat. Herb. 18: 352 (1917).
C. tenax (L. Rich.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 479 (1927).
C. trichorhachis (Hack.) Hitchc. in Contrib. U. S. Nat Herb. 24: 481 (1927).
C. vulpiseta (Lam.) Hitche. \& Chase in Contrib. U. S. Nat. Herb. 18: 350 (1917).

Chloris bahiensis Steud. Syn. Pl. Gram. 208 (1854).
C. Beyrichiana Kunth, Rév. Gram. 1: 289, t. 56 (1830).
C. distichophylla var. argentina Hack. in Stuckert, Contrib. Conoc. Gram. Argent. 113 (1904).
C. halophila Parodi in Rev. Argent. Agron. 12: 45 (1945).
C. polydactyla (L.) Sw. Prodr. 26 (1788).
C. radiata (L.) Sw. Prodr. 26 (1788).
C. virgata Sw. Fl. Ind. Occ. 1: 203 (1797).

Chusquea delicatula Hitchc. in Contrib. U. S. Nat. Herb. 24: 309 (1927).
C. longipendula O. Ktze. Rev. Gen. 3 (2) : 348 (1898) = C. uniflora ?
C. peruviana E. G. Camus, Bamb. Monog. 88, t. 53, fig. B (1913).
C. quitensis var. patentissima Hack. in Fedde, Repert. Spec. Nov. 6: 161 (1908) = C. scandens.
C. scandens Kunth, Syn. Pl. Aequin. 1: 254 (1822).
C. serrulata Pilg. in Engler, Bot. Jahrb. 25: 719 (1898).
C. spicata Munro in Trans. Linn. Soc. 26: 60 (1868).
C. uniflora Steud. Syn. Pl. Glum. 337 (1854).

Coix lachryma-jobi L. Sp. Pl. 972 (1753).
Cortaderia atacamensis (Phil.) Pilg. in Engler, Bot. Jahrb. 37: 374 (1906).
C. bifida Pilg. in Engler, Bot. Jahrb. 37: 374 (1906).
C. bifida var. grandiflora Henr. in Meded. Rijks Herbar. 40: 67 (1921) = C. bifida.
C. columbiana (Pilg.) Pilg. in Engler, Bot. Jahrb. 37, Beibl 85: 65 (1906) $=$ C. nitida.
C. jubata (Lemoine) Stapf in Bot. Mag. 124: t. 7607 (1898).
C. nitida (HBK.) Pilg. in Engler, Bot. Jahrb. 37: 375 (1906).
C. rudiuscula Stapf in Gard. Chron. (ser. 3) 22: 396 (1897).
C. Selloana (Schult.) Asch. \& Graebn. Synop. Mittel-Europ. F1. 2(1): 325 (1900).
C. speciosa (Nees) Stapf in Gard. Chron. (ser. 3) 22: 396 (1897).

Cynodon Dactylon (L.) Pers. Synops. Pl. 1: 85 (1805).
C. Dactylon var. maritimum (HBK.) Hack. in Fries in Ark. Bot. 8(8): 40 (1908) = C. Dactylon.

Dactyloctenium aegyptium (L.) Richt. Pl. Eur. 1: 68 (1890).
Danthonia cirrhata Hack. \& Arech. in Anal. Mus. Nac. Montevideo, 1: 367 (1897).

Deyeuxia Anthoxanthum Wedd. in Bull. Soc. Bot. France, 22: 156 (1875) = Calamagrostis sp.?
D. capitata Wedd. in Bull. Soc. Bot. France, 22: 156 (1875) = Calamagrostis sp.?
D. cephalotes Wedd. in Bull. Soc. Bot. France, 22: 178 (1875) $=$ Calamagrostis sp.?
D. festucoides Wedd. in Bull. Soc. Bot. France, 22: 178 (1875) $=$ Calamagrostis sp. ?
D. imberbis Wedd. in Bull. Soc. Bot. France, 22: 177 (1875) $=$ Calamagrostis rigescens.
L. Lagurus Wedd. in Bull. Soc. Bot France, 22: 156 (1875) = Calamagrostis sp.?
D. Mandoniana Wedd. in Bull. Soc. Bot. France, 22: 179 (1875) = Calamagrostis Humboldtiana.
D. mutica Wedd. in Bull. Soc. Bot. France, 22: 177 (1875) $=$ Calamagrostis sp.?
D. nematophylla Wedd. in Bull. Soc. Bot. France, 22: 179 (1875) = Calamagrostis sp.?
D. nivalis Wedd. in Bull. Soc. Bot. France, 22: 156 (1875) $=$ Calamagrostis ovata.
D. obtusata Wedd. in Bull. Soc. Bot. France, 22: 177 (1875) = Calamagrostis sp.?
D. phalaroides Wedd. in Bull. Soc. Bot. France, 22: 177 (1875) = Calamagrostis rigescens.
D. picta Wedd, in Bull. Soc. Bot. France, 22: 177 (1875) = Calamagrostis sp.?
D. setiflora Wedd. in Bull. Soc. Bot. France, 22: 178 (1875) = Calamagrostis sp.?
D. subsimilis Wedd. in Bull. Scc. Bot. France, 22: 178 (1875) $=$ Calamagrostis sp.?
D. sulcata Wedd. in Bull. Soc. Bot. France, 22: 178 (1875) = Calamagrostis sp.?
Dielsiochloa floribunda (Pilg.) Pilg. in Rev. Argent. Agron. 11: 257 (1944).
Digitaria Gerdesii var. boliviensis Henr. Monog. Digit. 287 (1950).
D. Lehmanniana Henr. in Blumea, 1(1): 107 (1934).

Dissanthelium calycinum (Presl) Hitchc. in Journ. Wash. Acad. Sci. 13: 224 (1923).
D. minimum Pilg. in Engler, Bot. Jahrb. 56, Beibl. 123: 28 (1920).
D. peruvianum (Nees \& Mey.) Pilg. in Engler, Bot. Jahrb. 37: 378 (1906).
D. Trollii Pilg. in Notizbl. 11: 778 (1933).

Distichlis humilis Phil. in Anal. Mus. Nac. Chile, 8: 86 (1891).
D. spicata (L.) Greene in Bull. Calif. Acad. 2: 415 (1887).

Echinochloa crusgalli var. crus-pavonis (HBK.) Hitchc. in Contrib. U. S. Nat. Herb. 22: 148 (1920).
Eleusine indica (L.) Gaertn. Fruct. 1: 8 (1788).
Elymus angulatus Presl, Rel. Haenk. 1: 264 (1830).
Elyonurus adustus (Trin.) Ekm. in Ark. Bot. 13(10): 6 (1913).
E. tripsacoides Humb. \& Bonpl. ex Willd. Sp. Pl. 4(2): 941 (1806).
E. tripsacoides var. ciliaris (Kunth) Hack. in DC. Monog. Phan. 6: 333 (1889) = E. tripsacoides.

Eragrostis articulata (Schrank) Nees, Agrost. Bras. 502 (1829).
E. articulata var. glabrescens Henr. in Meded. Rijks Herbar. 40: 69 (1921).
E. atrovirens (Desf.) Trin. in Steud. Nomencl. (ed. 2) 1: 562 (1840).
E. bahiensis Schrad. ex Roem. \& Schult. Mant. 2: 318 (1824).
E. bahiensis var. boliviensis Henr. in Meded. Rijks Herbar. 40: 68 (1921) = E. lurida.
E. boliviensis Jedw. in Bot. Archiv Mez, 5: 205 (1924) = E. montufari.
E. Buchtienii Hack. in Fedde, Repert. Spec. Nov. 6: 157 (1908) = E. montufari.
E. cilianensis (All.) Link ex Vign. Lut. in Malpighia, 18: 386 (1904).
E. ciliaris (L.) Link, Hort. Berol. 1: 192 (1827).
E. contristata Nees \& Meyen in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 163 (1843) = E. lurida.
E. expansa Link, Hort. Berol. 1: 190 (1827).
E. glomerata (Walt.) L. H. Dewey in Contrib. U. S. Nat. Herb. 2: 543 (1894).
E. hypnoides (Lam.) BSP. Prelim. Cat. N. Y. 69 (1888).
E. lugens Nees, Agrost. Bras. 505 (1829).
E. lugens subsp. flaccida (Lindm.) Hack. in Stuckert in Anal. Mus. Nac. Buenos Aires, 21: 134 (1911).
E. lurida Presl, Rel. Haenk. 1: 276 (1830).
E. maypurensis (HBK.) Steud. Syn. Pl. Glum. 1: 276 (1854).
E. mexicana (Lag.) Link. Hort. Berol. 1: 190 (1827).
E. montufari (HBK.) Steud. Nomencl. (ed. 2) 1: 563 (1840).
E. nigricans (HBK.) Steud. Nomencl. (ed. 2) 1: 563 (1840).
E. pilosa (L.) Beauv. Ess. Agrost. 71 (1812), combination implied but not actually made.
E. polytricha Nees, Agrost. Bras. 507 (1829).
E. reptans (Michx.) Nees, Agrost. Bras. 514 (1829).
E. solida Nees, Agrost. Bras. 501 (1829).
E. soratensis Jedw. in Bot. Archiv Mez, 5: 213 (1924) = E. lugens.
E. subatra Jedw. in Bot Archiv Mez, 5: 202 (1924) = E. nigricans.
E. tristis Jedw. in Bot. Archiv Mez, 5: 205 (1924) = E. nigricans.
E. villamontana Jedw. in Bot. Archiv Mez, 5: 197 (1924) =?

Erianthus angustifolius Nees, Agrost. Bras. 316 (1829).
E. Trinii (Hack.) Hack. in DC. Monog. Phan. 6: 135 (1889).

Eriochloa distachya HBK. Nov. Gen. \& Spec. 1: 95, t. 30 (1816).
E. punctata (L.) Desv. ex Hamilt. Prodr. Pl. Ind. Occ. 5 (1825).

Eriochrysis cayennensis Beauv. Ess. Agrost. 8, t. 4, fig. 11 (1812).
E. Warmingiana (Hack.) Kuhlm. in Comm. Linkas Telegr. Matto Grosso, 67: 29 (1922).
Festuca bromoides L. Sp. Pl. 75 (1753).
F. Buchtienii Hack. in Fedde, Repert. Spec. Nov. 6: 160 (1908) $=$ F. dolichophylla.
F. dissitiflora Steud. ex Griseb. in Goett. Abh. 24: 287 (1879) =F. rigescens.
F. dissitiflora subsp. eu-dissitiflora var. trachyphylla Hack. ex St.-Yves in Candollea, 3: 246 (1927) =?
F. dissitiflora subsp. loricata var. villipalea St.-Yves in Candollea, 3: 250 (1927) $=$ ?
F. dolichophylla Presl, Rel. Haenk. 1: 258 (1830).
F. Fiebrigii Pilg. in Engler, Bot. Jahrb. 37: 510 (1906) = F. procera
F. laetiviridis Pilg. in Engler, Bot. Jahrb. 37: 510 (1906) = F. dolichophylla.
F. megalura Nutt. in Journ. Acad. Philad. (ser. 2) 1: 188 (1848).
F. orthophylla Pilg. in Engler, Bot. Jahrb. 25: 717 (1898).
F. orthophylla var. boliviana Pilg. in Engler, Bot. Jahrb. 37: 508 (1906) $=$ F. orthophylla.
F. Pflanzii Pilg. in Engler, Bot. Jahrb. 49: 188 (1913) = F. dolichophylla.
F. procera HBK. Nov. Gen. \& Spec. 1: 154 (1816).
F. rigescens (Presl) Kunth, Rév. Gram. 3: 609 (1829).
F. scirpifolia (Presl) Kunth, Rév. Gram. 3: 609 (1829) =F. dolichophylla.
F. Stuebelii Pilg. in Engler, Bot. Jahrb. 25: 717 (1898) = F. rigescens.
F. sublimis Pilg. in Engler, Bot. Jahrb. 25. 718 (1898).
F. tectoria subsp. Mandoniana St.-Yves in Candollea, 3: 242 (1927).
F. tectoria subsp. Mandoniana var. mutica St.-Yves in Candollea, 3: 243 (1927).
F. ulochaeta Steud. Syn. Pl. Glum. 1: 305 (1854).

Gouinia latifolia (Griseb.) Vasey in Contrib. U. S. Nat. Herb. 1: 365 (1895).
G. virgata (Presl) Scribn. in U. S. Dept. Agric. Div. Agrost. Bull. 4: 10 (1897).

Gymnopogon jubiflorus Hitche. in Contrib. U. S. Nat. Herb. 24: 412 (1927).
G. spicatus (Spreng.) O. Ktze. Rev. Gen. 3(2): 354 (1898).
G. spicatus var. longiaristatus O. Ktze. Rev. Gen. 3(2): 354 (1898).

Gynerium atacamense Phil. in Linnaea, 33: 289 (1864-1865).
G. sagittatum (Aubl.) Beauv. Ess. Agrost. 138, t. 24, fig. 6 (1812).

Hackelochloa granularis (L.) O. Ktze. Rev. Gen. 2: 776 (1891).
Heteropogon contortus (L.) Beauv. ex Roem. \& Schult. Syst. Veg. 2: 836 (1817).
H. melanocarpus (Ell.) Benth. in Journ. Linn. Soc. 19: 71 (1882).
H. villosus Nees, Agrost. Bras. 362 (1829).

Holcus halepensis L. Sp. Pl. 1047 (1753).
H. lanatus L. Sp. Pl. 1048 (1753).
H. Sorghum L. Sp. Pl. 1047 (1753).

Homolepis aturensis (HBK.) Chase in Proc. Biol. Soc. Wash. 24: 146 (1911).
Hordeum halophilum Griseb. in Goett. Abh. 19: 249 (1874).
H. muticum Presl, Rel. Haenk. 1: 327 (1830).
H. muticum var. andicola (Griseb.) Thell. Fl. Advent. Montpellier, 157 (1912).
H. nodosum L. Sp. Pl. (ed. 2) 1: 126 (1762).
H. nodosum var. parviflorum (Hack.) Henr. \& Thell. in Meded. Rijks Herbar. 40: 75 (1921).
Hyparrhenia bracteata (Humb. \& Bonpl.) Stapf in Fl. Trop. Afr. 9: 360 (1919).
Ichnanthus breviscrobs Doell in Mart. Fl. Bras. 2(2): 294 (1877).
I. calvescens (Nees) Doell in Mart. Fl. Bras. 2(2): 285 (1877).

1. candicans (Nees) Doell in Mart, Fl. Bras. 2(2): 291 (1877).
2. minarum (Nees) Doell in Mart. Fl. Bras. 2(2): 294 (1877).
I. pallens (Sw.) Munro in Benth. Fl. Hongk. 414 (1861).
I. peruvianus Mez in Fedde, Repert. Spec. Nov. 15: 129 (1918).
I. Ruprechtii Doell in Mart. Fl. Bras. 2(2) : 293 (1877).

Imperata brasiliensis Trin. Mém. Acad. St. Pétersb. (ser. 6) 2: 331 (1832).
I. contracta (HBK.) Hitchc. in Rept. Missouri Bot. Gard. 4: 146 (1893).
I. minutiflora Hack. in DC. Monog. Phan. 6: 100 (1889).
I. tenuis Hack. in DC. Monog. Phan. 6: 689 (1889).

Isachne arundinacea (Sw.) Griseb. Fl. Brit. W. Ind. 553 (1864).
Koeleria cristata (L.) Pers. Synops. Pl. 1: 97 (1805).
K. gracilis Pers. Synops. Pl. 1: 97 (1805).
K. gracilis subsp. boliviensis (Domin) Domin in Biblioth. Bot. 65: 237 (1907).
K. pseudocristata var. andicola Domin in Fedde, Repert. Spec. Nov. 2: 94 (1906).

Lamprothyrsus Hieronymi (O. Ktze.) Pilg. in Engler, Bot. Jahrb. 37, Beibl. 85: 58 (1906).
L. Hieronymi var. pyramidata Pilg. in Engler, Bot. Jahrb. 37, Beibl. 85: 59 $(1906)=$ L. Hieronymi.
L. Hieronymi var. tincta Pilg. in Engler, Bot. Jahrb. 37, Beibl. 85: 59 (1906) $=$ L. Hieronymi.

Lasiacis divaricata (L.) Hitchc. in Contrib. U. S. Nat. Herb. 15: 16 (1910).
L. ligulata Hitchc. \& Chase in Contrib. U. S. Nat. Herb. 18: 337 (1917).
L. sorghoides (Desv.) Hitchc. \& Chase in Contrib. U. S. Nat. Herb. 18: 338 (1917).

Leersia hexandra Sw. Prodr. 21 (1788).
Leptochloa domingensis (Jacq.) Trin. Fund. Agrost. 133 (1820).
L. dubia (HBK.) Nees in Syllog. Pl. Ratisb. 1: 4 (1824).
L. uninervia (Presl) Hitchc. \& Chase in Contrib. U. S. Nat Herb. 18: 383 (1917).
L. virgata (L.) Beauv. Ess. Agrost. 71, t. 15, fig. 1 (1812).

Leptocoryphium lanatum (HBK.) Nees, Agrost. Bras. 84 (1829).
Lolium multiflorum Lam. Fl. Franc. 3: 621 (1778).
L. perenne L. Sp. Pl. 83 (1753).
L. temulentum L. Sp. Pl. 83 (1753).
L. temulentum var. arvense (With.) Bab. Man. Brit. Bot. 377 (1843).

Luziola peruviana Gmel. Syst. Nat. 1: 637 (1791).
Lycurus phalaroides HBK. Nov. Gen. \& Spec. 1: 142 (1816).
L. phleoides HBK. Nov. Gen. \& Spec. 1: 142, t. 45 (1816).

Manisuris aurita (Steud.) Hitchc. \& Chase in Contrib. U. S. Nat. Herb. 18: 276 (1917).
M. fasciculata (Lam.) Hitchc. in Amer. Journ. Bot. 2: 299 (1915).

Melica adhaerens Hack. in Fedde, Repert. Spec. Nov. 6: 158 (1908).
M. adhaerens var. tenuis (Papp) Papp in Notizbl. 10: 412 (1928).
M. Mandonii Papp in Notizbl. 10: 356 (1928).
M. scabra HBK. Nov. Gen. \& Spec. 1: 164 (1816).
M. scabra var. glabra Papp in Fedde, Repert. Spec. Nov. 25: 145 (1928).
M. violacea Cav. Ic. 5: 47, t. 472, fig. 2 (1799).

Mesosetum rottboellioides (HBK.) Hitchc. in Contrib. U. S. Nat. Herb. 12: 211 (1909).

Microchloa indica (L. f.) O. Ktze. Rev. Gen. 3(2): 356 (1898).
Muhlenbergia angustata (Presl) Kunth, Rév. Gram. 3: 594 (1829).
M. elegans var. atroviolacea O. Ktze. Rev. Gen. 3(2): 357 (1898).
M. elegans var. subviridis O. Ktze. Rev. Gen. 3(2): 357 (1898).
M. fastigiata (Presl) Henr. in Meded. Rijks Herbar. 40: 59 (1921).
M. Herzogiana Henr. in Meded. Rijks Herbar. 40: 58 (1921) = M. peruviana.
M. Holwayorum Hitche. in Contrib. U. S. Nat. Herb. 24: 389 (1927).
M. ligularis (Hack.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 388 (1927).
M. peruviana (Beauv.) Steud. Nomencl. (ed. 2) 1: 41 (1840).
M. phragmitoides Griseb. in Goett. Abh. 19: 255 (1874).
M. quitensis (HBK.) Hitchc. in Contrib. U. S. Nat. Herb. 17: 292 (1913).
M. rigida (HBK) Kunth, Rév. Gram. 1: 63 (1829).
M. tenuissima (Presl) Kunth, Rév. Gram. 3: 594 (1829).

Munroa andina Phil. in Anal. Mus. Nac. Chile, 8: 90 (1891).
M. andina var. breviseta Hack. ex Stuckert in Ann. Conserv. \& Jard. Bot. Genève, 17: 294 (1914).
M. argentina Griseb. in Goett. Abh. 24: 300 (1879).
M. decumbens R. A. Phil. in Anal. Mus. Nac. Chile, 8: 90 (1891).

Nassella Asplundii Hitchc. in Contrib. U. S. Nat. Herb. 24: 394 (1927).
N. corniculata Hack. in Fedde, Repert. Spec. Nov. 6: 155 (1908) = N. pubiflora.
N. deltoidea Hack. in Fedde, Repert. Spec. Nov. 11: 23 (1912) = N. pubiflora.
N. flaccidula Hack. in Fedde, Repert. Spec. Nov. 6: 154 (1908). = Stipa inconspicua.
N. flaccidula var. humilior Hack. in Fedde, Repert. Spec. Nov. 6: 155 $(1908)=\mathrm{N}$. pubiflora.
N. Meyeniana (Trin. \& Rupr.) Parodi in Darwiniana, 7: 379 (1947).
N. pubiflora (Trin. \& Rupr.) Desv. in Gay, Fl. Chile, 6: 264 (1853).
N. trachyphylla Henr. Meded. Rijks Herbar. 40: 57 (1921) $=$ N. pubiflora.

Olyra Buchtienti Hack. in Fedde, Repert. Spec. Nov. 11: 20 (1912).
O. ciliatifolia Raddi, Agrost. Bras. 19 (1823)).
O. ecaudata Doell in Mart. Fl. Bras. 2(2): 326 (1877).
O. Heliconia Lindm. in Kgl. Sv. Vet. Akad. Handl. 34 (6): 11, t. 6 (1900).
O. lateralis (Presl) Chase in Proc. Biol. Soc. Wash. 21: 179 (1908).
O. latifolia L. Syst. Nat. (ed. 10) 2: 1261 (1759).
O. micrantha HBK. Nov. Gen. \& Spec. 1: 199 (1816).
O. pauciflora var. atrocarpa O. Ktze. Rev. Gen. 3(2): 357 (1898).
O. pauciflora var. leucocarpa O. Ktze. Rev. Gen. 3(2): 357 (1898).

Oplismenus hirtellus (L.) Beauv. Ess. Agrost. 54, 168 (1812).
Orthoclada laxa (Rich.) Beauv. ex Nees, Agrost. Bras. 522 (1829).
Oryzopsis florulenta Pilg. in Engler, Bot. Jahrb. 27: 26 (1899).
O. Neesii Pilg. in Engler, Bot. Jahrb. 56, Beibl. 123: 26 (1920) = Stipa obtusa.
Panicum adustum var. leianthum Hack. in Fedde, Repert. Spec. Nov. 6: 342 (1909).
P. aquaticum Poir. in Lam. Encyc. Suppl. 4: 281 (1816).
P. Bergii var. leiophyllum Hack. \& Lindm. in Kgl. Sv. Vet. Akad. Handl. $34(6): 10$ (1900).
P. boliviense Hack. in Fedde, Repert. Spec. Nov. 11: 19 (1912).
P. caaguazense Henr. in Meded. Rijks Herbar. 47: 2 (1922).
P. cayennense Lam. Encyc. Tabl. 1: 173 (1791).
P. chloroticum Nees ex Trin. Gram. Pan. 236 (1826).
P. cordovense Fourn. Mex. Pl. 2: 26 (1886).
P. cyanescens Nees, Agrost. Bras. 220 (1829).
P. echinulatum Mez in Notizbl. 7: 62 (1917).
P. echinulatum var. boliviense Henr. in Meded. Rijks Herbar. 40: 50 (1921).
P. Friesii Hack. ex Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1(1): 170 (1905) $=$ Trichachne saccharata.
P. frondescens G.F.W. Meyer, Primit. Fl. Esseq. 56 (1818).
P. Gerdesii Hack. in Oesterr. Bot. Zeitschr. 51: 333 (1901).
P. Ghiesbreghtii Fourn, Mex. Pl. 2: 29 (1886).
P. glutinosum Sw. Prodr. 24 (1788).
P. granuliferum var. longifolium O. Ktze. Rev. Gen. 3(2): 361 (1898).
P. hebotes Trin. in Mém. Acad. St. Pétersb. (ser. 6.) 1: 30 (1834).
P. helobium Mez ex Henr. in Meded. Rijks Herbar. 40: 52 (1921).
P. hirticaule J. \& C. Presl. Rel. Haenk. 1: 308 (1830).
P. laxum forma minus Hack. ex Stuckert, Terc. Contrib. 39 (1911).
P. maximum Jacq. Collect. 1: 76 (1786).
P. megiston Schult. Mant. 2: 248 (1824).
P. nemorosum var. uncinatum O. Ktze. Rev. Gen. 3(2): 363 (1898).
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P. pantrichum Hack. in Verh. Zool.-Bot. Ges. Wien, 65: 72 (1915).
P. parvifolium Lam. Encyc. Tabl. 1: 173 (1791).
P. paucispicatum Morong in Ann. N. Y. Acad. Sci. 7: 262 (1893).
P. peladoënse Henr. in Blumea, 4 (3): 504 (1941).
P. pilosum Sw. Prodr. 22 (1788).
P. polygonatum Schrad. ex Schult. Mant. 2: 256 (1824).
P. procurrens Nees ex Trin. Gram. Pan. 183 (1826).
P. pulchellum Raddi, Agrost. Bras. 42 (1823).
P. pygmaeum var. glabrescens Hack. in Fedde, Repert. Spec. Nov. 11: 18 (1912).
P. quadriglume (Doell) Hitchc. in Contrib. U. S. Nat. Herb. 24: 460 (1927).
P. Rudgei Roem. \& Schult. Syst. Veg. 2: 444 (1817).
P. sciurotis Trin. Gram. Pan. 228 (1826).
P. Sellowii Nees, Agrost. Bras. 153 (1829).
P. (?) sempervirens O. Ktze. Rev. Gen. 3(2): 364 (1898).
P. stoloniferum Poir. in Lam. Encyc. Suppl. 4: 274 (1816).
P. stramineum Hitchc. \& Chase in Contrib. U. S. Nat. Herb. 15: 67 (1910).
P. trichanthum Nees, Agrost. Bras. 210 (1829).
P. tricholaenoides Steud. Syn. Pl. Glum. 1: 68 (1854).
P. uncinatum Raddi, Agrost. Bras. 41 (1823).
P. versicolor Doell in Mart. Fl. Bras. 2(2): 254 (1877).
P. zizanioides HBK. Nov. Gen. \& Spec. 1: 100 (1816).

Pappophorum mucronulatum Nees, Agrost. Bras. 412 (1829).
P. Wrightii S. Wats. in Proc. Amer. Acad. 18: 178 (1883).

Pariana bicolor Tutin in Journ. Linn. Soc. 50: 355 (1936).
P. gracilis Doell in Mart. Fl. Bras. 2(2): 377 (1877).
P. lunata Nees, Agrost. Bras. 295 (1829).
P. zingiberina Doell in Mart. Fl. Bras. 2(2): 337 (1877).

Paspalum attenuatum Presl, Rel. Haenk. 1: 212 (1830).
P. barbatum Nees, Agrost. Bras. 27 (1829).
P. boliviense Chase in Hitchc. in Contrib. U. S. Nat. Herb. 24: 454 (1927).
P. Buchtienii Hack. in Fedde, Repert. Spec. Nov. 6: 153 (1908).
P. candidum (Humb. \& Bonpl.) Kunth in Mém. Mus. Hist. Nat. 2: 68 (1815).
P. capillare Lam. Encyc. Tabl. 1: 176 (1791).
P. castaneum Remy in Ann. Sci. Nat. (ser. 3) 6: 348 (1846).
P. ceresia (O. Ktze.) Chase in Niles in Contrib. U. S. Nat Herb. 24: 153 (1925).
P. collinum Chase in Hitchc. in Contrib. U. S. Nat. Herb. 24: 451 (1927).
P. conjugatum Berg. in Act. Helv. Phys. Math. 7: 129 (1772).
P. conspersum Schrad. ex Schult. Mant. 2: 174 (1824).
P. decumbens Sw. Prodr. 22 (1788).
P. depauperatum Presl, Rel. Haenk. 1: 215 (1830).
P. densum Poir. in Lam. Encyc. 5: 32 (1804).
P. distichum L. Syst. Nat. (ed. 10) 2: 855 (1759).
P. Ekmanianum Henr. in Meded. Rijks Herbar. 40: 49 (1921).
P. Humboldtianum Fluegge, Monog. 1: 67 (1810).
P. inaequivalve Raddi, Agrost. Bras. 228 (1823).
P. intermedium Munro ex Morong \& Britton in Ann. N. Y. Acad. Sci. 7: 258 (1893).
P. inconstans Chase in Hitchc. in Contrib. U. S. Nat. Herb. 24: 446 (1927).
P. iridifolium Poepp. Reise, 2: 324 (1836).
P. Juergensii Hack. in Fedde, Repert. Spec. Nov. 7: 312 (1909).
P. lepidum Chase in Hitchc. in Contrib. U. S. Nat. Herb. 24: 447 (1927).
P. lineispathum Mez in Fedde, Repert. Spec. Nov. 15: 27 (1917).
P. macrophyllum HBK. Nov. Gen. \& Spec. 1: 92 (1816).
P. malacophyllum Trin. Sp. Gram. 3: t. 271 (1836).
P. marginatum Remy in Ann. Sci. Nat. (ser. 3) 6:348 (1846).
P. melanospermum Desv. in Lam. Encyc. Suppl. 4: 315 (1816).
P. membranaceum Lam. Encyc. Tabl. 1: 177 (1791).
P. membranaceum var. aequiglume Doell in Mart. Fl. Bras. 2(2): 94 (1877).
P. millegrana Schrad. ex Schult. Mant. 2: 175 (1824).
P. minus Fourn. Mex. Pl. 2:6 (1886).
P. multicaule Poir. in Lam. Encyc. Suppl. 4: 309 (1816).
P. notatum Fluegge, Monog. 1: 106 (1810).
P. paniculatum L. Syst. Nat. (ed. 10) 2: 855 (1759).
P. penicillatum Hook. f. in Trans. Linn. Soc. 20: 171 (1847).
P. pictum Ekm. in Ark. Bot. 10 (17): 11, t. 1, fig. 6 (1911).
P. pilosum Lam. Encyc. Tabl. 1: 175 (1791).
P. plicatulum Michx. Fl. Bor.-Am. 1: 45 (1803).
P. polyphyllum Nees in Trin. Gram. Pan. 114 (1826).
P. prostratum Scribn. \& Merr. in U. S. Dept. Agric. Div. Agrost. Bull. 24: 9 (1901).
P. pygmaeum Hack. in Fedde, Repert. Spec. Nov. 11: 18 (1912).
P. pygmaeum var. glabrescens Hack. in Fedde, Repert. Spec. Nov. 11: 18 $(1912)=P$. pygmaeum.
P. Regnellii Mez in Fedde, Repert. Spec. Nov. 15: 75 (1917).
P. remotum Remy in Ann. Sci. Nat. (ser. 3) 6: 349 (1846).
P. saccharoides Nees in Trin. Sp. Gram. 1: t. 107 (1828).
P. stellatum Humb. \& Bonpl. ex Fluegge, Monog. 1: 62 (1810).
P. tripinnatum Mez in Fedde, Repert. Spec. Nov. 15: 64 (1917).
P. Urvillei Steud. Syn. Pl. Glum. 1: 24 (1854).
P. vinosum Mez in Fedde, Repert. Spec. Nov. 15: 28 (1917) = P. depauperatum.
P. virgatum L. Syst. Nat. (ed. 10) 2: 855 (1759).

Pennisetum bambusiforme (Fourn.) Hemsl. Biol. Centr. Amer. Bot. 3: 506 (1885).
P. chilense (Desv.) Jacks. ex R. E. Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1: 172 (1905).
P. latifolium Spreng. Syst. Veg. 1: 302 (1825).
P. mutilatum (O. Ktze.) Hack. in O. Ktze. Rev. Gen. 3(2): 347 (1898), in synon.
P. sagittatum Henr. in Blumea, Suppl. 1: 229, t. 16 (1937).
P. setosum (Sw.) Pers. Synops. Pl. 1: 72 (1805).
P. tristachyum subsp. boliviense Chase in Hitchc. in Contrib. U. S. Nat. Herb. 24: 486 (1927).
P. villosum R. Br. in Fresen. in Mus. Senckenb. 2: 134 (1837).

Phalaris angusta Nees ex Trin. Sp Gram. 1: t. 78 (1827).
Pharus glaber HBK. Nov. Gen. \& Spec. 1: 196 (1816).
P. latifolius L. Syst. Nat. (ed. 10) 2: 1269 (1759).
P. parvifolius Nash in Bull. Torr. Bot. Club, 35: 301 (1908).

Phragmites communis (L.) Trin. Fund. Agrost. 134 (1820).
Piptochaetium laeve (Nees) Pilg. in Engler, Bot. Jahrb. 56, Beibl. 123: 26 (1920) $=$ Nassella pubiflora.
P. setifolium Presl, Rel. Haenk. 1: 222 (1830).
P. tuberculatum Desv. in Gay, Fl. Chile, 6: 272 (1853).

Poa androgyna Hack. in Fedde, Repert. Spec. Nov. 6: 159 (1908) = P. horridula.
P. annua L. Sp. Pl. 68 (1753).
P. asperiflora Hack. in Fedde, Repert. Spec. Nov. 11: 28 (1912).
P. boliviensis Hack. in Fedde, Repert. Spec. Nov. 11: 25 (1912) = P. pratensis.
P. bonariensis (Lam.) Kunth, Rév. Gram. 1: 115 (1829).
P. Buchtienii Hack. in Fedde, Repert. Spec. Nov. 11: 29 (1912).
P. Buchtienii var. subacuminata Hack. in Fedde, Repert. Spec. Nov. 11: 30 $(1912)=$ P. Buchtienii.
P. cañdamoana Pilg. in Engler, Bot. Jahrb. 37: 381 (1906).
P. chamaeclinos Pilg. in Engler, Bot. Jahrb. 37: 379 (1906).
P. denticulata Hack. in Fedde, Repert. Spec. Nov. 11: 27 (1912).
P. dumetorum Hack. in Fedde, Repert. Spec. Nov. 11: 26 (1912) = P. horridula.
P. dumetorum var. unduavensis Hack. in Fedde, Repert. Spec. Nov. 11: 27 (1912) $=$ P. horridula.
P. gymnantha Pilg. in Engler, Bot. Jahrb. 56, Beibl. 123: 28 (1920).
P. gymnantha var. aperta Pilg. in Notizbl. 11: 780 (1933).
P. horridula Pilg. in Engler, Bot. Jahrb. 37: 506 (1906).
P. humillima Pilg. in Engler, Bot. Jahrb. 37: 378 (1906).
P. Lilloi Hack. ex Stuckert in Anal. Mus. Nac. Buenos Aires, 21: 153 (1911).
P. myriantha Hack. ex Stuckert, Segunda Contrib. 517, t. 3 (1906).
P. perligulata Pilg. in Notizbl. 11: 779 (1933).
P. Pflanzii Pilg. in Engler, Bot. Jahrb. 49: 187 (1913) $=$ P. asperiflora.
P. pratensis L. Sp. Pl. 67 (1753).
P. scaberula Hook. f. Fl. Antarct. 2: 378 (1846).
P. subspicata (Presl) Kunth, Rév. Gram. 3: 606 (1829).

Polypogon elongatus HBK. Nov. Gen. \& Spec. 1: 134 (1816).
P. elongatus forma exaristatus Pilg. in Engler, Bot. Jahrb. 49: 182 (1913).
P. lutosus (Poir.) Hitchc. in U. S. Dept. Agric. Bull. 772: 138 (1920).

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Puccinellia oresigena (Phil.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 326 (1927).
P. parvula Hitchc. in Contrib. U. S. Nat. Herb. 24: 325 (1927).

Saccharum cayennense (P. Br.) Benth. in Journ. Linn. Soc. 19: 66 (1881).
S. officinarum L. Sp. Pl. 54 (1753).

Sacciolepis myuros (Lam.) Chase in Proc. Biol. Soc. Wash. 21: 7 (1908).
Setaria gracilis HBK. Nov. Gen. \& Spec. 1: 109 (1816).
S. gracilis forma brevispica (Hack.) Hack. in Stuckert in Anal. Mus. Nac. Buenoes Aires, 21: 48 (1911).
S. gracilis forma penicillata (Willd.) Mez ex Ekm. in Ark. Bot. 13(10): 33 (1910).
S. leiocarpa Herrm. in Beitr. Biol. Pflanz. 10: 62 (1910) $=$ Chaetochloa oblongata.
Sorghastrum minarum (Nees) Hitchc. in Contrib. U. S. Nat. Herb. 24: 501 (1927).
S. parviflorum (Desv.) Hitchc. \& Chase in Contrib. U. S. Nat. Herb. 18: 287 (1917).
S. stipoides (HBK).) Nash in N. Am. Fl. 17: 129 (1912).

Sporobolus aeneus (Trin.) Kunth, Rév. Gram. 3: 595 (1829).
S. argutus (Nees) Kunth, Enum. Pl. 1: 215 (1833).
S. asperifolius Nees \& Meyen in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 141 (1841).
S. Berteroanus (Trin.) Hitch. \& Chase in Contrib. U. S. Nat. Herb. 18: 370 (1917).
S. eximius (Nees) Ekm. in Ark. Bot. 13(10): 41 (1913).
S. indicus (L.) R. Br. Prodr. Fl. Nov. Holl. 1: 170 (1810).
S. Poiretii (Roem. \& Schult.) Hitchc. in Bartonia, 14: 32 (1932).
S. tenuissimus (Mart. \& Schrank) Hack. in Bull. Herb. Boiss. (ser. 2) 4(3): 278 (1904).
Stipa boliviensis Hack. in Fedde, Repert. Spec. Nov. 11: 21 (1912) = S. obtusa.
S. brachyphylla Hitchc. in Contrib. U. S. Nat. Herb. 24: 275 (1925).
S. capilliseta Hitchc. in Contrib. U. S. Nat. Herb. 24: 271 (1925).
S. curviseta Hitchc. in Contrib. U. S. Nat. Herb. 24: 282 (1925).
S. dasycarpa Hitchc. in Contrib. U. S. Nat. Herb. 24: 281 (1925).
S. depauperata Pilg. in Engler, Bot. Jahrb. 56, Beibl. 123: 23 (1920).
S. Hans-Meyeri Pilg. in Engler, Bot. Jahrb. 56, Beibl. 123: 24 (1920).
S. Holwayi Hitchc. in Contrib. U. S. Nat. Herb. 24: 287 (1927).
S. Ichu (R. \& P.) Kunth, Rév. Gram. 1: 60 (1829).
S. illimanica Hack. in Fedde, Repert. Spec. Nov. 11: 22 (1912).
S. inconspicua Presl, Rel. Haenk. 1: 227 (1830).
S. leptothera var. atroviolacea Hack. in Fedde, Repert. Spec. Nov. 6: 154 (1908) $=$ S. depauperata.
S. mucronata HBK. Nov. Gen. \& Spec. 1: 125 (1816).
S. nardoides (R. A. Phil.) Hack. ex Hitchc. in Contrib. U. S. Nat. Herb. 24: 271 (1925).
S. Neesiana Trin. \& Rupr. in Mém. Acad. St. Pétersb. (ser. 6) 5(1): 27 (1842).
S. obtusa (Trin \& Rupr.) Hitchc. in Contrib. U. S. Nat. Herb. 24: 284 (1925).
S. pampagrandensis Spegazz. in Anal. Mus. Nac. Montevideo, 4: 158, fig. 48 (1901).
S. Pflanzii Mez in Fedde, Repert. Spec. Nov. 17: 206 (1921) $=$ Nassella pubiflora.
S. plumosa Trin. in Mém. Acad. St. Pétersb. (ser. 6) 2(1): 37 (1836).
S. plumosula Nees in Steud. Syn. Pl. Gram. 127 (1854).
S. polyclada Hack. ex Stuckert in Anal. Mus. Nac. Buenos Aires, 21: 80 (1911).
S. pumila Mez in Fedde, Repert. Spec. Nov. 17: 205 (1921) = S. depauperata.
S. speciosa Trin. \& Rupr. in Mém. Acad. St. Pétersb. (ser. 6) 5(1): 45 (1842).
S. Trollii Pilg. in Notizbl. 11: 777 (1933).

Stylagrostis leiopoda (Wedd.) Mez in Bot. Archiv Mez, 1: 20 (1922).
Thrasya campylostochya (Hack.) Chase in Proc. Biol. Soc. Wash. 24: 115 (1911).

Trachypogon canescens Nees, Agrost. Bras. 343 (1829).
T. montufari (HKB.) Nees, Agrost. Bras. 342 (1829).
T. montufari var. bolivianus (Pilg.) Pilg. in Notizbl. 11: 777 (1933) = T. montufari.
T. plumosus (Humb. \& Bonpl.) Nees, Agrost. Bras. 344 (1829).

Tragus alienus (Spreng.) Schult. in Roem. \& Schult. Syst. Veg. Mant. 2: 205 (1824).

Trichachne saccharata (Buckl.) Nash ex Small, Fl. SE. U. S. 83 (1903).
T. sacchariflora (Raddi) Nees, Agrost. Bras. 87 (1829).

Trichloris mendozina (Phil.) Kurtz in Mem. Fac. Cienc. Exact. Univ. Córdoba, 1896: 37 (1897).
T. plurifiora Fourn. Mex. Pl. 2: 142 (1886).

Tricholena rosea Nees, Fl. Afr. Austr. 1: 17 (1841).
Trichopteryx flammida (Trin.) Benth. in Journ. Linn. Soc. 19: 59 (1882), combination implied but not actually made.
Triniochloa stipoides (HBK.) Hitchc. in Contrib. U. S. Nat. Herb. 17: 303 (1913).

Triodia avenacea HBK. Nov. Gen. \& Spec. 1: 156, t. 48 (1816).
Tripogon spicatus (Nees) Ekm. in Ark. Bot. 11(4): 36 (1912).
Tripsacum dactyloides (L.) L. Syst. Nat. (ed. 10) 2: 1261 (1759).
Trisetum oreophilum Louis-Marie in Rhodora, 30: 221 (1928).
T. spicatum (L.) Richt. Pl. Eur. 1: 59 (1890).
T. subspicatum (L.) Beauv. Ess. Agrost. 88 (1812).

Tristachya chrysothrix Nees, Agrost. Bras. 460 (1829).
Zea Mays L. Sp. Pl. 971 (1753).
Zeugites mexicana (Kunth) Trin. ex Steud. Nomencl. (ed. 2) 2: 798 (1841).
Z. mexicana var. glandulosa Hack. in Fedde, Repert. Spec. Nov. 6: 158 (1908).

## CYPERACEAE

Ascolepis brasiliensis (Kunth) Benth. ex C. B. Clarke in Dur. \& Schinz, Consp. Fl. Afr. 5: 651 (1894).
Becquerelia glomerulata Brongn. in Duperrey, Bot. Voy. Coq. 163 (1829).
Bulbostylis boliviana Palla in Oesterr. Bot. Zeitschr. 59: 191 (1909).
B. capillaris (L.) C. B. Clarke in Hook. Fl. Brit. India, 6: 652 (1893).
B. hirtella (Schrad.) Urb. Symb. Ant. 2: 166 (1900).
B. junciformis (HBK.) C. B. Clarke in Trans. Linn. Soc. (ser. 2) 4: 512 (1895).
B. juncoides (Vahl) Kükenth. ex Osten in Anal. Mus. Hist. Nat. Montevideo (ser. 2), 3: 187 (1931).
B. juncoides var. ampliceps Kükenth. ex Osten in Anal. Mus. Hist. Nat. Montevideo (ser. 2), 3: 188 (1931).
B. papillosa Kükenth. in Fedde, Repert. Spec. Nov. 23: 198 (1926).
B. sphaerocephala (Boeck.) C. B. Clarke in Bull. Herb. Boiss. (ser. 2) 3: 1018 (1903).
B. sphaerocephala var. macrocephala Kükenth. ex Osten in Anal. Mus. Hist. Nat. Montevideo (ser. 2), 3: 186 (1931).
B. sphaerolepis (Boeck.) Beetle in Amer. Midl. Nat. 41: 487 (1949).
B. tenuifolia (Rudge) Macbride in Field Mus. Publ. Bot. 11: 5 (1931).

Calyptrocarya fragifera (Rudge) Nees in Linnaea, 9: 304 (1834).
Carex boliviensis v. Heurck \& Muell. Arg. in v. Heurck, Obs. Bot. 32 (1870).
C. Bonplandii Kunth, Enum. Pl. 2: 380 (1837).
C. cladostachya var. maxima Kükenth. in Engler, Pflanzenr. IV, 20 (38): 268 (1909).
C. decidua var. Brehmeri (Boeck.) Kükenth. in Engler, Pflanzenr. IV, 20(38): 307 (1909).
C. fecunda Steud. Syn. Cyp. 194 (1855).
C. Goodenowii var. stolonifera (Hoppe) Aschers. Fl. Brandenb. 1: 777 (1864).
C. Jamesonii var. subfulva Kükenth. in Fedde, Repert. Spec. Nov. 8: 7 (1910).
C. lapazensis C. B. Clarke in Kew Bull. Add. Ser. 8: 76 (1908).
C. Mandoniana Boeck. in Allg. Bot. Zeit. no. 11: 174 (1896).
C. nebularum Phil. in Anal. Univ. Chile, 93: 492 (1896).
C. perprava C. B. Clarke in Kew Bull. Add. Ser. 8: 76 (1908).
C. phalaroides var. moesta (Kunth) Kükenth. in Verh. Bot. Ver. Brandenb. 47: 208 (1905).
C. pichinchensis HBK. Nov. Gen. \& Spec. 1: 233 (1816).
C. pichinchensis var. obtusisquama R. Gross in Notizbl. 14: 193 (1938).
C. pinetorum Liebm. in Vidensk. Selsk Skr. Kjøbenh. (ser. 2) 5: 263 (1851).

Cladium Mariscus R. Br. Prodr. 236 (1810).
C. Mariscus subsp. jamaicense var. ferruginescens Kükenth. in Fedde, Repert. Spec. Nov. 51: 192 (1942).
Cyperus albomarginatus Mart. \& Schrad. ex Nees in Mart. Fl. Bras. 2(1): 9 (1842) [this is the usual reference given, but actually the name published was Pycreus albo-marginatus].
C. andinus Palla ex Kükenth. in Engler, Pflanzenr. IV, 20 (101): 310 (1936).
C. Andreanus var. capitinduensis (Maury) Kükenth. in Engler, Pflanzenr. IV, $20(101)$ : 212 (1936).
C. aristatus var. inflexus (Muehl.) Boeck. in Linnaea, 35: 500 (1868), combination implied but not actually made.
C. articulatus var. nodosus (Willd.) Kükenth. in Engler, Pflanzenr. IV, 20(101): 79 (1935).
C. Bangianus Gandoger in Bull. Soc. Bot. France, 66: 297 (1920).
C. camphoratus var. boliviensis Kükenth. in Engler, Pflanzenr. IV, 20(101): 422 (1936).
C. cayennensis (Lam.) Britton in Bull. Dept. Agric. Jamaica, 5, Suppl. 1: 8 (1907).
C. compressus L. Sp. Pl. 46 (1753).
C. corymbosus var. subnodosus (Nees \& Mey.) Kükenth. ex Osten in Anal. Mus. Hist. Nat. Montevideo (ser. 2), 3: 147 (1931).
C. densicaespitosus Mattf. \& Kükenth. in Engler, Pflanzenr. IV, 20(101): 597 (1936).
C. diffusus subsp. chalaranthus (Presl) Kükenth. in Engler, Pflanzenr. IV, 20(101): 210 (1936).
C. diffusus subsp. chalaranthus var. tolucensis (HBK.) Kükenth. in Engler, Pflanzenr. IV, 20 (101): 211 (1936).
C. diffusus subsp. chalaranthus var. umbrosus (Lindl. \& Nees) Kükenth. in Engler. Pflanzenr. IV, 20 (101): 210 (1936).
C. digitatus var. obtusifructus Kükenth. in Engler, Pflanzenr. IV, 20(101): 56 (1935).
C. Eggersii Boeck. Cyper. Nov. 1: 53 (1888).
C. elegans L. Sp. Pl. 45 (1753).
C. entrerianus var. parvicapitulus Kükenth. in Engler, Pflanzenr. IV( 20(101): 170 (1936).
C. Eragrostis Lam. Encyc. Tabl. 1: 146 (1791).
C. esculentus var. leptostachyus Boeck. in Linnaea, 36: 290 (1870).
C. ferax L. C. Rich. in Act. Soc. Hist. Nat. Paris, 1: 106 (1792).
C. flavus var. aggregatus (Willd.) Kükenth. in Engler, Pflanzenr, IV, 20(101): 532 (1936).
C. flavus var. gigas (Lindm.) Kükenth. in Engler, Pffanzenr. IV, 20(101): 532 (1936).
C. flavus subsp. redolens (Maury) Osten in Anal. Mus. Hist. Nat. Montevideo (ser. 2), 3: 152 (1931).
C. friburgensis Boeck. Cyper. Nov. 2: 2 (1890).
C. giganteus Vahl, Enum. 2: 364 (1806).
C. Haspan var. americanus Boeck. in Linnaea, 35: 575 (1868).
C. Haspan subsp. juncoides (Lam.) Kükenth. in Fedde, Repert. Spec. Nov. 23: 184 (1926).
C. hermaphroditus (Jacq.) Standl. in Contrib. U. S. Nat. Herb. 18: 88 (1916).
C. hermaphroditus var. condensatus Kükenth. in Fedde, Repert. Spec. Nov. 26: 251 (1929).
C. Hieronymi var. Fiebrigii (Kükenth.) Kükenth. in Engler, Pflanzenr. IV, 20(101): 184 (1936).
C. incomtus Kunth, Enum. Pl. 2: 39 (1837).
C. incomtus var. dissolutior Kükenth. in Engler, Pflanzenr. IV, 20(101): 184 (1936).
C. incomtus var. Miguelii Kükenth. in Engler, Pflanzenr. IV, 20(101): 183 (1936).
C. laevigatus L. Mant. 2: 179 (1771).
C. laevigatus var. distachyus (All.) Coss. \& Durieu, Fl. Algér. 2: 251 (1854).
C. laevigatus var. reptans (Boeck.) C. B. Clarke in Journ. Linn. Soc. 21: 78 (1884).
C. lanceolatus Poir. in Lam. Encyc. 7: 245 (1806).
C. lanceolatus var. compositus Presl, Rel. Haenk, 1: 167 (1830).
C. ligularis L. Pl. Jamaic. Pugill. 3 (1759).
C. luzulae (L.) Retz, Obs. 4:11 (1786).
C. megapotamicus Kunth, Enum. Pl. 2: 10 (1837).
C. Meyenianus Kunth, Enum. Pl. 2: 88 (1837).
C. miliifolius var. saturatus (Donn. Sm.) Kükenth. in Engler, Pflanzenr. IV, 20(101): 221 (1936).
C. Mutisii (HBK.) Griseb. Fl. Brit. W. Ind. 567 (1864).
C. niger R. \& P. Fl. Peruv. 1: 47 (1789).
C. niger var. intricato-ramosus (Boeck.) Kükenth. in Engler, Pflanzenr. IV, 20(101): 345 (1936).
C. niger var. Lorentzianus (Boeck.) Kükenth. in Engler, Pflanzenr. IV, 20(101): 345 (1936).
C. obtusatus (Presl) Mattf. \& Kükenth. in Engler, Pflanzenr. IV, 20(101): 585 (1936).
C. ochraceus var. excelsior Kükenth. in Engler, Pflanzenr. IV, 20(101): 182 (1936).
C. Pearcei C. B. Clarke in Kew Bull. Add. Ser. 8: 7 (1908).
C. phaeocephalus Griseb. in Goett. Abh. 19: 214 (1874).
C. phaeocephalus var. major Kükenth. in Engler, Pflanzener. IV, 20 (101): 464 (1936).
C. piceus Liebm. in Vidensk. Selsk. Skr. Kjøbenh. 5(2): 200 (1851).
C. prolixus HBK. Nov. Gen. \& Spec. 1: 206 (1816).
C. reflexus Vahl, Enum. 2: 299 (1806).
C. retrorsus var. australis (Lindm.) Kükenth. in Engler, Pflanzenr. IV, 20 (101): 513 (1936).
C. rigens var. rufidulus (Steud.) Kükenth. in Fedde, Repert. Spec. Nov. 26: 252 (1929).
C. rigens var. tarijensis Kükenth. in Engler, Pflanzenr. IV, 20(101): 444 (1936).
C. rivularis subsp. lagunetto (Steud.) Kükenth. in Engler, Pflanzenr. IV, 20 (101): 383 (1936).
C. seslerioides HBK. Nov. Gen. \& Spec. 1: 209 (1816).
C. sesquiflorus (Torr.) Mattf. \& Kükenth. in Engler, Pflanzenr. IV, 20(101): 591 (1936).
C. simplex HBK. Nov. Gen. \& Spec. 1: 209 (1816).
C. sphacelatus Rottb. Descr. \& Icon. 26 (1773).
C. surinamensis Rottb. Descr. \& Icon. 35, t. 6, fig. 5 (1773).
C. surinamensis var. lutescens Boeck. in Linnaea, 35: 555 (1868).
C. tabina Steud. ex Boeck. in Linnaea, 35: 559 (1868).
C. uncinulatus Schrad. ex Nees in Mart. Fl. Bras. 2(1): 23 (1842).
C. unioloides R. Br. Prodr. Fl. Nov. Holl. 216 (1810).
C. vegetus var. obtusangulus O. Ktze. Rev. Gen. 3 (2): 334 (1898) = C. Eragrostis.
Dichromena ciliata Vahl, Enum. 2: 240 (1806).
D. Kuntzei (Clarke) Macbride in Field Mus. Publ. Bot. 11:42 (1931).
D. Mandonii (Clarke) Macbride in Field Mus. Publ. Bot. 4: 167 (1929).
D. monostachya (Boeck.) C. B. Clarke in Kew Bull. Add. Ser. 8: 32 (1908).
D. nervosa Vahl, Enum. 2: 241 (1806).

Diplacrum longifolium (Griseb.) C. B. Clarke in Dur. \& Schinz, Consp. Fl. Afr. 5: 669 (1894).
Eleocharis albibracteata Nees \& Meyen ex Kunth, Enum. Pl. 2: 143 (1837).
E. Brehmeriana Boeck. in Allg. Bot. Zeit. no. 11: 33 (1896).
E. capitata (L) R. Br. Prodr. Fl. Nov. Holl. 225 (1810).
E. caribaea (Rottb.) Blake in Rhodora, 20: 24 (1918).
E. costulata Nees \& Meyen ex Kunth, Enum. Pl. 2: 142 (1837).
E. crinalis (Griseb.) C. B. Clarke in Kew Bull. Add. Ser. 8: 23 (1908).
E. Dombeyana Kunth, Enum. Pl. 2: 145 (1937).
E. exigua (HBK.) Roem. \& Schult. Syst. Veg. 2: 154 (1817).
E. filiculmis Kunth, Enum. Pl. 2: 144 (1837).
E. fistulosa (Poir.) Schult. Mant. 2: 89 (1824).
E. geniculata (L.) Roem. \& Schult. Syst. Veg. 2: 150 (1817).
E. interstincta (Vahl) Roem. \& Schult. Syst. Veg. 2: 149 (1817).
E. maculosa R. Br. Prodr. Fl. Nov. Holl. 224 (1810).
E. minima Kunth, Enum. Pl. 2: 139 (1837).
E. nodulosa (Roth) Schult. Mant. 2: 87 (1824).
E. nubigena C. B. Clarke in Engler, Bot. Jahrb. 37: 518 (1906).
E. ochreata var. flaccida (Spreng.) Boeck. in Urb. Symb. Ant. 2: 63 (1900).
E. Sellowiana Kunth, Enum. P1. 2: 149 (1837).
E. sulcata (Roth) Nees in Linnaea, 9: 294 (1834) [combination was not actually made here].
Fimbristylis aestivalis Vahl, Enum. 2: 288 (1806).
F. annua (All.) Roem. \& Schult. Syst. Veg. 2: 95 (1817).
F. monostachya (L.) Hassk. Pl. Jav. Rar. 61 (1848).

Fuirena umbellata Rottb. Descr. \& Icon. 70, t. 19, fig. 3 (1773).
Lipocarpha Sellowiana Kunth, Enum. Pl. 2: 267 (1837).
Pleurostachys puberula var. Buchtienii (Kükenth.) Kükenth. in Fedde, Repert. Spec. Nov. 26: 254 (1929).
Rhynchospora andina Kükenth. in Fedde, Repert. Spec. Nov. 53: 73 (1944).
R. aristata Boeck. in Flora, 40: 36 (1857).
R. aristata var. latilaminata Kükenth. in Fedde, Repert. Spec. Nov. 26: 253 (1929).
R. boliviensis C. B. Clarke in Kew Bull. Add. Ser. 8: 37 (1908).
R. confinis (Nees) Clarke in Kew Bull. Add. Ser. 8: 40, 119 (1908).
R. corymbosa (L.) Britton in Trans. N. Y. Acad. 11: 84 (1892).
R. cyperoides (Sw.) Mart. in Denkschr. Akad. Muench. 6: 149 (1820).
R. emaciata (Nees) Boeck. in Vidensk. Meddel. Kjoebenh. 1869: 149 (1870).
R. exaltata var. cephalophora (Nees) Kükenth. in Engler, Bot. Jahrb. 74: 440 (1949).
R. exaltata var. ovalis Kükenth. in Engler, Bot. Jahrb. 74: 440 (1949).
R. glauca Vahl, Enum. 2: 233 (1806).
R. globosa (HBK.) Roem \& Schult. Syst. Veg. 2. 89 (1817).
R. globosa var. Loefgrenii (Boeck.) Kükenth. in Engler, Bot. Jahrb. 74: 465 (1949).
R. hirta (Nees) Boeck. in Vidensk. Meddel. Kjoebenh. 1869: 146 (1870).
R. Lundii Boeck. in Vidensk. Meddel. Kjoebenh. 1869: 147 (1870).
R. luzuliformis Boeck. in Linnaea, 37: 632 (1873).
R. macrochaeta Steud. ex Boeck. in Linnaea, 37: 632 (1873).
R. macrochaeta var. colombiensis forma condensata Kükenth. in Engler, Bot. Jahrb. 74: 394 (1949).
R. macrochaeta var. quinquespicata (Boeck.) Kükenth. in Engler, Bot. Jahrb. 74: 394 (1949).
R. macrochaeta var. Ruiziana (Boeck.) Kükenth. in Engler, Bot. Jahrb. 74: 393 (1949).
R. Marisculus Nees in Linnaea, 9: 297 (1834).
R. polyphlla Vahl, Enum. 2: 230 (1806).
R. polyphylla var. longispiculosa Kükenth. in Engler, Bot. Jahrb. 74: 406 (1949).
R. radicans (Schlechtd. \& Cham.) H. Pfeiff. in Fedde, Repert. Spec. Nov. 38: 93 (1935).
R. Schiedeana (Schlechtd.) Kunth, Enum. Pl. 2: 300 (1837).
R. setacea (Berg.) Boeck. in Vidensk. Meddel. Kjoebenh. 1869: 159 (1870).
R. tenerrima Nees ex Spreng. Syst. Veg. 4: Cur. Post. 26 (1827).
R. tenuis Link in Sprengel, Schrader \& Link, Jahrb. 1(3): 76 (1820).
R. tenuis var. emaciata (Boeck.) Lindm. in Bihang Kgl. Sv. Akad. Handl. 26, Afd. 3(9): 28 (1900).
R umbraticola var. Kuntzei (C. B. Clarke) Kükenth. in Engler, Bot. Jahrb. 74: 391 (1949).
R. velutina var. Sellowiana (Kunth) Boeck. in Linnaea, 37: 614 (1873).

Scirpus americanus Pers. Synops. Pl. 1: 68 (1805).
S. asper Presl, Rel. Haenk. 1: 194 (1830).
S. atacamensis (Phil.) O. Ktze. Rev. Gen. 2: 757 (1891).
S. cernuus Vahl, Enum. 2: 245 (1806).
S. deserticola Phil .Fl. Atac. 53 (1860).
S. inundatus Poir. in Lam. Encyc. Suppl. 5: 103 (1817).
S. micranthus Vahl, Enum. 2: 254 (1806).
S. rigidus Boeck. in Linnaea, 36: 492 (1869-1870).
S. riparius Presl, Rel. Haenk. 1: 193 (1830).

Scleria bracteata Cav. Icon. 5: 34, t. 457 (1799).
S. bracteata forma simplicior Kükenth. in Fedde, Repert. Spec. Nov. 26: 253 (1929).
S. castanea Core in Brittonia, 1: 239 (1934).
S. cyperina var. dentata H. Pfeiff. in Fedde, Repert. Spec. Nov. 52: 169 (1943).
S. hirtella 'Sw. Prodr. 19 (1788).
S. lithosperma (L.) Sw. Prodr. 18 (1788).
S. macrogyne C. B. Clarke in Kew Bull.. Add. Ser. 8: 59 (1908).
S. macrophylla Presl, Rel. Haenk. 1: 200 (1830).
S. microcarpa Nees in Linnaea, 9: 302 (1834), nomen nudum.
S. mitis Berg. in Vet. Akad. Handl. Stockh. 27: 145, t. 5 (1765).
S. obtusa Core in Brittonia, 1: 240 (1934).
S. paludosa Poepp. \& Endl. ex Kunth, Enum. Pl. 2: 344 (1837).
S. pleostachya Kunth, Enum. Pl. 2: 355 (1837).
S. reflexa HBK. Nov. Gen. \& Spec. 1: 232 (1816).
S. scabra Willd. Sp. Pl. 4 (1): 315 (1805).
S. stipularis Nees in Hook. Journ. Bot. 2: 394 (1840).
S. vaginata Steud. Syn. Pl. Cyp. 179 (1855).

Uncinia hamata (Sw.) Urb. Symb. Ant. 2: 169 (1900).
U. phleoides (Cav.) Pers. Synops. Pl. 2: 534 (1806).

## PALMAE

Acrocomia Totai Mart. Palmet. Orbign. 78, t. 9, fig. 1, t. 29B (1847).
Aiphanes caryotifolia (HBK.) Wendl. Kerch. Palm. 230 (1878).
A. truncata (Brongn. ex Mart.) Wendl. Kerch. Palm 230 (1878).

Astrocaryum Chonta Mart. Palmet. Orbign. 84, t. 4, fig. 1, t. 29C (1847).
A. Huaimi Mart. Palmet. Orbign. 86, t. 13, fig. 3, t. 30A (1847).
A. Huaimi var. Orbignyi Drude in Mart. Fl. Bras. 3(2): 380 (1882).

Bactris faucium Mart. Palmet. Orbign. 60, t. 6, fig. 2, t. 28B (1847).
B. inundata Mart. Palmet. Orbign. 58, t. 7, fig. 3, t. 27B (1847).

Ceroxylon pityrophyllum Mart. ex Wendl. Kerch. Palm. 239 (1878).
Chamaedorea boliviensis Dammer in Notizbl. 6: 262 (1915).
C. conocarpa Mart. Palmet. Orbign. 6, t. 6, fig. 1, t. 16B (1847).
C. fragrans (R. \& P.) Mart. Hist. Nat. Palm. 2: 4, t. 3, fig. 1-2 (1823).
C. lanceolata (R. \& P.) Kunth, Enum. Pl. 3: 172 (1841).
C. macroloba Burret in Notizbl. 11: 757 (1933).

Copernicia australis Becc. in Webbia, 2: 1.58 (1907).
Desmoncus Kuhlmannii Burrett in Notizbl. 14: 267 (1938).
D. latisectus Burret in Fedde, Repert. Spec. Nov. 36: 215 (1934).
D. rudentum Mart. Palmet. Orbign. 48, t. 14, fig. 3, t. 26A (1847).

Dictyocaryum Lamarckianum (Mart.) Wendl. in Bot. Zeit. 21: 131 (1863).
Diplothenium maritimum Mart. Hist. Nat. Palm. 2: 108, t. 75, t. 77, fig. 3 (1826).

Euterpe andicola Brongn. ex Mart. Palmet. Orbign. 8, t. 2, fig. 2, t. 17A (1847).
E. Haenkeana Brongn. ex Mart. Palmet. Orbign. 9, t. 2, fig. 3, t. 17B (1847).
E. longevaginata Mart. Palmet. Orbign. 11, t. 15, fig. 1, t. 17C (1847).
E. precatoria Mart. Palmet. Orbign. 10, t. 8, fig. 2, t. 18A (1847).

Geonoma Brongniartii Mart. Palmet. Orbign. 24, t. 12, fig. 1, t. 23C (1847).
G. Desmarestii Mart. Palmet. Orbign. 23, t. 11, fig. 3, t. 22B (1847).
G. Jussieuana Mart. Palmet. Orbign. 24, t. 12, fig. 2, t. 23A (1847).
G. Orbignyana Mart. Palmet. Orbign. 23, t. 11, fig. 1, t. 22A (1847).
G. pachydicrana Burret in Engler, Bot. Jahrb. 63: 206 (1930).
G. Werdermannii Burret in Engler, Bot. Jahrb. 63: 173 (1930).

Guilielma insignis Mart. Palmet. Orbign. 71, t. 10, fig. 3, t. 29A (1847).
Iriartea phaeocarpa Mart. Palmet. Orbign. 15, t. 5, fig. 3, t. 19 (1847).
Mauritia armata Mart. Hist. Nat. Palm. 2: 45, tt. 41-43 (1824).
M. vinifera Mart. Hist. Nat. Palm. 2: 42, t. 38, t. 39, fig. 1-2 (1824).

Maximiliana regia Mart. Hist. Nat. Palm. 2: 132, tt. 91, 93 (1826).
Oenocarpus tarampabo Mart. Palmet. Orbign. 12, t. 8, fig. 3, t. 18B (1847).
Orbignya humilis Mart. Palmet. Orbign. 129, t. 10, fig. 2 (1847).
O. phalerata Mart. Palm. Orbign. 126, t. 13, fig. 2, t. 32A (1847).

Parajubaea Torallyi (Mart.) Burret in Notizbl. 11: 50 (1930).
Pyrenoglyphis Brongniartii (Mart.) Burret in Fedde, Repert. Spec. Nov. 34: 251 (1934).
P. infesta (Mart.) Burret in Fedde, Repert. Spec. Nov. 34: 248 (1934).
P. socialis (Mart.) Burret in Fedde, Repert. Spec. Nov. 34: 246 (1934).

Scheelea blepharopus (Mart.) Burret in Notizbl. 10: 674 (1929).
S. princeps (Mart.) Karst. in Linnaea, 28: 269 (1856).

Socratea Orbignyana (Mart.) Karst. in Linnaea, 28: 264 (1856).
Syagrus petraea (Mart.) Becc.in L'Agric. Colon. 10(2): 467 (1916).
Taenianthera macrostachys (Mart.) Burret in Engler, Bot. Jahrb. 63: 268 (1930).

Tessmanniophoenix Chuco (Mart.) Burret in Notizbl. 10: 400 (1928).
Trithrinax schizophylla Drude in Mart. Fl. Bras. 3(2): 551, t. 130 (1882).

CYCLANTHACEAE
Carludovica palmata R. \& P. Syst. 291 (1798).

## ARACEAE

Anthurium apiculatum Krause in Engler, Bot. Jahrb. 44, Beibl. 101: 9 (1910).
A. Buchtienii Krause in Engler, Bot. Jahrb. 44, Beibl. 101: 10 (1910).
A. conjunctum Krause in Notizbl. 11: 612 (1932).
A. coripatense Engl. in Engler, Pflanzenr. IV, 23b: 255 (1905) = A. Miguelii.
A. gracile Lindl. in Bot. Reg. 19: t. 1635 (1833).
A. grande N. E. Br. in Engler, Pflanzenr. IV, 23b: 204 (1905).
A. indecorum Schott in Oesterr. Bot. Zeitschr. 8: 350 (1858).
A. Lechlerianum Schott, Prodr. Aroid. 534 (1860).
A. mapiriense Krause in Engler, Bot. Jahrb. 44, Beibl. 101: 10 (1910).
A. Miguelii Engl. in Engler, Pflanzenr. IV, 23b: 126 (1905).
A. Ottonis Krause in Notizbl. 11: 609 (1932).
A. paraguayense Engler, Bot. Jahrb. 25: 361 (1898).
A. parile N. E. Br. in Engler, Pflanzner. IV, 23b: 151 (1905).
A. rusticum N. E. Br. in Engler, Pflanzenr. IV, 23b: 82 (1905).
A. scandens Engl. in Mart. Fl. Bras. 3(2): 78 (1878).
A. scandens var. violaceum Engl. in Mart. Fl. Bras. 3(2): 78, t. 7 (1878).
A. trinerve Miq. in Linnaea, 17: 66 (1843).
A. trinerve var. angustifolium Krause in Engler, Bot. Jahrb. 54, Beibl. 118: 123 (1916).
A. triphyllum Brongn. ex Schott, Prodr. Aroid. 548 (1860).
A. violaceum (Sw.) Schott, Prodr. Aroid. 437 (1860).

Asterostigma Pavonii Schott, Prodr. Aroid. 339 (1860).
Caladium sororium Schott in Oesterr. Bot. Zeitschr. 9: 38 (1859).
Heteropsis boliviana Rusby in Bull. N. Y. Bot. Gard. 6: 493 (1910).
Monstera boliviana Rusby in Bull. N. Y. Bot. Gard. 6: 494 (1910).
M. falcifolia Engl. in Engler, Bot. Jahrb. 37: 117 (1905).
M. unilatera Rusby in Bull. N. Y. Bot. Gard. 6: 494 (1910).

Philodendron arcuatum Krause in Engler, Pflanzenr. IV, 23Db: 72 (1913).
P. Brandtianum Krause in Engler, Pflanzenr. IV, 23Db: 46 (1913).
P. Buchtienii Krause in Engler, Pflanzenr. IV, 23Db: 30 (1913).
P. caudatum Krause in Engler, Pflanzenr. IV, 23Db: 13 (1913).
P. Lechlerianum Schott, Prodr. Aroid. 250 (1860).
P. Paxianum Krause in Engler, Pflanzenr. IV, 23Db: 31 (1913).
P. rubens Schott, Syn. Aroid. 84 (1856).
? P tripartitum (Jacq.) Schott in Wien. Zeitschr. 3: 780 (1829).
Pistia Stratiotes L. Sp. Pl. 963 (1753).
Rhodospatha boliviensis Engl. \& Krause in Engler, Bot. Jahrb. 44, Beibl. 101: 13 (1910).
Scaphispatha gracilis Brongn. ex Schott, Prodr. Aroid. 214 (1860).
Spathanthium heterandrum (Baker) N. E. Br. in Gard. Chron. 20: 70 (1883).
S. Orbignyanum Schott in Bonplandia, 7: 165 (1859).

Spathicarpa hastifolia Hook. Bot. Misc. 2: 147 (1831).
Stenospermation Mathewsii Schott, Gen. Aroid. 70 (1858).
S. Rusbyi N. E. Br. in Bull. N. Y. Bot Gard. 4: 461 (1907).

Synandrospadix vermitoxicum (Griseb.) Engl. in Engler, Bot. Jahrb. 4: 62 (1883).

Taccarum caudatum Rusby in Mem. N. Y. Bot. Gard. 7: 210 (1927).
T. Weddellianum Brongn. ex Schott, Gen. Aroid. t. 65 (1858).

Xanthosoma Buchtienii Engl. in Engler, Pflanzenr. IV, 23E: 54 (1920).
X. hylaeae Engl. \& Krause in Notizbl. 6: 115 (1y14).
X. mafaffa var. Poeppigii (Schott) Engl. in Mart. Fl. Bras. 3(2): 193 (1878).
X. roseum Schott in Oesterr. Bot. Zeitschr. 8: 178 (1858).
X. syngoniifolium Rusby in Mem. N. Y. Bot. Gard. 7: 209 (1927).

## LEMNACEAE

Lemna gibba L. Sp. Pl. 970 (1753).
L. valdiviana Phil. in Linnaea, 33: 239 (1864).

## CENTROLEPIDACEAE

Gaimardia boliviana Pax in Fedde, Repert. Spec. Nov. 5: 225 (1908).

## MAYACACEAE

Mayaca boliviana Rusby in Mem. N. Y. Bot. Gard. 7: 211 (1927) = M. Sellowiana.
M. Sellowiana Kunth, Enum. Pl. 4: 32 (1843).

## XYRIDACEAE

Xyris caroliniana Walt. Fl. Carol. 69 (1788).
X. macrocephala Vahl, Enum. 'Pl. 2: 204 (1806).
X. savanensis Miq. in Linnaea, 18: 605 (1844).
X. simulans Alb. Nilsson in Kgl. Sv. Vet. Akad. Handl. 24 (14): 47 (1892).
X. subulata R. \& P. Fl. Peruv. 1: 46, t. 7, fig. 6 (1798).

## ERIOCAULACEAE

Eriocaulon Steinbachii (Moldenke) Moldenke in Phytologia, 2(9): 364 (1947).
Paepalanthus chiquitensis Herzog in Fedde, Repert. Spec. Nov. 20: 86 (1924).
P. manicatus var. pulvinatus Herzog in Fedde, Repert. Spec. Nov. 20: 86 (1924).
P. muscosus Koern. in. Mart. Fl. Bras. 3(1): 348 (1863).

Syngonanthus caulescens (Poir.) Ruhl. in Engler, Pflanzenr. IV, 30: 267 (1903).
S. Fischerianus (Bong.) Ruhl. in Engler, Pflanzenz. IV, 30: 256 (1903).
S. gracilis var. bolivianus Ruhl. in Engler, Pflanzenr. IV, 30: 252 (1903).

## BROMELIACEAE

Abromeitiella brevifolia (Griseb.) Castellanos in Anal. Mus. Nac. Hist. Nat. Buenos Aires, 36: 371, tt. 2, 3 (1931).
Aechmea angustifolia Poepp. \& Endl. Nov. Gen. \& Spec. 2: 43, t. 159 (1838).
Ae. boliviana Rusby in Bull. N. Y. Bot. Gard. 4: 456 (1907) $=$ Ae. angustifolia.
Ae. brachyclada Baker, Handbk. Bromel. 37 (1889).
Ae. bromeliaefolia (Rudge) Baker ex Benth. \& Hook. f. Gen. Pl. 3: 664 (1883).
Ae Castelnavii Baker, Handbk. Bromel. 39 (1889).
Ae. distichantha var. Schlumbergeri E. Morr. ex Mez in Mart. Fl. Bras. 3(3): 343 (1892).
Ae. ellipsoidea Rusby in Mem. N. Y. Bot. Gard. 7: 212 (1927) $=$ Ae. bromeliaefolia.
Ae. inconspicua Harms in Notizbl. 10: 786 (1929) $=$ Ae. angustifolia.
Ae. involucrata Rusby in Bull. N. Y. Bot. Gard. 4: 45̄6 (1907) $=$ Ae. distichantha var. Schlumbergeri.
Ae. involucrifera Mez in Enler, Pflanzenr. IV, $32(1): 157$ (1934) $=$ Ae. distichantha var. Schlumbergeri.

Ae. Kuntzeana Mez in DC. Monog. Phan. 9: 208 (1896).
Ae. tocantina Baker, Handbk. Bromel. 39 (1889).
Ananas ananassoides (Baker) L. B. Smith in Bot. Mus. Leafl. Harvard Univ. 7: 79 (1939).
Billbergia boliviensis Baker, Handbk. Bromel. 81 (1889) $=$ B. decora.
B. Cardenasii L. B. Smith in Phytologia, 4(6): 382 (1953).
B. decora Poepp. \& Endl. Nov. Gen. \& Spec. 2: 42, t. 157 (1838).

Bromelia Hieronymi Mez. in Mart. Fl. Bras. 3(3): 199 (1891).
B. serra Griseb. in Goett. Abh. 24: 328 (1879).

Cottendorfia Rusbyi Baker in Bull. Torr. Bot. Club, 29: 697 (1902) $=$ Lindmania villosula.
Deuterocohnia strobilifera Mez in Fedde, Repert. Spec. Nov. 3: 15 (1906).
D. strobilifera var. inermis L. B. Smith in Contrib. U. S. Nat. Herb. 29: 535 (1954).

Dyckia boliviensis Mez in DC. Monog. Phan. 9: 524 (1896).
D. gracilis Mez in DC. Monog. Phan. 9: 516 (1896).
? D. leptostachya Baker in Gard. Chron. 22: 198 (1884).
D. Meziana O. Ktze. Rev. Gen. 3(2): 302 (1898).
D. pulquinensis Wittm. in Meded. Rijks Herbar. 29: 88 (1916).

Guzmania calothyrsa (Beer) Mez in DC. Monog. Phan. 9: 910 (1896).
G. complanata Wittm. in Meded. Rijks Herbar. 29: 92 (1916) $=$ Tillandsia disticha.
G. lingulata (L.) Mez in DC. Monog. Phan. 9: 899 (1896).
G. Melinonis Regel in Gartenfl. 34: 116 (1885).
G. obtusa Rusby in Mem. N. Y. Bot. Gard. 7: 212 (1927) $=$ Vriesia heliconioides.
G. Roezlii (Morr.) Mez in DC. Monog. Phan. 9: 948 (1896).

Lindmania gracilis (Rusby) L. B. Smith in Contrib. Gray Herb. 104: 78 (1934).
L. graminea L. B. Smith in Lilloa, 14: 93 (1948).
L. Pearcei (Baker) Mez in DC. Monog. Phan. 9: 537 (1896).
L. penduliflora (C. H. Wright) Stapf in Bot. Mag. 150: t. 9029 (1924).
L. Rusbyi Mez in Engler, Bot. Jahrb. 30, Beibl. 67 :6 (1901).
L. villosula Harms in Notizbl. 10: 794 (1929).
L. Weberbaueri Mez in Fedde, Repert. Spec. Nov. 12: 417 (1913).
L. Weddelliana (Brongn.) Mez in DC. Monog. Phan. 9: 538 (1896).

Pitcairnia Bangii Baker in Mem. Torr. Bot. Club, 6: 124 (1896) = Puya stenothyrsa.
P. biattenuata Rusby in Bull. N. Y. Bot. Gard. 4: 457 (1907) $=$ P. paniculata.
P. Brittoniana Mez in DC. Monog. Phan. 9: 451 (1896).
P. consimilis Baker in Journ. Bot. 19: 266 (1881) $=$ P. ferruginea.
P. crassa L. B. Smith in Lilloa, 14: 94 (1948).
P. divaricata Wittm. in Meded. Rijks Herbar. 29: 81 (1916).
P. ferruginea R. \& P. Fl. Peruv. 3: 36 (1802).

Pt grandiflora Mez. in Fedde, Repert. Spec. Nov. 3: 5 (1906).
P. mirabilis Mez in Fedde, Repert. Spec. Nov. 3: 6 (1906).
P. multiramosa Mez in DC. Monog. Phan. 9: 419 (1896).
P. odontopoda Baker, Handbk. Bromel. 93 (1889).
P. paniculata R. \& P. Fl. Peruv. 3: 36, t. 260 (1802).
P. platystemon Mez in DC. Monog. Phan. 9: 421 (1896).
? P. rigida Mez in Bull. Herb. Boiss. (ser. 2) 4: 625 (1904).
P. robusta Rusby in Bull. N. Y. Bot. Gard. 6: 488 (1910) $=$ Puya sanctaecrucis.
P. sessiliflora Rusby in Bull. N. Y. Bot. Gard. 4: 457 (1907) $=$ P. subpetiolata.
P. subpetiolata Baker in Journ. Bot. 19: 267 (1881).

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P. Brittoniana Baker, Handbk. Bromel. 124 (1889).
P. Cardenasii L. B. Smith in Lilloa, 14: 94 (1948).
P. cristata L. B. Smith in Lilloa, 14: 95 (1948).
P. ctenorhyncha L. B. Smith in Phytologia, 5: 49 (1954).
P. dyckioides (Baker) Mez in DC. Monog. Phan. 9: 486 (1896).
P. Fiebrigii Mez. in Fedde, Repert. Spec. Nov. 3: 9 (1906).
P. Fosteriana L. B. Smith in Journ.. Wash. Acad. Sci. 40: 216 (1950).
P. glabrescens L. B. Smith in Contrib. U. S. Nat. Herb. 29: 537 (1954).
P. glareosa L. B. Smith in Lilloa, 14: 96 (1948).
P. Hauthalii Mez in Fedde, Repert. Spec. Nov. 16: 65 (1919).
P. Herzogii Wittm. in Meded. Rijks Herbar. $29: 86$ (1916).
P. Hofstenii Mez. in Fedde, Repert. Spec. Nov. 3: 8 (1906).
P. humilis Mez in DC. Monog. Phan. 9: 498 (1896).
P. Kuntzeana Mez in DC. Monog. Phan. 9: 490 (1896).
P. lasiopoda L. B. Smith in Proc. Amer. Acad. 70: 153 (1935).
P. leptostachya L. B. Smith in Lilloa, 14: 97 (1948).
P. Meziana Wittm. in Meded. Rijks Herbar. 29: 85 (1916).
P. micrantha Mez in Fedde, Repert. Spec. Nov. 3: 8 (1906).
P. mollis Baker ex Mez in DC. Monog. Phan. 9: 488 (1896).
P. nana Wittm. in Meded. Rijks Herbar. 29: 85 (1916).
P. olivacea Wittm. in Meded. Rijks Herbar. 29: 83 (1916).
P. paupera Mez in Fedde, Repert. Spec. Nov. 3: 14 (1906).
P. Pearcei (Baker) Mez in DC. Monog. Phan. 9: 480 (1896).
P. penduliflora L. B. Smith in Contrib. Gray Herb. 98: 12 (1932).
P. Raimondii Harms in Notizbl. 10: 213 (1928).
P. Rusbyi (Baker) Mez in DC Monog. Phan. 9: 482 (1896).
P. sanctae-crucis (Baker) L. B. Smith in Proc. Amer. Acad. 70: 154 (1935).
P. spathacea (Griseb.) Mez in DC. Monog. Phan. 9: 481 (1896).
P. stenothyrsa (Baker) Mez in DC. Monog. Phan. 9: 481 (1896).
P. tuberosa Mez in DC. Monog. Phan. 9: 483 (1896).
P. tunarensis Mez in DC. Monog. Phan. 9: 498 (1896).
P. ultima L. B. Smith in Contrib. U. S. Nat. Herb. 29: 540 (1954).
P. Weddelliana (Baker) Mez in DC. Monog. Phan. 9: 475 (1896).
P. Werdermannii Harms in Notizbl. 10: 793 (1929).

Tillandsia adpressa var. Tonduziana (Mez) L. B. Smith in Contrib. Gray Herb. 89: 8 (1930).
T. apoloënsis Rusby in Bull. N. Y. Bot. Gard. 6: 489 (1910) $=$ T. soratensis.
T. australis Mez in Fedde, Repert. Spec. Nov. 16: 75 (1919) $=$ T. maxima.
T. Bakeri L. B. Smith in Contrib. Gray Herb. 95: 45 (1931).
T. Bangii Baker in Mem. Torr. Bot. Club, 6: 124 (1896) = T. Deppeana.
T. biffora R. \& P. Fl. Peruv. 3:41, t. 268 (1802).
T. boliviana Mez in Bull. Herb. Boiss. (ser. 2) 4: 1130 (1904).
T. boliviensis Baker in Mem. Torr. Bot. Club, 4(3): 267 (1895).
T. Brittoniana Baker, Handbk. Bromel. 195 (1889).
T. bryoides Griseb. in Goett. Abh. 24: 334 (1879).
T. Buchtienii H. Winkl. in Fedde, Repert. Spec. Nov. 7: 107 (1909) = T. Rusbyi.
T. calocephala Wittm. in Meded. Rijks Herbar. 29: 90 (1916).
T. capillaris forma cordobensis (Hieron.) L. B. Smith in Proc. Amer. Acad. 70: 211 (1935).
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T. Cardenasii L. B. Smith in Proc. Amer. Acad. 70: 154 (1935).
T. caulescens Brongn. ex Baker, Handbk. Bromel. 168 (1889).
T. complanata Benth. Bot. Voy. Sulphur, 173 (1846).
T. condensata Baker, Handibk. Bromel. 164 (1889).
T. crocata (E. Morr.) Baker in Journ. Bot. 25: 214 (1887).
T. decomposita Baker, Handbk. Bromel. 168 (1889).
T. Deppeana Steud. Nomencl. (ed. 2) 2: 688 (1841).
T. didisticha Baker in Journ. Bot. 26: 16 (1888).
T. Duratii Vis. in Nuov. Sagg. Padov. 5: 271 (1841).
T. flexuosa (Baker) Mez in DC. Monog. Phan. 9: 774 (1896) $=$ T. Bakeri.
T. Friesii Mez in Fedde, Repert. Spec. Nov. 3: 37 (1906).
T. funebris Castellanos in Anal. Mus. Nac. Hist. Nat. Buenos Aires, 37: 502 (1933).
T. fusco-guttata Mez in Bull. Herb. Boiss. (ser. 2) 5: 101 (1905).
T. Gilliesii Baker in Journ. Bot. 16: 240 (1878).
T. Guentheri Harms in Notizbl. 10: 794 (1929) $=$ T. Rusbyi.
T. Herzogii Wittm. in Meded. Rijks Herbar. 29: 89 (1916) $=$ T. Reichenbachii.
T. incurvata Griseb. in Goett. Nachr. 1864: 15.
T. ixioides Griseb. in Goett. Abh. 24: 333 (1879).
T. juncea (R. \& P.) Poir. in Lam. Encyc. Suppl. 5: 309 (1818).
T. Krukoffiana L. B. Smith in Contrib. Gray Herb. 154: 36 (1945).
T. Kuntzeana Mez in DC. Monog. 9: 790 (1896).
T. laxissima Mez in Bull. Herb. Boiss. (ser. 2) 5:108 (1905).
T. loliacea Mart. ex Schult. f. Syst. Veg. 7: 1204 (1830).
T. longifolia Baker, Handbk. Bromel. 185 (1889).
T. Lorentziana Griseb. in Goett. Abh. 19: 217 (1874).
T. Mandonii Morr. ex Mez in DC. Monog. Phan. 9: 871 (1896) = T. crocata.
T. marantoidea Rusby, Descr. S. Amer. Pls. 4(1920).
T. maxima Lillo \& Hauman in Anal. Mus. Nac. Buenos Aires, 29: 416 (1917).
T. maxima var. densior L. B. Smith in Lilloa, 14: 97 (1948).
T. Maxoniana L. B. Smith in Contrib. Gray Herb. 124: 11 (1939).
T. micrantha Baker in Bull. Torr. Bot. Club, 29: 698 (1902) $=$ T. spiculosa.
T. monticola Mez \& Sodiro in Bull. Herb. Boiss. (ser. 2) 4: 1135 (1904).
T. myosura Griseb. in Goett. Abh. 24: 333 (1879).
T. paleacea Presl, Rel. Haenk. 1: 125 (1827).
T. paraënsis Mez in Mart. Fl. Bras. 3(3): 586 (1894).
T. pardina L. B. Smith in Lillloa, 14: 98 (1948).
T. parviflora R. \& P. Fl. Peruv. 3: 41, t. 259 (1802).
T. pendulispica Mez in DC. Monog. Phan. 9: 745 (1896).
T. polyphylla Baker, Handbk. Bromel. 178 (1889) = T. vernicosa.
T. polystachya L. Sp. Pl. (ed. 2) 1: 410 (1762).
T. pulchella Hook. Exot. Fl. 2: t. 154 (1825).
T. pulchella var. rosea (Lindl.) Mez. in Mart. Fl. Bras. 3(3): 603 (1894).
T. quadriflora Baker, Handbk. Bromel. 163 (1889) = T. loliacea.
T. recurvata L. Sp. Pl. (ed. 2) 1: 410 (1762).
T. Reichenbachii Baker, Handbk. Bromel. 166 (1889).
T. rubella Baker in Journ. Bot. 26: 44 (1888).
T. Rusbyi Baker, Handbk. Bromel. 176 (1889).
T. scalarifolia Baker in Journ. Bot. 25: 235 (1887) = T. paleacea.
T. Seemannii (Baker) Mez in DC. Monog. Phan. 9: 737 (1896).
T. soratensis Baker in Journ. Bot. 25: 235 (1887).
T. sphaerocephala Baker in Journ. Bot. 26: 141 (1888).
T. spiculosa Griseb. in Goett. Nachr. 1864: 17.
T. streptocarpa Baker in Journ. Bot. 25. 241 (1887).
T. triangularis Rusby, Descr. S. Amer. Pls. 3 (1920) = T. pendulispica.
T. tricholepis Baker in Journ. Bot. 25: 234 (1887) .
T. tricholepis var. macrophylla L. B. Smith in Lilloa, 14: 98 (1948).
T. triticea Burchell ex Baker in Journ. Bot. 26: 42 (1888).
T. tucumanensis Mez in DC. Monog. Phan. 9: 853 (1896) $=$ T. Reichenbachii.
T. usneoides L. Sp. Pl. (ed. 2) 1: 411 (1762).
T. Valenzuelana A. Rich. Fl. Cub. Fanerog. 2: 267 (1853).
T. vernicosa Baker in Journ. Bot. 25: 241 (1887).
T. violascens Mez in DC. Monog. Phan. 9: 797 (1896).
T. Walteri Mez in Fedde, Repert. Spec. Nov. 3: 43 (1906).
T. Weddellii Baker, Handbk. Bromel. 181 (1889) = T. decomposita.
T. Williamsii Rusby in Bull. N. Y. Bot. Gard. 6: 489 (1910) = T. capillaris.
Vriesia heliconioides (Kunth) Lindl. in Bot. Reg. 29: t. 10, in obs. (1843), combination implied, not made.
V. heterandra (E. André) L. B. Smith in Contrib. U. S. Nat. Herb. 29: 443 (1951).
V. icterica Castellanos in Lilloa, 11: 150 (1945).
V. rubra (R. \& P.) Beer, Bromel. 98 (1857).

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Aneilema ovato-oblongum Beauv. Fl. Owar. 2: 71, t. 104 (1807).
Athyrocarpus rufipes (Seub.) Standl. in Standley \& Calderón, Lista Prelim. Pl. El Salvador, 47 (1925).
Callisia repens L. Sp. Pl. (ed. 2) 1: 62 (1762).
C. repens var. Mandonii C. B. Clarke in DC. Monog. Phan. 3: 311 (1881).

Campelia Zanonia (L.) HBK. Nov. Gen. \& Spec. 1: 264 (1816).
Cochliostema odoratissimum Lem. in Illustr. Hortic. 6: Misc. 70, t. 217 (1859).
Commelina Bangii Rusby in Bull. N. Y. Bot. Gard. 6: 490 (1910).
C. elliptica HBK. Nov. Gen. \& Spec. 1: 259 (1816).
C. fasciculata R. \& P. Fl. Peruv. 1: 44, t. 72 (1798).
C. gracilis R. \& P. Fl. Peruv. 1: 44, t. 72, fig. a (1798).
C. hispida R. \& P. Fl. Peruv. 1: 43, t. 73 (1798).
C. hispida var. Gaudichaudii C. B. Clarke in DC. Monog. Phan. 3: 156 (1881).
C. nudiflora L. Sp. Pl. 41 (1753).
C. platyphylla var. Balansae C. B. Clarke in DC. Monog. Phan. 3: 177 (1881).
C. quitensis Benth. Pl. Hartw. 258 (1846).
C. quitensis var. Mandonii C. B. Clarke in DC. Monog. Phan. 3: 156 (1881).
C. reflexa Rusby in Phytologia, 1(2): 50 (1934).
C. robusta Kunth, Enum. Pl. 4: 52 (1843).
C. virginica L. Sp. Pl. (ed. 2) 1: 61 (1762).

Descantaria Pflanzii Brückn. in Notizbl. 10: 57 (1927).
Dichorisandra Aubletiana Schult. f. Syst. Veg. 7: 1181 (1830).
D. Gaudichaudiana Kunth, Enum. Pl. 4: 113 (1843).
D. hexandra (Aubl.) Standl. in Standley \& Calderón, Lista Prelim. Pl. El Salvador, 48 (1925).
D. inaequalis Presl, Rel. Haenk. 1: 140 (1828).
D. pubescens Mart. ex Schult. f. Syst. Veg. 7: 1186 (1830).
D. villosula Mart. ex Schult. f. Syst. Veg. 7: 1185 (1830).

Floscopa perforans Rusby in Bull. N. Y. Bot. Gard. 6: 490 (1910).

Mandonia boliviana Hassk. in Flora, 54: 260 (1871) = Tradescantia sp. ?
Phaeospherion persicariaefolium (Delile) C. B. Clarke in DC. Monog. Phan. 3: 137 (1881).
Tinantia fugax Scheidw. in Otto \& Dietr. Allg. Gartenzeit. 7: 365 (1839).
T. fugax var. erecta (Drummond) C. B. Clarke in DC Monog. Phan. 3: 286 (1881).

Tradescantia ambigua Mart. ex Schult. f. Syst. Veg. 7: 1170 (1830).
T. cymbispatha C. B. Clarke in DC. Monog. Phan. 3: 296 (1881).
T. elongata G. F. W. Meyer, Prim. Fl. Esseq. 146 (1818).
T. geniculata Jacq. Enum. Pl. Carib. 18 (1760).
T. multiflora Sw. Prodr. 57 (1788).
T. multiflora var. parviflora (R. \& P.) C. B. Clarke in DC. Monog. Phan. 3: 306 (1881).

## PONTEDERIACEAE

Eichhornia azurea (Sw.) Kunth, Enum. Pl. 4: 129 (1843).
E. crassipes (Mart.) Solms-Laubach in DC. Monog. Phan. 4: 527 (1883).
E. pauciflora Seub. in Mart. Fl. Bras. 3(1): 91 (1847).

Heteranthera limosa (Sw.) Vahl, Enum. 2: 44 (1806).
H. reniformis R. \& P. Fl. Peruv. 1: 43, t. 71 (1798).
H. zosteraefolia Mart. Nov. Gen. \& Spec. 1: 7, t. 3 (1823).

Pontederia rotundifolia L. f. Suppl. 192 (1781).
Reussia subovata (Seub.) Solms-Laubach in DC. Monog. Phan. 4: 534 (1883).

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Distichia filamentosa (Buch.) Griseb. in Abh. Nat. Ver. Bremen, 6: 369 (1879).
D. muscoides Nees \& Meyen in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 129 (1843).

Juncus andicola Hook. Ic. Pl. 8: t. 714 (1848).
J. brunneus Buch. in Abh. Nat. Ver. Bremen, 6: 403 (1879).
J. dichotomus Ell. Sketch, 1: 406 (1821).
J. imbricatus var. Chamissonis (Kunth) Buch. in Engler, Pflanzenr. IV, 36: 122 (1906).
J. involucratus Steud. ex Buch. in Abh. Nat. Ver. Bremen, 4: 121 (1874).
J. Mandonii Buch. in Abh. Nat. Ver. Bremen, 4: 121, t. 3 (1874).
J. microcephalus HBK. Nov. Gen. \& Spec. 1: 237 (1816).
J. microcephalus var. floribundus (HBK.) Kunth, Enum. Pl. 3: 324 (1841).

Luzula boliviensis Buch. in Abh. Nat. Ver. Bremen, 4: 128, t. 4 (1874) = L. peruviana.
L. excelsa Buch. in Abh. Nat. Ver. Bremen, 4: 126 (1874).
L. gigantea Desv. in Journ. Bot. 1: 145 (1808).
L. peruviana Desv. in Journ. Bot. 1: 160 (1808).
L. racemosa Desv. in Journ. Bot. 1: 162 (1808).

Oxychloe̊ andina Phil. Fl. Atac. 52, t. 6 (1860).

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Allium bivalve var. Bangii O. Ktze. Rev. Gen. 3(2): 313 (1898) $=$ Nothoscordum sp.?
Anthericum boliviense v. Poelln. in Rev. Sudam. Bot. 7: 99 (1942).
A. eccremorrhizum R. \& P. Fl. Peruv. 3: 67, t. 301 (1802).
A. glaucum R. \& P. Fl. Peruv. 3: 68 (1802).
A. glaucum var. andinum v. Poelln. in Rev. Sudam. Bot. 7: 157 (1943).
A. peruvianum Willd. ex Kunth, Enum. Pl. 4: 596 (1843), in synon.

Asagraea longiflora Rusby in Bull. N. Y. Bot. Gard. 6: 491 (1910).
Asparagus officinalis L. Sp. Pl. 313 (1753).
Asphodelus fistulosus L. Sp. Pl. 309 (1753).
Cordyline dracaenoides Kunth in Abh. Acad. Berl. 1842: 30.
Dianella boliviana Schlittler in Mitteil. Bot. Mus. Univ. Zürich, 163: 253 (1940).
Excremis coarctata (R. \& P.) Baker in Journ. Linn. Soc. 15: 320 (1876).
E. scabra O. Ktze. Rev. Gen. 3(2): 316 (1898).

Herreria montevidensis Klotzsch ex Griseb. in Mart. Fl. Bras. 3(1): 24 (1847).
Milla andicola (Kunth) Baker in Journ. Linn. Soc. 11: 381 (1870).
Nothoscordum flavescens Poepp. in Kunth, Enum. Pl. 4: 459 (1843).
N. bivalve (L.) Britton in Britton \& Brown, Illustr. Fl. 1: 415 (1896).

Smilax argyraea L. Lind. \& Rod. in Illustr. Hortic. 39: 51, t. 152 (1892).
S. flavicaulis Rusby in Mem. N. Y. Bot. Gard. 7: 213 (1927).
S. Kunthii Killip \& Morton in Carnegie Inst. Wash. Publ. 461: 269 (1936).
S. irrorata Mart. ex Griseb. in Mart. Fl. Bras. 3(1): 10 (1842).
S. mexicana Griseb. ex Kunth, Enum. Pl. 5: 167 (1850).
S. phylloloba Mart. ex Griseb. in Mart. Fl. Bras. 3(1): 21 (1842).
S. tomentosa HBK. Nov. Gen. \& Spec. 1: 272 (1816).

## HAEMODORACEAE

Xiphidium coeruleum Aubl. Pl. Guian. Franç. 1: 33, t. 11 (1775).

## AMARYLLIDACEAE

Alstroemeria Fiebrigiana Kränzl. in Engler, Bot. Jahrb. 40: 237 (1908).
A. pygmaea Herb. Amaryll. 100, t. 8, fig. 4-13 (1837).
? Amaryllis Aglaiae Castellanos in Herbertia, 7: 63 (1941).
A. Belladonna L. Sp. Pl. 293 (1753).
A. Belladonna var. Haywardii (Traub \& Uphof) Traub \& Moldenke, Amaryllidac. 123 (1949).
A. crociflora (Rusby) Traub \& Uphof in Herbertia, 5: 128 (1938).
A. Cybister (Herb.) Planch. in Fl. des Serres, 5: t. 455 (1849).
A. elegans Spreng. Pl. Min. Cognit. Pugill. 2: 59 (1815).
A. Mandonii (Baker) Traub \& Uphof in Herbertia, 5: 129 (1938).
A. scopulorum (Baker) Traub \& Uphof in Herbertia, 5: 129 (1938).
A. soratensis (Baker) Traub \& Uphof in Herbertia, 5: 123 (1938).
A. viridiflora (Rusby) Traub \& Uphof in Herbertia, 5: 124 (1938).

Atamosco microcarpa Rusby in Mem. N. Y. Bot. Gard. 7: 213 (1927).
? Bomarea acutifolia (Lk. \& Otto) Herb. Amaryll. 112 (1837).
B. aurantiaca Herb. Amaryll. 399, t. 46, fig. 1 (1837).
B. boliviensis Baker in Rusby in Bull. Torr. Bot. Club, 29: 700 (1902).
B. brevis (Herb.) Baker in Journ. Bot. 20: 202 (1882).
B. Bridgesiana Beauverd in Bull. Soc. Bot. Genève (ser. 2), 14: 173 (1922).
B. calyculata Kränzl. in Kew Bull. 1913: 189.
B. coccinea (R. \& P.) Baker in Journ. Bot. 20: 202 (1882).
B. crocea (R. \& P.) Herb. Amaryll. 119 (1837).
B. distichophylla (Herb.) Baker in Journ. Bot. 20: 202 (1882).
B. dulcis (Hook.) Beauverd in Bull. Soc. Bot. Genève (ser. 2), 14: 172 (1922).
B. edulis (Tussac) Herb. Amaryll. 111 (1837).
B. Fiebrigiana Kränzl. in Engler, Bot. Jahrb. 40: 230 (1908).
B. fimbriata (R. \&. P.) Herb. Amaryll. 116 (1837).
B. flava Baker in Rusby in Bull. N. Y. Bot. Gard. 4: 459 (1907).
B. formosissima (R. \& P.) Griseb. ex Baker, Handbk. Amaryll. 153 (1888).
B. glaucescens (Kunth) Baker in Journ. Bot. 20: 201 (1882).
B. Herbertiana Baker, Handbk. Amaryll. 155 (1888).
B. involucrosa (Herb.) Baker in Journ. Bot. 20: 201 (1882).
B. multiflora (L. f.) Mirbel in Hist. Nat. Pl. 9: 72 (1804).
B. ovata (Cav.) Mirbel in Hist. Nat. Pl. 9: 72 (1804).
B. petiolata Rusby in Mem. N. Y. Bot. Gard. 7: 216 (1927).
B. petraea Kränzl. in Engler, Bot. Jahrb. 40: 229 (1908).
B. polyphylla Kränzl. in Ann. Naturh. Hoîmus. Wien, 27: 158 (1913).
B. puberula (Herb.) Kränzl. in Engler, Bot. Jahrb. 49: 192 (1913).
B. salcilla Mirbel in Hist. Nat. Pl. 9:71 (1804).
B. sanguinea Kränzl. in Engler, Bot. Jahrb. 50, Beibl. 112: 6 (1913).
B. stans Kränzl. in Engler, Bot. Jahrb. 40: 231 (1908).
B. subsessilis Killip in Journ. Wash. Acad. Sci. 25: 373 (1935).
B. superba Herb. Amaryll. 117, t. 6, fig. 1 (1837).
B. tomentosa (R. \& P.) Herb. Amaryll. 117 (1837).
B. trachypetala Kränzl. in Engler, Bot. Jahrb. 50, Beibl. 112: 5 (1913).
B. uniflora (Mathews) Killip in Journ. Wash. Acad. Sci. 25: 372 (1935).

Chlidanthus fragrans Herb. App. 46 (1821).
Collania guadelupensis Kränzl. in Ann. Naturh. Hofmus. Wien, 27: 157 (1913).
C. Herzogiana Kränzl. in Engler, Bot. Jahrb. 50, Beibl. 111: 3 (1913).
C. subverticillata Kränzl. in Ann. Naturh. Hofmus. Wien, 27: 152 (1913).

Crocopsis fulgens Pax in Engler, Bot. Jahrb. 11: 324 (1889).
Curculigo scorzoneraefolia (Lam.) Baker in Journ. Linn. Soc. 17: 124 (1878).
Furcraea sp.
Habranthus brachyandrus (Baker) Sealy in Journ. Roy. Hort. Soc. 62: 208 (1937).

Haylockia andina R. E. Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1(1): 160, t. 9, fig. 1-2 (1905).
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H. pseudocrocus Solms-Laubach in Bot. Zeit. 65(1): 135 (1907).

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H. quitoënsis Herb. App. 45 (1821).

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H. humilis HBK. Nov. Gen. \& Spec. 1: 286 (1816).

Lepidopharynx deflexa Rusby in Mem. N. Y. Bot. Gard. 7: 214, fig. 1 (1927).
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S. Pearcei Baker in Saunder, Ref. Bot. 5: t. 308 (1873).
S. recurvatum (R. \& P.) Baker in Saunder, Ref. Bot. 5: sub t. 308 (1873).

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Wichuraea acicularis (Herb.) M. J. Roem. Syn. Ensat. 280 (1847) = Bomarea dulcis.
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Z. viridi-lutea Kränzl. in Fedde, Repert. Spec. Nov. 13: 118 (1914).

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D. angustifolia Rusby in Bull. Torr. Bot. Club, 29: 701 (1902).

Dioscorea acanthogyne Rusby in Bull. N. Y. Bot. Gard. 6: 492 (1910).
D. arcuata Rusby in Bull. N. Y. Bot. Gard. 4: 460 (1907) $=$ D. Mandonii.
D. Bangii R. Knuth in Engler, Pflanzenr. IV, 43: 324 (1924).
D. bermejensis R. Knuth in Notizbl. 7: 199 (1917).
D. boliviensis R. Knuth in Notizbl. 7: 188 (1917).
D. calderillensis R. Knuth in Notizbl. 7: (1917).
D. chacoënsis R. Knuth in Fedde, Repert. Spec. Nov. 21: 77 (1925).
D. chiquiacensis R. Knuth in Notizbl. 7: 196 (1917).
D. convolvulacea Schlechtd. \& Cham. in Linnaea, 6: 49 (1831).
D. coripatensis Macbride in Candollea, 6: 2 (1934).
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D. cymosula Hemsl. Biol. Centr. Am. Bot. 3: 355, t. 90 (1884).
D. ferruginicaulis Rusby in Mem. N. Y. Bot. Gard. 7: 217 (1927).
D. Friesii R. Knuth in Fedde, Repert. Spec. Nov. 21: 77 (1925).
D. fuliginosa R. Knuth in Fedde, Repert. Spec. Nov. 21: 78 (1925).
D. furcata Griseb. in Mart. Fl. Bras. 3(1): 45 (1842).
D. Galeottiana Kunth, Enum. Pl. 5: 409 (1850).
D. glauca Rusby in Bull. N. Y. Bot. Gard. 4: 459 (1907) $=$ D. coripatensis.
D. glomerulata var. Mandonii (Uline) R. Knuth in Engler, Pflanzenr. IV, 43: 59 (1924).
D. guanaiensis R. Knuth in Engler, Pflanzenr. IV, 43: 78 (1924).
D. hastiformis R. Knuth in Notizbl. 7: 197 (1917).
D. Herzogii R. Knuth in Meded. Rijks Herbar. 29: 56 (1916).
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D. Kuntzei Uline in O. Ktze. Rev. Gen. 3(2): 311 (1898).
D. lagoa-santa Uline ex R. Knuth in Notizbl. 7: 201 (1917) = D. monadelpha.
D. larecajensis Uline ex R. Knuth in Notizbl. 7: 195 (1917).
D. Lorentzii var. Mandonii Uline ex R. Knuth in Notizbl. 7: 187 (1917).
D. macrantha Uline ex R. Knuth in Notizbl. 7: 198 (1917).
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D. monadelpha (Kunth) Griseb in Vidensk. Medd. Kjoebenh. 1875: 164.
D. multiflora Griseb. in Mart. Fl. Bras. 3(1) : 35 (1842).
D. multispicata R. Knuth in Meded. Rijks Herbar. 29: 55 (1916).
D. nodosa R. Knuth in Notizbl. 7: 187 (1917).
D. oblongifolia Rusby in Bull. N. Y. Bot. Gard. 6: 492 (1901).
D. orthoneura var. acutissima Uline ex R. Knuth in Notizbl. 7: 216 (1917).
D. ovalifolia R. Knuth in Notizbl. 7: 200 (1917).
D. polygonoides Humb. \& Bonpl. ex Willd. Sp. Pl. 4 (2): 795 (1805).
D. racemosa Rusby in Bull. N. Y. Bot. Gard. 4: 459 (1907) $=$ D. Bangii.
D. Rusbyi Uline in Engl. \& Prantl, Nat. Pflanzenfam. Nachtr. II (5): 86 (1897).
D. sinuata Vell. Fl. Flum. 10: t. 129 (1827).
D. spectabilis R. Knuth in Meded. Rijks Herbar. 29: 55 (1916).
D. tarijensis R. Knuth in Notizbl. 7: 212 (1917).
D. toldosensis R. Knuth in Engler, Pflanzenr. IV, 43: 351 (1924).
D. Trollii R. Knuth in Fedde, Repert. Spec. Nov. 30: 161 (1932).
D. violacea R. Knuth in Notizbl. 7: 200 (1917) $=$ D. toldosensis.

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Calydorea approximata R. C. Foster in Contrib. Gray Herb. 155: 46 (1945).
C. azurea Klatt in Abh. Naturf. Ges. Halle, 15: 387 (1882).
C. campestris (Klatt) Baker in Journ. Bot. 14: 187 (1876).

Cardenanthus boliviensis R. C. Foster in Contrib. Gray Herb. 155: 4 (1945).
C. longitubus R. C. Foster in Contrib. Gray Herb. 171: 23 (1950).
C. orurensis R. C. Foster in Contrib. Gray Herb. 161: 14 (1946).
C. tunariensis R. C. Foster in Contrib. Gray Herb. 155: 5 (1945).

Cipura major Rusby in Bull. N .Y. Bot. Gard. 6: 493 (1910).
C. paludosa Aubl. Pl. Guian. Fr. 1: 38, t. 13 (1775).

Cypella linearis (HBK.) Baker, Handbk. Irid. 65 (1892).
C. peruviana Baker in Bot. Mag. 102: t. 6213 (1876).

Eleutherine bulbosa (Mill.) Urb. in Fedde, Repert. Spec. Nov. 15: 305 (1918).
Libertia boliviana R. C. Foster in Contrib. Gray Herb. 161: 4 (1946).
Mastigostyle brevicaulis (Baker) R. C. Foster in Contrib. Gray Herb. 161: 16 (1946).
M. Cardenasii R. C. Foster in Contrib. Gray Herb. 155: 23 ( 1945 ).

Orthrosanthus nigrorhynchus Rusby in Mem. Torr. Bot. Club, 6: 126 (1896).
O. tunarensis O.Ktze. Rev. Gen. 3(2): 309 (1898) =O. nigrorhynchus.

Phaiophleps acaulis (Klatt) R. C. Foster in Contrib. Gray Herb. 127: 43 (1939).

Sphenostigma boliviense Baker, Handbk. Irid. 107 (1892).
S. Goodspeedianum R. C. Foster in Contrib. Gray Herb. 171: 27 (1950).
S. Mandonii (Rusby) R. C. Foster in Contrib. Gray Herb. 161: 10 (1946).
S. Mandonii var. bulbilliferum R. C. Foster in Contrib. Gray Herb. 161: 11 (1946).
S. umbellatum (Klatt) Klatt in Abh. Naturf. Ges. Halle, 15: 363 (1882).

Sisyrinchium alatum var. minus Rusby in Bull. N. Y. Bot. Gard. 6: 493 (1910).
S. azureum Phil. Fl. Atac. 50 (1860).
S. Bakeri Klatt in Abh. Naturf. Ges. Halle, 15: 378 (1882) $=$ S. trinerve.
S. brevipes Baker, Handbk. Irid. 130 (1882).
S. cryptocarpum Rusby in Mem. Torr. Bot. Club, 6: 126 (1896) = S. trinerve.
S. hypsophilum I. M. Johnst. ex R. C. Foster in Contrib. Gray Herb. 166: 30 (1948).
S. Ivanii R. C. Foster in Contrib. Gray Herb. 166: 30 (1948).
S. junceum E. Mey. ex Presl, Rel. Haenk. 1: 118 (1827).
S. laterale Baker in Journ. Bot. 14: 269 (1876).
S. macrocephalum R. Graham in Edinb. New Philos. Journ. 176 (Jan. 1833).
S. Mandonii Baker in Journ. Bot. 14: 269 (1876).
S. Marchio (Vell.) Steud. Nomencl. (ed. 2) 2: 596 (1841).
S. micranthum Cav. Diss. 2: 345, t. 191, fig. 2 (1788).
S. pictum Kränzl. in Fedde, Repert. Spec. Nov. 13: 119 (1914) = S. laterale ?
S. rigidifolium Baker, Handbk. Irid. 131 (1892).
S. tinctorium HBK. Nov. Gen. \& Spec. 1: 324 (1816).
S. trinerve Baker in Journ. Bot. 14: 267 (1876).
S. unispathaceum Klatt in Linnaea, 34: 737 (1866).
S. vaginatum Spreng. Syst. Veg. 1: 166 (1825).

Tigridia bracteolata (Klatt) Macbride in Candollea, 5: 348 (1934).

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Heliconia acuminata A. Rich. in Nov. Act. Acad. Caes. Leop. 15, Suppl.: 26, t. 11 (1831).
H. Bihai sensu auctt. non L.
H. cannoides sensu auctt. non A. Rich.
H. Cardenasii L. B. Smith in Contrib. Gray Herb. 124: 5 (1939).
H. episcopalis Vell. Fl. Flum. 3: 107, t. 22 (1825).
H. Pearcei Rusby in Bull. N. Y. Bot. Gard. 6: 494 (1910) = H. acuminata.
H. psittacorum L. f. Suppl. 158 (1781).
H. robusta Pax in Fedde, Repert. Spec. Nov. 7: 107 (1909).
H. rostrata R. \& P. Fl. Peruv. 3: 71, t. 305 (1802).

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Costus cylindricus Jacq. Fragm. 34, t. 77 (1809).
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C. guanaiensis Rusby in Bull. Torr. Bot. Club, 29: 694 (1902).
C. longifolius Rusby in Phytologia, 1(2): 50 (1934).
C. Mooreanus Rusby in Bull. N. Y. Bot. Gard. 4: 454 (1907).
C. rurrenabaqueanus Rusby in Mem. N. Y. Bot. Gard. 7: 219 (1927).
C. sinningiaeflorus Rusby in Mem. N. Y. Bot. Gard. 7: 219 (1927).
C. spicatus (Jacq.) Sw. Prodr. 11 (1788).
C. Steinbachii Loes. in Notizbl. 10: 714 (1929).
C. Tatei Rusby in Phytologia, 1(2): 51 (1934).

Dimerocostus bolivianus (Rusby) Loes. in Notizbl. 10: 716 (1929).
D. Gutierrezii O. Ktze. Rev. Gen. 3(2): 301 (1898).

Renealmia Cardenasii Rusby in Mem. N. Y. Bot. Club, 7: 219 (1927).
R. dermatopetala K. Schum. in Engler, Pflanzenr. IV, 46: 304 (1904).
R. micrantha K. Schum. in Engler, Pflanzenr. IV, 46: 298 (1904).
R. Ruiziana (Steud.) Horan. Prodr. Monog. Scitam. 33 (1862).
R. spectabilis Rusby in Mem. N. Y. Bot. Gard. 7: 218 (1927).

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Canna Bangii Kränzl. in Engler, Pflanzenr. IV, 47: 38 (1912).
C. Brittonii Rusby in Bull. Torr. Bot. Club, 29: 695 (1902).
C. coccinea Mill. Dict. (ed. 8) no. 3 (1768).
C. edulis Ker in Bot. Reg. 9: t. 775 (1824).
C. glauca L. Sp. Pl. 1 (1753).
C. lanuginosa Rosc. Scit. t. 16 (1828).
C. pedunculatus Sims in Bot. Mag. 49: t. 2323 (1822).

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Calathea bracteosa Rusby in Mem. N. Y. Bot. Gard. 7: 220 (1927).
C. Buchtienii Pax in Fedde, Repert. Spec. Nov. 7: 107 (1909).
C. capitata (R. \& P.) Lindl. in Bot. Reg. 14: sub t. 1210 (1829).
C. Cardenasii Rusby in Mem. N. Y. Bot. Gard. 7: 222 (1927).
C. divaricata Rusby in Bull. Torr. Bott. Club, 29: 695 (1902).
C. exserta Rusby in Bull. N. Y. Bot. Gard. 6: 495 (1910).
C. gigas Gagnep. in Bull. Soc. Bot. France, 50: 589 (1904).
C. Mansonis Koern. in Bull. Soc. Nat. Mosc. 35(1): 119 (1862).
C. nigricans Rusby in Bull. N. Y. Bot. Gard. 6: 496 (1910) $=$ C. Rusbyi.
C. nodosa Rusby in Bull. N. Y. Bot. Gard. 4: 455 (1907).
C. Pearcei Rusby in Mem. Torr. Bot. Club, 6: 123 (1896).
C. pilosa Rusby in Bull. N. Y. Bot. Gard. 6: 496 (1910).
C. Rusbyi Loes, in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 15a: 678 (1930).
C. Sprucei Rusby in Bull. N. Y. Bot. Gard. 6: 495 (1910).
C. stenostachys Rusby in Mem. N. Y. Bot. Gard. 7: 221 (1927).
C. stromanthifolia Rusby in Bull. N. Y. Bot. Gard. 4: 456 (1907).
C. Whitei Rusby in Mem. N. Y. Bot. Gard. 7: 221 (1927).

Ethanium jamaicense (Gaertn.) O. Ktze. Rev. Gen. 2: 689 (1891).
Ischnosiphon Baenitzii Pax in Fedde, Repert. Spec. Nov. 7: 108 (1909).
I. bolivianus Loes. in Notizbl. 6: 280 (1915).
I. gracilis (Rudge) Koern. in Bull. Soc. Nat. Mosc. 35(1): 94 (1862).
I. lasiocoleus var. bolivianoides Loes. in Notizbl. 6: 280 (1915).
I. Parkeri (Rosc.) Koern. in Bull. Soc. Nat. Mosc. 35(1): 81 (1862).

Maranta amplifolia K. Schum. in Engler, Pflanzenr. IV, 48: 128 (1902).
M. Tonckat Aubl. Pl. Guian. Fr. 1: 3 (1775).

Myrosma boliviana Loes. in Notizbl. 6: 270 (1915).
M. boliviana var. acreana Loes. in Notizbl. 6: 270 (1915).

Stromanthe angustifolia Rusby in Mem. Torr. Bot. Club, 4 (3): 266 (1895).
S. boliviana K. Schum. in Engler, Pflanzenr. IV, 48: 151 (1902).
S. confusa K. Schum. in Engler, Pflanzenr. IV, 48: 150 (1902).
S. Porteana Griseb. in Ann. Sci. Nat. (ser. 4) 9: 185 (1858).

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Apteria aphylla (Nutt.) Barnh. ex Small, Fl. SE. U. S. 309 (1903).
A. boliviana Rusby in Bull. N. Y. Bot. Gard. 4: 447 (1907) $=$ A. aphylla.
A. gentianoides Jonker, Monog. Burmann. 211 (1938).

Burmannia capitata (Walt.) Mart. Nov. Gen. 1: 12 (1823).
B. flava Mart. Nov. Gen. 1: 11, t. 5 (1823).
B. tenella Benth. in Journ. Bot. 7: 12 (1855).

Dictyostega orobanchioides Miers in Proc. Linn. Soc. 1: 61 (1840).

## ORCHIDACEAE

Aa microtidis Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 35 (1922) = Altensteinia sp. ?
A. sphaeroglossa Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 36 (1922) $=$ Altensteinia sp. ?
A. trilobulata Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 37 (1922) = Altensteinia sp.?
Altensteinia calcarata Reichb. f. Xen. Orch. 3: 19 (1878).
A. boliviensis Rolfe in Mem. Torr. Bot. Club, 4 (3): 265 (1895) = A. fimbriata.
A. chiogena (Schltr.) C. Schweinf. in Bot. Mus. Leafl. Harvard Univ. 16(1): 2 (1953).
A. Fiebrigii Schltr. in Fedde, Repert. Spec. Nov. 10: 445 (1912).
A. fimbriata HBK. Nov. Gen. \& Spec. 1: 333, t. 72 (1816).
A. gymnandra Reichb. f. Xen. Orch. 3: 18 (1878).
A. inaequalis Reichb. f. Xen. Orch. 3: 19 (1878).
A. Mandonii Reichb. f. Xen. Orch. 3: 19 (1878).
A. marginata Reichb. f. Xen. Orch. 3: 19 (1878).
A. Matthewsii Reichb. f. Xen. Orch. 3: 19 (1878).
A. paludosa Reichb. f. Xen. Orch. 3: 19 (1878).
A. Weddelliana Reichb. f. Xen. Orch. 3: 19 (1878).

Amblostoma cernuum Scheidw. in Otto \& Dietr. Gartenzeit. 6: 383 (1838).
A. densum Reichb. f. Xen. Orch. 3: 22 (1878).

Beloglottis boliviensis Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 38 $(1922)=($ probably ) Spiranthes costaricensis.
Bletia catenulata R. \& P. Syst. 229 (1798).
B. Mandonii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 48 (1922).
B. Wageneri Reichb. f. in Bonplandia, 2: 22 (1854).

Brachionidium concolor Lindl. Fol. Orch. Brach. 1 (1859).
Brassia boliviensis Schltr. in Fedde, Repert. Spec. Nov. 12: 494 (1913).
B. caudata (L.) Lindl. in Bot. Reg. 10: t. 832 (1824).
B. Lanceana Lindl. in Bot. Reg. 21: t. 1754 (1835).
B. thyrsodes Reichb. f. in Gard. Chron. 1868: 342.

Buchtienia boliviensis Schltr. in Fedde, Repert. Spec. Nov. 27: 34 (1929).
Bulbophyllum amazonicum L. O. Wms. in Lilloa, 5: 7 (1940).
B. bolivianum Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 49 (1922).
B. tricolor Smith \& Harris in Contrib. Gray Herb. 114: 11 (1936).
B. Weberbauerianum var. angustius C. Schweinf. in Bot. Mus. Leafl. Harvard Univ. 11: 189 (1944).
Camaridium boliviense Rolfe in Mem. Torr. Bot. Club, 4 (3): 264 (1895) = Maxillaria sp. ?
C. flavum Schltr. in Fedde, Repert. Spec. Nov. 27: 76 (1929) $=$ Maxillaria sp.?
C. vagans Schltr. in Fedde, Repert. Spec. Nov. 27: 77 (1929) $=$ Maxillaria sp.?
Campylocentrum apiculatum Schltr. in Fedde, Repert. Spec. Nov. 27: 84 (1929).
C. Kuntzei Cogn. in O. Ktze. Rev. Gen. 3(2): 298 (1898).
C. neglectum (Reichb. f. \& Warm.) Cogn. ex Chod. in Bull. Herb. Boiss. (ser. 2) 1: 425 (1901).

Catasetum Buchtienii Kränzl. in Fedde, Repert. Spec. Nov. 25: 27 (1928).
C. cristatum Lindl. in Bot. Reg. 10: sub t. 840 (1824).
C. fimbriatum (C. Morr.) Lindl. in Paxt. Flow. Gard. 1: 124 (1850).
C. fimbriatum var. Morrenianum (Morr.) Mansf. in Fedde, Repert. Spec. Nov. 31: 108 (1932).
C. Pflanzii Schltr. in Fedde, Repert. Spec. Nov. 11: 45 (1912) = C. fimbriatum var. Morrenianum.
C. Wredeanum Schltr. in Orchis, 9:14 (1915), nomen nudum $=$ C. fimbriatum var. Morrenianum.
Cattleya luteola Lindl. in Gard. Chron. 1853: 774.
C. Walkeriana Gardn. in Hook. Lond. Journ. Bot. 2: 662 (1843).

Centrogenium roseoalbum (Reichb. f.) Schltr. in Beih. Bot. Centralbl. 37(2): 453 (1920).
Chloraea boliviana (Reichb. f.) Kränzl. Orch. Gen. \& Spec. 2: 139, t. 16 (1904).
C. calantha Kränzl. in Engler, Bot. Jahrb. 37: 395 (1906).
C. Fiebrigiana Kränzl. in Engler, Bot. Jahrb. 37: 396 (1906).
C. ignea Kränzl. in Engler, Bot. Jahrb. 37: 396 (1906).
C. reticulata Schltr. in Fedde, Repert. Spec. Nov. 15: 210 (1918).

Cochlioda Noezliana Rolfe in Lindenia, 6:55, t. 266 (1890).
Comparettia falcata Poepp. \& Endl. Nov. Gen. 1: 42, t. 73 (1835).
C. macroplectron Reichb. f. \& Triana in Gard. Chron. 1878 (II): 524.
C. splendens Schltr. in Fedde, Repert, Spec. Nov. Beih. 10: 51 (1922).

Corymborchis flava (Sw.) O. Ktze. Rev. Gen. 2: 658 (1891).
Cranichis ciliata (HBK.) Kunth, Syn. Pl. Aeq. 1: 324 (1822).
C. Mandonii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 38 (1922) = C. ciliata.

Cyclopogon casanaënsis Schltr. in Fedde, Repert. Spec. Nov. 27: 32 (1929) = Spiranthes sp.?
Cycnoches Buchtienii Kränzl. in Fedde, Repert. Spec. Nov. 25: 26 (1928).
? C. Haagei Rodr. Orch. Nov. 2: 221 (1882).
Cryrtopodium Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 25: 26 (1928).
C. Pflanzii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 49 (1922).
C. punctatum (L.) Lindl. Gen. \& Spec. Orch. 188 (1833).

Diadenium micranthum Poepp. \& Endl. Nov. Gen. 1: 41, t. 71 (1835).
Dichaea anguina Schltr. in Fedde, Repert. Spec. Nov. 27: 82 (1929):
D. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 53 (1922).
D. echinocarpa (Sw.) Lindl. Gen. \& Spec. Orch. 208 (1833).
D. hamata Rolfe in Mem. Torr. Bot. Club, 4 (3): 264 (1895).
D. laxa (R. \& P.) Poepp. \& Endl. Nov. Gen. 2: 4, t. 105 (1838).
D. longa Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 54 (1922).
? D. muricata (Sw.) Lindl. Gen. \& Spec. Orch. 209 (1833).
D. robusta Schltr. in Fedde, Repert. Spec. Nov. 27: 83 (1929).
D. stenophylla Schltr. in Fedde, Repert. Spec. Nov. 27: 84 (1929).
? Elleanthus brasiliensis Reichb. f. in Walp. Ann. 6: 475 (1861).
E. linifolius Presl, Rel. Haenk. 1: 97 (1827).
E. maculatus (Lindl.) Reichb. f. in Walp. Ann. 6: 482 (1861).
E. scopula Schltr. in Fedde, Repert. Spec. Nov. 10: 457 (1912).
E. setosus Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 34 (1922).
E. yungasensis Rolfe in Mem. Tomm. Bot. Club. 4(3): 262 (1895).

Encyclia Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 27: 62 (1929) = Epidendrum sp., not Epidendrum Buchtienii.
E. Pflanzii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 46 (1922) = Epidendrum sp.?
E. Steinbachii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 47 (1922) = Epidendrum sp.?
Epidendrum albiflorum Schltr. in Fedde, Repert. Spec. Nov. 12: 488 (1913).
E. alopecurum Schltr. in Fedde, Repert. Spec. Nov. 27: 58 (1929).
E. armeniacum Lindl. in Bot. Reg. 22: t. 1867 (1836).
E. Bangii Rolfe in Bull. N. Y. Bot Gard. 4: 451 (1907) = E. rostrigerum.
E. bolivianum Schltr. in Fedde, Repert. Spec. Nov. 10: 456 (1912).
E. brachycladium Lindl. Fol. Orch. Epid. 60 (1853) .
E. brachyglossum Lindl. Fol. Orch. Epid. 72 (1853).
E. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 10: 455 (1912).
E. buenavistae Kränzl. in Fedde, Repert. Spec. Nov. 6: 19 (1908).
E. cartilaginiflorum Reichb. f. Xen. Orch. 3: 24 (1878).
E. Christyanum Reichb. f. in Gard. Chron. 22: 38 (1884).
E. coroicoënse Schltr. in Fedde, Repert. Spec. Nov. 27: 60 (1929).
E. corymbosum Lindl. Fol. Orch. Epid. 61 (1853).
E. crassinervium Kränzl. in Fedde, Repert. Spec. Nov. 1: 182 (1905).
E. cristatum R. \& P. Syst. 243 (1798).
E. cuneatum Schltr. in Fedde, Repert. Spec. Nov. 10: 456 (1912).
E. difforme Jacq. Enum. Pl. Carib. 29 (1760).
? E. elongatum Jacq. Ic. Pl. Rar. 3:17, t. 604 (1793).
E. Evelynae Reichb. f. Xen. Orch. 3: 23 (1878).
E. exaltatum Kränzl. in Engler, Bot. Jahrb. 54, Beibl. 117: 26 (1916).
? E. fallax Lindl. Orch. Linden. 9 (1846).
E. fimbriatum var. rhomboglossum (Kränzl.) C. Schweinf. in Bot. Mus. Leafl. Harvard Univ. 11: 224 (1844).
E. fragrans Sw. Prodr. 123 (1788).
E. Friderici-Guglielmi Warsc. ex Reichb. f. in Bonplandia, 2: 110 (1854).
E. gladiatum Lindl. Gen. \& Spec. Orch. 106 (1831).
E. Guentherianum Kränzl. in Fedde, Repert. Spec. Nov. 25: 20 (1928).
E. Harrisoniae Hook. in Bot. Mag. 60: t. 3209 (1833).
E. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 489 (1913).
E. humidicola Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 44 (1922) = E. paniculatum.
E. ibaguense HBK. Nov. Gen. \& Spec. 1: 352 (1816).
E. insectiferum Lindl. Fol. Orch. Epid. 87 (1853).
E. integrilabium Ames \& Schweinf. Sched. Orch. 8: 46 (1925) $=$ E. fimbriatum var. rhomboglossum.
E. lanioides Schltr. in Fedde, Repert. Spec. Nov. 12: 389 (1913).
E. lanipes Lindl. Fol. Orch. Epid. 91 (1853).
E. mapiriense Kränzl. in Fedde, Repert. Spec. Nov. 25: 21 (1928).
E. mesomicron Lindl. Fol. Orch. Epid. 51 (1853).
E. Miguelii Schltr. in Fedde, Repert. Spec. Nov. 21: 337 (1925).
E. nigricans Schltr. in Fedde, Repert. Spec. Nov. 12: 490 (1913).
E. nocturnum Jacq. Enum. Pl. Carib. 29 (1760).
E. obliquum Schltr. in Fedde, Repert. Spec. Nov. 10: 457 (1912).
E. odontospathum Reichb. f. Xen. Orch. 3: 23 (1878).
E. oreonastes Reichb. f. Xen. Orch. 3: 22 (1878).
E. paniculatum R. \& P. Syst. 243 (1789).
E. Peperomia Reichb. f. in Bonplandia, 2: 20 (1854).
E. physophorum Schltr. in Fedde, Repert, Spec. Nov. 12: 490 (1913).
E. purum Lindl. in Bot. Reg. 30: Misc. 75 (1844).
E. pygmaeum Hook. in Bot. Mag. 60: t. 3233 (1833).
E. quinquepartitum Schltr. in Fedde, Repert. Spec. Nov. Beih. $10: 45$ (1922).
E. ramosum Jacq. Select. Stirp. Amer. 221 (1763).
E. rigidum Jacq. Enum. Pl. Carib. 29 (1760).
E. rostrigerum Reichb. f. in Linnaea, 41: 38 (1877).
E. scopulorum Reichb. f. Xen. Orch. 3: 23 (1873).
E. soratae Reichb. f. Xen. Orch. 3: 24 (1878).
E. Steinbachii Ames, Sched. Orch. 1: 20 (1922) = E. obliquum.
E. syringodes Schltr. in Fedde, Repert. Spec. Nov. 27: 61 (1929).
E. syringothyrsus Reichb. f. Xen. Orch. 3: 22 (1878).
E. Theodori Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 46 (1922).
E. trichopetalum Schltr. in Fedde, Repert. Spec. Nov. 12: 491 (1931).
E. trichorhizum Kränzl. in Fedde, Repert. Spec. Nov. 25: 21 (1928).
E. yungasense Rolfe in Mem. Torr. Bot. Club, 4 (3): 262 (1895).

Epistephium amplexicaule ((R. \& P.) Poepp. \& Endl. Nov. Gen. 1: 52, t. 91 (1836).
E. Herzogianum Kränzl. in Fedde, Repert. Spec. Nov. 6: 21 (1908).
E. sclerophyllum Lindl. Gen. \& Spec. Orch. 433 (1840).

Eulophidium maculatum (Lindl.) Pfitz. in Engl. \& Prantl, Nat. Pflanzenfam. 2(6): 188 (1889).
Galeandra Fiebrigii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 47 (1922).
? G. lagoënsis Reichb. f. \& Warsc. in Otia Bot. Hamb. fasc. 1: 88 (1881).
Gomphichis longifolia (Rolfe) Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 60 (1922).
G. plantaginifolia C. Schweinf. in Bot. Mus. Leaf. Harvard Univ. 11: 217 (1944).
G. valida Reichb. f. Xen. Orch. 3: 20 (1878).

Govenia boliviensis Rolfe in Mem. Torr. Bot. Club, 4(3): 263 (1895).
G. tingens Poepp. \& Endl. Nov. Gen.2: 5, t. 107 (1838) = G. utriculata.
G. utriculata (Sw.) Lindl. in Bot. Reg. 25: Misc. 47 (1839).

Habenaria Bangii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 30 (1922).
H. bermejoënsis Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 30 (1922).
H. boliviana Reichb. f. in Bonplandia, 3: 213 (1885).
H. bractescens Lindl. Gen. \& Spec. Orch. 308 (1835).
H. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 31 (1922).
H. flexa Reichb. f. ex Kränzl. in Engler, Bot. Jahrb. 16: 97 (1892).
H. Guentheriana Kränzl. in Fedde, Repert. Spec. Nov. 25: 18 (1928).
H. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 48 (1913).
H. leptantha Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 31 (1922).
H. leucosantha Rodr. Orch. Nov. 1: 151 (1877).
H. ligulata C. Schweinf. in Bot. Mus. Leafl. Harvard Univ. 9: 47 (1941).
H. maxillaris Lindl. in Hook. Journ. Bot. 1: 5 (1834).
H. microstylina Reichb. f. Xen. Orch. 3: 17 (1878).
H. Miguelii Schltr. in Fedde, Repert. Spec. Beih. 10: 32 (1922).
H. monorrhiza (Sw.) Reichb. f. in Ber. Deut. Bot. Ges. 3: 274 (1885).
H. Ottonis Schltr. in Fedde, Repert. Spec. Nov. 27: 28 (1929) $=$ H. Guentheriana.
H. Paiveana Reichb. f. Xen. Orch. 3: 17 (1878).
H. petrogeiton Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 33 (1922).
H. pseudorepens Schltr. in Fedde, Repert. Spec. Nov. 12: 481 (1913).
H. pratensis (Lindl.) Reichb. f. in Linnaea, 22: 813 (1849).
H. pungens Cogn. in O. Ktze. Rev. Gen. 3(2): 299 (1898).
H. repens Nutt. Gen. Am. Pl. 2: 190 (1818).
H. sartor Lindl. in Hook. Journ. Bot. 2: 662 (1843).
H. simillima Reichb. f. Xen. Orch. 3: 18 (1878).
H. speciosa Poepp. \& Endl. Nov. Gen. 1: 44 (1835).
H. subandina Schltr. in Fedde, Repert. Spec. Nov. 27: 29 (1929).
H. Theodori Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 33 (1922).
H. Williamsii Schltr. in Fedde, Repert. Spec. Nov. 10: 445 (1912).
H. yungasensis Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 34 (1922).

Hexadesmia boliviensis Rolfe in Mem. Torr. Bot. Club, 6: 122 (1896) = Scaphyglottis Summersii, at least in part.
Houlletia boliviana Schltr. in Fedde, Repert. Spec. Nov. 27: 65 (1929).
H. Buchtienii Kränzl. in Fedde, Repert. Spec. Nov. 25: 28 (1928).
H. odoratissima Lindl. in Paxt. Flow. Gard. 3: 172 (1853).
H. Sanderi Rolfe in Gard. Chron. (ser. 3) 47: 206 (1910).

Ionopsis utricularioides (Sw.) Lindl. Coll. Bot. t. 39A (1821-24).
Isochilus linearis (Jacq.) R. Br. in Ait. Hort. Kew. (ed. 2) 5:209 (1813).
Kefersteinia pulchella Schltr. in Fedde, Repert. Spec. Nov. 27: 68 (1929).
Koellensteinia boliviensis (Rolfe) Schltr. in Orchis, 12: 32 (1918).
Lacaena grandis Kränzl. in Fedde, Repert. Spec. Nov. 25: 25 (1928).
Laelia undulata (Lindl.) L. O. Wms. in Darwiniana, 5: 76 (1941).
Lepanthes Koehleri Schltr. in Fedde, Repert. Spec. Nov. 10: 386 (1912).
L. Paiveana Reichb. f. Xen. Orch. 3: 26 (1878).
L. rupicola Schltr. in Fedde, Repert. Spec. Nov. 12: 485 (1913).
L. sillarensis Schltr. in Fedde, Repert. Spec. Nov. 12: 486 (1913).

Liparis elata Lindl. in Bot. Reg. 14: t. 1175 (1828).
L. neuroglossa Reichb. f. Xen. Orch. 3: 26 (1878).
L. otophyllon Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 41 (1922).
L. ramosa Poepp. \& Endl. Nov. Gen. 2: 9, t. 112 (1837).
L. retusa Fawc. \& Rendl. in Journ. Bot. 47: 128 (1909).
L. Rusbyi Rolfe in Bull. N. Y. Bot. Gard. 4: 454 (1907).
L. vexillifera (Llave \& Lex.) Cogn. in Mart. Fl. Bras. 3(4): 289 (1895).
? Lockhartia lunifera (Lindl.) Reichb. f. in Bot. Zeit. 10: 767 (1852).
L. parthenocomos (Reichb. f.) Reichb. f. in Bot. Zeit. 10: 767 (1852).

Lycaste costata (Lindl.) Lindl. in Bot. Reg. 29: Misc. 15 (1843).
L. macrophylla (Poepp. \& Endl.) Lindl. in Bot. Reg. 28: Misc. 85 (1842).
L. neglecta Schltr. in Fedde, Repert. Spec. Nov. 27: 66 (1929).

Macradenia Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 27: 79 (1929).
Malaxis boliviana (Schltr.) Ames, Sched. Orch. 9: 18 (1925).
M. excavata (Lindl.) O. Ktze. Rev. Gen. 2: 673 (1891).
M. fastigiata (Reichb. f.) O. Ktze. Rev. Gen. 2: 673 (1891).
M. hastilabia (Reichb. f.) O. Ktze. Rev. Gen. 2: 673 (1891).
M. Hieronymi (Cogn.) L. O. Wms. in Lilloa, 4: 363 (1939).
M. major (Reichb. f.) León ex A. D. Hawkes in Phytologia, 3: 260 (1950).
M. Reichenbachiana (Schltr.) L. O. Wms. in Bot. Mus. Leafl. Harvard Univ. 5: 143 (1938).
Masdevallia aspera Reichb. f. ex Kränzl. in Fedde, Repert. Spec. Nov. Beih. 34: 82 (1925).
M. auropurpurea Reichb. f. \& Warsc. in Bonplandia, 2: 115 (1854).
M. Bangii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 41 (1922).

M, boliviensis Schltr. in Fedde, Repert. Spec. Nov. 12: 483 (1913) = M. scandens.
M. brachyantha Schltr. in Fedde, Repert. Spec. Nov. 27: 37 (1929).
M. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 10: 450 (1912) = M. scandens.
M. Herzogii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 42 (1922) = M. auropurpurea.
M. ionocharis Reichb. f. in Gard. Chron. 1875 (II) : 388.
M. Paiveana Reichb. f. Xen. Orch. 3: 25 (1878).
M. scandens Rolfe in Bull. N. Y. Bot. Gard. 4: 453 (1907).
M. setipes Schltr. in Fedde, Repert. Spec. Nov. 27: 38 (1929).
M. tubata Schltr. in Fedde, Repert. Spec. Nov. 27: 39 (1929).
M. xanthura Schltr. in Fedde, Repert. Spec. Nov. 27: 39 (1929) = M. auropurpurea.
Maxillaria aurea var. gigantea (Lindl.) C. Schweinf. in Bot. Mus. Leafl. Harvard Univ. 11: 263 (1945).
M. boliviensis Schltr. in Fedde, Repert. Spec. Nov. Beith. 10: 51 (1922).
? M. breviscapa Poepp. \& Endl. Nov. Gen. 1: 36 (1835).
M. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 27: 68 (1929).
M. casta Kränzl. in Fedde, Repert. Spec. Nov. 25: 30 (1928).
M. compressibulba Schltr. in Fedde, Repert. Spec. Nov. 27: 69 (1929).
M. densifolia (Poepp. \& Endl.) Reichb. f. in Walp. Ann. 6: 534 (1861).
M. divaricata (Barb. Rodr.) Cogn. in Mart. Fl. Bras. 3(6): 49, t. 4, fig. 1 (1904).
M. dolichophylla Schltr. in Fedde, Repert. Spec. Nov. 10: 458 (1912).
M. fallax Schltr. in Fedde, Repert. Spec. Nov. 27: 70 (1929) $=$ M. divaricata.
M. gracilipes Schltr. in Fedde, Repert. Spec. Nov. 27: 71 (1929).
M. grandiflora (HBK.) Lindl. Gen. \& Spec. Orch. 147 (1832).
M. Guentheriana Kränzl. in Fedde, Repert. Spec. Nov. 25: 31 (1928).
M. Herzogiana Kränzl. in Fedde, Repert. Spec. Nov. 6: 20 (1908).
M. leucantha Schltr. in Fedde, Repert. Spec. Nov. 27: 72 (1929).
M. longibracteata (Lindl.) Reichb. f. in Walp. Ann. 6: 540 (1861).
M. longicaulis Schltr. in Fedde, Repert. Spec. Nov. 27: 72 (1929).
M. mapiriensis (Kränzl.) L. O. Wms. in Caldasia, 5: 16 (1942).
M. nervosa Rolfe in Mem. Torr. Bot. Club, 4 (3): 263 (1895).
M. oxysepala Schltr. in Fedde, Repert. Spec. Nov. 27: 73 (1929).
M. poaefolia Schltr. in Fedde, Repert. Spec. Nov. 27: 74 (1929).
M. polybulbon Kränzl. in Fedde, Repert. Spec. Nov. 6: 19 (1908).
M. simacoana Schltr. in Fedde, Repert. Spec. Nov. 27: 75 (1929).
M. splendens Poepp. \& Endl. Nov.. Gen. 1: 38, t. 66 (1835).
M. xylobiiflora Schltr. in Fedde, Repert. Spec. Nov. 27: 76 (1929).

Miorostylis Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 10: 449 (1912) = Malaxis sp.?
M. Mandonii Reichb. f. in Flora, 71: 152 (1888) = Malaxis sp. ?
M. mixta Schltr. in Fedde, Repert. Spec. Nov. 10: 449 (1912) = Malaxis sp.?
M. nasuta Schltr. in Fedde, Repert. Spec. Nov. 27: 35 (1929) = Malaxis sp.?
M. Ottonis Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 39 (1922) = Malaxis hastilabia.
M. tridentula Schltr. in Fedde, Repert. Spec. Nov. 27: 36 (1929) = Malaxis sp.?
M. Weddellii Finet in Bull. Soc. Bot. France, 54: 532 (1907) = Malaxis sp. ?

Mormodes Guentherianum (Kränzl.) Mansf. in Fedde, Repert. Spec. Nov. 31: 112 (1932).
Neodryas Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 493 (1913).
N. latilabia Smith \& Harris in Contrib. Gray Herb. 117: 39 (1937) $=$ N. rhodoneura.
N. Mandonii Reichb. f. Xen. Orch. 3: 21 (1878) = N. rhodoneura.
N. reniformis Smith \& Harris in Contrib. Gray Herb. 117: 39 (1937) $=$ N. rhodoneura.
N. rhodoneura Reichb. f. in Bot. Zeit. 10: 835 (1852).
N. Sacciana Lind. Cogn. in Journ. Orch. 4: 73 (1893).

Notylia arachnites Reichb. f. in Nederl. Kruidk. Arch. 4: 326 (1859).
N. boliviensis Schltr. in Repert. Spec. Nov. Beih. 10: 53 (1922).
N. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 10: 458 (1912).
N. lilacina Kränzl. in Fedde, Repert. Spec. Nov. 25: 29 (1928).
? N. micrantha Lindl. in Bot. Reg. 24: Misc. 91 (1838).
Octomeria boliviensis Rolfe in Bull. N. Y. Bot. Gard. 4: 452 (1907).
O. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 27: 57 (1929).
O. grandiflora Lindl. in Bot. Reg. 28: Misc. 64 (1842).
O. Guentheriana Kränzl. in Fedde, Repert. Spec. Nov. 25: 19 (1928).
O. tenuis Schltr. in Fedde, Repert. Spec. Nov. 10: 455 (1912).
? Odontoglossum chiriquense Reichb. f. in Bot. Zeit. 10: 692 (1852).
O. coronarium Lindl. Fol. Orch. Odont. 21 (1852).
O. mapiriense Mansf. in Fedde, Repert. Spec. Nov. 36: 62 (1934).
O. mystacinum Lindl. Fol. Orch. Odont. 6 (1852).
O. rigidum Lindl. in Benth. Pl. Hartw. 152 (1844) = O. mystacinum.

Oncidium aurarium Reichb. f. in Gard. Chron. 22: 394 (1884).
O. aureum Lindl. Sert. Orch. sub t. 25 (1838).
O. barbatum Lindl. Coll. Bot. t. 27 (1821-24).
O. Batemannianum Parm. ex Knowl. \& Westc. Flor. Cab. 3: 183, t. 137 (1840).
O. Baueri Lindl. Illustr. Gen. \& Spec. Orch. t. 7 (1830).
O. Blanchetii Reichb. f. in Linnaea, 22: 845 (1849).
O. bolivianense Oppenheim in Orchis, 10: 93 (1916).
O. bolivianum Schltr. in Fedde, Repert. Spec. Nov. 10:459 (1912) = O. Baueri.
O. boliviense Rolfe in Bull. N. Y. Bot. Gard. 4: 452 (1907) = O. Batemannianum.
O. brachystegium Kränzl. in Engler, Pflanzenr. IV, 50: 229 (1922).
O. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 27: 81 (1929).
O. disciferum Lindl. Fol. Orch. Oncid. 24 (1855).
O. globuliferum HBK. Nov. Gen. \& Spec. 1: 347 (1816).
O. glossomystax Reichb. f. in Bot. Zeit. 10: 696 (1852).
O. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 494 (1913) $=$ O. barbatum.
O. heteranthum Poepp. \& Endl. Nov. Gen. 1: 34, t. 60 (1835).
O. Jonesianum Reichb. f. in Gard. Chron. 1883 (II) : 781.
O. lepturum Reichb. f. in Gard. Chron. 1886 (I): 41.
O. macropetalum Lindl. Sert. Orch. sub t. 48 (1841).
O. Mandonii Reichb. f. Xen. Orch. 3: 21 (1878).
O. Methonica Reichb. f. Linnaea, 41: 21 (1877).
O. microxiphium Reichb. f. in Linnaea, 41: 21 (1877).
O. otometon Kränzl. in Engler, Pflanzenr. IV, 50: 190 (1922).
O. pusillum (L.) Reichb. f. in Walp. Ann. 6: 714 (1861).
O. reductum Kränzl. in Fedde, Repert. Spec. Nov. 26: 344 (1929).
O. retusum Lindl. in Bot. Reg. 25: sub t. 1920 (1837).
O. Rusbyi Rolfe in Mem. Torr. Bot. Club, 4 (3) : 265 (1895).
O. subulifolium Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 79 (1922) $=0$. bolivianense.
O. superbiens Reichb. f. in Linnaea, 22: 843 (1849).
O. trilingue Lindl. \& Paxt. Flow. Gard. 1: 42 (1850).
O. varicosum Lindl. in Bot. Reg. 25: sub. t. 1920 (1837).
O. Weddellii Lindl. Fol. Orch. Oncid. 39 (1855).
O. Williamsii Schltr. in Fedde, Repert. Spec. N~v. 10: 459 (1912).
O. Wittii Oppenheim in Orchis, 10: 94 (1916).

Ornithidium bolivianum Schltr. in Fedde, Repert. Spec. Nov. 27: 78 (1929) $=$ Maxillaria aurea var. gigantea.
O. flaccidum Kränzl. in Fedde, Repert. Spec. Nov. 25:31 (1928) = Maxillaria sp.?
O. rhomboglossum Schltr. in Fedde, Repert. Spec. Nov. 27: 78 (1929) $=$ Maxillaria sp. ?

Ornithocephalus gladiatus Hook. Exot. Fl. 2: 127 (1825).
O. myrticola Lindl. in Ann. Mag. Nat. Hist. 4: 383 (1840).

Pachyphyllum Cardenasii Smith \& Harris in Contrib. Gray Herb. 114: 12 (1936).
P. confusum Kränzl. in Engler, Pflanzenr. IV, 50: 22 (1923) $=$ P. cyrtophyllum.
P. cyrtophyllum Schltr. in Fedde, Repert. Spec. Nov. 15: 217 (1918).
P. falcifolium Schltr. in Fedde, Repert. Spec. Nov. 10: 460 (1912) = P. cyrtophyllum.
P. Herzogii Schltr. in Meded. Rijks Herbar. 29: 80 (1916).
P. minus Schltr. in Fedde, Repert. Spec. Nov. 10: 460 (1912).
P. pectinatum Reichb. f. Xen. Orch. 3: 22 (1878).
P. pseudo-dichaea Reichb. f. Xen. Orch. 3: 22 (1878).

Pelexia bonariensis (Lindl.) Schltr. in Beih. Bot. Centralbl. 37(2): 400 (1920).
P. Fiebrigii Schltr. in Beih. Bot. Centralbl. 37(2): 402 (1920).

Phragmipedium caricinum (Lindl.) Rolfe in Orch. Rev. 4: 331 (1896).
Physosiphon andinum Schltr. in Fedde, Repert. Spec. Nov. 10: 451 (1912).
P. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 485 (1913).

Physurus anchoriferus Schltr. in Fedde, Repert. Spec. Nov. 12: 482 (1913) = Erythrodes sp.?
P. boliviensis Cogn. in O. Ktze. Rev. Gen. 3(2): 300 (1898) = Erythrodes sp. ?
P. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 27: 34 (1929) $=$ Erythrodes sp.?
P. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 482 (1913) $=$ Erythrodes sp.?
? Pleurothallis affinis Lindl. in Hook. Compan. Bot. Mag. 2: $£ 54$ (1837).
P. agathophylla Reichb. f. Xen. Orch. 3: 25 (1878).
P. amblyopetala Schltr. in Fedde, Repert. Spec. Nov. 12: 486 (1913).
P. boliviana Reichb. f. in Bonplandia, 3: 224 (1855).
P. Brittonii Rolfe in Bull. N. Y. Bot. Gard. 4: 449 (1907).
P. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 66 (1922).
P. bulbophylloides Schltr. in Fedde, Repert. Spec. Nov. 27: 50 (1929).
P. chamensis Lindl. Orch. Lindl. Orch. Linden. 2 (1846).
P. coffeicola Schltr. in Fedde, Repert. Spec. Nov. 27: 50 (1929).
P. complicata Rolfe in Mem. Torr. Bot. Club, 6: $121(1896)=$ P. semipellucida.
P. densifolia Rolfe in Mem. Torr. Bot. Club, 4 (3): 260 (1895).
P. diffusa Poepp. \& Endl. Nov. Gen. 1: 49, t. 86 (1835).
P. dolichocaulon Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 43 (1922).
P. fraterna Lindl. Fol. Orch. Pleur. 3 (1859).
P. frutex Schltr. in Fedde, Repert. Spec. Nov. 10: 454 (1912).
P. Guentheri Schltr. in Fedde, Repert. Spec. Nov. 27: 51 (1929).
P. herpethophyton Schltr. in Fedde, Repert. Spec. Nov. 27: 52 (1929).
P. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 487 (1913).
P. lamellaris Lindl. Fol. Orch. Pleur. 8 (1859).
P. linguifera Lindl. Fol. Orch. Pleur. 10 (1859).
P. Mandonii Reichb. f. Xen. Orch. 3: 24 (1878).
P. obovata (Lindl.) Lindl. in Bot. Reg. 28: Misc. 75 (1842).
P. Ottonis Schltr. in Fedde, Repert. Spec. Nov. 27: 52 (1929).
P. papuligera Schltr. in Fedde, Repert. Spec. Nov. 10: 453 (1912).
P. papuligera var. macra Schltr. in Fedde, Repert. Spec. Nov. 10: 454 (1912).
P. plumosa Lindl. in Bot. Reg. 28: Misc. 72 (1842).
P. rhopalocarpa Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 43 (1922).
? P. riograndensis Rodr. Orch. Nov. 2: 28 (1882).
P. ruscifolia (Jacq.) R. Br. in Ait. Hort. Kew. (ed. 2) 5: 211 (1813).
P. saltatoria Lindl. Fol. Orch. Pleur. 30 (1859).
P. sanjanae Schltr. in Fedde, Repert. Spec. Nov. 12: 487 (1913).
P. scabrata Lindl. Fol. Orch. Pleur. 30 (1859).
P. scabridula Rolfe in Mem. Torr. Bot. Club, 4 (3) : 260 (1895).
P. scleropus Schltr. in Fedde, Repert. Spec. Nov. 27: 53 (1929).
P. semipellucida Reichb. f. in Linnaea, 22: 823 (1855).
P. serrisepala Kränzl. in Fedde, Repert. Spec. Nov. 6: 18 (1908).
P. simacoana Schltr. in Fedde, Repert. Spec. Nov. 27: 54 (1929).
P. soratana Reichb. f. Xen. Orch. 3: 25 (1878).
P. spathata Schltr. in Fedde, Repert. Spec. Nov. 27: 54 (1929).
P. stenopetala Lindl. in Bot. Reg. 24: Misc. 95 (1838).
P. tenuiflora Schltr. in Fedde, Repert. Spec. Nov. 12: 488 (1913).
P. trialata Rolfe in Bull. N. Y. Bot. Gard. 4: 449 (1907) = P. triptera.
P. tricarinata Poepp. \& Endl. Nov. Gen. 1: 49, t. 87 (1835).
P. triptera Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 68 (1922).
P. tripterocarpa Schltr. in Fedde, Repert. Spec. Nov. 27: 55 (1929).
P. triquetra Schltr. in Fedde, Repert. Spec. Nov. 12: 488 (1913).
P. umbraticola Schltr. in Fedde, Repert. Spec. Nov. 27: 56 (1929) $=$ P. vaginata.
P. vaginata Schltr. in Fedde, Repert. Spec. Nov. Beih. 19: 197 (1923).
P. Weddelliana Reichb. f. Xen. Orch. 3: 24 (1878).
P. yungasensis Rolfe in Mem. Torr. Bot. Club, 4 (3): 259 (1895).

Polystachya boliviensis Schltr. in Fedde, Repert. Spec. Nov. 12: 483 (1913).
P. simacoana Schltr. in Fedde, Repert. Spec. Nov. 27: 63 (1929) 二P. boliviensis, at least in part.
Ponera mapiriensis Kränzl. in Fedde, Repert. Spec. Nov. 25: 22 (1928) $=$ Scaphyglottis cuneata.
Ponthieva cornuta Reichb. f. in Linnaea, 41: 18 (1877).
P. elegans (Kränzl.) Schltr. in Fedde, Repert. Spec. Nov. 10: 447 (1912).
P. Mandonii Reichb. f. Xen. Orch. 3: 18 (1878).
P. Mandonii var. bilobipetala Hoehne in Fl. Brasil. 12 (2) : 150 (1945).
P. montana Lindl. in Benth. Pl. Hartw. 155 (1845).
P. unguiculata Ames \& Schweinf. in Ames, Sched. Orch. 8: 9 (1925).

Pterichis Bangii Rolfe in Bull. N. Y. Bot. Gard. 4: 448 (1907).
P. boliviana Schltr. in Fedde, Repert. Spec. Nov. 9: 436 (1911).
P. galeata Lindl. Gen. \& Spec. Orch. 445 (1840).
P. Mandonii (Reichb. f.) Rolfe in Bull. N. Y. Bot. Gard. 4: 449 (1907).
P. saxicola Schltr. in Fedde, Repert. Spec. Nov. 12: 482 (1913).
P. silvestris Schltr. in Fedde, Repert. Spec. Nov. 10: 446 (1912).
P. yungasensis Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 37 (1922).

Rodriguezia corydaloides Kränzl in Fedde, Repert. Spec. Nov. 25: 24 (1928).
Rusbyella caespitosa Rolfe in Mem. Torr. Bot. Club, 6: 122 (1896).
Sarcoglottis Herzogii Schltr. in Fedde, Repert. Spec. Nov. 21: 332 (1925) = Spiranthes sp.?
S. picta (Anders.) Kl. in Allg. Gartenzeit. 10: 106 (1842) = Spiranthes sp. ?

Scaphyglottis boliviana Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 44: (1922).
S. cuneata Schltr. in Bot. Centralbl. Beih. 36(2): 398 (1918).
S. Summersii L. O. Wms. in Bot. Mus. Leaf. Harvard Univ. 9: 14, t. 4 (1940).

Sievekingia Trollii Mansf. in Fedde, Repert. Spec. Nov. 36: 61 (1934).
Sigmatostalix Buchtienii Kränzl. in Fedde, Repert. Spec. Nov. 25: 24 (1928).
S. graminea (Poepp. \& Endl.) Reichb. f. in Bot. Zeit. 10: 769 (1852).

Sobralia boliviensis Schltr. in Fedde, Repert. Spec. Nov. 12: 491 (1913).
S. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 27: 30 (1929).
S. caloglossa Schltr. in Fedde, Repert. Spec. Nov. 27: 31 (1929).
S. chrysoleuca Reichb. f. Xen. Orch. 2: 179 (1874).
S. dichotoma R. \& P. Syst. 232 (1798).
S. D'Orbignyana Reichb. f. Xen. Orch. 2: 179 (1874).
S. fruticetorum Schltr. in Fedde, Repert. Spec. Nov. 12: 492 (1913).
S. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 492 (1913).
S. Mandonii Reichb. f. Xen. Orch. 2: 175, t. 174 (1874) = S. dichotoma.
S. parviflora L. O. Wms. in Lilloa, 3: 475 (1938).
S. rupicola Kränzl. in Fedde, Repert. Spec. Nov. 6: 21 (1908).
S. sancti-josephi Kränzl. in Fedde, Repert. Spec. Nov. 25: 22 (1928).
S. scopulorum Reichb. f. Xen. Orch. 2: 176 (1874).
S. semperflorens Kränzl. in Viertelj. Naturf. Ges. Zürich, 60: 428 (1915).
S. setigera Poepp. \& Endl. Nov. Gen. 1: 54 (1835).
? S. violacea Lindl. Orch. Linden. 26 (1846).
Spiranthes acaulis (J. E. Sm.) Cogn. in Mart. Fl. Bras. 3(4): 221 (1895).
S. Castillonii (Haumann) L. (). Wms. in Lilloa, 3: 478 (1938).
S. chlorops Reichb. f. Xen. Orch. 3: 20 (1878).
? S. costaricensis Reichb. f. in Bonplandia, 3: 214 (1855).
S. elata (Sw.) L. C. Rich. in Mém. Mus. Paris, 4: 59 (1818).
S. goodyeroides Schltr. in Fedcic, Repert. Spec. Nov. 10: 448 (1912).
S. maculata (Rolfe) C. Schweinf. in Pot. Mus. Leafl. Harvard Univ. 10: 30 (1941).
S. Mandonii Reichb. f. Xen. Orch. 3: 21 (1878).
S. orchioides (Sw.) A. Rich. Fl. Cub. Fanerog. 2: 252 (1853).
S. plantaginea Lindl. Gen. \& Spec. Orch. 468 (1840).
S. yungasensis Rolfe in Mem. Torr. Bot. Club, 4 (3) : 266 (1895).
? Stanhopea eburnea Lindl. in Bot. Reg. 18: t. 1529 (1832).
Stelis atrobrunnea Schltr. in Fedde, Repert. Spec. Nov. 27: 40 (1929).
S. Bangii Rolfe in Mem. Torr. Bot. Club, 4 (3): 260 (1895).
S. boliviensis Rolfe in Bull. N. Y. Bot. Gard. 4: 450 (1907).
S. Brittoniana Rolfe in Mem. Torr. Bot. Club, 4 (3): 261 (1895).
S. Buchtienii Schltr. in Fedde, Repert. Spec. Nov. 10: 451 (1912).
S. campanulifera Lindl. Fol. Orch. Stel. 3 (1858),
S. casanaënsis Schltr. in Fedde, Repert. Spec. Nov. 27: 40 (1929).
S. connata Presl, Rel. Haenk. 1: 103 (1827).
S. discolor Reichb. f. in Bonplandia, 3: 240 (1855).
S. euspatha Reichb. f. in Bonplandia, 3: 225 (1855).
S. filiformis Lindl. Fol. Orch. Stel. 6 (1859).
S. flexa Schltr. in Fedde, Renert. Spec. Nov. 27: 41 (1929).
S. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 12: 484 (1913).
S. heterosepala Schltr. in Fedde, Repert. Spec. Nov. 27: 42 (1929).
S. iminapensis Reichb. f. Xen. Orch. 3: 25 (1878).
S. laxa Schltr. in Fedde, Repert. Spec. Nov. 10: 451 (1912).
S. macrantha Rolfe in Bull. N. Y. Bot. Gard. 4: 450 (1907).
S. Mandoniana Schltr. in Fedde, Repert. Spec. Nov. 27: 42 (1929).
S. microtatantha Schltr. in Fedde, Repert. Spec. Nov. 27: 43 (1929).
S. naviculigera Schltr. in Fedde, Repert. Spee. Nov. 27: 44 (1929).
S. Ottonis Schltr. in Fedde. Repert. Spec. Nov. 27: 45 (1929).
S. phaeomelana Schltr. in Fedde, Repert. Spee. Nov. 27: 45 (1929).
S. polycarpa Schltr. in Fedde, Repert. Spec. Nov. 27: 46 (1929).
S. Rusbyi Rolfe in Mem. Torr. Bot. Cluh, 4(3): 261 (1895).
S. saxicola Schltr. in Fedde. Repert. Spec. Nov. 10: 452 (1912).
S. scandens Rolfe in Bull. N. Y. Bot. Gard. 4: 451 (1907).
S. setacea Lindl. Fol. Orch. Stel. 3 (1859).
S. simacoënsis Schltr. in Fedde, Repert. Spee. Nov. 27: 47 (1929).
S. tenuicaulis Lindl. Fol. Orch. Stel. 16 (1859).
S. trianguliflora Schltr. in Fedde, Repert. Suee. Nov. 27: 48 (1929).
? S. tricardium Lindl. Fol. Orch. Stel. 14 (1859).
S. triseta Lindl. Fol. Orch. Stel. 17 (1859).
S. vagans Schltr. in Fedle, Repert. Sinee. Nov. 27: 48 (1929).
S. virens Schltr. in Fedde, Repert. Spec. Nov. 12: 484 (1913).
S. xanthantha Schltr. in Fedde, Repert. Spec. Nov. 10: 452 (1912).
S. yungasensis Schltr. in Fedde, Repert. Spec. Nov. 27: 49 (1929).

Stenoptera acuta Lindl. Gen. \& Spec. Orch. 447 (1840).
S. Guentheriana Kränzl. in Fedde, Repert. Spec. Nov. 25: 19 (1928).
S. plantaginea Schltr. in Fedde, Repert. Spec. Nov. 10: 446 (1912).

Stenorrhynchus apetalus Kränzl. in Fedde, Repert. Spec. Nov. 6: 23 (1908).
S. aphyllus Lindl. Gen. \& Spec. Orch. 478 (1840).
S. australis Lindl. Gen. \& Spec. Orch. 477 (1840).
S. comosus Cogn. in O. Ktze. Rev. Gen. 3(2): 299 (1898).
S. macranthus (Reichb. f.) Cogn. in Mart. Fl. Bras. 3(4): 176, t. 40 (1895).
S. sancti-josephi Kränzl. in Fedde, Repert. Spec. Nov. 6: 22 (1908).

Telipogon Benedicti Reichb. f. in Linnaea, 41: 3 (1877).
Trichoceros parviflorus HBK. Nov. Gen. \& Spec. 1: 337, t. 76 (1816).
Trichopilia fragrans (Lindl.) Reichb. f. in Hamb. Gartenzeit. 14: 229 (1858).
Trizeuxis andina Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 52 (1922) = T. falcata.
T. falcata Lindl. Coll. Bot. t. 2 (1821).

Vanilla odorata Presl, Rel. Haenk. 1: 101 (1827).
V. palmarum Lindl. Gen. \& Spec. Orch. 436 (1840).
V. pompona Schiede in Linnaea, 4: 573 (1829).

Xylobium Buchtienianum Kränzl. in Orchis, 2: 129 (1908).
X. flavescens Schltr. in Fedde, Repert. Spec. Nov. 12: 493 (1913).
X. latifolium Schltr. in Fedde, Repert. Spec. Nov. 27: 66 (1929) $=$ X. pallidiflorum.
X. miliaceum (Reichb. f.) Rolfe in Orch. Rev. 20: 43 (1912).
X. pallidiflorum (Hook.) Nicholson, Dict. Gard. 4: 225 (1887).
X. scabrilingue (Lindl.) Rolfe ex Gentil, Pl. Cult. Jard. Bot. Bruxelles, 194 (1905) $=$ X. squalens.
X. squalens (Lindl.) Lindl. in Bot. Reg. 11: sub t. 897 (1825).
X. varicosum (Lindl.) Rolfe in Mem. Torr. Bot. Club, 4 (3): 263 (1895).

Zygopetalum bolivianum Schltr. in Fedde, Repert. Spec. Nov. Beih. 10: 50 $(1922)=$ Z. intermedium var. peruvianum.
Z. intermedium var. peruvianum Rolfe in Lindenia, 9: 71, t. 418 (1893).

## DICOTYLEDONEAE

## PIPERACEAE

Peperomia aceramarcana Trel. in Bull. Torr. Bot. Club, 55: 169 (1928).
P. aceramarcana var. variifolia Yuncker in Lilloa, 27: 199, t. 76 (1955).
P. aceroana C. DC. in Bull. Torr. Bot. Club, 25: 572 (1898).
P. adenocarpa C. DC. in Bull. Torr. Bot. Club, 25: 569 (1898).
P. alata R. \& P. Fl. Peruv. 1: 31, t. 48 (1798).
P. alata var. angustifolia C. DC. Prodr. 16(1): 418 (1869).
P. angustata HBK. Nov. Gen. \& Spec. 1: 68 (1815).
P. apodostachya Yuncker in Lilloa, 27: 251, t. 128 (1955).
P. argyreia (Miq.) E. Morr. in Belg. Hort. 17: 2, t. 2 (1867).
P. Balansana C. DC. in Mém. Soc. Phys. Hist. Nat. Genève, 27(2): 313, t. 10 (1882).
P. Bangii C DC. in Bull. Torr. Bot. Club. 19: 49 (1892).
P. barbaranoides Yuncker in Lilloa, 27: 173, t. 53 (1955).
P. blanda HBK. Nov. Gen. \& Spec. 1: 67 (1815).
P. blanda var. Langsdorfii (Miq.) Henschen in Nov. Act. Soc. Sci. U'psal. (ser. 3) 8: 39 (1873).
P. blanda var. pseudo-dindygulensis (C. DC.) Yuncker in Lilloa, 27: 218 (1955).
P. boliviensis C. DC. in DC. Prodr. $16(1): 453$ (1898) $=$ P. reflexa ?
P. bopiana Trel. in Mem. N. Y. Bot. Gard. 7: 227 (1927).
P. brevispica C. DC. in Bull. Torr. Bot. Club, 25: 570 (1898).
P. Brittonii C. DC. in Bull. Torr. Bot. Club, 19: 254 (1892).
P. Buchtienii Yuncker in Lilloa, 27: 241, t. 118 (1955).
P. canaminana Trel. in Mem. N. Y. Bot. Gard. 7: 228 (1927).
P. Cardenasii Trel. in Mem. N. Y. Bot. Gard. 7: 227 (1927).
P. carnifolia Yuncker in Lilloa, 27: 193, t. 70 (1955).
P. chromatogena Yuncker in Lilloa, 27: 278, t. 159 (1955).
P. chromatogena var. subpeltata Yuncker in Lilloa, 27: 279 (1955).
P. circinnata Link in Bot. Jahrb. 1: 64 (1820).
P. comarapana C. DC. in Meded. Rijks Herbar. 27: 8 (1915).
P. coroicensis Yuncker in Lilloa, 27: 237, t. 114 (1955).
P. cyclaminoides A. W. Hill in Ann. Bot. 21: 149, t. 15, fig. 16-17 (1907).
P. cyclophylla Miq. ex Seeman, Bot. Voy. Herald, 198 (1854).
P. divaricata Yuncker in Lilloa, 27. 203, t. 81 (1955).
P. duidana Trel. in Bull. Torr. Bot. Club, 58: 354 (1931).
P. dumeticola C. DC. in Bull. Torr. Bot. Club, 25: 569 (1898) = P. trinervis ?
P. effusa Yuncker in Lilloa, 27: 240, t. 117 (1955).
P. efimbriata Trel. in Mem. N. Y. Bot. Gard. 7: 226 (1927).
P. elegans C. DC. in DC. Prodr. 16 (1) : 430 (1869).
P. elongata HBK. Nov. Gen. \& Spec. 1: 62 (1815).
P. elongata var. piliramea Trel. \& Yuncker, Piperac. North. S. Amer. 659 (1950).
P. emarginella (Sw.) C. DC. in DC. Prodr. 16 (1): 437 (1869).
P. emarginella forma glabrior C. DC. in Fedde, Repert. Spec. Nov. 9: 235 (1911) $=$ P. emarginella.
P. Fiebrigii C. DC. in Fedde, Repert. Spec. Nov. 14: 397 (1916).
P. Fiebrigii forma glabrata Yuncker in Lilloa, 27: 185 (1955).
P. galiifolia Trel. in Mem. N. Y. Bot. Gard. 7: 227 (1927) $=$ P. galioides.
P. galioides HBK. Nov. Gen. \& Spec. 1: 71, t. 17 (1815).
P. galioides var. longifolia C. DC. in DC. Prodr. $16(1): 464$ (1869) $=$ P. galioides.
P. glabella (Sw.) A. Dietr. Sp. Pl. 1: 156 (1831).
P. glabella var. nervulosa (C. DC.) Yuncker in Ann. Missouri Bot. Gard. 37: 98 (1950).
P. Herzogii C. DC. in Meded. Rijks Herbar. 27: 9 (1915).
P. heterophylla Miq. in Hook. Lond. Journ. Bot. 4: 415 (1845).
P. heterophylla var. grandis Yuncker in Lilloa, 27: 244, t. 121 (1955).
P. hispidula (Sw.) A. Dietr. Sp. Pl. 1: 165 (1831).
P. hispidula var. muscophila (C. DC.) C. DC. in Candollea, 1: 335, 392 (1923).
P. hispiduliformis Trel. in Lilloa, 6: 295 (1941).
P. imbracteata Yuncker in Lilloa, 27: 175, t. 55 (1955).
P. Klotzschiana Miq. Syst. Pip. 145 (1843).
P. Kuntzei C. DC. in O. Ktze. Rev. Gen. 3 (2): 272 (1898).
P. lancifolia Hook. Ic. Pl. 4: t. 332 (1841).
P. larecajana C. DC. in DC. Prodr. 16(1): 406 (1869).
P. larecajana var. angustifolia Yuncker in Lilloa, 27: 170 (1955).
P. Lorentzii var. boliviensis Yuncker in Lilloa, 27: 198, t. 75 (1955).
P. macrostachya (Vahl) A. Dietr. Sp. Pl. 1: 149 (1831).
P. Mandonii C. DC. in DC. Prodr. 16 (1) : 395 (1869).
P. Mandonii var. excelsis C. DC. in Bull. Torr. Bot. Club, 21: 161 (1894) = P. Mandonii.
P. marcapatana Trel. in Macbr. in Field. Mus. Publ. Bot. 13 (2): 61 (1936).
P. multifolia Yuncker in Lilloa, 27: 227, t. 103 (1955).
P. multispica C. DC. in Bull. Torr. Bot. Club, 25: 571 (1898).
P. nequejahuirana Trel. in Bull. Torr. Bot. Club, 55: 169 (1928).
P. nudicaulis C. DC. in Bull. Torr. Bot. Club, 19: 48 (1892).
P. obtusifolia (L.) A. Dietr. Sp. Pl. 1: 154 (1831).
P. okarana Trel. in Bull. Torr. Bot. Club, 55: 170 (1928) $=\mathrm{P}$. galioides.
P. olens C. DC. in Fedde, Repert. Spec. Nov. 13: 307 (1914).
P. Ottoniana forma boliviensis C. DC. in Fedde, Repert. Spec. Nov. 13: 308 (1914) $=$ P. Buchtienii.
P. parvifolia C. DC. in Journ. Bot. 4: 133 (1866).
P. peltifolia C. DC. in Bull. Torr. Bot. Club, 25: 570 (1898).
P. pentadactyla Yuncker in Lilloa, 27: 283, t. 164 (1955).
P. perlongipes C. DC. in Fedde, Repert. Spec. Nov. 13: 308 (1914).
P. perlongispica Yuncker in Lilloa, 27: 277, t. 157 (1955).
P. peruviana (Miq.) Dahlst. in Kgl. Sv. Vet. Akad. Handl. 33 (2): 32 (1900).
P. peruviana var. major A. W. Hill in Ann. Bot. 21: 151 (1907).
P. pitiguayana Trel. in Bull. Torr. Bot. Club, $55: 169$ (1928).
P. procumbens C. DC. in DC Prodr. 16(1): 435 (1869).
P. pseudo-cobana Yuncker in Lilloa, 27: 256, t. 133 (1955).
P. pseudofurcata C. DC. in DC. Prodr. 16 (1): 399 (1869).
P. pseudo-rufescens C. DC. in I3ull. Torr. Bot. Club, 21: 160 (1894).
P. pseudosilvarum Yuncker in Lilloa, 27: 200, t. 77 (1955).
P. pseudo-umbilicata Yuncker in Lilloa, 27: 275, t. 155 (1955).
P. psilophylla C. DC. in Bull. Torr. Bot. Club, 21: 160 (1894).
P. psilostachya C. DC. in Mém. Soc. Phys. Hist. Nat. Genève, 32 (pt. 1, no. 2): 9, t. 54, fig. 6-9 (1893).
P. punctulatissima Trel. in Mem. N. Y. Bot. Gard. 7: 228 (1927).
P. quaesita Trel. in Macbr. in Field Mus. Publ. Bot. 13 (2) : 83 (1936).
P. reflexa (L. f.) A. Dietr. Sp. Pl. 1: 180 (1831).
P. reflexa forma robustior C. DC. in Fedde, Repert. Spec. Nov. 13: 304 (1914).
P. reflexa forma variipila Yuncker in Lilloa, 27: 192 (1955).
P. retropuberula Yuncker in Lilloa, 27: 184, t. 64 (1955).
P. rhombea R. \& P. Fl. Peruv. 1: 31, t. 46, fig. b. (1798).
P. rhombifolia Trel. in Mem. N. Y. Bot. Gard. 7: 226 (1927).
P. rotundifolia HBK. Nov. Gen. \& Spec. 1: 67, t. 12 (1815).
P. rotundifolia var. pilosior (Miq.) C. DC. in Urb. Symb. Ant. 3: 230 (1902).
P. rurrenabaqueana Trel. in Mem. N. Y. Bot. Gard. 7: 226 (1927).
P. Rusbyi C. DC. in Bull. Torr. Bot. Club, 19: 49 (1892).
P. saxicola C. DC. in Bull. Torr. Bot. Cluh, 25: 571 (1898).
P. scutifolia C. DC. in Notizbl. 7: 497 (1917).
P. scutilimba Yuncker in Lilloa, 27: 275, t. 154 (1955).
P. semimetralis C. DC. in Fedde, Repert. Spec. Nov. 13: 305 (1914) $=$ P. angustata.
P. serpens (Sw.) Loud. Hort. Brit. 13 (1830).
P. silvarum C. DC. in Fedde, Repert. Spec. Nov. 13: 305 (1914).
P. sirupayana C. DC. in Candollea, 1: 361 (1923).
P. soratana C. DC. Bull. Torr. Bot. Club, 25: 569 (1898).
P. Steinbachii Yuncker in Lilloa, 27: 234, t. 113 (1955).
P. Stuebelii C. DC. in Bull. Torr. Bot. Club, 19: 255 (1892).
P. Stuebelii var. glabrata Yuncker in Lilloa, 27: 181 (1955).
P. suspensa C. DC. in Fedde, Repert. Spec. Nov. 13: 304 (1914).
P. Swartziana Miq. Syst. Pip. 155 (1843).
P. talinifolia HBK. Nov. Gen. \& Spec. 1: 62, t. 8 (1815).
P. talinifolia var. longipetiolata C. DC. in Bull. Torr. Bot. Club, 27: 132 (1900) $=$ P. talinifolia.
P. Tatei Yuncker in Lilloa, 27: 220, t. 95 (1955).
P. tenuipeduncula C. DC. in Fedde, Repert. Spec. Nov. 13: 306 (1914).
P. ternata C. DC. in Bull. Herb. Boiss. 6: 509 (1898).
P. tetragona R. \& P. Fl. Peruv. 1: 31, t. 47 (1798).
P. Theodori Trel. in Lilloa, 5: 356 (1940).
P. Theodori var. glabricaulis Yuncker in Lilloa, 27: 189 (1955).
P. ticunhuayana Trel. in Bull. Torr. Bot. Club, 55: 170 (1928).
P. tominana C. DC. in Bull. Torr. Bot. Club, 25. 572 (1898).
P. tominana forma pubifolia Yuncker in Lilloa, 27: 186 (1955).
P. trinervis R. \& P. Fl. Peruv. 1: 32, t. 48, fig. b (1798).
P. unduavina C. DC. in Fedde, Repert. Spec. Nov. 13: 306 (1914).
P. vestita C. DC. in Bull. Torr. Bot. Club, 25: 568 (1898).
P. Williamsii C. DC. in Ann. Conserv. \& Jard. Bot. Genève, 21: 248 (1920).
P. yanacachiana Yuncker in Lilloa, 27: 228, t. 104 (1955).
P. yungasana C. DC. in Fedde, Repert. Spec. Nov. 13: 306 (1914).

Piper acutifolium R. \& P. Fl. Peruv. 1: 38, t. 64, fig. a (1798).
P. aduncum L. Sp. Pl. 1: 29 (1753).
P. aduncum var. cordulatum (C. DC.) Yuncker in Lilloa, 27: 129 (1955).
P. aduncum var. Garcia-Barrigae Trel. \& Yuncker, Pip. North. S. Amer. 251 (1950).
P. arboreum Aubl. Pl. Guian. Fr. 1: 23 (1775).
P. Bangii C. DC. in Bull. Torr. Bot. Club, 19: 254 (1892).
P. Bangii var. pubinervium Yuncker in Lilloa, 27: 105 (1955).
P. Bartlingianum (Miq.) C. DC. in DC. Prodr. 16 (1) : 257 (1869).
$P$. benianum Trel. in Mem. N. Y. Bot. Gard. 7: 222 (1927) = P. callosum.
P. bolivianum C. DC. in DC. Prodr. 16 (1) : 280 (1869).
P. bopianum Trel. in Mem. N. Y. Bot. Gard. 7: 223 (1927) = P. longestylosum.
P. Buchtienii C. DC. in Fedde, Repert. Spec. Nov. 9: 230 (1911).
P. Buchtienii var. charopampanum (C. DC.) Yuncker in Lilloa, 27: 161 (1955).
P. callosum R. \& P. Fl. Peruv. 1: 34, t. 53, fig. a (1798).
P. Cardenasii Trel. in Mem. N. Y. Bot. Gard. 7: 223 (1927) $=$ P. aduncum var. cordulatum.
P. cataractarum Trel. in Mem. N. Y. Bot. Gard. 7: 224 (1927) = P. hispidum.
P. cingens C. DC. in Fedde, Repert. Spec. Nov. 13: 311 (1914).
P. coriaceilimbum C. DC. in Fedde, Repert. Spec. Nov. 9: 234 (1911).
P. cuspidibracteatum Yuncker in Lilloa, 27: 107, t. 4, fig. 4 (1955).
P. duidaënse var. bolivianum Yuncker in Lilloa, 27: 162, t. 42 (1955).
P. elliptico-oblongifolium Trel. in Mem. N. Y. Bot. Gard. 7: 224 (1927) = P. Buchtienii var. charopampanum.
P. elongatum Vahl, Enum. 1: 312 (1805).
P. guanaianum C. DC. in Fedde, Repert. Spec. Nov. 9: 232 (1911) $=$ P. aduncum var. cordulatum.
P. Herzogii C. DC. in Meded. Rijks Herbar. 27: 7 (1915) = P. aduncum var. Garcia-Barrigae.
P. Hieronymi C. DC. in O. Ktze. Rev. Gen. 3(2) : 273 (1898).
P. hispidum Sw. Prodr. 15 (1788).
P. hispidum var. magnifolium (C. DC.) C. DC. in Urb. Symb. Ant. 3: 188 (1902).
P. hispidum var. trachydermum (Trel.) Yuncker in Ann. Missouri Bot. Gard. 37:33 (1950).
P. Kuntzei C. DC. in O. Ktze. Rev. Gen. 3(2): 274 (1898) = P. aduncum.
P. laevigatum HBK. Nov. Gen. \& Spec. 1: 56 (1815).
P. laevilimbum C. DC. in Fedde, Repert. Spec. Nov. 9: 232 (1911).
P. lanceolatum R. \& P. Fl. Peruv. 1:36, t. 61, fig. b (1798).
P. longestylosum C. DC. in Bull. Torr. Bot. Club, 21: 161 (1894).
P. longichaetum Yuncker in Lilloa, 27: 127, t. 15 (1955).
P. mapirense C. DC. in Bull. Torr. Bot. Club, 19: 47 (1892).
P. mapirense var. magnifolium C. DC. in Fedde, Repert. Spec. Nov. 9: 230 (1911) $=$ P. mapirense.
P. marequitense C. DC. in DC. Prodr. 16(1): 290 (1869).
P. medium Jacq. Ic. Pl. Rar. 1: 2, t. 8 (1781).
P. medium var. perglabrum Yuncker in Lilloa, 27: 118 (1955).
P. mercens Yuncker in Lilloa, 27: 135, t. 19, fig. 1 (1955).
P. microtrichum C. DC. in Fedde, Repert. Spec. Nov. 13: 310 (1914).
P. nigriconnectivum C. DC. in Meded. Rijks Herbar. 27: 7 (1915).
P. nigro-granulatum Trel. in Mem. N. Y. Bot. Gard. 7: 224 (1927) = P. lanceolatum.
P. obovatum var. bolivianum C. DC. in Ann. Conserv. \& Jard. Bot. Genève, 21: 237 (1920) = P. Buchtienii.
P. oxyphyllum C. DC. in Bull. Torr. Bot. Club, 19: 48 (1892).
P. pachyphloium C. DC. in O. Ktze. Rev. Gen. 3(2): 274 (1898).
P. pachyphloium var. macrophyllum Yuncker in Lilloa, 27: 107, t. 4, fig. 1 (1955).
P. peltilimbum Yuncker in Lilloa, $27: 155$, t. 37 (1955).
P. percostatum Yuncker in Lilloa, 27: 157, t. 39 (1955).
P. perscabrifolium Yuncker in Lilloa, 27: 111, t. 7, fig. 1 (1955).
P. pilirameum C. DC. in Fedde, Repert. Spec. Nov. 9: 229 (1911).
P. pilirameum var. subglabrum Yuncker in Lilloa, 27: 110 (1955).
P. praeacutilimbum C. DC. in Fedde, Repert. Spec. Nov. 9: 231 (1911).
P. pseudogrande Yuncker in Lilloa, $27: 146$, t. 27, fig. 1 (1955).
P. psilophyllum C. DC. in Bull. Torr. Bot. Club, 19: 47 (1892).
P. psilophyllum forma longepedunculatum Yuncker in Lilloa, 27: 148, t. 28 (1955).
P. puberulinerve C. DC. in Fedde, Reeprt. Spec. Nov. 9: 231 (1911).
P. puberulinerve var. subarborescens (C. DC.) Yuncker in Lilloa, 27: 149 (1955).
P. pubiovarium Yuncker in Lilloa, 27: t. 25, fig. 2 (1955).
P. punctulantherum C. DC. in Fedde, Repert. Spec. Nov. 9: 233 (1911).
P. rectispicum Trel. in Mem. N. Y. Bot. Gard. 7: 225 (1927) $=$ P. mapirense.
P. rogaguanum Trel. in Mem. N. Y. Bot. Gard. 7: 225 (1927).
P. rurrenabaqueanum Trel. in Mem. N. Y. Bot. Gard. 7: 225 (1927) = P. Buchtienii.
P. Rusbyi C. DC. in Bull. Torr. Bot. Club, 19: 47 (1892).
P. Rusbyi var. hirsutum Yuncker in Lilloa, 27: 139 (1955).
P. sanctae-crucis C. DC. in O. Ktze. Rev. Gen. 3(2): 274 (1898) = P. mapirense.
P. semimetrale C. DC. in Fedde, Repert. Spec. Nov. 9: 232 (1911).
P. Steinbachii Yuncker in Lilloa, 27: 136, t. 136 (1955).
P. subsilvulanum C. DC. in Notizbl. 6: 453 (1917).
P. svidaefolium Trel in Mem. N. Y. Bot. Gard. 7: 225 (1927) = P. subsilvulanum.
P. trichogynum C. DC. in Fedde, Repert. Spec. Nov. 9: 233 (1911).
P. trichorhachis C. DC. in Bull. Torr. Bot. Club, 25: 566 (1898).
P. trigoniastrifolium C. DC. in Bull. Torr. Bot. Club, 25: 567 (1898).
P. tuberculatum Jacq. Collect. 2: 2, t. 211 (1788).
P. tuberculatum var. minus C. DC. in DC. Prodr. 16(1): 266 (1869).
P. tumupasense Yuncker in Lilloa, 27: 106, t. 2, fig. 2 (1955).
P. umbrigaudens C. DC. in Fedde, Repert. Spec. Nov. 13: 310 (1914) $=$ P. Rusbyi.
P. unduavinum C. DC. in Fedde, Repert. Spec. Nov. 13: 309 (1914) $=$ P. psilophyllum.
Pothomorphe peltata (L.) Miq. Comm. Phyt. 37 (1840).
P. umbellata var. vestita (C. DC.) Yuncker in Lilloa, 27: 166 (1955).

## CHLORANTHACEAE

Hedyosmum brasiliense Miq. in Mart. Fl. Bras. 4(1): 3 (1852).
H. bolivianum Cordem. in Adansonia, 3: 306 (1863) $=$ H. racemosum.
H. Mandonii Solms-Laub. in DC. Prodr. 16(1): 480 (1869).
H. maximum (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1): 345 (1900).
H. racemosum (R. \& P.) G. Don, Gen. Hist. 3: 434 (1834).

## SALICACEAE

Salix Humboldtiana Willd. Sp. Pl. 4(2): 657 (1806).

## MYRICACEAE

Myrica arguta HBK. Nov. Gen. \& Spec. 2: 17, t. 98 (1817).
M. costata Rusby, Descr. S. Am. Pls. 8 (1920).
M. macrocarpa HBK. Nov. Gen. \& Spec. 2: 16 (1817).
M. xalapensis HBK. Nov. Gen. \& Spec. 2: 16 (1817).

## JUGLANDACEAE

Juglans boliviana Dode in Bull. Soc. Dendrol. France, 13: 211 (1909).

## CORYLACEAE

Alnus acuminata HBK. Nov. Gen. \& Spec. 2: 20 (1817).
A. jorullensis var. ferruginea (HBK.) O. Ktze. Rev. Gen. 3(2): 295 (1898).
A. jorullensis var. Mirbelii (Spach) H. Winkl. in Engler, Pflanzenr. IV, 61: 126 (1904).

## ULMACEAE

Ampelocera sp.
Celtis boliviana Planch. in Ann. Sci. Nat. (ser. 3) 10:311 (1848) = C. pubescens.
C. brasiliensis Planch. in Ann. Sci. Nat. (ser. 3) 10: 310 (1848).
C. iguanaea (Jacq.) Sarg. Silv. N. Am. 7: 64 (1895).
C. morifolia Planch. in Ann. Sci. Nat. (ser. 3) 10: 311 (1848).
C. pubescens (HBK.) Spreng. Syst. Veg. 1: 931 (1825).
C. pubescens var. Chichape (Wedd.) Baehni in Candollea, 7: 201 (1936).
C. spinosa Spreng. Syst. Veg. 1: 931 (1825).
C. spinosa var. Weddelliana (Planch.) Baehni in Candollea, 7: 204 (1936).
C. Tala var. Gilliesiana forma velutina Herzog in Meded. Rijks Herbar. 27: 72 (1915) = C. pubescens var. Chichape.
C. triflora (Klotzsch) Miq. in Mart. Fl. Bras. 4(1): 181 (185今).
C. Williamsii Rusby in Bull. N. Y. Bot. Gard. 6: 497 (1910) = C. iguanaea.

Lozanella permollis Killip \& Morton in Journ. Wash. Acad. Sci. 21: 338 (1931).
Momisia crenata Wedd. in Ann. Sci. Nat. (ser. 3) 18: 195 (1852) = Celtis pubescens.
M. flexuosa Wedd. in Ann. Sci. Nat. (ser. 3) 18: 195 (1852) = Celtis pubescens.
M. tarijensis Wedd. in Ann. Sci. Nat. (ser. 3) 18: 194 (1852) $=$ Celtis triflora.
Phyllostylum orthopterum Hall. f. in Meded. Rijks Herbar. 27: 70 (1915).
Trema affinis (Planch.) Blume in Mus. Bot. Lugd. Bat. 2: 58 (1852).
T. micrantha (L.) Blume in Mus. Bot. Lugd. Bat. 2: 58 (1852).

## MORACEAE

Batocarpus amazonicus (Ducke) Fosberg in Proc. Biol. Soc. Wash. 55: 101 (1942).

Brosimum Gaudichaudii Trécul in Ann. Sci. Nat. (ser.3) 8: 140 (1847).
B. guianense (Aubl.) Huber ex Ducke in Bol. Mus. Goëldi, 7: 172 (1913).

Cecropia angustifolia Trécul in Ann. Sci. Nat. (ser. 3) 8: 83 (1847).
C. elongata Rusby in Bull. N. Y. Bot. Gard. 4: 446 (1907).
C. ficifolia Warb. ex Snethlage in Notizbl. 8: 365 (1923).
C. latiloba Miq. in Mart. Fl. Bras. 4(1): 147 (1853).
C. leucocoma Miq. in Mart. Fl. Bras. 4 (1): 142 (1853).
C. obovata Rusby in Bull. N. Y. Bot. Gard. 6: 498 (1910).
C. Tessmannii Mildbr. in Notizbl. 9: 260 (1925).

Chlorophora reticulata Herzog in Meded. Rijks Herbar. 27: 73 (1915).
C. tinctoria (L.) Gaud. in Freyc. Voy. Bot. 508 (1827), combination implied but not actually made.
Clarisia biflora R. \& P. Syst. 256 (1798).
C. ilicifolia (Spreng.) Lanj. \& Rossb. in Meded. Bot. Mus. Utrecht, 36: 717 (1936).

Coussapoa asperifolia Trécul in Ann. Sci. Nat. (ser. 3) 8: 96 (1847).
C. boliviana Standl. in Field Mus. Publ. Bot. 17: 159 (1937).
C. ovalifolia Trécul in Ann. Sci. Nat. (ser. 3) 8: 95 (1847).

Dorstenia brasiliensis Lam. Encyc. 2: 317 (1786).
Duguetia glabra Britton in Bull. Torr. Bot. Club, 16: 14 (1889) = Ogcodeia Sandwithiana.
D. montana Herzog in Meded. Rijks Herbar. 27: 73 (1915).

Ficus bopiana Rusby in Mem. N. Y. Bot. Gard. 7: 230 (1927).
F. caballina Standl. in Field Mus. Publ. Bot. 13: 301 (1937).
F. coerulescens (Rusby) Rossberg in Fedde, Repert. Spec. Nov. 42: 61 (1937).
F. elliptica (Herzog) Herter in Rev. Sudam. Bot. 6: 151 (1940).
F. gemina Ruiz ex Miq. in Mart. Fl. Bras. 4(1): 98 (1853), in synon.
F. Katherinae A. D. Hawkes in Phytologia, 3:32 (1948).
F. Killipii Standl. in Field Mus. Publ. Bot. 13: 304 (1937).
F. Macbridei Standl. in Field Mus. Publ. Bot. 13: 305 (1937).
F. Matthewsii (Miq.) Miq. in Ann. Mus. Bot. Lugd. Bat. 3: 298 (1867).
F. oblanceolata Rusby in Bull. N. Y. Bot. Gard. 4: 446 (1907) =F. Matthewsii.
F. oblanceolata Rusby in Bull. N. Y. Bot. Gard. 6: 498 (1910) = F. Katherinae.
F. paraënsis Miq. in Ann. Mus. Bot. Lugd. Bat. 3: 298 (1867).
F. radula Willd. Sp. Pl. 4(2): 1144 (1806).
F. regularis Standl. in Field Mus. Publ. Bot. 17: 175 (1937).
F. Ruiziana Standl. in Field Mus. Publ. Bot. 13(2): 307 (1937).
F. Whitei Rusby in Mem. N. Y. Bot. Gard. 7: 230 (1927).
F. Williamsii (Rusby) Rossberg in Fedde, Repert. Spec. Nov. 42: 61 (1937).
F. Wuiana Rossberg in Fedde, Repert. Spec. Nov. 42: 61 (1937).

Helicostylis tomentosa (Poepp. \& Endl.) Rusby in Mem. Torr. Bot. Club, 6: 120 (1896).
Morus alba L. Sp. PI. 986 (1753).
Ogcodeia acreana Mildbr. in Notizbl. 11: 421 (1932).
O. pseudo-naga Mildbr. in Notizbl. 11: 419 (1932).
O. Sandwithiana Mildbr. in Notizbl. 11: 422 (1932).
O. ternstroemiiflora Mildbr. in Notizbl. 10: 188 (1927).

Olmedia aspera R. \& P. Syst. 257 (1798).
O. Habas Pax in Fedde, Repert. Spec. Nov. 7: 108 (1909).

Pharmacosycea Brittonii Rusby in Bull. Torr. Bot. Club, 28: 309 (1901).
Poulsenia armata (Miq.) Standl. in Trop. Woods, 33: 4 (1933).

Pourouma crassivenosa Mildbr. in Notizbl. 10: 419 (1928).
P. scabra Rusby in Bull. N. Y. Bot. Gard. 6: 498 (1910).
P. subtriloba Rusby in Mem. N. Y. Bot. Gard. 7: 232 (1927).
P. uvifera Rusby in Mem. N. Y. Bot. Gard. 7: 231 (1927).

Pseudolmedia alnifolia Rusby in Mem. N. Y. Bot. Gard. 7: 229 (1927).
P. hirtellaefolia Rusby in Mem. N. Y. Bot. Gard. 7: 228 (1927).
P. laevigata Trécul in Ann. Sci Nat. (ser. 3) 8: 131 (1847).
P. laevis (R. \& P.) Macbr. in Field Mus. Publ. Bot. 11: 16 (1931).
P. Mildbraedii Macbr. in Field Mus. Fubl. Bot. 11: 61 (1931).

Sorocea ilicifolia Miq. in Mart. Fl. Bras. 4(1): 114 (1853).
S. muriculata Miq. in Mart. Fl. Bras 4(1): 113 (1853).

Trophis aurantiaca Herzog in Fedde, Repert. Spec. Nov. 7: 51 (1909).
Urostigma costata Rusby in Bull. N. Y. Bot. Gard. 6: 499 (1910) $=$ Ficus Wuiana.

## URTICACEAE

Boehmeria brevirostris Wedd. in Ann. Sci. Nat. (ser. 4) 1: 201 (1854).
B. caudata Sw. Prodr. 34 (1788).
B. fallax Wedd. in Arch. Mus. Paris, 9: 346 (1856-57).
B. pallida (Rusby) Killip in Journ. Wash. Acad. Sci. 21: 347 (1931).
B. Pavonii Wedd. in Ann. Sci. Nat. (ser. 4) 1: 202 (1854).
B. sordida Rusby, Descr. S. Am. Pls. 9 (1920).
B. tenuistachys Rusby in Bull. Torr. Bot. Club, 28: 312 (1901).

Goethartia edentata (O. Ktze.) Herzog in Meded. Rijks Herbar. 27: 77 (1915).
Myriocarpa densiflora Benth. Bot. Voy. Sulphur, 169 (1846) = M. stipitata.
M. filiformis Rusby in Bull. N. Y. Bot. Gard. 6: 500 (1910).
M. obscura Rusby, Descr. S. Am. Pls. 11 (1920).
M. purpurascens Rusby in Mem. N. Y. Bot. Gard. 7: 233 (1927).
M. stipitata Benth. Bot. Voy. Sulphur, 168, t. 55 (1846).
M. Tatei Rusby in Phytologia, 1: 52 (1934).

Parietaria debilis Forst. f. Fl. Ins. Austral. Prodr. 73 (1786).
Phenax angustifolius (HBK.) Wedd. in Ann. Sci. Nat. (ser. 4) 1: 193 (1854).
P. bullatus Rusby in Phytologia, 1: 52 (1934).
P. flavifolius Rusby in Phytologia, 1: 53 (1934).
P. globuliferus Rusby in Mem. Torr. Bot. Club. 6: 120 (1896).
P. laevigatus Wedd. in Ann. Sci. Nat. (ser. 4) 1: 192 (1854).
P. laevigatus var. serratus Wedd. in DC. Prodr. 16(1): $235^{40}$ (1869).
P. pallidus Rusby in Mem. Torr. Bot. Club, 4 (3): 259 (1895) $=$ Boehmeria Pavonii.
P. pauciserratus (Wedd.) Rusby in Bull. Torr. Bot. Club, 28: 313 (1901).
P. rugosus (Poir.) Wedd. in DC. Prodr. 16(1): $235^{38}$ (1869).
P. rugosus var. Mandonii Wedd. in DC. Prodr. 16(1): $235^{38}$ (1869).
P. Sonnerattii Wedd. in DC. Prodr. 16(1): $235^{37}$ (1869).

Pilea anomala Wedd. in Ann. Sci. Nat. (ser. 3) 18: 217 (1852) $=$ P. multiflora.
P. Buchtienii Killip in Journ. Wash. Acad. Sci. 15: 297 (1925).
P. capitellata Wedd. in Arch. Mus. Paris. 9: 220 (1856-57).
P. cymbifolia Rusby in Bull. Torr. Bot. Club, 28: 311 (1901).
P. dauciodora (R. \& P.) Wedd. in Ann. Sci. Nat. (ser.3) 18: 233 (1852).
P. filipes Rusby in Bull. Torr. Bot. Club, 28: 311 (1901).
P. hyalina Fenzl in Denkschr. Akad. Wiss. Math. Naturw. Wien, 1: 256 (1850).
P. macrophylla Rusby, Descr. S. Am. Pls. $10(1920)=$ P. picta.
P. multiflora (Poir.) Wedd. in Ann. Sci. Nat. (ser. 3) 18: 217 (1852).
P. nutans (Poepp.) Wedd. in Arch. Mus. Paris, 9: 196, t. 7 (1856-57).
P. pauciserrata Killip in Journ. Wash. Acad. Sci. 15: 293 (1925).
P. picta Herzog in Meded. Rijks Herbar. 27: 76 (1915).
P. rotundata Griseb. Fl. Brit. W. Ind. 158 (1859).
P. Rusbyi (Britton) Killip in Journ. Wash. Acad. Sci. 15: 293 (1925).
P. serpyllacea (HBK.) Wedd. in Ann. Sci. Nat. (ser. 3) 18: 207 (1852).
P. Spruceana Wedd. in DC. Prodr. 16(1): 161 (1869).
P. strigosa Wedd. in Ann. Sci. Nat. (ser. 3) 18: 225 (1852).
P. sublobata Rusby in Bull. Torr. Bot. Club, 28: 311 (1901).
P. uncidens Wedd. in Ann. Sci. Nat. (ser. 3) 18: 224 (1852) = P. dauciodora.
P. urerifolia Rusby in Bull. Torr. Bot. Club, 28: 312 (1901) $=$ P. cymbifolia.

Pouzolzia asper (Wedd.) Wedd. in DC. Prodr. 16(1): 233 (1869) = P. Poeppigiana.
P. discolor Wedd. in Arch. Mus. Paris, 9: 408 (1856-57) $=$ P. Poeppigiana.
P. Poeppigiana (Wedd.) Killip in Journ. Wash. Acad. Sci. 21: 347 (1931).

Urera alceaefolia Gaud. in Freyc. Voy. Bot. 407 (1830).
U. baccifera (L.) Gaud. in Freyc. Voy. Bot. 497 (1830), combination implied but not actually made.
U. boliviensis Herzog in Meded. Rijks Herbar. 27: 75 (1915).
U. capitata Wedd. in Ann. Sci. Nat. (ser. 3) 18: 201 (1852).
U. caracasana (Jacq.) Griseb. Fl. Brit. W. Ind. 154 (1859).
U. filiformis Rusby in Bull. Torr. Bot. Club, 28: 310 (1901).
U. laciniata Wedd. in Ann. Sci. Nat. (ser. 3) 18: 203 (1952).
U. rugosa Rusby in Bull. Torr. Bot. Club, 28: 310 (1901).
U. sinuata Wedd. in Ann. Sci. Nat. (ser. 3) 18: 201 (1852).
U. viridisetosa Rusby in Mem. N. Y. Bot. Gard. 7: 232 (1927).

Urtica ballotaefolia Wedd. in Ann. Sci. Nat. (ser. 3) 18: 197 (1852).
U. echinata Benth. Pl. Hartw. 252 (1846).
U. echinata var. trichantha Wedd. in DC. Prodr. 16(1): 42 (1869).
U. flabellata HBK. Nov. Gen. \& Spec. 2: 40 (1817).
U. magellanica Juss. ex Poir. in Lam. Encyc. Suppl. 4: 223 (1816).
U. purpurascens Nutt. in Trans. Amer. Phil. Soc. 5: 169 (1837).
U. subincisa Benth. Pl. Hartw. 292 (1848).
U. Trianae Rusby in Bull. N. Y. Bot. Gard. 4: 319 (1907).

## PROTEACEAE

Orites Fiebrigii (Perkins) Sleumer in Engler, Bot. Jahrb. 76: 141 (1954).
Panopsis Pearcei Rusby in Bull. N. Y. Bot. Gard. 4: 439 (1907) = P. rubescens var. Sprucei.
P. rubescens var. Sprucei (Meisn. ex Rusby) Sleumer in Engler, Bot. Jahrb. 76: 180 (1954).
Roupala Meisneri Sleumer in Engler, Bot. Jahrb. 76: 162 (1954).
R. montana Aubl. Pl. Guian. Fr. 1: 83, t. 32 (1775).
R. montana var. dentata (R. Br.) Sleumer in Engler, Bot. Jahrb. 76: 173 (1954).
R. Steinbachii Sleumer in Engler, Bot. Jahrb. 76: 157 (1954).

## LORANTHACEAE

Antidaphne viscoidea Poepp. \& Endl. Nov. Gen. 2: 70, t. 199 (1838).
Dendrophthora buxifolia (Lam). Eichl. in Mart. Fl. Bras. 5(2): 105 (1868).
D. clavata (Benth.) Urb. in Ber. Deut. Bot. Ges. 14: 285 (1896).
D. inaequidenatta (Rusby) Trel. Genus Phorad. 218 (1916).
D. mesembryanthemifolia (Griseb.) Urb. in Ber. Deut. Bot. Ges. 14: 285 (1896).
D. Rusbyi (Britton) Trel. Genus Phorad. 218 (1916).
D. striata Rusby, Descr. S. Am. Pls. 14 (1920).
D. subtrinervis Urb. in Ber. Deut. Bot. Ges, 14: 285 (1896).
D. subtrinervis (Rusby) Trel. Genus Phorad. 218 (1916).

Loranthus concinnus Mart. in Schult. Syst. Veg. 7: 150 (1829) $=$ Phrygilanthus sp.?
L. cubeboides Rusby in Bull. Torr. Bot. Club, 27: 135 (1900) = Phrygilanthus sp.?
L. flexilis Rusby in Mem. Torr. Bot. Club, 4 (3): 253 (1895) $=$ Phrygilanthus sp.?
Oryctanthus botryostachys Eichl. in Mart. Fl. Bras. 5(2): 89, t. 29 (1868).
Phoradendron angustifolium (HBK.) Eichl. in Mart. Fl. Bras. 5(2) : 115 (1868).
P. argentinum Urb. in Engler, Bot. Jahrb. 23, Beibl. 57: 14 (1897).
P. Balleanum (Seem.) Eichl. in Mart. Fl. Bras. 5(2): 134m (1868).
P. bathyoryctorum Eichl. in Mart. Fl. Bras. 5(2): 123, t. 43 (1868).
P. bolivianum Trel. Genus Phorad. 138 (1916).
P. Brittonianum Rusby in Mem. Torr. Bot. Club, 4 (3): 254 (1895).
P. clavatum (Benth.) Eichl. in Mart. Fl. Bras. 5(2): 107 (1868),
P. crassifolium (Pohl) Eichl. in Mart. Fl. Bras. 5(2): 125, t. 40 (1868).
P. emarginatum Eichl. in Mart. Fl. Bras. 5(2): 118, t. 38 (1868).
P. Kuntzei Urb. in Engler, Bot. Jahrb. 23, Beibl. 58: 11 (1897).
P. latifolium (Sw.) Griseb. in Mem. Amer. Acad. (ser. 2) 8: 191 (1861).
P. Liga (Gill.) Eichl. in Mart. Fl. Bras. 5(2): 134m (1868).
P. Mandonii Eichl. in Mart. Fl. Bras. 5(2): 124 (1868).
P. meliae Trel. Genus Phorad. 121 (1916).
P. paucifolium Rusby in Bull. N. Y. Bot. Gard. 6: 501 (1910).
P. Pearcei Rusby in Bull. Torr. Bot. Club, 27: 136 (1900).
P. pennivenium (DC.) Eichl. in Mart. Fl. Bras. 5(2): 128 (1868).
P. piperoides (HBK.) Trel. Genus Phorad. 145 (1916).
P. Rusbyanum Trel. in Mem. N. Y. Bot. Gard. 7: 234 (1927).
P. semiteres Trel. Genus Phorad. 69 (1916).
P. tafallaeoides Rusby in Bull. N. Y. Bot. Gard. 4: 441 (1907).
P. tucumanense Urb. in Engler, Bot. Jahrb. 23, Beibl. 57: 16 (1897).
P. undulatum (Pohl) Eichl. in Mart. Fl. Bras. 5(2): 122, t. 39 (1868).

Phrygilanthus bolivianus Engl. in Engl. \& Prantl, Nat. Pflanzenfam. Nachtr. 133 (1897).
P. cordifolius Rusby in Mem. N. Y. Bot. Gard. 7: 233 (1927).
P. cuneifolius (R. \& P.) Eichl. in Mart. Fl. Bras. 5(2): 49, t. 11 (1868).
P. eugenioides (HBK.) Eichl. in Mart. Fl. Bras. 5(2): 50, t. 12 (1868).
P. falcatus Rusby in Mem. N. Y. Bot. Gard. 7: 233 (1927).
P. falcatus var. (?) macrocalyx Rusby in Mem. N. Y. Bot. Gard. 7: 234 (1927).
P. mapirensis (Rusby) Engl. in Engl. \& Prantl, Nat. Pflanzenfam. Nachtr. 134 (1897).
P. punctatus (R. \& P.) Eichl. in Mart. Fl. Bras. 5(2): 47 (1868).
P. tetrandrus (R. \& P.) Eichl. in Mart. Fl. Bras. 5(2): 47 (1868).
P. verticillatus (R. \& P.) Eichl. in Mart. Fl. Bras 5(2): 47 (1868).

Phthirusa heterophylla Rusby in Bull. N. Y. Bot. Gard. 6: 500 (1910).
P. paniculata (HBK.) Macbr. in Field Mus. Publ. Bot. 11: 17 (1931).
P. pyrifolia (HBK.) Eichl. in Mart. Fl. Bras. 5(2): 63 (1868).
P. robusta Rusby in Bull. N. Y. Bot. Gard. 6: 501 (1910).

Psittacanthus cupulifer (HBK.) G. Don, Gen. Hist. 3: 417 (1834).
Struthanthus concinnus Mart. in Flora, 13(1): 104 (1830).
S. divaricatus Rusby, Descr. S. Am. Pls. 12 (1920).
S. nudipes Rusby in Mem. Torr. Bot. Club, 6: 116 (1896).
S. oblongifolius Rusby in Bull. N. Y. Bot. Gard. 4: 440 (1907).

## SANTALACEAE

Acanthosyris falcata Griseb. in Goett. Abh. 24: 151 (1879).
Iodina rhombifolia Hook. \& Arn. in Hook. Bot. Misc. 3: 172 (1833).

Quinchamalium chilense Lam. Illustr. 2: 125, t. 142 (1793).
Q. gracile Brongn. in Duperr. Voy. Coq. Bot. 231, t. 52 (1829).
Q. majus Brongn. in Duperr. Voy. Coq. Bot. 229, t. 51 (1829).
Q. Stuebelii Hieron. in Engler, Bot. Jahrb. 21: 306 (1896).

## OPILIACEAE

Agonandra brasiliensis Miers in Ann. \& Mag. Nat. Hist. (ser. 2) 8: 172 (1851).

## OLACACEAE

Heisteria biflora Rusby in Mem. Torr. Bot. Club, $6: 18(1896)=$ H. brasiliensis.
H. brasiliensis Engl. in Mart. Fl. Bras. 12(2): 19 (1872).
? H. caloneura Sleurner in Notizbl. 12: 66 (1934).
H. ixiamensis Rusby in Mem. N. Y. Bot. Gard. 7: 234 (1927).
H. scandens Ducke in Archiv. Jard. Bot. Rio Janeiro, 4: 9 (1925).
H. yapacaniensis (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1) : 360 (1900).

Schoepfia obliquifolia Turcz. in Bull. Soc. Imp. Nat. Mosc. 31(1): 249 (1858).
S. tetramera Herzog in Meded. Rijks Herbar. 29: 4 (1916).

Ximenia americana L. Sp. Pl. 1197 (1753).

## BALANOPHORACEAE

## ? Helosis sp.

Juelia subterranea Asplund in Sv. Bot. Tidskr. 22: 274 (1928).
Lophophytum bolivianum Wedd. in Ann. Sci. Nat. (ser. 3) 14: 185, t. 10 (1850).
Ombrophytum zamioides Wedd. in Ann. Sci. Nat. (ser. 3) 14: 184, t. 10 (1850).

## ARISTOLOCHIACEAE

Aristolochia angustifolia Cham. in Linnaea, 7: 211, t. 5 (1832).
A. apoloënsis Rusby in Bull. N. Y. Bot. Gard. 6: 502 (1910).
A. asperifolia Ule in Verh. Bot. Ver. Brandenb. 47: 121 (1905).
A. boliviensis O. Ktze. Rev. Gen. 3(2) : 271 (1898).
A. Buchtienii O. C. Schmidt in Fedde, Repert. Spec. Nov. 27: 292 (1930).
A. Burelae Herzog in Meded. Rijks Herbar. 40: 2 (1921).
A. Cardenasii Standl. in Field Mus. Publ. Bot. 17: 237 (1937).
A. ceresensis O. Ktze. Rev. Gen. 3(2): 272 (1898).
A. chiquitensis Duchtr. in Ann. Sci. Nat. (ser. 4) 2: 49 (1854).
A. cymbifera var. abbreviata Duchtr. in DC. Prodr. 15(1): 470 (1864).
A. didyma Sp. Moore in Journ. Bot. 53: 7, t. 535, fig. 1 (1915).
A. eriantha Mart. \& Zucc. Nov. Gen. 1: 78, t. 53 (1824).
A. esperanzae O. Ktze. Rev. Gen. 3(2): 272 (1898).
A. Gibertii Hook. in Bot. Mag. 88: t. 5345 (1862).
A. Guentheri O. C. Schmidt in Fedde, Repert. Spec. Nov. 27: 292 (1930).
A. Hoehneana O. C. Schmidt in Notizbl. 12: 390 (1935).
A. Joergensenii Haum, in Anal. Mus. Nac. Buenos Aires, 32: 323, t. 1 (1923).
A. Lindneri Berger in Notizbl. 10: 129 (1927).
A. lingulata Ule in Verh. Bot. Ver. Brandenb. 47: 123 (1905).
A. lingulata var. parviflora Herzog in Meded. Rijks Herbar. 40: 3 (1921).
A. macroura Gomez in Act. Olyss. 77 (1812).
A. odoratissima L. Sp. Pl. (ed. 2) 2: 1362 (1763).
A. pandurata Jacq. Hort. Schoenbr. 4: 49, t. 497 (1804).
? A. peruviana O. C. Schmidt in Notizbl. 9: 136 (1924).
A. pilosa HBK. Nov. Gen. \& Spec. 2: 146, t. 113 (1817).
A. prostrata Duchtr. in Ann. Sci. Nat. (ser. 4) 2: 63 (1854).
A. pseudo-triangularis O. C. Schmidt in Fedde, Repert. Spec. Nov. 38: 110 (1935).
A. Rimbachii O. C. Schmidt in Fedde, Repert. Spec. Nov. 23: 287 (1927).
A. Rodriguesii Hoehne in Mem. Inst. Oswaldo Cruz, $20(1): 140$ (1927).
A. sessilifolia (Klotzsch) Duchtr. in DC. Prodr. 15(1): 464 (1864).
A. stenocarpa O. Ktze. Rev. Gen. 3(2) : 271 (1898).
A. triangularis Cham. in Linnaea, 7: 209, t. 6 (1832).
A. Trollii O. C. Schmidt in Fedde, Repert. Spec. Nov. 30: 68 (1932).
A. Weddellii Duchtr. in Ann. Sci. Nat. (ser. 4) 2: 62 (1854).
A. Werdermanniana O. C. Schmidt in Fedde, Repert. Spec. Nov. 30: 67 (1932).
A. Williamsii Rusby in Bull. N. Y. Bot. Gard. 6: 501 (1910).
A. yungasensis Rusby in Bull. N. Y. Bot. Gard. 4: 437 (1907).

## RAFFLESIACEAE

Apodanthes tribracteata Rusby, Descr. S. Am. Pls. 15 (1920). ? Pilostyles sp.

## POLYGONACEAE

Coccoloba chacoënsis Standl. in Field Mus. Publ. Bot. 17: 239 (1937).
C. illheënsis Wedd. in Ann. Sci. Nat. (ser. 3) 13: 258 (1850).
C. Meissneriana (Britton) K. Schum. in Just, Bot. Jahresber. 28(1): 451 (1902).
C. padifolia Rusby in Mem. N. Y. Bot. Gard. 7: 235 (1927).
C. Persicaria Wedd. in Ann. Sci. Nat. (ser. 3) 13: 256 (1850).
C. polystachya Wedd. in Ann. Sci. Nat. (ser. 3) 13: 261 (1850).
C. strobilulifera Meissn. in Mart. Fl. Bras. 5(1) : 25 (1855).
C. tiliacea Lindau in Engler, Bot. Jahrb. 13: 198, t. 5 (1890).

Enneatypus Nordenskjoeldii Herzog in Meded. Rijks Herbar. 46: 4 (1922).
Muehlenbeckia chilensis Meissn. in DC. Prodr. 14: 148 (1856).
M. dumosa I. M. Johnst. in Contrib. Gray Herb. 81: 87 (1928).
M. fruticulosa (Walp.) Standl. in Field Mus. Publ. Bot. 13: 453 (1937).
M. hastulata (Smith) I. M. Johnst. in Contrib. Gray Herb. 81: 88 (1928).
M. rupestris Wedd. in Ann. Sci. Nat. (ser. 3) 13: 256 (1850) = M. fruticulosa.
M. rupestris var. nivalis Wedd. in Ann. Sci. Nat. (ser. 3) 13: 256 (1850) = ?
M. tamnifolia (HBK.) Meissn. Pl. Vasc. Gen. Comm. 2: 227 (1843).
M. tiliaefolia Wedd. in Ann. Sci. Nat. (ser. 3) 13: 255 (1850).
M. vulcanica (Benth.) Endl. Gen. Suppl. 4, pt. 2: 51 (1847).

Polygonum acuminatum HBK. Nov. Gen. \& Spec. 2: 178 (1817).
P. fallax Small in Bull. Torr. Bot. Club, 24: 46 (1897).
P. lacerum HBK. Nov. Gen. \& Spec. 2: 179 (1817).
P. persicarioides HBK. Nov. Gen. \& Spec. 2: 179 (1817).

Rumex conglomeratus Murr. Prodr. Fl. Gotting. 52 (1770).
R. crispus L. 'Sp. Pl. 335 (1753).
R. cuneifolius Campd. Monog. Rum. 66, 95 (1819).

Ruprechtia apetala Wedd. in Ann. Sci. Nat. (ser. 3) 13: 268 (1850).
R. boliviensis Herzog in Meded. Rijks Herbar. 46: 5 (1922).
R. mollis Wedd. in Ann. Sci. Nat. (ser. 3) 13: 268 (1850).
R. scandens Rusby in Mem. N. Y. Bot. Gard. 7: 237 (1927).
R. triflora Griseb. in Goett. Abh. 24: 89 (1879).

Triplaris boliviana Britton ex Rusby in Bull. Torr. Bot. Club, 27: 130 (1900) $=\mathrm{T}$. Pavonii.
T. caracasana Cham. in Linnaea, 8: 137 (1833).
T. corylifolia var. intermedia O. Ktze. Rev. Gen. 3(2): 271 (1898).
T. efistulifera Rusby in Bull. Torr. Bot. Club, 27: 129 (1900).
T. estriata O. Ktze. Rev. Gen. 3(2): 271 (1898).
T. guanaiensis Rusby in Mem. Torr. Bot. Club, 6: 111 (1896).
T. hispida Britton ex Rusby in Mem. Torr. Bot. Club, 6:111 (1896) = T. Poeppigiana.
T. Pavonii Meissn. in DC. Prodr. 14: 172 (1856).
T. peruviana Fisch. \& Mey. ex C. A. Mey. in Mém. Acad. St. Pétersb. (ser. 6) Sci. Nat. 4: 149 (1845).
T. Poeppigiana Wedd. in Ann. Sci. Nat. (ser. 3) 13: 265 (1850).
T. setosa Rusby in Mem. N. Y. Bot. Gard. 7: 237 (1927).
T. vestita Rusby in Mem. N. Y. Bot. Gard. 7: 236 (1927).
T. Williamsii Rusby in Mem. N. Y. Bot. Gard. 7: 235 (1927).

## CHENOPODIACEAE

Atriplex Asplundii Standl. in Field Mus. Publ. Bot. 11: 125 (1931).
A. cristata Humb. \& Bonpl. ex Willd. Sp. Pl. 4(2): 959 (1806).
A. cristata var. depauperata O. Ktze. Rev. Gen. 3 (2): 266 (1898) = A. Herzogii.
A. cristata var. pulvinata O. Ktze. Tev. Gen. 3 (2): 266 (1898) = A. Herzogii.
A. Herzogii Standl. in Field Mus. Publ. Bot. 11: 125 (1931).
A. imbricata (Moq.) D. Dietr. Syn. Pl. 5: 536 (1852).
A. Lampa Gill. ex Moq. in DC. Prodr. 13(2): 110 (1849).
A. Rusbyi Britton in Rusby in Mem. Torr. Bot. Club, 4(3): 250 (1895).
A. semibaccata R. Br. Prodr. 406 (1810).
A. serpyllifolia Herzog in Meded. Rijks Herbar. 27: 11 (1915) = A. Herzogii.

Chenopodium ambrosioides L. Sp. Pl. 219 (1753).
C. ambrosioides subsp. chilense (Schrad.) Aellen in Fedde, Repert. Spec. Nov. 26: 36 (1929).
C. ambrosioides subsp. chilense var. andicola (Phil.) Aellen in Fedde, Repert. Spec. Nov. 26: 37 (1929).
C. ambrosioides forma minus (Murr.) Aellen in Fedde, Repert. Spec. Nov. 26: 37 (1929).
C. ambrosioides var. querciforme (Murr.) Aellen in Fedde, Repert. Spec. Nov. 26: 37 (1929).
C. bolivianum Murr. in Magyar Bot. Lapok. 1: 359 (1902) = C. petiolare.
C. carnosulum Moq. in DC. Prodr. 13(2): 64 (1849).
C. graveolens var. Bangii (Murr.) Aellen in Verh. Naturf. Ges. Basel, 41: 107 (1931).
C. hircinum Schrad. Ind. Sem. Hort. Goett. 1832: 2 (1833).
C. hircinum var. rhombicum Aellen in Fedde, Repert. Spec. Nov. 26: 122 (1929).
C. incisum Poir. in Lam. Encyc. Suppl. 1: 392 (1810).
C. macrospermum var. halophilum (Phil.) Standl. in Field Mus. Publ. Bot. 11: 118 (1931).
C. macrospermum subsp. halophilum forma angustius Thell. \& Aellen in Fedde, Repert. Spec. Nov. 26: 44 (1929).
C. macrospermum forma farinosum (S. Wats.) Aellen in Fedde, Repert. Spec. Nov. 26: 43 (1929).
C. macrospermum forma nonum Aellen in Fedde, Repert. Spec. Nov. 26: 44 (1929) $=$ C. macrospermum forma angustius.
C. murale L. Sp. Pl. 219 (1753).
C. pallidicaule Aellen in Fedde, Repert. Spec. Nov. 26: 126 (1929).
C. paniculatum Hook. ex Moq. in DC. Prodr. 13(2): 65 (1849).
C. paniculatum var. incanum (Wats.) Murr. in Allg. Bot. Zeitschr. 12: 54 (1906).
C. petiolare HBK. Nov. Gen. \& Spec. 2: 191 (1817).
C. petiolare forma hastatum (Phil.) Aellen in Fedde, Repert. Spec. Nov. 26: 150 (1929).
C. petiolare forma incanum (Murr.) Aellen in Fedde, Repert. Spec. Nov. 26: 150 (1929).
C. petiolare forma scutatum Aellen in Fedde, Repert. Spec. Nov. 26: 151 (1929).
C. petiolare forma trilobum Aellen in Fedde,Repert. Spec. Nov. 26: 151 (1929).
C. Quinoa Willd. Sp. Pl. 1: 1301 (1798).
C. Quinoa var. melanospermum Hunziker in Revist. Argent. Agron. 10: 317 (1943).
C. Quinoa forma purpureum Aellen in Fedde, Repert. Spec. Nov. 26: 124 (1929).
C. rigidum Lingelsh. in Fedde, Repert. Spec. Nov. 7: 241 (1909) = C. graveolens var. Bangii.
Salicornia andina Phil. in Anal. Mus. Nac. Chile, Bot. 8: 75 (1891).
S. fruticosa L. Sp. Pl. (ed. 2) 1: 5 (1762).

Suaeda foliosa Moq. in DC. Prodr. 13(2): 156 (1849).
S. fruticosa var. crassifolia Moq. in DC. Prodr. 13 (2) : 157 (1849) = S. foliosa.

Teloxys Mandonii S. Wats. in Proc. Amer. Acad. 9:91 (1874) 三 Chenopodium graveolens var. Bangii.

## AMARANTHACEAE

Achyranthes aspera L. Sp. Pl. 204 (1753).
A. aspera var. indica L. Sp. Pl. 204 (1753).
A. Bangii Standl. in Journ. Wash. Acad. Sci. 5: 74 (1915) = Alternanthera paniculata.
Alternanthera altacruzensis Suesseng. in Mitteil. Bot. Staatss. Münch. 1: 3 (1950).
A. boliviana (Rusby) Standl. in Journ. Wash. Acad. Sci. 5: 74 (1915).
A. coriacea Herzog in Meded. Rijks Herbar. 46: 6 (1922).
A. lanceolata (Benth.) Schinz in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 16C: 75 (1934).
A. mexicana forma lanuginosa Suesseng. in Fedde, Repert. Spec. Nov. 35: 301 (1934).
A. microcephala (Moq.) Schinz in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 16C: 75 (1934).
A. microphylla R. E. Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1(1): 154 (1905).
A. Moquinii (Webb) Dusén in Arch. Mus. Nac. Rio Janeiro, 13: 63 (1903).
A. paniculata HBK. Nov. Gen. \& Spec. 2: 208 (1818).
A. paronychioides St. Hil. Voy. Brés. 2(2): 439 (1833).
A. philoxeroides (Moq.) Griseb. in Goett. Abh. 24: 36 (1879).
A. pilosa Moq. in DC. Prodr. 13(2): 357 (1849).
A. polygonoides (L.) R. Br. Prodr. 417 (1810), combination implied but not actually made.
A. pubiflora (Benth.) O. Ktze. Rev. Gen. 2: 538 (1891).
A. pungens HBK. Nov. Gen. \& Spec. 2: 206 (1818).
A. repens (L.) O. Ktze. Rev. Gen. 2: 536, 540 (1891).
A. scandens Herzog in Meded. Rijks Herbar. 46: 7 (1922).
A. tomentosa (Moq.) Schinz in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 16C: 76 (1934).
Amaranthus affinis Thell. in Fedde, Repert. Spec. Nov. 21: 324 (1925).
A. Asplundii Thell. in Fedde, Repert. Spec. Nov. 21: 322 (1925).
A. Buchtienianus Thell. in Fedde, Repert. Spec. Nov. 21: 323 (1925).
A. Cardenasianus Hunziker in Bol. Soc. Argent. Bot. 4: 136 (1952).
A. caudatus L. Sp. Pl. 990 (1753).
A. chlorostachys Willd. Amaranth. 34, t. 10, fig. 19 (1790).
A. muricatus Gill. ex Moq. in DC. Prodr. 13(2): 276 (1849).
A. peruvianus (Schauer) Standl. in Field Mus. Publ. Bot. 13(2): 487 (1937).
A. retroflexus L. Sp. Pl. 991 (1753).

Chamissoa altissima (Sw.) HBK. Nov. Gen \& Spec. 2: 197, t. 125 (1817).
C. altissima subsp. albo-grisea Suesseng. in Fedde, Repert. Spec. Nov. 39: 6 (1935).
C. altissima var. rubella Suesseng. in Fedde, Repert. Spec. Nov. 35: 306 (1934).
C. celosioides Griseb. in Goett. Abh. 19: 79 (1874).

Cyathula achyranthoides (HBK.) Moq. in DC. Prodr. 13(2): 326 (1849).
Gomphrena acaulis Remy in Ann. Sci. Nat. (ser. 3) 6: 350 (1846) = G. Meyeniana.
G. boliviana Moq. in DC. Prodr. 13 (2) : 401 (1849).
G. cinnabarina Suesseng. in Fedde, Repert. Spec. Nov. 35: 309 (1934).
G. Conwayi Rusby in Bull. N. Y. Bot. Gard. 8: 89 (1912) = G. Meyeniana.
G. decumbens Jacq. Hort. Schoenbr. 5: 41, t. 482 (1804).
G. decumbens var. boliviana Stuchlik in Fedde, Repert. Spec. Nov. 12: 519 (1913).
G. discolor R. E. Fries in Ark. Bot. 16(12): 34 (1920).
G. elegans var. mandonioides Suesseng. in Fedde, Repert. Spec. Nov. 35: 310 (1934).
G. Gardneri Moq. in DC. Prodr. $13(2)$ : 404 (1849).
G. glabrata (Mart.) Moq. in DC. Prodr. 13(2): 388 (1849).
G. glutinosa R. E. Fries in Ark. Bot. 16(12): 28 (1920).
G. hygrophila forma luteiflora Herzog in Meded. Rijks Herbar. $46: 8$ (1922).
G. hygrophila forma subecristata Herzog in Meded. Rijks Herbar. 46: 8 (1922).
G. ixiamensis Rusby in Bull. N. Y. Bot. Gard. 6: 502 (1910) $=$ G. decumbens.
G. lutea Rusby in Mem. N. Y. Bot. Gard. 7: 238 (1927).
G. Mandonii R. E. Fries in Ark. Bot. 16(12): 22 (1920).
G. Meyeniana Walp. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 404 (1843).
G. oligocephala Remy in Ann. Sci. Nat. (ser. 3) 6: 350 (1846).
G. oligocephala var. pallida Suesseng. in Fedde, Repert. Spec. Nov. 49: 9 (1940).
G. perennis L. Sp. Pl. 224 (1753).
G. perennis var. boliviana Stuchlík in Fedde, Repert. Spec. Nov. 12: 521 (1913).
G. perennis var. saxatilis R. E. Fries in Ark. Bot. 16(12): 40 (1920).
G. potosiana Suesseng. \& Benl in Mitteil. Bot. Staatss. Münch. 1: 6 (1950).
G. pulchella forma nana Suesseng. in Fedde, Repert. Spec. Nov. 35: 315 (1934).
G. pulchella var. rosea Stuchlík in Fedde, Repert. Spec. Nov. 12: 523 (1913).
G. subalpina Herzog in Meded. Rijks Herbar. 46: 7 (1922).
G. tarijensis R. E. Fries in Ark. Bot. 16(12): 27 (1920).
G. Trollii Suesseng. in Fedde, Repert. Spec. Nov. 35: 315 (1934).
G. umbellata Remy in Ann. Sci. Nat. (ser. 3) 6: 349 (1846).
G. vaga Mart. Nov. Gen. 2: 17, t. 120 (1826).

Guilleminia densa (Willd.) Moq. in DC. Prodr. 13(2): 338 (1849).
Hebanthe holosericea Mart. in Flora, 21, II Beibl.: 65 (1838) = Pfaffia sp. ?
Iresine angustifolia Euphr. Beskr. St. Barthel. 165 (1795).
I. Cardenasii Standl. in Field Mus. Publ. Bot. 17: 241 (1937).
I. Celosia L. Syst. (ed. 10) 1291 (1759).
I. celosioides L. Sp. Pl. (ed. 2) 2: 1456 (1763) $=$ I. Celosia.
I. celosioides var. nicotianoides Suesseng. in Fedde, Repert. Spec. Nov. 39: 11 (1935).
I. Hassleriana Chod. in Bull. Herb. Boiss. (ser. 2) 3: 390 (1903).
I. Hassleriana var. guaranoides Suesseng. in Fedde, Repert. Spec. Nov. 35: 321 (1934).
I. paniculata (L.) O. Ktze. Rev. Gen. 2: 542 (1891).
I. spiculigera forma pauciglandulosa Herzog in Meded. Rijks Herbar. 46: 9 (1922).

Mogiphanes soratensis Rusby in Bull. N. Y. Bot. Gard. 6: 503 (1910) $=$ Alternanthera lanceolata.
Pfaffia Bangii R. E. Fries in Ark. Bot. 16(12): 11 (1920).
P. brachiata Chod. in Chod. \& Rehf. in Bull. Soc. Bot. Genève, 14: 285 (1927).
P. brachiata var. grandiflora (Fries) Stützer in Fedde, Repert. Spec. Nov. Beih. 88: 8 (1935).
P. Dunaliana (Moq.) Schinz in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 16C: 68 (1934).
P. Fiebrigii Suesseng. in Fedde, Repert. Spec. Nov. 35: 329 (1934).
P. fruticulosa Suesseng. in Fedde, Repert. Spec. Nov. 35: 330 (1934).
P. glabrata Mart. Nov. Gen. 2: 21, t. 122 (1826).
P. gnaphalioides (L. f.) Mart. Nov. Gen. 2: 24 (1826).
P. gnaphalioides var. floccosa (Seub.) Stützer in Fedde, Repert. Spec. Nov. Beih. 88: 26 (1935).
P. grandiflora var. prominulifera Stützer in Fedde, Repert. Spec. Nov. Beih. 88: 10 (1935).
P. holosericea (Moq.) Standl. in Field Mus. Publ. Bot. 13(2): 491 (1937).
P. luzulaeflora forma gracilis Stützer in Fedde, Repert. Spec. Nov. Beih. 88: 34 (1935).
P. paniculata (Mart.) O. Ktze. Rev. Gen. 2: 543 (1891).
$\boldsymbol{P}$. soratensis Rusby in Bull. N .Y. Bot. Gard. 6: 502 (1910) $=$ Gomphrena, aff. G. elegans var. mandonioides.
P. stenophylla (Spreng.) Stuchlík in Fedde, Repert. Spec. Nov. 12: 357 (1913).

Pleuropetalum Sprucei (Hook. f.) Standl. in N. Am. Fl. 21: 96 (1917).
Telanthera Bangii Rusby in Mem. Torr. Bot. Club, 6: 110 (1896) $=$ Alternanthera paniculata.

## NYCTAGINACEAE

Allionia incarnata L. Syst. (ed. 10) 2: 890 (1759).
Boerhaavia caribaea Jacq. Obs. Bot. 4: 5, t. 84 (1771).
B. coccinea Mill. Gard. Dict. (ed. 8) no. 4 (1768).
B. coccinea var. leiocarpa (Heimerl) Standl. in Field Mus. Publ. Bot. 11: 108 (1931).
B. erecta L. Sp. Pl. 3 (1753).
B. Friesii Heimerl in Oesterr. Bot. Zeitschr. $56: 253(1906)=$ B. coccinea var. leiocarpa.
B. scandens L. Sp. Pl. 3 (1753).
B. viscosa Lag. \& Rod. in Anal. Cienc. Nat. 4: 256 (1801).

Bougainvillea berberidifolia Heimerl in Denkschr. Akad. Wiss. Wien, 70: 121, t. 1 (1900).
B. campanulata Heimerl in Meded. Rijks Herbar. 19: 33 (1913).
B. Herzogiana Heimerl in Meded. Rijks Herbar. 27: 12 (1915).
B. infesta Griseb. in Goett. Abh. 24: 40 (1879).
B. longispinosa Rusby in Mem. Torr. Bot. Club, 6: 109 (1896).
B. modesta Heimerl in Denkschr. Akad. Wiss. Wien, 70: 118 (1900).
B. praecox Griseb. in Goett. Abh. 24: 40 (1879).
B. praecox var. rhombifolia Heimerl in Verh. Zool.-Bot. Ges. Wien, 62: 4 (1912).
B. praecox var. spinosa Chod. \& Hassl. in Bull. Herb. Boiss. (ser. 2) 3: 415 (1903).
B. spectabilis Willd. Sp. Pl. 2: 348 (1799).
B. spinosa (Cav.) Heimerl in Engl. \& Prantl, Nat. Pflanzenfam. 3 (lb): 27 (1889).
B. stipitata Griseb. in Goett. Abh. 24: 39 (1879), nomen nudum.
B. stipitata var. Fiebrigii Heimerl in Engler, Bot. Jahrb. 42: 76 (1908).
B. stipitata var. Grisebachiana Heimerl in Denkschr. Akad. Wiss. Wien, 70: 116 (1900).
B. stipitata var. Kuntzeana Heimerl in Denksch. Akad. Wiss. Wien, 70: 117 (1900).
B. Trollii Heimerl in Notizbl. 11: 464 (1932).

Colignonia glomerata Griseb. in Goett. Abh. 19: 87 (1874).
C. glomerata var. boliviana Heimerl in Denkschr. Akad. Wiss. Wien, 70: 136 (1900).
C. parviflora (HBK.) Endl. Gen. 311 (1837), combination implied but not actually made.
C. rufopilosa O. Ktze. Rev. Gen. 3(2): 264 (1898).

Commicarpus crassifolius Heimerl in Notizbl. 11: 461 (1932).
Cryptocarpus pyriformis HBK. Nov. Gen. \& Spec. 2: 188, t. 124 (1817).
Mirabilis Jalapa L. Sp. Pl. 177 (1753).
M. micrantha (Chois.) Heimerl in Engl. \& Prantl, Nat. Pflanzenfam. 3(lb): 24 (1889).
M. prostrata (R. \& P.) Heimerl, Beitr. Syst. Nyct. 21 (1897).

Neea Bangii Rusby in Bull. N. Y. Bot. Gard. 4: 435 (1907).
N. boliviana Standl. in Field Mus. Publ. Bot. 11: 81 (1931).
N. Brittonii Standl. in Field Mus. Publ. Bot. 11: 80 (1931).
N. dimorphophylla Standl. in Field Mus. Publ. Bot. 11: 78 (1931).
N. divaricata Poepp. \& Endl. Nov. Gen. 2: 45, t. 161 (1838).
N. longipedunculata Britton in Rusby in Bull. Torr. Bot. Club, 27: 126 (1900).
N. macrophylla Britton in Rusby in Bull. Torr. Bot. Club, 27; 126 (1900) = N. Brittonii.
N. mapirensis Standl. in Field Mus. Publ. Bot. 11: 78 (1931).

Oxybaphus bracteosus Griseb. in Goett. Abh. 19: 86 (1874).
Pisonia aculeata forma inermis O. Ktze. Rev. Gen. 3(2): 265 (1898) = P. Zapallo.
P. hirtella HBK. Nov. Gen. \& Spec. 2: 217 (1818).
P. indecora Heimerl in Notizbl. 11: 469 (1932).
P. Zapallo Griseb. in Goett. Abh. 24: 39 (1879).

Pisoniella arborescens var. glabrata (Heimerl) Heimerl in Meded. Rijks Herbar. 19: 35 (1913).
Torrubia boliviana (Britton) Standl. in Contrib. U. S. Nat. Herb. 18: 100 (1916).
T. Hassleriana (Heimerl) Standl. in Contrib. U. S. Nat. Herb. 18: 100 (1916).
T. Olfersiana (Lk. Kl. \& Otto) Standl. in Contrib. U. S. Nat. Herb. 18: 101 (1916).
T. suspensa (Heimerl) Standl. in Contrib. U. S. Nat. Herb. 18: 101 (1916).

## PHYTOLACCACEAE

Achatocarpus microcarpus Schinz \& Autran in Bull. Herb. Boiss. 1: 8 (1893).
A. praecox Griseb. in Goett. Abh. 24: 32 (1879).

Gallesia Gorazema (Vell.) Moq. in DC. Prodr. 13(2): 8 (1849).
Microtea maypurensis (HBK.) G. Don in Loud. Hort. Brit. (ed. 2) 98 (1832).
M. paniculata var. latifolia O. Ktze. Rev. Gen. 3(2): 268 (1898).
M. scandens Rusby in Mem. N. Y. Bot. Gard. 7: 239 (1927).

Mohlana nemoralis Mart. Nov. Gen. 3: 171, t. 290 (1829).
M. secunda (R. \& P.) Mart. Nov. Gen. 3: 172 (1829).

Petiveria alliacea L. Sp. Pl. 342 (1753).
Phytolacca australis Phil. in Anal. Univ. Chile, 1873: 536.
P. icosandra L. Sp. Pl. (ed. 2) 1: 631 (1762).
P. octandra L. Sp. Pl. (ed. 2) 1: 631 (1762).
P. rivinoides Kunth \& Bouché, Ind. Sem. Hort. Berol. 15 (1848).
P. thyrsiflora Fenzl in Mart. Fl. Bras. 14(2): 343 (1872).

Rivina humilis L. Sp. Pl. 121 (1753).
R. humilis var. glabra L. Sp. Pl. 122 (1753).

Schindleria densiflora (O. Ktze.) Monachino in Phytologia, 4: 39 (1952).
S. mollis H. Walt. in Engler, Pflanzenr. IV, 83: 116 (1909).
S. racemosa (Britton) H. Walt. in Engler, Bot. Jahrb. 37, Beibl. 85: 24 (1906).
S. rivinoides (Rusby) H. Walt. in Engler, Bot. Jahrb. 37, Beibl. 85: 24 (1906).
S. rosea H. Walt. in Engler, Bot. Jahrb. 37, Beibl. 85: 24 (1906).

Seguieria brevithyrsa H. Walt. in Engler, Pflanzenr. IV, 83: 87 (1909).
S. guaranitica Speg. in Anal. Soc. Cient. Argent. 16: 88 (1883).
S. macrophylla Benth. in Trans. Linn. Soc. 18: 235 (1839).
S. paraguayensis Morong in Ann. N. Y. Acad. Sci. 7: 210 (1893).
S. parvifolia Benth. in Trans. Linn. Soc. 18: 235 (1839).

Trichostigma octandrum (L.) H. Walt. in Engler, Pflanzenr. IV, 83: 109 (1909).

## AIZOACEAE

Mollugo verticillata L. Sp. Pl. 89 (1753).

## PORTULACACEAE

Calandrinia acaulis HBK. Nov. Gen. \& Spec. 6: 78 (1823).
C. chromantha Griseb. in Goett. Abh. 24: 30 (1879).
C. ciliata (R. \& P.) DC. Prodr. 3: 359 (1828).

Portulaca elongata Rusby in Mem. Torr. Bot. Club, 6: 7 (1896).
P. fragilis v. Poelln. in Fedde, Repert. Spec. Nov. 50: 61 (1941).
P. Gilliesii var. pedicellata Legrand in Lilloa, 17: 351 (1949).
P. gracilis v. Poelln. in Fedde, Repert. Spec. Nov. 50: 107 (1941).
P. grandiflora var. macrophylla Rohrb. in Mart. Fl. Bras. 14 (2): 302 (1872).
P. longiusculo-tuberculata v. Poelln. in Fedde, Repert. Spec. Nov. 33: 161 (1933).
P. marginata HBK. Nov. Gen. \& Spec. 6: 72 (1823).
P. pedicellata var. cochabambensis Legrand in Lilloa, 17: 356 (1949).
P. perennis R. E. Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1(1): 151, t. 8 (1905).
P. Philippii I. M. Johnst. in Contrib. Gray Herb. 85:39 (1929).
P. pilosa L. Sp. Pl. 445 (1753).
P. rotundifolia R. E. Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1(1): 149 (1905).
P. simpliciuscula Mart. ex Rohrb. in Mart. Fl. Bras. 14(2): 301, t. 68 (1872).

Talinum patens (L.) Willd. Sp. Pl. 2: 863 (1799).

## BASELLACEAE

? Boussingaultia baselloides HBK. Nov. Gen. \& Spec. 7: 196, t. 645 bis (1825).
B. boliviensis (Hauman) Macbr. in Field Mus. Publ. Bot. 13: 577 (1937).
B. tucumanensis Lillo \& Hauman ex Haum. in Anal. Mus. Hist. Nat. Buenos Aires, 33: 353 (1925).
Ullucus tuberosus Caldas, Seman. Nuov. Granad. 185 (1809).

## CARYOPHYLLACEAE

Acanthonychia polycnemoides Rohrb. in Mart. Fl. Bras. 14 (2): 250 (1872).
A. ramosissima (Weinm.) Rohrb. in Mart. Fl. Bras. 14 (2): 249, t. 56 (1872).

Alsine yungasensis Rusby in Phytologia, 1: 53 (1934) =?

Arenaria alsinoides (Michx.) Rohrb. in Mart. Fl. Bras. 14 (2): 274 (1872), in synon.
A. andina Rohrb. in Linnaea, 37: 255 (1871-73).
A. boliviana Williams in Journ. Linn. Soc. 33: 425 (1898).
A. catamarcensis Pax in Engler, Bot. Jahrb. 18: 29 (1893).
A. conferta Wedd. in Ann. Sci. Nat. (ser. 5) 1: 293 (1864) $=$ A. boliviana.
A. conferta var. villosa Wedd. in Ann. Sci. Nat. (ser. 5) 1: 293 (1864) =?
A. digyna Schlechtd. in Ges. Naturf. Fr. Berl. Mag. 7: 201 (1813).
A. lanuginosa (Michx.) Rohrb. in Mart. Fl. Bras. 14(2): 274 (1872).
A. Mandoniana Wedd. in Ann. Sci. Nat. (ser. 5) 1: 294 (1864).
A. Orbignyana Wedd. in Ann.Sci. Nat. (ser. 5) 1: 293 (1864).
A. pedunculosa Wedd. in Ann. Sci. Nat. (ser. 5) 1: 294 (1864).
A. pycnophylla Rohrb. in Linnaea, 37: 250 (1871-73).
A. soratensis Rohrb. in Linnaea, 37: 266 (1871-73).
A. Stuebelii Hieron. in Engler, Bot. Jahrb. 21: 307 (1895).

Cerastium arvense L. Sp. Pl. 438 (1753).
C. arvense var. arvensiforme (Wedd.) Rohrb. in Linnaea, 37: 305 (1871-73).
C. arvensiforme var. glandulosum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 296 (1864).
C. Behmianum Muschl. in Engler, Bot. Jahrb. 45: 446 (1911).
C. brevicarpum Rusby in Phytologia,1: 54 (1934).
C. consanguineum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 296 (1864).
C. crassipes Bartl. in Presl, Rel. Haenk. 2: 18 (1831).
C. humifusum Camb. ex St. Hil. Fl. Bras. Mer. 2: 166 (1829).
C. imbricatum HBK. Nov. Gen. \& Spec. 6: 28 (1823).
C. imbricatum var. Mandonianum Rohrb. in Linnaea, 37: 293 (1871-73).
C. mucronatum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 294 (1864).
C. nutans Raf. Préc. Découv. 36 (1814).
C. orophilum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 295 (1864).
C. soratense Rohrb. in Linnaea, 37: 291 (1871-73).
C. subspicatum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 295 (1864).
C. viscosum L. Sp. Pl. 437 (1753).
C. vulgatum L. Fl. Suec. (ed. 2) 158 (1755).
C. vulgatum var. peruvianum A. Gray in Bot. U. S. Explor. Exped. 1: 120 (1854).

Colobanthus bolivianus Pax in Fedde, Repert. Spec. Nov. 7: 109 (1909).
Drymaria cordata (L.) Willd. ex Roem. \& Schult. Syst. Veg. 5: 406 (1819).
D. glandulosa Bartl. in Presl, Rel. Haenk. 2: 9 (1831).
D. hirsuta Bartl. in Presl, Rel. Haenk. 2: 8 (1831).
D. Ladewii Rusby in Phytologia, 1: 54 (1934).
D. pauciflora Bartl. in Presl, Rel. Haenk. 2: 8 (1831).
D. sperguloides A. Gray, Pl. Fendl. 11 (1849).
D. stricta Rusby in Phytologia, 1: 55 (1934).

Herniaria setigera Gill. in Hook. Bot. Misc. 3: 337 (1833).
Lychnis andicola (Gill.) Britton in Bull. Torr. Bot. Club, 16: 61 (1889).
Melandrium cucubaloides Fenzl ex Rohrb. in Linnaea, 36: 223 (1869-70) =?
M. Mandonii Rohrb. in Linnaea, 36: 222 (1869-70) = Lychnis andicola ?

Paronychia andina A. Gray in Bot. U. S. Explor. Exped. 1: 128 (1854).
P. chilensis DC. Prodr. 3: 370 (1828).
P. Mandoniana Rohrb. in Linnaea, 37: 208 (1871-73).
P. microphylla Phil. in Anal. Mus. Nac. Chile, Bot. 8: 26 (1891).
P. sessiliflora Nutt. Gen. Am. Pl. 1: 160 (1818).

Pentacaena ramosissima (Weinm.) Hook. \& Arn. in Hook. Bot. Misc. 3: 338 (1833).

Polycarpaea Hassleriana Chod. in Bull. Herb. Boiss. (ser.2) 3: 791 (1903).

Pycnophyllopsis keraiopetala Mattf. in Schr. Ver. Naturf. Unterwes. 7: 22 (1934).

Pycnophyllum dicranoides (HBK.) Muschl. in Engler, Bot. Jahrb. 45: 454 (1911).
P. kobalanthum Mattf. in Fedde, Repert. Spec. Nov. 36: 274 (1934).
P. molle Remy in Ann. Sci. Nat. (ser. 3) 6: 355, t. 20 (1846).
P. Pilgerianum Muschl. in Engler, Bot. Jahrb. 45: 454 (1911).
P. spathulatum Mattf. in Fedde, Repert. Spec. Nov. 18: 175 (1922).
P. Stuebelii Mattf. in Fedde, Repert. Spec. Nov. 18: 171 (1922).
P. tetrastichum Remy in Ann. Sci. Nat. (ser. 3) 6: 356, t. 20 (1846).

Sagina graminifolia Wedd. in Ann. Sci. Nat. (ser. 5) 1: 292 (1864).
Silene gallica L. Sp. Pl. 417 (1753).
Spergularia andina Rohrb. in Linnaea, 37: 234 (1871-73).
S. firma Kze. ex Kindb. Monog. Lepig. 34 (1863), in synon.
S. floribunda Rohrb. in Linnaea, 37: 230 (1871-73).
S. pazensis (Rusby) R. P. Rossbach in Rhodora, 42: 205 (1940).
S. ramosa Camb. in St. Hil. Fl. Bras. Mer. 2: 178 (1829).

Stellaria leptopetala Benth. Pl. Hartw. 163 (1845).
S. media (L.) Sowerby \& Smith, English Bot. 8: t. 537 (1799).
S. nemorum L. Sp. Pl. 42 1(1753).

## NYMPHAEACEAE

Cabomba piauhyensis Gardn. in Hook. Ic. Pl. 7: t. 641 (1844).

## RANUNCULACEAE

Anemone decapetala var. foliolosa Eichl. in Mart. Fl. Bras. 13(1): 151, t. 35 (1864).

Caltha alata A. W. Hill in Ann. Bot. 32: 428, fig. 3-4 (1918) = C. sagittata.
C. sagittata Cav. Ic. 5: 8, t. 414 (1799).

Clematis alborosea Ulbr. in Notizbl. 8: 325 (1923).
C. Bangii Rusby in Mem. Torr. Bot. Club, $3(3): 3:(1893)=$ C. Hilarii.
C. cochabambensis Rusby in Mem. Torr. Bot. Club, 3(3): 3 (1893) = C. millefoliata.
C. dioica var. brasiliana (DC.) Eichl. in Mart. Fl. Bras. 13(1): 148 (1864).
C. Hilarii Spreng. Syst. Veg. 5: 177 (1828).
C. millefoliata Eichl. in Mart. Fl. Bras. 13(1): 150 (1864).
C. sericea HBK. Nov. Gen. \& Spec. 5: 37 (1821).

Ranunculus breviscapus DC. Syst. 1: 253 (1817).
R. Cymbalaria Pursh, Fl. Am. Sept. 2: 392 (1814).
R. Cymbalaria var. exilis R. E. Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1(1): 145 (1905).
R. filamentosus Wedd. Chlor. And. 2: 301 (1861).
R. flagelliformis Smith in Rees, Cycl. 29: no. 13 (1819).
R. Guzmannii Humb. Tabl. Reg. Eq. 69 (1805).
R. haemanthus Ulbr. in Engler, Bot. Jahrb. 37: 404 (1906).
R. Mandonianus Wedd. Chlor. And. 2: 299 (1861).
R. minutiusculus Ulbr. in Engler, Bot. Jahrb. 37: 403 (1906) $=$ R. Cymbalaria. var. exilis.
R. praemorsus HBK. Nov. Gen. \& Spec. 5:47 (1821).
R. psychrophilus Wedd. Chlor. And. 2: 300 (1861).
R. repens L. Sp. Pl. 554 (1753).
R. trichophyllus Chaix in Vill. Hist. Pl. Dauph. 1: 335 (1786), nomen nudum.

Rhopalodium Gusmanni var. bolivianum Ulbr. in Notizbl. 8: 259 (1922) = Ranunculus Guzmannii ?

Thalictrum Cardenasianum Boivin in Bull. Torr. Bot. Club, 80: 136 (1953).
T. cincinnatum Boivin in Rhodora, 46: 398 (1944).
T. decipiens Boivin in Rhodora, 46: 405 (1944).
T. inuncans Boivin in Rhodora, 46: 404 (1944) $=$ T. decipiens .
T. Steinbachii Boivin in Rhodora, 46:397 (1944) = T. cincinnatum.
T. Venturii Boivin in Rhodora, 46: 422 (1944).

## BERBERIDACEAE

Berberis agapatensis Lechl. Berb. Amer. Austr. 44 (1857).
B. bumeliaefolia C. K. Schneider in Bull. Herb. Boiss. (ser. 2) 5: 818 (1905).
B. carinata Lechl. Berb. Amer. Austr. 41 (1857).
B. chrysacantha C. K. Schneider in Engler, Bot. Jahrb. 42: 81 (1908).
B. ciliaris Lindl. in Journ. Hort. Soc. 5: 5 (1850).
B. commutata Eichl. in Mart. Fl. Bras. 13(1): 231 (1864).
B. conferta var. boliviana (Lechl.) C. K. Schneider in Bull. Herb. Boiss. (ser. 2) 5: 393 (1905).
B. densifolia Rusby, Descr. S. Am. Pls. 16 (1920).
B. divaricata Rusby in Mem. Torr. Bot. Club, 4 (3): 203 (1895) = B. commutata.
B. edentata Rusby in Mem. N. Y. Bot. Gard. 7: 239 (1927).
B. ferruginea Lechl. Berb. Amer. Austr. 9 (1857).
B. Fiebrigii C. K. Schneider in Engler. Bot. Jahrb. 42: 85 (1908).
B. Keissleriana C. K. Schneider in Bull. Herb. Boiss. (ser. 2) 5: 808 (1905).
B. laurina Thunb. Pl. Bras. 1: 8 (1817).
B. Lobbiana (Schneid.) C. K. Schneider in Engler, Bot. Jahrb. $42: 83$ (1908).
B. ovalifolia Rusby, Descr. S. Am. Pls. 16 (1920).
B. paucidentata Rusby in Bull. N. Y. Bot. Gard. 4: 321 (1907).
B. phyllacantha Rusby in Mem. Torr. Bot. Club, 6: 4 (1896).
B. pseudo-spinulosa Job in Not. Mus. La Plata, 8: 129 (1943)
B. rariflora Lechl. Berb. Amer. Austr. 33 (1857).
B. Rechingeri C. K. Schneider in Bull. Herb. Boiss. (ser. 2) 5: 808 (1905).
B. rectinervia Rusby in Mem. Torr. Bot. Club, 3(3): 5 (1893).
B. Trollii Diels in Notizbl. 11: 781 (1933).
B. Weddellii Lechl. Berb. Amer. Austr. 21 (1857).
B. Wettsteiniana C. K. Schneider in Bull. Herb. Boiss. (ser. 2) 5: 809 (1905).

## MENISPERMACEAE

Abuta boliviana Rusby in Mem. N. Y. Bot. Gard. 7: 241 (1927) $=$ Chondodendron tomentocarpum.
A. Candollei Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 17: 47 (1862).
A. concolor Poepp. \& Endl. Nov. Gen. 2: 64, t. 188 (1838).
A. grandifolia (Mart.) Sandw. in Kew Bull. 1937: 397.
A. splendida Krukoff \& Moldenke in Bull. Torr. Bot. Club, 68: 241 (1941).
A. trinervis (Rusby) Moldenke in Brittonia, 3: 59 (1938).

Anomospermum bolivianum Krukoff \& Moldenke in Lilloa, 5: 234 (1940).
A. Schomburgkii Miers, Contrib. Bot. 3: 71 (1871).

Chondodendron tomentocarpum (Rusby) Moldenke in Brittonia, 3: 21 (1938).
C. tomentosum R. \& P. Syst. 261 (1798).

Cissampelos ciliata Rusby in Mem. N. Y. Bot. Gard. 7: 240 (1927).
C. ovalifolia DC. Syst. 1: 537 (1818).
C. Pareira L. Sp. Pl. 1031 (1753).
C. Pareira var. Gardneri Diels in Engler, Pflanzenr. IV, 94: 294 (1910).
C. Pareira var. Haenkeana (Presl) Diels in Engler, Pflanzenr. IV, 94: 292 (1910).
C. sympodialis var. grandifolia Britton in Bull. Torr. Bot. Club, 16: 15 (1889).
C. tropaeolifolia DC. Syst. 1: 532 (1818).
C. violaefolia Rusby in Mem. N. Y. Bot. Gard. 7: 240 (1927).

Disciphania clausa Diels in Engler, Pflanzenr. IV, 94: 176 (1910).
D. cubijensis (R. Knuth) Sandw. in Kew Bull. 1954: 614 (1955).

Hyperbaena domingensis (P. DC.) Benth. in Journ. Linn. Soc. 5, Suppl. 2: 50 (1861).
H. Hassleri Diels in Engler, Pflanzenr. IV, 94: 201 (1910).
? Somphoxylon sp.

## ANNONACEAE

Annona Cherimola Mill. Gard. Dict. (ed. 8) no. 5 (1768).
A. dioica St. Hil. Fl. Bras. Mer. 1: 34 (1825).
A. hypoglauca Mart. Fl. Bras. 13(1): 13 (1841).
A. nano-fruticosa Herzog in Fedde, Repert. Spec. Nov. 7: 51 (1909).
A. nutans (R. E. Fries) R. E. Fries in Bull. Herb. Boiss. (ser. 2) 4: 1171 (1904).
A. reticulata L. Sp. Pl. 537 (1753).

Cardiopetalum calophyllum Schlechtd. in Linnaea, 9: 328 (1835).
Crematosperma leiophyllum (Diels) R. E. Fries in Act. Hort. Berg. 10(2): 328 (1931).
C. monospermum (Rusby) R. E. Fries in Act. Hort. Berg. 10(2): 327 (1931).

Cymbopetalum longipes Diels in Verh. Bot. Ver. Brandenb. 47: 132 (1906).
C. parvifolium Rusby in Bull. N. Y. Bot. Gard. 6:505 (1910) = Cardiopetalum calophyllum.
Duguetia ibonensis Rusby in Mem. N. Y. Bot. Gard. 7: 246 (1927) = D. quitarensis.
D. quitarensis Benth. in Hook. Lond. Journ. Bot. 2: 361 (1843).

Guatteria alutacea var. Steinbachii R. E. Fries in Act. Hort. Berg. 12(3): 362 (1939).
G. boliviana H. Winkl. in Fedde, Repert. Spec. Nov. 7: 242 (1909).
G. Buchtienii R. E. Fries in Act. Hort. Berg. 12 (3): 388 (1939).
G. cuspidata Rusby in Mem. N. Y. Bot. Gard. 7: 245 (1927) $=$ ? (not Annonaceae, fide R. E. Fries).
G. Guentheriana Diels in Notizbl. 11: 75 (1931).
G. lasiocalyx R. E. Fries in Act. Hort. Berg. 12(3): 388 (1939).
G. lucida Rusby in Mem. N. Y. Bot. Gard. 7: 245 (1927) = Crematosperma monospermum.
G. oblongifolia Rusby in Bull. N. Y. Bot. Gard. 4: 320 (1907).
G. Rusbyi Macbr. in Field Mus. Publ. Bot. 4: 171 (1929) = Crematosperma monospermum.
G. setosa Rusby in Phytologia, 1: 55 (1934) = G. trichoclonia.
G. tomentosa Rusby in Bull. N. Y. Bot. Gard. 6: 504 (1910).
G. trichoclonia Diels in Notizbl. 11: 77 (1931).

Oxandra Espintana (Spruce) Baill. Hist. Pl. 1: 207 (1868).
O. ovata Rusby, Descr. S. Am. Pls. 19 (1920) = O. Espintana.

Porcelia nitidifolia R. \& P. Syst. 144 (1798).
P. ponderosa (Rusby) Rusby in Mem. N. Y. Bot. Gard. 7: 245 (1927) $=$ P. nitidifolia.
P. Saffordiana Rusby in Mem. N. Y. Bot. Gard. 7: 242, fig. 2 (1927) = P. nitidifolia.
P. Steinbachii (Diels) R. E. Fries in Act. Hort. Berg. 10 (1): 35 (1930).

Rollinia boliviana R. E. Fries in Act. Hort. Berg. 13(3): 115 (1941).
R. Hassleriana var. vestita R. E. Fries in Act. Hort. Berg. 12(1): 171 (1934).
R. Herzogii R. E. Fries in Act. Hort. Berg. 12(1): 177 (1934).
R. Williamsii Rusby ex R. E. Fries in Act. Hort. Berg. 12(1): 186 (1934).

Ruizodendron ovale (R. \& P.) R. E. Fries in Ark. Bot. 28B (4) : 3 (1936).
Trigynaea Periquino Rusby in Mem. N. Y. Bot. Gard. 7: 247 (1927) = Unonopsis sp.
Unonopsis boliviensis (Britton) R. E. Fries in Kgl. Sv. Vet. Akad. Handl. 34 (5): 28 (1900).
U. Buchtienii R. E. Fries in Fedde, Repert. Spec. Nov. 24: 247 (1928).
U. Guaraya Herzog in Fedde, Repert. Spec. Nov. 7: 52 (1909).
U. Matthewsii (Benth.) R. E. Fries in Kgl. Sv. Vet. Akad. Handl. 34(5): 28 (1900).

## MYRISTICACEAE

Dialyanthera parvifolia Markgraf in Notizbl. 9: 964 (1926).
Virola boliviensis Warb. in Nov. Act. Acad. Caes. Leop. 68: 184 (1897) = V. sebifera.
V. flexuosa A. C. Smith in Brittonia, 2: 151 (1936).
V. sebifera Aubl. Pl. Guian. Fr. 2: 904, t. 345 (1775).

## MONIMIACEAE

Mollinedia boliviensis A. DC. in Journ. Bot. 3: 220 (1865).
M. caloneura Perk. in Engler, Bot. Jahrb. 27: 663 (1900).
M. ovata R. \& P. Syst. 143 (1798).
M. Rusbyana Perk. in Engler, Bot. Jahrb. 27: 682 (1900).
M. Steinbachiana Perk. in Notizbl.. 10: 160 (1927).

Siparuna Apiosyce (Mart.) A. DC. in DC. Prodr. 16(2): 645 (1864).
S. bifida (Poepp. \& Endl.) A. DC. in DC. Prodr. 16(2): 652 (1864).
S. boliviensis Herzog in Meded. Rijks Herbar. 40: 3 (1921).
S. chrysantha Perk. in Engler, Bot. Jahrb. 28: 685 (1901).
S. cinerea Perk. in Engler, Bot. Jahrb. 28: 695 (1901).
S. dasyantha Perk. in Notizbl. 6: 134 (1914).
S. guianensis Aubl. Pl. Guian. Fr. 2: 865, t. 333 (1775).
S. hispida A. DC. in Journ. Bot. 3: 219 (1865).
S. hypoglauca Perk. in Engler, Bot. Jahrb. 28: 691 (1901).
S. limoniodora (R. \& P.) A. DC. in DC. Prodr. 16(2): 646 (1864).
S. macrophylla (HBK.) A. DC. in Prodr. 16(2): 646 (1864).
S. muricato-alata Herzog in Meded. Rijks Herbar. 40: 4 (1921).
S. nigra Rusby in Mem. Torr. Bot. Club, 4(3): 252 (1895).
S. obovata (Gardn.) A. DC. in DC. Prodr. 16(2) : 644 (1864).
S. pellita (Tul.) A. DC. in DC. Prodr. 16(2): 645 (1864).
S. polyantha (Tul.) A. DC. in DC. Prodr. 16(2): 646 (1864).
S. pseudospectabilis Sleumer in Fedde, Repert. Spec. Nov. 39: 276 (1935).
S. spectabilis Perk. in Engler, Bot. Jahrb. 28: 686 (1901).
S. Sprucei A. DC. in Journ. Bot. 3: 219 (1865).
S. tetradenia Perk. in Notizbl. 10: 163 (1927).
S. tomentosa (R. \& P.) Perk. in Engler, Bot. Jahrb. 28: 691 (1901).

## LAURACEAE

Acrodiclidium benense Rusby in Bull. Torr. Bot. Club, 49: 262 (1922) $=$ Licaria limbosa.
Aniba Coto (Rusby) Kosterm. in Macbr. in Field Mus. Publ. Bot. 13: 863 (1937).
A. gigantifolia O. C. Schmidt in Notizbl. 10: 225 (1928).
A. Muca (R. \& P.) Mez. in Jahrb. Bot. Gart. Berl. 5: 57 (1889).
A. perutilis Hemsl. in Kew Bull. 1894: 197.
A. pseudo-coto (Rusby) Kosterm. in Rec. Trav. Bot. Néerl. 35: 872 (1938).
A. Puchury-minor (Mart.) Mez in Jahrb. Bot. Gart. Berl. 5: 70 (1889).

Endlicheria boliviensis Kosterm. in Rec. Trav. Bot Néerl. 34: 553 (1937).
E. dysodantha (R. \& P.) Mez in Jahrb. Bot. Gart. Berl. 5: 119 (1889).
E. Lhotzkyi (Nees) Mez in Jahrb. Bot. Gart. Berl. 5: 122 (1889).
E. pyriformis (Nees) Mez in Jahrb. Bot. Gart. Berl. 5: 116 (1889).
E. Szyszylowiczii Mez in Jahrb. Bot. Gart. Berl. 5: 121 (1889).
E. tomentella Mez in Jahrb. Bot. Gart. Berl. 5:115 (1889).

Licaria amara (Mez) Kosterm. in Rec. Trav. Bot. Néerl. 34: 583 (1937).
L. limbosa (R. \& P.) Kosterm. in Rec. Trav. Bot. Néerl. 34: 585 (1937).

Nectandra acutifolia (R. \& P.) Mez in Jahrb. Bot. Gart. Berl. 5: 409 (1889).
N. Brittonii Mez in Jahrb. Bot. Gart. Berl. 5: 435 (1889).
N. citrifolia Mez \& Rusby in Mem. Torr. Bot. Club, 6: 115 (1896).
N. cuspidata Nees \& Mart. in Nees, Syst. Laur. 330 (1836).
N. guanaiensis Rusby in Bull. N. Y. Bot. Gard. 6: 508 (1910).
N. laevis Mez in Jahrb. Bot. Gart. Berl. 5: 451 (1889).
N. lanceolata Nees \& Mart. in Linnaea, 8: 47 (1833).
N. Laurel Klotzsch ex Nees in Linnaea, 21: 505 (1848).
N. Pichurim (HBK.) Mez in Jahrb. Bot. Gart. Berl. 5: 449 (1889).
N. pisi Miq. Stirp. Surin. Sel. 199 (1850).
N. pulverulenta Nees, Syst. Laurin. 283 (1836).
N. reticulata (R. \& P.) Mez in Jahrb. Bot. Gart. Berl. 5: 404 (1889).
N. Steinbachii O. C. Schmidt in Fedde, Repert. Spec. Nov. 31: 186 (1933).
N. Warmingii Meissn. in Warm. in Vid. Medd. 1870: 141.

Octea albida Mez \& Rusby in Mem. Torr. Bot. Club, 6: 114 (1896).
O. Bangii Mez \& Rusby in Mem. Torr. Bot. Club, 6: 115 (1896) = Endlicheria pyriformis.
O. cuneifolia (R. \& P.) Mez in Jahrb. Bot. Gart. Berl. 5: 259 (1889).
O. cuprea (Meissn.) Mez in Jahrb. Bot. Gart. Berl. 5: 299 (1889).
O. guianensis Aubl. Pl. Guian. Fr. 2: 781, t. 310 (1775).
O. illustris Rusby in Bull. N. Y. Bot. Gard. 6: 507 (1910).
O. Jelskii Mez in Jahrb. Bot. Gart. Berl. 5: 261 (1889).
O. laxiflora (Meissn.) Mez in Jahrb. Bot. Gart. Berl. 5: 371 (1889).
O. Mandonii Mez in Jahrb. Bot. Gart. Berl. 5: 311 (1889).
O. maranhana Rusby in Bull. N. Y. Bot. Gard. 6: 507 (1910), nomen nudum.
O. marmellensis Mez in Bull. Herb. Boiss. (ser. 2) 3: 238 (1903).
O. marowynensis Mez in Jahrb. Bot. Gart. Berl. 5: 380 (1889).
O. oblanceolata Rusby in Bull. N. Y. Bot. Gard. 6: 507 (1910) $=$ Aniba Muca.
O. oblonga (Meissn.) Mez in Jahrb. Bot. Gart. Berl. 5: 367 (1889).
O. proboscidea Rusby in Bull. N. Y. Bot. Gard. 4: 318 (1907).
O. prunifolia Rusby in Bull. N. Y. Bot. Gard. 4: 439 (1907).
O. reticulata Mez in Jahrb. Bot. Gart. Berl. 5: 303 (1889).
O. rubrinervis Mez in Jahrb. Bot. Gart. Berl. 5: 351 (1889).
O. Rusbyana Mez in Jahrb. Bot. Gart. Berl. 5: 303 (1889).
O. suaveolens var. robusta Hassl. in Ann. Conserv. \& Jard. Bot. Genève, 21: 90 (1919).
Persea boliviensis Mez \& Rusby in Mem. Torr. Bot. Club, 6: 113 (1896).
P. Buchtienii O. C. Schmidt in Fedde, Repert. Spec. Nov. 31: 179 (1933).
P. caerulea (R. \& P.) Mez in Jahrb. Bot. Gart. Berl. 5: 171 (1889).
P. filipes Rusby in Bull. N. Y. Bot. Gard. 6: 505 (1910).
P. gratissima Gaertn. Fruct. 3: 222, t. 221 (1805).
P. laevigata HBK. Nov. Gen. \& Spec. 2: 157 (1817).
P. negracotensis O. C. Schmidt in Fedde, Repert. Spec. Nov. 31: 180 (1933).
P. scoparia Mez in Arb. Bot. Gart. Breslau, 1: 115 (1892).
P. Trollii O. C. Schmidt in Fedde, Repert. Spec. Nov. 31: 180 (1933).
P. vestita Mez in Jahrb. Bot. Gart. Berl. 5: 154 (1889).

Phoebe porphyria (Griseb.) Mez in Jahrb. Bot. Gart. Berl. 5: 199 (1889).

## HERNANDIACEAE

Sparattanthelium acreanum Pilger in Notizbl. 6: 295 (1915).
S. botocudorum Mart. ex Meissn. in Mart. Fl. Bras. 5(2): 293 (1866).
S. Burchellii Rusby in Bull. N. Y. Bot. Gard. 8: 109 (1912).
S. glabrum Rusby in Mem. Torr. Bot. Club, 6: 35 (1896).

## PAPAVERACEAE

Argemone mexicana L. Sp. Pl. 508 (1753).
Bocconia integrifolia Humb. \& Bonpl. Pl. Aequin. 1: 119, t. 35 (1807).
B. Pearcei Hutchinson in Kew Bull. 1920: 278.

## CAPPARIDACEAE

Atamisquea emarginata Miers, Trav. Chile, 2: 529 (1826), nomen nudum.
Capparis Bangii Rusby in Mem. Torr. Bot. Club, 6:5 (1896).
C. cordata R. \& P. ex DC. Prodr. 1: 251 (1824).
C. retusa Griseb. in Goett. Abh. 24: 18 (1879).
C. salicifolia Griseb. in Goett. Abh. 24: 17 (1879).
C. Tweediana Eichl. in Mart. Fl. Bras. 13(1): 273 (1865).

Cleome aculeata L. Syst. (ed. 12) 3: 232 (1768).
C. Bangiana Gilg ex Heilborn in Ark. Bot. 23A (10): 12 (1930).
C. chilensis DC. Prodr. 1: 238 (1824).
C. consimilis A. Ernst in Notizbl. 13: 379 (1936).
C. cordobensis Eichl. ex Griseb. in Goett. Abh. 19: 73 (1874).
C. Eyerdamii Standl. \& Barkl. in Madroño, 9: 150 (1948).
C. Friesii O. Heilborn in Ark. Bot. 23A (10): 7 (1930).
C. gigantea L. Mant. 430 (1771).
C. glandulosa R. \& P. ex DC. Prodr. 1: 238 (1824).
C. Trollii A. Ernst in Notizbl. 13: 380 (1936).
C. tunarensis O. Ktze. Rev. Gen. 3(2): 7 (1898).
C. Werdermannii A. Ernst in Notizbl. 13: 378 (1936).

Morisonia oblongifolia Britton in Bull. Torr. Bot. Club, 16: 17 (1889).

## CRUCIFERAE

Alyssum boliviense Muschl. in Engler, Bot. Jahrb. 40: 275 (1908) $=$ Lesquerella mendocina.
A. Pflanzii Muschl. in Engler, Bot. Jahrb. 49: 201 (1913) = Draba scopulorum.
A. Urbanianum Muschl. in Engler, Bot. Jahrb. 40: 274 (1908) $=$ Lesquerella mendocina.
Arabis bracteata Wedd. in Ann. Sci. Nat. (ser. 5) 1: 291 (1864).
Aschersoniodoxa Mandoniana (Wedd.) Gilg \& Muschl. in Engler, Bot. Jahrb. 42: 469 (1908).
A. Rusbyi O. E. Schulz in Notizbl. 10: 115 (1927).

Brassica juncea Coss. in Bull. Soc. Bot. France, 6: 609 (1859).
Brayopsis calycina (Desv.) Gilg \& Muschl. in Engler, Bot. Jahrb. 42: 484 (1908).
B. calycina var. filiformis O. E. Schulz in Engler, Pflanzenr. IV, 105: 240 (1924).
B. calycina var. filiformis forma leiophylla O. E. Schulz in Engler, Pflanzenr. IV, 105: 240 (1924).
B. calycina var. filiformis forma trichophylla O. E. Schulz in Engler, Pflanzenr. IV, 105: 240 (1924).
B. pycnophylla Gilg \& Muschl. in Engler, Bot. Jahrb. 42: 484 (1909).

Capsella Bursa-pastoris var. rubriflora Muschl. in Engler, Bot. Jahrb. 49: 199 (1913).

Cardamine africana L. Sp. Pl. 655 (1753).
C. axillaris Wedd. in Ann. Sci. Nat. (ser. 5) 1: 290 (1864).
C. chenopodifolia Pers. Synops. Pl. 2: 195 (1807).
C. flaccida subsp. minima (Steud.) O. E. Schulz in Engler, Bot. Jahrb. 32: 451 (1903).
C. hispidula Phil. in Anal. Univ. Chile, 81: 79 (1892).
C. ibaguensis Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 17: 60 (1862).
C. Jamesonii var. speciosa (Britton) O. E. Schulz in Engler, Bot. Jahrb. 32: 422 (1903).
C. ovata Benth Pl. Hartw. 158 (1845).
C. ovata var. corymbosa Britton in Bull. Torr. Bot. Club, 16: 16 (1889).

Cremolobus bolivianus Britton in Bull. Torr. Bot. Club, 16: 17 (1889).
C. parviflorus Wedd. in Ann. Sci. Nat. (ser. 5) 1: 283 (1864).
C. subscandens O. Ktze. Rev. Gen. 3(2): 4 (1898).

Descurainia athroöcarpa (A. Gray) O. E. Schulz in Engler, Pflanzenr. IV, 105: 340 (1924).
D. athroöcarpa var. Gilgiana (Muschl.) O. E. Schulz in Engler, Pflanzenr. IV, 105: 341 (1924).
D. athroöcarpa var. macrorrhiza O. E. Schulz in Engler, Pflanzenr. IV, 105: 341 (1924).
D. depressa (Phil.) Prantl in Anal. Univ. Chile, 90: 148 (1895).
D. depressa var. Pflanzii (Muschl.) O. E. Schulz in Engler, Pflanzenr. IV, 105: 339 (1924).
D. latisiliqua O. E. Schulz in Engler, Pflanzenr. IV, 105: 336 (1924).
D. leptoclada Muschl. in Engler, Bot. Jahrb. 40: 272 (1908).
D. Perkinsiana Muschl. in Engler, Bot. Jahrb. 49: 199 (1913).
D. pulcherrima Muschl. in Engler, Bot. Jahrb 49: 200 (1913).
D. Urbaniana Muschl. in Engler, Bot. Jahrb. 40: 271 (1908) = D. athroöcarpa.

Draba affinis Hook. f. Fl. Antarct. 2: 235 (1847).
D. boliviana O. E. Schulz in Engler, Pflanzenr. IV, 105: 168 (1927).
D. Brackenridgei A. Gray in Bot. U. S. Explor. Exped. 1: 53 (1854).
D. cephalantha Gilg in Engler, Bot. Jahrb. $42: 477$ (1908) $=$ D. Brackenridgei.
D. discoidea Wedd. in Ann. Sci. Nat. (ser. 5) 1: 286 (1864).
D. discoidea var. leiocarpa O. E. Schulz in Engler, Pflanzenr. IV, 105: 167 (1927).
D. discoidea var. minor Wedd. ex O. E. Schulz in Engler, Pflanzenr. IV, 105: 167 (1927).
D. Herzogii O. E. Schulz in Engler, Pflanzenr. IV, 105: 168 (1927).
D. Macleanii Hook. f. Fl. Antarct. 2: 235 (1847).
D. Pickeringii var. Pearcei O. E. Schulz in Engler, Pflanzenr. IV, 105: 135 (1927).
D. scopulorum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 286 (1864).
D. scopulorum forma elongata Wedd. in Ann. Sci. Nat. (ser. 5) 1: 287 (1864).
D. soratensis Wedd. in Ann. Sci. Nat. (ser. 5) 1: 287 (1864).

Erysimum laxum Muschl. in Engler, Bot. Jahrb. 40: 273 (1908) = Sisymbrium peruvianum.
Eudema diapensioides (Wedd.) O. E. Schulz in Engler, Pflanzenr. IV, 105: 245 (1924).

Halimolobos adpressa O. E. Schulz in Engler, Pflanzenr. IV, 105: 293 (1924).
H. hispidula var. Weddellii (Fourn.) Rollins in Contrib. Dudley Herb. 3: 252 (1943).
H. montana (Griseb.) O. E. Schulz in Engler, Pflanzenr. IV, 105: 292 (1924).

Heterothrix gracilis (Wedd.) O. E. Schulz in Engler, Pflanzenr. IV, 105: 297 (1924).

Hutchinsia pusillima Wedd. in Ann. Sci. Nat. (ser. 5) 1: 284 (1864).
Lepidium abrotanifolium Turcz. in Bull. Soc. Nat. Mosc. 27 (2): 308 (1854).
L. abrotanifolium var. Steinmannii Thell. in Denkschr. Schweiz. Ges. Naturwiss. 41(1): 247 (1906).
L. affine Wedd. in Ann. Sci. Nat. (ser. 5) 1: 284 (1864) = L. Weddellii.
L. angustifolium Rusby, Descr. S. Am. Pls. 23 (1920) [possibly not Lepidium].
L. bipinnatifidum Desv. in Journ. Bot. 3: 165 (1814), nomen nudum.
L. Chichicara Desv. in Journ. Bot. 3: 165 (1814), nomen nudum.
L. Chichicara var. rhombocarpum Thell. in Fedde, Repert. Spec. Nov. 11: 309 (1912).
L. depressum Thell. in Denkschr. Schweiz. Ges. Naturwiss. 41 (1): 201 (1906).
L. demissum C. L. Hitchc. in Lilloa, 11: 121 (1945).
L. Meyenii subsp. gelidum (Wedd.) Thell. in Denkschr. Schweiz. Ges. Naturwiss. 41(1): 203 (1906).
L. Meyenii subsp. gelidum forma rhombicum Thell. in Mitteil. Bot. Mus. Univ. Zürich, 28: 203 (1906).
L. Meyenii subsp. gelidum forma rotundatum Thell. in Mitteil. Bot. Mus. Univ. Zürich, 28: 203 (1906).
L. Philippianum (O. Ktze.) Thell. in Denkschr. Schweiz. Ges. Naturwiss. 41(1): 200 (1906).
L. Philippianum var. boliviense Thell. in Denkschr. Schweiz. Ges. Naturwiss. 41(1): 201 (1906).
L. quitense var. integrifolium Thell. in Denkschr. Schweiz. Ges. Naturwiss. 41(1): 213 (1906).
L. reticulatum var. austro-americanum Thell. in Bull. Herb. Boiss. (ser. 2) 8: 914 (1908).
L. scabrifructum C. L. Hitchc. in Lilloa, 11: 119 (1945).
L. Steinbachii O. E. Schulz in Notizbl. 9: 1037 (1926).
L. Trianae Thell. in Denkschr. Schweiz. Ges. Naturwiss. 41(1): 214 (1906).
L. Walpersii Macbr. in Candollea, 5: 357 (1934) $=$ L. depressum.
L. Weddellii O. E. Schulz in Notizbl. 11: 391 (1932).

Lesquerella mendocina (Phil.) Kurtz in Rev. Mus. LaPlata, 5: 286 (1893).
Mancoa foliosa (Wedd.) O. E. Schulz in Engler , Bot. Jahrb. 66: 98 (1933).
M. hispida Wedd. in Ann. Sci. Nat. (ser. 5) 1: 285 (1864).
M. laevis Wedd. in Ann. Sci. Nat. (ser. 5) 1: 285 (1864).
M. minima Rollins in Contrib. Dudley Herb. 3: 194 (1941).

Mathewsia boliviana Gilg \& Muschl. in Engler, Bot. Jahrb. 42: 464 (1908) = Rorippa nana.
M. diffusa Rusby in Bull. N. Y. Bot. Gard. $4: 322$ (1907) = Rorippa sp. ?

Nasturtium bonariense var. erectum (Trev.) O. E. Schulz in Fedde, Repert. Spec. Nov. 33: 283 (1934).
N. clandestinum var. brevistylum O. E. Schulz in Fedde, Repert. Spec. Nov. 33: 283 (1934).
N. pubescens var. punense O. Ktze. Rev. Gen. 3(2): 6 (1898).
N. pubescens var. serratifolium O. Ktze. Rev. Gen. 3(2): 6 (1898).

Polypsecadium Harmsianum (Muschl.) O. E. Schulz in Engler, Pflanzenr. IV, 105: 177 (1924).
P. Harmsianum var. dentatum (Muschl.) O. E. Schulz in Engler, Pflanzenr. IV, 105: 177 (1924).
Radicula scabra Rusby, Descr. S. Am. Pls. 23 (1920) = Mancoa hispida.
R. nana (Wedd.) Rusby, Descr. S. Am. Pls. 23 (1920) = Rorippa nana.

Rorippa nana (Schlechtd.) Macbr. in Field Mus. Publ. Bot. 13(2): 965 (1938).
R. Nasturtium-aquaticum (L.) G. Beck, Fl. Nied.-Oesterr. 1: 463 (1892).

Sarcodraba Herzogii O. E. Schulz in Notizbl. 10: 563 (1929).
Sisymbrium anomalum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 289 (1864) $=$ S. peruvianum.
S. calycinum (Desv.) Wedd. in Ann. Sci. Nat. (ser. 5) 1: 289 (1864).
S. fragile Wedd. in Ann. Sci. Nat. (ser. 5) 1: 288 (1864).
S. lanatum (Walp.) O. E. Schulz in Notizbl. 11: 642 (1932).
S. Mandonii Fourn. Thèse Crucif. 109 (1865).
S. officinale (L.) Scopoli, Fl. Carn. (ed. 2) 2: 26 (1772).
S. oliganthum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 289 (1864) $=$ Weberbauera pusilla.
S. Orbignyanum Fourn. Thèse Crucif. 107 (1865).
S. orophilum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 288 (1864).
S. pazensis Rusby in Mem. Torr. Bot. Club, 3 (3): 5 (1893) $=$ Halimolobos Weddellii.
S. peruvianum DC. Syst. Nat. 2: 477 (1821).
S. Rusbyi Britton in Bull. Torr. Bot. Club, 16: 16 (1889).
S. setaceum Wedd. in Ann. Sci. Nat. (ser. 5) 1: 289 (1864).

Streptanthus boliviensis Muschl. in Engler, Bot. Jahrb. 40: 268 (1908) = Heterothrix gracilis.
Thlaspi alpestre L. Sp. Pl. (ed. 2) 2: 903 (1763).
Weberbauera pusilla (Gill.) O. E. Schulz in Engler, Pflanzenr. IV, 105: 194 (1924).

## TOVARIACEAE

Tovaria pendula R. \& P. Fl. Peruv. 3: 73, t. 306 (1802).

## DROSERACEAE

Drosera montana St. Hil. Pl. Remarq. Brés. 260 (1824).

## PODOSTEMACEAE

Apinagia boliviana v. Roy. in Meded. Bot. Mus. Utrecht, 107: 130 (1951).
A. fluitans v. Roy. in Meded. Bot. Mus. Utrecht, 107: 128 (1951).

## CRASSULACEAE

Cotyledon peruvianum Baker in Saund. Ref. Bot. 1: sub t. 58 (1869).
Echeveria Buchtienii v. Poelln. in Fedde, Repert. Spec. Nov. 36: 193 (1934).
E. chilonensis (O. Ktze.) E. Walther in Cact. \& Succ. Journ. 7: 40 (1935).
E. quitensis (HBK.) Lindl. in Journ. Hort. Soc. 7: 268 (1852).
E. Whitei Rose in Addisonia, 10: 47, t. 344 (1925).

Sedum cymatopetalum Fröd. in Act. Hort. Gotoberg. 10: 83 (1935).
Tillaea connata R. \& P. Fl. Peruv. 1: 70, t. 106 (1798).

## SAXIFRAGACEAE

Escallonia aculeata O. Ktze. Rev. Gen. 3(2): 81 (1898).
E. adscendens Rusby in Mem. Torr. Bot. Club, 6: 32 (1896) = E. corymbosa.
E. Bridgesii Rusby in Mem. Torr. Bot. Club. 6: 32 (1896).
E. corymbosa (R. \& P.) Pers. Synops. Pl. 1: 234 (1805).
E. hypoglauca Herzog in Meded. Rijks Herbar. 27: 88 (1915).
E. Mandonii Rusby in Mem. Torr. Bot. Club, 3(3): 25 (1893).
E. Mandonii var. microphylla Herzog in Meded. Rijks Herbar. 27: 89 (1915).
E. millegrana Griseb. in Goett. Abh. 24: 141 (1879).
E. myrtilloides L. f. Suppl. 156 (1781).
E. paniculata var. acuminatissima O. Ktze. Rev. Gen. 3(2): 81 (1898).
E. resinosa (R. \& P.) Pers. Synops. Pl. 1: 235 (1805).

Hieronymusia alchemilloides (Griseb.) Engl. in Notizbl. 7: 267 (1918).
Hydrangea Bangii Engl. in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 18A: 207 $(1930)=\mathrm{H}$. tarapotensis.
H. scandens Poepp. ex DC. Prodr. 4: 666 (1830).
H. tarapotensis Briq. in Ann. Conserv. \& Jard. Bot. Genève, 20: 415 (1919).

Phyllonoma integerrima (Turcz.) Britton in Bull. Torr. Bot. Club, 17: 11 (1890).
P. ruscifolia Willd. ex Roem. \& Schult. Syst. Veg. 6: 210 (1820).

Ribes albifolium R, \& P. Fl. Peruv. 3: 12, t. 232 (1802).
R. bolivianum Jancz. in Bull. Acad. Sci. Cracov. 1905: 759.
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A. elongata L. Mant. 200 (1771).
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A. hirsuta HBK. Nov. Gen. \& Spec. 6: 224 (1824) = Lachemilla sp.
A. pinnata forma rosulata Pilg. ex Rothm. in Trab. Mus. Nac. Cienc. Nat. 21: 33 (1935) = Lachemilla sp.
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H. Sprucei Benth. ex Hook. f. in Mart. Fl. Bras. 14 (2): 30 (1867).
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H. triandra Sw. Prodr. 51 (1788).

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P. incana subsp. brachypoda Bitter in Engler, Bot. Jahrb. 45: 644 (1911).
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P. racemosa var. lanata O. Ktze. Rev. Gen. 3(2): 77 (1898).
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P. tomentella Wedd. Chlor. And. 2: 237, t. 78 (1861).
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R. nubigenus HBK. Nov. Gen. \& Spec. 6: 220 (1824).
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R. camptoneura Radlk. in Sitzb. Bayer. Akad. Wiss. Münch. 14: 375 (1886).
R. glabra var. trifoliolata Britton in Bull. Torr. Bot. Club, 16: 192 (1889) $=$ R. camptoneura.
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A. boliviana Rusby in Bull. N. Y. Bot. Gard. 4: 348 (1907).
A. bonariensis Gill. ex Hook. Bot. Misc. 3: 207 (1832).
A. Farnesiana (L.) Willd. Sp. Pl. 4 (2): 1083 (1806).
A. Feddeana Harms in Fedde, Repert. Spec. Nov. 16: 450 (1920).
A. Fiebrigii Harms in Fedde, Repert. Spec. Nov. 16: 351 (1920) = A. Feddeana.
A. furcata Gill in Hook. Bot. Misc. 3: 206 (1832).
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A. Michelii Rusby in Mem. Torr. Bot. Club, 6: 28 (1896).
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A. praecox Griseb. in Goett. Abh. 19: 136 (1874).
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A. patancana Ulbr. in Engler, Bot. Jahrb. 37: 554 (1906).
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A. polyacantha Wedd. Chlor. And. 2: 265 (1861).
A. rupicola Wedd. Chlor. And. 2: 266, t. 79 bis (1861).
A. Schickendantzii Griseb. in Goett. Abh. 24: 104 (1879).
A. spinosissima Meyen, Reise, 2: 27 (1835).

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Ae. apoloana Rusby in Bull. N. Y. Bot. Gard. 6: 511 (1910) $=$ Ae. falcata.
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Ae. denticulata Rudd in Contrib. U. S. Nat. Herb. 32: 69 (1955).
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Ae. evenia Wright in Sauvalle in Anal. Acad. Cienc. Habana, 5: 334 (1868).
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Ae. pratensis var. caribaea Rudd in Contrib. U. S. Nat. Herb. 32: 47 (1955).
Ae. rudis Benth. Pl. Hartw. 116 (1843).
Ae. sensitiva Sw. Prodr. 107 (1788).
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A. cearensis (Allem.) A. C. Smith in Trop. Woods, 62: 30 (1940).

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Amicia fimbriata Harms ex O. Ktze. Rev. Gen. 3(2): 49 (1898).
A. Lobbiana Benth. ex Rusby in Mem. Torr. Bot. Club, 3(3): 20 (1893).
A. medicaginea Griseb. in Goett. Abh. 24: 105 (1879).
A. micrantha Harms ex O. Ktze. Rev. Gen. 3(2): 49 (1898).
A. parvula Rusby in Mem. Torr. Bot. Club, 6: 23 (1896).

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A. prostrata Benth. in Trans. Linn. Soc. 18: 159 (1839).

Astragalus arequipensis Vog. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 17 (1843).
A. bolivianus Phil. Cat. Pl. Itin. Tarapaca, 15 (1891) $=$ A. arequipensis.
A. capitellus Britton in Bull. Torr. Bot. Club, 16: 260 (1889) =A. micranthellus.
A. colliculus Rusby in Mem. Torr. Bot. Club, 3 (3) : 19 (1893). = A. minimus.
A. crymophilus I. M. Johnst. in Journ. Arnold Arb. 28: 400 (1947).
A. cryptanthus Wedd. Chlor. And. 2: 259 (1861).
A. deminutivus I. M. Johnst. in Journ. Arnold Arb. 28: 406 (1947).
A. flavocreatus I. M. Johnst. in Journ. Arnold Arb. 28: 405 (1947).
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A. gracilis Romero in Bol. Direc. Nac. Estad. y Estud. Geogr. La Paz, sec. Epoc. III, nos. 31-33: 45 (1920).
A. Herzogii Ulbr. in Meded. Rijks Herbar. 27: 53 (1915) = A. uniflorus.
A. Hieronymi Ulbr. in Engler, Bot. Jahrb. 37: 418 (1906) $=$ A. tarijensis.
A. hypsogenus I. M. Johnst. in Journ. Arnold Arb. 28: 399 (1947).
A. Mandonii Rusby in Mem. Torr. Bot. Club, $3(3): 19$ (1893) $=$ A. Garbancillo.
A. micranthellus Wedd. Chlor. And. 2: 262 (1861).
A. minimus Vog. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 18 (1843).
A. minutissimus Wedd. Chlor. And. 2: 257 (1861).
A. modestus Wedd. Chlor. And. 2: 262 (1861) $=$ A. Weddellianus.
A. Orbignyanus Wedd. Chlor. And. 2: $260(1861)=$ A. arequipensis.
A. patancanus Ulbr. in Engler, Bot. Jahrb. 37: 417 (1906) = A. micranthellus.
A. peruvianus Vog. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 18 (1843).
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A. Reichei Speg. in Anal. Mus. Nac. Buenos Aires (ser. 2), 4: 264 (1902).
A. sinocarpus Rusby in Mem. Torr. Bot. Club, $3(3): 19$ (1893) $=$ A. arequipensis.
A. tarijensis Wedd. Chlor. And. 2: 262 (1861).
A. uniflorus (Dombey) DC. Astrag. 243 (1802).
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B. Conwayi Rusby in Bull. N. Y. Bot. Gard. 8: 92 (1912).
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B. Langsdorffiana Bong. in Mém. Acad. St. Pétersb. (ser. 4) 6: 109 (1836).
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B. Rusbyi Britton in Bull. Torr. Bot. Club, 16: 326 (1889).
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C. coluteifolia Griseb. in Goett. Abh. 24: 111 (1879).
C. coulterioides Griseb. in Goett. Abh. 24: 113 (1879).
C. fimbriata Tul. in Arch. Mus. Paris, 4: 145 (1845).
C. Fisheriana Rusby in Mem. Torr. Bot. Club, 3(3): 23 (1893).
C. floribunda Tul. in Arch. Mus. Paris, 4: 140 (1845).
C. Herzogii Harms in Meded. Rijks Herbar. 27: 38 (1915) = C. Steckertii.
C. mimosifolia Griseb. in Goett. Abh. 19: 128 (1874).
C. pulcherrima (L.) Swartz, Obs. 166 (1791).
C. rosulata Rusby in Mem. Torr. Bot. Club, 3(3): 23 (1893).
C. Stuckertii Hassl. in Fedde, Repert. Spec. Nov. 12: 201 (1913).

Cajanus indicus Spreng. Syst. Veg. 3: 248 (1826).
Calliandra boliviana Britton in Bull. Torr. Bot. Club, 16: 327 (1889).
C. formosa (Kunth) Benth. in Hook Lond. Journ. Bot. 3: 98 (1844).
C. inaequilatera Rusby in Mem. Torr. Bot. Club, 6: 28 (1896).
C. portoricensis (Jacq.) Benth. in Hook. Lond. Journ. Bot. 3: 99 (1844).
C. stricta Rusby in Mem. N. Y. Bot. Gard. 7: 255 (1927).

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C. brasiliensis Mart. ex Benth. in Ann. Naturh. Hofmus. Wien, 2: 135 (1838).
C. ensiformis (L.) DC. Prodr. 2: 404 (1825).
C. lasiocalyx O. Ktze. Rev. Gen. 3(2): 55 (1898).
C. obtusifolia DC. Prodr. 2: 404 (1825).
C. villosa Benth. in Ann. Naturh. Hofmus. Wien, 2: 135 (1838).

Cardenasia setacea Rusby in Mem. N. Y. Bot. Gard. 7: 259, fig. 3 (1927).
Cascaronia astragalina Griseb. in Goett. Abh. 24: 100 (1879).
Cassia Absus L. Sp. Pl. 376 (1753).
C. acinicarpa Rusby in Bull. N. Y. Bot. Gard. 4: 311 (1907).
C. affinis Benth. in Mart. Fl. Bras. 15(2): 98 (1870).
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M. boliviana Benth. in Trans. Linn. Soc. 30: 396 (1875).
M. carinata Griseb. in Goett. Abh. 24: 120 (1879).
M. eurycarpa Herzog in Fedde, Repert. Spec. Nov. 7: 53 (1909) =M. Herzogii.
M. floribunda Willd. Sp. Pl. 4(2): 1031 (1806).
M. glaucescens var. ramosa Benth. in Mart. Fl. Bras. 15(2): 308 (1876).
M. gonoclada Benth. in Trans. Linn. Soc. 30: 427 (1875).
M. grandistipula Herzog in Fedde, Repert. Spec. Nov. 7: 53 (1909).
M. Herzogii Macbr. in Contrib. Gray Herb. 59: 14 (1919).
M. insidiosa Mart. Herb. Fl. Bras. 134 (1837).
M. invisa Mart. ex Colla, Herb. Pedem. 2: 255 (1834).
M. ixiamensis Rusby in Bull. N. Y. Bot. Gard. 8: 91 (1912).
M. Kuntzei Harms in O. Ktze. Rev. Gen. 3(2): 67 (1898) $=$ M. boliviana.
M. lepidota Herzog in Fedde, Repert. Spec. Nov. 7: 53 (1909).
M. Lorentzii Griseb. in Goett. Abh. 19: 134 (1874).
M. neptunioides Harms ex O. Ktze. Rev. Gen. 3(2): 67 (1898).
M. nuda Benth. in Hook. Journ. Bot. 4: 362 (1841).
M. orthacantha Benth. in Hook. Journ. Bot. 4: 365 (1841).
M. parapitiensis Burkart in Bol. Soc. Argent. Bot. 1(1): 36 (1945).
M. pigra L. Cent. Pl. 1: 13 (1755).
M. polycarpa Kunth, Mimos. 8, t. 3 (1819).
M. revoluta (Kunth) Benth. in Hook. Journ. Bot. 4: 409 (1841).
M. rixosa Mart. in Flora, 21 (II Beibl.) : 57 (1838).
M. rufescens Benth. in Mart. Fl. Bras. 15(2): 362 (1876).
M. sensibilis Griseb. in Goett. Abh. 24: 119 (1879).
M. somnians Humb. \& Bonpl. ex Willd. Sp. Pl. 4 (2): 1036 (1806).
M. soratensis Benth. in Trans. Linn. Soc. 30: 427 (1875).
M. 'Steinbachii Harms in Notizbl. 9: 1038 (1926).
M. stenoptera Benth. in Trans. Linn. Soc. 30: 395 (1875).
M. subsericea Benth. in Hook. Journ. Bot. 4: 380 (1841).
M. velascoënsis Harms ex O. Ktze. Rev. Gen. 3(2): 68 (1898).
M. Velloziana Mart. in Flora, 22 (I Beibl.): 9 (1839).
M. Williamsii Rusby in Bull. N. Y. Bot. Gard. 8: 91 (1912).

Mucuna mapirensis (Rusby) Macbr. in Field Mus. Publ. Bot. 13(3): 315 (1943).
M. rostrata Benth. in Mart. Fl. Bras. 15(1): 171, t. 47 (1859).

Myroxylon peruiferum L. f. Suppl. 233 (1781).
Neocracca Kuntzei O. Ktze. Rev. Gen. 3 (2): 68 (1898) = Cracca heterantha.
Nissolia fruticosa Jacq. Enum. Pl. Carib. 27 (1760).
Ormosia bopiensis Pierce ex Macbr. in Field Mus. Publ. Bot. 13: 248 (1943).
Pachyrhizus bulbosus (L.) Britton in Bull. Torr. Bot. Club, 16: 324 (1889).
P. tuberosus (Lam.) Spreng. Syst. 4: Cur. Post. 281 (1827).

Parkinsonia aculeata L. Sp. Pl. 375 (1753).
Parosela oblongifolia Rusby in Mem. N. Y. Bot. Gard. 7: 262 (1927) = Dalea sp.
P. pilocarpa Rusby in Mem. N. Y. Bot. Gard. 7: 261 (1927) = Dalea sp.

Patagonium alcicornutum Rusby in Bull. N. Y. Bot. Gard. 6: 512 (1910) $=$ Adesmia sp.?
P. grandidentatum Rusby in Mem. Torr. Bot. Club, 6: 24 (1896) $=$ Adesmia sp. ?
P. scabridum Rusby in Bull. N. Y. Bot. Gard. 6: 512 (1910) $=$ Adesmia sp.?

Phaseolus adenanthus var. radicans (Benth.) Hassl. in Candollea, 1: 443 (1923).
P. Augustii Harms in Notizbl. 7: 503 (1921).
P. bolivianus Piper in Contrib. U. S. Nat. Herb. 22: 694 (1926).
P. bracteolatus Nees \& Mart. in Nov. Act. Acad. Caes. Leop. 12: 27 (1824).
P. campestris (Benth.) Mart. ex Benth. in Mart. Fl. Bras. 15(1): 188 (1859).
P. caracalla L. Sp. Pl. 725 (1753).
P. erythroloma (Benth.) Mart. ex Benth. in Mart. Fl. Bras. 15(1): 191 (1859).
P. fraternus Piper in Contrib. U. S. Nat. Herb. 22: 679 (1926).
P. lathyroides L. Sp. Pl. (ed. 2) 1018 (1763).
P. ligulatus Piper in Contrib. U. S. Nat. Herb. 22: 676 (1926).
P. longipedunculatus var. linearifoliolatus forma boliviensis Hassl. in Candollea, 1: 453 (1923).
P. ovatus (Benth.) Benth. in Mart. Fl. Bras. 15(1): 188 (1859).
P. peduncularis HBK. Nov. Gen. \& Spec. 6: 447 (1824).
P. prostratus Benth. in Mart. Fl. Bras. 15(1): 192 (1859).
P. prostratus var. angustifolius forma flavoviridis O. Ktze. Rev. Gen. 3(2): 70 (1898).
P. prostratus forma macrophyllus Hassl. in Candollea, 1: 459 (1923).
P. rigidus Piper in Contrib. U. S. Nat. Herb. 22: 699 (1926).
P. truxillensis HBK. Nov. Gen. \& Spec. 6: 451 (1824).
P. vignoides Rusby in Bull. N. Y. Bot. Gard. 4: 345 (1907) $=$ Canavalia lasiocalyx.

Piptadenia colubrina (Vell.) Benth. in Hook. Journ. Bot. 4: 341 (1841).
P. communis Benth. in Hook. Journ. Bot. 4: 337 (1841).
P. macrocarpa Benth. in Hook. Journ. Bot. 4: 341 (1841).

Pithecellobium angustifolium (Rusby) Rusby in Mem. N. Y. Bot. Gard. 7: 253 (1927) = P. sophorocarpum.
P. bifoliolum Rusby in Mem. N. Y. Bot. Gard. 7: 254 (1927).
P. dependens Rusby in Mem. N. Y. Bot. Gard. 7: 253 (1927).
P. divaricatum Benth. in Hook. Lond. Journ. Bot. 3: 213 (1844).
P. latifolium (L.) Benth. in Hook. Lond. Journ. Bot. 2: 214 (1844).
P. laxiforum Rusby in Mem. Torr. Bot. Club, 3(3): 24 (1893).
P. niopoides Spruce ex Benth. in Mart. Fl. Bras. 15(2): 447 (1876).
P. pedicellare Benth. in Hook. Lond. Journ. Bot. 3: 219 (1844).
? P. pendulum Lindm. in Bihang Kgl. Sv. Vet. Akad. Handl. 24 (Afd. 3, no. 7): 51 (1898).
P. Saman (Jacq.) Benth. in Hook. Lond. Journ. Bot. 3: 216 (1844).
P. scalare Griseb. in Goett. Abh. 24: 123 (1879).
P. sophorocarpum Benth. in Benth. \& Hook. f. Gen. Pl. 1: 598 (1865).
P. trapezifolium (Vahl) Benth. in Hook. Lond. Journ. Bot. 3: 204 (1844).
P. tortum Mart. Herb. Fl. Bras. 114 (1837).
P. venosum Rusby in Mem. Torr. Bot. Club, 6: 29 (1896).

Platymiscium cochabambense Rusby in Mem. Torr. Bot. Club, 6: 26 (1896).
P. ellipticum Rusby in Bull. N. Y. Bot. Gard. 6: 514 (1910).
P. fragrans Rusby in Mem. N. Y. Bot. Gard. 7: 267 (1927).

Poiretia scandens Vent. Choix de Pl. t. 42 (1803).
Prosopis Algarobillo Griseb. in Goett. Abh. 19: 131 (1874).
P. ferox Griseb. in Goett. Abh. 24: 118 (1879).
P. Herzogii Harms in Meded. Rijks Herbar. 27: 35 (1915).
P. juliflora (Sw.) DC. Prodr. 2: 447 (1825).
P. Kuntzei Harms ex O. Ktze. Rev. Gen. 3(2): 71 (1898).
P. nigra (Griseb.) Hieron. in Bol. Acad. Nac. Córdova, 4: 283 (1881).
P. ruscifolia Griseb. in Goett. Abh. 19: 130 (1874).

Psoralea glandulosa L. Sp. Pl. (ed. 2) 1075 (1763).
P. lasiostachys Vog. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 13 (1843).
P. lasiostachys var. potens (Macbr.) Macbr. in Field Mus. Publ. Bot. 8: 88 (1930).
P. mexicana (L. f.) A. M. Vail in Bull. Torr. Bot. Club, 21: 119 (1894).
P. Mutisii HBK. Nov. Gen. \& Spec. 6: 487 (1824).
P. timorata Macbr. in Field Mus. Publ. Bot. 8: 89 (1930).

Pterocarpus Steinbachianus Harms in Notizbl. 9: 1039 (1926).
P. violaceus Vog. in Linnaea, 11: 416 (1837).

Pterogyne nitens Tul. ex Benth. in Mart. Fl. Bras. 15(2): 245, t. 64 (1870),
Rhynchosia apoloënsis (Rusby) Macbr. in Field Mus. Publ. Bot. 4: 91 (1925).
R. caribaea (Jacq.) DC. Prodr. 2: 384 (1825).
R. corylifolia Mart. ex Benth. in Mart. Fl. Bras. 15(1): 202 (1859).
R. minima (L.) DC. Prodr. 2: 385 (1825).

Samanea coripatensis (Rusby) Killip ex Record in Trop. Woods, 63: 6 (1940).
Sclerolobium Radlkoferi Rusby in Mem. Torr. Bot. Club, 6: 26 (1896).
S. tinctorium Benth. in Hook. Journ. Bot. Misc. 2: 236 (1850).

Sophora macrocarpa Smith in Rees, Cycl. 33: no. 6 (1819).
Spartium junceum L. Sp. Pl. 708 (1753).
Steinbachiella leptoclada Harms in Notizbl. 10: 345 (1928).
Stylosanthes Bangii Taub. in Rusby in Mem. Torr. Bot. Club, 4(3): 206 (1895).
S. gracilis var. vulgaris Burkart in Darwiniana, 3: 247 (1939).
S. guianensis (Aubl.) Sw. in Vet. Acad. Stockh. 1789: 296.
S. guianensis var. subviscosa Benth. in Mart. Fl. Bras. 15(1): 92 (1859).
S. hamata (L.) Taub. in Abh. Bot. Ver. Brandenb. 32: 22, fig. 22 (1890).
S. juncea Micheli in Mém. Soc. Phys. Hist. Nat. Genève, 28 (7): 19 (1883).
S. montevidensis Vog. in Linnaea, 12: 67 (1838).
S. scabra Vog. in Linnaea, 12: 69 (1838).

Swartzia Jorori Harms in Meded. Rijks Herbar. 27: 39 (1915).
S. Matthewsii Benth. in Hook. Ic. Pl. 11: 51, t. 1064 (1870).

Tamarindus indica L. Sp. Pl. 34 (1753).
Tephrosia adunca Benth. in Ann. Nat. Hist. (ser. 1) 3: 432 (1839).
T. leptostachya DC. Prodr. 2: 251 (1825).
T. toxicaria Pers. Synops. Pl. 2: 329 (1807).

Teramnus uncinatus (L.) Sw. Fl. Ind. Occ. 3: 1239 (1806).
Tipuana speciosa Benth. in Journ. Linn. Soc. 4: Suppl. 72 (1860).
Tounatea arborescens (Aubl.) Britton in Bull. Torr. Bot. Club, 16: 325 (1889).
T. costata Rusby, Descr. S. Am. Pls. 28 (1920).
T. fugax (Spruce) Britton in Bull. Torr. Bot. Club, 16: 325 (1889).

Tragacantha arequibensis var. minima O. Ktze. Rev. Gen. 3 (2): 73 (1898) $=$ Astragalus micranthellus.
T. arequibensis var. tenuifolia O. Ktze. Rev. Gen. 3(2): 73 (1898) = Astragalus micranthellus.
Trifolium amabile HBK. Nov. Gen. \& Spec. 6: 503, t. 593 (1824).
T. peruvianum Vog. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 12 (1843).

Vicia acerosa Clos in Gay, Hist. Chile, 2: 137 (1846).
V. graminea Smith in Rees, Cycl. 37: no. 27 (1819).
V. montevidensis Vog. in Linnaea, 13: 34 (1839).
V. setifolia HBK. Nov. Gen. \& Spec. 6: 500 (1824).

Vigna myrtifolia Piper in Contrib. U. S. Nat. Herb. 22: 666 (1926).
Zornia diphylla (L.) Pers. Synops. Pl. 2: 318 (1807).
Z. diphylla var. latifolia (DC.) Benth. in Mart. Fl. Bras. 15(1): 81 (1859).

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Biophytum bolivianum R. Knuth in Engler, Pflanzenr. IV, 130: 403 (1930).
B. ferrugineum Rusby in Bull. N. Y. Bot. Gard. 8: 95 (1912).
B. globuliflorum R. Knuth in Engler, Pflanzenr. IV, 130: 403 (1930).
B. mapirense R. Knuth in Engler, Pflanzenr. IV, 130: 405 (1930).
B. mapirense var. hirtum R. Knuth in Engler, Pflanzenr. IV, 130: 405 (1930).
B. peruvianum R. Knuth in Engler, Pflanzenr. IV, 130: 402 (1930).

Hypseocharis corydalifolia R. Knuth in Engler, Bot. Jahrb. 41: 173 (1908).
H. Fiebrigii R. Knuth in Engler, Bot. Jahrb. 41: 173 (1908).
H. malpasensis R. Knuth in Fedde, Repert. Spec. Nov. 29: 219 (1931).
H. moschata R. Knuth in Meded. Rijks Herbar. 27: 67 (1915).
H. pedicularifolia R. Knuth in Engler, Bot. Jahrb. 41: 173 (1908).
H. pimpinellifolia Remy in Ann. Sci. Nat. (ser. 3) 8: 239 (1847).
H. tridentata Griseb. in Goett. Nachr. 1877: 495.

Ionoxalis canaminensis Rusby in Mem. N. Y. Bot. Gard. 7: 269 (1927) $=$ Oxalis sp.
Lotoxalis pseudosepium Rusby in Mem. N. Y. Bot. Gard. 7: 269 (1927) = Oxalis sepium.
Oxalis aetheria Macbr. in Candollea, 6:8(1934) $=$ O. pygmaea.
O. adpressa R. Knuth in Engler, Pflanzenr. IV, 130: 160 (1930).
O. affinis R. Knuth in Meded. Rijks Herbar. 27: 61 (1915) = O. cognita.
O. albicans var. sericea DC. Prodr. 1: 693 (1824).
O. andina Britton in Bull. Torr. Bot. Club, 16: 159 (1889).
O. aphylla Rusby in Bull. N. Y. Bot. Gard. 8: 95 (1912).
O. arenaria Bert. in Merc. Chil. 16: 739 (1829).
O. Asplundii R. Knuth in Fedde, Repert. Spec. Nov. 24: 53 (1927).
O. azanaquensis R. Knuth in Fedde, Repert. Spec. Nov. 29: 217 (1931).
O. Bangii Rusby in Bull. N. Y. Bot. Gard. 4: 337 (1907).
O. Barrelieri L. Sp. Pl. (ed. 2) 1: 624 (1762).
O. bermejensis R. Knuth in Notizbl. 7: 312 (1919).
O. bipartita St. Hil. Fl. Bras. Mer. 1: 125, t. 25 (1825).
O. bisfracta Turcz. in Bull. Soc. Nat. Mosc. 36(1): 595 (1863),
O. boliviana Britton in Bull. Torr. Bot. Club, 16: 159 (1889).
O. breviramulosa Rusby in Mem. Torr. Bot. Club, 3(3): 13 (1893)
O. brunneo-pilosa R. Knuth in Fedde, Repert. Spec. Nov. 29: 215 (1931).
O. Buchtienii (Rusby) R. Knuth in Fedde, Repert. Spec. Nov. 24: 55 (1927).
O. bulbifera R. Knuth in Notizbl. 7: 310 (1919).
O. calachaccensis R. Knuth in Meded. Rijks Herbar. 27: 64 (1915) $=0$. breviramulosa.
O. capitata R. Knuth in Meded. Rijks Herbar. 27: 61 (1915).
O. carnosa Molina, Sagg. Stor. Nat. Chil. (ed. 2) 288 (1810).
O. chacoënsis R. Knuth in Fedde, Repert. Spec. Nov. 23: 138 (1926).
O. charaguensis R. Knuth in Meded. Rijks Herbar. 27: 62 (1915).
O. cognita R. Knuth in Fedde, Repert. Spec. Nov. 23: 141 (1926).
O. Commersonii Pers. Synops. Pl. 1: 519 (1805).
O. corniculata L. Sp. Pl. 435 (1753).
O. cotagaitensis R. Knuth in Fedde, Repert. Spec. Nov. 29: 215 (1931).
O. cuzcensis R. Knuth in Notizbl. 7: 303 (1919).
O. densissima Rusby in Phytologia, 1: 61 (1934).
O. dolichopoda Diels in Engler, Bot. Jahrb. 37: 423 (1906).
O. elegans HBK. Nov. Gen. \& Spec. 5: 234, t. 466 (1822).
O. eriolepis Wedd. Chlor. And. 2: 290 (1861).
O. erythropoda Rusby in Mem. Torr. Bot. Club, 6: 16 (1896).
O. filiformis HBK. Nov. Gen. \& Spec. 5: 245, t. 469 (1822).
O. glaberrima Norlind in Ark. Bot. 20A (4): 26, t. 3, fig. 4 (1926).
O. guaquiensis R. Knuth in Meded. Rijks Herbar. 27: 63 (1915) $=$ O. breviramulosa.
O. Harmsiana R. Knuth in Engler, Pflanzenr. IV, 130: 431 (1930).
O. Hauthalii R. Knuth in Notizbl. 7: 305 (1919).
O. Herzogii R. Knuth in Meded. Rijks Herbar. 27: 63 (1915).
O. irregularis R. Knuth in Fedde, Repert. Spec. Nov. 23: 141 (1926).
O. lepidocaulis Norlind in Ark. Bot. 20A (4): 22, t. 2, fig. 1 (1926).
O. Lilloana R. Knuth in Fedde, Repert. Spec. Nov. 23: 140 (1926).
O. longissima (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1): 360 (1898).
O. lotoides HBK. Nov. Gen. \& Spec. 5: 241 (1822).
O. magellanica Forst. in Comm. Goett. 9: 33 (1789).
O. manihotoides (Rusby) R. Knuth in Fedde, Repert. Spec. Nov. 23: 141 (1926).
O. mapirensis R. Knuth in Engler, Pflanzenr. IV, 130: 174 (1930).
O. Martiana Zucc. in Denkschr. Akad. Münch. 9: 144 (1825).
O. medicaginea HBK. Nov. Gen. \& Spec. 5: 242 (1822).
O. megalorrhiza Jacq. Oxal. 33 (1794).
O. microcarpa Benth. Pl. Hartw. 115 (1843).
O. mollis HBK. Nov. Gen. \& Spec. 5: 241 (1822).
O. mollissima (Rusby) R. Knuth in Fedde, Repert. Spec. Nov. 23: 275 (1927).
O. nubigena Walp. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 320 (1843).
O. ollantaytambensis R. Knuth in Fedde, Repert. Spec. Nov. 23: 142 (1926) = O. cuzcensis.
O. oxyptera Prog. in Mart. Fl. Bras. 12(2): 489, t. 103 (1877).
O. parapitensis R. Knuth in Meded. Rijks Herbar. 27: 62 (1915).
O. parvifolia DC. Prodr. 1: 693 (1824).
O. parvifolia var. pluriflora R. Knuth in Notizbl. 7: 301 (1919).
O. parvula Remy in Ann. Sci. Nat. (ser. 3) 6: 354 (1846).
O. pazensis (Rusby) R. Knuth in Fedde, Repert. Spec. Nov. 24: 55 (1927).
O. phaseolifolia (Rusby) R. Knath in Fedde, Repert. Spec. Nov. 23: 140 (1926).
O. Philippii R. Knuth in Meded. Rijks Herbar. 27: 67 (1915).
O. pinguiculacea R. Knuth in Notizbl. 7: 311 (1919).
O. pinoënsis R. Knuth in Fedde, Repert. Spec. Nov. 29: 213 (1931).
O. platylepis Wedd. Chlor. And. 2: 290 (1861).
O. pseudo-violacea R. Knuth in Fedde, Repert. Spec. Nov. 24: 55 (1927).
O. pubescens HBK. Nov. Gen. \& Spec. 5: 240 (1822).
O. pycnophylla Wedd. Chlor. And. 2: 291 (1861).
O. pygmaea A. Gray in Bot. U. S. Explor. Exped. 1: 322 (1854).
O. Regnellii Miq. in Linnaea, 22: 545 (1849).
O. renifolia R. Knuth in Notizbl. 7: 296 (1919).
O. rubrovenosa Norlind in Ark. Bot. 20A (4): 21 (1926).
O. scandens HBK. Nov. Gen. \& Spec. 5: 242 (1822).
O. soldanelliflora R. Knuth in Fedde, Repert. Spec. Nov. 23: 275 (1926).
O. Steinbachii R. Knuth in Fedde, Repert. Spec. Nov. 24: 55 (1927).
O. Steinmannii Solms-Laub. in Bot. Zeitung, 65(1): 132, t. 2, fig. 7 (1907).
O. Tatei Rusby in Phytologia, 1: 62 (1934).
O. teneriensis R. Knuth in Meded. Rijks Herbar. 27: 64 (1915).
O. tenerrima R. Knuth in Fedde, Repert. Spec. Nov. 23: 277 (1926).
O. tenuiscaposa R. Knuth in Meded. Rijks Herbar. 27: 66 (1915).
O. tocoranensis R. Knuth in Meded. Rijks Herbar. 27: 65 (1915).
O. Trollii R. Knuth in Fedde, Repert. Spec. Nov. 29: 218 (1931).
O. tuberosa Molina, Sagg. Stor. Nat. Chile, 132 (1782).
O. unduavensis (Rusby) R. Knuth in Fedde, Repert. Spec. Nov. 23: 142 (1926).
O. violacea L. Sp. Pl. 434 (1753).
O. virgata Rusby in Phytologia, 1: 62 (1934).
O. yapacaniensis (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1) : 360 (1898).
O. yungasensis Rusby in Mem. Torr. Bot. Club, $3(3): 12$ (1893).

Xanthoxalis biflexa Rusby, Descr. S. Am. Pls. 31 (1920) = Oxalis breviramulosa.
X. flagellata Rusby, Descr. S. Am. Pls. 31 (1920) $=$ Oxalis andina.

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Balbisia integrifolia R. Knuth in Engler, Pflanzenr. IV, 129: 558 (1912).
B. Meyeniana Klotzsch in Linnaea, 10: 432 (1836).

Erodium cicutarium (L.) L'Hérit. ex Ait. Hort. Kew. 2: 414 (1789).
E. moschatum L'Hérit. ex Ait. Hort. Kew. 2: 414 (1789).

Geranium album R. Knuth in Engler, Bot. Jahrb. 37: 557 (1906).
G. amoenum R. Knuth in Fedde, Repert. Spec. Nov. 40: 217 (1936).
G. Bangii Hieron. in Engler, Bot. Jahrb. 21: 314 (1895).
G. bolivianum R. Knuth in Engler, Pflanzenr. IV, 129: 575 (1912).
G. carolinianum L. Sp. Pl. 682 (1753).
G. chaparense R. Knuth in Fedde, Repert. Spec. Nov. 28: 4 (1930).
G. comarapense R. Knuth in Meded. Rijks Herbar. 27: 69 (1915).
G. cuchillense R. Knuth in Fedde, Repert. Spec. Nov. 34: 144 (1933).
G. diffusum HBK. Nov. Gen. \& Spec. 5: 230 (1822).
G. escalonense R. Knuth in Fedde, Repert. Spec. Nov. 34: 145 (1933).
G. Fiebrigianum R. Knuth in Engler, Bot. Jahrb. 37: 560 (1906).
G. fuscicaule R. Knuth in Fedde, Repert. Spec. Nov. 28: 7 (1930).
G. Herzogii R. Knuth in Meded. Rijks Herbar. 27: 69 (1915).
G. Lechleri R. Knuth in Engler, Pflanzenr. IV, 129: 80 (1912).
G. malpasense R. Knuth in Fedde, Repert. Spec. Nov. 34: 146 (1933).
G. mexicanum var. minoriflorum (Briq.) R. Knuth in Engler, Pflanzenr. IV, 129: 197 (1912).
G. palcaënse R. Knuth in Meded. Rijks Herbar. 27: 68 (1915).
G. pallidifolium R. Knuth in Fedde, Repert. Spec. Nov. 28: 3 (1930).
G. patagonicum Hook. f. Fl. Antarct. 2: 252 (1845).
G. Pflanzii R. Knuth in Engler, Pflanzenr. IV, 129: 576 (1912).
G. rupicola Wedd. Chlor. And. 2: 285 (1861).
G. sepalo-roseum Rusby in Mem. Torr. Bot. Club, 3(3): 12 (1893).
G. sessiliflorum Cav. Diss. 4: 198, t. 77, fig. 2 (1787).
G. sessiliflorum var. compactum R. Knuth in Engler, Pflanzenr. IV, 129: 85 (1912).
G. sessiliflorum var. lanatum R. Knuth in Engler, Bot. Jahrb. $37: 565$ (1906).
G. sessiliflorum var. microphyllum O. Ktze. Rev. Gen. 3(2): 33 (1898).
G. soratae R. Knuth in Engler, Pflanzenr. IV, 129: 212 (1912).
G. superbum R. Knuth in Engler, Bot. Jahrb. 37: 561 (1906).
G. tablasense R. Knuth in Meded. Rijks Herbar. 27: 68 (1915) = G. patagonicum.
G. titicacaënse R. Knuth in Fedde, Repert. Spec. Nov. 45: 60 (1938) = G. patagonicum.
G. totorense R. Knuth in Fedde, Repert. Spec. Nov. 28: 7 (1930).
G. Weddellii Briq. in Ann. Conserv. \& Jard. Bot. Genève, 11-12: 183 (1908).

## TROPAEOLACEAE

Tropaeolum boliviense Loes. in Engler, Bot. Jahrb. 45: 462 (1911).
T. cochabambense Buchenau in Engler, Bot. Jahrb. 22: 161 (1895).
T. cuspidatum Buchenau in Engler, Bot. Jahrb. 26: 581 (1899).
T. infundibularum Rusby in Bull. N. Y. Bot. Gard. 4: 336 (1907) $=$ T. cuspidatum.
T. Kuntzeanum Buchenau in Engler, Bot. Jahrb. 22: 163 (1895).
T. maculatum Rusby in Mem. Torr. Bot. Club, 6: 15 (1896).
T. pentaphyllum var. megapetalum Buchenau in Engler, Bot. Jahrb. 22: 169 (1895).
T. peregrinum L. Sp. Pl. 345 (1753).
T. rectangulum Buchenau in Engler, Bot. Jahrb. 22: 165 (1895).
T. rectangulum var. bicolor O. Ktze. Rev. Gen. 3(2): 33 (1898).
T. rectangulum var. pallidum O. Ktze. Rev. Gen. 3(2): 33 (1898).
T. Seemannii Buchenau in Engler, Bot. Jahrb. 15: 226 (1892).
T. Smithii DC. Prodr. 1: 684 (1824).
T. tuberosum R. \& P. Fl. Peruv. 3: 77, t. 314 (1802).
T. umbellatum Hook. in Bot. Mag. 73: t. 4337 (1847).

## LINACEAE

Linum filiforme Urb. in Linnaea, 41: 643 (1877).
? L. scoparium Griseb. in Goett. Abh. 19: 103 (1874).
Roucheria laxiflora H. Winkl. in Fedde, Repert. Spec. Nov. 7: 109 (1909).

## ERYTHROXYLACEAE

Erythroxylon anguifugum Mart. in Abh. Akad. Wiss. Münch. 1840: 361.
E. Bangii Rusby in Mem. Torr. Bot. Club, 3(3): 11 (1893).
E. bolivianum Burck. in Teysmannia, 1: 456, t. 3 (1890).
E. Coca Lam. Encyc. 2: 393 (1786).
E. cuneifolium var. silvaticum O. E. Schulz in Engler, Pflanzenr. IV, 134: 122 (1907).
E. Herzogii O. E. Schulz in Fedde, Repert. Spec. Nov. 7: 57 (1909).
E. lucidum HBK. Nov. Gen. \& Spec. 5: 179 (1822).
E. macrophyllum Cav. Diss. 8: 401 (1789).
E. opacum Rusby in Mem. N. Y. Bot. Gard. 7: 270 (1927).
E. pauciflorum Rusby in Mem. Torr. Bot. Club, 6: 13 (1806).
E. paraënse Peyr. in Mart. Fl. Bras. 12(1): 164, t. 30 (1878).
E. Trollii O. E. Schulz in Notizbl. 11: 723 (1933).
E. Ulei O. E. Schulz in Engler, Pflanzenr. IV, 134: 62 (1907).
E. venosum Rusby in Mem. N. Y. Bot. Gard. 7: 270 (1927).

## ZYGOPHYLLACEAE

Bulnesia bonariensis Griseb. in Goett. Abh. 19: 105 (1874).
B. foliosa Griseb. in Goett. Abh. 19: 106 (1874).
B. Sarmienti Lor. ex Griseb. in Goett. Abh. 24: 75 (1879).

Kallstroemia boliviana Standl. in Field Mus. Publ. Bot. 11: 161 (1936).
K. maxima (L.) Torr. \& Gray, N. Am. Fl. 1: 213 (1838).
K. tribuloides (Mart.) Wight \& Arn. Prodr. 145 (1834), combination implied but not actually made.
Larrea divaricata Cav. in Anal. Hist. Nat. Madrid, 2: 122, t. 19, fig. 1 (1800).
Porliera arida Rusby in Mem. Torr. Bot. Club, 6: 15 (1896).
P. hygrometra R. \& P. Fl. Peruv. 4: t. 343 (1802).
P. Lorentzii Engl. in Engl. \& Prantl, Nat. Pflanzenfam. 3 (4): 84 (1890) $=$ P. microphylla.
P. microphylla (Baill.) Desc. O'Don. \& Lourt. in Lilloa, 5: 329 (1940).
P. Steinbachii Standl. in Field Mus. Publ. Bot. 11: 162 (1936) = P. microphylla.
Tribulus cistoides L. Sp. Pl. 387 (1753).
T. maximus var. roseus O. Ktze. Rev. Gen. 3(2): 30 (1898) $=$ ?
T. terrestris L. Sp. Pl. 387 (1753).

## RUTACEAE

Citrus acida Roxb. Fl. Ind. 3: 390 (1832).
Cusparia pilocarpidia Rusby in Bull. N. Y. Bot. Gard. 8: 98 (1912).
Dictyoloma peruvianum Planch. in Hook. Lond. Journ. Bot. 5: 583 (1846).
Erythrochiton brasiliensis Nees \& Mart. in Nov. Act. Acad. Caes. Leop. 11: 166 (1823).

Esenbeckia lucida Rusby in Bull. N. Y. Bot. Gard. 8: 98 (1912).
Fagara aculeatissima Engl. in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 19A: 220 (1931).
F. comosa Herzog in Meded. Rijks Herbar. 27: 80 (1915).
F. cuiabensis var. axillaris O. Ktze. Rev. Gen. 3(2): 34 (1898).
F. Naranjillo (Griseb.) Engl. in Engl. \& Prantl, Nat. Pflanzenfam. 3(4): 117 (1896).
F. nebuletorum Herzog in Meded. Rijks Herbar. 27: 79 (1915).
F. nigrescens R. E. Fries in Ark. Bot. 8(8): 12, t. 1, fig. 4-5 (1908).
F. Pterota L. Syst. (ed. 10) 897 (1759).
F. rhoifolia (Lam.) Engl. in Engl. \& Prantl, Nat. Pflanzenfam. 3(4): 118 (1897).
F. rigidifolia Herzog in Meded. Rijks Herbar. 27: 78 (1915).
F. tenuifolia forma aculeata Herzog in Meded. Rijks Herbar. 27: 80 (1915).

Ruta graveolens L. Sp. Pl. 383 (1753).
Ticorea longiflora DC. in Mém. Mus. Paris, 9: 146, t. 9 (1822).
Zanthoxylum annulatum Rusby in Mem. N. Y. Bot. Gard. 7: 277 (1927).
Z. Cardenasii Rusby in Mem. N. Y. Bot. Gard. 7: 277 (1927).
B. Coco Gill. ex Hook. \& Arn. in Hook. Bot. Misc. 3: 168 (1833).
Z. pubescens St. Hil. \& Tul. in Ann. Sci. Nat. (ser. 2) 17: 141 (1842).
Z. stipitatum Engl. in Mart. Fl. Bras. 12(2): 161, t. 34 (1874).

## SIMAROUBACEAE

Alvaradoa amorphoides Liebm. in Vidensk. Meded. för 1853: 101 (1854).
A. subovata Cronquist in Brittonia, 5: 134 (1944).

Icica rhynchophylla Rusby in Mem. N. Y. Bot. Gard. 7: 278 (1927) $=$ Protium insigne.
Picramnia Corallodendron Tul. in Ann. Sci. Nat. (ser. 3) 7: 259 (1847).
P. magnifolia Macbr. in Candollea, 5: 376 (1934).
P. monninaefolia Rusby in Mem. N. Y. Bot. Gard. 7: 278 (1927).
P. pendula Herzog in Fedde, Repert. Spec. Nov. 7: 58 (1909).
P. Sellowii Planch. in Hook. Lond. Journ. Bot. 5: 578 (1846).
P. Spruceana Engl. in Mart. Fl. Bras. 12(2): 238 (1874).

Simarouba amara Aubl. Pl. Guian. Fr. 2: 860, tt. 331-332 (1775).
S. versicolor var. pallida Engl. in Mart. Fl. Bras. 12(2): 226 (1874).

## BURSERACEAE

Bursera amplifolia Rusby in Bull. N. Y. Bot. Gard. 4: 338 (1907).
Protium Bangii Swart in Act. Bot. Neerland. 1: 244 (1952).
P. bolivianum Britton in Bull. Torr. Bot. Club, 16: 189 (1899) = Mauria ferruginea.
P. guianense (Aubl.) Planch. in Adansonia, 8: 52 (1867).
P. heptaphyllum var. brasiliense Engl. in Mart. Fl. Bras. 12(2): 263 (1874).
P. insigne (Tr. \& Pl.) Engl. in DC. Monog. Phan. 4: 77 (1883).
P. Llewelynii Macbr. in Candollea, 5: 378 (1934).
P. meridionale Swart in Act. Bot. Neerland. 1: 246 (1952).
P. montanum Swart in Act. Bot. Neerland. 1: 247 (1952).
P. ovatum Engl. in Mart. Fl. Bras. 12(2): 264, t. 52 (1874).
P. tenuifolium Engl. in DC. Monog. Phan. 4: 76 (1883).

Tetragastris sp.
Trattinickia Lawrancei var. boliviana Swart in Act. Bot. Neerland. 1: 249 (1952).
T. rhoifolia subsp. Sprucei var. pubescens Swart in Act. Bot. Neerland. 1: 249 (1952).

## MELIACEAE

Cedrela boliviana Rusby, Descr. S. Am. Pls. 36 (1920).
J. brunellioides Rusby in Bull. N. Y. Bot. Gard. 8: 99 (1912).
C. odorata L. Syst. (ed. 10) 940 (1759).
C. Steinbachii Harms in Notizbl. 11: 381 (1932).

Guarea alborosea Rusby in Bull. Torr. Bot. Club, 49: 263 (1922) $=$ G. pendulispica.
G. Bangii Rusby in Bull. Torr. Bot. Club, 49: 262 (1922).
G. membranacea Rusby in Mem. N. Y. Bot. Gard. 7: 279 (1927).
G. ovalis (Rusby) Rusby in Mem. Torr. Bot. Club, 4(3): 205 (1895).
G. pendulispica C. DC. in Fedde, Repert. Spec. Nov. 7: 59 (1909).
G. Steinbachii Harms in Notizbl. 10: 348 (1928).
G. trichilioides L. Mant. 228 (1771).
G. yungasana Briq. in Candollea, 6: 20 (1935).

Melia Azedarach L. Sp. Pl. 384 (1753).
Moschoxylon viride Rusby in Mem. Torr. Bot. Club, 6: 18 (1896) =?
Ruagea surutensis Harms in Notizbl. 10: 347 (1928) = Guarea sp.
Swietenia Mahagani Jacq. Enum. Pl. Carib. 20 (1760).
Sycocarpus Rusbyi Britton in Bull. Torr. Bot. Club, 14: 143 (1887) = Guarea trichilioides.

Trichilia Buchtienii Harms in Notizbl. 11: 386 (1932).
T. Cardenasii Rusby in Mem. N. Y. Bot. Gard. 7: 279 (1927).
T. Catigua A. Juss. in St. Hil. Fl. Bras. Mer. 2: 77 (1829).
T. Claussenii C. DC. in Mart. Fl. Bras. 11(1): 207 (1878).
T. elegans A. Juss. in St. Hil. Fl. Bras. Mer. 2: 79, t. 98 (1829).
T. guayaquilensis C. DC. in DC. Monog. Phan. 1: 682 (1878).
T. guayaquilensis var. Candollei O. Ktze. Rev. Gen. 3(2): 36 (1898).
T. Harmsii Rusby in Bull. N. Y. Bot. Gard. 4: 338 (1907).
T. longifolia C. DC. in Meded. Rijks Herbar. 27: 82 (1915).
T. multifoliola C. DC. in Meded. Rijks Herbar. 27: 82 (1915).
T. pachypoda (Rusby) C. DC. ex Harms in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 19b: 114 (1940).
T. pauciflora Rusby in Mem. N. Y. Bot. Gard. 7: 280 (1927).
T. sexanthera C. DC. in Notizbl. 6: 501 (1917).
T. Steinbachii Harms in Notizbl. 9: 1156 (1927).
T. stellato-tomentosa O. Ktze. Rev. Gen. 3(2): 36 (1898).
T. stellipila C. DC. in Bull. Herb. Boiss. (ser. 2) 3: 412 (1903) = T. stellatotomentosa.
T. subarborescens C. DC. in Fedde, Repert. Spec. Nov. 7: 58 (1909).
T. tartagalensis C. DC. in Meded. Rijks Herbar. 27: 81 (1915).
T. Trollii Harms in Notizbl. 11: 385 (1932).
T. viridis var. puberula Lingelsh. in Fedde, Repert. Spec. Nov. 8: 1 (1910).

## MALPIGHIACEAE

Acmanthera Radlkoferi O. Ktze. Rev. Gen. 3 (2): 27 (1898) $=$ Bunchosia Lindeniana var. boliviensis.
Aspicarpa argentea var. tenuifolia Niedenzu in Engler, Pflanzenr. IV, 141: 557 (1928).
A. boliviensis Ndzu. in Meded. Rijks Herbar. 19: 72 (1913).
A. lanata (Chod.) Ndzu. in Verz. Vorles. Akad. Braunsberg, 1912-13: 59 (1912).
A. sericea Griseb. in Goett. Abh. 24: 68 (1879).

Banisteria argentea var. acuminata forma eglandulosa Ndzu. in Engler, Pflanzenr. IV, 141: 436 (1928).
B. argentea var. obtusiuscula forma glandulifera Ndzu. in Engler, Pfanzenr. IV, 141: 436 (1928).
B. atrosanguinea Juss. in Ann. Sci. Nat. (ser.2) 13: 281 (1840).
B. cinerascens var. platyphylla Ndzu. in Engler, Pflanzenr. IV, 141: 406 (1928).
B. cinerea Rusby in Bull. N. Y. Bot. Gard. 4: 335 (1907) = B. Gardneriana ?
B. cristata Griseb. in Linnaea, 22: 16 (1849).
B. crotonifolia Juss. in St. Hil. Fl. Bras. Mer. 3: 36 (1832).
B. Gardneriana Juss. in Arch. Mus. Paris, 3: 421 (1843).
B. illustris (Rusby) Ndzu. in Engler, Pflanzenr. IV, 141: 451 (1928).
B. lutea Griseb. in Linnaea, 22: 15 (1849).
B. metallicolor var. aurea forma eglandulosa Ndzu. in Engler, Pflanzenr. IV, 141: 434 (1928).
B. metallicolor var. aurea forma glandulifera Ndzu. in Engler, Pflanzenr. IV, 141: 434 (1928).
B. metallicolor var. subrotunda forma glandulifera Ndzu. in Engler, Pflanzenr. IV, 141: 433 (1928).
B. metallicolor var. subsalicina forma eglandulosa Ndzu. in Engler, Pflanzenr. IV, 141: 435 (1928).
B. muricata Cav. Diss. 9: 423, t. 246 (1790).
B. nigrescens Juss. in St. Hil. Fl. Bras. Mer. 3: 44 (1832).
B. nitrosiodora Griseb. in Goett. Abh. 24: 65 (1879).
B. oxyclada Juss. in Arch. Mus. Paris, 3: 396 (1843).
B. oxyclada forma brevialata Ndzu. De Gen. Banist. pt. 1: 26 (1900).
B. parviflora var. boliviensis Ndzu. in Fedde, Repert. Spec. Nov. 26: 345 (1929).
B. Pearcei Rusby in Bull. N. Y. Bot. Gard. 4: 334 (1907) = B. argentea.
B. pubipetala Juss. in St. Hil. Fl. Bras. Mer. 3: 41, t. 169 (1832).
B. Rusbyana Ndzu. in Ind. Lect. Lyc. Braunsberg, 1901: 19 (1901).
B. sanguinea Rusby in Bull. N. Y. Bot. Gard 4: 335 (1907) $=$ Heteropterys Beecheyana var. andina.
B. Sellowiana var. Blanchetiana (Juss.) Ndzu. in Ind. Lect. Lyc. Braunsberg p. hiem. 1900-1901: 8 (1900).
B. Sellowiana var. Blanchetiana forma grandifolia Ndzu. in Engler, Pflanzenr. IV, 141: 409 (1928).
B. Spruceana Griseb. in Mart. Fl. Bras. 12(1): 45 (1858).
B. sublucida (Rusby) Ndzu. in Engler, Pflanzenr. IV, 141: 452 (1928).
B. Whitei (Rusby) Ndzu. in Engler, Pflanzenr. IV, 141: 453 (1928).
B. Williamsii (Rusby) Ndzu. in Engler, Pflanzenr. IV, 141: 453 (1928).

Brittonella pilosa Rusby in Bull. Torr. Bot. Club, 20: 430 (1893) = Mionandra camareoides.
Bunchosia angustifolia forma parvifolia Ndzu. in Meded. Rijks Herbar. 19: 75 (1913).
B. armeniaca (Cav.) Rich. in A. Juss. in Ann. Mus. Paris, 18: 481 (1811), combination implied, but not actually made.
B. armeniaca forma systyla Ndzu. in Arb. Bot. Inst. Akad. Braunsberg, 5: 42 (1914).
B. lanceolata Turcz. in Bull. Soc. Nat. Mosc. 36(1): 582 (1863).
B. Lindeniana var. boliviensis Ndzu. in Ind. Lect. Lyc. Braunsb. p. hiem. 189899: 10 (1898).
B. pilocarpa Rusby in Bull. N. Y. Bot. Gard. 4: 333 (1907) = B. armeniaca. Byrsonima biacuminata Rusby in Mem. Torr. Bot. Club, 6: 13 (1896) $=$ B. coriacea var. spicata forma angustifolia.
B. coccolobifolia HBK. Nov. Gen. \& Spec. 5: 148 (1822).
B. coriacea var. spicata (Cav.) Ndzu. in Engler, Pflanzenr. IV, 141: 700 (1928).
B. coriacea var. spicata forma angustifolia (Benth.) Ndzu. in Engler, Pflanzenr. IV, 141: 701 (1928).
B. crassifolia (L.) HBK. Nov. Gen. \& Spec. 5: 149 (1822).
B. cydoniaefolia Juss. in St. Hil. Fl. Bras. Mer. 3: 77 (1832).
B. cydoniaefolia var. chiquitensis Juss. in Arch. Mus. Paris, 3:281 (1843).
B. laevigata (Poir.) DC. Prodr. 1: 580 (1824).
B. Orbignyana Juss. in Ann. Sci. Nat. (ser. 2) 13:332 (1840).
B. Poeppigiana var. velutina Ndzu. in Engler, Pflanzenr. IV, 141: 715 (1928).
B. spicata (Cav.) Rich. ex Juss. in Ann. Mus. Paris, 18: 481 (1812), combination implied, but not actually made.
B. variabilis Juss. in St. Hil. Fl. Bras. Mer. 3: 78 (1832).

Dicella Conwayi Rusby in Bull. N. Y. Bot. Gard. 8: 98 (1912).
D. macroptera (Mart.) Juss. in Ann. Sci. Nat. (ser. 2) 13: 323 (1840).

Galphimia brasiliensis (L.) Juss. in St. Hil. Fl. Bras. Mer. 3: 71, t. 178 (1832).
Heteropterys aceroides forma Grisebachiana subf. elongata Ndzu. in Arb. Bot. Inst. Lyc. Hos. 2: 34 (1903).
H. anoptera var. eglandulosa subvar. latifolia Ndzu. in Arb. Bot. Inst. Lyc. Hos. 2: 49 (1903).
H. anoptera var. glandulifera subvar. ovata Ndzu. in Arb. Bot. Inst. Lyc. Hos. 2: 48 (1903).
H. Beecheyana var. andina Ndzu. in Arb. Bot. Inst. Lyc. Hos. 2: 55 (1903).
H. bopiana (Rusby) Ndzu. in Engler, Pflanzenr. IV, 141: 377 (1928).
H. campestris Juss. in St. Hil. Fl. Bras. Mer. 3: 33 (1832).
H. canaminensis (Rusby) Ndzu. in Engler, Pflanzenr. IV, 141: 378 (1928).
H. cochleosperma forma glandulifera Ndzu. in Arb. Bot. Inst. Lyc. Hos. 2: 11 (1903).
H. dumetorum (Griseb.) Ndzu. in Engler, Pflanzenr. IV, 141: 336 (1928).
H. falcifera Juss. in Ann. Sci. Nat. (ser. 2) 13: 274 (1840).
H. hypericifolia Juss. in St. Hil. Fl. Bras. Mer. 3: 24 (1832).
H. macrostachya A. Juss. in Arch. Mus. Paris, 3: 450 (1843).
H. ovalifolia Rusby in Bull. N. Y. Bot. Gard. 4: 334 (1907) = H. falcifera.
H. rufula forma hirta Ndzu. in Fedde, Repert. Spec. Nov. 26: 345 (1929).
H. sphaerandra (Rusby) Ndzu. in Engler, Pflanzenr. IV, 141: 380 (1928).
H. suberosa var. Candolleana (Juss.) Ndzu. in Arb. Bot. Inst. Lyc. Hos. 2: 51 (1903).
H. suberosa var. Lessertiana (Juss.) Griseb. in Mart. Fl. Bras. 12(1): 69 (1858).
H. sylvatica Juss. in Ann. Sci. Nat. (ser. 2) 13: 277 (1840).
H. syringifolia Griseb. in Linnaea, 13: 224 (1830).
H. syringifolia var. Pilgeri Ndzu. in Arb. Bot. Inst. Lyc. Hos. 2: 20 (1903).
H. tenuifolia (Ndzu.) Ndzu. in Engler, Pflanzenr. IV, 141: 333 (1928).
H. tomentosa Juss. in St. Hil. Fl. Bras. Mer. 3: 31 (1832).
H. trichanthera A. Juss. in Arch. Mus. Paris, 3: 438 (1843).
H. trigoniifolia forma glandulifera Ndzu. in Arb. Bot. Inst. Lyc. Hos. 2: 8 (1903).
H. umbellata Juss. in St. Hil. Fl. Bras. Mer. 3: 25, t. 166 (1832).

Hiraea chlorocarpa A. Juss. in Ann. Sci. Nat. (ser. 2) 13: 259 (1840).
H. fagifolia var. Blanchetiana forma longifolia Ndzu. in Verz. Vorles. Lyc. Hos. W.-S. 1906-07: 14 (1906).
H. fagifolia var. Blanchetiana forma longifolia subf. parvifolia Ndzu. in Meded. Rijks Herbar. 19: 71 (1913).
H. Jussieana Miq. in Linnaea, 19: 142 (1847).
H. Kunthiana Juss. in Arch. Mus. Paris, 3: 571 (1843).
H. strigulosa Rusby in Bull. N. Y. Bot. Gard. 8: 95 (1912).
H. transiens Ndzu. in Verz. Vorles. Lyc. Hos. W.-S. 1906-07: 8 (1906).

Janusia guaranitica (St. Hil.) Juss. in Ann. Sci. Nat. (ser. 2) 13: 251 (1840).
J. guaranitica var. vulgaris forma sericans Ndzu. in Verz. Vorles. Akad. Braunsberg im W.-S. 1912-13: 49 (1912).
Jubistylis mollis Rusby in Mem. N. Y. Bot. Gard. 7: 274, fig. 4 (1927) = Banisteria cristata.
Mascagnia anisopetala (Juss.) Griseb. in Mart. Fl. Bras. 12(1): 95 (1858).
M. brevifolia Griseb. in Goett. Abh. 24: 67 (1879).
M. brevifolia var. paniculata Ndzu. in Arb. Bot. Inst. Lyc. Braunsberg, 3: 15 (1908).
M. chlorocarpa var. cristata Ndzu. in Arb. Bot. Inst. Lyc. Braunsberg, 3: 21 (1908).
M. ixiamensis Rusby in Mem. N. Y. Bot. Gard. 7: 271 (1927) = M. ovatifolia.
M. macrophylla Rusby in Mem. N. Y. Bot. Gard. 7: 272 (1927).
M. ovatifolia (HBK.) Griseb. Fl. Brit. W. Ind. 121 (1864).
M. ovatifolia forma cordata Ndzu. in Arb. Bot. Inst. Lyc. Braunsberg, 3: 13 (1908).
M. pachyptera Rusby in Mem. N. Y. Bot. Gard. 7: 271 (1927) = M. psilophylla.
M. psilophylla (Juss.) Griseb. in Mart. Fl. Bras. 12(1): 94 (1858).
M. rigida (Juss.) Griseb. in Mart. F1. Bras. 12(1): 92 (1858).
M. rigida subsp. coriacea (Griseb.) Ndzu. in Arb. Bot. Inst. Lyc. Braunsberg, 3: 19 (1908).
M. sepium var. rufescens Griseb. in Mart. Fl. Bras. 12 (1): 96 (1858).
M. sericans var. boliviensis Ndzu. in Arb. Bot. Inst. Lyc. Braunsberg, 3: 21 (1908).

Mionandra camareoides Griseb. in Goett. Abh. 19: 102 (1874).
Peixotoa reticulata Griseb. in Linnaea, 13: 213 (1839).
Ptilochaeta nudipes Griseb. in Goett. Abh. 24: 66 (1879).
Stigmatophyllum bogotense Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 18: 320 (1862).
S. calcaratum N. E. Brown in Trans. Bot. Soc. Edinb. 20: 48 (1894).
S. coloratum Rusby in Mem. Torr. Bot. Club, 6: 14 (1896).
S. tiliaefolium (HBK.) Ndzu. De Gen. Stigmat. pt. 2: 16 (1900).
S. tomentosum Juss. in St. Hil. Fl. Bras. Mer. 3: 53 (1832).

Tetrapterys acapulcensis HBK. Nov. Gen. \& Spec. 5: 168 (1821).
T. ambigua var. paraguayensis (Ndzu.) Ndzu. in Engler, Pflanzenr. IV, 141: 169 (1928).
T. boliviensis Ndzu. in Verz. Vorles. Lyc. W.-S. 1909-10: 17 (1909).
T. calophylla var. boliviana Rusby in Mem. Torr. Bot. Club, 6: 14 (1896).
T. calophylla var. glabrior Ndzu. in Verz. Vorles. Lyc. W.-S. 1909-10: 47 (1909).
T. discolor (G. Meyer) DC. Prodr. 1: 587 (1824).
T. discolor var. andina Ndzu. in Verz. Vorles. Lyc. W.-S. 1909-10: 42 (1909).
T. elliptica Rusby in Bull. N. Y. Bot. Gard. 8: 96 (1912).
T. mucronata var. boliviensis Ndzu. in Verz. Vorles. Lyc. W.-S. 1909-10: 55 (1909).
T. multiglandulosa Juss. in Ann. Sci. Nat. (ser. 2) 13: 264 (1840).
T. suaveolens Juss. in Ann. Sci. Nat. (ser. 2) 13: 263 (1840).

Thryallis latifolia var. ovatifolia (Ndzu.) Ndzu. in Arb. Bot. Inst. Akad. Braunsberg, 5: 12 (1914).

## TRIGONIACEAE

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T. boliviana Warm. in Mart. Fl. Bras. 13(2): 134 (1875).
f. echitifolia Rusby in Bull. N. Y. Bot. Gard. 4: 324 (1907).
T. floccosa Rusby in Bull. N. Y. Bot. Gard. 4: 325 (1907).
T. parviflora Benth. in Hook. Journ. Bot. 3: 163 (1851).
T. pubescens Camb. in St. Hil. Fl. Bras. Mer. 2: 114 (1829).
T. simplex var. pilosula O. Ktze. Rev. Gen. 3(2): 12 (1898).

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Callisthene fasciculata Mart. Nov. Gen. \& Spec. 1: 126, t. 100 (1824).
Erisma calcaratum (Link) Warm. in Mart. Fl. Bras. 13(2): 111 (1875).
Qualea acuminata Spruce ex Warm. in Mart. Fl. Bras. 13(2): 40 (1875).
Q. grandiflora Mart. Nov. Gen. \& Spec. 1: 133, t. 79 (1826).
Q. multiflora subsp. pubescens (Mart.) Stafleu in Act. Bot. Neerland. 2: 196 (1953).
Q. parviflora Mart. Nov. Gen. \& Spec. 1: 135, t. 81 (1826).
Q. pilosa var. heterophylla O. Ktze. Rev. Gen. 3(2): 11 (1898).
Q. pilosa var. multinervia O. Ktze. Rev. Gen. 3(2): 11 (1898).
Q. Tessmannii Mildbr. in Notizbl. 9: 141 (1924).
Q. virgata Rusby in Bull. N. Y. Bot. Gard. 8: 99 (1912) = Q. multiflora subsp. pubescens.
Salvertia convallariodora St. Hil. in Mém. Mus. Paris, 6: 266 (1820).
Vochysia boliviana Rusby in Mem. Torr. Bot. Club, 3(3): 7 (1893).
V. caesia Stafleu in Rec. Trav. Bot. Néerl. 41: 488 (1948).
V. divergens Pohl, Fl. Bras. 2: 19, t. 3 (1831).
V. Haenkeana Mart. Nov. Gen. \& Spec. 1: 147, t. 89 (1826).
V. Leguiana Macbr. in Field Mus. Publ. Bot. 8: 121 (1930).
V. mapirensis Rusby in Mem. Torr. Bot. Club, 6: 7 (1826).
V. Radlkoferi O. Ktze. Rev. Gen. 3(2): 12 (1898).
V. rufa Mart. Nov. Gen. \& Spec. 1: 144, t. 86 (1826).

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B. floribunda Willd. in Ges. Naturf. Freunde Neue Schr. 3: 412 (1801).

Monnina aestuans (L. f.) DC. Prodr. 1: 338 (1824).
M. alatodrupacea O. Ktze. Rev. Gen. 3(2): 10 (1898).
M. Arbutus Chod. in Meded. Rijks Herbar. 27: 30 (1915).
M. Autraniana Chod. in Bull. Herb. Boiss. (ser.1) 3: 543 (1895).
M. Bangii Chod. in Bull. Herb. Boiss. (ser. 1) 4: 243 (1896).
M. boliviana Chod. in Bull. Herb. Boiss. (ser. 1) 3: 543 (1895).
M. boliviensis A. W. Bennett in Bull. Torr. Bot. Club, 16: 20 (1889).
M. brachystachya Griseb. in Goett. Abh. 19: 75 (1874).
M. Bridgesii Chod. in Bull. Herb. Boiss. (ser. 1) 3: 542 (1895).
M. Buchtienii Rusby, Descr. S. Am. Pls. 41 (1920).
M. eriocarpa Chod. in Meded. Rijks Herbar. 27: 29 (1915).
M. Franchetii Chod. in Bull. Herb. Boiss. (ser. 1) 4: 248 (1896).
M. gracilis Chod. in Bull. Herb. Boiss. (ser. 1) 4: 244 (1896).
M. Hassleri Chod. in Engler, Bot. Jahrb. 42: 100 (1908).
M. herbacea DC. Prodr. 1: 340 (1824).
M. Herzogii Chod. in Meded. Rijks Herbar. 27: 31 (1915).
M. Laureola Chod. in Bull. Herb. Boiss. (ser. 1) 4: 245 (1896).
M. macroclada Chod. in Bull. Herb. Boiss. (ser. 1) 4: 246 (1896).
M. macrostachya var. stenophylla O. Ktze. Rev. Gen. 3(2): 10 (1898).
M. nigrescens Rusby in Bull. N. Y. Bot. Gard. 4: 324 (1907).
M. Pearcei Chod. in Bull. Herb. Boiss (ser. 1) 4:243 (1896).
M. pseudostipulata Chod. in Bull. Herb. Boiss. (ser. 1) 4: 245 (1896).
M. resedoides St. Hil. Fl. Bras. Mer. 2: 61 (1829).
M. rupestris HBK. Nov. Gen. \& Spec. 5: 415 (1822).
M. Rusbyi Chod. in Rusby in Mem. Torr. Bot. Club, 6: 6 (1896).
M. salicifolia R. \& P. Syst. 172 (1798).
M. stipulata Chod. in Bull. Herb. Boiss. (ser. 1) 2: 170 (1894).
M. Weddelliana Chod. in Bull. Herb. Boiss. (ser. 1) 4: 244 (1896).

Polygala acuminata (Willd.) Chod. Monog. Polyg. 2: 46 (1893).
P. andina A. W. Bennett in Bull. Torr. Bot. Club, 16: 19 (1889).
P. angustifolia HBK. Nov. Gen. \& Spec. 5: 405, t. 511 (1822).
P. Bangiana Chod. in Bull. Herb. Boiss. (ser. 1) 4: 234 (1896).
P. boliviensis A. W. Bennett in Journ. Bot. 17: 171 (1879).
P. cisandina Chod. in Meded. Rijks Herbar. 27: 28 (1915).
P. filiformis St. Hil. Fl. Bras. Mer. 2: 7 (1829).
P. formosa A. W. Bennett in Bull. Torr. Bot. Club, 16: 19 (1889).
P. gymnosepala Chod. in Meded. Rijks Herbar. 27: 26 (1915).
P. hebeclada DC. Prodr. 1: 331 (1824).
P. macerrima Blake in Proc. Biol. Soc. Wash. 43: 5 (1930).
P. Mandonii Chod. in Engler, Bot. Jahrb. 42: 98 (1908).
P. molluginifolia St. Hil. Fl. Bras. Mer. 2: 25 (1829).
P. monodonta Chod. in Meded. Rijks Herbar. 27: 28 (1915).
P. myurus Chod. in Meded. Rijks Herbar. 27: 27 (1915).
P. nemoralis A. W. Bennett in Journ. Bot. 17: 172 (1879).
P. paludosa var. angustocarpa Chod. in Mém. Soc. Phys. Hist. Nat. Genève, 30 (pt. 2, no. 8): 106 (1889).
P. paniculata L. Sp. Pl. (ed. 2) 2: 987 (1763).
P. Pearcei A. W. Bennett in Journ. Bot. 17: 201 (1879).
P. spectabilis var. minor Chod. ex Rusby in Bull. N. Y. Bot. Gard. 4: 323 (1907).

Securidaca volubilis L. Sp. Pl. 707 (1753).

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Acalypha alchorneoides Rusby in Bull. N. Y. Bot. Gard. 8: 101 (1912).
A. amblyodonta var. villosa Muell. Arg. in Mart. Fl. Bras. $11(2): 366$, t. 53 (1874).
A. arvensis Poepp. \& Endl. Nov. Gen. 3: 21 (1845).
A. Baenitzii Pax in Fedde, Repert. Spec. Nov. 5: 227 (1908) = A. stenoloba.
A. benensis Britton ex Rusby in Bull. Torr. Bot. Club, 28: 304 (1901).
A. boliviensis Muell. Arg. in Linnaea, 34: 162 (1865).
A. bopiana Rusby in Mem. N. Y. Bot. Gard. 7: 287 (1927).
A. Brittonii Rusby in Bull. Torr. Bot. Club, 28: 303 (1901).
A. Buchtienii Pax in Fedde, Repert. Spec. Nov. 5: 227 (1908).
A. callosa Benth. Pl. Hartw. 252 (1846).
A. capillaris Rusby in Mem. Torr. Bot. Club, 4 (3): 257 (1895) $=$ A. stenoloba.
A. communis Muell. Arg. in Linnaea, 34: 23 (1865).
A. communis var. guaranitica Chod. \& Hassl. in Bull. Herb. Boiss. (ser. 2) 5: 605 (1905).
A. communis var. hirta (Spreng.) Muell. Arg. in Linnaea, 34: 24 (1865).
A. communis var. tomentella Muell. Arg. in Linnaea, 34: 24 (1865).
A. controversa (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26 (1) : 348 (1898).
A. cuprea Herzog in Fedde, Repert. Spec. Nov. 7: 60 (1909).
A. cuspidata Jacq. Hort. Schoenbr. 2: 63, t. 243 (1797).
A. diversifolia Jacq. Hort. Schoenbr. 2: 63, t. 244 (1797).
A. diversifolia var. carpinifolia (Poepp.) Muell. Arg. in DC. Prodr. 15(2): 854 (1866).
A. Douilleana Rusby in Mem. N. Y. Bot. Gard. 7: 285 (1927).
A. erosa Rusby in Bull. Torr. Bot. Club, 28: 305 (1901).
A. eugenifolia Rusby in Bull. N. Y. Bot. Gard. 4: 443 (1907).
A. flabellifera Rusby in Mem. Torr. Bot. Club, 6: 119 (1896) =A. plicata.
A. foliosa Rusby in Bull. N. Y. Bot. Gard. 4: 443 (1907).
A. grandispicata Britton ex Rusby in Bull. Torr. Bot. Club, 28: 304 (1901).
A. Herzogiana Pax \& Hoffm. in Meded. Rijks Herbar. 40: 24 (1921).
A. heteromorpha Rusby in Mem. N. Y. Bot. Gard. 7: 286 (1927).
A. hibiscifolia Britton ex Rusby in Mem. Torr. Bot. Club, 4 (3): 257 (1895).
A. inaequalis Rusby in Bull. Torr. Bot. Club, 28: 303 (1901).
A. jubifera Rusby, Descr. S. Am. Pls. 48 (1920).
A. Lechleri Britton ex Rusby in Bull. Torr. Bot. Club, 28: 304 (1901).
A. lucida Rusby in Bull. N. Y. Bot. Gard. 4: 444 (1907).
A. lycioides Pax. \& Hoffm. in Meded. Rijks Herbar. 40: 24 (1921).
A. macrophylla Ule in Verh. Bot. Ver. Brandenb. 50: 79 (1908).
A. macrostachya Jacq. Hort. Schoenbr. 2: 63, t. 245 (1797).
A. macrostachya var. sidaefolia (HBK.) Muell. Arg. in Linnaea, 34: 11 (1865).
A. macrostachya var. tristis Muell. Arg. in Mart. Fl. Bras. 11(2): 345 (1874).
A. Mandonii Muell. Arg. in Linnaea, 34: 162 (1865-66).
A. mapirensis Pax in Fedde, Repert. Spec. Nov. 7: 110 (1909).
A. mapirensis var. pubescens Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xvi): 65 (1924).
A. Nitschkeana Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xvi): 88 (1924).
A. ovata Pax \& Hoffm. in Meded. Rijks Herbar. 40: 23 (1921) = A. stenoloba.
A. paupercula Pax \& Hoffm. in Meded. Rijks Herbar. 40: 24 (1921).
A. plicata Muell. Arg. in DC. Prodr. 15(2): 855 (1866).
A. Poiretii Spreng. Syst. Veg. 3: 879 (1826).
A. soratensis Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xvi): 126 (1924).
A. stachyura Pax in Fedde, Repert. Spec. Nov. 7: 110 (1909) = A. macrophylla.
A. stenoloba Muell. Arg. in Flora, 55: 41 (1872).
A. variegata Rusby in Mem. N. Y. Bot. Gard. 7: 285 (1927).
A. vermifera Rusby in Mem. N. Y. Bot. Gard. 7: $286(1927)=$ A. diversifolia.
A. villosa Jacq. Enum. Pl. Carib. 32 (1760).
A. villosa var. latiuscula Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xvi): 17 (1924).
A. Williamsii Rusby in Bull. N. Y. Bot. Gard. 8: 101 (1912).
A. Williamsii Rusby, Descr. S. Am. Pls. 47 (1920).

Alchornea castaneifolia var. salicifolia (Baill.) Baill. in Adansonia, 5: 238 (1865).
A. iricurana forma pubescens (Britton) Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (vii): 233 (1914).
A. latifolia Sw. Prodr. 98 (1788).
A. megalostylis Rusby in Phytologia, 1: 63 (1934).
A. Pearcei Britton ex Rusby in Bull. Torr. Bot. Club, 28: 305 (1901).
A. sclerophylla Pax in Fedde, Repert. Spec. Nov. 7: 242 (1909).
A. triplinervia (Spreng.) Muell. Arg. in DC. Prodr. 15(2): 909 (1866).
A. triplinervia var. boliviana Pax \&.Hoffm. in Engler, Pflanzenr. IV, 147 (vii): 229 (1914).
A. triplinervia var. janeirensis (Casar.) Muell. Arg. in DC. Prodr. 15(2): 909 (1866).

Amanoa muricata Rusby in Bull. N. Y. Bot. Gard. 8: 100 (1912).
Aparisthmium cordatum (Juss.) Baill. in Adansonia, 5: 307 (1865).
Apodandra Buchtienii (Pax) Pax in Engler, Pflanzenr. IV, 147 (ix): 21 (1919).
Astrocasia sp.
Bernardia paraguariensis var. orbiculata Chod. \& Hassl. in Bull. Herb. Boiss. (ser. 2) 5: 504 (1905).
B. rotundifolia Herzog in Fedde, Repert. Spec. Nov. 7: 59 (1909).

Caperonia castaneifolia (L.) St. Hil. Pl. Remarq. Brésil, 245 (1824).
Chaetocarpus Pearcei Rusby in Bull. N. Y. Bot. Gard. 8: 102 (1912).
Chiropetalum boliviense (Muell. Arg.) Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (vi): 94 (1912).
Cleidion amazonicum Ule in Verh. Bot. Ver. Brandenb. 50: 76 (1908).
C. tricoccum (Casar.) Baill. in Adansonia, 4: 370 (1863-64).

Cnidoscolus tubulosus var. trilobus (Muell. Arg.) Lourt. \& O'Don. in Lilloa, 9: 113 (1943).
Conceveiba guianensis Aubl. Pl. Guian, Fr. 2: 924, t. 353 (1775).
Croton abutilifolius Croiz. in Darwiniana, 6: 448 (1944).
C. andinus Muell. Arg. in Linnaea, 34: 126 (1865).
C. apicifolius Croiz. in Darwiniana, 6: 447 (1944).
C. avulsus Croiz. in Darwiniana, 6: 450 (1944).
C. Bangii Rusby in Mem. Torr. Bot. Club, 4 (3): 256 (1895).
C. boliviensis Muell. Arg. in Linnaea, 34: 91 (1895).
C. Bonplandianus Baill. in Adansonia, 4: 339 (1864).
C. Bridgesii Muell. Arg. in Linnaea, 34: 115 (1865) = C. Orbignyanus.
C. Buchtienii Rusby in Mem. N. Y. Bot. Gard. 7: 284 (1927).
C. caladiifolius Croiz. in Journ. Arnold Arb. 21: 96 (1940) $=$ C. peltophorus.
C. callicarpifolius var. pubescens Muell. Arg. in Linnaea, 34: 85 (1865).
C. Cardenasii Standl. in Field Mus. Publ. Bot. 22: 34 (1940).
C. chamaedryfolius Lam. ex Griseb. Fl. Brit. W. Ind. 41 (1859).
C. charaguensis Standl. in Field Mus. Publ. Bot. 22: 35 (1940).
C. densiflorus Pax \& Hoffm. in Meded. Rijks Herbar. 40: 19 (1921).
C. emporiorum Croiz. in Journ. Arnold Arb. 21: 97 (1940).
C. erythrochyloides Croiz. in Darwiniana, 6: 449 (1944).
C. Frieseanus Muell. Arg. in DC. Prodr. 15(2): 543 (1866).
C. glandulosus L. Syst. (ed. 10) 1275 (1759).
C. Hieronymi Griseb. in Goett. Abh. 24: 54 (1879).
C. laeticapsulus Croiz. in Darwiniana, 6: 448 (1944).
C. lobatus L. Sp. Pl. 1005 (1753).
C. Mandonis Muell. Arg. in Linnaea, 34: 85 (1865).
C. matourensis Aubl. Pl. Guian. Fr. 2: 879, t. 338 (1775).
C. nudulus Croiz in Journ. Arnold Arb. 21: 98 (1940).
C. Orbignyanus Muell. Arg. in Linnaea, 34: 123 (1865-66).
C. pedicellatus HBK. Nov. Gen. \& Spec. 2: 75 (1817).
C. peltophorus Muell. Arg. in Mart. Fl. Bras. 11 (2): 154 (1873).
C. perintricatus Croiz. in Darwiniana, 6: 450 (1944).
C. piluliferus Rusby in Mem. Torr. Bot. Club, 4(3): 256 (1895).
C. pseudogracilipes Pax \& Hoffm. in Meded. Rijks Herbar. 40: 20 (1921) = C. peltophorus.
C. pungens Jacq. Ic. Pl. Rar. 3: 19, t. 622 (1794).
C. rhamnifolius var. boliviensis Pax \& Hoffm. in Meded. Rijks Herbar. 40: 21 (1921) $=$ C. Orbignyanus.
C. roborensis Standl. in Field Mus. Publ. Bot. 22: 36 (1940).
C. Rusbyi Britton in Rusby in Mem. Torr. Bot. Club, 6: 119 (1898).
C. sarcopetalus var. longipetiolatus Pax \& Hoffm. in Meded. Riiks Herbaï. 40: 21 (1921).
C. Sellowii Baill. in Adansonia, 4: 304 (1864).
C. soratensis Muell. Arg. in Linnaea, 34: 115 (1865-66).
C. soratensis var. intermedius Muell. Arg. in Linnaea, 34: 116 (1865-66).
C. soratensis var. leptobotryus Muell. Arg. in Linnaea, 34: 116 (1865-66).
C. soratensis var. pycnanthus Muell. Arg. in Linnaea, 34: 116 (1865-66).
C. tartonrairoides Pax \& Hoffm. in Meded. Rijks Herbar. 40: 20 (1921).
C. triqueter Lam. Encyc. 2: 214 (1786).
C. Urucurana Baill. in Adansonia, 4: 335 (1863-64).
C. Williamsii Rusby in Bull. N. Y. Bot. Gard. 8: 100 (1912) $=$ C. peltophorus.
C. yungensis Croiz. in Journ. Arnold Arb. 21: 103 (1940).

Dalechampia adscendens (Muell. Arg.) Muell. Arg. in Mart. Fl. Bras. 11(2): 640 (1874).
D. albibracteosa Rusby in Mem. N. Y. Bot. Gard. 7: 287 (1927).
D. Bangii Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xii): 24 (1919).
D. boliviana Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xii): 50 (1919).
D. boliviana Gandog. in Bull. Soc. Bot. France, 66: 286 (1920).
D. Burchellii Muell. Arg. in Mart. Fl. Bras. 11(2): 649 (1874).
D. cujabensis Muell. Arg. in Linnaea, 34: 222 (1865-66).
D. Herzogiana Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xii): 36 (1919).
D. humilis var. adscendens Muell. Arg. in Linnaea, 34: 224 (1865-66).
D. scandens L. Sp. Pl. 2: 1054 (1753).
D. scandens var. fimbriata Muell. Arg. in DC. Prodr. 15 (2): 1244 (1866).

Ditaxis breviramea (Muell. Arg.) Pax \& Hoffm. in Engler, Pflanzenr. IV, 147(vi): 65 (1912).
Euphorbia acerensis Boiss. in DC. Prodr. 15(2): 55 (1862).
E. boerhaavioides Rusby in Bull. N. Y. Bot. Gard. 4: 441 (1907).
E. boliviana Rusby in Bull. N. Y. Bot. Gard. 4: 442 (1907).
E. caecorum Mart. ex Boiss. in DC. Prodr. 15 (2): 51 (1862).
E. Chamaesyce L. Sp. Pl. 455 (1753).
E. cymbiformis Rusby in Mem. Torr. Bot. Club, 4 (3): 255 (1895).
E. dentata Michx. Fl. Bor. Am. 2: 211 (1803).
E. duriuscula Pax \& Hoffm. in Blumea, 5(3): 641 (1945).
E. eanophylla Croiz. in Rev. Sudam. Bot. 6: 10 (1939).
E. geniculata Orteg. in Hort. Matrit. Dec. 2: 18 (1797).
E. Huanchahana var. peperomioides Croiz. in Journ. Arnold Arb. 24: 179 (1943).
E. hypericifolia L. Sp. Pl. 454 (1753).
E. hyssopifolia L. Syst. (ed. 10) 2: 1048 (1759).
E. insulana subsp. tovarensis (Boiss.) Croiz. in Journ. Arnold Arb. 24: 178 (1943).
E. lasiocarpa Klotzsch in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 414 (1843).
E. lasiocarpa var. subprostrata Boiss. in DC. Prodr. 15(2): 1262 (1866).
E. Lathyrus L. Sp. Pl. 457 (1753).
E. longipila Rusby in Bull. N. Y. Bot. Gard. 4: 442 (1907) $=$ E. acerensis.
E. Mandoniana Boiss. in DC. Prodr. 15(2): 1264 (1866).
E. Meyeniana Klotzsch in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 414 (1843).
E. nutans Lag. Gen. \& Spec. Nov. 17 (1816).
E. orbiculata HBK. Nov. Gen. \& Spec. 2: 52 (1817).
E. Peplus L. Sp. Pl. 456 (1753).
E. pilulifera L. Sp. Pl. 454 (1753).
E. Poeppigii (Kl. \& Gke.) Boiss. in DC. Prodr. 15(2): 56 (1862).
E. portulacoides L. Sp. Pl. 456 (1753).
E. Preslii var. andicola Danguy \& Cherm. in Bull. Mus. Hist. Nat. Paris, 28: 438 (1922).
E. prostrata Ait. Hort. Kew. 2: 138 (1789).
E. prunifolia Jacq. Hort. Schoenbr. 3: 15, t. 277 (1798).
E. serpens HBK. Nov. Gen. \& Spec. 2: 52 (1817).

Hevea brasiliensis (Willd.) Muell. Arg. in Linnaea, 34: 204 (1865-66).
H. Spruceana Muell. Arg. in Linnaea, 34: 204 (1865-66).

Hieronyma andina Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xv) : 37 (1922).
H. boliviana Pax in Fedde, Repert. Spec. Nov. 7: 109 (1909).
H. Buchtienii Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xv): 33 (1922).
H. Moritziana var. yungasensis Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xv): 33 (1922).
H. oblonga (Tul.) Muell. Arg. in Linnaea, 34: 66 (1865-66).
H. reticulata (Pl.) Britton ex Rusby in Mem. Torr. Bot. Club, 4(3): 255 (1895).

Hura crepitans L. Sp. Pl. 1008 (1753).
Jatropha clavuligera Muell. Arg. in Linnaea, 34: 209 (1865-66).
J. Curcas L. Sp. Pl. 1006 (1753).
J. elliptica (Pohl) Muell. Arg. in Mart. Fl. Bras. 11(2): 489 (1874).
J. gossypifolia var. staphysagrifolia (Mill.) Muell. Arg. in DC. Prodr. 15(2): 1087 (1866).
J. grossidentata Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (vii) : 398 (1914).
J. Hieronymi O. Ktze. Rev. Gen. 3(2): 287 (1898).
J. intercedens Pax in Engler, Pflanzenr. IV, 147: 31 (1910).
J. pachypoda Pax in Engler, Pflanzerr. IV, 147: 47 (1910).
J. papyrifera Pax \& Hoffm. in Notizbl. 10: 385 (1928).
J. pedatipartita O. Ktze. Rev. Gen. 3(2): 287 (1898).
J. thyrsantha Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (vii): 397 (1914).
J. tubulosa var. triloba Muell. Arg. in Linnaea, 34: 212 (1865-66).

Julocroton Herzogii Pax \& Hoffm. in Meded. Rijks Herbar. 40: 21 (1921).
J. malvoides Croiz. in Rev. Argent. Agron. 10: 139 (1943).
J. paniculatus Pax \& Hoffm. in Meded. Rijks Herbar. 40: 22 (1921).
J. peruvianus var. flavispicatus (Rusby) Croiz. in Rev. Argent. Agron. 10: 136 (1943).
Mabea anadena Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xiv): 55 (1919).
M. elegans Rusby in Mem. N. Y. Bot. Gard. 7: 288 (1927).
M. fistulifera Mart. in Spix \& Mart. Reise Bras. 2: 479 (1828).
M. longifolia (Britton) Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (v): 30 (1912).
M. paniculata Spruce ex Benth. in Hook. Journ. Bot. 6: 367 (1854).

Manihot boliviana Pax \& Hoffm. in Engler, Pflanzenr. IV, 147(vii): 402 (1914).
M. glabrata (Chod. \& Hassl.) Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (ii): 43 (1910).
M. Pavoniana Muell. Arg. in Linnaea, 34: 205 (1865-66).
M. Rusbyi Britton in Bull. Torr. Bot. Club, 28: 302 (1901).
M. utilissima Pohl, Pl. Bras. 1: 32, t. 24 (1827).

Maprounea guianensis Aubl. Pl. Guian. Fr. 2: 895, t. 342 (1775).
Margaritaria nobilis L. f. Suppl. 428 (1781).
Omphalea diandra L. Syst. (ed. 10) 1264 (1759).
Pachystroma ilicifolium var. longifolium Muell. Arg. in Linnaea, 34: 178 (1865-66).
Pera benensis Rusby, Descr. S. Am. Pls. 49 (1920).
P. elliptica Rusby in Mem. N. Y. Bot. Gard. 7: 288 (1927).

Phyllanthus acuminatus Vahl, Symb. 2: 95 (1791).
P. biflorus Rusby in Mem. N. Y. Bot. Gard. 7: 282 (1927).
P. bolivianus Pax \& Hoffm. in Meded. Rijks Herbar. 40: 18 (1921).
P. brasiliensis (Aubl.) Poir. Encyc. 5: 296 (1804).
P. caroliniensis Walt. Fl. Car. 228 (1788).
P. cassioides Rusby in Bull. N. Y. Bot. Gard. 8: 100 (1912).
P. graveolens var. glaber Pax \& Hoffm. in Meded. Rijks Herbar. 40: 18 (1921).
P. ibonensis Rusby in Mem. N. Y. Bot. Gard. 7: 281 (1927) = Margaritaria nobilis.
P. ichthyomethius Rusby in Mem. N. Y. Bot. Gard. 7: 282 (1927).
P. inaequalis Rusby in Mem. Torr. Bot. Club, 6: 118 (1896) = Astrocasia sp.
P. microphyllus var. Orbignyanus Muell. Arg. in Linnaea, 32: 45 (1863).
P. Niruri subsp. lathyroides (HBK.) Webster in Contrib. Gray Herb. 176: 52 (1955).
P. orbiculatus L. C. Rich. in Act. Soc. Hist. Nat. Paris, 1: 113 (1792).
P. prunifolius Rusby in Mem. N. Y. Bot. Gard. 7: 283 (1927).
P. pseudo-nobilis Rusby in Mem. N. Y. Bot. Gard. 7: 281 (1927) = Margaritaria nobilis.
P. rupestris HBK. Nov. Gen. \& Spec. 2: 110 (1817).

Plukenetia volubilis L. Sp. Pl. 1192 (1753).
Ricinus communis L. Sp. Pl. 1007 (1753).
Sapium bolivianum Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (v) : 221 (1912).
S. haematospermum Muell. Arg. in Linnaea, 34: 217 (1865-66).
S. montevidense Klotzsch ex Baill. in Adansonia, 5: 320 (1865), nomen nudum in synon.
S. Peloto Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (v): 210 (1912).
S. rhombifolium Rusby in Bull. Torr. Bot. Club, 28: 307 (1901).

Sebastiania boliviana Rusby, Descr. S. Am. Pls. 50 (1920).
S. brasiliensis Spreng. in Neue Entdeck. 2: 118, t. 3 (1821).
S. brasiliensis var. divaricata (Muell. Arg.) Muell. Arg. in DC. Prodr. 15(2): 1187 (1866).
S. brasiliensis var. ramosissima (St. Hil.) Muell. Arg. in DC. Prodr. 15(2): 1187 (1866).
S. Bridgesii (Muell. Arg.) Pax in Engler, Pflanzenr. IV, 147 (v): 143 (1912).
S. Fiebrigii Pax in Engler, Pflanzenr. IV, 147 (v): 142 (1912).
S. hispida var. paraguayensis (Chod. \& Hassl.) Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (v): 111 (1912).
S. nervosa (Muell. Arg.) Muell. Arg. in DC. Prodr. 15(2): 1183 (1866).

Stillingia salpingadenia (Muell. Arg.) Huber in Bull. Herb. Boiss. (ser. 2) 6: 452 (1906).
Tragia aurea Rusby in Bull. N. Y. Bot. Gard. 4: 444 (1907).
T. Bangii Rusby in Bull. N. Y. Bot. Gard. 4: 445 (1907).
T. Fendleri Muell. Arg. in Linnaea, 34: 179 (1865-66).
T. Friesii Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xvii) : 186 (1924).
T. geraniifolia Klotzsch ex Baill. Étude générale Euphorb. 461 (1858).
T. oligantha Pax \& Hoffm. in Engler, Pflanzenr. IV, 147 (xvii) : 187 (1924).
T. Sellowiana var. glabrifolia Britton ex Rusby in Bull. Torr. Bot. Club, 28: 307 (1901).
T. tristis Muell. Arg. in Mart. Fl. Bras. 11(2): 410 (1874).
T. volubilis L. Sp. Pl. 980 (1753).

## CALLITRICHACEAE

Callitriche heteropoda Engelm. ex Hegelm. in Verh. Bot. Ver. Brandenb. 9: 40 (1867).

## BUXACEAE

Styloceras columnare Muell. Arg. in DC. Prodr. 16(1): 10 (1869).

## ANACARDIACEAE

Anacardium occidentale L. Sp. Pl. 383 (1753).
Astronium fraxinifolium forma glaberrimum Mattick in Notizbl. 11: 1005 (1934).
A. fraxinifolium forma mollissimum Mattick in Notizbl. 11: 1003 (1934).
A. fraxinifolium forma subglabrum Mattick in Notizbl. 11: 1004 (1934).
A. urundueva (Allem.) Engl. in Engler, Bot. Jahrb. 1: 45 (1881).

Cardenasiodendron brachypterum (Loesen.) Barkley in Lloydia, 17: 242 (1954).
Lithraea molleoides (Vell.) Engl. in Mart. Fl. Bras. 12(2): 394, t. 83 (1876).
L. Huasango Spruce ex Engl. in DC. Monog. Phan. 4: 461 (1883).

Mauria Biringo Tul. in Ann. Sci. Nat. (ser. 3) 6: 365 (1846).
M. boliviana Herzog in Fedde, Repert. Spec. Nov. 7: 60 (1909).
M. ferruginea Tul. in Ann. Sci. Nat. (ser. 3) 6: 366 (1846).
M. suaveolens Poepp. \& Endl. Nov. Gen. \& Spec. 3: 77 (1845).
M. thaumatophylla Loesen. in Engler, Bot. Jahrb. 37: 573 (1906).

Protium bolivianum Britton in Bull. Torr. Bot. Club, 16: 189 (1889) = Mauria ferruginea.
Schinopsis Balansae Engl. in Engler, Bot. Jahrb. 6: 286 (1885).
S. cornuta Loesen. in Meded. Rijks Herbar. 27: 86 (1915).
S. Lorentzii (Griseb.) Engl. in Engler, Bot. Jahrb. 1: 46 (1881).
S. marginata Engl. in DC. Monog. Phan. 4: 464 (1883).

Schinus andinus (Engl.) I. M. Johnst. in Journ. Arnold Arb. 19: 259 (1938).
S. andinus var. subtridentatus (O. Ktze.) Barkley in Brittonia, 5: 179 (1944).
S. dependems var. andinus forma grandifolius Loesen. in Meded. Rijks Herbar. 27: 84 (1915) $=\mathrm{S}$. andinus.
S. dependens var. crenatus Engl. in Mart. Fl. Bras. 12(2): 388 (1876).
S. dependens var. obovatus Engl. in Mart. Fl. Bras. 12(2): 387 (1876).
S. dependens var. tomentosus R. E. Fries in Ark. Bot. 8(8): 11 (1908).
S. diversifolius Rusby in Mem. Torr. Bot. Club, 4 (3): 206 (1895) $=$ S. Pearcei.
S. Engleri Barkley in Brittonia, 5: 178 (1944).
S. fasciculatus var. boliviensis Barkley in Brittonia, 5: 177 (1944).
S. ferox Hassl. in Fedde, Repert. Spec. Nov. 12: 373 (1913).
S. maurioides Rusby in Bull. N. Y. Bot. Gard. 8: 102 (1912).
S. Molle L. Sp. Pl. 388 (1753).
S. myrtifolius (Griseb.) Cabrera in Inst. Mus. Univ. Nac. La Plata, Obra del Cincuentario, 2: 269 (1937).
S. Pearcei Engl. in Engler, Bot. Jahrb. 1: 423 (1881).
S. polygamus (Cav.) Cabrera in Inst. Mus. Univ. Nac. La Plata, Obra del Cincuentario, 2: 269 (1937).
S. polygamus forma parviflorus (March.) Cabrera in Rev. Mus. La Plata, secc. Bot. 2: 34 (1938).
S. tomentosus Rusby in Bull. N. Y. Bot. Gard. 8: 102 (1912).
S. Venturii Barkley in Brittonia, 5: 179 (1944).

Tapirira guianensis Aubl. Pl. Guian. Fr. 1: 470, t. 188 (1775).
T. Pearcei Rusby in Mem. Torr. Bot. Club, 6: 22 (1896).

## AQUIFOLIACEAE

Hex aggregata (R. \& P.) Loesen. in Notizbl. 11: 95 (1931).
I. amboroica Loesen. in Fedde, Repert. Spec. Nov. 7: 61 (1909).
I. amplifolia Rusby in Mem. Torr. Bot. Club, 6: 20 (1896).

1. amygdalifolia Rusby in Mem. Torr. Bot. Club, 3(3): 15 (1893) = I. aggregata.
I. andicola Loesen. in Nov. Act. Acad. Caes. Leop. 78: 161 (1901).
I. boliviana Britton ex Rusby in Mem. Torr. Bot. Club, 3(3): 15 (1893).
I. boliviana var. acutata Loesen. in Nov. Act. Acad. Caes. Leop. 78: 155 (1901).
I. boliviana var. Brittoniana Loesen. in Nov. Act. Acad. Caes. Leop. 78: 155 (1901).
I. boliviana var. Rusbyana Loesen. in Nov. Act. Acad. Caes. Leop. 78: 155 (1901).
I. buxifolioides Loesen. in Nov. Act. Acad. Caes. Leop. 78: 225 (1901).
I. buxifolioides var. fastigiata Loesen. in Nov. Act. Acad. Caes. Leop. 78: 226 (1901).
I. Herzogii Loesen. in Meded. Rijks Herbar. 29: 3 (1916).
I. imbricata Rusby, Descr. S. Am. Pls. 52 (1920).
I. Mandonii Loesen. in Nov. Act. Acad. Caes. Leop. 78: 226 (1901).
I. minimifolia Loesen. in Nov. Act. Acad. Caes. Leop. 78: 174 (1901).
I. parviflora Benth. in Hook. Kew Journ. 4: 11 (1852).
I. pseudoëbenacea Loesen. in Nov. Act. Acad. Caes. Leop. 78: 386 (1901).
I. sessiliflora Tr. \& Pl. in Ann. Sci. Nat. (ser. 5) 16: 378 (1872).
I. sessiliflora var. Pearcei Loesen. in Nov. Act. Acad. Caes. Leop. 78: 168 (1901).
I. teratops Loesen. in Engl. \& Prantl, Nat. Pflanzenfam. Nachtr. 3: 218 (1897).
I. trichoclada Loesen. in Nov. Act. Acad. Caes. Leop. 78: 178 (1901).

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Maytenus apurimacensis var. Trollii Loesen. in Notizbl. 13: 219 (1936).
M. Cardenasii Rusby in Mem. N. Y. Bot. Gard. 7: 290 (1927).
M. erythrocarpa Rusby in Mem. N. Y. Bot. Gard. 7: 290 (1927).
M. flagellata Rusby in Mem. Torr. Bot. Club, 6: 20 (1896).
M. ilicifolia var. boliviana Loesen. in Notizbl. 13: 218 (1936).
M. meguillensis Rusby in Mem. N. Y. Bot. Gard. 7: 289 (1927).
M. pseudoboaria Loesen. in Notizbl. 12: 29 (1934).
M. pseudoboaria var. monantha Loesen. in Notizbl. 12: 29 (1934).
M. subalata Reiss. in Mart. Fl. Bras. 11(1): 12, t. 2 (1861).
M. tunarina Loesen. ex O. Ktze. Rev. Gen. 3(2): 37 (1898).
M. verticillata (R. \& P.) DC. Prodr. 2: 10 (1825).
M. Vitis-Idaea Griseb. in Goett. Abh. 19: 110 (1874).

Moya boliviana (Loesen.) Loesen. in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 20b: 147, 405 (1942).
Plenckia integerrima (Lundell) Lundell in Phytologia, 1: 284 (1938).
Schaefferia Dietheri Herter in Rev. Sudam. Bot. 6: 155 (1940).
S. uruguayensis Speg. in Physis, 3: 346 (1917).

## HIPPOCRATEACEAE

Anthodon decussatum R. \& P. Fl. Peruv. 1: 45, t. 74 (1798).
Cheiloclinium cognatum (Miers) A. C. Smith in Brittonia, 3: 529 (1940).
C. hippocrateoides (Peyr.) A. C. Smith in Brittonia, 3: 546 (1940).

Hippocratea volubilis L. Sp. Pl. 1191 (1753).
Prionostemma aspera (Lam.) Miers in Trans. Linn. Soc. 28: 355 (1872).
Pristimera andina Miers in Trans. Linn. Soc. 28: 364 (1872).
P. nervosa (Miers) A. C. Smith in Brittonia, 3: 370 (1940).

Salacia arborescens Rusby in Mem. N. Y. Bot. Gard. 7: 290 (1927) = Pristimera nervosa.
S. impressifolia (Miers) A. C. Smith in Bull. Torr. Bot. Club, 66: 247 (1939).
S. notundifolia Rusby in Bull. N. Y. Bot. Gard. 4: 339 (1907) = Pristimera andina.
Tontelea cuspidata A. C. Smith in Brittonia, 3: 490 (1940).
T. fluminensis (Peyr.) A. C. Smith in Brittonia, 3: 477 (1940).
T. glabra A. C. Smith in Brittonia, 3: 500 (1940).
T. mauritioides (A. C. Smith) A. C. Smith in Brittonia, 3: 481 (1940).
T. Ulei (Loesen.) A. C. Smith in Brittonia, 3: 498 (1940).

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## ? Turpinia sp.

## ICACINACEAE

Citronella apogon (Griseb.) Howard in Contrib. Gray Herb. 142: 75 (1942).
Dendrobangia boliviana Rusby in Mem. Torr. Bot. Club, 6: 19 (1896).

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Allophylus angustatus (Tr. \& Pl.) Radlk. in Engl. \& Prantl, Nat. Pflanzenfam. $3(5): 312$ (1895).
A. cinnamomeus Radlk. in Bull. Torr. Bot. Club, 25: 336 (1898).
A. edulis (St. Hil.) Niederlein in Bol. Mens. Mus. Prod. Argent. 3: 180 (1890).
A. edulis var. gracilis Radlk. in Mart. Fl. Bras. 13(3): 385 (1900).
A. leptostachys Radlk. in Mart. Fl. Bras. 13(3): 489 (1900).
A. pauciflorus Radlk. in Meded. Rijks Herbar. 19: 61 (1913).
A. petiolulatus var. pulverulentus Radlk. in Mart. Fl. Bras. 13(3): 491 (1900).
A. punctatus (Poepp.) Radlk. in Mem. Torr. Bot. Club, 6: 21 (1896).
A. strictus Radlk. in Engl. \& Prantl, Nat. Pflanzenfam. 3(5): 312, fig. 162 (1895).

Athyana weinmannifolia (Griseb.) Radlk. in Durand, Ind. Gen. 73 (1888).
Cardiospermum corindum L. Sp. Pl. (ed. 2) 1: 526 (1762).
C. corindum forma angustisectum (Griseb.) Radlk. in Engler, Pflanzenr. IV, 165(1): 406 (1932).
C. corindum forma elongatum Radlk. in Engler, Pflanzenr. IV, 165(1): 406 (1932).
C. corindum forma loxense (HBK.) Radlk. in Engler, Pflanzenr. IV, 165(1): 402 (1932).
C. corindum forma subsetulosum Radlk. in Engler, Pflanzenr. IV, 165(1): 404 (1932).
C. corindum forma villosum (Mill.) Radlk. in Engler, Pflanzenr. IV, 165(1): 403 (1932).
C. grandiflorum Sw. Prodr. 64 (1788).
C. grandiflorum forma elegans (HBK.) Radlk. in Sitzber. Bayer. Akad. 8: 260 (1878).
C. grandiflorum forma hirsutum (Willd.) Radlk. in Sitzber. Bayer. Akad. 8: 260 (1878).
C. Halicacabum L. Sp. Pl. 366 (1753).

Cupania cinerea Poepp. \& Endl. Nov. Gen. 3: 38 (1845).
C. vernalis Camb. in St. Hil. Fl. Bras. Mer. 1: 387 (1827).

Diatenopteryx sorbifolia Radlk. in Sitzber. Bayer. Akad. 8: 285 (1878).
Dilodendron bipinnatum Radlk. in Sitzber. Math.-Phys. Akad. Muench. 8: 357 (1878).

Diplokeleba Herzogii Radlk. in Meded. Rijks Herbar. 40: 11 (1921).
Dodonaea viscosa Jacq. Enum. Pl. Carib. 19 (1760).
D. viscosa var. vulgaris forma Burmanniana (DC.) Radlk. in Mart. Fl. Bras. 13(3): 646 (1900).
Llagunoa Mandonii Rusby in Bull. N. Y. Bot. Gard. 4: 341 (1907) = L. nitida.
L. nitida R. \& P. Syst. 252 (1798).
L. nitida var. mollis (HBK.) O. Ktze. Rev. Gen. 3(2): 43 (1898).

Lophostigma plumosum Radlk. in Engl. \& Prantl, Nat. Pflanzenfam. Nachtr. 228 (1897).
Magonia glabrata St. Hil. Pl. Remarq. Brés. 241 (1824).
M. pubescens St. Hil. Pl. Remarq. Brés. 239, t. 23, fig. A, t. 24, fig. A (1824).

Matayba boliviana Radlk. in Bull. Torr. Bot. Club, 25: 336 (1898).
M. scrobiculata (HBK.) Radlk. in Sitzber. Bayer. Akad. 9: 536 (1879).
M. Steinbachii Melch. in Notizbl. 10: 349 (1928).

Melicocca lepidopetala Radlk. in Sitzber. Bayer. Akad. 8: 344 (1878).
Paullinia acutangula (R. \& P.) Pers. Synops. Pl. 1: 443 (1805).
P. bilobulata Radlk. in Engler, Bot. Jahrb. 37: 152 (1905).
P. boliviana Radlk. in Mem. Torr. Bot. Club, 4(3): 206 (1895).
P. boliviana forma glabrescens Radlk. in Mem. Torr. Bot. Club, 4(3): 206 (1895).
P. cuneata Radlk. in Notizbl. 6: 150 (1914).
P. dasystachya Radlk. in Abh. Math.-Phys. Bayer. Akad. Wiss. 19: 119, 270 (1896).
P. dasystachya forma hirta Radlk. in Abh. Math.-Phys. Bayer. Akad. Wiss. 19: 271 (1896).
P. elegans Camb. in St. Hil. Fl. Bras. Mer. 1: 370 (1827).
P. ingaefolia Rusby in Mem. N. Y. Bot. Gard. 7: 291 (1927).
P. neglecta Radlk. in Abh. Math.-Phys. Bayer. Akad. Wiss. 19: 167 (1896).
P. pendulifolia Rusby in Mem. N. Y. Bot. Gard. 7: 291 (1927).
P. pinnata L. Sp. Pl. 366 (1753).
P. quercifolia Rusby in Mem. N. Y. Bot. Gard. 7: 292 (1927).
P. rhizantha Poepp. \& Endl. Nov. Gen. 3: 36, t. 243 (1845).
P. ribesiaecarpa Rusby in Mem. N. Y. Bot. Gard. 7: 293 (1927).
? P. riparia HBK. Nov. Gen. \& Spec. 5: 116 (1821).
P. Tatei Rusby in Phytologia, 1: 64 (1934).

Sapindus Saponaria L. Sp. Pl. 367 (1753).
Serjania altissima (Poepp.) Radlk. Serj. Monog. 125 (1875).
S. areolata Radlk. Monog. Serj. Suppl. 87 (1886).
S. caracasana Willd. Sp. Pl. 2(1): 465 (1799).
S. caracasana forma flavoviridis Radlk. in Fedde, Repert. Spec. Nov. 7: 356 (1909).
S. caracasana forma puberula Radlk. in Trab. Mus. Farm. Fac. Cienc. Med. Buenos Aires, 21: 78 (1909).
S. caracasana forma Radlkoferi O. Ktze. Rev. Gen. 3(2): 44 (1898).
S. chaetocarpa Radlk. in Engl. \& Prantl, Nat. Pflanzenfam. 3(5): 302 (1895).
S. confertiflora Radlk. Consp. Serj. 4 (1874).
S. confertiflora var. dasycephala Radlk. in Mem. Torr. Bot. Club, 6: 21 (1896).
S. crassifolia Radlk. Serj. Monog. 225 (1875).
S. dibotrya Poepp. \& Endl. Nov. Gen. 3: 35, t. 242 (1844).
S. didymadenia Radlk. in Bull. Herb. Boiss. (ser. 1) 1: 467 (1893).
S. diffusa Radlk. Serj. Monog. 302 (1875).
S. dumicola Radlk. Consp. Serj. 4 (1874).
S. erecta Radlk. Consp. Serj. 8 (1874).
S. glabrata HBK. Nov. Gen. \& Spec. 5: 110 (1821).
S. glabrata forma mollior Radlk. Serj. Monog. 169 (1875).
S. glabrata forma mollissima Radlk. Serj. Monog. 168 (1875).
S. grandiceps Radlk. in Bull. Torr. Bot. Club, 25: 336 (1898).
S. humifusa Radlk. in Fedde, Repert. Spec. Nov. 7: 355 (1909).
S. leptocarpa Radlk. Serj. Monog. 112 (1875).
S. lethalis St. Hil. Pl. Remarq. Brés. 235 (1825).
S. leucocephala Radlk. in Meded. Rijks Herbar. 19: 59 (1913).
S. lyrata Rusby in Phytologia, 1: 64 (1934).
S. Mansiana Mart. in Flora, 22, Beibl. 1: 9 (1839).
S. marginata Casar. Decad. Stirp. Nov. Bras. 5: 44 (1843).
S. marginata forma pluridentata Radlk. Serj. Monog. 160 (1875).
S. meridionalis Camb. in St. Hil. Fl. Bras. Mer. 1: 366, t. 76 (1827).
S. nutans Poepp. \& Endl. ex Walp. Repert. 2: 813 (1843).
S. ovalifolia Radlk. Serj. Monog. 218 (1875).
S. pannifolia Radlk. in Engler, Bot. Jahrb. 37: 146 (1905).
S. perulacea Radlk. Serj. Monog. 227 (1875).
S. reticulata Camb. in St. Hil. Fl. Bras. Mer. 1: 359 (1827).
S. reticulata forma platyptera Radlk. Serj. Monog. 159 (1875).
S. rigida Radlk. Serj. Monog. 283 (1875).
S. rubicaulis Benth. ex Radlk. Serj. Monog. 254 (1875).
S. rubicunda Radlk. in Meded. Rijks Herbar. 19: 58 (1913).
S. sphaerococca Radlk. Serj. Monog. 153 (1875).
S. sufferruginea Radlk. Serj. Monog. 299 (1875).
S. trirostris Radlk. in Notizbl. 6: 149 (1914).

Talisia esculenta (Camb.) Radlk. in Sitzber. Bayer. Akad. 8: 345 (1878).
Thinouia coriacea Britton in Bull. Torr. Bot. Club, 16: 191 (1889).
T. paraguariensis (Britton) Radlk. in Engl. \& Prantl, Nat. Pflanzenfam. 3(5): 308 (1895).
T. repanda Radlk. in Engl. \& Prantl, Nat. Pflanzenfam. 3(5): 308 (1895).

Urvillea filipes Radlk. in Fedde, Repert. Spec. Nov. 7: 354 (1909).
U. laevis Radlk. in Att. Congr. Internat. Bot. Firenze, 1874: 63 (1876), nomen nudum.
U. rufescens Camb. in St. Hil. Fl. Bras. Mer. 1: 354 (1827).
U. ulmacea HBK. Nov. Gen. \& Spec. 5: 106, t. 440 (1821).

## VITACEAE

Cissus alata Jacq. Sel. Stirp. Amer. 23 (1763).
C. erosa L. C. Rich. in Act. Soc. Hist. Nat. Paris, 1: 106 (1792).
C. gongyloides (Baker) Planch. in DC. Monog. Phan. 5: 550 (1887).
C. paraguayensis Planch. in DC. Monog. Phan. 5: 554 (1887).
C. pruinosa Herzog in Meded. Rijks Herbar. 40: 30 (1921).
? C. salutaris (Baker) Herzog in Meded. Rijks Herbar. 40: 30 (1921).
C. sicyoides L. Sp. Pl. (ed. 2) 1: 170 (1762).
C. sicyoides forma canescens (Lam.) Planch. in DC. Monog. Phan. 5: 531 (1887).
C. sicyoides forma ovata (Lam.) Planch. in DC. Monog. Phan. 5: 526 (1887).
C. trifoliolata L. Sp. Pl. (ed. 2) 1: 170 (1762).

Vitis obliqua (R. \& P.) O. Ktze. Rev. Gen. 3(2): 41 (1898).

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Colletia foliosa var. microphylla O. Ktze. Rev. Gen. $3(2)$ : 38 (1898).
C. spinosa Lam. Tabl. Encyc. 2: 91, t. 129 (1793).

Condalia Weberbaueri Perkins in Engler, Bot. Jahrb. 45: 463 (1911).
Discaria Weddelliana (Miers) Escalante in Bol. Soc. Argent. Bot. 1: 223 (1946)
Gouania Blanchetiana Miq. in Linnaea, 22: 797 (1847).
G. colurnaefolia Reiss. in Mart. Fl. Bras. 11(1): 107 (1861).
G. latifolia Reiss. in Mart. Fl. Bras. 11(1): 103 (1861).
G. polygama Urb. Symb. Ant. 4: 378 (1910).
G. sepiaria Mart. ex Britton in Bull. Torr. Bot. Club, 16: 189 (1889) = G. Blanchetiana.
G. tomentosa Jacq. Sel. Stirp. Amer. 263 (1763).
G. ursinicarpa Rusby in Bull. N. Y. Bot. Gard. 8: 103 (1912).

Karwinskia oblongifolia Rusby in Mem. N. Y. Bot. Gard. 7: 293 (1927).
Kentrothamnus foliosus (Rusby) Suesseng. \& Overk. in Fedde, Repert. Spec. Nov. 50: 327 (1941).
K. penninervius Suesseng. \& Overk. in Fedde, Repert. Spec. Nov. 50: 327 (1941).

Rhamnidium elaeocarpum Reiss. in Mart. Fl. Bras. 11(1): 94 (1861).
R. glabrum Reiss. in Mart. Fl. Bras. 11(1): 95 (1861).

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S. hastata St. Hil. Fl. Bras. Mer. 1: 190, t. 36, fig. 2 (1827).
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S. macrodon DC. Prodr. 1: 464 (1824).
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S. rhombifolia var. canariensis (Willd.) Griseb. Fl. Brit. W. Ind. 74 (1859).
S. rufescens St. Hil. Fl. Bras. Mer. 1: 185 (1827).
S. supina L'Hérit. Stirp. 109 bis, t. 52 (1785).
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W. excelsior (Cav.) Presl, Rel. Haenk. 2: 118 (1836).
W. filipes Rusby in Mem. N. Y. Bot. Gard. 7: 296 (1927).
W. grandifolia Baker f. in Bull. N. Y. Bot. Gard. 4: 328 (1907).
W. Grisebachii R. E. Fries in Kgl. Sv. Vetensk. Akad. Handl. 43(4): 74 (1908).
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B. scabra L. Sp. Pl. (ed. 2) 1: 284 (1762).

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Waltheria americana L. Sp. Pl. 673 (1753).
W. communis St. Hil. Fl. Bras. Mer. 1: 155 (1825).
W. Ladewii Rusby in Phytologia, 1: 65 (1934).

## DILLENIACEAE

Davilla grandiflora St. Hil. \& Tul. in Ann. Sci. Nat. (ser. 2) 17: 131 (1842).
D. Lechleri Rusby in Mem. Torr. Bot. Club, 6: 2 (1896).
D. microcalyx Herzog in Fedde, Repert. Spec. Nov. 7: 62 (1909).
D. rugosa Poir. Encyc. Suppl. 2: 457 (1811).
D. rugosa var. capitata Rusby in Mem. Torr. Bot. Club, 6: 2 (1896).

Doliocarpus dentatus (Aubl.) Standl. in Journ. Wash. Acad. Sci. 15: 286 (1925).
D. ferrugineus Rusby in Mem. Torr. Bot. Club, 6: 3 (1896).
D. magnificus Sleumer in Fedde, Repert. Spec. Nov. 39: 45 (1935).
D. rufescens Sleumer in Fedde, Repert. Spec. Nov. 39: 46 (1935).
D. semidentatus Garcke in Linnaea, 22: 48 (1849).

Saurauia brevipes Rusby, Descr. S. Am. Pls. 57 (1920).
S. coroicana Busc. in Malpighia, 26: t. 9, fig. 17 (1913).
S. excelsa Willd. in Ges. Naturf. Freunde, Berlin, Neue Schr. 3: 407 (1801).
S. parviflora Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 18: 268 (1862).
S. pseudoparviflora Busc. in Malpighia, 30: 158 (1927).
S. pyramidata Sleumer in Notizbl. 12: 145 (1934).
S. Rusbyi Britton in Bull. Torr. Bot. Club, 16: 64 (1889).
S. scabra var. boliviana Busc. in Malpighia, 25: 11 (1912), nomen nudum.
S. serrata DC. Prodr. 1: 526 (1824).
S. Trolliana Sleumer in Notizbl. 12: 148 (1934).

Tetracera aspera var. boliviana O. Ktze. Rev. Gen. 3(2):2 (1898) = T. parviflora.
T. parviflora (Rusby) Sleumer in Fedde, Repert. Spec. Nov. 39: 47 (1935).

## OCHNACEAE

Cespedezia excelsa Rusby in Mem. Torr. Bot. Club, 6: 17 (1896).
C. spathulata Planch. in Hook. Lond. Journ. Bot. 5: 647 (1846).

Godoya oblonga R. \& P. Fl. Peruv. Prodr. 58 (1794).
Ouratea boliviana v. Tiegh. in Ann. Sci. Nat. (ser. 8) 16: 263 (1902).
O. castaneaefolia (DC.) Engler in Mart. Fl. Bras. 12(2): 309 (1876).
O. denudata v. Tiegh. in Ann. Sci. Nat. (ser. 8) 16: 263 (1902).
O. flexuosa Rusby in Mem. N. Y. Bot. Gard. 7: 303 (1927).
O. macrobotrys Rusby in Mem. N. Y. Bot. Gard. 7: 303 (1927).
O. oblongifolia Rusby in Bull. N. Y. Bot. Gard. 8: 103 (1912).
O. Trollii Sleumer in Notizbl. 13: 354 (1936).
O. Werdermannii Sleumer in Notizbl. 13: 356 (1936).

Sauvagesia deflexifolia Gardn. in Hook. Ic. Pl. 5(1): t. 484 (1842) .
S. erecta L. Sp. Pl. 203 (1753).

## CARYOCARACEAE

Caryocar glabrum (Aubl.) Pers. Synops. Pl. 2: 84 (1807).
C. parviflorum A. C. Smith in Journ. Arnold Arb. 20: 298 (1939).

## MARCGRAVIACEAE

Marcgravia peduncularis Poepp. ex Rusby in Mem. Torr. Bot. Club, 3 (3): 8 (1893) $=$ Souroubea crassipes ?
M. rectiflora Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 17: 364 (1862).
M. rectiflora var. macrophylla Wittm. in Mart. Fl. Bras. $12(1): 222$, t. 40, fig. 2 (1878).
Norantea anomala HBK. Nov. Gen. \& Spec. 7: 218, t. 647 bis (1825).
N. droseriformis Rusby ex Gilg \& Werdermann in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 21: 101 (1925).
N. macrostoma Gilg in Engler, Bot. Jahrb. 25, Beibl. 60: 30 (1898).
N. oxystilis Baill. in Adansonia, 10: 243 (1872).
N. Weddelliana Baill. in Adansonia, 10: 242 (1872).

Souroubea brachystachya Rusby in Bull. N. Y. Bot. Gard. 8: 103 (1912).
S. crassipes Wittm. in Mart. Fl. Bras. 12(1): 254 (1878).
S. guianensis Aubl. Pl. Guian. Fr. 1: 244, t. 97 (1775).

## QUIINACEAE

Quiina Blackii Pires in Bol. Técn. Inst. Agron. Norte, Pará, no. 20: 44, t. 8 (1950).

## THEACEAE

Freziera angulosa Tul. in Ann. Sci. Nat. (ser. 3) 8: 332 (1847.)
F. boliviensis Wawra in Mart. Fl. Bras. 12(1): 284 (1886) = F. lanata.
F. caloneura Kobuski in Journ. Arnold Arb. 22: 477 (1941).
F. maequalifolia (Lingelsh.) Kobuski in Ann. Missouri Bot. Gard. 25: 354 (1938) $=\mathrm{F}$. inaequilatera.
F. inaequilatera Britton in Bull. Torr. Bot. Club, 16: 63 (1889).
F. lanata (R. \& P.) Tul. in Ann. Sci. Nat. (ser. 3) 8: 334 (1847).
F. subintegrifolia (Rusby) Kobuski in Ann. Missouri Bot. Gard. 25: 355 (1938).
F. yungasia Tul. in Ann. Sci. Nat. (ser. 3) 8: 333 (1847) =F. lanata.

Laplacea fruticosa (Schreb.) Kobuski in Journ. Arnold Arb. 28: 437 (1947).
L. pubescens Planch. \& Lind. in Ann. Sci. Nat. (ser. 4) 18: 269 (1862).
L. pubescens var. subcaudata Kobuski in Journ. Arnold Arb. 31: 427 (1950).
L. symplocoides Planch. \& Lind. in Ann. Sci. Nat. (ser. 4) 18: 269 (1862).

Taomabo flavifolia Rusby in Bull. N. Y. Bot. Gard. 8: 104 (1912) $=$ Ternstroemia asymmetrica.
Ternstroemia asymmetrica Rusby in Bull. N. Y. Bot. Gard. 4: 327 (1907).
T. brasiliensis Camb. in St. Hil. Fl. Bras. Mer. 1: 298 (1827).
T. circumscissilis Kobuski in Journ. Arnold Arb. 23: 304 (1942).
T. polyandra Kobuski in Journ. Arnold Arb. 23: 333 (1942).
T. subserrata (Rusby) Melchior in Engl. \& Prantl, Nat. Pflanzenfam. (ed. 2) 21: 142 (1925).

## GUTTIFERAE

Calophyllum ellipticum Rusby in Mem. N. Y. Bot. Gard. 7: 303 (1927).
Caopia cordata Rusby in Bull. N. Y. Bot. Gard. 8: 105 (1912) = Vismia sp. ?
C. crassa Rusby in Mem. Torr. Bot. Club, 4 (3) : 204 (1895) = Vismia sp.?
C. parvifolia Rusby in Phytologia, 1: 65 (1934) = Vismia sp.?

Chrysochlamys macrophylla Pax in Fedde, Repert. Spec. Nov. 7:111 (1909).
C. myrcioides Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 14: 260 (1860).

Clusia amazonica Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 13: 358 (1860).
C. criuva Camb. in St. Hil. Fl. Bras. Mer. 1: 317 (1827).
C. elongata Rusby in Bull. N. Y. Bot. Gard. 8: 105 (1912).
C. insignis Mart. Nov. Gen. 3: 164 (1829).
C. latipes Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 13: 365 (1860).
C. Lechleri Rusby in Bull. N. Y. Bot. Gard. 8: 105 (1912).
C. multiflora HBK. Nov. Gen. \& Spec. 5: 200 (1822).
C. pseudomangle Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 13: 370 (1860).
C. ramosa Rusby in Mem. Torr. Bot. Club, 4 (3): 204 (1895).
C. ternstroemioides Rusby, Descr. S. Am. Pls. 59 (1920).
C. trochiformis Vesque, Epharmosis, 3: 4, t. 3 (1892).

Havetia laurifolia HBK. Nov. Gen. \& Spec. 5: 204, t. 462 (1822).
Havetiopsis flavida (Benth.) Pl. \& Tri. in Ann. Sci. Nat. (ser. 4) 14: 247 (1860).
H. glauca Rusby in Bull. N. Y. Bot. Gard. 4: 309 (1907).

Hypericum andinum Gleason in Torreya, 29: 137 (1929).
H. bolivianum Keller in Bull. Herb. Boiss. (ser. 2) 8: 189 (1908).
H. brasiliense Chois. ex DC. Prodr. 1: 547 (1824).
H. brevistylum Chois. Prodr. Hyper. 51 (1821).
H. connatum Lam. Encyc. 4: 168 (1797).
H. connatum var. Fiebrigii Briq. in Ann. Conserv. \& Jard. Bot. Genève, 20: 390 (1919).
H. connatum var. paraguariense Briq. in Ann. Conserv. \& Jard. Bot. Genève, 20: 390 (1919).
H. laricifolium Juss. in Ann. Mus. Paris, 3: 160, t. 16 (1804).
H. struthiolaefolium Juss. in Ann. Mus. Paris, 3: 160 (1804).
H. struthiolaefolium var. parviflorum Keller in Bull. Herb. Boiss. (ser. 2) 8: 182 (1908).
H. stylosum Rusby in Bull. N. Y. Bot. Gard. 4: 326 (1907).
H. thesiifolium HBK. Nov. Gen. \& Spec. 5: 192 (1822).

Kielmeyera paniculata Rusby in Mem. Torr. Bot. Club, 6: 9 (1896).
Marila laxifiora Rusby in Mem. Torr. Bot. Club, 6: 9 (1896).
Rengifa acuminata Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 14: 243 (1860).
Rheedia Achachairu Rusby in Mem. N. Y. Bot. Gard. 7: 304 (1927).
R. floribunda (Miq.) Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 14: 319 (1860).
R. rogaguensis Rusby in Mem. N| Y. Bot. Gard. 7: 304 (1927).
R. Spruceana Engl. in Mart. Fl. Bras. 12 (1): 463 (1888).

Symphonia globulifera L. f. Suppl. 302 (1781).
Tovomita alatopetiolata O. Ktze. Rev. Gen. 3(2): 16 (1898).
T. micrantha A. C. Smith in Phytologia, 1: 123 (1935).
T. umbellata Benth. in Hook. Lond. Journ. Bot. 2: 367 (1843).
T. Weddelliana Tri. \& Pl. in Ann. Sci. Nat. (ser. 4) 14: 277 (1860).

Vismia cayennensis (L.) Pers. Synops. Pl. 2: 86 (1807).
V. dealbata HBK. Nov. Gen. \& Spec. 5: 184, t. 454 (1822).
V. glabra R. \& P. Syst. 183 (1798).
V. guianensis (Aubl.) Pers. Synops. Pl. 2: 86 (1807).
V. magnoliifolia Cham. \& Schlechtd. in Linnaea, 3: 118 (1828).
V. plicatifolia Hochr. in Ann. Conserv. \& Jard. Bot. Genève, 21: 54 (1919).
V. tomentosa R. \& P. Syst. 183 (1798).

Anthobryum tetragonum Phil. in Anal. Mus. Nac. Chile, Bot. 1891: 51, t. 2 (1891).
A. triandrum (Remy) Surgis in Rev. Gén. Bot. 34: 455 (1922).

Frankenia farinosa Remy in Ann. Sci. Nat. (ser. 3) 8: 236 (1847).

## BIXACEAE

Bixa Orellana L. Sp. Pl. 512 (1753).

## COCHLOSPERMACEAE

Amoureuxia unipora v. Tiegh. in Journ. de Bot. 14: 48 (1900).
Cochlosperum hibiscioides Kunth, Syn. Pl. Aequin. 3: 214 (1824).
C. insigne St. Hil. Pl. Us. Bras. t. 57 (1824-28).
C. tetraporum Hall. f. in Meded. Rijks Herbar. 19: 39 (1913).
C. trilobum Standl. in Field Mus. Publ. Bot. 22: 92 (1940).

## KOEBERLINIACEAE

Koeberlinia spinosa Zucc. in Abh. Akad. Muench. 1: 359 (1832).

## VIOLACEAE

Anchietea parviflora Hall. f. in Meded. Rijks Herbar. 19: 64 (1913).
Calceolaria appendiculata Rusby in Mem. N. Y. Bot. Gard. 7: 305 (1927) $=$ Hybanthus sp.
C. balaënsis Rusby in Mem. N. Y. Bot. Gard. 7: 306 (1927) $=$ Hybanthus sp.
C. sessiliflora O. Ktze. Rev. Gen. 3(2): 8 (1898) $=$ Hybanthus sp.

Hybanthus atropurpureus (St. Hil.) Taub. in Engl. \& Prantl, Nat. Pflanzenfam. 3(6): 333 (1895).
H. biacuminatus (Rusby) G. K. Schulze in Notizbl. 12: 114 (1934).
H. Calceolaria (L.) G. K. Schulze in Notizbl. 12: 114 (1934).
H. communis (St. Hil.) Taub. in Engl. \& Prantl, Nat. Pflanzenfam. 3(6): 333 (1895).
H. oppositifolius (L.) Taub. in Engl. \& Prantl, Nat. Pflanzenfam. 3(6): 333 (1895).
H. parviflorus (Mut.) Baill. Bot. Médic. 841 (1884).
H. parviflorus var. Bangii (Rusby) Sparre in Lilloa, 23: 535 (1950).
H. parviflorus var. glutinosus (Vent.) Hassl. in Bull. Soc. Bot. Genève (ser. 2), 1: 214 (1909).

Ionidium subglaucum Herzog in Meded. Rijks Herbar. 40: 15 (1921) $=$ Hybanthus sp .
Leonia glycycarpa R. \& P. Fl. Peruv. 2: 69, t. 222 (1799).
Rinorea albicaulis (Turcz.) Blake in Contrib. U. S. Nat. Herb. 20: 517 (1924).
R. gracilis Rusby in Bull. N. Y. Bot. Gard. 8: 106 (1912).
R. juruana Ule in Verh. Bot. Ver. Brandenb. 47: 158 (1905).
R. Lindeniana (Tul.) O. Ktze. Rev. Gen. 1: 42 (1891).
R. ovalifolia (Britton) Blake in Contrib. U. S. Nat. Herb. 20: 513 (1924).
R. viridifolia Rusby in Mem. Torr. Bot. Club, 6: 5 (1896).

Viola Bangiana W. Becker in Beih. Bot. Centralbl. 22(2): 89 (1907).
V. Bangii Rusby in Mem. Torr. Bot. Club, 6: 5 (1896).
V. boliviana W. Becker in Beih. Bot. Centralbl. 22 (2) : 88 (1907) $=$ V. Steinbachii.
V. boliviana Britton in Bull. Torr. Bot. Club, 16: 18 (1889).
V. Bridgesii Britton in Bull. Torr. Bot. Club, 16: 18 (1889).
V. Cumingii W. Becker in Beih. Bot. Centralbl. 22(2): 94 (1907).
V. exigua W. Becker in Engler, Bot. Jahrb. 37: 590 (1906).
V. flavicans Wedd. in Ann. Sci. Nat. (ser. 5) 1: 292 (1864).
V. Hillii W. Becker in Kew Bull. 1928: 134.
V. Humboldtii var. renifolia Britton in Bull. Torr. Bot. Club, 16: 18 (1889).
V. Mandonii W. Becker in Beih. Bot. Centralbl. 22(2): 95 (1907).
V. micranthella Wedd. in Ann. Sci. Nat. (ser. 5) 1: 291 (1864).
V. Orbignyana Remy in Ann. Sci. Nat. (ser. 3) 6: 353 (1846).
V. producta W. Becker in Engler, Bot. Jahrb. 37: 591 (1906).
V. pusillima Wedd. in Ann. Sci. Nat. (ser. 5) 1: 291 (1864).
V. pygmaea Juss. ex Poir. in Lam. Encyc. 8: 630 (1808).
V. scandens Humb. \& Bonpl. ex Roem. \& Schult. Syst. 5: 391 (1819).
V. Steinbachii W. Becker in Notizbl. 9: 1040 (1926).
V. thymifolia Britton in Bull. Torr. Bot. Club, 16: 18 (1889).
V. veronicaefolia Pl. \& Lind. in Ann. Sci. Nat. (ser. 4) 17: 121 (1862).

## FLACOURTIACEAE

Abatia boliviana (Mand. \& Wedd.) Britton in Bull. Torr. Bot. Club, 17: 214 (1890) =A. stellata.
A. stellata Lillo in Act. 1 Reunión Nac. Soc. Arg. Cienc. Nat. Tucumán, 1916: 223 (1919).
Azara salicifolia Griseb. in Goett. Abh. 24: 20 (1879).
Banara amazonica Sleumer in Notizbl. 12: 50 (1934).
B. laxiffora Benth. in Journ. Linn. Soc. 5, Suppl. 2: 91 (1861).
B. pyramidata Rusby in Mem. Torr. Bot. Club, 3(3): 33 (1893).

Casearia aculeata Jacq. Enum. Pl. Carib. 21 (1760).
C. acuminata DC. Prodr. 2: 50 (1825).
C. albicaulis Rusby in Mem. N. Y. Bot. Gard. 7: 307 (1927).
C. arborea (L. C. Rich.) Urb. Symb. Ant. 4: 421 (1910).
C. attenuata Rusby in Mem. Torr. Bot. Club, 6: 41 (1896).
C. Bangii Rusby in Mem. Torr. Bot. Club, $3(3): 34$ (1893) $=$ C. Cambessedesii.
C. berberoidia Rusby in Mem. N. Y. Bot. Gard. 7: 307 (1927) = C. aculeata.
C. boliviana Briq. in Ann. Conserv. \& Jard. Bot. Genève, 2: 69 (1898).
C. brasiliensis Eichl. in Mart. Fl. Bras. 13(1): 477 (1872).
C. Cambessedesii Eichl. in Mart. Fl. Bras. 13(1): 475 (1872).
C. combaymensis Tul. in Ann. Sci. Nat. (ser. 3) 7: 362 (1847).
C. commutata Briq. in Ann. Conserv. \& Jard. Bot. Genève, 2: 65 (1898).
C. membranacea Britton in Bull. Torr. Bot. Club, 17: 214 (1890) = C. combaymensis.
C. oblongifolia Camb. in St. Hil. Fl. Bras. Mer. 2: 234 (1829).
C. obtusifolia Rusby in Bull. N. Y. Bot. Gard. 4: 362 (1907) = C. boliviana.
C. punctata Spreng. Neue Entdeck. 2: 154 (1821).
C. sylvestris Sw. Fl. Ind. Occ. 2: 752 (1800).
C. sylvestris var. tomentella Rusby in Mem. Torr. Bot. Club, 6: 41 (1896).

Prockia completa Hook. Ic. Pl. 1: t. 94 (1828).
P. crucis L. Sp. Pl. (ed. 2) 1: 745 (1762).
P. grandiflora Herzog in Fedde, Repert. Spec. Nov. 7: 62 (1909).
P. septemnervia Spreng. Syst. 2: 609 (1825).

Xylosma ellipticum (Clos) Hemsl. Biol. Centr. Am. Bot. 1: 57 (1879).
X. ovatum Rusby in Bull. N. Y. Bot. Gard. 4: 323 (1907) = X. Rusbyanum.
X. Rusbyanum Sleumer in Notizbl. 12: 56 (1934).
X. venosum N. E. Br. in Trans. \& Proc. Bot. Soc. Edinb. 20: 46 (1894).

## LACISTEMACEAE

Lacistema aggregatum (Berg) Rusby in Bull. N. Y. Bot. Gard. 4: 447 (1907).
L. bolivianum Gandog. in Bull. Soc. Bot. France, 66: 288 (1920) = L. aggregatum.

## TURNERACEAE

Piriqueta Duarteana var. grandifolia Urb. in Jahrb. Bot. Gart. Berlin, 2: 67 (1883).
P. seticarpa Rusby in Mem. N. Y. Bot. Gard. 7: 308 (1927).

Turnera melochioides var. oblongifolia Urb. in Jahrb. Bot. Gart. Berlin, 2: 116 (1883).
T. muricata Rusby in Mem. N. Y. Bot. Gard. 7: 308 (1927).
T. sidoides var. lycopifolia (DC.) Urb. in Jahrb. Bot. Gart. Berlin, 2: 102 (1883).
T. ulmifolia var. caerulea (DC.) Urb. in Jahrb. Bot. Gart. Berlin, 2: 144 (1883).
T. ulmifolia var. elegans (Otto) Urb. in Jahrb. Bot. Gart. Berlin, 2: 139 (1883).
T. ulmifolia var. grandidentata Urb. in Jahrb. Bot. Gart. Berlin, 2: 139 (1883).
T. Weddelliana Urb. \& Rolfe in Jahrb. Bot. Gart. Berlin, 2: 90 (1883).
T. Weddelliana var. brachyphylla Urb. in Engler, Bot. Jahrb. 25, Beibl. 60: 3 (1898).
T. Whitei Rusby in Mem. N. Y. Bot. Gard. 7: 309 (1927).

## PASSIFLORACEAE

Passiflora auriculata HBK. Nov. Gen. \& Spec. 2: 131 (1817).
P. Bangii Masters in Rusby in Bull. N. Y. Bot. Gard. 4: 363 (1907) $=$ P. violacea.
P. Buchtienii Killip in Journ. Wash. Acad. Sci. 14: 115 (1924).
P. callimorpha Harms in Fedde, Repert. Spec. Nov. 18: 295 (1922).
P. Candollei Tri. \& Pl. in Ann. Sci. Nat. (ser. 5) 17: 161 (1873), nomen provisorium.
P. cayaponioides Rusby in Bull. N. Y. Bot. Gard. 8: 107 (1912) $=$ P. auriculata.
P. cincinnata Mast. in Gard. Chron. 1868: 966.
P. coccinea Aubl. Pl. Guian. Fr. 2: 828, t. 324 (1775).
P. coriacea Juss. in Ann. Mus. Hist. Nat. Paris, 6: 109, t. 39, fig. 2 (1805).
P. dalechampioides Killip in Journ. Wash. Acad. Sci. 17: 429 (1927).
P. erosa Rusby in Bull. N. Y. Bot. Gard. 4: 363 (1907) = P. morifolia.
P. exoperculata Mast. in Mart. Fl. Bras. 13(1): 556 (1872).
P. foetida L. Sp. Pl. 959 (1753).
P. foetida var. gossypifolia (Desv.) Mast. in Trans. Linn. Soc. 27: 631 (1871).
P. gracilens (A. Gray) Harms in Engl. \& Prantl, Nat. Pflanzenfam. 3(6a): 91 (1893).
P. Guentheri Harms in Notizbl. 10: 811 (1929).
P. hastifolia Killip in Journ. Wash. Acad. Sci. 14: 115 (1924).
P. ianthina Mast. in Journ. Bot. 21: 36 (1883) $=$ P. umbilicata.
P. ichthyura Mast. in Mart. Fl. Bras. 13(1): 587 (1872).
P. ligularis Juss. in Ann. Mus. Hist. Nat. 6: 113, t. 40 (1805).
P. Mandonii (Mast.) Killip in Journ. Wash. Acad. Sci. 14: 213 (1924).
P. mapiriensis Harms in Notizbl. 10: 810 (1929).
P. misera HBK. Nov. Gen. \& Spec. 2: 136 (1817).
P. mixta L. f. Suppl. 408 (1781).
P. mollissima (HBK.) Bailey in Rhodora, 18: 156 (1916).
P. Mooreana Hook. f. in Bot. Mag. 66: t. 3773 (1840).
P. morifolia Mast. in Mart. Fl. Bras. 13(1): 555 (1872).
P. naviculata Griseb. in Goett. Abh. 19: 149 (1874).
P. nephrodes Mast. in Bull. Torr. Bot. Club, 17: 282 (1890).
P. nigradenia Rusby in Mem. N. Y. Bot. Gard. 7: 311 (1927).
P. palmatisecta Mast. in Mart. Fl. Bras. 13(1): 564 (1872).
P. pinnatistipula Cav. Icon. 5: 16, t. 428 (1799).
P. Pohlii Mast. in Mart. Fl. Bras. 13(1): 586 (1872).
P. punctata L. Sp. Pl. 957 (1753).
P. quadrangularis L. Syst. (ed. 10) 1248 (1759).
P. quadriglandulosa Rodschied, Med. Chir. Bemerk. Esseq. 77 (1796).
P. Rojasii Hassl. ex Harms in Notizbl. 10: 812 (1929).
P. rubra L. Sp. Pl. 956 (1753).
P. rubrotincta Killip in Journ. Wash. Acad. Sci. 17: 429 (1929).
P. Rusbyi Masters in Bull. Torr. Bot. Club, 17: 282 (1890).
P. serrato-digitata L. Sp. Pl. 960 (1753).
P. Steinbachii Harms in Notizbl. 10: 815 (1920) $=$ P. Mandonii.
P. suberosa L. Sp. Pl. 958 (1753).
P. Tatei Killip \& Rusby in Phytologia, 1: 66 (1934).
P. tenuifila Killip in Journ. Wash. Acad. Sci. 17: 430 (1927).
P. translinearis Rusby in Mem. N. Y. Bot. Gard. 7: 309 (1927) $=$ P. misera as to foliage and P. quadriglandulosa as to flowers.
P. tricuspis Masters in Mart. Fl. Bras. 13(1): 587 (1872).
P. triloba R. \& P. ex DC. Prodr. 3: 330 (1828).
P. trisecta Masters in Mart. Fl. Bras. 13(1): 564 (1872).
P. umbilicata (Griseb.) Harms in Engl. \& Prantl, Nat. Pflanzenfam. 3 (pt. 6a) : 91 (1893).
P. urnaefolia Rusby in Mem. Torr. Bot. Club, 6: 42 (1896).
P. venosa Rusby in Mem. Torr. Bot. Club, 6: 42 (1896).
P. vespertilio L. Sp. Pl. 597 (1753).
P. violacea Vell. Fl. Flum. 9: t. 84 (1827).
P. Warmingii, subsp. chacoënsis R. E. Fries in Ark. Bot. 8 (no. 8) : 4, t. 1, fig. $7-8$ (1908) = P. morifolia.
P. yacumensis Rusby in Mem. N. Y. Bot. Gard. 7: 310 (1927) $=$ P. quadriglandulosa.
Tacsonia boliviana Rusby in Mem. Torr. Bot. Club, 3(3): 37 (1893) $=$ Passiflora gracilens.

## CARICACEAE

Carica boliviana Rusby in Bull. N. Y. Bot. Gard. 4: 364 (1907).
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M. molybdea var. titanea (Naud.) Cogn. in DC. Monog. Phan. 7: 827 (1891).
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M. plumifera Triana in Trans. Linn. Soc. 28: 124 (1871).
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M. polygama Cogn. in Bull. Torr. Bot. Club, 17: 92 (1890).
M. prasina (Sw.) DC. Prodr. 3: 188 (1828).
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E. ebracteatum Lam. Encycl. 4: 759 (1796).
E. bracteatum var. poterioides (Griseb.) Urb. in Linnaea, 43: 297 (1882).
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Sanicula mexicana DC. Prodr. 4: 84 (1830).
Spananthe paniculata Jacq. Collect. 3: 247 (1789).
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C. peruviana Macbr. in Trop. Woods, 19: 5 (1929).

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B. denticulata Remy in Ann. Sci. Nat. (ser. 3) 8: 230 (1847) = B. hispida.
B. glauca Humb. \& Bonpl. Pl. Aequin. 2: 118, t. 117 (1809).
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C. Martii (Meissn.) A. C. Smith in Bull. Torr. Bot. Club, 63: 313 (1936).
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E. racemosum Herzor in Meded. Rijks Herbar. 27: 22 (1915).

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G. barosmoides Rusby in Bull. N. Y. Bot. Gard. 4: 313 (1907).
G. brachybotrys DC. Prodr. 7: 595 (1839).
G. conferta Benth. Pl. Hartw. 219 (1846).
G. cordifolia HBK. Nov. Gen. \& Spec. 3: 285, t. 261 (1819).
G. formosa Remy in Ann. Sci. Nat. (ser. 3) 8: 231 (1847).
G. glabra DC. Prodr. 7: 596 (1839).
G. mucromata Remy in Ann. Sci. Nat. (ser. 3) 8: 232 (1847) = G. Remyana.
G. odorata Willd. in Ges. Naturf. Freunde Neue Schr. 3: 425 (1801).
G. pichinchensis Benth. Pl. Hartw. 225 (1846).
G. Remyana A. C. Smith in Contrib. U. S. Nat. Herb. 29: 347 (1950).
G. reticulata HBK. Nov. Gen. \& Spec. 3: 284 (1819).
G. rufescens DC. Prodr. 7: 595 (1839).
G. saxicola Wedd. Chlor. And. 2: 174 (1860).
G. secunda Remy in Ann. Sci. Nat. (ser. 3) 8: 231 (1847).
G. serrulata Herzog in Meded. Rijks Herbar. 27: 19 (1915).
G. tetriches Rusby, Descr. S. Am. Pls. 74 (1920).
G. tomentosa HBK. Nov. Gen. \& Spec. 3: 287, t. 262 (1819).
G. vaccinioides Griseb. ex Wedd. Chlor. And. 2: 176 (1860).

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P. phyllyraefolia (Pers.) DC. Prodr. 7: 587 (1839).
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P. prostrata var. Pentlandii (DC.) Sleumer in Notizbl. 12: 290 (1935).
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S. magnifica Sleum. in Notizbl. 12: 132 (1934).
S. pilosa A. C. Smith in Contrib. U. S. Nat. Herb. 28: 355 (1932).

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Sphyrospermum buxifolium Poepp. \& Endl. Nov. Gen. 1: 4, t. 8 (1835).
S. cordifolium Benth. Pl. Hartw. 222 (1846).

Thibaudia axillaris Rusby in A. C. Smith in Contrib. U. S. Nat. Herb. 28: 417 (1932).
T. crenulata Remy in Ann. Sci. Nat. (ser. 3) 8: 234 (1847).
T. densiflora (Herzog) A. C. Smith in Bull. Torr. Bot. Club, 60: 114 (1933).
T. macrocalyx Remy in Ann. Sci. Nat. (ser. 3) 8: 235 (1847).
T. oblongifolia Remy in Ann. Sci. Nat. (ser. 3) 8: 233 (1847) = Cavendishia pubescens?
Vacciniopsis tetramera Rusby, Descr. S. Am. Pls. 77 (1920) = Disterigma alaternoides var. parvifolium.
Vaccinium didymanthum Dun. in DC. Prodr. 7: 575 (1839).
V. empetrifolium HBK. Nov. Gen. \& Spec. 3: 263, t. 248 (1819).
V. epacridifolium Benth. Pl. Hartw. 221 (1846).
V. floribundum HBK. Nov. Gen. \& Spec. 3: 226, t. 251 (1819).
V. floribundum var. ramosissimum (Dun.) Sleum. in Notizbl. 13: 131 (1936).
V. floribundum var. Tatei (Rusby) Sleum. in Notizbl. 13: 132 (1936).
V. marginatum Dun. in DC. Prodr. 7: 570 (1839).
V. penaeoides HBK. Nov. Gen. \& Spec.. 3: 264 (1819).
V. polystachyum Benth. Pl. Hartw. 140 (1844).
$V$. thibaudioides Sleum. in Notizbl. 12: 140 (1934) $=$ Eleutherostemon racemosum.

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Clavija boliviensis Mez in Engler, Pflanzenr. IV, 236a: 26, (1903).
C. Cardenasii Rusby in Mem. N. Y. Bot. Gard. 7: 318 (1927).
C. formosa Remy in Ann. Sci. Nat. (ser. 3) 8: 227 (1847).
C. Hassleri Mez in Bull. Herb. Boiss. (ser. 2) 3: 238 (1903).
C. spathulata R. \& P. Syst. 285 (1798).
C. tarapotana Spruce ex Rusby in Bull. N. Y. Bot. Gard. 4: 406 (1907).
C. tarapotana Rusby in Bull. N. Y. Bot. Gard. 8: 111 (1912).

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Conomorpha peruviana A. DC. in Ann. Sci. Nat. (ser. 2) 16: 92 (1841).
Cybianthus glaucus Rusby in Mem. N. Y. Bot. Gard. 7: 318 (1927).
C. lanceolatus Pax in Fedde, Repert. Spec. Nov. 7: 112 (1909).
C. psychotriaefolius (Rusby) Rusby ex Mez in Engler, Pflanzenr. IV, 236: 227 (1902).

Geissanthus Bangii Rusby in Mem. Torr. Bot. Club, 4(3): 217 (1895).
G. bolivianus Britton in Bull. Torr. Bot. Club, 20: 140 (1893).
G. Haenkeanus Mez in Engler, Pflanzenr. IV, 236: 236 (1902).
G. multiflorus Mez in Engler, Pflanzenr. IV, 236: 239 (1902).
G. Pentlandii Mez in Engler, Pflanzenr. IV, 236: 236 (1902).

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R. lucida Herzog in Meded. Rijks Herbar. 27: 25 (1915).
R. Mandonii Mez in Engler, Pflanzenr. IV, 236: 378 (1902).
R. pseudocrenata Mez in Engler, Pflanzenr. IV, 236: 393 (1902).
R. sessiliflora Mez in Fedde, Repert. Spec. Nov. 3: 103 (1906).
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Weigeltia Buchtienii Pax in Fedde, Repert. Spec. Nov. 7: 112 (1909).

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Samolus Valerandi var. floribundus BSP. Prelim. Cat. N. Y. Pls. 34 (1888).

Plumbago coerulea HBK. Nov. Gen. \& Spec. 2: 220 (1817).
P. scandens L. Sp. Pl. (ed. 2) 1: 215 (1762).

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B. sartorum Mart. Herb. Fl. Bras. 233 (1837).

Chrysophyllum gonocarpum (Mart. \& Eichl.) Engler in Engler, Bot. Jahrb. 12: 523 (1892).
C. ilicioides Rusby in Bull. N. Y. Bot. Gard. 4: 406 (1907) = C. gonocarpum.
C. marginatum (Hook. \& Arn.) Radlk. in Act. Congr. Bot. Anvers, 170 (1887).
C. maytenoides Mart. in Flora, 22, I Beibl.: 1 (1839).
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Lucuma reticulata Remy in Ann. Sci. Nat. (ser. 3) 8: 228 (1847).
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P. boliviana (Rusby) Baehni in Candollea, 9: 419 (1942).
P. catoclantha (Eichl.) Baehni in Candollea, 9: 232 (1942).
P. nemorosa Baehni in Candollea, 9: 348 (1942).
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S. Pearcei Perkins in Engler, Pflanzenr. IV, 241: 46 (1907).
S. Pearcei var. bolivianus Perkins in Engler, Pflanzenr. IV, 241: 46 (1907).
S. Pentlandianus Remy in Ann. Sci. Nat. (ser. 3) 8: 229 (1847).
S. subheterotrichus Herzog in Meded. Rijks Herbar. 40: 31 (1921).
S. tarapotensis Perkins in Engler, Bot. Jahrb. 31: 479 (1902).

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S. castanea Brand in Fedde, Repert. Spec. Nov. 14: 324 (1916).
S. colorata Brand in Engler, Pflanzenr. IV, 242: 74 (1901).
S. flavescens Rusby in Bull. N. Y. Bot. Gard. 4: 407 (1907).
S. hiemalis Lingelsh. in Fedde, Repert. Spec. Nov. 8: 3 (1910).
S. mapiriensis Brand in Engler, Pflanzenr. IV, 242: 74 (1901).
S. Matthewsii A. DC. Prodr. 8: 250 (1844).
S. parvifolia var. subcuneata Herzog in Meded. Rijks Herbar. 40: 7 (1921).
S. theaeformis (L. f.) Gürke in Engl. \& Prantl, Nat. Pflanzenfam. 4(1): 172 (1891).

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Mayepea implicata Rusby in Bull. N. Y. Bot. Gard. 4: 314 (1907).
Menodora chlorargantha (Remy) Steyerm. in Ann. Missouri Bot. Gard. 19: 156 (1932).
M. helianthemoides Humb. \& Bonpl. Pl. Aequin. 2: 98, t. 110 (1809).
M. integrifolia (Cham. \& Schlechtd.) Steud. Nomencl. (ed. 2) 2: 124 (1841).
M. integrifolia var. trifida (Cham. \& Schlechtd.) Steyerm. in Ann. Missouri Bot. Gard. 19: 131 (1932).
M. pulchella Markgraf in Notizbl. 8: 219 (1922).

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B. anchoënsis O. Ktze. Rev. Gen. 3(2) : 200 (1898).
B. andina Britton ex Rusby in Mem. Torr. Bot. Club, 4 (3): 222 (1895).
B. aromatica Remy in Ann. Sci. Nat. (ser. 3) 8: 227 (1847).
B. Bangii Kränzl. in Ann. Naturh. Hofmus. Wien, 26: 395 (1912).
B. boliviana Pax in Fedde, Repert. Spec. Nov. 5: 227 (1908) = Cordia bifurcata.
B. brasiliensis Jacq. ex Spreng. Syst. 1: 430 (1825).
B. canescens Rusby in Mem. Torr. Bot. Club, 6: 78 (1896).
B. cochabambensis Rusby, Descr. S. Am. Pls. 81 (1920).
B. coriacea Remy in Ann. Sci. Nat. (ser. 3) 8: 226 (1847).
B. coroicensis Rusby in Bull. N. Y. Bot. Gard. 4: 412 (1907).
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B. inconspicua Kränzl. in Engler, Bot. Jahrb. 40: 310 (1908).
B. ledifolia Kränzl. in Engler, Bot. Jahrb. 50, Beibl. 111: 42 (1913).
B. microcephala Rusby in Bull. N. Y. Bot. Gard. 8: 113 (1912).
B. misera Kränzl. in Engler, Bot. Jahrb. 40: 308 (1908).
B. monocephala Kränzl. in Engler, Bot. Jahrb. 40: 309 (1908).
B. montana Britton ex Rusby in Bull. Torr. Bot. Club, 25: 544 (1898).
B. oblongifolia Rusby in Bull. N. Y. Bot. Gard. 8: 112 (1912).
B. rhododendroides Kränzl. in Ann. Naturh. Hofmus. Wien, 26: 395 (1912).
B. soratae Kränzl. in Engler, Bot. Jahrb. 50, Beibl. 111: 47 (1913).
B. tiraquiensis O. Ktze. Rev. Gen. 3(2): 201 (1898).
B. tucumanensis Griseb. in Goett. Abh. 19: 213 (1874).
B. Urbaniana Kränzl. in Engler, Bot. Jahrb. 40: 310 (1908).
B. verbascifolia HBK. Nov. Gen. \& Spec. 2: 351 (1818).

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D. spinosa R. \& P. Fl. Peruv. 2: 47, t. 186 (1799).

Spigelia elongata Rusby in Bull. Torr. Bot. Club, 25: 542 (1898).
S. Herzogiana Kränzl. in Fedde, Repert. Spec. Nov. 13: 117 (1914).
S. sessilifolia Rusby in Bull. Torr. Bot. Club, 25: 543 (1898).

Strychnos brachiata R. \& P. Fl. Peruv. 2: 30, t. 157 (1799).
S. darienensis Seem. Bot. Voy. Herald, 166 (1854).
S. Mitscherlichii Rich. Schomb. Reisen, 2: 451 (1848).
S. parvifolia DC. Prodr. 9: 16 (1845).
S. Peckii Robinson in Proc. Amer. Acad. 49: 504 (1913).
S. rondeletioides Spruce ex Benth. in Journ. Linn. Soc. 1: 104 (1856).

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C. Whitei Rusby in Mem. N. Y. Bot. Gard. 7: 322 (1927).

Curtia tenuifolia (Aubl.) Knobl. in Bot. Centralbl. 60: 323 (1894).
Deianira chiquitana Herzog in Fedde, Repert. Spec. Nov. 7: 65 (1909).
Gentiana albido-coerulea Gilg in Engler, Bot. Jahrb. 22: 323 (1896).
G. alticola R. C. Foster in Rhodora, 56: 103 (1954).
G. anthosphaera Gilg in Fedde, Repert. Spec. Nov. 2: 46 (1906).
G. armerioides Griseb. ex Gilg in Engler, Bot. Jahrb. 22: 306 (1896), nomen mudum.
G. Bangiana Gilg in Engler, Bot. Jahrb. 22: 335 (1896).
G. Bangii Gilg in Engler, Bot. Jahrb. 22: 324 (May 22, 1896).
G. Bangii Rusby in Mem. Torr. Bot. Club, 6: 79 (Nov. 17, 1896) = G. albidocoerulea.
G. bellatula Gilg in Engler, Bot. Jahrb. 50, Beibl. 111: 49 (1913).
G. Benedictae Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 80 (1916).
G. Bockii Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 34 (1916).
G. boliviana Pax in Fedde, Repert. Spec. Nov. 7: 243 (1909).
G. Bridgesii Gilg in Engler, Bot. Jahrb. 22: 316 (1896).
G. Briquetiana Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 32 (1916).
G. Buchtienii Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 66 (1916).
G. cerastioides var. emarginata Gilg in Engler, Bot. Jahrb. 22: 328 (1896) = G. palcana.
G. chrysantha Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 81 (1916).
G. cochabambensis Rusby in Mem. Torr. Bot. Club, 6: 79 (1896) = G. Kuntzei.
G. comarapana Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 82 (1916).
G. dasythamna Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 63 (1916).
G. Dielsiana Gilg in Engler, Bot. Jahrb. 22: 316 (1896).
G. dolichantha Gilg in Torreya, 5: 109 (1905).
G. erythrochrysea Gilg in Fedde, Repert. Spec. Nov. 2: 38 (1906).
G. Fiebrigii Gilg in Fedde, Repert. Spec. Nov. 2: 45 (1906).
G. florida Griseb. in Goett. Abh. 24: 236 (1879).
G. gageoides Gilg in Engler, Bot. Jahrb. 22: 320 (1896).
G. gynophora Gilg in Engler, Bot. Jahrb. 22: 305 (1896).
G. Hauthalii Gilg ex Perkins in Engler, Bot. Jahrb. 49: 212 (1913) $=$ G. Dielsiana.
G. Herzogii Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 57 (1916).
G. hygrophiloides Gilg in Fedde, Repert. Spec. Nov. 2: 40 (1906) $=$ G. Kuntzei.
G. inaequicalyx Gilg in Engler, Bot. Jahrb. 22: 324 (1896).
G. incurva Hook. in Bot. Misc. 2: 228 (1831).
G. Krauseana Gilg in Fedde, Repert. Spec. Nov. 2: 45 (1906).
G. Kuntzei Gilg in Engler, Bot. Jahrb. 22: 326 (1896).
G. Kusnezowii Gilg in Engler, Bot. Jahrb. 22: 325 (1896).
G. lancifolia Gilg in Engler, Bot. Jahrb. 22: 326 (1896) $=$ G. alticola.
G. larecajensis Gilg in Engler, Bot. Jahrb. 54. Beibl. 118: 31 (1916).
G. lilacino-flavescens Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 38 (1916).
G. limoselloides HBK. Nov. Gen. \& Spec. 3: 167, t. 220, fig. 1 (1819).
G. lithophila Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 39 (1916).
G. longipes Rusby in Mem. N. Y. Bot. Gard. 7: 321 (1927).
G. lythroides Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 24 (1916).
G. macroclada Gilg in Fedde, Repert. Spec. Nov. 2: 47 (1906).
G. macrorrhiza Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 40 (1916).
G. Mandonii Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 37 (1916) = G. neomandonii.
G. Mandonii Rusby in Mem. Torr. Bot. Club, 6: 80 (1896) $=$ G. inaequicalyx.
G. myriantha Gilg in Fedde, Repert. Spec. Nov. 2: 43 (1906).
G. narcissoides Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 65 (1916).
G. neomandonii R. C. Foster in Rhodora, 56: 103 (1954).
G. odontosepala Gilg in Fedde, Repert. Spec. Nov. 2: 48 (1906).
G. orobanchoides Gilg in Engler, Bot. Jahrb. 22: 333 (1896).
G. palcana Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 47 (1916).
G. pallide-lilacina Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 58 (1916).
G. Pilgeriana Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 42 (1916).
G. pinifolia R. \& P. ex G. Don, Gen. Syst. 4: 182 (1837).
G. praticola Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 46 (1916) 二 G. sanctimatthaei.
G. primulifolia Griseb. Gen. \& Spec. Gent. 221 (1839).
G. primuloides Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 31 (1916).
G. prostrata Jacq. Collect. 2: 66, t. 17 (1788).
G. prostrata var. podocarpa (Griseb.) Kusnez. in Act. Hort. Petrop. 15: 373 (1904).
G. pseudocrassula Gilg in Fedde, Repert. Spec. Nov. 2: 44 (1906).
G. pseudolycopodium Gilg in Fedde, Repert. Spec. Nov. 2: 38 (1906).
G. punicea Wedd. Chlor. And. 2: 70 (1859).
G. purpureiflora Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 65 (1916).
G. rupicola HBK. Nov. Gen. \& Spec. 3: 167, t. 220, fig. 2 (1819).
G. sancti-matthaei R. C. Foster in Rhodora, 56: 103 (1954).
G. sandiensis Gilg in Fedde, Repert. Spec. Nov. 2: 36 (1906).
G. scopulorum Wedd. Chlor. And. 2: 67 (1859).
G. sedifolia HBK. Nov. Gen. \& Spec. 3: 173, t. 225 (1819).
G. seminuda Rusby in Mem. Torr. Bot. Club, 6: 81 (1896) $=$ G. gynophora.
G. silenoides Gilg in Engler, Bot. Jahrb. 22: 319 (1896).
G. soratensis Gilg in Engler, Bot. Jahrb. 22: 332 (1896).
G. spectabilis Rusby in Mem. Torr. Bot. Club, 6: 80 (1896) $=$ G. Dielsiana.
G. stenocephala Gilg in Engler, Bot. Jahrb. 22: 331 (1896).
G. striaticalyx Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 56 (1916).
G. Tatei Rusby in Phytologia, 1: 72 (1934).
G. thiosphaera Gilg in Fedde, Repert. Spec. Nov. 2: 46 (1906).
G. totorensis Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 84 (1916).
G. tradescantiifolia Britton ex Rusby in Bull. Torr. Bot. Club, 25: 545 (1898).
G. virgata Rusby in Mem. Torr. Bot. Club, 6: 81 (1896) = G. Kusnezowii.

Halenia bifida Rusby \& Allen in Ann. Missouri Bot. Gard. 20: 201 (1933).
H. Dombeyana (Griseb.) Wedd. Chlor. And. 2: 76 (1859).
H. gracilis (HBK.) G. Don. Gen. Hist. 4: 177 (1837).
H. Herzogii Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 113 (1916).
H. Hieronymi Gilg in Fedde, Repert. Spec. Nov. 2: 52 (1906).
H. penduliflora Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 116 (1916).
H. pusilla Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 107 (1916).
H. robusta Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 110 (1916).
H. Rusbyi Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 117 (1916).
H. silenoides Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 113 (1916).
H. valerianoides Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 106 (1916).
H. vincetoxicoides Gilg in Engler, Bot. Jahrb. 54, Beibl. 118: 108 (1916).

Leiphaimos aphylla (Jacq.) Gilg in Engl. \& Prantl, Nat. Pflanzenfam. 4(2): 104 (1895).
Limnanthemum Humboldtianum (HBK.) Griseb. Gen. \& Spec. Gent. 347 (1839).
L. verrucosum R. E. Fries in Ark. Bot. 6(11): 25 (1906).

Lisianthus calycogonus R. \& P. Fl. Peruv. 2: 14, t. 126 (1799).
L. ovalis R. \& P. Fl. Peruv. 2: 13 (1799).

Macrocarpaea Bangiana Gilg in Engler, Bot. Jahrb. 22: 335 (1896).
M. cochabambensis Ch. Gilg in Notizbl. 13: 381 (1936).

Microcala quadrangularis (Lam.) Griseb. in DC. Prodr. 9: 63 (1845).
Rusbyanthus cinchonifolius (Britton) Gilg in Engl. \& Prantl, Nat. Pflanzenfam. 4(2): 95 (1895).
Schultesia Pohliana Progel in Mart. Fl. Bras. 6(1): 205 (1865).
Symbolanthus Brittonianus Gilg in Engler, Bot. Jahrb. 22: 342 (1896).
S. Rusbyanus Gilg in Engler, Bot. Jahrb. 22: 344 (1896).

## Tachia sp.

Tetragonanthus Whitei Rusby in Mem. N. Y. Bot. Gard. 7: 321 (1927) = Halenia vincetoxicoides.
Zygostigma australe (Cham. \& Schlechtd.) Griseb. Gen. \& Spec. Gent. 150 (1839).

## APOCYNACEAE

Aspidosperma australe Muell. Arg. in Mart. Fl. Bras. 6(1): 58 (1860).
A. brevifolium Rusby in Bull. N. Y. Bot. Gard. 8: 113 (1912) = A. cylindrocarpon.
A. cylindrocarpon Muell. Arg. in Mart. Fl. Bras. 6(1): 54 (1860).
A. macrocarpon Mart. Nov. Gen. 1: 59 (1826).
A. Marcgravianum Woodson in Ann. Missouri Bot. Gard. 38: 170 (1951).
A. Quebracho-blanco Schlechtd. in Bot. Zeit. 19: 137 (1861).
A. ramiflorum Muell. Arg. in Mart. Fl. Bras. 6(1): 55 (1860).
A. rauwolfioides Markgraf in Notizbl. 12: 300 (1935) = A. rigidum.
A. rigidum Rusby in Mem. N. Y. Bot. Gard. 7: 323 (1927).
A. Steinbachii Markgraf in Notizbl. 9: 1158 (1927).
A. tomentosum Mart. Nov. Gen. 1: 58 (1826).

Bonafousia juruana Markgraf in Notizbl. 14: 181 (1938).
Dipladenia Buchtienii Rusby, Descr. S. Am. Pls. 87 (1920) = Mandevilla cuspidata.
D. glabra Rusby, Descr. S. Am. Pls. 88 (1920) = Mandevilla pulchra.
D. mollis Rusby in Bull. N. Y. Bot. Gard. 8: 114 (1912) = Mandevilla cuspidata.
D. piladenia Rusby, Descr. S. Am. Pls. 87 (1920) $=$ Mandevilla cuspidata.
D. rotundifolia Rusby in Mem. N. Y. Bot. Gard. 7: 326 (1927) = Mandevilla cuspidata.
D. tetradenia Rusby, Descr. S. Am. Pls. 88 (1920) = Mandevilla cuspidata.

Echites altescandens H. Winkl. in Fedde, Repert. Spec. Nov. 7: 243 (1909) = Mandevilla antennacea.
E. Bangii Rusby in Bull. N. Y. Bot. Gard. 4: 409 (1907) $=$ Prestonia acutifolia.
E. boliviana Britton ex Rusby in Mem. Torr. Bot. Club, 4 (3): 219 (1895) $=$ Mandevilla antennacea.
E. mapirensis H. Winkl. in Fedde, Repert. Spec. Nov. 7: 113 (1909) = Mesechites acuminata ?
E. rigida Rusby in Mem. N. Y. Bot. Gard. 7: 325 (1927) $=$ Mesechites trifida.
E. trifida forma puberula Markgraf in Notizbl. 9: 80 (1924) $=$ Mesechites acuminata.
Forsteronia amblybasis Blake in Journ. Wash. Acad. Sci. 14: 292 (1924).
F. glabrescens Muell. Arg. in Mart. Fl. Bras. 6(1): 102 (1860).
F. mollis Rusby in Mem. Torr. Bot. Club, 4(3): 218 (1895).
F. mollis var. foliosa (Rusby) Woodson in Ann. Missouri Bot. Gard. 22: 188 (1935).
F. obscura Rusby in Mem. Torr. Bot. Club, 4 (3): 219 (1895) $=$ F. thyrsoidea var. glabriuscula.
F. pubescens A. DC. Prodr. 8: 436 (1844).
F. Sellowii Muell. Arg. in Mart. Fl. Bras. 6(1): 101 (1860).
F. thyrsoidea var. glabriuscula (A. DC.) Woodson in Ann. Missouri Bot. Gard. 22: 201 (1935).
Himatanthus obovatus (Muell. Arg.) Woodson in Ann. Missouri Bot. Gard. 25: 201 (1938).
H. Sucuuba (Spruce) Woodson in Ann. Missouri Bot. Gard. 25: 198 (1937).

Landolphia boliviensis Markgraf in Notizbl. 9: 1041 (1926).
Laseguea Mandonii Britton ex Rusby in Mem. Torr. Bot. Club, 4 (3) : 220
(1895) $=$ Mandevilla Pentlandiana.

Macropharynx fistulosa Rusby in Mem. N. Y. Bot. Gard. 7: 329, fig. 6 (1927) $=\mathrm{M}$. spectabilis.
M. spectabilis (Stadelm.) Woodson in Ann. Missouri Bot. Gard. 18: 552 (1931).

Macrosiphonia longiflora (Desf.) Muell. Arg. in Mart. Fl. Bras. 6(1): 140, t. 43 (1860).
Mandevilla antennacea (A. DC.) K. Schum. in Engl. \& Prantl, Nat. Pflanzenfam. 4(2): 171 (1895).
M. Bangii Rusby in Mem. Torr. Bot. Club, 6: 76 (1896) = M. Bridgesii.
M. boliviensis (Hook. f.) Woodson in Ann. Missouri Bot. Gard. 20: 716 (1933).
M. brachyloba (Muell. Arg.) K. Schum. in Engl. \& Prantl, Nat. Pflanzenfam. 4(2): 171 (1895).
M. bracteosa (Rusby) Woodson in Ann. Missouri Bot. Gard. 20: 742 (1933).
M. Bridgesii (Muell. Arg.) Woodson in Ann. Missouri Bot. Gard. 19: 67 (1932).
M. cereola Woodson in Ann. Missouri Bot. Gard. 20: 712 (1933).
M. collium Woodson in Ann. Missouri Bot. Gard. 23: 380 (1936).
M. cuspidata (Rusby) Woodson in Ann. Missouri Bot. Gard. 20: 730 (1933?).
M. erecta (Vell.) Woodson in Ann. Missouri Bot. Gard. 19: 62 (1932).
M. fragilis Woodson in Ann. Missouri Bot. Gard. 19: 59 (1932).
M. hirsuta (A. Rich.) K. Schum. in Engl. \& Prantl, Nat. Pflanzenfam. 4(2): 171 (1895).
M. laxa (R. \& P.) Woodson in Ann. Missouri Bot. Gard. 19: 68 (1932).
M. Mandonii Britton ex Rusby in Bull. Torr. Bot. Club, 25: 496 (1898) $=$ M. Bridgesii.
M. oblongifolia (Woodson) Woodson in Ann. Missouri Bot. Gard. 20: 708 (1933).
M. Pentlandiana (A. DC.) Woodson in Ann. Missouri Bot. Gard. 19: 63 (1932).
M. pulchra Woodson in Ann. Missouri Bot. Gard. 23: 376 (1936).
M. Rusbyi Britton ex Rusby in Bull. N. Y. Bot. Gard. 4: 409 (1907) = M. hirsuta.
M. rutila Woodson in Ann. Missouri Bot. Gard. 19: 385 (1932).
M. subcordata Rusby in Bull. N. Y. Bot. Gard. 4: 315 (1907).
M. superba Herzog in Fedde, Repert. Spec. Nov. 7: 65 (1909).
M. tenuicarpa Rusby in Bull. N. Y. Bot. Gard. 8: 114 (1912) $=$ M. antennacea.

Mesechites acuminata (R. \& P.) Muell. Arg. in Linnaea, 30: 446 (1860).
M. Mansoana (A. DC.) Woodson in Ann. Missouri Bot. Gard. 20: 636 (1936).
M. trifida ( Jacq.) Muell. Arg. in Mart. Fl. Bras. 6(1): 151 (1860).

Odontadenia boliviana Rusby in Mem. Torr. Bot. Club, 6: 76 (1896).
O. laxiflora (Rusby) Woodson in Ann. Missouri Bot. Gard. 19: 386 (1932).

Peltastes giganteus Woodson in Ann. Misouri Bot. Gard. 19: 373 (1932).
Plumeria bracteata A. DC. Prodr. 8: 394 (1844).
P. tarapotensis K. Schum. ex Markgraf in Notizbl. 11: 339 (1932).
P. velutina var. boliviana O. Ktze. Rev. Gen. 3(2): 198 (1898).

Prestonia acutifolia (Benth.) K. Schum. in Engl. \& Prantl, Nat. Pflanzenfam. 4(2): 188 (1895).
P. cephalantha Rusby in Mem. N. Y. Bot. Gard. 7: 330 (1927).
P. cornutisepala Rusby in Mem. N. Y. Bot. Gard. 7: 329 (1927).
P. cyaniphylla (Rusby) Woodson in Ann. Missouri Bot. Gard. 23: 284 (1936).
P. Muelleri Rusby in Mem. Torr. Bot. Club, 4 (3): 217 (1895) = P. Riedelii.
P. Phenax Woodson in Ann. Missouri Bot. Gard. 23: 314 (1936).
P. Riedelii (Muell. Arg.) Markgraf in Fedde, Repert. Spec. Nov. 20: 26 (1924).
P. robusta Rusby, Descr. S. Am. Pls. 91 (1920).
P. sericocalyx Malme in Bih. Sv. Vet. Akad. Handl. 24 (10): 29, t. 3 (1899).
P. tomentosa R. Br. in Mem. Wern. Soc. 1: 70 (1811).

Rauwolfia boliviana Markgraf in Fedde, Repert. Spec. Nov. 20: 122 (1924).
R. ternifolia HBK. Nov. Gen. \& Spec. 3: 232 (1819).

Secondatia densiflora A. DC. Prodr. 8: 445 (1844).
Stemmadenia obovata var. mollis (Benth.) Woodson in Ann. Missouri Bot. Gard. 15: 358 (1928).
Tabernaemontana Buchtienii H. Winkl. in Fedde, Repert. Spec. Nov. 7: 244 (1909).
T. laeta Mart. in Flora, 20, II Beibl.: 98 (1837).
T. macrosiphon Herzog in Fedde, Repert. Spec. Nov. 7: 66 (1909).
T. mapirensis Rusby in Bull. N. Y. Bot. Gard. 8: 115 (1912).
T. myriantha Britton ex Rusby, Descr. S. Am. Pls. 84 (1920).
T. undulata Mey. Primit. Fl. Esseq. 135 (1818).
T. unguiculata Rusby in Mem. N. Y. Bot. Gard. 7: 324 (1927).

Vallesia glabra (Cav.) Link, Enum. Hort. Berol. 1: 207 (1821).

## ASCLEPIADACEAE

Amblystigma hypoleucum Benth. in Hook. Ic. Pl. 12: 76, t. 1188 (1876).
A. pedunculare Benth. in Hook. Ic. Pl. 12: 77, sub t. 1188 (1876) = Sarcostemma Gilliesii.
Amphistelma Pearcei Rusby in Bull. N. Y. Bot. Gard. 4: 411 (1907).
Aphanostelma parviflorum (Malme) Maime in Ark. Bot. 25A(7): 11 (1932).
Araujia grandiflora (Mart. \& Zucc.) Morong in Ann. N. Y. Acad. Sci. 7: 161 (1893).
A. plumosa Schltr. in Oesterr. Bot. Zeitschr. 45: 449 (1895).

Asclepias barjoniaefolia Fourn. in Ann. Sci. Nat. (ser. 6) 14: 372 (1882).
A. boliviensis Fourn. in Ann. Sci. Nat. (ser. 6) 14: 381 (1882).
A. brasiliensis (Fourn.) Schltr. in Meded. Rijks Herbar. 29: 12 (1916).
A. Bridgesii Fourn. in Ann. Sci. Nat. (ser. 6) 14: 383 (1882).
A. campestris Decne. in DC. Prodr. 8: 566 (1844).
A. cochabambensis Rusby in Mem. Torr. Bot. Club, 4(3): 221 (1895).
A. curassavica L. Sp. Pl. 215 (1753).
A. Fiebrigii Schltr. in Engler, Bot. Jahrb. 37: 608 (1906).
A. Kuntzei Schltr. in Oesterr. Bot. Zeitschr. 49: 450 (1895).
A. marginata Decne, in DC. Prodr. 8: 566 (1844).
A. nervosa Decne. in DC. Prodr. 8: 568 (1844).
A. Pilgeriana Schltr. in Engler, Bot. Jahrb. 37: 608 (1906).
A. ramosa Fourn. in Ann. Sci. Nat. (ser. 6) 14: 373 (1882).
A. Weddellii Fourn. in Ann. Sci. Nat. (ser. 6) 14: 381 (1882).

Blepharodon bolivianum Malme in Ark. Bot. 25A (7): 17 (1932).
B. mucronatum (Schlechtd.) Decne. in DC. Prodr. 8: 603 (1844).
B. philibertioides Schltr. in Fedde, Repert. Spec. Nov. 13: 440 (1914).
B. Rahmeri Phil. in Anal. Mus. Nac. Chile, Bot. 8: 52, t. 2 (1891).

Corollonema boliviense Schltr. in Fedde, Repert. Spec. Nov. 13: 441 (1914).
Cynanchum Rusbyi Malme in Ark. Bot. 25A (7): 9 (1932).
Dactylostelma boliviense Schltr. in Oesterr. Bot. Zeitschr. 45: 452 (1895).
Ditassa apiculata Rusby in Bull. N. Y. Bot. Gard. 4: 412 (1907).
D. aristata Benth. ex Fourn. in Mart. Fl. Bras. 6(4): 247 (1885).
D. bonariensis Decne. in DC. Prodr. 8: 577 (1844).
D. Fiebrigii Malme in Ark. Bot. 28A (5) : 22 (1936).
D. lanceolata Decne. in DC. Prodr. 8: 576 (1844).
D. Mandonii Rusby, Descr. S. Am. Pls. 97 (1920).
D. montana Schltr. in Fedde, Repert. Spec. Nov. 13: 439 (1914) $=$ D. Schlechteri.
D. racemosa Britton ex Rusby in Bull. Torr. Bot. Club, 25: 498 (1898).
D. Schlechteri Macbr. in Field Mus. Publ. Bot. 11: 34 (1931).
D. subalpina Schltr. in Fedde, Repert. Spec. Nov. 13: 439 (1914).

Fischeria boliviana Blake in Journ. Wash. Acad. Sci. 14: 292 (1924).
F. Martiana Decne. in DC. Prodr. 8: 601 (1844).

Funastrum fragile Rusby in Mem. N. Y. Bot. Gard. 7: 332 (1927) = Sarcostemma clausum.
F. lanceolatum Rusby in Mem. N. Y. Bot. Gard. 7: 332 (1927) = Sarcostemma clausum.
Gonolobus andinus Malme in Ark. Bot. 25A (7): 21 (1932).
G. Asplundii Malme in Ark. Bot. 25A (7): 20 (1932).
G. attenuatus Rusby, Descr. S. Am. Pls. 101 (1920).
G. boliviensis (Schltr.) T. Meyer in Lilloa, 23: 57 (1950).
G. Brittonii Rusby in Bull. Torr. Bot. Club, 25: 500 (1898).
G. ellipticus Rusby in Mem. Torr. Bot. Club, 4(3): 222 (1895).
G. Fiebrigii Schltr. in Engler, Bot. Jahrb. 37: 625 (1906).
G. floribundus Malme in Ark. Bot. 25A (7): 19 (1932).
G. hirsutissimus Schltr. in Engler, Bot. Jahrb. 37: 625 (1906).
G. leucodermis Rusby, Descr. S. Am. Pls. 102 (1920).

Gothofreda andina Rusby in Mem. Torr. Bot. Club, $4(3): 220$ (1895) $=$ Oxypetalum sp.?
G. apoloënsis Rusby in Bull. N. Y. Bot. Gard. 8: 113 (1912) $=$ Oxypetalum sp. ?
G. consimilis Rusby in Mem. N. Y. Bot. Gard. 7: 334 (1927) $=$ Oxypetalum sp. ?
G. macroglossa Rusby in Mem. N. Y. Bot. Gard. 7: 334 (1927) $=$ Oxypetalum sp.?
G. Pearsomii Rusby in Mem. N. Y. Bot. Gard. 7: 335 (1927) = Oxypetalum sp.?
Hemipogon andinum Rusby, Descr. S. Am. Pls. 92 (1920).
H. Williamsii Rusby, Descr. S. Am. Pls. 92 (1920).

Jobinia chlorantha (K. Schum.) Malme in Ark. Bot. 25A (7): 3 (1932).
Macroditassa tassadioides (Schltr.) Malme in Ark. Bot. 28A (5): 6 (1936).
Marsdenia Hilariana Fourn. in Mart. Fl. Bras. 6(4): 322 (1885).
Melinia campanulata Schltr. in Engler, Bot. Jahrb. 37: 615 (1906).
M. discolor Schltr. in Engler, Bot. Jahrb. 37: 615 (1906).

Metastelma ditassoides Schltr. in Fedde, Repert. Spec. Nov. 13: 438 (1914).
M. ditassoides Schltr. in Meded. Rijks Herbar. 29: 12 (1916) $=$ M. Schlechteri.
M. Fiebrigii Schltr. in Engler, Bot. Jahrb. 37: 609 (1906).
M. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 13: 438 (1914).
M. Mathewsii Rusby in Bull. Torr. Bot. Club, 25: 497 (1898).
M. myrianthum Schltr. in Oesterr. Bot. Zeitschr. 45: 451 (1895).
M. parviflorum (Sw.) R. Br. in Mem. Wern. Soc. 1: 52 (1811), combination implied but not actually made.
M. retinaculatum Schltr. in Engler, Bot. Jahrb. 37: 610 (1906).
M. Schlechteri Macbr. in Field Mus. Publ. Bot. 11: 34 (1931).

Mitostigma boliviense Schltr. in Engler, Bot. Jahrb. 37: 601 (1906).
M. Fiebrigii Schltr. in Engler, Bot. Jahrb. 37: 602 (1906).
M. grandiflorum Schltr. in Engler, Bot. Jahrb. 37: 603 (1906).
M. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 13: 441 (1914).
M. niveum Griseb. in Goett. Abh. 24: 266 (1879).
M. subniveum Malme in Ark. Bot. 3(1): 9 (1904).

Morrenia brachystephana Griseb. in Goett. Abh. 19: 205 (1874).
M. *grandiflora Malme in Ark. Bot. 8(1): 21 (1909) [but called "subsp. nov."].
M. Herzogii Schltr. in Fedde, Repert. Spec. Nov. 13: 440 (1914).
M. odorata (Hook. \& Arn.) Lindl. in Bot. Reg. 24: Misc. 71 (1838).

Nephradenia pendula Rusby in Mem. N. Y. Bot. Gard. 7: 336 (1927).
Oxypetalum albiflorum Schltr. in Engler, Bot. Jahrb. 37: 621 (1906).
O. attenuatum (Rusby) Malme in Ark. Bot. 25A (14): 15 (1933).
O. Balansae Malme in Kgl. Sv. Vet. Akad. Handl. 34(7): 51 (1900).
O. boliviense Schltr. in Engler, Bot. Jahrb. 37: 622 (1906).
O. brachystemma Malme in Ark. Bot. 3(8): 2, t. 1, fig. 3 (1904).
O. Schlechteri Malme in Ark. Bot. 25A (7): 15 (1932).

Phaeostemma grandifolium Rusby, Descr. S. Am. Pls. 101 (1920).
Philibertia hypoleuca Schltr. in Oesterr. Bot. Zeitschr. 45: 450 (1895) = Sarcostemma campanulatum.
P. picta Schltr. in Engler, Bot. Jahrb. 37: 606 (1906) $=$ Sarcostemma, probably a hybrid.
Pseudibatia Herzogii Schltr. in Fedde, Repert. Spec. Nov. 13: 443 (1914).
Roulinia Mannii Rusby in Mem. N. Y. Bot. Gard. 7: 333 (1927).
Sarcostemma campanulatum Lindl. in Bot. Reg. 32: t. 36 (1846).
S. clausum (Jacq.) Roem. \& Schult. Syst. Veg. 6: 114 (1820).
S. Gilliesii (Hook. \& Arn.) Decne. in DC. Prodr. 8: 542 (1844).
S. gracile Deene. in DC. Prodr. 8: 539 (1844).
S. lysimachioides (Wedd.) R. Holm in Ann. Missouri Bot. Gard. 37: 547 (1950).
S. solanoides (HBK.) Decne. in DC. Prodr. 8: 541 (1844).
S. Vaileae (Rusby) R. Holm in Ann. Missouri Bot. Gard. 37: 543 (1950).

Schistogyne boliviensis Schltr. in Fedde, Repert. Spec. Nov. 13: 442 (1914).
S. Fiebrigii Malme in Ark. Bot. 25A (14): 14 (1933).
S. Mandonii Malme in Ark. Bot. 25A (14): 12 (1933).
S. oxypetaloides Schltr. in Fedde, Repert. Spec. Nov. 13: 442 (1914) $=$ Oxypetalum attenuatum.
S. pentaseta Rusby, Descr. S. Am. Pls. 98 (1920).

Steleostemma pulchellum Schltr. in Engler, Bot. Jahrb. 37: 604 (1906).
Stelmatocodon Fiebrigii Schltr. in Engler, Bot. Jahrb. 37: 618 (1906).
Tassadia Hutchisoniana Rusby in Mem. N. Y. Bot. Gard. 7: 331 (1927).
T. rhombifolia Rusby in Mem. N. Y. Bot. Gard. 7: 331 (1927).
T. Rusbyi Macbr. in Field Mus. Publ. Bot. 11: 34 (1931).
T. Sprucei Rusby in Bull. Torr. Bot. Club, $25: 498$ (1898) = T. Rusbyi.

Tweedia brunonis Hook. \& Arn. in Hook. Journ. Bot. 1: 292 (1934).
Vailia mucronata Rusby in Bull. Torr. Bot. Club, 25: 542 (1898).
Vincetoxicum cuspidatum Rusby in Mem. N. Y. Bot. Gard. 7: 333 (1927).
V. umbellatum Rusby in Mem. Torr. Bot. Club, 6: 78 (1896) $=$ Cynanchum Rusbyi.
V. unguiculatum (R. \& P.) Britton ex Rusby in Bull. Torr. Bot. Club, 25: 499 (1898).

## CONVOLVULACEAE

Bonamia boliviana O'Donell in Lilloa, 23: 458 (1950).
Calonyction aculeatum (L.) House in Bull. Torr. Bot. Club, 31: 590 (1904).
Convolvulus Blanchetii forma albiflorus O. Ktze. Rev. Gen. 3(2): 212 (1898).
C. Blanchetii forma coeruleus O. Ktze. Rev. Gen. 3(2): 212 (1898).
C. bogotensis forma albiflorus O. Ktze. Rev. Gen. 3(2): 212 (1898).
C. bogotensis forma lilacinus O. Ktze. Rev. Gen. 3(2): 212 (1898).
C. bonariensis Cav. Ic. 5: 54, t. 480, fig. 2 (1799).
C. crenatifolius R. \& P. Fl. Peruv. 2: 10, t. 118 (1799).
C. crenatifolius var. argentinicus Hall. f. in Jahrb. Hamb. Wiss Anst. 16, 3 Beih.: 35 (1899).
C. crenatifolius var. peruvianus Hall. f. in Jahrb. Hamb. Wiss. Anst. 16, 3 Beih.: 34 (1899).
C. laciniatus Desv. in Lam. Encycl. 3: 546 (1789).
C. Ottonis (Chois.) Meissn. in Mart. Fl. Bras. 7: 311 (1869).
C. pauciflorus var. chilensis O. Ktze. Rev. Gen. 3(2): 214 (1898).
C. venustus Spreng. Syst. 1: 600 (1825).

Cuscuta acutiloba Engelm. in Trans. Acad. Sci. St. Louis, 1: 478 (1859).
C. boliviana Yuncker in Amer. Journ. Bot. 9: 565, t. 1, fig. 3a-e (1922).
C. fragrans Rusby in Mem. Torr. Bot. Club, 6: 85 (1896) $=$ C. odorata.
C. grandiflora HBK. Nov. Gen. \& Spec. 3: 123, t. 213 (1819).
C. insquamata Yuncker in Amer. Journ. Bot. 10: 12, t. 5, fig. 30a-d (1923).
C. odorata R. \& P. Fl. Peruv. 1: 69, t. 105, fig. a (1798).
C. odorata var. Holwayana Yuncker in Amer. Journ. Bot. 9: 564, t. 4, fig. 21f (1922).
C. partita Choisy in Mém. Soc. Phys. Hist. Nat. Genève, 9: 284, t. 5 (1841).
C. Rojasii Hunziker in Darwiniana, 7: 323 (1947).

Dichondra argentea Willd. Enum. Hort. Berol. 297 (1809).
D. evolvulacea var. villosa (Parodi) O. Ktze. Rev. Gen. 3(2): 216 (1898).
D. repens Forst. Char. Gen. 40, t. 20 (1776).
D. repens var. microcalyx Hall. f. in Engler, Bot. Jahrb. 18: 84 (1893).

Evolvulus alsinoides var. debilis (HBK.) v. Ooststr. in Meded. Bot. Mus. Utrecht, 14: 33 (1934).
E. argyreus Choisy in Mém. Soc. Phys. Hist. Nat. Genève, 8: 75 (1837).
E. boliviensis v. Ooststr. in Meded. Bot. Mus Utrecht, 14: 83 (1934).
E. columbianus var. incanus Hall. f. in Meded. Rijks Herbar. 46: 13 (1922) = E. tenuis subsp. longifolius.
E. corumbaënsis Hoehne in Anex. Mem. Inst. Butantan Bot. 1(6): 38, t. 1 (1922).
E. elegans Moric. Pl. Nouv. Amér. 53, t. 36 (1838).
E. frankenioides Moric Pl. Nouv. Amér. 49, t. 33 (1838).
E. frankenioides var. subglaber v. Ooststr. in Meded. Bot. Mus. Utrecht, 14: 149 (1934).
E. glaber Spreng. Syst. Veg. 1: 862 (1825).
E. glomeratus subsp. eu-glomeratus forma echioides (Moric.) v. Ooststr. in Meded. Bot. Mus. Utrecht, 14: 228 (1934).
E. linoides Moric. Pl. Nouv. Amér. 139, t. 83 (1844).
E. nummularius (L.) L. Sp. Pl. (ed. 2) 1: 391 (1762).
E. pterocaulon var. floccosus Meissn. in Mart. Fl. Bras. 7: 333 (1869).
E. sericeus Sw. Prodr. 55 (1788).
E. sericeus var. holosericeus (HBK.) v. Ooststr. in Meded. Bot. Mus. Utrecht, 14: 130 (1934).
E. tenuis subsp. longifolius (Choisy) v. Ooststr. in Meded. Bot. Mus. Utrecht, 14: 61 (1934).
Ipomoea alba L. Sp. Pl. 161 (1753).
I. Batatas Poir. in Lam. Encycl. 6: 14 (1804).
I. bona-nox L. Sp. Pl. (ed. 2) 1: 228 (1762).
I. carnea Jacq. Enum. Pl. Carib. 13 (1760).
I. chiliantha Hall. f. in Bull. Herb. Boiss. (ser. 1) 7, App. 1: 50 (1899).
I. coccinea L. Sp. Pl. (ed. 2) 1: 228 (1762).
I. densibracteata O'Donell in Lilloa, 23: 438 (1950).
I. edulis (Choisy) Niederl. in Bol. Mens. Mus. Prod. Argent. 3(29) : 190 (1890).
I. fastigiata (Roxb.) Sweet, Hort. Brit. (ed. 1) 288 (1827).
I. filipedunculata Rusby in Bull. Torr. Bot. Club, 26: 150 (1899).
I. fistulosa Mart. ex Choisy in DC. Prodr. 9: 349 (1845).
I. floribunda Moric. Pl. Nouv. Amér. 46, t. 31 (1838).
I. hederacea Jacq. Collect. 1: 124 (1786).
I. indivisa (Vell.) Hall. f. in Meded. Rijks Herbar. 46: 20 (1922).
I. magnifolia Rusby in Mem. Torr. Bot. Club, 6: 84 (1896).
I. neurocephala Hall. f. in Jahrb. Hamb. Wiss. Anst. 16, 3 Beih.: 40 (1899).
I. Nil (L.) Roth, Catalect. Bot. 1: 36 (1797).
I. opulifolia Rusby in Bull. Torr. Bot. Club, 26: 150 (1899).
I. palmata Forsk. Fl. Aegypt. Arab. 43 (1775).
I. pes-caprae (L.) Roth, Nov. Pl. Sp. 109 (1821).
I. Plummerae A. Gray, Syn. Fl. (ed. 2) 2(1) : 434 (1886).
I. Plummerae forma rhombifolia v. Ooststr. in Rec. Trav. Bot. Néerl. 33: 221 (1936).
I. Pseudomina (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1): 383 (1900).
I. Regnellii Meissn. in Mart. Fl. Bras. 7: 266 (1869).
I. scabra Forsk. Fl. Aegypt. Arab. 44 (1775).
I. setifera Poir. in Lam. Encycl. 6: 17 (1804).
I. sidaefolia Choisy in Mém. Soc. Phys. Hist. Nat. Genève, 6: 459 (1833).
I. suburceolata O'Donell in Lilloa, 26: 394 (1953).
I. trifida (HBK.) G. Don, Gen. Syst. 4: 280 (1837).

Jacquemontia acuminata Rusby in Mem. Torr. Bot. Club, 6: 84 (1896).
J. agricola Rusby in Mem. N. Y. Bot. Gard. 7: 337 (1927).
J. bifurcata Rusby in Mem. N. Y. Bot. Gard. 7: 336 (1927).
J. densiflora Rusby in Bull. Torr. Bot. Club, 26: 151 (1899) = J. Rusbyana.
J. evolvuloides var. longepedunculata Meissn. in Mart. Fl. Bras. 7: 307, t. 112 (1869).
J. pedunculata Rusby in Mem. Torr. Bot. Club, 6: 85 (1896).
J. Rusbyana Standl. in Field Mus. Publ. Bot. 11: 172 (1936).
J. Sphaerostigma (Cav.) Rusby in Bull. Torr. Bot. Club, 26: 151 (1899).
J. unilateralis (Roem. \& Schult.) O'Donell in Lilloa, 23: 470 (1950).

Merremia aegyptia (L.) Urb. Symb. Ant. 4: 505 (1910).
M. cissoides (Lam.) Hall. f. in Engler, Bot. Jahrb. 16: 552 (1893).
M. dissecta (Jacq.) Hall. f. in Engler, Bot. Jahrb. 16: 552 (1893).
M. dissecta var. chacoënsis O'Donell in Lilloa, 6: 504 (1941).
M. dissecta var. Maximilianii (Meissn.) Hall. f. in Engler, Bot. Jahrb. 16: 552 (1893).
M. macrocalyx (R. \& P.) O'Donell in Lilloa, 6: 506 (1941).
M. pentaphylla (L.) Hall. f. in Engler, Bot. Jahrb. 16: 552 (1893).
M. umbellata (L.) Hall. f. in Engler, Bot. Jahrb. 16: 552 (1893).
M. umbellata var. occidentalis Hall. f. in Verslag. Plantent. Buitenz. 1895: 127 (1896).
Pharbitis hederacea Choisy in Mém. Soc. Phys. Hist. Nat. Genève, 6: 440 (1833).
P. heterophylla (Ortega) Choisy in DC. Prodr. 9: 344 (1845).
P. purpurea (L.) Voigt, Hort. Suburb. Calc. 354 (1845).

Quamoclit hederifolia (L.) G. Don, Gen. Syst. 4: 259 (1837).

## POLEMONIACEAE

Cantua bicolor Lem. in Fl. des Serres (ser. 1) 3: 242 (1847).
C. buxifolia Juss. in Lam. Encycl. 1: 603 (1785).
C. pyrifolia Juss. in Lam. Encycl. 1: 603 (1785).

Collomia biflora (R. \& P.) Brand in Engler, Bot. Jahrb. 36: 72 (1905).
Gilia alpina (Wedd.) Brand in Engler, Pflanzenr. IV, 250: 107 (1907).
G. gracilis (Dougl.) Hook. in Bot. Mag. 56: t. 2924 (1829).
G. gracilis var. congesta (Wedd.) Borsini in Lilloa, 8: 214 (1942).
G. laciniata R. \& P. Fl. Peruv. 2: 17, t. 123, fig. b (1799).

## HYDROPHYLLACEAE

Hydrolea spinosa L. Sp. Pl. (ed. 2) 1: 328 (1762).
H. spinosa var. inermis Chod. in Bull. Herb. Boiss. (ser. 2) 2: 737 (1902).

Nama dichotomum (R. \& P.) Choisy in Mém. Soc. Phys. Hist. Nat. Genève, 6: 113 (1833).
N. dichotomum var. amplifolium (Brand) C. L. Hitchc. in Amer. Journ. Bot. 20: 530 (1933).
N. jamaicense L. Sp. Pl. (ed. 2) 1: 327 (1762).
N. longifolium Rusby in Mem. N. Y. Bot. Gard. 7: 337 (1927) = Hydrolea sp.

Phacelia boliviana Brand in Engler, Pflanzenr. IV, 251: 77 (1913).
P. circinata (Willd.) Jacq. f. Eclog. Amer. 1: 135, t. 91 (1813).
P. magellanica (Lam.) Coville in Contrib. U. S. Nat. Herb. 4: 159 (1893).
P. nana Wedd. Chlor. And. 2: 86, t. 58C (1859).
P. peruviana Spreng. Syst. Veg. 1: 584 (1825).
P. pinnatifida Griseb. ex Wedd. Chlor. And. 2: 85 (1869).
P. viscosa Phil. Fl. Atac. 37 (1860).

## BORAGINACEAE

Amsinckia hispida (R. \& P.) I. M. Johnst. in Contrib. Gray Herb. 73: 75 (1924).

Borago officinalis L. Sp. Pl. 137 (1753).
Coldenia dichotoma (R. \& P.) Lehm. Asperifol. 9 (1818).
C. elongata Rusby, Descr. S. Am. Pls. 107 (1920) = C. parviflora.
C. paronychioides Phil. in Anal. Mus. Nac. Chile, Bot. 8: 55 (1891).
C. parviflora Phil. in Anal. Mus. Nac. Chile, Bot. 8: 55 (1891).

Cordia alliodora (R. \& P.) Cham. in Linnaea, 8: 121 (1833), combination implied but not actually made.
C. andina Chod. in Bull. Soc. Bot. Genève (ser. 2), 12: 211 (1921) = C. alliodora.
C. bicolor A. DC. in DC. Prodr. 9: 485 (1845).
C. bifurcata Roem. \& Schult. Syst. 4: 466 (1819).
C. boliviana Gandog. in Bull. Soc. Bot. France, $65: 62$ (1918) = C. bifurcata.
C. Bridgesii (Friesen) I. M. Johnst. in Journ. Arnold Arb. 33: 64 (1952).
C. buddleoides Rusby in Mem. Torr. Bot. Club, 6: 83 (1896).
C. caracasana var. velutina Britton ex Rusby in Bull. Torr. Bot. Club, 26: 147 (1899).
C. chacoënsis Chod. in Bull. Soc. Bot. Genève (ser. 2) 12: 218 (1921).
C. coriacea Killip in Journ. Wash. Acad. Sci. 17: 329 (1927).
C. curassavica Roem. \& Schult. Syst. 4: 460 (1819).
? C. cylindrostachya Roem. \& Schult. Syst. 4: 459 (1819).
C. discolor Cham. \& Schlechtd. in Linnaea, 4: 482 (1829).
C. excelsa (Mart.) A. DC. Prodr. 9: 473 (1845).
C. expansa Lingelsh. in Fedde, Repert. Spec. Nov. 7: 244 (1909).
C. ferruginea (Lam.) Roem. \& Schult. Syst. 4: 458 (1819).
C. Gerascanthus L. Syst. (ed. 10) 936 (1759).
C. glabrata var. orbicularis Chod. \& Visch. in Bull. Soc. Bot. Genève (ser. 2) 12: 212 (1921).
C. guaranitica Chod. \& Hassl. in Bull. Herb. Boiss. (ser. 2) 5: 305 (1905).
C. guayaquilensis A. DC. Prodr. 9: 496 (1845).
C. hispidissima A. DC. Prodr. 9: 475 (1845).
C. insignis Cham. in Linnaea, 8: 122 (1833).
C. laxiflora HBK. Nov. Gen. \& Spec. 3: 72 (1818).
C. lutea Lam. Tabl. Encycl. 1: 421 (1791).
C. multicapitata Britton ex Rusby in Bull. Torr. Bot. Club, 26: 146 (1899).
C. nodosa Lam. Tabl. Encycl. 1: 422 (1791).
C. pauciflora Rusby in Mem. Torr. Bot. Club, 6: 83 (1896) $=$ C. ferruginea.
C. Poeppigii DC. Prodr. 9: 492 (1845).
C. Rusbyi Britton ex Rusby in Mem. Torr. Bot. Club, 6: 82 (1896).
C. Salzmannii DC. Prodr. 9: 494 (1845).
C. trichotoma (Vell.) Arrab. ex Steud. Nomencl. (ed. 2) 419 (1840).
C. umbrosa Spruce ex Rusby in Bull. Torr. Bot. Club, 26: 147 (1899).
C. Weddellii I. M. Johnst. in Journ. Arnold Arb. 16: 173 (1935).

Cryptantha debilis (Phil.) Reiche in Anal. Univ. Chile, 121: 830 (1908).
C. peruviana I. M. Johnst. in Contrib. Gray Herb. 73: 74 (1924).

Cynoglossum Fiebrigii Krause in Engler, Bot. Jahrb. 37: 634 (1906) = Hackelia revoluta.
Eritrichium Mandonii Ball in Journ. Linn. Soc. 22: 51 (1885) =Amsinckia hispida.
E. pachnophilum Wedd. Chlor. And. 2: 87 (1859) $=$ Amsinckia hispida.
E. Walpersii (A. DC.) Wedd. Chlor. And. 2: 90 (1859) = Plagiobothrys sp.

Hackelia revoluta (R. \& P.) I. M. Johnst. in Contrib. Gray Herb. 68: 45 (1923).
Heliotropium abbreviatum Rusby in Mem. Torr. Bot. Club, 4(3): 224 (1895).
H. amplexicaule Vahl, Symb. Bot. 3: 21 (1794).
H. anchusaefolium Poir. in Lam. Encycl. Suppl. 3: 23 (1803).
H. andinum Rusby in Mem. Torr. Bot. Club, 4 (3): 224 (1895) $=$ H. campestre.
H. angiospermum Murray, Prodr. Stirp. Gött. 217 (1770).
H. arborescens L. Syst. (ed. 10) 913 (1759).
H. Bangii Rusby in Bull. N. Y. Bot. Gard. 4: 414 (1907) = H. microstachyum.
H. barbatum DC. Prodr. 9: 541 (1845).
H. bolivianum Rusby in Mem. Torr. Bot. Club, 4 (3): 225 (1895) = H. amplexicaule.
H. Bridgesii Rusby in Mem. Torr. Bot. Club, 4 (3): 224 (1895) $=$ H. procumbens.
H. campestre Griseb. in Goett. Abh. 19: 234 (1874).
H. corymbosum R. \& P. Fl. Peruv. 2: 2, t. 107 (1799).
H. curassavicum L. Sp. Pl. 130 (1753).
H. elongatum Hoffm. ex Roem. \& Schult. Syst. 4: 736 (1819).
H. filiforme Lehm. in Gött. Gelehrt. Anz. 1817: 1515.
H. fruticosum L. Sp. Pl. (ed. 2) 1: 187 (1762).
H. hispidum HBK. Nov. Gen. \& Spec. 3: 87 (1819).
H. indicum L. Sp. Pl. 130 (1753).
H. inundatum var. chacoënse R. E. Fries in Ark. Bot. 6(11): 22 (1906) = H. procumbens.
H. lagoënse (Warm.) Gürke in Engl. \& Prantl, Nat. Pflanzenfam 4(3a): 97 (1893).
H. leiocarpum Morong in Ann. N. Y. Acad. Sci. 7: 168 (1893).
H. Mandonii I. M. Johnst. in Contrib. Gray Herb. 81: 43 (1928).
H. microstachyum R. \& P. Fl. Peruv. 2: 3. t. 110 (1799).
H. monostachyum Cham. in Linnaea, 4: 455 (1829).
H. nicotianaefolium Poir. in Lam. Encycl. Suppl. 3: 23 (1813).
H. paronychioides DC. Prodr. 9: 565 (1845).
H. parviflorum L. Mant. 2: 201 (1771).
H. procumbens Mill. Gard. Dict. (ed. 8) no. 10 (1768).
H. rufipilum var. anadenum I. M. Johnst. in Contrib. Gray Herb. 81 : 44 (1928).
H. salicoides Cham. in Linnaea, 8: 117 (1833).
H. tiaridioides Cham. in Linnaea, 4: 453 (1829).
H. veronicifolium Griseb. in Goett. Abh. 19: 232 (1874).

Lithocardium guazumifolium var. santacruzense O. Ktze. Rev. Gen. 3 (2): 206 (1898) $=$ Cordia buddleoides.

Myosotis azorica H. C. Wats. in Bot. Mag. 70: t. 4122 (1844).
Pectocarya boliviana (I. M. Johnst.) I. M. Johnst. in Contrib. Gray Herb. 78: 118 (1927).
Plagiobothrys congestus (Wedd.) I. M. Johnst. in Contrib. Gray Herb. 68: 75 (1923).

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P. humilis (R. \& P.) I. M. Johnst. in Contrib. Gray Herb. 68: 75 (1923).
P. Kunthii (Walp.) I. M. Johnst. in Contrib. Gray Herb. 68: 74 (1923).

Saccellium lanceolatum Humb. \& Bonpl. Pl. Aequin. 1: 47, t. 13 (1806).
S. Oliveri Britton ex Rusby in Bull. Torr. Bot. Club, 26: 147 (1899).

Tournefortia andina Britton ex Rusby in Bull. Torr. Bot. Club, 26: 148 (1899).
T. bicolor Sw. Prodr. 40 (1788).
T. Buchtienii Killip in Journ. Wash. Acad. Sci. 17: 334 (1927).
T. curvilimba Killip in Journ. Wash. Acad. Sci. 19: 195 (1929).
T. cuspidata HBK. Nov. Gen. \& Spec. 3: 83 (1818).
T. fuliginosa HBK. Nov. Gen. \& Spec. 3: 81, t. 203 (1818).
T. graciliflora Rusby in Bull. Torr. Bot. Club, 26: 148 (1899) =T. paniculata.
T. Herzogii Vaupel in Meded. Rijks Herbar. 46: 10 (1922) $=$ T. rubicunda.
T. laevigata Lam. Encycl. Tabl. 1: 416 (1791).
T. Lilloi I. M. Johnst. in Contrib. Gray Herb. 92: 71 (1930).
T. mapirensis Lingelsh. in Fedde, Repert. Spec. Nov. 7: 244 (1909).
T. obscura A. DC. Prodr. 9: 517 (1845).
T. ovalifolia Rusby in Bull. N. Y. Bot. Gard. 4: 414 (1907).
T. paniculata Cham. in Linnaea, 4: 468 (1829).
T. polystachya R. \& P. Fl. Peruv. 2: 24, t. 149, fig. a (1799).
T. psilostachya HBK. Nov. Gen. \& Spec. 3: 78 (1818).
T. rubicunda Salzm. ex DC. Prodr. 9: 526 (1845).
T. Salzmannii A. DC. Prodr. 9: 524 (1845).
T. setacea Killip in Journ. Wash. Acad. Sci. 17: 332 (1927).
T. subrotunda Rusby in Bull. N. Y. Bot. Gard. 8: 115 (1912) = T. mapirensis.
T. surinamensis A. DC. Prodr. 9: 526 (1845).
T. Ulei Vaupel in Notizbl. 6: 186 (1914).
T. vestita Killip in Journ. Wash. Acad. Sci. 17: 333 (1927).

## VERBENACEAE

Acantholippia deserticola (R. A. Phil.) Moldenke in Lilloa, 5: 370 (1940).
Aegiphila boliviana Moldenke in Fedde, Repert. Spec. Nov. 33: 114 (1933).
Ae. breviflora (Rusby) Moldenke in Phytologia, 1: 95 (1934).
Ae. Buchtienii Moldenke in Fedde, Repert. Spec. Nov. 33: 116 (1933).
Ae. chrysantha Hayek in Engler, Bot. Jahrb. 42: 171 (1909).
Ae. densiflora Rusby in Mem. Torr. Bot. Club, 6: 107 (1896) $=$ Ae. setiformis.
Ae. elegans Moldenke in Brittonia, 1: 186 (1932).
Ae. elongata Moldenke in Fedde, Repert. Spec. Nov. 33: 121 (1933).
Ae. filipes Mart. \& Schauer in DC. Prodr. 11: 652 (1847).
Ae. Herzogii Moldenke in Fedde, Repert. Spec. Nov. 33: 126 (1933).
Ae. hirsuta Moldenke in Fedde, Repert. Spec. Nov. 33: 127 (1933).
Ae. integrifolia (Jacq.) Jackson in Ind. Kew. 1: 46 (1893).
A. mollis HBK. Nov. Gen. \& Spec. 2: 250, t. 130 (1818).

Ae. multiflora R. \& P. Fl. Peruv. 1: 50, t. 76 (1798).
Ae. oblongifolia Rusby in Bull. Torr. Bot. Club, 27: 81 (1900) $=$ Ae. filipes.
Ae. ovata Moldenke in Brittonia, 1: 189 (1932).
Ae. peruviana Turcz. in Bull. Soc. Imp. Nat. Mosc. 36(2): 219 (1863).
Ae. Sellowiana Cham. in Linnaea, 7: 111 (1831).
Ae. setiformis Rusby in Mem. Torr. Bot. Club, 4 (3): 245 (1895).
Ae. spicata (Rusby) Moldenke in Fedde, Repert. Spec. Nov. 33: 139 (1933).
Ae. Steinbachii Moldenke in Phytologia, 2: 9 (1941).
Ae. vitelliniflora Klotzsch ex Walp. Repert. 4: 123 (1845).
Aloysia Fiebrigi (Hayek) Moldenke in Revist. Sudam. Bot. 4: 15 (1937).
A. ligustrina (Lag.) Small, Fl. SE. U. S. 1013 (1903).
A. scorodonioides (HBK.) Cham. in Linnaea, 7: 234 (1832), combination implied but not actually made.
A. Sellowii (Briq.) Moldenke in Revist. Sudam. Bot. 4: 15 (1937).
A. virgata (R. \& P.) A. Juss. in Ann. Mus. Paris, 7: 73 (1806), combination implied but not actually made.
Baillonia amabilis Bocq. in Adansonia, 2: 252, t. 7 (1862).
B. amabilis var. longifolia O. Ktze. Rev. Gen. 3(2): 250 (1898).

Bouchea boliviana (O. Ktze.) Moldenke in Phytologia, 1: 18 (1933).
B. fluminensis (Vell.) Moldenke in Fedde, Repert. Spec. Nov. 49: 117 (1940).
B. incisa Rusby in Bull. N. Y. Bot. Gard. 4: 432 (1907) = B. Rusbyi.
B. pseudogervao forma pilosa Herzog in Meded. Rijks Herbar. 29: 46 (1916) $=\mathrm{B}$. boliviana.
B. Rusbyi Moldenke in Torreya, 34: 8 (1934).

Callicarpa acuminata HBK. Nov. Gen. \& Spec. 2: 252 (1818).
C. minutiflora Rusby in Mem. N. Y. Bot. Gard. 7: 339 (1927).

Castelia cuneato-obovata Cav. in Anal. Cienc. Nat. 3: 134 (1801).
Citharexylum andinum Moldenke in Fedde, Repert. Spec. Nov. 37: 217 (1934).
C. ilicifolium HBK. Nov. Gen. \& Spec. 2: 256 (1818).
C. laurifolium Hayek in Engler, Bot. Jahrb. 42: 170 (1908).
C. megacanthum Rusby in Bull. N. Y. Bot. Gard. 8: 115 (1912).
C. mendocinum R. A. Phil. Sert. Mend. Alt. 193 (1870).
C. Poeppigii var. margaritaceum Poepp. \& Moldenke in Fedde, Repert. Spec. Nov. 37: 233 (1934).
C. punctatum Greenm. in Field Columb. Mus. Bot. Ser. 2: 189 (1907).

Clerodendron bolivianum Britton ex Rusby in Bull. Torr. Bot. Club, 27: 82 $(1900)=$ Aegiphila multiflora.
C. fragrans var. pleniflorum Schauer in DC. Prodr. 11: 666 (1847).

Duranta Benthamii Briq. in Bull. Herb. Boiss. (ser. 1) 4: 343 (1896).
D. Mandonii Moldenke in Lilloa, 5: 390 (1940).
D. Pearcei Rusby in Bull. N. Y. Bot. Gard. 4: 433 (1907).
D. recurvistachys Rusby in Phytologia, 1: 73 (1934).
D. repens L. Sp. Pl. 637 (1753).
D. rupestris Hayek in Engler, Bot. Jahrb. 42: 171 (1908).
D. serratifolia (Griseb.) O. Ktze. Rev. Gen. 3(2): 251 (1898).

Ghinia Cardenasii Moldenke in Bull. Torr. Bot. Club, 68: 504 (1941).
Junellia aretioides (R. E. Fries) Moldenke in Lilloa, 5: 393 (1940).
J. bisulcata (Hayek) Moldenke, Known Geogr. Distrib. Verb. \& Avicenn. 77 (1942).
J. minima (Meyen) Moldenke in Lilloa, 5: 398 (1940).

Lantana achyranthifolia Desf. Cat. Hort. Paris (ed. 3) 392 (1829).
L. aristata var. Cabrerae Moldenke in Lilloa, 5: 404 (1940).
L. aristata var. pluripedunculata (O. Ktze.) Moldenke in Phytologia, 1: 170 (1935).
L. Balansae Briq. in Ann. Conserv. \& Jard. Bot. Genève, 7-8: 300 (1904).
L. Balansae var. peduncularis Briq. in Bull. Herb. Boiss. (ser. 2) 4: 1063 (1904).
L. brachypoda Hayek in Engler, Bot. Jahrb. 42: 167 (1908).
L. Camara L. Sp. Pl. 627 (1753).
L. Camara var. mista (L.) L. H. Bailey, Cycl. Am. Hort. 884 (1900).
L. Camara var. nivea (Vent.) L. H. Bailey, Cycl. Am. Hort. 883 (1900).
L. canescens HBK. Nov. Gen. \& Spec. 2: 259 (1818).
L. Chamissonis (D. Dietr.) Benth. \& Hook. f. Gen. Pl. 2: 1142 (1876), combination implied but not actually made.
L. cujabensis Schauer in DC. Prodr. 11: 599 (1847).
L. Fiebrigii Hayek in Engler, Bot. Jahrb. 42: 169 (1908).
L. foetida Rusby in Bull. N. Y. Bot. Gard. 4: 431 (1907).
L. fucata Lindl. in Bot. Reg. 10: t. 798 (1824).
L. hyptoides Rusby in Bull. N. Y. Bot. Gard. 4: 431 (1907).
L. micrantha Briq. in Ann. Conserv. \& Jard. Bot. Genève, 7-8: 299 (1904).
L. micrantha var. armata Moldenke in Phytologia, 2: 468 (1948).
L. montevidensis (Spreng.) Briq. in Ann. Conserv. \& Jard. Bot. Genève, 7-8: 301 (1904).
L. ovata Hayek in Fedde, Repert. Spec. Nov. 2: 163 (1906).
L. procurrens Schauer in DC. Prodr. 11: 596 (1847).
L. rugulosa HBK. Nov. Gen. \& Spec. 2: 261 (1818).
L. Rusbyana Moldenke in Lilloa, 8: 422 (1942).
L. tenuifolia Rusby in Phytologia, 1: 74 (1934) $=$ L. cujabensis.
L. trifolia L. Sp. Pl. 626 (1753).

Lippia affinis Schauer in DC. Prodr. 11: 576 (1847).
L. alba (L.) N. E. Br. in Britt. \& Wils. Sci. Surv. Porto Rico, 6: 141 (1925).
L. aristata Schauer in DC. Prodr. 11: 581 (1847).
L. asperrima Cham. in Linnaea, 7: 215 (1832).
L. boliviana Rusby in Mem. Torr. Bot. Club, 4(3): 243 (1895).
L. chacensis Moldenke in Phytologia, 2: 414 (1948).
L. dumetorum Herzog in Meded. Rijks Herbar. 29: 45 (1916).
L. fimbriata Rusby in Mem. Torr. Bot. Club, 4 (3): 244 (1895) = Lantana achyranthifolia.
L. hirsuta var. vernonioides (Cham.) O. Ktze. Rev. Gen. 3(2): 252 (1898).
L. imbricata O. Ktze. Rev. Gen. 3(2): 252 (1898).
L. lasiocalycina Cham. in Linnaea, 7: 231 (1832).
L. lasiocalyx Herzog in Meded. Rijks Herbar. 29: 44 (1916).
L. laxibracteata Herzog in Meded. Rijks Herbar. 29: 45 (1916).
L. lupulina Cham. in Linnaea, 7: 222 (1832).
L. origanoides HBK. Nov. Gen. \& Spec. 2: 267 (1818).
L. pendula Rusby in Bull. N. Y. Bot. Gard. 8: 116 (1912).
L. salviaefolia Cham. in Linnaea, 7: 227 (1832).
L. suffruticosa (Griseb.) O. Ktze. Rev. Gen. 3(2): 253 (1898).
L. turnerifolia Cham. in Linnaea, 7: 217 (1832).
L. venosa Rusby in Mem. N. Y. Bot. Gard. 7: 338 (1927).

Parodianthus ilicifolius (Moldenke) Troncoso in Darwiniana, 5: 39 (1941).
Petrea fragrantissima Rusby in Mem. N. Y. Bot. Gard. 7: 338 (1927).
P. maynensis Huber in Bol. Mus. Goëldi, 4: 602 (1906).

Phyla betulaefolia (HBK.) Greene in Pittonia, 4: 48 (1899).
P. caespitosa (Rusby) Moldenke in Rev. Sudam. Bot. 5: 2 (1937).
P. nodiflora (L) Greene in Pittonia, 4: 46 (1899).
P. nodiflora var. reptans (HBK.) Moldenke, Alph. List. Inval. Names Verb. 31 (1942).
P. nodiflora var. rosea (D. Don) Moldenke in Phytologia, 2: 22 (1941).

Priva boliviana Moldenke in Phytologia, 3: 172 (1949).
P. lappulacea (L.) Pers. Synops. Pl. 2: 139 (1806).

Recordia boliviana Moldenke in Phytologia, 1: 99 (1934).
Stachytarphaeta canescens HBK. Nov. Gen. \& Spec. 2: 281 (1818).
S. cajanensis (L. C. Rich.) Vahl, Enum. 1: 208 (1804).
S. elatior Schrad. ex Schult. Mant. 1: 172 (1822).

Timotocia Mansoi (Schauer) Moldenke in Fedde, Repert. Spec. Nov. 39: 142 (1936).

Verbena Bangiana Moldenke in Phytologia, 3: 63 (1949).
V. bonariensis L. Sp. Pl. 20 (1753).
V. brasiliensis Vell. Fl. Flum. 17 (1825).
V. cochabambensis Moldenke in Castanea, 10: 45 (1945).
V. dissecta Willd. ex Spreng. Syst. Veg. 2: 750 (1825).
V. gracilescens (Cham.) Herter in Rev. Sudam. Bot. 4: 186 (1937).
V. hispida R. \& P. Fl. Peruv. 1: 22, t. 34, fig. a (1798).
V. laciniata (L.) Briq. in Ann. Conserv. \& Jard. Bot. Genève, 7-8: 296 (1904).
V. littoralis HBK. Nov. Gen. \& Spec. 2: 276, t. 137 (1818).
V. microphylla HBK. Nov. Gen. \& Spec. 2: 272, t. 133 (1818).
V. officinalis L. Sp. Pl. 20 (1753).
V. parvula Hayek in Engler, Bot. Jahrb. 42: 162 (1908).
V. peruviana (L.) Britton in Ann. N. Y. Acad. Sci. 7: 197 (1893).
V. rigida Spreng. Syst.: Cur. Post. 230 (1827).
V. seriphioides Gill. \& Hook. in Bot. Misc. 1: 164 (1829).
V. tenera Spreng. Syst. Veg. 2: 750 (1825).
V. tenuisecta Briq. in Ann. Conserv. \& Jard. Bot. Genève, 7-8: 294 (1904).

Vitex cymosa Bert. ex Spreng. Syst. Veg. 2: 757 (1925).
V. pseudolea Rusby in Mem. N. Y. Bot. Gard. 7: 341 (1927).
V. triflora Vahl, Symb. 2: 49 (1798).

## LABIATAE

Bystropogon andinus var. hypoleucus Briq. in Bull. Herb. Boiss. (ser. 1) 4: 799 (1896) = Minthostachys ovata.
B. minutus Briq. in Bull. Herb. Boiss. (ser. 1) 4: 803 (1896) = Satureja parvifolia.
B. uniflorus Rusby ex Briq. in Bull. Herb. Boiss. (ser. 1) 4: 802 (1896) $=$ Satureja axillaris.
Ceratominthe Kuntzeana Briq. in Bull. Herb. Boiss. (ser. 1) 4: 877 (1896) = Satureja odora.
Clinopodium Kuntzeanum O. Ktze. Rev. Gen. 3 (2): 259 (1898) = Satureja boliviana.
Eriope crassipes Benth. Lab. Gen. 144 (1833).
Hedeoma adscendens Rusby in Phytologia, 1: 74 (1934).
H. Mandoniana Wedd. Chlor. And. 2: 148 (1860).

Hyptis arborea Benth. in DC. Prodr. 12: 132 (1848).
H. brevipes Poit. in Ann. Mus. Paris, 7: 465 (1806).
H. canaminensis Rusby in Mem. N. Y. Bot. Gard. 7: 342 (1927) = H. mutabilis var. canescens.
H. carpinifolia Benth. Lab. Gen. 115 (1833).
H. compacta Rusby in Mem. N. Y. Bot. Gard. 7: 343 (1927).
H. conferta var. angustifolia Benth. in DC. Prodr. 12: 112 (1848), nomen nudum.
H. dumetorum Morong in Ann. N. Y. Acad. Sci. 7: 200 (1893).
H. duplicato-dentata Pohl ex Benth. Lab. Gen. 114 (1833).
H. eriocephala Benth. in DC. Prodr. 12: 124 (1848).
H. goyazensis St. Hil. ex Benth. Lab. Gen. 92 (1833) [as H. goyavensis].
H. gymnodonta Briq. in Bull. Herb. Boiss. (ser. 1) 4: 795 (1896) = H. dumetorum.
H. hirsuta HBK. Nov. Gen. \& Spec. 2: 318, t. 161 (1818).
H. idiocephala Briq. in Bull. Herb. Boiss. (ser. 1) 4: 792 (1896) $=$ H. Lorentziana.
H. inundata Herzog in Fedde, Repert. Spec. Nov. 7: 66 (1909) = H. microphylla.
H. Kuntzeana Briq. in Bull. Herb. Boiss. (ser. 1) 4: 787 (1896).
H. lantanaefolia Poit. in Ann. Mus. Paris, 7: 468, t. 29, fig. 1 (1806).
H. lappacea Benth. Lab. Gen. 103 (1833).
H. lappulacea Mart. ex Benth. Lab. Gen. 104 (1833).
H. longifrons Briq. in Bull. Herb. Boiss. (ser. 1) 4: 793 (1896) $=$ H. velutina.
H. Lorentziana O. Hoffm. in Linnaea, 43: 137 (1880).
H. lutescens Pohl ex Benth. Lab. Gen. 109 (1833).
H. microphylla Pohl ex Benth. Lab. Gen. 82 (1833).
H. mutabilis (A. Rich.) Briq. in Bull. Herb. Boiss. (ser. 1) 4: 788 (1896).
H. mutabilis var. canescens (HBK.) Briq. in Bull. Herb. Boiss. (ser. 1) 4: 788 (1896).
H. mutabilis var. spicata (Poit.) Briq. in Bull. Herb. Boiss. (ser. 1) 4: 788 (1896).
H. obtusiflora Presl ex Benth. Lab. Gen. 107 (1833).
H. odorata Benth. Lab. Gen. 81 (1833).
H. pectinata Poit. in Ann. Mus. Paris, 7: 474, t. 30 (1806).
H. recurvata Poit. in Ann. Mus. Paris, 7: 467, t. 28, fig. 2 (1806).
H. recurvata var. megacephala Benth. in DC. Prodr. 12: 90 (1848).
H. rugosa var. canescens (Briq.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 275 (1937).
H. sinuata Pohl ex Benth. Lab. Gen. 103 (1833).
H. spicigera Lam. Encycl. 3: 185 (1789).
H. suaveolens Poit. in Ann. Mus. Paris, 7: 472, t. 29, fig. 2 (1806).
T. Tafallae Benth. Lab. Gen. 132 (1833).
H. trachychroa Briq. in Bull. Herb. Boiss. (ser. 1) 4: 790 (1896) $=$ H. lutescens.
H. umbrosa var. Mikanii Benth. in DC. Prodr. 12: 124 (1848).
H. uncinata Benth. Lab. Gen. 80 (1833).
H. velascana Briq. in Bull. Herb. Boiss. (ser. 1) 4: 798 (1896) $=$ H. virgata.
H. velutina Pohl ex Benth. Lab. Gen. 90 (1833).
H. virgata Benth. Lab. Gen. 77 (1833).

Lepechinia aurifera (Rusby) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 25 (1935).
L. bella Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 21 (1935).
L. confusa (Briq.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 25 (1935).
L. floribunda (Benth.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 22 (1935).
L. graveolens (Regel) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 25 (1935).
L. heteromorpha (Briq.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 26 (1935).
L. inflata (Briq.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 24 (1935).
L. lancifolia (Rusby) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 23 (1935).
L. Meyenii (Walp.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 20 (1935).

Marrubium vulgare L. Sp. Pl. 583 (1753).
Marsypianthes Chamaedrys (Vahl) O. Ktze. Rev. Gen. 2: 524 (1891).
Mentha aquatica L. Sp. Pl. 576 (1753).
Mesosphaerum arboreum var. bracteosum Rusby in Mem. Torr. Bot. Club, 6: 107 (1896) = Hyptis arborea.
M. crenatum var. albiflorum O. Ktze. Rev. Gen. 3 (2): 260 (1898) = Hyptis sp.?
M. crenatum var. subviolaceum O. Ktze. Rev. Gen. 3 (2): 259 (1898) = Hyptis sp.?
M. grandiflorum Rusby in Bull. N. Y. Bot. Gard. 8: 116 (1912) $=$ Hyptis Tafallae.
M. pallidum Rusby in Bull. N. Y. Bot. Gard. 4: 433 (1907) $=$ Hyptis obtusiflora.
M. yungasense Britton ex Rusby in Mem. Torr. Bot. Club, 4 (3): 246 (1895) $=$ Hyptis mutabilis var. canescens.
Minthostachys acutifolia Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 166 (1936).
M. andina (Britton) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 166 (1936)).
M. diffusa Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 167 (1936).
M. Mandoniana (Briq.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 167 (1936).
M. ovata (Briq.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 167 (1936).
M. setosa (Briq.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 166 (1936).

Ocimum micranthum Willd. Enum. Hort. Berol. 630 (1809).
Perilomia ocimoides HBK. Nov. Gen. \& Spec. 2: 328 (1818).
Rosmarinus officinalis L. Sp. Pl. 23 (1753).
Salvia amplifrons Briq. in Bull. Herb. Boiss. (ser. 1) 4: 863 (1896).
S. atrocyanea Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 98 (1936).
S. australis Epl. in Rev. Sudam. Bot. 4: 43 (1937).
S. avicularis Briq. in Bull. Herb. Boiss. (ser. 1) 4:866 (1896) = S. Haenkei.
S. Bangii Rusby in Mem. Torr. Bot. Club, 4(3): 246 (1895).
S. Bridgesii Britton ex Rusby in Bull. Torr. Bot. Club, 27: 124 (1900) = S. Haenkei.
S. cardiophylla Benth. Lab. Gen. 721 (1835).
S. chariantha Briq. in Bull. Herb. Boiss. (ser. 1) 4: 861 (1896) = S. Orbignaei.
S. chorianthos Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 57 (1935).
S. cochabambensis Rusby in Mem. Torr. Bot. Club, 6: 108 (1896) = S. Orbignaei.
S. Dombei Epl. in Rev. Sudam. Bot. 4: 47 (1937).
S. erythradenia Briq. in Bull. Herb. Boiss. (ser. 1) 4: 853 (1896) = S. Bangii.
S. Gilliesii Benth. Lab. Gen. 265 (1833).
S. grewiaefolia S. Moore in Journ. Bot. 42: 109 (1904).
S. Haenkei Benth. Lab. Gen. 283 (1833).
S. Kuntzeana Briq. in Bull. Herb. Boiss. (ser. 1) 4: 859 (1896) = S. Orbignaei.
S. longiflora R. \& P. Fl. Peruv. 1: 23, t. 40 (1798).
S. occidentalis Sw. Prodr. 14 (1788).
S. Orbignaei Benth. in DC. Prodr. 12: 338 (1848).
S. oxyphora Briq. in Bull. Herb. Boiss. (ser. 1) 4: 864 (1896).
S. personata Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 73 (1935).
S. platystoma Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 81 (1935).
S. praeclara Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 121 (1936).
S. pseudoavicularis Briq. in Bull. Herb. Boiss. (ser. 1) 4: 867 (1896) = S. Haenkei.
S. retinervia Briq. in Bull. Herb. Boiss. (ser. 1) 4: 857 (1896).
S. rhombifolia R. \& P. Fl. Peruv. 1: 26, t. 36 (1798).
S. Rusbyi Britton ex Rusby in Mem. Torr. Bot. Club, 4 (3): 247 (1895).
S. mppara Briq. in Bull. Herb. Boiss. (ser. 1) 4: 850 (1896) = S. tiraquensis.
S. sophrona Briq. in Bull. Herb. Boiss. (ser. 1) 4: 854 (1896).
S. stachydifolia Benth. in DC. Prodr. 12: 311 (1848).
S. tiliaefolia Vahl, Symb. 3: 7 (1794).
S. tiraquensis Briq. in Bull. Herb. Boiss. (ser. 1) 4: 851 (1896).

Satureja axillaris (Rusby) Epl. in Ann. Missouri Bot. Gard. 14: 82 (1927).
S. boliviana (Benth.) Briq. in Engl. \& Prantl, Nat. Pflanzenfam. 4(3a): 300 (1896).
S. boliviana var. tarijensis (Wedd.) Epl. in Ann. Missouri Bot. Gard. 14: 81 (1927).
S. Kuntzeana Briq. in Bull. Herb. Boiss. (ser. 1) 4:874 (1896) = S. boliviana.
S. odora (Griseb.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 158 (1936).
S. pallida Epl. in Ann. Missouri Bot. Gard. 14: 65 (1927).
S. parvifolia (Phil.) Epl. in Fedde, Repert. Spec. Nov. Beih. 85: 159 (1936).
S. simulans Epl. in Ann. Missouri Bot. Gard. 14: 81 (1927).

Scutellaria breviflora Benth. in Bot. Reg. 18: sub t. 1493, no. 7 (1832).
S. racemosa Pers. Synops. Pl. 2: 136 (1806).
S. uliginosa St. Hil. ex Benth. Lab. Gen. 427 (1834).

Sphacele cochabambana Briq. in Bull. Herb. Boiss. (ser. 1) 4: 807 (1896) = Lepechinia aurifera.
S. Kuntzeana Briq. in Bull. Herb. Boiss. (ser. 1) 4: 805 (1896) $=$ Lepechinia aurifera.
S. Mandoniana Briq. in Ann. Conserv. \& Jard. Bot. Genève, 2: 176 (1898) = Lepechinia inflata.

Stachys boliviana Briq. in Bull. Herb. Boiss. (ser. 1) 4: 871 (1896) = S. petiolosa.
S. Mandoniana Briq. in Ann. Conserv. \& Jard. Bot. Genève, 2: 118 (1898).
S. petiolosa Briq. in Bull. Herb. Boiss. (ser. 1) 4: 868 (1896).
S. pusilla (Wedd.) Briq. in Ann. Conserv. \& Jard. Bot. Genève, 2: 120 (1898).

Teucrium vesicarium Mill. Gard. Dict. (ed. 8) no. 17 (1768).

## SOLANACEAE

Acnistus oblongifolius Rusby in Mem. Torr. Bot. Club, 4(3): 232 (1895) $=$ Dunalia breviflora var. glabrata.
Bassovia anceps (R. \& P.) Rusby in Bull. Torr. Bot. Club, 26: 197 (1899).
B. Fendleri Rusby in Bull. Torr. Bot. Club, 26: 197 (1899).
B. minutiflora Rusby in Mem. N. Y. Bot. Gard. 7: 343 (1927).
B. platyneura H. Winkl. in Fedde, Repert. Spec. Nov. 7: 248 (1909).
B. solanacea (Miers) Benth. \& Hook. f. Gen. Pl. 2: 891 (1876), combination implied but not actually made.
Brachistus hebephyllus Miers in Ann. \& Mag. Nat. Hist. (ser. 2) 3: 266 (1849).
B. lasiophyllus (Humb. \& Bonpl.) Rusby in Bull. Torr. Bot. Club, 26: 198 (1899).
B. virgatus H. Winkl. in Fedde, Repert. Spec. Nov. 7: 245 (1909) $=$ Lycianthes actinocalyx.
Browallia viscosa HBK. Nov. Gen. \& Spec. 2: 273 (1818).
Brugmansia arborea (L.) Steud. Nomencl. (ed. 2) 1: 230 (1840).
B. bicolor (R. \& P.) Pers. Synops. Pl. 1: 216 (1805).
B. sanguinea (R. \& P.) D. Don in Sweet, Brit. Fl. Gard. (ser 2) 3: t. 272 (1835).
B. suaveolens (Humb. \& Bonpl.) Bercht. \& Presl, Rostl. 1. Solanac. 45 (1823).

Brunfelsia Mire Monachino in Phytologia, 4:342 (1953).
B. latifolia (Pohl) Benth. in DC. Prodr. 10: 199 (1846).

Cacabus parviflorus Rusby in Mem. Torr. Bot. Club, 4(3): 233 (1895).
Capsicum baccatum L. Mant. 47 (1767).
C. frutescens L. Sp. Pl. 189 (1753).
C. glomeruliflorum (Sendt.) O. Ktze. Rev. Gen. 3(2): 218 (1898).
C. grandiflorum O. Ktze. Rev. Gen. 3(2): 218 (1898) = Dunalia fasciculata.
C. punctatum (R. \& P.) O. Ktze. Rev. Gen. 3(2): 219 (1898).
C. solanaceum (L'Hérit.) O. Ktze. Rev. Gen. 3(2): 219 (1898).

Cestrum albotomentosum U. Damm. ex Francey in Candollea, 6: 152 (1936).
C. atroxanthum O. Ktze. Rev. Gen. 3(2): 219 (1898).
C. Baenitzii Lingelsh. in Fedde, Repert. Spec. Nov. 7: 248 (1909).
C. Baenitzii var. angustifolium Francey in Candollea, 6: 312 (1936).
C. bolivianum Francey in Candollea, 6: 230 (1936).
C. Buchtienii Francey in Candollea, 6: 300 (1936).
C. calycinum Willd. ex Roem. \& Schult. Syst. Veg. 4: 808 (1819).
C. ellipticum Francey in Candollea, 6: 216 (1936).
C. floribundum Britton in Mem. Torr. Bot. Club, 6: 92 (1896) = C. reflexum.
C. foliosum Francey in Candollea, 6: 260 (1936).
C. Herzogii E. Damm. in Meded. Rijks Herbar. 29: 28 (1916).
C. impressum Rusby in Bull. N. Y. Bot. Gard. 4: 425 (1907) = C. calycinum.
C. Mandonii Rusby in Bull. N. Y. Bot. Gard. 4: 425 (1907) = C. Parqui.
C. Mathewsii Dunal in DC. Prodr. 13(1): 637 (1852).
C. papyraceum Rusby, Descr. S. Am. Pls. 120 (1920).
C. Parqui L'Hérit. Stirp. Nov. 4: 73, t. 36 (1788)
C. Parqui var. macrocalyx Francey in Candollea, 7 (preprint): 45 (1936).
C. Parqui var. oranense Scolnik in Revist. Argent. Agron. 21: 30 (1954).
C. Parqui var. tomentistipes O. Ktze. Rev. Gen. 3(2): 219 (1898).
C. plicatum Francey in Candollea, 7: 52 (1936).
C. racemosum var. bolivianum Francey in Candollea, 6: 274 (1936).
C. reflexum Sendt. in Mart. Fl. Bras. 10: 218 (1846).
C. reflexum var. densiflorum Francey in Candollea, 6: 267 (1936).
C. rigidum Rusby in Mem. Torr. Bot. Club, 4(3): 234 (1895).
C. sparsiflorum Britton ex Rusby in Bull. Torr. Bot. Club, 27: 22 (1900).
C. strigillatum R. \& P. Fl. Peruv. 2: 29, t. 156 (1799) [as C. strigilatum].
C. strigillatum var. calycinum (HBK.) O. Ktze. Rev. Gen. 3 (2): 220 (1898).
C. tenuissimum Francey in Candollea, 6: 248 (1936).

Chamaesaracha boliviensis U. Damm. in Engler, Bot. Jahrb. 49: 215 (1913) $=$ Solanum chamaesarachidium.
Cyphomandra acuminata Rusby in Bull. Torr. Bot. Club, 26: 196 (1899).
C. arborea H. Winkl. in Fedde, Repert. Spec. Nov. 7: 246 (1909).
C. artocarpophylla H. Winkl. in Fedde, Repert. Spec. Nov. 7: 246 (1909).
C. benensis Britton ex Rusby in Bull. Torr. Bot. Club, 26: 196 (1899).
C. crassifolia (Ort.) O. Ktze. Rev. Gen. 3(2): 220 (1898).
C. Fraxinella Sendt. in Mart. Fl. Bras. 10: 122 (1846).
C. subcordata Rusby in Bull. N. Y. Bot. Gard. 8: 119 (1912).
C. uniloba Rusby in Mem. Torr. Bot. Club, 6: 90 (1896).
C. yungasensis Rusby in Bull. Torr. Bot. Club, 26: 195 (1899).

Datura Stramonium L. Sp. Pl. 179 (1753).
D. Tatula L. Sp. Pl. (ed. 2) 1: 256 (1762).

Dunalia brachyantha Miers in Hook. Lond. Journ. Bot. 7: 339 (1848).
D. breviflora var. glabrata (Sendt.) Sleum. in Lilloa, 23: 131 (1950).
D. fasciculata (Miers) Sleum. in Lilloa, 23: 135 (1950).
D. Hauthalii U. Damm. in Engler, Bot. Jahrb. 50, Beibl. 111: 55 (1913).
D. Herzogii U. Damm. in Meded. Rijks Herbar. 29: 25 (1916) = D. senticosa.
D. lycioides Miers in Hook. Lond. Journ. Bot. 4: 334 (1845).
D. Pflanzii U. Damm. in Engler, Bot. Jahrb. 50, Beibl. 111: 57 (1913) = D. lycioides.
D. senticosa Miers in Hook. Lond. Journ. Bot. 4: 340 (1848).
D. Steinbachii Sleum. in Lilloa, 23: 136 (1950).

Fabiana densa Remy in Ann. Sci. Nat. (ser. 3) 8: 225 (1847).
Fregirardia Dunaliana Wedd. Chlor. And. 2: 100 (1859).
Grabowskia boerhaaviaefolia var. obtusifolia O. Ktze. Rev. Gen. 3(2): 221 (1898).
G. schizocalyx U. Damm. in Meded. Rijks Herbar. 29: 22 (1916).

Iochroma lyciifolium U. Damm. in Engler, Bot. Jahrb. 37: 637 (1906).
Jaborosa floccosa U. Damm. in Engler, Bot. Jahrb. 37: 641 (1906).
J. leiocalyx U. Damm. in Meded. Rijks Herbar. 29: 27 (1916).

Juanulloa Hookeriana Miers in Ann. \& Mag. Nat. Hist. (ser. 2) 4: 189 (1849).
J. membranacea Rusby in Mem. Torr. Bot. Club, 4 (3): 233 (1895).
J. mexicana (Schlechtd.) Miers in Ann. \& Mag. Nat. Hist. (ser. 2) 4: 188 (1849).
J. pedunculata Rusby in Mem. Torr. Bot. Club, 4 (3): 234 (1895).

Lonchestigma crispum (Miers) Dunal in DC. Prodr. 13(1): 477 (1852).
Lycianthes actinocalyx (H. Winkl.) Bitter in Abh. Naturw. Ver. Bremen, 24: 338 (1920).
L. apiculata Bitter in Abh. Naturw. Ver. Bremen, 24: 452 (1920).
L. Buchtienii Bitter in Abh. Naturw. Ver. Bremen, 24: 337 (1920) = L. actinocalyx.
L. candicans (Dun.) Hassl. in Ann. Conserv. \& Jard. Bot. Genève, 20: 181 (1917).
L. coccinea (Rusby) Rusby in Bull. Torr. Bot. Club, 53: 210 (1926).
L. fasciculata (Rusby) Bitter in Abh. Naturw. Ver. Bremen, 24: 334 (1920).
L. Fendleri (Rusby) Rusby in Bull. Torr. Bot. Club, 53: 210 (1926).
L. heterodoxa Bitter in Abh. Naturw. Ver. Bremen, 24: 333 (1920).
L. hispida (Rusby) Rusby in Bull. Torr. Bot. Club, 53: 210 (1926).
L. hylophila Bitter in Abh. Naturw. Ver. Bremen, 24: 336 (1920).
L. inaequilatera (Rusby) Bitter in Abh. Naturw. Ver. Bremen, 24: 439 (1920).
L. leptocaulis (Rusby) Rusby in Bull. Torr. Bot. Club, 53: 218 (1926).
L. lycioides (L.) Hassl. in Ann. Conserv. \& Jard. Bot. Genève, 20: 181 (1917).
L. lycioides var. parvifolia (Wedd.) Bitter in Abh. Naturw. Ver. Bremen, 24: 328 (1920).
L. medians Bitter in Fedde, Repert. Spec. Nov. 18: 317 (1922).
L. polycarpa Rusby in Bull. Torr. Bot. Club, 53: 212 (1926).
L. pseudolycioides (Chod. \& Hassl.) Bitter in Abh. Naturw. Ver. Bremen, 24: 352 (1920).
L. pyrifolia Rusby in Bull. Torr. Bot. Club, 53: 212 (1926).
L. reflexa Rusby in Bull. Torr. Bot. Club, 53: 211 (1926).
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S. Mandonis var. tardecalvescens Bitter in Fedde, Repert. Spec. Nov. 11: 487 (1913).
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S. minutibaccatum var. curtipedunculatum Bitter in Fedde, Repert. Spec. Nov. 11: 205 (1912).
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S. nitidibaccatum var. robusticalyx Bitter in Fedde, Repert. Spec. Nov. 11: 209 (1912).
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S. Pearcei Britton ex Rusby in Mem. Torr. Bot. Club, 4(3): 227 (1895).
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S. Phureja var. Pujeri Hawkes, Potato Coll. Exped. 2: 128 (1944).
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S. stenotomum var. cyaneum Hawkes, Potato Coll. Exped. 2: 57 (1944).
S. stenotomum var. megalocalyx Hawkes, Potato Coll. Exped. 2: 59 (1944).
S. stenotomum var. Pitiquilla Hawkes, Potato Coll. Exped. 2: 54 (1944).
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S. suaveolens var. heterotrichostylum Bitter in Fedde, Repert. Spec. Nov. 11: 356 (1912).
S. suaveolens subsp. microphyllidium Bitter in Fedde, Repert. Spec. Nov. 11: 357 (1912).
S. subandigenum Hawkes, Potato Coll. Exped. 2: 128 (1944).
S. subauriferum Bitter in Fedde, Repert. Spec. Nov. 10: 559 (1912).
S. subtusviolaceum Bitter in Fedde, Repert. Spec. Nov. 11: 207 (1912)
S. sucrense Hawkes, Potato Coll., Exped. 2: 126 (1944).
S. sucrense var. brevifolium Hawkes, Potato Coll. Exped. 2: 51 (1944).
S. symmetricum Rusby in Mem. Torr. Bot. Club, 6: 89 (1896).
S. symmetrifolium Rusby in Bull. N. Y. Bot. Gard. 4: 418 (1907).
S. tabacifolium Salzm. ex Dunal in DC. Prodr. 13(1): 261 (1852).
S. tarijense Hawkes, Potato Coll. Exped. 2: 114 (1944).
S. tenuifilamentum Juz. \& Buk. in Trudy Vsecouz. Sezda Genetike, 3: 603 (1929).
S. tenuispinum Rusby in Phytologia, 1: 75 (1934).
S. ternatum R. \& P. Fl. Peruv. 2: 38, t. 172 (1799).
S. Theresiae A. Zahlbr. in Beih. Bot. Centralbl. 13: 83 (1902).
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S. toralopanum var. subintegrifolium Cárd. \& Hawkes in Journ. Linn. Soc. 53: 99 (1946).
S. trifurcum Dunal in DC. Prodr. 13(1): 272 (1852).
S. tripartitum Dunal in DC. Prodr. 13(1): 72 (1852).
S. tuberosum L. Sp. Pl. 185 (1753).
S. tuberosum subsp. sparsipilum Bitter in Fedde, Repert. Spec. Nov. 12: 152 (1913).
S. tunariense O. Ktze. Rev. Gen. 3(2): 228 (1898).
S. turneroides Chod. in Bull. Herb. Boiss. (ser. 2) 2: 814) (1902).
S. ursinum Rusby in Mem. Torr. Bot. Club, 4(3): 227 (1895).
S. urticans Dunal in DC. Prodr. 13(1): 324 (1852).
S. utile Klotzsch in Allg. Gartenz. 17: 315 (1839).
S. validum Rusby in Mem. Torr. Bot. Club, 4(3): 230 (1895).
S. velutissimum Rusby in Mem. Torr. Bot. Club, 6: 89 (1896).
S. verbascifolium L. Sp. Pl. 184 (1753).
S. verbascifolium var. caducum O. Ktze. Rev. Gen. 3(2): 228 (1898).
S. verniciflorum Bitter in Fedde, Repert. Spec. Nov. 18: 66 (1922).
S. violaceimarmoratum Bitter in Fedde, Repert. Spec. Nov. 11: 389 (1912).
S. violaceimarmoratum var. papillosum Hawkes, Potato Coll. Exped. 2: 113 (1944).
S. violaceistriatum Bitter in Fedde, Repert. Spec. Nov. 9: 550 (1912).
S. violifolium Schott ex Spreng. Syst. Veg. 4: Cur. Post. 403, no. 5 (1827).
S. volubilis Rusby in Bull. Torr. Bot. Club, 26: 194 (1899).
S. vulpinum Rusby in Bull. N. Y. Bot. Gard. 4: 418 (1907).
S. Williamsii Rusby in Bull. N. Y. Bot. Gard. 8: 118 (1912).
S. Wrightii Benth. Fl. Hongk. 243 (1861).
S. yapacaniense O. Ktze. Rev. Gen. 3(2): 228 (1898).
S. yungasense Hawkes in Ann. \& Mag. Nat. Hist. 7 (81): 697 (1954).

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A. incisaefolia R. \& P. Syst. 154 (1798).

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A. chiquitensis Herzog in Meded. Rijks Herbar. 29: 33 (1916).

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B. breviflora Benth. in DC. Prodr. 10: 545 (1846).
B. ciliolata Wedd. Chlor. And. 2: 123 (1860).
B. crenoloba Wedd. Chlor. And. 2: 124 (1860).
B. diffusa Benth. in DC. Prodr. 10: 546 (1846).
B. Fiebrigii Diels in Engler, Bot. Jahrb. 37: 430 (1906).
B. filiformis Wedd. Chlor. And. 2: 126 (1860).
B. Guggenheimiana Rusby in Phytologia, 1: 76 (1934).
B. hispida Benth. in DC. Prodr. 10: 547 (1846).
B. inaequalis Benth. in DC. Prodr. 10: 547 (1846).
B. laxiflora Benth. in DC. Prodr. 10: 547 (1846).
B. Meyeniana Benth. in DC. Prodr. 10: 546 (1846).
B. mutica (HBK). Benth. in DC. Prodr. 10: 548 (1846).
B. patens Benth. in DC. Prodr. 10: 546 (1846).
B. peruviana Walp. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 400 (1843).
B. pumila Benth. in DC. Prodr. 10: 546 (1846).
B. sanguinea Diels in Engler, Bot. Jahrb. 37: 433 (1906).

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B. spinosum (Chod.) Moldenke in Bull. Torr. Bot. Club, 63: 347 (1936).

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B. elongata forma rigidior O. Ktze. Rev. Gen. 3(2): 230 (1898).

Calceolaria aquatica A. Br. \& Bouché, Ind. Sem. Hort. Berol. 2 (1852).
C. Atahualpae Kränzl. in Engler, Pflanzenr. IV, 257C: 107 (1907).
C. bartsiaefolia Wedd. Chlor. And. 2: 134 (1860).
C. boliviana (Britton) Pennell in Proc. Acad. Nat. Sci. Philad. 97: 170 (1945).
C. Buchtieniana Kränzl. in Fedde, Repert. Spec. Nov. 5: 369 (1908).
C. camptoclada Kränzl. in Engler, Pflanzenr. IV, 257C: 74 (1907).
C. canescens Willd. ex Roem. \& Schult. Syst. Mant. 1: 165 (1822).
C. chelidonioides HBK. Nov. Gen. \& Spec. 2: 378 (1818).
C. conocarpa Pennell in Proc. Acad. Nat. Sci. Philad. 97: 172 (1945).
C. cryptantha Rusby in Phytologia, 1: 77 (1934).
? C. cuneiformis R. \& P. Fl. Peruv. 1: 19, t. 27, fig. 6 (1798).
C. deflexa R. \& P. Fl. Peruv. 1: 18, t. 30b (1798).
C. dichotoma Lam. Encycl. 1: 555 (1783).
C. elatior Griseb. in Goett. Abh. 24: 237 (1879).
C. elliptica Wedd. Chlor. And. 2: 137 (1860).
C. endotrachys Kränzl. in Fedde, Repert. Spec. Nov. 27: 22 (1929) = C. Engleriana.
E. Engleriana Kränzl. in Fedde, Repert. Spec. Nov. 1: 106 (1905).
C. epilobioides Kränzl. in Ann. Naturh. Hofm. Wien, 22: 194 (1907) = C. Engleriana.
C. Ernestii Kränzl. in Fedde, Repert. Spec. Nov. 27: 24 (1929).
C. extensa Benth. in DC. Prodr. 10: 214 (1846).
C. Fiebrigiana Kränzl. in Fedde, Repert. Spec. Nov. 1: 84 (1905).
C. glacialis Wedd. Chlor. And. 2: 143, t. 59A (1860).
C. Guentheri Kränzl. in Fedde, Repert. Spec. Nov. 27: 17 (1929).
C. Halliana Kränzl. in Fedde, Repert. Spec. Nov. 1: 85 (1905).
C. Herzogiana Kränzl. in Engler, Bot. Jahrb. 50, Beibl. 111: 69 (1913).
C. hypericina Poepp. ex Benth. in DC. Prodr. 10: 222 (1846).
C. hypoleuca Kränzl. in Fedde, Repert. Spec. Nov. 27: 25 (1929).
C. incachacensis Kränzl. in Fedde, Repert. Spec. Nov. 27: 20 (1929) = C. Engleriana.
C. inflexa R. \& P. Fl. Peruv. 1: 16, t. 25 (1798).
C. larecajensis Kränzl. in Fedde, Repert. Spec. Nov. 16: 450 (1920).
C. lechioides Rusby in Phytologia, 1: 77 (1934) = C. parvifolia.
C. leiophylla Kränzl. in Engler, Bot. Jahrb. 50, Beibl. 111: 70 (1913).
C. lobata Cav. Ic. 5: 26, t. 443 (1799).
C. malacophylla Kränzl. in Engler, Bot. Jahrb. 50, Beibl. 111: 67 (1913) = C. larecajensis.
C. melissaefolia Benth. in DC. Prodr. 10: 214 (1846).
C. monantha Kränzl. in Fedde, Repert. Spec. Nov. 27: 20 (1929).
C. palustris Sodiro \& Kränzl. in Engler, Pflanzenr. IV, 257C: 27 (1907).
C. parvifolia Wedd. Chlor. And. 2: 134 (1860).
C. Pavonii Benth. in DC. Prodr. 10: 211 (1846).
C. Pearceana Kränzl. in Engler, Pflanzenr. IV, 257C: 107 (1907).
C. Pflanzii Perkins in Engler, Bot. Jahrb. 49: 218 (1913).
C. pinnata L. Mant. 171 (1771).
C. poikilantha Kränzl. in Fedde, Repert. Spec. Nov. 27: 12 (1929).
C. polyclada Kränzl. in Fedde, Repert. Spec. Nov. 1: 105 (1905).
C. ribesiaefolia Rusby in Phytologia, 1: 78 (1934).
C. rivularis Kränzl. in Fedde, Repert. Spec. Nov. 1: 83 (1905).
? C. saxatilis HBK. Nov. Gen. \& Spec. 2: 382 (1818).
C. scabra R. \& P. Fl. Peruv. 1: 19, t. 29, fig. a (1798).
C. soratensis Kränzl. in Engler, Pflanzenr. IV, 257C: 105 (1907).
C. teucrioides Griseb. in Goett. Abh. 19: 212 (1874).
C. trilobata Hemsl. in Biol. Centr. Am. Bot. 2: 439 (1882).
C. tripartita Mandoniana (Kränzl.) Pennell in Proc. Acad. Nat. Sci. Philad. 97: 175 (1945).
C. umbellata Wedd. Chlor. And. 2: 142 (1860).
C. vaccinioides Kränzl. in Fedde, Repert. Spec. Nov. 27: 17 (1929).
C. virgata R. \& P. Fl. Peruv. 1: 20, t. 31 (1798).

Capraria biflora L. Sp. Pl. 628 (1753).
Castilleja communis Benth. in DC. Prodr. 10: 529 (1846).
C. fissifolia L. f. Suppl. 293 (1781).
C. fissifolia subsp. fruticosa Wedd. Chlor. And. 2: 118 (1860).
C. fissifolia subsp. pumila (Benth.) Wedd. Chlor. And. 2: 119 (1860).

Escobedia brevipes Pennell in Proc. Acad. Nat. Sci. Philad. 83: 418 (1931).
E. obtusifolia Pennell in Proc. Acad. Nat. Sci. Philad. 83: 419 (1931).
E. scabrifolia R. \& P. Syst. 159 (1798).

Esterhazya andina Herzog in Meded. Rijks Herbar. 29: 36 (1916).
Fagelia Bangii Rusby in Mem. Torr. Bot. Club, 4 (3): 236 (1895) = Calceolaria bartsiifolia ?
F. boliviana Britton ex Rusby in Bull. Torr. Bot. Club, 27: 24 (1900) = Calceolaria sp.
Gerardia Bangii O. Ktze. Rev. Gen. 3(2): 233 (1898).
G. brevifolia Rusby in Bull. Torr. Bot. Club, 27: 25 (1900).
G. Fiebrigii Diels in Engler, Bot. Jahrb. 37: 428 (1906).
G. Fiebrigii var. brevidens Herzog in Meded. Rijks Herbar. 29: 38 (1916).
G. genistifolia Cham. \& Schlechtd. in Linnaea, 3: 15 (1828).
G. humilis Diels in Engler, Bot. Jahrb. 37: 429 (1906).
G. lanceolata (R. \& P.) Benth. in Hook. Compan. Bot. Mag. 1: 207 (1836).
G. lanceolata var. revoluta (R. \& P.) O. Ktze. Rev. Gen. 3(2): 233 (1898).
G. linarioides Cham. \& Schlechtd. in Linnaea, 3: 13 (1828).
G. macrodonta var. latifolia O. Ktze. Rev. Gen. 3(2): 234 (1898).
G. ovatifolia Rusby in Bull. N. Y. Bot. Gard. 4: 427 (1907).
G. reflexidens Herzog in Meded. Rijks Herbar. 29: 37 (1916).
G. rigida Gill. ex Benth. in Hook. Compan. Bot. Mag. 1: 206 (1836).
G. scarlatina Herzog in Meded. Rijks Herbar. 29: 38 (1916).
G. splendida (Mikan) O. Ktze. Rev. 3(2): 234 (1898).
G. tarijensis R. E. Fries in Ark. Bot. 6(11): 19 (1906).

Ilysanthes gratioloides (L.) Benth. in DC. Prodr. 10: 419 (1846)).
Lendneria humilis (Soland.) Minod in Bull. Soc. Bot. Genève, 10: 241 (1918) $=$ Capraria sp. ?
Leucocarpus alatus G. Don ex Sweet, Brit. Fl. Gard. 2: t. 124 (1831).
Limosella americana Glück in Notizbl. 12: 75 (1934).
L. aquatica L. Sp. Pl. 631 (1753).

Linaria canadensis var. texana (Scheele) Pennell in Proc. Acad. Nat. Sci Philad. 73: 502 (1922).
Mimulus glabratus HBK. Nov. Gen. \& Spec. 2: 370 (1818).
M. parviflorus var. nanus Wedd. Chlor. And. 2: 132 (1860).

Ourisia biflora Wedd. Chlor. And. 2: 117 (1860).
O. chamaedrifolia Benth. in DC. Prodr. 10: 493 (1846).
O. chamaedrifolia var. elegans Wedd. Chlor. And. 2: 114 (1860).
O. muscosa Benth. in DC. Prodr. 10: 493 (1846).
O. nana Benth. in DC. Prodr. 10: 493 (1846).
O. pulchella Wedd. Chlor. And. 2: 116 (1860).
O. rupicola Wedd. Chlor. And. 2: 115 (1860).

Saccanthus violaceus Herzog in Meded. Rijks Herbar. 29: 47 (1916) $=$ Basistemon spinosum.
Scoparia annua Cham. \& Schlechtd. in Linnaea, 6: 375 (1831).
S. dulcis L. Sp. Pl. 116 (1753).
S. nudicaulis subsp. praedensa R. E. Fries in Ark. Bot. 6(9) : 12 (1906).

Sibthorpia conspicua Diels in Engler, Bot. Jahrb. 37: 428 (1906).
S. nectarifera Wedd. Chlor. And. 2: 211, t. 60B (1859).
S. pichinchensis HBK. Nov. Gen. \& Spec. 2: 390, t. 176 (1818) .
S. retusa HBK. Nov. Gen. \& Spec. 2: 391, t. 177 (1818).

Stemodia lanceolata Benth. in DC. Prodr. 10: 384 (1846).
S. parviflora Ait. Hort. Kew. (ed. 2) 4: 52 (1812).
S. stricta Cham. \& Schlechtd. in Linnaea, 3: 10 (1828).

Vandellia diffusa L. Mant. 89 (1767).
Verbascum virgatum Stokes in With. Bot. Arr. Brit. Pls. (ed. 2) 1: 227 (1781).
Veronica peregrina L. Sp. Pl. 14 (1753).
Virgularia ochrophylla Rusby in Mem. N. Y. Bot. Gard. 7: 350 (1927) = Gerardia sp.

## BIGNONIACEAE

Adenocalymma bracteatum (Cham.) DC. Prodr. 9: 200 (1845).
A. densiflorum Rusby in Mem. N. Y. Bot. Gard. 7: 355 (1927).
A. impressum (Rusby) Sandw. in Rec. Trav. Bot. Néerl. 34: 212 (1937).
A. latifolium Rusby, Descr. S. Am. Pls. 121 (1920).

Amphilophium molle Cham. \& Schlechtd. in Linnaea, 5: 120 (1830).
A. paniculatum (L.) HBK. Nov. Gen. \& Spec. 3: 149 (1818).
A. Vauthieri DC. Prodr. 9: 193 (1845).

Anemopaegma huachianum Rusby in Mem. N. Y. Bot. Gard. 7: 352 (1927).
A. leptosiphon Rusby in Mem. N. Y. Bot. Gard. 7: 354 (1927).
A. symmetricum Rusby in Mem. N. Y. Bot. Gard. 7: 353 (1927).

Arrabidaea arthrerion (DC.) Bureau ex K. Schum. in Engl. \& Prantl, Nat. Pflanzenfam. 4(3b): 213 (1894).
A. Bangii Sprague in Bull. Herb. Boiss. (ser. 2) 6: 371 (1906).
A. candicans (Rich.) DC. Prodr. 9: 185 (1845).
A. Cardenasii Rusby in Mem. N. Y. Bot. Gard. 7: 351 (1927).
A. floribunda (HBK.) Loes. in Fedde, Repert. Spec. Nov. 16: 209 (1919).
A. florida DC. Prodr. 9: 184 (1845).
A. macrocarpa O. Ktze. Rev. Gen. 3(2): 242 (1898).
A. obovata DC. Prodr. 9: 185 (1845).
A. Orbignyana DC. Prodr. 9: 184 (1845).
A. pachycalyx Sprague in Bull. Herb. Boiss. (ser. 2) 6: 373 (1906).
A. pentstemonoides Kränzl. in Notizbl. 6: 370 (1915).
A. platyphylla (Cham.) Bur. \& K. Schum. in Mart. Fl. Bras. 8(2): 38 (1896).

Bignonia benensis Britton ex Rusby in Bull. Torr. Bot. Club, 27: 70 (1900).
B. boliviana Rusby in Bull. Torr. Bot. Club, 27: 70 (1900).
B. brachypoda DC. Prodr. 9: 145 (1845).
B. brevipes Rusby in Bull. Torr. Bot. Club, 27: 71 (1900).
B. capreolata L. Sp. Pl. 624 (1753).
B. glutinosa DC. Prodr. 9: 162 (1845).
B. nivea Kränzl. in Engler, Bot. Jahrb. 54, Beibl. 119: 26 (1916).
B. Pearcei Rusby in Mem. Torr. Bot. Club, 6: 100 (1896).
B. pyramidata Rich. in Act. Soc. Hist. Nat. Paris, 1: 110 (1792).
B. Rusbyi Britton ex Rusby in Bull. Torr. Bot. Club, 27: 71 (1900).
B. tecomaeflora Rusby in Mem. Torr. Bot. Club, 6: 101 (1896).
B. unguis-cati L. Sp. Pl. 623 (1753).
B. venusta Ker in Bot. Reg. 3: t. 249 (1818).

Callichlamys riparia Miq. in Linnaea, 18: 254 (1844).
Cremastus pulcher (Cham.) Bureau in Vidensk. Meddel. Kjoebenh. 1893: 101 (1894).
C. rufo-villosus Herzog in Meded. Rijks Herbar. 29: 40 (1916).

Crescentia Cujete L. Sp. Pl. 626 (1753).
Cuspidaria ovalis Rusby, Descr. S. Am. Pls. 120 (1920).
C. Schumanniana O. Ktze. Rev. Gen. 3(2): 243 (1898).

Cybistax antisiphilitica Mart. ex DC. Prodr. 9: 199 (1845).
Gelseminum amoenum var. tomentosum O. Ktze. Rev. Gen. 3(2): 245 (1898).
G. amoenum var. pubescens O. Ktze. Rev. Gen. 3(2): 245 (1898).
G. Avellanedae (Griseb.) O. Ktze. Rev. Gen. 3(2): 245 (1898).
G. Garrocha var. bicolor O. Ktze. Rev. Gen. 3(2): 245 (1898).
G. Garrocha var. rubrum O. Ktze. Rev. Gen. 3(2): 245 (1898).
G. molle (HBK.) O. Ktze. Rev. Gen. 3(2): 245 (1898).

Glaziova sp.
Godmania aesculifolia (HBK.) Standl. in Standl. \& Calderón, List. Prelim. Pl. El Salvador, 200 (1925).
Jacaranda acutifolia Humb. \& Bonpl. Pl. Aequin. 1: 59, t. 17 (1805).
J. atropurpurea Rusby in Mem. N. Y. Bot. Gard. 7: 357 (1927).
J. Copaia var. spectabilis (Mart. ex DC.) Bureau in Mart. Fl. Bras. 8(2): 387 (1897).
J. cuspidifolia Mart. in Flora, 24, II Beibl.: 51 (1841).
J. longiflora Britton ex Rusby in Bull. Torr. Bot. Club, 27: 73 (1900).

Lundia densiflora DC. Prodr. 9: 181 (1845).
L. phaseolifolia Rusby in Mem. Torr. Bot. Club, 6: 99 (1896).
L. Spruceana Bureau in Adansonia, 8: 279 (1867-68).
L. truncata Rusby in Mem. N. Y. Bot. Gard. 7: 356 (1927).

Macfadyena Bangii Rusby in Bull. Torr. Bot. Club, 27: 72 (1900).
M. uncata (Andr.) Sprague \& Sandw. in Meded. Bot. Mus. Utrecht, 40: 215 (1937).
M. undulata K. Schum. in Engl. \& Prantl, Nat. Pflanzenfam. 4 (3b) : 227 (1894), nomen nudum.
M. violacea Rusby in Mem. N. Y. Bot. Gard. 7: 356 (1927).

Martinella obovata (Spreng.) Bur. \& K. Schum. in Mart. Fl. Bras. 8(2): 161 (1896).

Melloa populifolia (DC.) Britton in Ann. N. Y. Acad. Sci. 7: 188 (1893).
Mussatia hyacinthina (Standl.) Sandw. in Rec. Trav. Bot. Néerl. 34: 218 (1937).

Paragonia pyramidata (Rich.) Bureau in Vidensk. Medd. Naturh. Foren. 1893: 104 (1894).
Petastoma laurifolium Kränzl. in Fedde, Repert. Spec. Nov. 17: 57 (1921).
P. multiglandulosum (Benth.) Kränzl. in Fedde, Repert. Spec. Nov. 17: 58 (1921).
P. patelliferum (Schlechtd.) Miers in Proc. Roy. Hort. Soc. 3: 195 (1863).
P. samydoides Miers in Proc. Roy. Hort. Soc. 3: 195 (1863).
P. truncatum (Sprague) Hassl. in Fedde, Repert. Spec. Nov. 9: 53 (1910).
P. Whitei (Rusby) Sandw. in Kew Bull. 1953: 462.

Pithecoctenium cynanchoides DC. Prodr. 9: 195 (1845).
P. echinatum K. Schum. in Mart. Fl. Bras. 8(2): 168, t. 86 (1896).
P. glaucum Rusby in Mem. N. Y. Bot. Gard. 7: 354 (1927).
P. Lundii P. DC. Prodr. 9: 196 (1845).

Pleonotoma jasminifolium (HBK.) Miers in Proc. Roy. Hort. Soc. 3: 184 (1863).

Pyrostegia venusta Miers in Proc. Roy. Hort. Soc. 3: 188 (1863).
Saldanhaea confertiflora Bureau in Adansonia, 8: 356 (1867-68).
? S. mollis Kränzl. in Engler, Bot. Jahrb. 54, Beibl. 119: 26 (1916).

## Scobinaria sp.

Stenolobium Garrocha (Hieron.) R. E. Fries in Ark. Bot. 6(11): 16 (1904).
Tabebuia nodosa Griseb. in Goett. Abh. 24: 258 (1879).
T. Caraiba (Mart.) Bureau in Vidensk. Meddel. 1893: 113 (1894).
T. roseo-alba (Ridley) Sandw. in Kew Bull. 1954: 597 (1955).
T. serratifolia (Vahl) Nicholson, Dict. Gard. 4: 1 (1888).
T. suberosa Rusby in Mem. N. Y. Bot. Gard. 7: 358 (1927).

Tecoma capensis Lindl. in Bot. Reg. 13: t. 1117 (1828).
T. cochabambensis (Herzog) Sandw. in Kew Bull. 1953: 455.
T. Gaudichaudii DC. Prodr. 9: 223 (1845).
T. mollis HBK. Nov. Gen. \& Spec. 3: 144 (1819).
T. sambucifolia HBK. Nov. Gen. \& Spec. 3: 143 (1819).

Tynnanthus micranthus Mello in Arq. Mus. Paranaënse, 9: 63 (1952).
T. myrianthus (Poepp.) Bur. \& K. Schum. in Mart. Fl. Bras. 8(2) : 197 (1896).
T. polyanthus (Bur.) Sandw. in Kew Bull. 1953: 465.

Zeyhera Kuntzei K. Schum. in O. Ktze. Rev. Gen. 3(2): 246 (1898).

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Craniolaria integrifolia Cham. in Linnaea, 7: 725 (1832).

## GESNERIACEAE

Achimenes flaccida Rusby in Mem. Torr. Bot. Club, 6: 95 (1896).
A. gracilis Britton ex Rusby in Bull. Torr. Bot. Club, 27: 27 (1900).
A. heppielloides Fritsch in Bull. Torr. Bot. Club, 23: 151 (1896).
A. Rusbyi Britton ex Rusby in Mem. Torr. Bot. Club, 6: 95 (1896).

Alloplectus dichrous DC. Prodr. 7: 546 (1839).
A. grandifolius Britton ex Rusby in Bull. Torr. Bot. Club, 27: 30 (1900).
A. Patrisii DC. Prodr. 7: 545 (1839).
A. solitarius Rusby in Mem. Torr. Bot. Club, 4 (3): 238 (1895).

Besleria aurantiaca Fritsch in Meded. Rijks Herbar. 29: 51 (1916) = B. longipedunculata.
B. boliviana Morton in Contrib. U. S. Nat. Herb. 26: 432 (1939).
B. elegans HBK. Nov. Gen. \& Spec. 2: 397 (1817).
B. foliacea Rusby in Mem. Torr. Bot. Club, 4(3): 240 (1895).
B. longipedunculata Britton ex Rusby in Bull. Torr. Bot. Club, 27: 69 (1900).
B. montana Britton ex Rusby in Mem. Torr. Bot. Club, 4 (3): 240 (1895).
B. ovalifolia Rusby in Mem. Torr. Bot. Club, 4 (3): 240 (1895).
B. pauciflora Rusby in Bull. Torr. Bot. Club, 27: 31 (1900).
B. Rhytidophyllum Hanst. in Linnaea, 34: 332 (1865-66)).
B. rotundifolia Rusby in Mem. Torr. Bot. Club, 6: 98 (1896).
B. Sprucei Britton ex Rusby in Bull. Torr. Bot. Club, 27: 31 (1900).
B. Uleana Fritsch in Engler, Bot. Jahrb. 37: 483 (1906) = B. Sprucei.

Columnea ascendens Rusby in Mem. Torr. Bot. Club, 4 (3): 239 (1895).
C. boliviana Britton ex Rusby in Mem. Torr. Bot. Club, 4 (3): 238 (1895).
C. grandifolia Rusby, Descr. S. Am. Pls. 126 (1920).
C. inaequilatera Poepp. \& Endl. Nov. Gen. 3: 1 (1845).
C. latisepala Rusby in Mem. Torr. Bot. Club, 4 (3): 239 (1895).
C. oblongifolia Rusby in Mem. Torr. Bot. Club, 6: 98 (1896).
C. pallida Rusby, Descr. S. Am. Pls. 125 (1920).
C. stricta Rusby, Descr. S. Am. Pls. 125 (1920).
C. Trollii Mansf. in Fedde, Repert. Spec. Nov. 36: 122 (1934).

Corytholoma paludosum Rusby in Mem. N. Y. Bot. Gard. 7: 360 (1927).
Diastema galeopsis Fritsch in Engler, Bot. Jahrb. 50: 405 (1913).
D. latiflorum Rusby in Mem. Torr. Bot. Club, 6: 96 (1896).
D. parviflorum (Rusby) Fritsch in Engler, Bot. Jahrb. 50: 406 (1913).
D. purpurascens Rusby in Bull. Torr. Bot. Club, 27: 28 (1900).
D. Williamsii Rusby, Descr. S. Am. Pls. 124 (1920).

Diplolegnon Riceanum Rusby in Bull. Torr. Bot. Club, 27: 30 (1900).
Drymonia Campbellii Rusby in Mem. N. Y. Bot. Gard. 7: 359 (1927).
D. serrata (Jacq.) Mart. Nov. Gen. \& Spec. 3: 59 (1829), combination implied but not actually made.
Episcia Buchtienii Mansf. in Fedde, Repert. Spec. Nov. 38: 25 (1935).
Fiebrigia digitaliflora Fritsch in Engler, Bot. Jahrb. 50: 397 (1913).
Fritschiantha nematanthoides O. Ktze. Rev. Gen. 3(2): 241 (1898).
Gesneria stachydifolia Benth. Pl. Hartw. 230 (1846).
Gloxinia perennis (L.) Fritsch in Engl. \& Prantl, Nat. Pflanzenfam. 4(3b): 174 (1894).
G. reflexa Rusby in Mem. Torr. Bot. Club, 6: 94 (1896).

Isoloma flexuosa Rusby in Bull. Torr. Bot. Club, 27: 28 (1900).
I. urticifolia Rusby in Bull. Torr. Bot. Club, 27: 28 (1900).

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K. major Fritsch in Engler, Bot. Jahrb. 50: 398 (1913).

Kohleria patentipilosa (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1): 386 (1900).
K. Sprucei (Britton) Fritsch in Engler, Bot. Jahrb. 50: 429 (1913).

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Monopyle divaricata Rusby in Bull. N. Y. Bot. Gard. 8: 119 (1912).
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N. rigidus Rusby in Mem. Torr. Bot. Club, 6: 99 (1896).

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R. sulcata (Rusby) Fritsch in Engler, Bot. Jahrb. 50: 436 (1913).

Seemannia albescens (Rusby) Fritsch in Engler, Bot. Jahrb. 50: 403 (1913).
S. cuneata Rusby in Mem. Torr. Bot. Club, 6: 96 (1896).
S. dioica Rusby in Mem. N. Y. Bot. Gard. 7: 360 (1927).
S. latifolia Fritsch in Meded. Rijks Herbar. 29: 52 (1916).
S. major Baill. in Bull. Mens. Soc. Linn. Paris, 1: 710 (1887).
S. purpurascens Rusby in Mem. Torr. Bot. Club, 4 (3): 237 (1895).
S. silvatica (HBK.) Hanst. in Linnaea, 29: 540 (1857-58).
S. ternifolia Regel in Gartenfl. 4: 183, t. 126 (1855).
S. uniflora Baill. in Bull. Mens. Soc. Linn. Paris, 1: 710 (1887).

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Columellia serrata Rusby in Mem. Torr. Bot. Club, 6: 93 (1896).
C. subsessilis Schltr. in Notizbl. 7: 12 [356]. (1920).

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Utricularia alpina Jacq. Enum. Pl. Carib. 11 (1760).
U. cornuta Michx. Fl. Bor.-Am. 1: 12 (1803).
U. globulariaefolia Mart. ex Benj. in Mart. Fl. Bras. 10: 241 (1847).
U. Herzogii Lützelberg in Fedde, Repert. Spec. Nov. 7: 356 (1909).
U. obtusa Sw. Prodr. 14 (1788).
U. pusilla Vahl, Enum. 1: 202 (1804).
U. subulata L. Sp. Pl. 18 (1753).
U. unifolia R. \& P. Fl. Peruv. 1: 20, t. 31 (1798).
U. velascoënsis O. Ktze. Rev. Gen. 3(2): 240 (1898).

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A. albadenia Rusby in Mem. N. Y. Bot. Gard. 7: 364 (1927).
A. castanaefolia Britton ex Rusby in Bull. Torr. Bot. Club, 27: 76 (1900).
A. cryptantha Rusby in Mem. N. Y. Bot. Gard. 7: 364 (1927).
A. Hieronymi Griseb. in Goett. Abh. 24: 260 (1879).
A. inaequalis Lindau in Bull. Herb. Boiss. (ser. 1) 3: 368 (1895).
A. kolobantha Lindau in Ann. Conserv. \& Jard. Bot. Genève, 2: 39 (1898).
A. longibracteolata Lindau in Bull. Herb. Boiss. (ser. 1) 3: 367 (1895).
A. macrosiphon Lindau in Bull. Herb. Boiss. (ser. 1) 3: 367 (1895).
A. Rusbyi Britton ex Rusby in Bull. Torr. Bot. Club, 27: 77 (1900).
A. simplex Lindau in Bull. Herb. Boiss. (ser. 1) 3: 366 (1895).
A. tetragona (Vahl) Nees in DC. Prodr. 11: 295 (1847).

Beloperone Amherstiae Nees ex Wall. Pl. As. Rar. 3: 102 (1832).
B. Baenitzii H. Winkl. in Fedde, Repert. Spec. Nov. 7: 113 (1909).
B. Bangii Rusby in Mem. Torr. Bot. Club, 6: 104 (1896).
B. cochabambensis Rusby in Mem. Torr. Bot. Club, 6: 103 (1896).
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B. consanguinea var. pubescens Lindau in Bull. Herb. Boiss. (ser. 1) 5: 676 (1897).
B. denudata Nees in DC. Prodr. 11: 423 (1847).
B. Mandonii Lindau in Bull. Herb. Boiss. (ser. 1) 5: 675 (1897).
B. Matthewsii Lindau in Bull. Herb. Boiss. 6, App. 1: 30 (1898).
B. nuda Rusby in Mem. Torr. Bot. Club, 6: 103 (1896).
B. pseudociliata Mildbr. in Notizbl. 9: 1159 (1927).
B. ramulosa Morong in Ann. N. Y. Acad. Sci. 7: 194 (1893).
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B. velascana Lindau in Bull. Herb. Boiss. (ser. 1) 3: 489 (1895).
B. viridissima Rusby in Mem. N. Y. Bot. Gard. 7: 367 (1927).

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C. macrosiphon Lindau in Bull. Herb. Boiss. (ser. 1) 3: 490 (1895).
C. Rusbyi Lindau in Bull. Herb. Boiss. (ser. 1) 3: 491 (1895).

Chaetothylax boliviensis Lindau in Eull. Herb. Boiss. (ser. 1) 3: 492 (1895).
C. tocantinus Nees in Mart. Fl. Bras. 9: 153 (1847).

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D. multicaule Rusby in Mem. Torr. Bot. Club, 6: 105 (1896).
D. resupinatum (Juss.) O. Ktze. Rev. Gen. 3(2): 248 (1898).
D. scutellatum var. coeruleum O. Ktze. Rev. Gen. 3(2): 248 (1898).
D. scutellatum var. flavum O. Ktze. Rev. Gen. 3(2): 248 (1898).

Dicliptera cochabambensis Lindau in Bull. Herb. Boiss. (ser. 1) 3: 479 (1895).
D. Niederleiniana Lindau in Engler, Bot. Jahrb. 19, Beibl. 48: 15 (1894).

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E. minimiflorum O. Ktze. Rev. Gen. 3(2): 248 (1898).
E. oreadum (S. Moore) O. Ktze. Rev. Gen. 3(2): 248 (1898).

Elytraria imbricata (Vahl) Pers. Synops. Pl. 1: 23 (1805).
Eranthemum cordatum Nees ex Benth. Bot. Voy. Sulphur, 147 (1846).
Geissomeria cincinnata Nees in Mart. Fl. Bras. 9: 81 (1847).
Habracanthus pyramidalis Lindau in Bull. Herb. Boiss. (ser. 1) 3: 482 (1895).
H. sanguinalis Nees in DC. Prodr. 11: 312 (1847).

Hansteinia crenulata Britton ex Rusby in Mem. Torr. Bot. Club, 4(3): 242 (1895).

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J. tenuistachys Rusby in Mem. Torr. Bot. Club, 6: 105 (1896).

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J. comata (L.) Sw. Obs. 14 (1791).
J. Kuntzei Lindau in Bull. Herb. Boiss. (ser. 1) 3: 483 (1895).
J. laeta (Nees) Lindau in Engl. \& Prantl, Nat. Pflanzenfam. 4 (3b): 350 (1895).
J. longiacuminata Rusby in Bull. Torr. Bot. Club, 27: 78 (1900).
J. Lorentziana Lindau in Engler, Bot. Jahrb. 19, Beibl. 48: 20 (1894).
J. obtusifolia (Nees) Lindau in Engler, Bot. Jahrb. 19, Beibl. 48: 20 (1894).
J. parviflora (Nees) Lindau in Engl. \& Prantl, Nat. Pflanzenfam. 4(3b): 350 (1895).
J. reisensis Rusby in Bull. Torr. Bot. Club, 27: 79 (1900).
J. riojana Lindau in Engler, Bot. Jahrb. 19, Beibl. 48: 19 (1894).
J. robusta Rusby in Bull. N. Y. Bot. Gard. 4: 430 (1907).
J. Rusbyana Lindau in Mem. Torr. Bot. Club, 4(3): 243 (1895).
J. subintegrifolia Rusby in Bull. N. Y. Bot. Gard. 4: 430 (1907).
J. velascana Lindau in Bull. Herb. Boiss. (ser. 1) 3: 484 (1895).

Lepidagathis justicioides Britton ex Rusby in Bull. Torr. Bot. Club, 27: 76 (1900).

Lophostachys conferta Rusby in Mem. Torr. Bot. Club, 6: 103 (1896).
? Mendoncia glabra Nees in DC. Prodr. 11: 52 (1847).
M. hirsuta Poepp. \& Endl. Nov. Gen. 3: 10 (1845).
M. Lindavii Rusby in Mem. Torr. Bot. Club, 4(3): 241 (1895).
M. puberula var. micropus (Mart.) Nees in DC. Prodr. 11: 53 (1847).
M. robusta Rusby in Mem. N. Y. Bot. Gard. 7: 361 (1927).
M. robusta var. alba Rusby in Mem. N. Y. Bot. Gard. 7: 362 (1927).
M. Schomburgkiana Nees in DC. Prodr. 11: 50 (1847).
M. Velloziana Nees in DC. Prodr. 11: 52 (1847).

Pachystachys Riedeliana Nees in Mart. Fl. Bras. 9: 99 (1847).
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Ruellia amoena Nees ex Rusby in Mem. Torr. Bot. Club, 6: 102 (1896).
R. bahiensis (Nees) Morong in Ann. N. Y. Acad. Sci. 7: 192 (1893).
R. Bangii Rusby in Mem. Torr. Bot. Club, 6: 102 (1896).
R. chiquitensis Baill. in Bull. Mens. Soc. Linn. Paris, 2: 853 (1890).
R. elliptica Rusby in Bull. Torr. Bot. Club, 27: 74 (1900).
R. euantha Lindau in Bull. Herb. Boiss. (ser. 1) 3: 366 (1895).
R. filicalyx Lindau in Bull. Herb. Boiss. (Ser. 1) 3: 362 (1895).
R. geminiflora HBK. Nov. Gen. \& Spec. 2: 240 (1817).
R. gracilis Rusby in Mem. Torr. Bot. Club, 6: 102 (1896).
R. Herzogii Lindau in Fedde, Repert. Spec. Nov. 7: 67 (1909).
R. Humboldtiana (Nees) Lindau in Bull. Herb. Boiss. (ser. 1) 3: 366 (1895).
R. hypericifolia Rusby in Mem. N. Y. Bot. Gard. 7: 363 (1927).
R. Kuntzei Lindau in Bull. Herb. Boiss. (ser. 1) 3: 365 (1895).
R. Lechleri Britton ex Rusby in Bull. Torr. Bot. Club, 27: 75 (1900).
R. Lechleri var. grandifolia Britton ex Rusby in Bull. Torr. Bot. Club, 27: 75 (1900).
R. longipedunculata Lindau in Bull. Herb. Boiss. (ser.1) 3: 365 (1895).
R. Lorentziana Griseb. in Goett. Abh. 24: 259 (1879).
R. Morongii Britton in Ann. N. Y. Acad. Sci. 7: 192 (1893).
R. multisetosa Rusby in Mem. N. Y. Bot. Gard. 7: 362 (1927).
R. paniculata L. Sp. Pl. 635 (1753).
R. Pearcei Rusby in Bull. N. Y. Bot. Gard. 4: 429 (1907).
R. pedunculosa (Nees) Lindau in Engl. \& Prantl, Nat. Pflanzenfam. 4(3b): 311 (1895).
R. proxima Lindau in Bull. Herb. Boiss. (ser. 1) 3: 365 (1895).
R. Puri Mart. ex Nees in Mart. Fl. Bras. 9: 35 (1847), in synon.
R. Ruiziana (Nees) Lindau in Engl. \& Prantl, Nat. Pflanzenfam. 4(3b): 311 (1895).
R. sanguinea Griseb. in Goett. Abh. 24: 260 (1879).
R. serratitheca Rusby in Mem. N. Y. Bot. Gard. 7: 362 (1927).
R. tuberosa L. Sp. Pl. 635 (1753).
R. velascana Lindau in Bull. Herb. Boiss. (ser. 1) 3: 363 (1895).
R. Willdenowiana (Nees) Lindau ex Rusby in Bull. N. Y. Bot. Gard. 4: 429 (1907).

Sanchezia peruviana (DC.) Rusby in Mem. Torr. Bot. Club, 6: 103 (1896).
Schaueria azaleaeflora Rusby in Mem. N. Y. Bot. Gard. 7: 365 (1927).
Staurogyne diantheroides Lindau in Bull. Herb. Boiss. (ser. 1) 5: 645 (1897).
Stenandrium diphyllum Nees in Mart. Fl. Bras. 9: 75 (1847).
S. dulce (Cav.) Nees in DC. Prodr. 11: 282 (1847).
S. mandioccanum Nees in Mart. Fl. Bras. 9: 76 (1847).
S. trinerve Nees in Mart. Fl. Bras. 9: 75 (1847).

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P. Durvillei subsp. mollior (Pilg.) Pilger in Engler, Pflanzenr. IV, 269: 234 (1937).
P. Durvillei subsp. Pflanzii (Pilg.) Yilger in Engler, Pflanzenr. IV, 269: 232 (1937).
P. Durvillei subsp. Pflanzii var. chamaeclina (Pilg.) Pilger in Engler, Pflanzenr. IV, 269: 232 (1937).
P. Durvillei subsp. Pflanzii var. grandidens (Pilg.) Pilger in Engler, Pflanzenr. IV, 269: 233 (1937).
P. Durvillei subsp. Pflanzii var. Hauthalii (Pilg.) Pilger in Engler, Pflanzenr. IV, 269: 233 (1937).
P. Durvillei subsp. Pflanzii var. latifolia (Pilg.) Pilger in Engler, Pflanzenr. IV, 269: 233 (1937).
P. Fiebrigii Pilger in Fedde, Repert. Spec. Nov. 15: 420 (1919).
P. Hillii Pilger in Notizbl. 10: 833 (1929).
P. hirtella HBK. Nov. Gen. \& Spec. 2: 229, t. 127 (1818).
P. hirtella forma minor Pilger in Engler, Bot. Jahrb. 50: 276 (1913).
P. humilior Pilger in Field Mus. Publ. Bot. 13(6): 271 (1937).
P. lanceolata L. Sp. Pl. 113 (1753).
P. litorea Phil. Fl. Atac. 46 (1860).
P. major L. Sp. Pl. 112 (1753).
P. major forma sinuata (Lam.) Pilger in Fedde, Repert. Spec. Nov. 18: 271 (1922).
P. monticola Decne. in DC. Prodr. 13(1): 711 (1852).
P. monticola subsp. angusta Pilger in Engler, Bot. Jahrb. 62: 80 (1928).
P. monticola subsp. crispula Pilger in Engler, Bot. Jahrb. 62: 81 (1928).
P. monticola subsp. eumonticola var. humillima Pilger in Engler, Bot. Jahrb. 62: 80 (1928).
P. monticola subsp. sericans Pilger in Engler, Bot. Jahrb. 62: 80 (1928).
P. Orbignyana Steinh. ex Decne. in DC. Prodr. 13 (1): 704 (1852).
P. paralias subsp. affinis (Decne.) Pilger in Notizbl. 11: 328 (1932).
P. paralias subsp. Grisebachii (Hieron.) Pilger in Notizbl. 11: 328 (1932).
P. Psyllium L. Sp. Pl. 115 (1753).
P. rigida HBK. Nov. Gen. \& Spec. 2: 227, t. 126, fig. 2 (1818).
P. sericea R. \& P. Fl. Peruv. 1: 51, t. 79, fig. b (1798).
P. tarijensis Pilger in Fedde, Repert. Spec. Nov. 15: 420 (1919).
P. truncata Barn. Monog. Plantag. 14 (1845).
P. tubulosa Decne. in DC. Prodr. 13(1): 728 (1852).
P. tubulosa forma maxima Pilger in Engler, Bot. Jahrb. 62: 92 (1928).
P. virginica L. Sp. Pl. 113 (1753).
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A. Tutumilla Rusby in Mem. N. Y. Bot. Gard. 7: 375 (1927).

Amaioua corymbosa HBK. Nov. Gen. \& Spec. 3: 419, t. 294 (1820).
Anisomeris albicaulis (Rusby) Standl. in Field Mus. Publ. Bot. 4: 293 (1929).
A. apodantha Standl. in Field Mus. Publ. Bot. 4: 293 (1929).
A. boliviana (Standl.) Rusby in Bull. Torr. Bot. Club, 52: 142 (1925).
A. rauwolfioides Standl. in Field Mus. Publ. Bot. 4: 292 (1929).

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A. nodosum Rusby in Phytologia, 1: 78 (1934).
A. setosum (R. \& P.) Schlechtd. in Linnaea, 28: 492 (1856).

Basanacantha erythropoda Rusby in Mem. N. Y. Bot. Gard. 7: 373 (1927) = Randia spinosa.
B. macrocarpa Rusby in Mem. N. Y. Bot. Gard. 7: 374 (1927) = Randia formosa.
B. mollis Rusby in Mem. N. Y. Bot. Gard. 7: 375 (1927) = Randia formosa.
B. mucromata Rusby in Mem. N. Y. Bot. Gard. 7: 373 (1927) $=$ Randia spinosa.

Bathysa obovata Schum. ex Standl. in Field Mus. Publ. Bot. 7: 280 (1931).
Bertiera guianensis Aubl. Pl. Guian. Fr. 1: 180, t. 69 (1775).
Borreria Brownii (Rusby) Standl. in Field Mus. Publ. Bot. 7: 333 (1931).
B. capitata (R. \& P.) DC. Prodr. 4: 545 (1830).
B. corymbosa (R. \& P.) DC. Prodr. 4: 550 (1830).
B. densiflora var. perennis Standl. in Field Mus. Publ. Bot. 7: 334 (1931).
B. exigua S. Moore in Meded. Rijks Herbar. 46: 28 (1922).
B. Herzogii S. Moore in Meded. Rijks Herbar. 46: 26 (1922).
B. laevis (Lam.) Griseb. in Goett. Abh. 7: 231 (1857).
B. latifolia (Aubl.) K. Schum. in Mart. Fl. Bras. 6(6): 61 (1888).
B. nectarifera Rusby in Mem. N. Y. Bot. Gard. 7: 381 (1927) = B. capitata.
B. ocimoides (Burm.) DC. Prodr. 4: 544 (1830).
B. staurochlamys R. E. Fries in Ark. Bot. $6(11): 9$, t. 2 (1907) = B. Brownii.
B. suaveolens Meyer, Prim. Fl. Esseq. 81, t. 1 (1818).

Calycophyllum multiflorum Griseb. in Goett. Abh. 24: 155 (1879).
C. Spruceanum (Benth.) Hook. f. ex K. Schum. in Mart. Fl. Bras. 6(6): 191, t. 106 (1889).

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C. tomentosa (Aubl.) Vahl, Eclog. Amer. 1: 19 (1796).
C. umbellata (R. \& P.) Standl. in Field Mus. Publ. Bot. 7: 301 (1931).

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C. unguis-cati Standl. in Field Mus. Publ. Bot. 8: 172 (1930).

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Cinchona asperifolia Wedd. in Ann. Sci. Nat. (ser. 3) 10: 7 (1848).
C. calisaya Wedd. in Ann. Sci. Nat. (ser. 3) 10: 6 (1848).
C. Humboldtiana Lamb. Ill. Cinch. 7 (1821).
C. Josephiana Wedd. in Ann. Sci. Nat. (ser. 5) 12: 58 (1869).
C. micrantha R. \& P. Fl. Peruv. 2: 52, t. 194 (1799).
C. officinalis L. Sp. Pl. 172 (1753).
C. ovata R. \& P. Fl. Peruv. 2: 52, t. 195 (1799).
C. pubescens Vahl in Skrivt. Naturh. Selsk. 1: 19 (1790).

Coccocypselum Brittonii Rusby in Bull. N. Y. Bot. Gard. 4: 368 (1907) $=$ C. Condalia.
C. Condalia Pers. Synops. P1. 1: 132 (1805).
C. cordatum Krause in Anex. Mem. Inst. Butantan, 1(3): 13, t. 1 (1922).
C. glabrum Britton in Bull. Torr. Bot. Club, 18: 108 (1891) = C. Condalia.
C. hirsutum Bartl. ex DC. Prodr. 4: 396 (1830).
C. lanceolatum (R. \& P.) Pers. Synops. Pl. 1: 132 (1805).

Coffea arabica L. Sp. Pl. 172 (1753).
Condaminea angustifolia Rusby in Mem. Torr. Bot. Club, 6: 45 (1896) $=$ C. corymbosa var. pubescens.
C. corymbosa (R. \& P.) DC. Prodr. 4: 402 (1830).
C. corymbosa var. pubescens Spruce ex K. Schum. in Mart. Fl. Bras. 6(6) : 258 (1889).

Corynula pilosa (Benth.) Hook. f. in Hook. Ic. Pl. 12: 22, t. 1123 (1872).
Cosmibuena grandiflora (R. \& P.) Rusby in Bull. N. Y. Bot. Gard. 4: 368 (1907).

Coussarea auriculata Standl. in Field Mus. Publ. Bot. 4: 330 (1929).
C. benensis Britton ex Standl. in Field Mus. Publ. Bot. 7: 296 (1931) $=$ C. brevicaulis.
C. brevicaulis Krause in Verh. Bot. Ver. Brandenb. 50: 117 (1908).
C. hydrangeaefolia (Benth.) Benth. \& Hook. f. ex Muell. Arg. in Mart. Fl. Bras. 6(5): 94 (1881).
C. rudgeoides Rusby in Mem. Torr. Bot. Club, 6: 48 (1896).
C. urophylla Standl. in Field Mus. Publ. Bot. 7: 298 (1931).

Diodia hyssopifolia (Willd.) Cham. \& Schlechtd. in Linnaea, 3: 350 (1828), combination implied but not actually made.
D. Kuntzei K. Schum. in Mart. Fl. Bras. 6(6): 15 (1888).
D. rogaguana Rusby in Mem. N. Y. Bot. Gard. 7: 380 (1927).

Duroia Steinbachii Standl. in Field Mus. Publ. Bot. 7: 290 (1931).
Elaeagia glomiflora Standl. in Field Mus. Publ. Bot. 7: 281 (1931).
E. grandis (Rusby) Rusby in Mem. Torr. Bot. Club, 4(3): 208 (1895).
E. Mariae Wedd. Hist. Nat. Quinq. 94 (1849).
E. mollis Rusby, Descr. S. Am. Pls. 130 (1920).
E. obovata Rusby, Descr. S. Am. Pls. 130 (1920).
E. utilis (Goud.) Wedd. Hist. Nat. Quinq. 94 (1849).

Emmeorrhiza umbellata (Spreng.) K. Schum. in Mart. Fl. Bras. 6(6): 408 (1889).

Evea radiata Rusby in Phytologia, 1: 79 (1934).
Faramea anisocalyx Poepp. \& Endl. Nov. Gen. 3: 28 (1845).
F. Bangii Rusby in Mem. Torr. Bot. Club, 3(3): 45 (1893).
F. benensis Rusby in Mem. N. Y. Bot. Gard. 7: 379 (1927) = F. maynensis.
F. candelabrum Standl. in Field Mus. Publ. Bot. 7: 299 (1931).
F. glandulosa Poepp. \& Endl. Nov. Gen. 3: 29 (1845).
F. maynensis Spruce ex Rusby in Bull. N. Y. Bot. Gard. 4: 370 (1907).
F. tenuifolia Rusby in Mem. N. Y. Bot. Gard. 7: 380 (1927).

Ferdinandusa Paxii H. Winkl. in Fedde, Repert. Spec. Nov. 7: 249 (1909).
Galium Aparine L. Sp. Pl. 108 (1753).
G. canescens HBK. Nov. Gen. \& Spec. 3: 336 (1819).
G. charoides Rusby in Phytologia, 1: 80 (1934).
G. cochabambense Rusby in Mem. Torr. Bot. Club, 6: 52 (1896) $=$ G. plumosum.
G. larecajense Wernh. in Journ. Bot. 50: 244 (1912).
G. Mandonii Britton in Bull. Torr. Bot. Club, 18: 263 (1891).
G. obovatum HBK. Nov. Gen. \& Spec. 2: 336, t. 227 (1819).
G. plumosum Rusby in Mem. Torr. Bot. Club, 3(3): 49 (1893).

Genipa americana L. Syst. (ed. 10) 931 (1759).
G. Caruto HBK. Nov. Gen. \& Spec. 3: 407 (1820)

Geophila herbacea (L.) Morong in Ann. N. Y. Acad. Sci. 7: 129 (1893).
Gomozia granadensis L. f. Suppl. 129 (1781).
Gonzalagunia Whitei (Rusby) Standl. in Field Mus. Publ. Bot. 4: 280 (1929).
Guettarda boliviana Standl. in Field Mus. Publ. Bot. 4: 289 (1929).
G. Spruceana Muell. Arg. in Flora, 58: 449 (1875).
G. Tournefortiopsis Standl. in Field Mus. Publ. Bot. 7: 293 (1931).

Hamelia lutea Rohr ex Smith in Rees, Cycl. 17: no. 4 (1819).
H. patens Jacq. Enum. Pl. Carib. 16 (1760).
H. pedicellata Wernh. in Journ. Bot. 49: 212 (1911).

Hemidiodia ocimifolia (Willd.) K. Schum. in Mart. Fl. Bras. 6(6): 29 (1888).
Heterophyllaea Fiebrigii (Krause) Standl. in Field Mus. Publ. Bot. 11: 214 (1936).
H. lycioides (Rusby) Sandw. in Kew Bull. 1949: 256.
H. pustulata Hook. f. in Hook. Ic. P1. 12: 31, t. 1134 (1873).

Hillia boliviana Britton in Mem. Torr. Bot. Club, 3(3): 43 (1893).
H. parasitica Jacq. Enum. Pl. Carib. 18 (1760), nomen nudum.
H. Ulei Krause in Verh. Bot. Ver. Brandenb. 50: 97 (1908).

Hoffmannia brachycarpa Britton in Bull. Torr. Bot. Club, 18: 108 (1891) = H. latifolia.
H. latifolia (Bartl.) O. Ktze. Rev. Gen. 1: 284 (1891).
H. pallida Rusby in Mem. Torr. Bot. Club, 3(3): 44 (1893).
H. Pearcei Rusby in Mem. Torr. Bot. Club, 3(3): 44 (1893).

Isertia reticulata Britton in Mem. Torr. Bot. Club, 6: 46 (1896).
Ixora Killipii Standl. in Field Mus. Publ. Bot. 8: 174 (1930).
I. peruviana (Spruce) Standl. in Field Mus. Publ. Bot. 7: 296 (1931).

Ladenburgia Carua (Wedd.) Standl. in Field Mus. Publ. Bot. 7: 274 (1931).
L. magnifolia (R. \& P.) Klotzsch in Hayne, Arzneigew. 14: sub t. 15 (1856).
L. magnifolia var. rostrata (Wedd.) Standl. in Field Mus. Publ. Bot. 7: 275 (1931.)
L. Riveroana (Wedd.) Standl. in Field Mus. Publ. Bot. 7: 201 (1931).
L. sericea Standl. in Field Mus. Publ. Bot. 7: 275 (1931).

Limnosipanea Kuntzei Standl. in Field Mus. Publ. Bot. 7: 280 (1931).
Macrocnemum hirsutum Rusby in Mem. N. Y. Bot. Gard. 7: 370 (1927) $=$ M. roseum.
M. roseum (R. \& P.) Wedd. in Ann. Sci. Nat. (ser. 4) 1: 76 (1854).
M. Sprucei Rusby in Mem. Torr. Bot. Club, 6: $44(1896)=$ M. roseum.
M. tortuosum Herzog in Fedde, Repert. Spec. Nov. 7: 68 (1909).

Malanea boliviana Standl. in Field Mus. Publ. Bot. 7: 295 (1931).
Manettia asperifolia Standl. in Field Mus. Publ. Bot. 4: 270 (1929).
M. Bangii (Rusby) Standl. in Field Mus. Publ. Bot. 4: 271 (1929).
M. boliviana Wernh. in Journ. Bot. 57, Suppl.: $20(1919)=$ M. cordifolia var. glabra.
M. coccinea (Aubl.) Willd. Sp. Pl. 1(2) : 625 (1798).
M. cordifolia Mart. Spec. Mat. Med. Bras. 19, t. 7 (1824).
M. cordifolia var. glabra (Cham. \& Schlechtd.) Standl. in Field Mus. Publ. Bot. 7: 263 (1931).
M. divaricata Wernh. in Journ. Bot. 57, Suppl.: 41 (1919).
M. Fiebrigii Standl. in Field Mus. Publ. Bot. 7: 264 (1931).
M. hispida Poepp. \& Endl. Nov. Gen. 3: 24, t. 228 (1845).
M. Pearcei Wernh. in Journ. Bot. 57, Suppl.: 36 (1919).
M. Tatei Standl. in Field Mus. Publ. Bot. 7: 265 (1931).
M. tenuis (Britton) Wernh. in Journ. Bot. 57, Suppl.: 33 (1919).
M. tomentosa (Rusby) Standl. in Field Mus. Publ. Bot. 7: 265 (1931).

Mapouria rigida Rusby in Mem. N. Y. Bot. Gard. 7: 376 (1927) = Psychotria alba.
Mitracarpus frigidus (Willd.) K. Schum. in Mart. Fl. Bras. 6(6): 81, t. 85 (1888).
M. hirtus (L.) DC. Prodr. 4: 572 (1830).
M. megapotamicus (Spreng.) Standl. in Field Mus. Publ. Bot. 7: 331 (1931).
M. simplex Rusby in Mem. N. Y. Bot. Gard. 7: 381 (1927) $=$ M. hirtus.

Paederia diffusa (Britton) Standl. in Field Mus. Publ. Bot. 7: 330 (1931).
Palicourea amethystina (R. \& P.) DC. Prodr. 4: 527 (1830).
P. attenuata Rusby in Bull. N. Y. Bot. Gard. 4: 371 (1907).
P. Buchtienii Standl. in Field Mus. Publ. Bot. 7: 317 (1931).
P. Cardenasii Standl. in Field Mus. Publ. Bot. 22: 119 (1940).
P. cornifolia Standl. in Field Mus. Publ. Bot. 7: 318 (1931).
P. corymbifera (Muell. Arg.) Standl. in Field Mus. Publ. Bot. 7: 127 (1930).
P. crocea (Sw.) Roem. \& Schult. Syst. Veg. 5: 193 (1819).
P. exiguiflora Standl. in Field Mus. Publ. Bot. 7: 319 (1931).
P. fastigiata HBK. Nov. Gen. \& Spec. 3: 368 (1819).
P. flavifolia (Rusby) Standl. in Field Mus. Publ. Bot. 7: 320 (1931).
P. glabrata H. Winkl. in Fedde, Repert. Spec. Nov. 8: 3 (1910).
P. Herzogii Standl. in Field Mus. Publ. Bot. 11: 226 (1936).
P. lasiantha Krause in Engler, Bot. Jahrb. 40: 341 (1908).
P. longipes Rusby in Bull. N. Y. Bot. Gard. 8: 121 (1912) = P. triphylla.
P. macrobotrys (R. \& P.) DC. Prodr. 4: 527 (1830).
P. macrophylla (HBK.) Standl. in Field Mus. Publ. Bot. 7: 321 (1931).
P. malacophylla Standl. in Field Mus. Publ. Bot. 7: 322 (1931).
P. mapirensis Standl. in Field Mus. Publ. Bot. 7: 322 (1931).
P. mollis H. Winkl. in Fedde, Repert. Spec. Nov. 8: $4(1910)=P$ triphylla.
P. obliqua H. Winkl. in Fedde, Repert. Spec. Nov. 8: 4 (1910) $=$ P. ovalifolia.
P. ovalifolia (Rusby) Standl. in Field Mus. Publ. Bot. 7: 323 (1931).
P. papyracea Rusby in Bull. N. Y. Bot. Gard. 4: 370 (1907).
P. Pearcei Standl. in Field Mus. Publ. Bot. 7: 324 (1931).
P. punicea (R. \& P.) DC. Prodr. 4: 526 (1830).
P. radicans Standl. in Field Mus. Publ. Bot. 7: 325 (1931).
P. rigida HBK. Nov. Gen. \& Spec. 3: 370 (1819).
P. stipularis Benth. Pl. Hartw. 133 (1844).
P. tenuis Standl. in Field Mus. Publ. Bot. 7: 326 (1931).
P. triphylla DC. Prodr. 4: 526 (1830).

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P. verrucifera Standl. in Field Mus. Publ. Bot. 7: 327 (1931).
P. Williamsii Rusby, Descr. S. Am. Pls. 142 (1920) = P. macrobotrys.

Pogonopus febrifugus var. macrosema Hutchinson in Kew Bull. 1910: $200=$ P. tubulosus.
P. tubulosus (DC.) K. Schum. in Mart. Fl. Bras. 6 (6) : 265 (1889).

Posoqueria latifolia (Rudge) Roem. \& Schult. Syst. Veg. 5: 227 (1819).
Psychotria alba R. \& P. Fl. Peruv. 2: 58, t. 205, fig. a (1799).
P. axillaris Willd. Sp. Pl. 1(2): 962 (1798).
B. Bangii Rusby in Mem. Torr. Bot. Club, 3 (3) : 47 (1893).
P. Bangii Romero in Caldasia, 7: $50(1955)=P$. salicifolia Rusby $=$ Palicourea attenuata Rusby.
P. boliviana Standl. in Field Mus. Publ. Bot. 7: 303 (1931).
P. brachiata Sw. Prodr. 45 (1788).
P. Buchtienii (H. Winkl.) Standl. in Field Mus. Publ. Bot. 7: 303 (1931).
P. capitata R. \& P. Fl. Peruv. 2: 59 (1799).
P. Cardenasii Standl. in Field Mus. Publ. Bot. 7: 303 (1931).
P. carthagenensis Jacq. Enum. Pl. Carib. 16 (1760).
P. chlorotica Muell. Arg. in Flora, 59: 542 (1876) = P. capitata.
P. costata (Rusby) Standl. in Field Mus. Publ. Bot. 7: 305 (1931).
P. cuspidata Bredem. ex Roem. \& Schult. Syst. Veg. 5: 192 (1819).
P. emetica L. f. Suppl. 144 (1781).
P. falcata Rusby in Mem. Torr. Bot. Club, 3 (3): 47 (1893).
P. Hartwegiana Standl. in Field Mus. Publ. Bot. 7: 95 (1930).
P. Herzogii S. Moore in Meded. Rijks Herbar. 46: 25 (1922).
P. involucrata (Aubl.) Sw. Prodr. 45 (1788).
P. lassula Standl. in Field Mus. Publ. Bot. 7: 100 (1930).
P. lupulina Benth. in Hook. Journ. Bot. 3: 230 (1841).
P. luxurians Rusby in Mem. Torr. Bot. Club, 6: 50 (1896).
P. macrophylla R. \& P. Fl. Peruv. 2: 56, t. 202, fig. a (1799).
P. mapirensis Standl. in Field Mus. Publ. Bot. 7: 308 (1931).
P. marginata Sw. Prodr. 43 (1788).
P. microbotrys Ruiz ex Standl. in Field Mus. Publ. Bot. 8: 204 (1930).
P. nana Krause in Verh. Bot. Ver. Brandenb. 50: 109 (1908).
P. niveo-barbata (Muell. Arg.) Britton in Bull. Torr. Bot. Club, 18: 110 (1891).
P. olyphylla Rusby, Descr. S. Am. Pls. 138 (1920) = Palicourea triphylla.
P. Ottonis Standl. in Field Mus. Publ. Bot. 7: 310 (1931).
P. pallescens (Rusby) Standl. in Field Mus. Publ. Bot. 7: 310 (1931).
P. patens Sw. Prodr. 45 (1788).
P. Pearcei Standl. in Field Mus. Publ. Bot. 7: 311 (1931).
P. pervicax Standl. in Field Mus. Publ. Bot. 7: 311 (1931).
P. pilosa R. \& P. Fl. Peruv. 2: 50, t. 208, fig. a (1799).
P. racemosa (Aubl.) Willd. Sp. Pl. 1: 966 (1797).
P. ramiflora Rusby in Mem. N. Y. Bot. Gard. 7: 377 (1927).
P. reticulata R. \& P. Fl. Peruv. 2: 56, t. 202, fig. b (1799).
P. rhodothamna Standl. in Field Mus. Publ. Bot. 8: 210 (1930).
P. rigida var. brevipes Rusby in Mem. Torr. Bot. Club, 6:50 (1896) = Palicourea papyracea.
P. Ruizii Standl. in Field Mus. Publ. Bot. 7: 313 (1931).
P. salicifolia Rusby, Descr. S. Am. Pls. 140 (1920) = Palicourea attenuata.
P. scabrifolia Rusby, Descr. S. Am. Pls. 137 (1920).
P. Steinbachii Standl. in Field Mus. Publ. Bot. 7: 314 (1931).
P. tipuanensis Standl. in Field Mus. Publ. Bot. 7: 315 (1931).
P. tristis H. Winkl. in Fedde, Repert. Spec. Nov. 7: 249 (1909).
P. trivialis Rusby in Mem. N. Y. Bot. Club, 6: 50 (1896).
$\boldsymbol{P}$. viburnifolia Rusby in Mem. N. Y. Bot. Gard. 7: 378 (1927) =Rudgea tomentosa.
P. viridis R. \& P. Fl. Peruv. 2: 61, t. 210, fig. b (1799).
P. yungasensis Rusby in Mem. Torr. Bot. Club, 3(3): 46 (1893).

Randia boliviana Rusby in Bull. N. Y. Bot. Gard. 4: 368 (1907).
R. calycina Cham. in Linnaea, 9: 246 (1835).
R. formosa (Jacq.) K. Schum. in Mart. Fl. Bras. 6(6) : 342 (1889).
R. oblanceolata Rusby in Bull. N. Y. Bot. Gard. 8: 120 (1912) = R. spinosa.
R. spinosa (Jacq.) Karst. Fl. Colomb. 2: 128 (1869).

Relbunium alpicola K. Schum. \& R. E. Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1(1): 101 (1905).
R. Bangii Rusby in Bull. N. Y. Bot. Gard. 4: 374 (1907) $=$ R. ovale.
R. ciliatum (R. \& P.) Hemsl. in Biol. Centr. Am. Bot. 2: 62 (1881).
R. compactum Rusby in Mem. Torr. Bot. Club, 3 (3): 49 (1893) = R. ciliatum.
R. croceum (R. \& P.) K. Schum. in Mart. Fl. Bras. 6(6): 116 (1888).
R. hirsutum (R. \& P.) K. Schum. in Mart. Fl. Bras. 6(6): 116 (1888).
R. hypocarpium (L.) Hemsl. in Biol. Centr. Am. Bot. 2: 63 (1881).
R. nitidum (HBK.) K. Schum. in Mart. Fl. Bras. 6(6): 114 (1888).
R. ovale (R. \& P.) K. Schum. in Mart. Fl. Bras. 6(6): 115 (1888).
R. tenuissimum Krause in Engler, Bot. Jahrb. 40: 350 (1908).
R. vile (Cham. \& Schlechtd.) K. Schum. in Mart. Fl. Bras. 6 (6) : 116 (1888).

Richardia brasiliensis Gomez, Mem. Ipecac. 31, t. 2 (1801).
R. coldenioides Rusby in Mem. Torr. Bot. Club, 4(3): 208 (1895).
R. cruciata Rusby in Mem. Torr. Bot. Club, 6: 51 (1896).
R. grandiflora (Cham. \& Schlechtd.) Steud. Nomencl. (ed. 2) 2: 459 (1841).

Rudgea acuminata (R. \& P.) Standl. in Field Mus. Publ. Bot. 7: 327 (1931).
R. amazonica Muell. Arg. in Flora, 59: 449 (1876).
R. Buchtienii Standl. in Field Mus. Publ. Bot. 7: 328 (1931).
R. ciliata (R. \& P.) Spreng. Syst. Veg. 1: 755 (1825).
R. fimbriata (Benth.) Standl. in Standl. \& Calderón, List. Pl. Salvador, 274 (1925).
R. tomentosa Rusby in Mem. Torr. Bot. Club, 3(3): 48 (1893).
R. valida Rusby in Mem. Torr. Bot. Club, 6:51 (1896) = Psychotria reticulata.
R. viburnoides (Cham. \& Schlechtd.) Benth. in Linnaea, 23: 458 (1850).

Sabicea acutissima Rusby in Mem. N. Y. Bot. Gard. 7: 371 (1927) = S. erecta.
S. boliviensis Wernh. Monog. Sabicea, 37 (1914).
S. brasiliensis Wernh. Monog. Sabicea, 51 (1914).
S. cuneata Rusby in Mem. Torr. Bot. Club, 6: 47 (1896).
S. erecta Rusby ex Wernh. Monog. Sabicea, 36, t. 12, fig. 23 (1914).
S. Pearcei Wernh. Monog. Sabicea, 38, t. 3, fig. 1 (1914).
S. setiloba Wernh. Monog. Sabicea, 37 (1914).
S. villosa Roem. \& Schult. Syst. Veg. 5: 265 (1819).
S. villosa var. adpressa (Wernh.) Standl. in Field Mus. Publ. Bot. 7: 52 (1930).

Sickingia catappifolia Standl. in Field Mus. Publ. Bot. 7: 279 (1931).
S. fragrans (Rusby) Standl. in Field Mus. Publ. Bot. 7: 279 (1931).

Sipanea hispida Benth. ex Wernh. in Journ. Bot. 55: 173 (1917).
Spermacoce cephalophora Rusby in Bull. N. Y. Bot. Gard. 4: 374 (1907) = Borreria latifolia.
S. tenuior L. Sp. Pl. 102 (1753).

Staelia filifolia Rusby in Mem. Torr. Bot. Club, 4 (3): 209 (1895).
Tocoyena formosa (Cham. \& Schlechtd.) K. Schum. in Mart. Fl. Bras. 6(6): 347 (1889).
Tournefortiopsis reticulata Rusby in Bull. N. Y. Bot. Gard. 4: 369 (1907) $=$ Guettarda Tournefortiopsis.
Uncaria guianensis (Aubl.) Gmel. Syst. Veg. 370 (1791).
Warscewiczia coccinea (Vahl) Klotzsch in Monatsber. Akad. Berlin, 1853: 497 (1853).
W. splendens Wedd. in Ann. Sci. Nat. (ser. 4) 1: 72 (1854) = W. coccinea. Watsonamra sordidiflora Rusby in Mem. N. Y. Bot. Gard. 7: 372 (1927) = Palicourea lasiantha.
Wernhamia boliviensis S. Moore in Meded. Rijks Herbar. 46: 23 (1922).

## CAPRIFOLIACEAE

Sambucus peruviana HBK. Nov. Gen. \& Spec. 3: 429 (1820).
Viburnum ayavacense HBK. Nov. Gen. \& Spec. 3: 428 (1820).
? V. glabratum HBK. Nov. Gen. \& Spec. 3: 428 (1820).
V. lasiophyllum Benth. Pl. Hartw. 189 (1845).
V. pichinchense Benth. Pl. Hartw. 188 (1845).
V. Seemenii Graebn. in Engler, Bot. Jahrb. 37: 435 (1906).
V. Seemenii forma bolivianum (Gandog.) Killip \& Smith in Bull. Torr. Bot. Club. 57: 258 (1930).
V. Seemenii forma minus Killip \& Smith in Bull Torr. Bot. Club, 57: 258 (1930).
V. Spruceanum Rusby in Bull. N. Y. Bot. Gard. 8: 121 (1912).
? V. tinoides L. f. Suppl. 184 (1781).

## VALERIANACEAE

Belonanthus angustifolius Schmale in Notizbl. 13: 25 (1936).
B. crassipes (Wedd.) Graebn. in Engler, Bot. Jahrb. 37: 447 (1906).
B. hispidus (Wedd.) Graebn. in Engler, Bot. Jahrb. 37: 447 (1906).

Phyllactis corymbulosa Wedd. Chlor. And. 2: 34 (1858).
P. densa Wedd. Chlor. And. 2: 31 (1858).
P. inconspicua Wedd. Chlor. And. 2: 31 (1858).
P. Mandoniana Wedd. Chlor. And. 2: 34 (1858).
P. mapirensis Britton in Bull. Torr. Bot. Club, 18: 263 (1891).

Valeriana andina Britton in Bull. Torr. Bot. Club, 18: 264 (1891).
V. Bangiana Graebn. in Engler, Bot. Jahrb. 37: 437 (1906).
V. boliviana Britton in Bull Torr. Bot. Club, 18: 263 (1891).
V. bulbosa Wedd. Chlor. And. 2: 24 (1858).
V. calvescens Briq. in Ann. Conserv. \& Jard. Bot. Genève, 17: 334 (1914).
V. decussata R. \& P. Fl. Peruv. 1: 42, t. 70 (1798).
V. effusa Griseb. in Goett. Abh. 19: 162 (1874).
V. effusa var. Fiebrigii Briq. in Anr. Conserv. \& Jard. Bot. Genève, 20: 434 (1919).
V. glauca Poepp. ex DC. Prodr. 4: 639 (1830).
V. hyalinorrhiza R. \& P. Fl. Peruv. 1: 41, t. 67 (1798).
V. jasminoides Briq. in Ann. Conserv. \& Jard. Bot. Genève, 17: 336 (1914).
V. leptothyrsos Graebn. in Engler, Bot. Jahrb. 26: 425 (1899).
V. macrorhiza Poepp. ex DC. Prodr. 4: 635 (1830).
V. Mandonii Britton in Bull. Torr. Bot. Club, 18: 264 (1891).
V. micropterina Wedd. Chlor. And. 2: 26, t. 49B (1858).
V. niphobia Briq. in Ann. Conserv. \& Jard. Bot. Genève, 17: 347 (1914) = Belonanthus hispidus.
V. nivalis Wedd. Chlor. And. 2: 23, t. 48A (1858).
V. paniculata R. \& P. Fl. Peruv. 1: 41, t. 70 (1798).
V. Pavonii Poepp. \& Endl. Nov. Gen. 3: 16, t. 215 (1845).
V. Pavonii var. yungasensis Briq. in Ann. Conserv. \& Jard. Bot. Genève, 17: 337 (1914).
V. polemonioides HBK. Nov. Gen. \& Spec. 3: 332 (1819).
V. polyclada Briq. in Ann. Conserv. \& Jard. Bot. Genève, 17: 343 (1914).
V. poterioides Graebn. in Engler, Bot. Jahrb. 37: 441 (1906).
V. potopensis Briq. in An. Conserv. \& Jard. Bot. Genève, 17: 335 (1914).
V. psychrophila Briq. in Ann. Conserv. \& Jard. Bot. Genève, 17: 331 (1914).
V. pygmaea Graebn. in Engler, Bot. Jahrb. 37: 446 (1906).
V. Rusbyi Britton in Bull. Torr. Bot. Club, 18: 264 (1891).
V. scandens L. Sp. Pl. (ed. 2) 1: 47 (1762).
V. soratensis Briq. in Ann. Conserv. \& Jard. Bot. Genève, 17: 346 (1914).
V. tuberifera Graebn. in Engler, Bot. Jahrb. 26: 428 (1899).

## DIPSACACEAE

Dipsacus fullonum L. Sp. Pl. 97 (1753).

## CUCURBITACEAE

Anguria bignoniacea Poepp. \& Endl. Nov. Gen. 2: 53 (1838).
A. grandiflora Cogn. in Mém. Cour. Acad. Belg. 28: 22 (1877).
A. longipedunculata Cogn. in Mém. Cour. Acad. Belg. 28: 21 (1877).
A. spinulosa Poepp. \& Endl. Nov. Gen. 2: 52, t. 170 (1838).
A. Warszewiczii Hook. in Bot. Mag. 88: t. 5304 (1862).

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C. pentaphylla Cogn. in DC. Monog. Phan. 3: 760 (1881).
C. Tayuya (Vell.) Cogn. in DC. Monog. Phan. 3: 772 (1881).

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C. brachybotrys (Poepp. \& Endl.) Cogn. in Mém. Cour. Acad. Belg. 28: 73 (1877).
C. explodens var. intermedia Cogn. in O. Ktze. Rev. Gen. 3(2): 103 (1898).
C. explodens var. trifida Cogn. in O. Ktze. Rev. Gen. 3(2): 103 (1898).
C. Hystrix (Gill.) Arn. in Hook. Journ. Bot. 3: 280 (1841).
C. Matthewsii Arn. in Hook. Journ. Bot. 3: 280 (1841), nomen nudum.
C. microcarpa Cogn in Mém. Cour. Acad. Belg. 28: 75 (1877).
C. montana Cogn. in Meded. Rijks Herbar. 19: 69 (1913).
C. pedata Schrad. in Ind. Sem. Hort. Gotting. (1831).
C. pedata var. edulis (Naud.) Cogn. in DC. Monog. Phan. 3: 826 (1881).
C. quinquelobata (Vell.) Cogn. in Mém. Cour. Acad. Belg. 28: 64 (1877).
C. Rusbyi Britton in Bull. Torr. Bot. Club, 17: 284 (1890).
C. tomentosa Cogn. in Mém. Cour. Acad. Belg. 28: 77 (1877).

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F. pergamentacea Cogn. ex O. Ktze. Rev. Gen. 3(2): 104 (1898).

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G. boliviana Rusby in Mem. Torr. Bot. Club, 3(3): 38 (1893).
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G. lanata Cogn. in Mém. Cour. Acad. Belg. 27: 26 (1876).
G. latifolia Rusby in Mem. N. Y. Bot. Grad. 7: 383 (1927).
G. neogranatensis Cogn. in Mém. Cour. Acad. Belg. 27: 34 (1876).
G. plumosa Rusby in Mem. N. Y. Bot. Gard. 7: 382 (1927).
G. repandodentata Herzog in Fedde, Repert. Spec. Nov. 7: 69 (1909).
G. spinulosa (Poepp. \& Endl.) Cogn. Mém. Cour. Acad. Belg. 27: 17 (1876).
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Marah Rusbyi (Greene) Greene in Leafl. Bot. Obs. 2: 36 (1910).
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M. fluminensis Gardn. in Hook. Journ. Bot. 1: 173 (1842).
M. Hookeri Cogn. in DC. Monog. Phan. 3: 588 (1881).

Momordica Charantia L. Sp. Pl. 1009 (1753).
M. Charantia var. abbreviata Ser. in DC. Prodr. 3: 311 (1828).
M. balsamina L. Sp. Pl. 1009 (1753).

Sicydium tamnifolium (HBK.) Cong. in DC. Monog. Phan. 3: 905 (1881).
S. tamnifolium var. grandifolium Cogn. in Engler, Pflanzenr. IV, 275(I): 259 (1916).

Sicyos aculeatus R. E. Fries in Ark. Bot. 6(11): 5, t. 2, fig. 6-7 (1906).
S. australis Endl. Prodr. Fl. Norf. 67 (1833).
S. debilis Cogn. in O. Ktze. Rev. Gen. 3(2): 104 (1898).
S. Kuntzei Cogn. in O. Ktze. Rev. Gen. 3(2): 104 (1898).
S. malvifolius Griseb. in Goett. Abh. 19: 147 (1874).
S. montanus Poepp. \& Endl. Nov. Gen. 2: 53 (1838).
S. subcorymbosus Cogn. in DC. Monog. Phan. 3: 887 (1881).
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C. aquilinus var. campestris E. Wimm. in Engler, Pflanzenr. IV, 276b: 260 (1943).
C. aquilinus var. integer E. Wimm. in Engler, Pflanzenr. IV, 276b: 260 (1943).
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C. Brittonianus A. Zahlbr. in Bull. Torr. Bot. Club, 24: 373 (1897).
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C. cardinalis A. Zahlbr. \& Rech. in Meded. Rijks Herbar. 19: 51 (1913).
C. cornutus (L.) Druce in Rept. Bot. Exch. Club Brit. Isl. 3: 416 (1914).
C. fulvus Gleason in Buli. Torr. Bot. Club, 52: 7, t. 1, fig. 10 (1925).
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C. gloriosus (Britton) A. Zahlbr. in Bull. Torr. Bot. Club, 24: 373 (1897).
C. Herzogii A. Zahlbr. \& Rech. in Meded. Rijks Herbar. 19: 49 (1913).
C. incanus (Britton) A. Zahlbr. in Bull. Torr. Bot. Club, 24: 374 (1897).
C. macrophyllus (G. Don) E. Wimm. in Notizbl. 10: 733 (1929).
C. magnificus A. Zahlbr. \& Rech. in Meded. Rijks Herbar. 19: 50 (1913).
C. Mandonis A. Zahlbr. in Ann. Naturh. Hofmus. Wien, 6: 438 (1891).
C. roseus Rusby in Bull. N. Y. Bot. Gard. 8: 123 (1912).
C. unduavensis (Britton) A. Zahlbr. in Bull. Torr. Bot. Club, 24: 374 (1897).
C. unduavensis var. aduanus E. Wimm. in Engler, Pflanzenr. IV, 276b: 230 (1943).
C. yungasensis Britton in Bull. Torr. Bot. Club, 19: 371 (1892).

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L. nana HBK. Nov. Gen. \& Spec. 3: 317, t. 272 (1819).
L. nana var. cymbalarioides (A. Zahlbr.) E. Wimm. in Macbr. in Field Mus. Publ. Bot. 13(6): 479 (1937).
L. nana var. flagelliformis Wedd. Chlor. And. 2: 13 (1857).
L. ruderalis Willd. ex Roem. \& Schult. Syst. Veg. 6: 56 (1819).
L. xalapensis HBK. Nov. Gen. \& Spec. 3: 315 (1819).

Lysipomia glandulifera Schlechtd. in Lechl. Berb. Am. Aust. 58 (1857), nomen nudum.
L. laciniata A. DC. Prodr. 7(2): 349 (1839).
L. laciniata var. vulgaris (Wedd.) E. Wimm. in Macbr. in Field Mus. Publ. Bot. 13(6): 486 (1937).
L. linearifolia E. Wimm. in Macbr. in Field Mus. Publ. Bot. 13(6): 487 (1937).
L. pumila (Wedd.) E. Wimm. in Macbr. in Feld Mus. Publ. Bot. 13(6): 488 (1937).

Pratia boliviensis A. DC. Prodr. $7(2): 340$ (1839) $=$ Lobelia nana var. cymbalarioides.
P. hederacea Cham. in Linnaea, 8: 212 (1833).

Siphocampylus altiscandens Gleason in Bull. Torr. Bot. Club, 48: 198 (1921) $=$ S. flagelliformis.
S. andinus Britton in Bull. Torr. Bot. Club, 19: 373 (1892).
S. andinus var. elegantissimus E. Wimm. in Fedde, Repert, Spec. Nov. 38: 22 (1935).
S. andinus var. solemnis E. Wimm. in Fedde, Repert. Spec. Nov. 38: 23 (1935).
S. angustiflorus Schlechtd. ex A. Zahlbr. in Bull. Torr. Bot. Club, 24: 379 (1897).
S. argutus A. Zahlbr. in Bull. Torr. Bot. Club, 24: 383 (1897).
S. aureus Rusby in Mem. Torr. Bot. Club, 6: 72 (1896).
S. aureus var. latior A. Zahlbr. in Bull. Torr. Bot. Club, 24: 378 (1897).
S. bilabiatus A. Zahlbr. in Bull. Torr. Bot. Club, 24: 382 (1897).
S. bilabiatus var. dives (E. Wimm.) E. Wimm. in Engler, Pflanzenr. IV, 276b: 343 (1953).
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S. boliviensis A. Zahlbr. in Ann. Naturh. Hofmus. Wien, 6: 443 (1891).
S. correoides A. Zahlbr. in Bull. Torr. Bot. Club, 24: 382 (1897).
S. corymbiferus Pohl, Pl. Bras. 2: 112, t. 175 (1831).
S. corymbiferus var. gracilis (Britton) A. Zahlbr. in Bull. Torr. Bot. Club, 24: 384 (1897).
S. crenatus (E. Wimm.) E. Wimm. in Ann. Naturh. Mus. Wien, 56: 323 (1948).
S. elegans var. boliviensis A. Zahlbr. in Bull. Torr. Bot. Club, 24: 381 (1897) $=S$. soraticus in part and S. andinus var. solemnis in part.
S. elegans var. cordatus A. Zahlbr. in Bull. Torr. Bot. Club, 24: 381 (1897) = S. reflexus.
S. Fiebrigii E. Wimm. in Fedde, Repert, Spec. 'Nov. 22: 209 (1926).
S. Fiebrigii var. intermedius E. Wimm. in Engler, Pflanzenr. IV, 276b: 310 (1953).
S. flagellformis A. Zahlbr. in Bull. Torr. Bot. Club, 24: 380 (1897).
S. flagelliformis var. glaber E. Wimm. in Ann. Naturh. Mus. Wien, 56: 324 (1948).
S. flavoruber Gleason in Torreya, 25: 94 (1925).
S. foliosus var. subcanus E. Wimm. in Macbr. in Field Mus. Publ. Bot. 13(6): 453 (1937).
S. Kuntzeanus A. Zahlbr. in Bull. Torr. Bot. Club, 24: 378 (1897).
S. Lorentzii E. Wimm. in Fedde, Repert. Spec. Nov. 29: 85 (1931).
S. membranaceus Britton in Bull. Torr. Bot. Club, 19: 372 (1892).
S. nemoralis var. tarijanus E. Wimm. in Revist. Sudam. Bot. 2: 92 (1935).
S. neurotrichus E. Wimm. in Fedde, Repert. Spec. Nov. 38: 24 (1935).
S. nummularius E. Wimm. in Fedde, Repert. Spec. Nov. 38: 18 (1935).
S. oblongifolius Rusby in Mem. Torr. Bot. Club, 6: 73 (1896).
S. Orbignyanus DC. Prodr. 7(2): 405 (1839).
S. Orbignyanus var. discurrens E. Wimm. in Ann. Naturh. Mus. Wien, 56: 323 (1948).
S. puberulus E. Wimm. in Fedde, Repert. Spec. Nov. 26: 13 (1929).
S. radiatus Rusby in Mem. Torr. Bot. Club, 6: 73 (1896).
S. radiatus var. brevidentatus (A Zahlbr. \& Rech.) E. Wimm. in Ann. Naturh. Mus. Wien, 56: 331 (1948).
S. radiatus var. minor A. Zahlbr. in Bull. Torr. Bot. Club. 24: 376 (1897).
S. reflexus Rusby in Bull. N. Y. Bot. Gard. 4: 403 (1907).
S. Rusbyanus Britton in Bull. Torr. Bot. Club, 19: 372 (1892).
S. soraticus E. Wimm. in Fedde, Repert. Spec. Nov. 38: 23 (1935).
S. soraticus var. angustatus E. Wimm. in Fedde, Repert. Spec. Nov. 38: 23 (1935).
S. sparsipilus E. Wimm. in Fedde, Repert. Spec. Nov. 19: 388 (1924).
S. subcordatus Rusby in Bull. N. Y. Bot. Gard. 8: 121 (1912).
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S. tunicatus A. Zahlbr. ex O. Ktze. Rev. Gen. 3(2): 189 (1898).
S. tupaeformis A. Zahlbr. in Ann. Naturh. Hofmus. Wien, 6: 440 (1891).
S. tupaeformis var. diversifolius Hicken in Darwiniana, 1: 142 (1924).
S. Vatkeanus A. Zahlbr. in Bull. Torr. Bot. Club, 24: 377 (1897).
S. virgatus A. DC. Prodr. 7(2): 398 (1839).
S. Werdermannii E. Wimm. in Fedde, Repert. Spec. Nov. 38: 76 (1935).
S. Williamsii Rusby in Bull. N. Y. Bot. Gard. 8: 122 (1912).

Sphenoclea zeylanica Gaertn. Fruct. 1: 113, t. 24 (1788).
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W. linarioides (Lam.) A. DC. Monog. Campan. 158 (1830).
W. peruviana A. Gray in Proc. Amer. Acad. 5: 152 (1861).

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A. tribuloides Juss. in Ann. Mus. Paris, 2: 348, t. 58, fig. 1 (1803).

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A. hispidum DC. Prodr. 5: 522 (1836).

Achyrocline alata DC. Prodr. 6: 221 (1838).
A. candicans (HBK.) DC. Prodr. 6: 221 (1838).
A. celosioides (HBK.) DC. Prodr. 6: 221 (1838).
A. hyperchlora Blake in Bot. Gaz. 74: 415 (1922).
A. latifolia Wedd. Chlor. And. 1: 148 (1856).
A. polycephala Rusby in Bull. N. Y. Bot. Gard. 4: 388 (1907).
A. ramosissima Britton ex Rusby in Mem. Torr. Bot. Club, 3(3): 57 (1893).
A. rufescens (HBK.) DC. Prodr. 6: 220 (1838).
A. satureioides (Lam.) DC. Prodr. 6: 220 (1838).
A. tomentosa Rusby in Bull. N. Y. Bot. Gard. 4: 388 (1907).
A. Vauthieriana DC. Prodr. 6: 220 (1838).
A. venosa Rusby in Mem. Torr. Bot. Club, 3(3): 57 (1893).

Addisonia boliviana Rusby, Descr. S. Am. Pls. 147 (1920).

Adenostemma triangulare DC. Prodr. 5: 113 (1836).
A. viscosum var. brasilianum (Cass.) Baker in Mart. Fl. Bras. 6(2): 185 (1876).

Ageratum conyzoides L. Sp. Pl. 839 (1753).
Ambrosia elatior L. Sp. Pl. 987 (1753).
Anthemis Cotula L. Sp. Pl. 894 (1753).
Artemisia Absinthium L. Sp. Pl. 848 (1753).
Aspilia lucidula Blake in Proc. Biol. Soc. Wash. 36: 52 (1923).
Aster acaulis Wedd. Chlor. And. 1: 189, t. 33A (1857).
A. Bangii Rusby in Mem. Torr. Bot. Club, 4(3): 213 (1895).
A. divaricatus var. graminifolius (Spreng.) Baker in Mart. Fl. Bras. 6(3): 22 (1882).
A. exilis Ell. Sketch, 2: 344 (1823).
A. exilis forma subalpinus R. E. Fries in Ark. Bot. 5(13): 12 (1906).
A. limophilus (Sch. Bip.) Hemsl. \& Pearson in Journ. Linn. Soc. 35: 86 (1901).
A. marginatus HBK. Nov. Gen. \& Spec. 4: 91 (1820).
A. Vahlii (Gaud.) Hook. \& Arn. in Hook. Compan. Bot. Mag. 2: 49 (1836).

Baccharis alpina HBK. Nov. Gen. \& Spec. 4: 48 (1820).
B. alpina var. nummularioides Heering in Jahrb. Hamb. Wiss. Anst. 21, Beih. 3: 35 (1904).
B. alpina var. serpyllifolia Wedd. Chlor. And. 1: 168 (1856).
B. aphylla var. boliviensis Sch. Bip. in Bull. Soc. Bot. France, 12: 81 (1865), nomen nudum.
B. articulata (Lam.) Pers. Synops. Pl. 2: 425 (1807).
B. caespitosa (R. \& P.) Pers. Synops. Pl. 2: 425 (1807).
B. capitalensis Heering in Jahrb. Hamb. Wiss. Anst. 31, Beih. 3: 102 (1915).
B. caprariaefolia DC. Prodr. 5: 416 (1836).
B. cassinoides DC. Prodr. 5: 412 (1836).
B. condensata Rusby, Descr. S. Am. Pls. 148 (1920).
B. Conwayi Rusby in Bull. N. Y. Bot. Gard. 8: 130 (1912).
B. coridifolia DC. Prodr. 5: 422 (1836).
B. cylindrica (Less.) DC. Prodr. 5: 426 (1836).
B. debilis Rusby in Mem. Torr. Bot. Club, 6: 60 (1896).
B. densiflora Wedd. Chlor. And. 1: 175 (1856).
B. dracunculifolia DC. Prodr. 5: 421 (1836).
B. dracunculifolia var. integerrima O. Ktze. Rev. Gen. 3(2): 132 (1898).
B. dracunculifolia var. integerrima forma subviscosa O. Ktze. Rev. Gen. 3(2): 132 (1898).
B. effusa Griseb. in Goett. Abh. 19: 177 (1874).
B. fallax O. Ktze. Rev. Gen. 3(2): 132 (1898).
B. floribunda HBK. Nov. Gen. \& Spec. 4: 64, t. 325 (1820).
B. genistelloides (Lam.) Pers. Synops. Pl. 2: 425 (1807).
B. Gilliesii A. Gray in Proc. Am. Acad. 5: 123 (1861).
B. glutinosa Pers. Synops. Pl. 2: 425 (1807).
B. grandicapitulata Hieron. in Engler, Bot. Jahrb. 36: 481 (1905).
B. grindeliaefolia Wedd. Chlor. And. 1: 176 (1856).
B. Grisebachii Hieron. in Bol. Acad. Nac. Córdova, 4: 36 (1881).
B. hemiprionoides Buek, Ind. 1: x $(1842)=$ B. Sternbergiana.
B. heterothalamoides Britton in Bull. Torr. Bot. Club, 19: 4 (1892).
B. juncea Desf. Cat. Hort. Paris (ed. 3), 163 (1829).
B. Kuntzeana Teodoro in Contrib. Inst. Geobiol. La Salle, Canoas, no. 2: 46 (1952).
B. lanceolata HBK. Nov. Gen. \& Spec. 4: 63 (1820).
B. latifolia Pers. Synops. Pl. 2: 424 (1807).
B. laxiflora Rusby in Bull. N. Y. Bot. Gard. 8: 129 (1912).
B. magellanica var. subviscosa O. Ktze. Rev. Gen. 3(2): 133 (1898).
B. Mandonii Sch. Bip. in Leopoldina, 25: 108 (1889).
B. mapirensis Rusby in Mem. Torr. Bot. Club, 6: 61 (1896).
B. marginalis var. coerulescens (DC.) Heering ex Reiche, Fl. Chil. 4: 11 (1905).
B. marginalis var. viminea Heering ex Reiche, Fl. Chil. 4: 10 (1905).
B. medullosa DC. Prodr. 5: 405 (1836).
B. microphylla HBK. Nov. Gen. \& Spec. 4: 55 (1820).
B. microphylla var. incarum Wedd. Chlor. And. 1: 170 (1856).
B. microphylla var. linearifolia Wedd. ex Sch. Bip. in Bull. Soc. Bot. France, 12: 81 (1865), nomen nudum.
B. microphylla var. pulverulenta Rusby in Mem. Torr. Bot. Club, 3(3): 56 (1893).
B. myriocephala Baker in Mart. Fl. Bras. 6(3): 93 (1882).
B. nitida (R. \& P.) Pers. Synops. Pl. 2: 425 (1807).
B. oblanceolata Rusby in Mem. Torr. Bot. Club, 6: 61 (1896).
B. obtusifolia HBK. Nov. Gen. \& Spec. 4: 51 (1820).
B. odorata HBK. Nov. Gen. \& Spec. 4: 52 (1820).
B. oppositifolia O. Ktze. Rev. Gen. 3(2): 133 (1898).
B. Orbignyana Klatt in Abh. Naturf. Ges. Halle, 15: 327 (1881).
B. oxyodonta var. punctulata (DC.) Baker in Mart. Fl. Bras. 6(3): 77 (1882).
B. papillosa Rusby in Bull. N. Y. Bot. Gard. 8: 129 (1912).
B. paucidentata DC. Prodr. 5: 420 (1836).
B. Pentlandii DC. Prodr. 5: 416 (1836).
B. perulata O. Ktze. Rev. Gen. 3(2): 133 (1898).
B. Pflanzii Perkins in Engler, Bot. Jahrb. 49: 224 (1913).
B. polycephala Wedd. Chlor. And. 1: 173 (1856).
B. prostrata (R. \& P.) Pers. Synops. Pl. 2: 425 (1807).
B. pulchella Sch. Bip. in Bull. Soc. Bot. France, 12: 81 (1865), nomen nudum.
B. pulverulenta Klatt in Abh. Naturf. Ges. Halle, 15: 327 (1881).
B. quitensis HBK. Nov. Gen. \& Spec. 4: 57 (1820).
B. resinosa var. truncatifolia Perkins in Engler, Bot. Jahrb. 49: 224 (1913).
B. retusa DC. Prodr. 5: 412 (1836).
B. rhexioides HBK. Nov. Gen. \& Spec. 4: 66 (1820).
B. riparia HBK. Nov. Gen. \& Spec. 4: 65 (1820).
B. rubricaulis Rusby in Bull N. Y. Bot. Gard. 8: 129 (1912).
B. salicifolia (R. \& P.) Pers. Synops. Pl. 2: 425 (1807).
B. saliens Rusby in Bull. N. Y. Bot. Gard. 4: 387 (1907).
B. scandens (R. \& P.) Pers. Synops. Pl. 2: 424 (1807).
B. semiserrata DC. Prodr. 5: 404 (1836).
B. serrulata Pers. Synops. Pl. 2: 423 (1807).
B. spartea Benth. Bot. Voy. Sulphur, 114 (1845).
B. Sternbergiana Steud. Nomencl. (ed. 2) 1: 179 (1840).
B. Sternbergiana var. pubescens Perkins in Engler, Bot. Jahrb. 49: 225 (1913).
B. subalata Wedd. Chlor. And. 1: 174 (1856).
B. subpenninervis Sch. Bip. in Linnaea, 34: 532 (1865-66), nomen nudum.
B. synncephala Sch. Bip. ex Rusby in Bull. N. Y. Bot. Gard. 4: 386 (1907).
B. tomentosa Pers. Synops. Pl. 2: 424 (1807).
B. trichoclada DC. Prodr. 5: 400 (1836).
B. tridentata DC. Prodr. 5: 409 (1836).
B. tridentata var. pluridentata DC. Prodr. 5: 409 (1836).
B. trinervis (Lam.) Pers. Synops. Pl. 2: 423 (1807).
B. tucumanensis Hook. \& Arn. in Hook. Journ. Bot. 3: 34 (1841).
B. ulicina var. multifida (Griseb.) O. Ktze. Rev. Gen. 3(2): 135 (1898).
B. viscosa var. nigricans O. Ktze. Rev. Gen. 1: 320 (1891).
B. Vitis-Idaea O. Ktze. Rev. Gen. 3 (2): 135 (1898) = B. Kuntzeana.

Barnadesia glomerata O. Ktze. Rev. Gen. 3(2): 135 (1898).
B. inermis Rusby in Bull. N. Y. Bot. Gard. 4: 399 (1907).
B. macrocephala O. Ktze. Rev. Gen. 3(2): 135 (1898).
B. polyacantha Wedd. Chlor. And. 1: 13, t. 1A (1855).
B. Seleriana Muschl. in Engler, Bot. Jahrb. 50, Beibl. 111: 99 (1913).
B. spinosa L. f. Suppl. 348 (1781).
B. venosa Rusby in Mem. Torr. Bot. Club, 6: 69 (1896).

Bidens andicola HBK. Nov. Gen. \& Spec. 4: 237 (1820).
B. andicola var. Cosmantha (Griseb.) Sherff in Bot. Gaz. 85: 2 (1928).
B. andicola var. Cosmantha forma Buchtienii (Sherff) Sherff in Field Mus. Publ. Bot. 16: 502 (1937).
B. andicola var. decomposita O. Ktze. Rev. Gen. 3(2): 136 (1898).
B. andicola var. Mandonii Sherff in Bot. Gaz. 80: 380 (1925).
B. andicola var. tarijensis Sherff in Bot. Gaz. 85: 14 (1928).
B. andicola var. tarijensis forma dissecta Sherff in Bot. Gaz. 85: 14 (1928).
B. grandiflora var. breviloba O. Ktze. Rev. Gen. 3(2): 136 (1898) = B. andicola var. decomposita.
B. grandiflora var. longiloba O. Ktze. Rev. Gen. 3(2): 136 (1898).
B. humilis HBK. Nov. Gen. \& Spec. 4: 234 (1820).
B. humilis var. tenuifolia Sch. Bip. ex Griseb. in Goett. Abh. 24: 198 (1879) $=\mathrm{B}$. triplinervia var. macrantha.
B. longipetiolata Rusby in Bull. N. Y. Bot. Gard. 8: 131 (1912) = B. segetum var. patula.
B. macrantha Griseb. in Goett. Abh. 19: 186 (1874).
B. pallida Rusby in Bull. N. Y. Bot. Gard. 4: 389 (1907) = B. segetum.
B. peucedanifolia var. soratensis O. Ktze. Rev. Gen. 3(2): 137 (1898) = Cosmos peucedanifolius.
B. pilosa L. Sp. Pl. 832 (1753).
B. pilosa var. alausensis (HBK.) Sherff in Bot. Gaz. 81: 35 (1926).
B. pilosa var. alausensis forma scandicina (HBK.) Sherff in Bot. Gaz. 81: 36 (1926).
B. pilosa var. minor (Blume) Sherff in Bot. Gaz. 80: 387 (1925).
B. pilosa var. radiata (Sch. Bip.) J. A. Schmidt, Beitr. Fl. Cap Verdischer Ins. 197 (1852).
B. pseudocosmos Sherff in Bot. Gaz. 76: 151 (1923).
B. rubifolia HBK. Nov. Gen. \& Spec. 4: 237, t. 381 (1820).
B. segetum Mart. ex Colla, Herb. Pedem. 3: 307 (1835).
B. segetum var. patula (Gardn.) Sherff in Field Mus. Publ. Bot. 16: 197 (1937).
B. squarrosa HBK. Nov. Gen. \& Spec. 4: 238 (1820).
B. tenera var. tetracera Sherff in Bot. Gaz. 88: 293 (1929).
B. triplinervia var. macrantha (Wedd.) Sherff in Bot. Gaz. 80: 383 (1925).
B. triplinervia var. macrantha forma octoradiata Sherff in Bot. Gaz. 92: 203 (1931).
B. triplinervia var. mollis (Poepp. \& Endl.) Sherff in Bot. Gaz. 80: 384, t. 22, fig. a-i (1925).
Brickellia diffusa (Vahl) A. Gray, Pl. Wright. 1: 86 (1852).
B. paucidentata Klatt in Abh. Naturf. Ges. Halle, 15: 326 (1881) =?

Cacalia Hieronymi O. Ktze. Rev. Gen. 3(2): 138 (1898) = Vernonia echitifolia
Calea anomala Hassl. in Fedde, Repert. Spec. Nov. 7: 356 (1909).
C. brevifolia Rusby in Bull. N. Y. Bot. Gard. 8: 132 (1912).
C. coriacea DC. Prodr. 5: 675 (1836).
C. cymosa Less. in Linnaea, 5: 158 (1830).
C. rhombifolia Blake in Proc. Biol. Soc. Wash. 36: 53 (1923).
C. robusta Britton in Bull. Torr. Bot. Club, 19: 151 (1892) = C. coriacea.
C. solidaginea HBK. Nov. Gen. \& Spec. 4: 295 (1820).

Cephalophora robusta Rusby in Mem. Torr. Bot. Club, $3(3): 63$ (1893) $=$ Helenium sp.?

Chaetanthera boliviensis Koster in Blumea, 5: 673 (1945).
C. Stuebelii Hieron. in Engler, Bot. Jahrb. 21: 368 (1895).

Chaptalia ebracteata (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1): 376 (1900).
C. integrifolia (Cass.) Baker in Mart. Fl. Bras. 6(3): 377 (1884).
C. majuscula Greene, Leafl. Bot. Obs. 1: 196 (1905).
C. Mandonii Burkart in Darwiniana, 6: 551 (1944).
C. microdonta Greene, Leafl. Bot. Obs. 1: 196 (1905).
C. nutans (L.) Hemsl. in Biol. Centr. Am. Bot. 2: 255 (1881).
C. piloselloides (Vahl) Baker in Mart. Fl. Bras. 6(3): 378 (1884).
C. rotundifolia D. Don in Trans. Linn. Soc. 16: 242 (1830).

Chersodoma Antennaria (Wedd.) Cabrera in Rev. Mus. La Plata, 6: 352 (1946).
C. candida Phil. in Anal. Mus. Nac. Chile, Sec. 2, Bot. 8: 33 (1891).
C. diclina (Wedd.) Cabrera in Rev. Mus. La Plata, 6: 353 (1946).
C. iodopappa (Sch. Bip.) Cabrera in Rev. Mus. La Plata 6: 350 (1946).

Chevreulia elegans Rusby in Bull. N. Y. Bot. Gard. 4: 389 (1907).
C. sarmentosa (Pers.) Blake in Proc. Biol. Soc. Wash. 38: 85 (1925).

Chiliotrichiopsis Keidelii Cabrera in Not. Mus. La Plata, 2: 172, fig. 1 (1937).
Chrysanthellum americanum (L.) Vatke in Bremen Abh. 9: 122 (1885).
Chrysanthemum Parthenium Bernh. Syst. Verz. Erf. 145 (1800).
Chuquiraga acanthophylla Wedd. Chlor. And. 1: 5 (1855).
C. armata Koster in Blumea, 5: 662 (1945).
C. brasiliensis (Spreng.) O. Ktze. Rev. Gen. 3(2): 141 (1898).
C. brasiliensis var. divaricata (Griseb.) O. Ktze. Rev. Gen. 3(2): 141 (1898).
C. ferox (Wedd.) Britton in Bull. Torr. Bot. Club, 19: 266 (1892).
C. insignis var. armata Wedd. Chlor. And. 1: 3 (1855).
C. Jussieui var. lanceifolia (Humb. \& Bonpl.) Koster in Blumea, 5:662 (1945).
C. longiflora (Griseb.) Hieron. Plantae Diaphoricae, 165 (1882).
C. oppositifolia Gill. \& Don in Phil. Mag. 11: 392 (1832).
C. oppositifolia var. macrocephala Wedd. Chlor. And. 1: 3 (1855).
C. oppositifolia var. microcephala Wedd. Chlor. And. 1: 3 (1855).
C. parviflora (Griseb.) Hieron. in Engler, Bot. Jahrb. 49: 231 (1913).
C. rotundifolia Wedd. Chlor. And. 1: 4. t. 4A (1855).
C. varians (Gardn.) Rusby in Bull. N. Y. Gard. 4: 399 (1907).

Clibadium asperum (Aubl.) DC. Prodr. 5: 506 (1836).
C. heterotrichium Blake in Contrib. Gray Herb. 52: 3 (1917).
C. peruvianum Poepp. in DC. Prodr. 5: 505 (1836).
C. remotiflorum O. E. Schulz in Engler, Bot. Jahrb. 46: 621 (1912).
C. surinamense L. Mant. 2: 294 (1771).

Cnicothamnus Azafran (Cabr.) Cabrera in Not. Mus. La Plata, 9: 256 (1944).
C. Lorentzii Griseb. in Goett. Abh. 19: 197 (1874).

Conyza andicola Phil. in Anal. Mus. Nac. Chile, 8: 38 (1891).
C. artemisioides Meyen \& Walp. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 262 (1843).
C. chilensis Spreng. Novi Proventus, 14 (1819).
C. evacioides Rusby in Bull. N. Y. Bot. Gard. 4: 385 (1907) = C. gnaphalioides.
C. gnaphalioides HBK. Nov. Gen. \& Spec. 4: 73, t. 327 (1820).
C. lignescens Rusby in Bull. N. Y. Bot. Gard. 4: 385 (1907).
C. lyrata HBK. Nov. Gen. \& Spec. 4: 70 (1820).
C. obtusa HBK. Nov. Gen. \& Spec. 4: 71 (1820).
C. suffruticosa Phil. in Linnaea, 28: 735 (1858).
C. yungasensis Rusby in Mem. Torr. Bot. Club, 3(3): 55 (1893).

Coreopsis boliviana Blake in Contrib. U. S. Nat. Herb. 22: 644 (1924) = C. Pickeringii.
C. fasciculata Wedd. Chlor. And. 1: 71 (1856).
C. Pickeringii A. Gray in Proc. Am. Acad. 5: 124 (1861).
C. spectabilis A. Gray in Proc. Am. Acad. 5: 125 (1861).
C. Townsendii Blake in Contrib. U. S. Nat. Herb. 22: 643 (1924).

Cosmos caudatus HBK. Nov. Gen. \& Spec. 4: 240 (1820).
C. diversifolius Otto in Knowles \& Westc. Fl. Cab. 2: 6, t. 47 (1838).
C. Herzogii Sherff in Bot. Gaz. 96: 148 (1934).
C. integrifolius Wedd. Chlor. And. 1: 70 (1856) = C. peucedanifolius var. cochabambensis.
C. peucedanifolius Wedd. Chlor. And. 1: 70 (1856).
C. peucedanifolius var. cochabambensis (O. Ktze.) Sherff in Bot. Gaz. 88: 307 (1929).
C. peucedanifolius var. tiraquensis (O. Ktze.) Sherff in Bot. Gaz. 88: 307 (1929).

Cotula pygmaea (HBK.) Hemsl. in Biol. Centr. Am. Bot. 2: 230 (1881).
Crepis heterophylla Klatt in Ann. Naturh. Hofmus. Wien, 9: 368 (1894) = Hieracium sp.?
Culcitium Neaei (DC). Sch. Bip. ex Wedd. Chlor. And 1: 140 (1856).
C. nivale HBK. Nov. Gen. \& Spec. 4: 171, t. 363 (1820).

Dimerostemma asperatum Blake in Contrib. Gray Herb. 52: 12 (1917).
Diplostephium atropurpureum Rusby in Bull. N. Y. Bot. Gard. 4: 384 (1907) $=$ D. Haenkei.
D. Haenkei (DC.) Wedd. Chlor. And. 1: 203 (1857).
D. liaboides Rusby in Bull. N. Y. Bot. Gard. 4: 384 (1907) $=$ D. Haenkei.
D. Mandonii Rusby in Bull. N. Y. Bot. Gard. 4: 383 (1907) = D. Haenkei.
D. sejaënse (O. Ktze.) Blake in Contrib. U. S. Nat. Herb. 24: 80 (1929) = D. Haenkei.
Dyssodia fastigiata DC. Prodr. 5: 640 (1836).
Eclipta alba (L.) Hassk. Pl. Rar. Jav. 528 (1848).
Egletes viscosa (L.) Less. Syn. 252 (1832).
Elephantopus angustifolius Sw. Prodr. 115 (1788).
E. scaber L. Sp. Pl. 814 (1753).
E. spicatus B. Juss. ex Aubl. Pl. Guian. Fr. 2: 808 (1775).
E. tomentosus L. Sp. Pl. 814 (1753).

Eleutheranthera ruderalis Sch. Bip. in Bot. Zeit. 24: 165 (1866).
Elvira biflora (L.) DC. Prodr. 5: 503 (1836).
Encelia hirsuta O. Ktze. Rev. Gen. 3(2): 145 (1898).
E. soratensis Rusby, Descr. S. Am. Pls. 154 (1920).

Erechtites hieracifolia (L.) Raf. ex DC. Prodr. 6: 294 (1838).
E. valerianaefolia (Wolf) DC. Prodr. 6: 295 (1838).

Erigeron bonariensis L. Sp. Pl. 863 (1753).
E. Brittonianus Rusby in Mem. Torr. Bot. Club, $3(3): 54$ (1893) $=$ E. rosulatus.
E. canadensis L. Sp. Pl. 863 (1753).
E. canescens Sch. Bip. in Linnaea, 34: 534 (1866), nomen nudum.
E. cinerascens Sch. Bip. in Bonplandia, 4: 54 (1856), nomen rudum.
E. ferrugineus Wedd. Chlor. And. 1: 195 (1857).
E. floribundus (HBK.) Sch. Bip. in Bull. Soc. Bot. France, 12: 81 (1865).
E. frigidus Wedd. Chlor. And. 1: 231 (1857).
E. hieracioides Wedd. Chlor. And. 1: 194, t. 34B (1857).
E. Hillii Domke in Notizbl. 13: 244 (1936).
E. lanceolatus Wedd. Chlor. And. 1: 193 (1857).
E. lanceolatus var. subacaulis Wedd. Chlor. And. 1: 193 (1857).
E. laxiflorus Baker in Mart. F1. Bras 6(3): 31 (1882).
E. pazensis Sch. Bip. ex Rusby in Mem. Torr. Bot. Club, 3(3): 54 (1893).
E. pulvinatus Wedd. Chlor. And. 1: 194, t. 33B (1857).
E. rosulatus Wedd. Chlor. And. 1: 193, t. 33C (1857).
E. semiamplexicaulis Meyen, Reise, 1: 311 (1834).
E. seneciiformis Blake in Biol. Soc. Wash. 36: 51 (1923).
E. senecioides Wedd. Chlor. And. 1: 198 (1857).
E. tunariensis O. Ktze. Rev. Gen. 3(2): 146 (1898).

Eupatorium alternifolium var. genuinum forma nitidum Koster in Blumea, 5: 651 (1945).
E. amygdalinum Lam. Encycl. 2: 408 (1786).
E. Arnottianum Griseb. in Goett. Abh. 19: 167 (1874).
E. austerum Robinson in Contrib. Gray Herb. 68: 9 (1923).
E. azarangoënse Sch. Bip. ex Wedd. Chlor. And. 1: 217 (1857).
E. Bangii Rusby in Mem. Torr. Bot. Club, 6: 56 (1896).
E. betonicaeforme (DC.) Baker in Mart. Fl. Bras. 6(2) : 362, t. 96 (1876).
E. Bridgesii Robinson in Proc. Am. Acad. 55: 7 (1919).
E. buniifolium Hook. \& Arn. in Compan. Bot. Mag. 1: 240 (1836).
E. bupleurifolium DC. Prodr. 5: 149 (1836).
E. calderillense Hieron. in Engler, Bot. Jahrb. 40: 381 (1908).
E. camachense Hieron. in Engler, Bot. Jahrb. 40: 386 (1908).
E. camataquiense Hieron. in Engler, Bot. Jahrb. 40: 377 (1908).
E. chaparense Robinson in Contrib. Gray Herb. 90: 24 (1930).
E. chiquitense Robinson in Contrib. Gray Herb. 68: 11 (1923).
E. clematideum Griseb. in Goett. Abh. 24: 172 (1879).
E. cochabambense Hieron. in Engler, Bot. Jahrb. 22: 745 (1897) E E. connivens.
E. confluentis Robinson in Contrib. Gray Herb. 77: 11 (1926).
E. connivens Rusby in Mem. Torr. Bot. Club, 6: 57 (1896).
E. conoclinanthium Hieron. in Engler, Bot. Jahrb. 40: 388 (1908).
E. conyzoides var. ciliatum (Hook. \& Arn.) Hieron. in Engler, Bot. Jahrb. 22: 741 (1897).
E. crenulatum Spreng. ex Hieron. in Engler, Bot. Jahrb. 22: 776 (1897).
E. dejectum Robinson in Contrib. Gray Herb. 77: 12 (1926).
E. dentatum Gardn. in Hook. Journ. Bot. 6: 443 (1847).
E. desmocephalum Robinson in Contrib. Gray Herb. 68: 14 (1923).
E. didymum Klatt in Ann. Naturh. Hofmus. Wien, 9: 356 (1894).
E. endyturn Robinson in Proc. Am. Acad. 55: 13 (1919).
E. eucosmum Robinson in Contrib. Gray Herb. 61: 6 (1920) = E. saltense.
E. euphyes Robinson in Contrib. Gray Herb. 68: 16 (1923).
E. extensum Gardn. in Hook. Journ. Bot. 6: 440 (1847).
E. Fiebrigii Hieron. in Engler, Bot. Jahrb. $40: 371$ (1908).
E. gloeocladum Robinson in Proc. Am. Acad. 55: 17 (1919).
E. grossidentatum Hieron. in Engler, Bot. Jahrb. 40: 377 (1908).
E. guanaiense Britton in Bull. Torr. Bot. Club, 18: 333 (1891) = E. ivaefolium.
E. gymoxioides Rusby in Bull. N. Y. Bot. Gard. 4: 380 (1907) = E. gynoxomorphum.
E. gynoxomorphum Rusby in Robinson in Contrib. Gray Herb. 61: 7 (1920).
E. hecatanthum (DC.) Baker in Mart. Fl. Bras. 6(2): 365 (1876).
E. Herzogii Robinson in Contrib. Gray Herb. 68: 19 (1923).
E. hirsutum Hook. \& Arn. in Compan. Bot. Mag. 1: 239 (1836).
E. hosanense Robinson in Contrib. Gray Herb. 100: 14 (1932).
E. ignoratum Hieron. in Engler, Bot. Jahrb. 40: 379 (1908).
E. inulaefolium HBK. Nov. Gen. \& Spec. 4: 109 (1820).
E. inulaefolium forma suaveolens (HBK.) Hieron. in Engler, Bot. Jahrb. 29: 11 (1900).
E. iresinoides HBK. Nov. Gen. \& Spec. 4: 106, t. 340 (1820).
E. ivaefolium L. Syst. (ed. 10) 1205 (1759).
E. ivaefolium var. extrorsum Baker in Mart. Fl. Bras. 6(2): 290 (1876).
E. jugipaniculatum Rusby in Bull. N. Y. Bot. Gard. 4: 379 (1907).
E. kleinioides HBK. Nov. Gen. \& Spec. 4: 120 (1820).
E. Kuntzei Hieron. in Engler, Bot. Jahrb. 22: 766 (1897) $=$ Ophryosporus macrodon.
E. laevigatum Lam. Encycl. 2: 408 (1786).
E. laevigatum forma albiflorum O. Ktze. Rev. Gen. 3(2): 147 (1898).
E. laevigatum forma flavidum O. Ktze. Rev. Gen. 3(2): 147 (1898).
E. laevigatum forma lilacinum O. Ktze. Rev. Gen. 3(2): 147 (1898).
E. lanigerum var. longicuneatum Robinson in Ostenia, 354 (1933).
E. lasiophthalmum Griseb. in Goett. Abh. 19: 167 (1874).
E. latipaniculatum Rusby in Bull. N. Y. Bot. Gard. 4: 380 (1907).
E. leptocephalum DC. Prodr. 5: 148 (1836).
E. leptocephalum var. hypomalacum Robinson in Contrib. Gray Herb. 80: 24 (1928).
E. lobatum Robinson in Proc. Am. Acad. 55: 21 (1919).
E. Lobbii Klatt in Ann. Naturh. Hofmus. Wien, 9: 356 (1894).
E. longipetiolatum Sch. Bip. ex Rusby in Mem. Torr. Bot. Club, 3(3): 52 (1893).
E. macrocephalum Less. in Linnaea, 5: 136 (1830).
E. macrophyllum L. Sp. Pl. (ed. 2) 2: 1175 (1763).
E. mallotum Robinson in Proc. Am. Acad. 55: 22 (1919).
E. mallotum var. aporum Robinson in Proc. Am. Acad. 55: 23 (1919).
E. Mandonii Sch. Bip. in Linnaea, 34: $533(1865-66)=$ E. bupleurifolium.
E. mapiriense Hieron. in Engler, Bot. Jahrb. 40: 374 (1908).
E. marginatum Poepp. \& Endl. Nov. Gen. 3: 54 (1845).
E. microstemon Cass. in Dict. Sci. Nat. 25: 432 (1822).
E. morifolium Mill. Gard. Dict. (ed. 8) no. 10 (1768).
E. patens var. rhodolaenum Griseb. in Goett. Abh. 24: 170 (1879).
E. patens var. tomentosum Hieron. in Engler, Bot. Jahrb. 22: 773 (1897).
E. Pentlandianum DC. Prodr. 5: 157 (1836).
E. phyllocephalum Klatt in Ann. Naturh. Hofmus. Wien, 9: 358 (1894).
E. polopolemse Robinson in Contrib. Gray Herb. 61: 10 (1920) = E. pycnocephalum.
E. porophylloides Robinson in Contrib. Gray Herb. 68: 29 (1923).
E. pteropodum Hieron. in Engler, Bot. Jahrb. 29: 15 (1900) = E. nemorosum.
E. pycnocephalum Less. in Linnaea, 6: 404 (1831).
E. pyramidale Klatt in Abh. Naturf. Ges. Halle, 15: 323 (1881).
E. pyramidale forma angustifolium (Hieron.) Robinson in Contrib. Gray Herb. 61: 56 (1920).
E. rufescens var. glabratum Hieron. ex Robinson in Contrib. Gray Herb. 61: 67 (1920).
E. Rusbyi Britton in Bull. Torr. Bot. Club, 18: 334 (1891) = E. nemorosum.
E. santacruzense Hieron. in Engler, Bot. Jahrb. 22: 762 (1897).
E. scopulorum Wedd. Chlor. And. 1: 216, t. 40 B (1857) = E. azangaroënse.
E. simillimum Robinson in Contrib. Gray Herb. 77: 38 (1926).
E. soratae Sch. Bip. ex Robinson in Contrib. Gray Herb. 61: 51 (1920).
E. solidaginoides HBK. Nov. Gen. \& Spec. 4: 126 (1820).
E. sordescens var. bolivianum Rusby in Mem. Torr. Bot. Club, 6: 56 (1896) $=$ E. endytum.
E. squalidum var. Rusbyanum Robinson in Proc. Am. Acad. 55: 34 (1919).
E. squarroso-ramosum Hieron. in Engler, Bot. Jahrb. 22: 753 (1897).
E. stachyophyllum Spreng. Syst. Veg. 3: 420 (1826).
E. Sternbergianum DC. Prodr. 5: 167 (1836).
E. steviaefolium DC. Prodr. 5: 158 (1836).
E. stipuliferum Rusby in Mem. Torr. Bot. Club, 4 (3): 210 (1895) = E. solidaginoides.
E. subscandens Hieron. in Engler, Bot. Jahrb. 22: 742 (1897).
E. tamboënse Hieron. in Engler, Bot. Jahrb. 22: 770 (1897).
E. thymifolium Britton in Bull. Torr. Bot. Club, 19: 1 (1892).
E. toldense Hieron. in Engler, Bot. Jahrb. 40: 378 (1908).
E. triosteifolium Rusby in Bull. N. Y. Bot. Gard. 4: 379 (1907).
E. tucumanense Lillo \& Robinson in Contrib. Gray Herb. 90: 32 (1930).
E. tunariense (Hieron.) Robinson in Contrib. Gray Herb. 61: 39 (1920).
E. vitalbae DC. Prodr. 5: 163 (1836).
E. yungasense Robinson in Contrib. Gray Herb. 104: 30 (1934).

Facelis capillaris Rusby in Mem. Torr. Bot. Club, 6: 62 (1896).
F. Schultziana Beauverd in Bull. Soc. Bot. Genève (ser. 2), 5: 219 (1913).
F. Weddelliana Beauverd in Bull. Soc. Bot. Genève (ser. 2), 5: 217 (1913).

Filago lasiocarpa Griseb. in Goett. Abh. 19: 180 (1874).
Flaveria chilensis J. F. Gmel. Syst. 1269 (1791).
F. contrayerba (Cav.) Pers. Synops. Pl. 2: 489 (1807).

Flourensia Fiebrigii Blake in Engler, Bot. Jahrb. 54, Beibl. 119: 47 (1916).
F. heterolepis Blake in Contrib. Gray Herb. 54: 186 (1918).

Franseria artemisioides Willd. Sp. Pl. 4(1): 378 (1805).
F. Conwayi Rusby in Bull. N. Y. Bot. Gard. 8: 130 (1912).
F. recurva Rusby in Bull. N. Y. Bot. Gard. 8: 131 (1912).

Galinsoga calva Rusby in Mem. Torr. Bot. Club, 3(3): 61 (1893).
G. parviflora Cav. Icon. 3: 41, t. 281 (1795).
G. parviflora var. hispida DC. Prodr. 5: 677 (1836).
G. purpurea St. John \& White in Rhodora, 22: 98 (1920).
G. unxioides Griseb. in Goett. Abh. 24: 198 (1879).

Gnaphalium alatum HBK. Nov. Gen. \& Spec. 4: 79 (1820).
G. badium Wedd. Chlor. And. 1: 145 (1856).
G. cheiranthifolium Lam. Encycl. 2: 752 (1786).
G. cheiranthifolium var. multiflorum Koster in Blumea, 5: 655 (1945).
G. cymatoides Kze. ex DC. Prodr. 6: 225 (1838).
G. ecuadorense Hieron. in Engler, Bot. Jahrb. 21: 347 (1895).
G. ecuadorense var. boliviense Cuatr. in Pl. Isernianae, 1: 223 (1935).
G. frigidum Wedd. Chlor. And. 1: 147, t. 24A (1856).
G. Gaudichaudiana DC. Prodr. 6: 226 (1838).
G. helichrysoides Wedd. Chlor. And. 1: 146 (1856).
G. Kunthianum (Wedd.) O. Ktze. Rev. Gen. 3(2): 152 (1898).
G. lacteum Meyen \& Walp. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 276 (1843).
G. melanosphaeroides Sch. Bip. ex Wedd. Chlor. And. 1: 148 (1856).
G. monticola Phil. in Anal. Univ. Chile, 112: 117 (1903).
G. purpureum L. Sp. Pl. 854 (1753).
G. satureioides var. candicans (HBK.) O. Ktze. Rev. Gen. 3(2): 153 (1898).
G. sphacelatum HBK. Nov. Gen. \& Spec. 4: 86 (1820).
G. spicatum Lam. Encycl. 2: 757 (1786).
G. tunariense O. Ktze. Rev. Gen. 3(2): 155 (1898).
G. versatile Rusby in Mem. Torr. Bot. Club, 6: 62 (1896).
G. Weddellianum var. nanum Cuatr. in Pl. Isernianae, 1: 225 (1935).

Gochnatia boliviana Blake in Contrib. U. S. Nat. Herb. 22: 651 (1924).
G. Cardenasii Blake in Journ. Wash. Acad. Sci. 25: 324 (1925).
G. curviflora (Griseb.) O. Hoffm. in Engl. \& Prantl, Nat. Pflanzenfam. 4(5): 337 (1893).
G. macrocephala (Rusby) Cabrera in Not. Mus. La Plata, 15, Bot. 74: 41 (1950).
G. Rusbyana Cabrera in Not. Mus. La Plata, 15, Bot. 74: 41 (1950).

Grindelia boliviana Rusby in Mem. Torr. Bot. Club, 6: 60 (1896).
Gutierrezia Gilliesii var. scabriuscula Griseb. in Goett. Abh. 19: 173 (1874).
Gynoxys baccharoides Cass. in Dict. Sci. Nat. 48: 455 (1827).
G. boliviana (Klatt) Blake in Contrib. Gray Herb. 53: 28 (1918).
G. cochabambensis Cabrera in Not. Mus. La Plata, 14: 194 (1949).
G. cruzensis Cuatr. in Collect. Bot. [Barcelona] 3(3): 295 (1953).
G. discolor Rusby in Bull. N. Y. Bot. Gard. 4: 398 (1907).
G. follosa (Rusby) Blake in Contrib. U. S. Nat. Herb. 24: 86 (1922).
G. glabriuscula Rusby in Mem. Torr. Bot. Club, 6: 68 (1896).
G. Hallii Hieron. in Engler, Bot. Jahrb. 19: 64 (1894).
G. Hoffmannii O. Ktze. Rev. Gen. 3(2): 156 (1898).
G. hypomalaca Blake in Bot. Gaz. 74: 427 (1922).
G. laurifolia (HBK.) Cass. in Dict. Sci. Nat. 48: 435 (1827), combination implied but not actually made.
G. Mandonii Sch. Bip. ex Rusby in Mem. Torr. Bot. Club, 6: 67 (1896).
G. megacephala Rusby in Bull. N. Y. Bot. Gard. 4: 398 (1907).
G. neovelutina Cuatr. in Fieldiana, Bot. 27(2): 11 (1951).
G. psilophylla Klatt in Ann. Naturh. Hofmus. Wien, 9: 367 (1894).
G. repanda Wedd. Chlor. And. 1: 77 (1856).
G. Rusbyi Cuatr. in Fieldiana, Bot. $27(2)$ : 10 (1951).
G. sorataënsis Cuatr. in Fieldiana, Bot. 27(2): 12 (1951).
G. tablaënsis Cabrera in Blumea, 7: 197 (1952).

Haplopappus boliviensis Cabrera in Blumea, 7: 193 (1952).
Heliopsis buphthalmoides (Jacq.) Dunal in Mém. Mus. Paris, 5: 57 (1819).
Helogyne Fiebrigii Hieron. in Engler, Bot. Jahrb. 40: 368 (1908).
H. virgata (Rusby) Robinson in Proc. Am. Acad. 42: 31 (1906).

Heterosperma diversifolium HBK. Nov. Gen. \& Spec. 4: 246 (1820).
H. maritimum HBK. Nov. Gen. \& Spec. 4: 245, t. 383 (1820).
H. pinnatum Cav. Icon. 3: 34, t. 267 (1795).
H. pinnatum var. biternatum O. Ktze. Rev. Gen. 3(2): 158 (1898).
H. rhombifolium Griseb. in Goett. Abh. 19: 187 (1874).

Heterotheca deltoidea Klatt in Ann. Naturh. Hofmus. Wien, 9: 358 (1894) = Liabum hastifolium.
Hieracium adenocephalum (Sch. Bip.) Arvet-Touvet, Spicil. 8 (1881).
H. apoloënse Rusby in Bull. N. Y. Bot. Gard. 8: 135 (1912).
H. Bangii Rusby in Mem. Torr. Bot. Club, 3(3): 66 (1893).
H. Bangii subsp. austroboliviense Zahn in Engler, Pflanzenr. IV, 280: 1099 (1922).
H. boliviense (Wedd.) Sch. Bip. in Bonplandia, 9: 173 (1861).
H. eriocephalum Wedd. Chlor. And. 1: 226 (1857).
H. Fiebrigianum Zahn in Engler, Pflanzenr. IV, 280 : 1098 (1922).
H. fimbriatum Arvet-Touvet, Spicil. 6 (1881).
H. Hauthalianum Zahn in Engler, Pflanzenr. IV, 280: 1090 (1922).
H. lagopus D. Don in Trans. Linn. Soc. 16(2): 176 (1830).
H. leptocephalum var. microcephalum (Sch. Bip.) Zahn in Engler, Pflanzenr. IV, 280: 1096 (1922).
H. Mandonii (Sch. Bip.) Arvet-Touvet, Spicil. 16 (1881).
H. mapirense Britton in Bull. Torr. Bot. Club, 19: 371 (1892).
H. megalochaetum Zahn in Engler, Pflanzenr. IV, 280: 1144 (1922).
H. pazense Blake in Bot. Gaz. 74: 429 (1922).
H. stachyoideum Arvet-Touvet, Spicil. 21 (1881).
H. strigosum D. Don in Trans. Linn. Soc. 16: 175 (1830).
H. tacense Hieron. in Engler, Bot. Jahrb. 21: 375 (1896).
H. trichodontum (Sch. Bip.) Arvet-Touvet, Spicil. 16 (1881).
H. trichodontum Rusby in Bull. N. Y. Bot. Gard. 4: 402 (1907).
H. Trollii Sleumer in Fedde, Repert. Spec. Nov. 41: 119 (1936).

Hyalis lancifolia Baker in Mart. Fl. Bras. 6(3): 368 (1884).
Hyaloseris boliviensis Koster in Blumea, 5: 668 (1945).
H. camataquiensis Hieron. ex Fiebrig in Engler, Bot. Jahrb. 45: 43 (1910).
H. quadriflora Koster in Blumea, 5: 667 (1945).

Hypochoeris acaulis (Remy) Britton in Bull. Torr. Bot. Club, 19: 371 (1892).
H. brasiliensis var. sulfurea O. Ktze. Rev. Gen. 3(2): 159 (1898).
H. chilensis Britton in Bull. Torr. Bot. Club, 19: 371 (1892).
H. elata (Wedd.) Griseb. in Goett. Abh. 24: 218 (1879).
H. Meyeniana (Walp.) Griseb. in Goett. Abh. 19: 199 (1874).
H. Meyeniana var. ciliata (Wedd.) Perkins in Engler, Bot. Jahrb. 49: 232 (1913).
H. ornata Koster in Blumea, 5: 660 (1945).
H. parvifolia Koster in Blumea, 5: 661 (1945).
H. sessiliflora HBK. Nov. Gen. \& Spec. 4: 2 (1820).
H. setosa (Wedd.) Rusby in Bull. N. Y. Bot. Gard. 4: 402 (1907).
H. stenocephala (A. Gray) O. Ktze. Rev. Gen. 3(2): 160 (1898).
H. stenocephala var. integrifolia O. Ktze. Rev. Gen. 3(2): 160 (1898).
H. taraxacoides (Meyen \& Walp.) Ball in Journ. Linn. Soc. 22: 48 (1885).

Hysterionica nidorelloides (DC.) Baker in Mart. Fl. Bras. 6(3): 12 (1882).
Isostigma Herzogii Hassl. in Fedde, Repert. Spec. Nov. 7: 358 (1909).
I. Hoffmannii O. Ktze. Rev. Gen. 3(2): 160 (1898).

Jaegeria hirta (Lag.) Less. Syn. Comp. 223 (1832).
Jungia affinis Gardn. in Hook. Journ. Bot. 6: 460 (1847).
J. divaricata Rusby in Mem. Torr. Bot. Club, 6: 71 (1896).
J. ferruginea L. f. Suppl. 390 (1781).
J. floribunda Less. in Linnaea, 5: 38 (1830).
J. grossulariaefolia Rusby, Descr. S. Am. Pls. 164 (1920).
J. Herzogiana Beauverd ex Koster in Blumea, 5: 683 (1945).
J. orbicularis Rusby in Bull. N. Y. Bot. Gard. 4: 401 (1907).
J. pauciflora Rusby in Bull. N. Y. Bot. Gard. 4: 401 (1907).
J. polita var. tomentosa O. Ktze. Rev. Gen. 3(2): 161 (1898).
J. pubescens var. boliviensis O. Ktze. Rev. Gen. 3(2): 161 (1898).
J. sordida Koster in Blumea, 5: 683 (1945).

Laestadia Lechleri Wedd. Chlor. And. 1: 184 (1856).
Lagascea mollis Cav. in Anal. Cienc. Nat. 6: 332, t. 44 (1803).
Leontopodium linearifolium (Wedd.) Britton in Bull. Torr. Bot. Club, 19: 148 (1892).

Lepidophyllum lucidum (Meyen) Cabrera in Bol. Soc. Argent. Bot. 1: 51 (1945).
L. phylicaeforme (Meyen) Hieron. ex Fries in Nov. Act. Soc. Sci. Upsal. (ser. 4) 1(1): 77 (1905).
L. quadrangulare (Meyen) Benth. \& Hook. f. Gen. Pl. 2(1): 258 (1873).
L. teretiusculum O. Ktze. Rev. Gen. 3(2): 162 (1898).
L. Tola Cabrera in Bol. Soc. Argent. Bot. 1: 56 (1945).

Liabum acuminatum Rusby, Descr. S. Am. Pls. 161 (1920).
L. asperifolium Muschl. in Engler, Bot. Jahrb. 50, Beibl. 111: 78 (1913).
L. Cardenasii Cabrera in Not. Mus. La Plata, 14: 191 (1949).
L. corymbosum Sch. Bip. ex Klatt in Ann. Naturh. Hofmus. Wien, 9: 363 (1894).
L. foliosum (Rusby) Cabrera in Not. Mus. La Plata, 14: 193 (1949).
L. fulvotomentosum O. Ktze. Rev. Gen. 3(2): 163 (1898).
L. giganteum Rusby in Bull. N. Y. Bot. Gard. 4: 391 (1907).
L. glandulosum O. Ktze. Rev. Gen. 3(2): 163 (1898).
L. hastatum (Wedd.) Britton in Bull. Torr. Bot. Club, 19: 263 (1892).
L. hastifolium Poepp. \& Endl. Nov. Gen. 3: 43 (1845).
L. hexagonum Blake in Journ. Wash. Acad. Sci. 25: 322 (1935) = L. longifolium.
L. hirtum O. Ktze. Rev. Gen. 3(2): 163 (1898).
L. isodontum Blake in Journ. Wash. Acad. Sci. 17: 298 (1927).
L. Jelskii Hieron. in Engler, Bot. Jahrb. 36: 499 (1905).
L. longifolium (Rusby) Blake in Journ. Wash. Acad. Sci. 25: 322 (1935).
L. mulgediifolium Muschl. in Engler, Bot. Jahrb. 50, Beibl. 111: 85 (1913).
L. ovatum (A. Gray) Ball in Journ. Linn. Soc. 22: 46 (1885).
L. ovatum var. hirtum Perkins in Engler, Bot. Jahrb. 49: 229 (1913).
L. pinnulosum O. Ktze. Rev. Gen. 3(2): 163 (1898).
L. Rusbyi Britton in Bull. Torr. Bot. Club, 19: 263 (1892).
L. subviride Blake in Journ. Wash. Acad. Sci. 17: 294 (1927).
L. uniflorum (Poepp. \& Endl.) Sch. Bip. in Flora, 36: 34 (1853).

Lophopappus cuneatus R. E. Fries in Ark. Bot. 5(13): 29, t. 1 (1906).
L. foliosus Rusby in Bull. Torr. Bot. Club, 21: 487 (1894).

Loricaria graveolens Wedd. Chlor. And. 1: 167, t. 27C (1856).
L. thuyoides (Lam.) Sch. Bip. in Bjnplandia, 8: 260 (1860).
L. unduaviensis Cuatr. in Fedde, Repert. Spec. Nov. 56: 170 (1954).

Lucilia affinis Wedd. Chlor. And. 1: 230 (1857).
L. flagelliformis Wedd. Chlor. And. 1: 157, t. 26D (1856).
L. Jamesonii Baker in Mart. Fl. Bras. 6(3): 113 (1882).
L. recurva Wedd. Chlor. And. 1: 156, t. 25B (1856).
L. Schultzii (Wedd.) A. Gray in Proc. Am. Acad. 5: 138 (1862).
L. squarrosa Baker in Mart. Fl. Bras. 6(3): 114 (1882).
L. subspicata (Wedd.) Hieron. in Engler, Bot. Jahrb. 29: 29 (1900).
L. tomentosa Wedd. Chlor. And 1: 157 (1856).
L. tunariensis (O. Ktze.) K. Schum. in Just, Bot. Jahresber. 26(1): 378 (1900).
L. violacea Wedd. Chlor. And. 1: 155 (1856).

Luciliopsis perpusilla Wedd. Chlor. And. 1: 160, t. 26A (1856).
Lycoseris boliviana Britton in Bull. Torr. Bot. Club, 19: 266 (1892).
L. retroflexa Koster in Blumea, 5: 664 (1945).

Mikania baccharoidea Rusby in Bull. N. Y. Bot. Gard. 8: 127 (1912).
M. Buchtienii Robinson in Contrib. Gray Herb. 64: 7 (1922).
M. cinnamomifolia Lingelsh. in Fedde, Repert. Spec. Nov. 7: 251 (1909).
M. cochabambana Robinson in Contrib. Gray Herb. 90: 33 (1930).
M. comarapana Robinson in Contrib. Gray Herb. 90: 34 (1930).
M. cordifolia (L. f.) Willd. Sp. Pl. 3(1): 1746 (1804).
M. decora Poepp. in Poepp. \& Endl. Nov. Gen. 3: 53 (1845).
M. desmocephala Robinson in Contrib. Gray Herb. 64: 7 (1922).
M. dictyota Robinson in Contrib. Gray Herb. 68: 37 (1923).
M. dioscoreoides (Rusby) Robinson in Contrib. Gray Herb. 64: 97 (1922).
M. eucosma Robinson in Contrib. Gray Herb. 64: 9 (1922).
M. ferruginea (Rusby) Rusby ex Robinson in Contrib. Gray Herb. 64: 101 (1922).
M. ferruginea var. subglabra Robinson in Contrib. Gray Herb. 104: 36 (1934).
M. Fiebrigii Hieron. in Engler, Bot. Jahrb. 40: 390 (1908).
M. flaccida Robinson in Contrib. Gray Herb. 64: 9 (1922).
M. Guaco Humb. \& Bonpl. Pl. Aequin. 2: 84, t. 105 (1809).
M. Haenkeana DC. Prodr. 5: 196 (1836).
M. lanuginosa DC. Prodr. 5: 201 (1836).
M. leucophylla (Rusby) Robinson in Proc. Am. Acad. 47: 196 (1911).
M. longiacuminata (Rusby) Rusby ex Robinson in Contrib. Gray Herb. 64: 103 (1922).
M. longiflora (Rusby) Robinson in Proc. Am. Acad. 47: 196 (1911).
M. Mandonii Sch. Bip. ex Baker in Mart. Fl. Bras. 6(2): 188 (1876) = Ophryosporus piquerioides.
M. micrantha HBK. Nov. Gen. \& Spec. 4: 134 (1820).
M. micrantha forma congesta (DC). Robinson in Contrib. Gray Herb. 64: 43 (1922).
M. microptera DC. Prodr. 5: 196 (1836).
M. officinalis Mart. Reise, 1: 283 (1823).
M. oreimeles Robinson in Contrib. Gray Herb. 68: 39 (1923).
M. Pennellii Robinson in Contrib. Gray Herb. 61: 19 (1920).
M. periplocifolia Hook. \& Arn. in Hook. Compan. Bot. Mag. 1: 243 (1836).
M. phyllopoda Griseb. in Goett. Abh. 19: 170 (1874).
M. platyphylla DC. Prodr. 5: 195 (1836).
M. psilostachya DC. Prodr. 5: 190 (1836).
M. rubella Lingelsh. in Fedde, Repert. Spec. Nov. 7: 250 (1909).
M. Rusbyi Robinson in Contrib. Gray Herb. 64: 18 (1922) .
M. Schultzii Robinson in Contrib. Gray Herb. 64: 19 (1922).
M. sinuata Rusby in Bull. N. Y. Bot. Gard. 8: 127 (1912) = M. micrantha.
M. speciosa DC. Prodr. 5: 196 (1836).
M. Steinbachii Robinson in Contrib. Gray Herb. 80: 40 (1928).
M. stygia Robinson in Contrib. Gray Herb. 90: 36 (1930).
M. trifolia (Rusby) Robinson in Contrib. Gray Herb. 64: 107 (1922).
M. vitifolia forma boliviensis (Lingelsh.) Robinson in Contrib. Gray Herb. 104: 54 (1934).
M. Werdermannii Robinson in Contrib. Gray Herb. 104: 47 (1934).
M. Williamsii Robinson in Contrib. Gray Herb. 64: 19 (1922).

Montanoa Orbignyana Klatt in Abh. Naturf. Ges. Halle, 15: 328 (1881).
Moquinia boliviana Rusby in Bull. N. Y. Bot. Gard. 4: 399 (1907) = Gochnatia Rusbyana.
Mutisia Bipontina Sch. Bip. ex Rusby in Mem. Torr. Bot. Club, 6: 68 (1896).
M. camptosorifolia Rusby in Mem. Torr. Bot. Club, 4 (3): 213 (1895) = M. cochabambensis.
M. Clematis L. f. Suppl. 373 (1781).
M. cochabambensis Hieron. in Engler, Bot. Jahrb. 19: 74 (1894).
M. comptoniaefolia Rusby in Mem. Torr. Bot. Club, 3(3): 65 (1893).
M. Flagellaria Koster in Blumea, 5: 672 (1945).
M. hastata Cav. Icon. 5: 64, t. 494 (1799).
M. homoeantha Wedd. Chlor. And. 1: 21, t. 2A (1855).
M. Isernii Phil. in Anal. Univ. Chile, 85: 823 (1894).
M. lanigera Wedd. Chlor. And. 1: 16 (1855).
M. ledifolia Decne. ex Wedd. Chlor. And. 1: 20 (1855).
M. ledifolia forma glabrata Cuatr. Pl. Isernianae, 1: 236 (1935).
M. ledifolia forma longiflora Koster in Blumea, 5: 673 (1945).
M. Orbignyana Wedd. Chlor. And. 1: 22 (1855).
M. subulata R. \& P. Syst. 193 (1798).
M. Vicia Koster in Blumea, 5: 670 (1945).
M. viciaefolia Cav. Icon. 5: 62, t. 490 (1799).
M. viciaefolia var. Candolleana (Gardn. \& Field) Wedd. Chlor. And. 1: 15 (1855).
M. viciaefolia var. hirsuta (Meyen ex Walp.) Wedd. Chlor. And. 1: 15 (1855).
M. viciaefolia forma intermedia Cuatr. Pl. Isernianae, 1: 237 (1935).

Nardophyllum armatum (Wedd.) Reiche in Anal. Univ. Chile, 109: 29 (1901).
Onoseris acerifolia HBK. Nov. Gen. \& Spec. 4: 8 (1820).
O. alata Rusby, Descr. S. Am. Pls. 163 (1920).
O. albicans (D. Don) Ferreyra in Journ. Arnold Arb. 25: 389 (1944).
O. fraterna Blake in Journ. Wash. Acad. Sci. 33: 368 (1943).
O. gnaphalioides Muschl. in Engler, Bot. Jahrb. 50, Beibl. 111: 94 (1913).
O. hastata Wedd. Chlor. And. 1: 9, t. 7 (1855).
O. hyssopifolia HBK. Nov. Gen. \& Spec. 4: 9, t. 306 (1820).
O. sagittata (Rusby) Rusby, Descr. S. Am. Pls. 164 (1920).

Ophryosporus angustifolius Robinson in Contrib. Gray Herb. 90: 3 (1930).
O. Cumingii (Sch. Bip.) Benth. ex Baker in Mart. Fl. Bras. 6(2): 188 (1876).
O. eleutheranthus (Rusby) Robinson in Contrib. Gray Herb. 61: 27 (1920).
O. Kuntzei Hieron. in Engler, Bot. Jahrb. 22: 707 (1897).
O. origanoides var. microcephalus Hieron. in Engler, Bot. Jahrb. 22: 708 (1897).
O. piquerioides (DC.) Benth. ex Baker in Mart. Fl. Bras. 6(2): 188 (1876).
O. Steinbachii Robinson in Contrib. Gray Herb. 77: 5 (1926).
O. venosissimus (Rusby) Robinson in Proc. Am. Acad. 42: 24 (1906).

Oyedaea boliviana Britton in Bull. Torr. Bot. Club, 19: 149 (1892).
O. bullata Koster in Blumea, 6: 269 (1948).
O. lanceolata (Rusby) Blake in Contrib. U. S. Nat. Herb. 20: 416 (1921).
O. Pearcei Rusby in Mem. Torr. Bot. Club, 3 (3): 59 (1893) $=0$. boliviana.
O. Rusbyi Blake in Contrib. U. S. Nat. Herb. 20: 416 (1921).

Pappobolus macranthus Blake in Hook. Ic. Pl. 31: t. 3057 (1916).
Parthenium cineraceum Rollins in Contrib. Gray Herb. 172: 32 (1950).
P. glomeratum Rollins in Contrib. Gray Herb. 172: 59 (1950).
P. Hysterophorus L. Sp. Pl. 988 (1753).

Pectis linifolia L. Sp. Pl. (ed. 2) 2: 1150 (1763).
P. odorata Griseb. in Goett. Abh. 24: 200 (1879).
P. sessiliflora Sch. Bip. ex Rusby in Mem. Torr. Bot. Club, 3(3): 62 (1893).
P. substriata Rusby in Bull. N. Y. Bot. Gard. 4: 390 (1907).
P. Swartziana Less. in Linnaea, 6: 711 (1831).

Perezia aracensis Koster in Blumea, 5: 678 (1945).
P. coerulescens Wedd. Chlor. And. 1: 39, t. 10A (1855).
P. cirsiifolia Wedd. Chlor. And. 1: 41 (1855).
P. elongata O. Ktze. Rev. Gen. 3(2): 166 (1898).
P. foliosa Rusby in Mem. Torr. Bot. Club, 6: 71 (1896).
P. glomerata Rusby in Mem. Torr. Bot. Club, 4(3): 214 (1895).
P. integrifolia Wedd. Chlor. And. 1: 40 (1855).
P. laurifolia O. Ktze. Rev. Gen. 3(2): 166 (1898).
P. Mandonii Rusby in Mem. Torr. Bot. Club, 3(3): 66 (1893).
P. multiflora (HBK.) Less. in Linnaea, 5: 19 (1830).
P. nitidifolia Koster in Blumea, 5: 677 (1945).
P. obtusisquama Koster in Blumea, 5: 680 (1945).
P. pungens (HBK.) Less. in Linnaea, 5: 20 (1830).
P. pungens var. cernua Rusby in Mem. Torr. Bot. Club, 6: 70 (1896).
P. purpurata Wedd. Chlor. And. 1: 43 (1855).
P. pygmaea Wedd. Chlor. And. 1: 40 (1855).
P. scalpellifolia Koster in Blumea, 5: 680 (1945).
P. scalpellifolia var. parvifolia Koster in Blumea, 5: 680 (1945).
P. violacea Wedd. Chlor. And. 1: 42 (1855).

Picrosia longifolia D. Don in Trans. Linn. Soc. 16: 184 (1830).
Piptocarpha laxa Rusby in Bull. N. Y. Bot. Gard. 8: 123 (1912).
P. Lechleri (Sch. Bip.) Baker in Mart. Fl. Bras. 6(2): 127 (1873).

Plagiochilus ciliaris Wedd. Chlor. And. 1: 227 (1857).
$P$. erectus Rusby in Mem. Torr. Bot. Club, 4 (3): 212 (1895) $=$ Chrysanthellum sp.?
P. solivaeformis DC. Prodr. 6: 142 (1838).

Plazia acaciifolia Koster in Blumea, 5: 665 (1945).
P. argentea (D. Don) O. Ktze. Rev. Gen. 3(2): 167 (1898).
P. daphnoides var. glabrescens Wedd. Chlor. And. 1: 13, t. 2B (1855).
P. spartioides (Wedd.) O. Ktze. Rev. Gen. 3(2): 167 (1898).

Pluchea fastigiata Griseb. in Goett. Abh. 24: 184 (1879).
P. glabra Griseb. in Goett. Abh. 24: 183 (1879).
P. odorata var. ferruginea Rusby in Mem. Torr. Bot. Club, 4 (3): 211 (1895).
P. suaveolens (Vell.) O. Ktze. Rev. Gen. 3(2): 168 (1898).

Podocoma hieracifolia (Poir.) Cass. in Dict. Sci. Nat. 42: 60 (1826).
Polyachyrus oblongiflorus Koster in Blumea, 5: 675 (1945).
Polymnia edulis Wedd. in Ann. Sci. Nat. (ser. 4) 7: 114 (1857).
P. glabrata DC. Prodr. 5: 515 (1836).
P. Siegesbeckia DC. Prodr. 5: 515 (1836).

Porophyllum lanceolatum DC. Prodr. 5: 649 (1836).
P. oblanceolatum Rusby in Mem. Torr. Bot. Club, 6: 64 (1896).
P. platyphyllum Chod. in Bull. Herb. Bois. (ser. 2) 2: 397 (1902).
P. ruderale (Jacq.) Cass. in Dict. Sci. Nat. 43: 56 (1826).
P. ruderale var. angustifolium Hassl. in Trab. Mus. Farm. Med. Buenos Aires, 21: 131 (1909).
P. ruderale var. ellipticum (Cass.) Gray ex Robinson \& Greenman in Proc. Am. Acad. 49: 509 (1913).
Proustia angustifolia Wedd. Chlor. And. 1: 24 (1855).
P. angustifolia var. mollis O. Ktze. Rev. Gen. 3 (2): 168 (1898).
P. pungens Poepp. ex Less. Syn. Comp. 110 (1832).
P. pungens var. cuneifolia (Don) Wedd. Chlor. And. 1: 23 (1855).
P. pungens var. oblongifolia Wedd. Chlor. And. 1: 23 (1855).

Fseudobaccharis acaulis (Wedd.) Cabrera in Not. Mus. La Plata, 9: 248 (1944).
P. boliviensis (Wedd.) Cabrera in Not. Mus. La Plata, 9: 249 (1944).

Pseudogynoxys Benthamii Cabrera in Brittonia, 7: 56 (1950).
Pterocaulon alopecuroideum (Lam.) DC. Prodr. 5: 454 (1836).
P. lanatum O. Ktze. Rev. Gen. 3(2): 169 (1898).
P. latifolium O. Ktze. Rev. Gen. 3(2): 169 (1898).
P. Lorentzii Malme in Kgl. Sv. Vet. Akad. Handl. 27: 22 (1901).
P. purpurascens Malme in Kgl. Sv. Vet. Akad. Handl. 32 (5) : 55 (1899), nomen nudum.
P. virgatum DC. Prodr. 5: 454 (1836).

Salmea scandens (L.) DC. Prodr. 5: 493 (1836).
Sanvitalia versicolor Griseb. in Goett. Abh. 24: 189 (1879).
Schistocarpha Hoffmannii O. Ktze. Rev. Gen. 3(2): 170 (1898).
S. paniculata Klatt in Bull. Soc. Bot. Belg. 31: 210 (1892).
S. triangularis Rusby in Bull. N. Y. Bot. Gard. 4: 392 (1907).

Schkuhria degenerica (O. Ktze.) R. E. Fries in Ark. Bot. 5(13): 22 (1906).
S. multiflora Hook. \& Arn. in Journ. Bot. 3: 322 (1841).
S. mutiflora var. pusilla (Wedd.) Cabrera in Anal. Soc. Cient. Argent. 114: 192 (1932).
S. pinnata (Lam.) O. Ktze. Rev. Gen. 3(2): 170 (1898), in synon.
S. pinnata var. abrotanoides (Roth) Cabrera in Anal. Soc. Cient. Argent. 114: 189 (1932).
S. pinnata var. octoaristata (DC.) Cabrera in Anal. Soc. Cient. Argent. 114: 190 (1932).
Senecio adamantinus Bong. in Bull. Sc. Acad. Pétersb. 5: 97 (1838).
S. adenophyllus Meyen \& Walp. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 282 (1843).
S. agapatensis Sch. Bip. in Bonplandia, 4: 55 (1856), nomen nudum.
S. algens Wedd. Chlor. And. 1: 104 (1856).
S. alternifolius (Rusby) Greenm. in Ann. Missouri Bot. Gard. 10: 76 (1923).
S. amphibolus Wedd. Chlor. And. 1: 109 (1856).
S. attenuatus Sch. Bip. ex Rusby in Mem. Torr. Bot. Club, 3(3): 63 (1893).
S. attenuatus var. microphyllus Britton in Bull. Torr. Bot. Club, 19: 264 $(1892)=$ S. clavifolius.
S. ayopayensis Cuatr. in Fieldiana, Bot. 27 (2): 50 (1951).
S. baccharidifolius Rusby in Bull. N. Y. Bot. Gard. 4: 397 (1907).
S. Bangii Rusby in Mem. Torr. Bot. Club, 3(3): 64 (1893).
S. biacuminatus Rusby in Bull. N. Y. Bot. Gard. 4: 394 (1907).
S. biserrifolius O. Ktze. Rev. Gen. 3(2) : 171 (1898).
S. boliviensis Sch. Bip. ex Klatt in Leopoldina, 24: 127 (1888).
S. Brittonianus Hieron. in Engler, Bot. Jahrb. 29: 72 (1900).
S. Buchtienii Greenm. in Ann. Missouri Bot. Gard. 10: 78 (1923).
S. Cabrerae Cuatr. in Fieldiana, Bot. 27(2): 61 (1951).
S. Cabrerianus Greenm. \& Cuatr. in Fedde, Repert. Spec. Nov. 55: 134 (1953)
S. campanulatus Sch. Bip. ex Klatt in Leopoldina, 24: 126 (1888).
S. campanulatus var. glabrescens Cabrera in Blumea, 7: 198 (1952).
S. canescens (Humb. \& Bonpl.) Cuatr. in Fieldiana, Bot. 27: 43 (1950).
S. canescens var. monocephalus (Wedd.) Cuatr. in Fieldiana, Bot. 27(2): 37 (1951).
S. Cardenasii Cuatr. in Fieldiana, Bot. 27(2): 48 (1951).
S. Chaenocephalus Cabrera in Not. Mus. La Plata, 9: 192 (1944).
S. charaguensis Cuatr. in Fieldiana, Bot. 27(2): 59 (1951).
S. Chodatianus Cuatr. in Collect. Bot. [Barcelona] 3(3): 278 (1953).
S. clavifolius Rusby in Mem. Torr. Bot. Club, 3(3): 64 (1893).
S. clivicola Wedd. Chlor. And. 1: 130 (1856).
S. cochabambensis Cabrera in Blumea, 7: 201 (1952).
S. colaminus Cuatr. in Fieldiana, Bot. 27(2): 58 (1951).
S. comarapensis Cabrera in Darwiniana, 10: 599 (1954).
S. coroicensis Rusby in Bull. N. Y. Bot. Gard. 4: 395 (1907).
S. culcitioides Sch. Bip. ex Wedd. Chlor. And. 1: 103 (1856).
S. dictyophlebius Greenm. in Ann. Missouri Bot. Gard. 25: 801 (1938).
S. epiphyticus O. Ktze. Rev. Gen. 3(2): 173 (1898).
S. expansus Wedd. Chlor. And. 1: 107 (1856).
S. evacoides Sch. Bip. in Bonplandia, 4: 52 (1856).
S. floscosus Britton in Bull. Torr. Bot. Club, 19: 264 (1892).
S. formosus HBK. Nov. Gen. \& Spec. 4: 177 (1820).
S. glacialis Wedd. Chlor. And. 1: 113, t. 18A (1856).
S. glacialis var. adenophylloides (Sch. Bip.) Perkins in Engler, Bot. Jahrb. 49: 230 (1913).
S. glacialis (Meyen \& Walp.) Cuatr. in Fieldiana, Bot. 27: 44 (1950).
S. graveolens Wedd. Chlor. And. 1: 111 (1856).
S. helianthemoides Wedd. Chlor. And. 1: 115 (1856).
S. Herzogii Cabrera in Blumea, 7: 202 (1952).
S. heterotrichius DC. Prodr. 6: 419 (1838).
S. Hohenackeri Sch. Bip. ex Wedd. Chlor. And. 1: 131 (1856).
S. Hualtata Bert. ex DC. Prodr. 6: 417 (1838).
S. humillimus var. vegetus Wedd. Chlor. And. 1: 104 (1856).
S. icoglossus var. araneosus DC. Prodr. 6: 420 (1838).
S. innovans Klatt in Ann. Naturh. Hofmus. Wien, 9: 365 (1894).
S. Jarae Phil. in Anal. Mus. Nac. Chile, Bot. 8: 44 (1891).
S. Klattii Greenm. in Ann. Missouri Bot. Gard. 1: 281 (1914).
S. Kosterae Cabrera in Blumea, 7: 201 (1952).
S. Krukoffii Cuatr. in Fieldiana, Bot. 27(2): 60 (1951).
S. leuceria Cabrera in Blumea, 7: 202 (1952).
S. liabifolius Rusby in Bull. N. Y. Bot. Gard. 4: 396 (1907).
S. longilinguae Cuatr. in Fieldiana, Bot. 27(2): 51 (1951).
S. Mandonianus Wedd. Chlor. And. 1: 228 (1857).
S. medullosus Sch. Bip. ex Greenm. in Ann. Missouri Bot. Gard. 10: 85 (1923).
S. melanolepis DC. Prodr. 6: 424 (1838).
S. Miguelii Cuatr. in Fieldiana, Bot. 27(2): 54 (1951).
S. modestus Wedd. Chlor. And. 1: 105, t. 18B (1856).
S. multinervis Sch. Bip. ex Klatt in Leopoldina, 24: 127 (1888).
S. myrianthus Klatt in Leopoldina, 24: 127 (1888).
S. oblanceolatus Rusby in Bull. N. Y. Bot. Gard. 4: 394 (1907).
S. octophyllus Sch. Bip. ex Rusby in Bull. N. Y. Bot. Gard. 4: 393 (1907).
S. oronocensis DC. Prodr. 6: 423 (1837).
S. pampae Lingelsh. in Fedde, Repert. Spec. Nov. 8: 6 (1910).
S. pampae var. penicillatus Lingelsh. in Fedde, Repert. Spec. Nov. 8: 6 (1910).
S. pectioides Rusby in Bull. $\mathfrak{N}$. Y. Bot. Gard. 4: 395 (1907).
S. pensilis Greenm. in Ann. Missouri Bot. Gard. 25: 813 (1938).
S. pentamerus Cuatr. in Fieldiana, Bot. 27 (2): 57 (1951).
S. Pentlandianus DC. Prodr. 6: 421 (1838).
S. Pflanzii (Perkins) Cuatr. in Fieldiana, Bot. 27: 44 (1950).
S. pongoënsis Cuatr. in Fieldiana, Bot. 27(2): 61 (1951).
S. potosianus Klatt in Abh. Naturf. Ges. Halle, 15: 331 (1881).
S. praeruptorum Sch. Bip. ex Klatt in Leopoldina, 24: 127 (1888).
S. prunifolius Wedd. Chlor. And. 1: 102 (1856).
S. prunioides Rusby in Bull. N. Y. Bot. Gard. 4: 396 (1907).
S. psidiifolius Rusby in Mem. Torr. Bot. Club, 6: 66 (1896).
S. psychrophilus Wedd. Chlor. And. 1: 112 (1856).
S. pulviniformis Hieron. in Engler, Bot. Jahrb. 21: 359 (1895).
S. Reicheanus Cabrera in Lilloa, 15: 403 (1949).
S. repens DC. Prodr. 6: 423 (1838).
S. rhizomatus Rusby in Mem. Torr. Bot. Club. 6: 66 (1896).
S. rudbeckiaefolius Meyen \& Walp. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 283 (1843).
S. rufescens (Humb. \& Bonpl.) Cuatr. in Fieldiana, Bot. 27: 45 (1950).
S. sailapatensis Cuatr. in Fieldiana, Bot. 27(2): 52 (1951).
S. senecioides (HBK.) O. Ktze. Rev. Gen. 3(2): 177 (1898).
S. Sepium Sch. Bip. ex Rusby in Bull. N. Y. Bot. Gard. 4: 394 (1907).
S. serratifolius (Meyen \& Walp.) Cuatr. in Fieldiana, Bot. 27: 45 (1950).
S. sinapoides Rusby in Mem. Torr. Bot. Club, 6: 65 (1896).
S. Smithii DC. Prodr. 6: 412 (1838).
S. Sprucei Britton in Bull. Torr. Bot. Club, 19: 265 (1892) $=$ S. Brittonianus.
S. Steinbachianus Cuatr. in Fieldiana, Bot. 27(2): 55 (1951).
S. stylotrichus Cabrera in Not. Mus. La Plata, 15: 107 (1950).
S. subdecurrens Sch. Bip. ex Wedd. Chlor. And. 1: 109 (1856).
S. subglomerosus Greenm. in Ann. Missouri Bot. Gard. 10: 93 (1923).
S. subvulgaris O. Ktze. Rev. Gen. 3(2): 178 (1898).
S. tabacifolius Rusby in Bull. N. Y. Bot. Gard. 4: 396 (1907).
S. tablensis Cabrera in Blumea, 7: 203 (1952).
S. tenuicaulis Sch. Bip. ex Klatt in Leopoldina, 24: 128 (1888).
S. tephrosioides Turcz. in Bull. Soc. Nat. Mosc. 24(2): 92 (1851).
S. unduavianus Cuatr. in Fieldiana, Bot. 27(2): 49 (1951).
S. viridilacus Cabrera in Blumea, 7: 199 (1952).
S. vulgaris L. Sp. Pl. 867 (1753).
S. Weddellii Cabrera in Not. Prelim. Mus. La Plata, 3: 122 (1934).
S. Williamsii Rusby in Bull. N. Y. Bot. Gard. 8: 134 (1912) = S. Cabrerianus.
S. yungasensis Britton in Bull. Torr. Bot. Club, 19: 264 (1892).
S. yurensis Rusby in Bull. N. Y. Bot. Gard. 8: 133 (1912).

Siegesbeckia flosculosa L'Hérit. Stirp. Nov. 37, t. 19 (1786).
S. orientalis L. Sp. Pl. 900 (1753).

Solidago microglossa DC. Prodr. 5: 332 (1836).
S. polyglossa DC. Prodr. 5: 332 (1836).

Sonchus asper (L.) Vill. Hist. Pl. Dauph. 3: 158 (1789).
S. oleraceus L. Sp. Pl. 794 (1753).

Sphaereupatorium Hoffmannii O. Ktze. Rev. Gen. 3(2): 147 (1898).
Spilanthes Acmella L. Mant. 2: 475 (1771).
S. ocymifolia forma radiifera A. H. Moore in Proc. Am. Acad. 42: 533 (1907).

Stemodontia elongata Rusby in Mem. Torr. Bot. Club, 3 (3): 58 (1893) = Heliopsis buphthalmoides.
Stevia Bangii Rusby in Mem. Torr. Bot. Club, 4 (3): 209 (1895).
S. Bangii var. dyscrita Robinson in Contrib. Gray Herb. 100: 3 (1932).
S. Benderi Perkins in Engler, Bot. Jahrb. 49: 221 (1913).
S. Benderi var. Cardenasii Robinson in Contrib. Gray Herb. 104: 7 (1934).
S. bermejensis Hieron. in Engler, Bot. Jahrb. 40: 361 (1908).
S. boliviensis Sch. Bip. ex Griseb. in Goett. Abh. 24: 166 (1879).
S. brevipapposa Hieron. in Engler, Bot. Jahrb. 22: 718 (1897) $=$ S. boliviensis.
S. Bridgesii Rusby in Bull. N. Y. Bot. Gard. 4: 377 (1907).
S. calderillensis Hieron. in Engler, Bot. Jahrb. 40: 356 (1908).
S. camachensis Hieron. in Engler, Bot. Jahrb. 40: 359 (1908).
S. cardiatica Perkins in Engler, Bot. Jahrb. 49: 222 (1913).
S. chacoënsis R. E. Fries in Ark. Bot. 5(13): 7, t. 2 (1906).
S. Chamaedrys Griseb. in Goett. Abh. 24: 167 (1879).
S. clivicola Robinson in Contrib. Gray Herb. 100: 4 (1932).
S. cochabambensis Hieron. in Engler, Bot. Jahrb. 22: 726 (1897).
S. copiosa Koster in Blumea, 5: 645 (1945).
S. discolor Robinson in Contrib. Gray Herb. 100: 5 (1932).
S. eclipes Robinson in Contrib. Gray Herb. 96: 5 (1931).
S. elatior var. austrina Robinson in Contrib. Gray Herb. 96: 7 (1931).
S. Fiebrigii Hieron. in Engler, Bot. Jahrb. 40: 365 (1908).
S. filipes Rusby in Bull. N. Y. Bot. Gard. 8: 126 (1912).
S. fruticosa Griseb. in Goett. Abh. 24: 167 (1879).
S. galeopsidifolia Hieron. in Engler, Bot. Jahrb. 22: 719 (1897).
S. glanduloso-pubescens Hieron. in Engler, Bot. Jahrb. 40: 360 (1908).
S. glomerata Hieron. in Engler, Bot. Jahrb. 40: 357 (1908).
S. grandidentata Sch. Bip. ex Rusby in Mem. Torr. Bot. Club, 6: 55 (1896) $=$ S. soratensis.
S. humilis Hieron. in Engler, Bot. Jahrb. 22: 730 (1897) $=$ S. obovata.
S. kuhnioides Rusby ex Robinson in Contrib. Gray Herb. 96: 7 (1931).
S. Kuntzei Hieron. in Engler, Bot. Jahrb. 22: 733 (1897).
S. Mandonii Sch. Bip. ex Robinson in Contrib. Gray Herb. 77: 6 (1926).
S. melancolica Robinson in Contrib. Gray Herb. 90: 15 (1930).
S. mercedensis Hieron. in Engler, Bot. Jahrb. 22: 735 (1897).
S. mercedensis var. glanditecta Robinson in Contrib. Gray Herb. 90: 16 (1930).
S. neglecta Rusby in Mem. Torr. Bot. Club. 4(3): 209 (1895).
S. obovata Rusby in Mem. Torr. Bot. Club, 6: 55 (1896).
S. obovata var. aristifera Robinson in Contrib. Gray Herb. 90: 17 (1930).
S. pauciflora Koster in Blumea, 6: 266 (1948).
S. reclinata Rusby in Bull. N. Y. Bot. Gard. 8: 127 (1912).
S. samaipatensis Robinson in Contrib. Gray Herb. 96: 15 (1931).
S. santacruzensis Hieron. in Engler, Bot. Jahrb. 22: 731 (1897).
S. sarensis Robinson in Contrib. Gray Herb. 100: 9 (1932).
S. sarensis var. dissiticeps Robinson in Contrib. Gray Herb. 100: 10 (1932).
S. Schultzii Hieron. in Engler, Bot. Jahrb. 22: 721 (1897) = S. boliviensis.
S. setifera Rusby ex Robinson in Contrib. Gray Herb. 100: 10 (1932).
S. soratensis Hieron. in Engler, Bot. Jahrb. 40: 356 (1908).
S. soratensis var. mecoyensis Robinson in Contrib. Gray Herb. 100: 11 (1932).
S. soratensis var. subeglandulosa (Hieron.) Hieron. in Engler, Bot. Jahrb. 40: 359 (1908).
S. Stuebelii Hieron. in Engler, Bot. Jahrb. 21: 328 (1895).
S. tapacariensis Hieron. in Engler, Bot. Jahrb. 22: 734 (1897) = S. Bangii.
S. tarijensis Hieron. in Engler, Bot. Jahrb. 40: 362 (1908).
S. totorensis Robinson in Contrib. Gray Herb. 96: 16 (1931).
S. triaristata Hieron. in Engler, Bot. Jahrb. 40: 358 (1908).
S. tunariensis Hieron. in Engler, Bot. Jahrb. 22: 713 (1897).
S. urticaefolia var. boliviensis (Hieron.) Robinson in Contrib. Gray Herb. 100: 44 (1932).
S. urticaefolia var. pallidiflora Robinson in Contrib. Gray Herb. 96: 16 (1931).
S. vaccinioides Koster in Blumea, 5: 646 (1945).
S. yaconensis var. subeglandulosa Hieron. in Engler, Bot. Jahrb. 40: 366 (1908).

Stuckertiella capitata (Wedd.) Beauverd in Bull. Soc. Bot. Genève (ser. 2), 5: 206 (1913).
Synedrellopsis Grisebachii Hieron. ex O. Ktze. Rev. Gen. 3(2): 180 (1898).
Tagetes daucoides Schrad. Ind. Sem. Hort. Gotting. 5 (1833).
T. erythrocephala Rusby in Bull. N. Y. Bot. Gard. 8: 133 (1912).
T. gigantea Carr. in Rev. Hort. 58: 107 (1886).
T. graveolens L'Hérit. in DC. Prodr. 5: 644 (1836).
T. Mandonii Sch. Bip. ex Klatt in Leopoldina, $25: 109$ (1889).
T. maxima O. Ktze. Rev. Gen. 3(2) : 181 (1898).
T. micrantha Cav. Icon. 4: 31, t. 352 (1797).
T. multiflora HBK. Nov. Gen. \& Spec. 4: 197 (1820).
T. pusilla HBK. Nov. Gen. \& Spec. 4: 194 (1820).
T. silenoides Meyen \& Walp. in Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 272 (1843).
Tessaria absinthoides (Hook. \& Arn.) DC. Prodr. 5: 457 (1836).
T. integrifolia R. \& P. Syst. 213 (1798).

Trichocline incana (Lam.) Cass. in Dict. Sci. Nat. 55: 216 (1828).
T. reptans (Wedd.) Robinson in Proc. Am. Acad. 49: 515 (1913).

Trichogonia capitata (Rusby) Robinson in Proc. Am. Acad. 47: 193 (1911).
Tridax boliviensis (Wedd.) R. E. Fries in Ark. Bot. 5(13) : 21 (1906).
T. procumbens L. Sp. Pl. 900 (1753).

Trixis aggregata Rusby in Mem. Torr. Bot. Club, 6: 71 (1896).
T. antimenorrhoea var. heterophylla O. Ktze. Rev. Gen. 3(2) : 183 (1898).
T. antimenorrhoea var. petiolata O. Ktze. Rev. Gen. 3(2): 183 (1898).
T. diffusa Rusby in Bull. N. Y. Bot. Gard. 8: 134 (1912).
T. divaricata (HBK.) Spreng. Syst. Veg. 3: 501 (1826).
T. rigida Koster in Blumea, 5: 682 (1945).

Verbesina australis Baker in Mart. Fl. Bras. 6(3): 215 (1884).
V. Benderi Perkins in Engler, Bot. Jahrb. 49: 227 (1913).
V. boliviana Klatt in Ann. Naturh. Hofmus. Wien, 9: 361 (1894).
V. Bridgesii Rusby in Mem. Torr. Bot. Club, $4(3): 212(1895)=$ V. boliviana.
V. cinerea Rusby in Mem. Torr. Bot. Club, 6: 63 (1896).
V. Cumingii Sch. Bip. ex Blake in Amer. Journ. Bot. 12: 634 (1925).
V. elegans HBK. Nov. Gen. \& Spec. 4: 204 (1820).
V. flavovirens R. E. Fries in Ark. Bot. 5(13): 19, t. 3 (1906).
V. leucactinota Robinson in Proc. Am. Acad. 47: 213 (1911).
V. macrophylla (Cass.) Blake in Bull. Torr. Bot. Club, 51: 430 (1924).
V. Mandonii Sch. Bip. ex Robinson \& Greenm. in Proc. Am. Acad. 34: 547 (1899).
V. Pflanzii Perkins in Engler, Bot. Jahrb. 49: 227 (1913).
V. rhomboidea Koster in Blumea, 6: 270 (1948).
V. semidecurrens O. Ktzę. Rev. Gen. 3(2) : 183 (1898).
V. soratae Sch. Bip. ex Robinson \& Greenm. in Proc. Am. Acad. 34: 551 (1899).
V. subcordata DC. Prodr. 5: 614 (1836).

Vernonia apiculata Mart. ex DC. Prodr. 5: 51 (1836).
V. arborescens Sw. Fl. Ind. Occ. 3: 1320 (1806).
V. arborescens var. cuneifolia Britton in Bull. Torr. Bot. Club, 18: 331 (1891) $=\mathrm{V}$. Rusbyi.
V. argyropappa Buek, Index Prodr. 2: v (1840).
V. aristosquamea Britton in Bull. Torr. Bot. Club, 18: 332 (1891) = V. argyropappa ?
V. auriculata Griseb. in Goett. Abh. 24: 163 (1879).
V. baccharoides HBK. Nov. Gen. \& Spec. 4: 40 (1820).
V. Bakerana Britton in Bull. Torr. Bot. Club, 18: 331 (1891).
V. Bangii Rusby in Mem. Torr. Bot. Club, 6: 52 (1896) $=$ V. baccharoides.
V. boliviana Britton in Bull. Torr. Bot. Club, 18: 332 (1891).
V. brachylepis Griseb. in Goett. Abh. 24: 164 (1879).
V. brasiliana (L.) Druce in Rept. Bot. Exch. Club Brit. Isl. 3: 426 (1914).
V. brevipetiolata Sch. Bip. ex Baker in Mart. Fl. Bras. 6(2): 85 (1873).
V. breviramosa Rusby in Bull. N. Y. Bot. Gard. 8: 123 (1912) $=$ V. scorpioides.
V. Buchtienii Gleason in Amer. Journ. Bot. 10: 302 (1923).
V. canaminana Gleason in Amer. Journ. Bot. 10: 309 (1923).
V. centauropsidea Hieron. in Engler, Bot. Jahrb. 40: 353 (1908).
V. Conwayi Rusby in Bull. N. Y. Bot. Gard. 8: 125 (1912).
V. cordiaefolia HBK. Nov. Gen. \& Spec. 4: 38 (1820).
V. coriacea Less. in Linnaea, 6: 661 (1831).
V. costata Rusby in Mem. Torr. Bot. Club, 6: 53 (1896).
V. crassifolia Rusby in Bull. N. Y. Bot. Gard. 8: 124 (1912).
V. deflexa Rusby in Bull. N. Y. Bot. Gard. 4: 376 (1907).
V. densipaniculata Rusby in Bull. N. Y. Bot. Gard. 8: 126 (1912).
V. digitata Rusby in Bull. N. Y. Bot. Gard. 8: 125 (1912) $=$ V. megaphylla.
V. echitifolia Mart. ex DC. Prodr. 5: 60 (1836).
V. ferruginea Less. in Linnaea, 4: 271 (1829).
V. fulta Griseb. in Goett. Abh. 24: 164 (1879).
V. fulta forma tomentosa Koster in Blumea, 5: 643 (1945).
V. grandiflora Less. in Linnaea, 6: 660 (1831).
V. herbacea (Vell.) Rusby in Mem. Torr. Bot. Club, 4(3): 209 (1895).
V. ixiamensis Rusby in Bull. N. Y. Bot. Gard. 8: 125 (1912).
V. jubifera Rusby in Mem. Torr. Bot. Club, 6: 53 (1896).
V. Kuntzei Hieron. in Engler, Bot. Jahrb. 22: 678 (1897).
V. laurifolia DC. Prodr. 5: 30 (1836).
V. Lehmannii Hieron. in Engler, Bot. Jahrb. 19: 44 (1894).
V. ligulaefolia Mart. ex DC. Prodr. 5: 45 (1836).
V. Mandonii Sch. Bip. ex Gleason in Amer. Journ. Bot. 10: 301 (1923).
V. mapirensis Gleason in Amer. Journ. Bot. 10: 307 (1923).
V. mattogrossensis Hieron. in Engler, Bot. Jahrb. 22: 696 (1897).
V. megaphylla Hieron. in Verh. Bot. Ver. Brandenb. 48: 195 (1907).
V. membranacea Gardn. in Hook. Journ. Bot. 5: 217 (1846).
V. mollis HBK. Nov. Gen. \& Spec. 4: 36 (1820).
V. myriocephala DC. Prodr. 5: 40 (1836).
V. obtusata Less. in Linnaea, 6: 662 (1831).
V. patuliflora Rusby in Bull. N. Y. Bot. Gard. 4: 376 (1907) $=$ V. cordiaefolia.
V. paucifolia Rusby in Mem. Torr. Bot. Club, 3 (3): 50 (1893) $=$ V. membranacea.
V. paucisquamata Rusby in Bull. N. Y. Bot. Gard. 4: 376 (1907).
V. pinguis Griseb. in Goett. Abh. 24: 165 (1879).
V. polycephala DC. Prodr. 5: 39 (1836).
V. prenanthoides Gleason in Amer. Journ. Bot. 10: 308 (1923).
V. pseudomollis Gleason in Amer. Journ. Bot. 10: 307 (1923).
V. pyenantha Benth. Pl. Hartw. 134 (1844).
V. remotiflora L. C. Rich. in Act. Soc. Hist. Nat. Paris, 1: 112 (1792).
V. robusta Rusby in Mem. Torr. Bot. Club, 6: 54 (1896).
V. rubricaulis HBK. Nov. Gen. \& Spec. 4: 33 (1820).
V. rufo-papposa var. latifolia Hieron. in Engler, Bot. Jahrb. 22: 700 (1897) = V. membranacea.
V. Rusbyi Gleason in Amer. Journ. Bot. 19: 753 (1932).
V. saltensis Hieron. in Engler, Bot. Jahrb. 22: 691 (1897).
V. santacruzensis Hieron. in Engler, Bot. Jahrb. 22: 699 (1897).
V. scorpioides (Lam.) Pers. Synops. Pl. 2: 404 (1807).
V. scorpioides var. sororia (DC.) Baker in Mart. Fl. Bras. 6(2): 101 (1873).
V. senecionaefolia Britton in Bull. Torr. Bot. Club, 18: 331 (1891) = V. fulta.
V. setososquamosa Hieron. in Engler, Bot. Jahrb. 22: 684 (1897).
V. simplex Less. in Linnaea, 4: 280 (1829).
V. sordido-papposa Hieron. in Engler, Bot. Jahrb. 22: 697 (1897).
V. squamipes Rusby in Bull. N. Y. Bot. Gard. 8: 124 (1912) = V. membranacea.
V. squamulosa Hook. \& Arn. in Hook. Compan. Bot. Mag. 2: 44 (1836).
V. subacuminata Hieron. in Engler, Bot. Jahrb. 22: 691 (1897).
V. tarijensis (Griseb.) Hieron. in Engler, Bot. Jahrb. 22: 682 (1897).
V. tricholepis DC. Prodr. 5: 54 (1836).
V. tristis Hieron. in Engler, Bot. Jahrb. 22: 683 (1897).
V. trixioides Rusby in Mem. Torr. Bot. Club, 6: 54 (1896) $=$ V. fulta.
V. varroniaefolia DC. Prodr. 5: 56 (1836).
V. yungasensis Britton in Bull. Torr. Bot. Club, 18: 332 (1891).

Viguiera anchusaefolia (DC.) Baker in Mart. Fl. Bras. 6(3): 222 (1884).
V. australis Blake in Contrib. Gray Herb. 54: 148 (1918).
V. fusiformis Blake in Contrib. Gray Herb. 54: 145 (1918).
V. glutinosa Rusby in Mem. Torr. Bot. Club, 4 (3): 211 (1895) $=$ Flourensia heterolepis.
V. lanceolata Britton in Bull. Torr. Bot. Club, 19: 149 (1892).
V. macrorhiza Baker in Mart. Fl. Bras. 6(3): 225 (1884).
V. Mandonii Sch. Bip. ex Rusby in Mem. Torr. Bot. Club, 3 (3): 60 (1893) = V. lanceolata.
V. pazensis Rusby in Mem. Torr. Bot. Club, 3(3): 59 (1893).
V. Pflanzii Perkins in Engler, Bot. Jahrb. 49: 226 (1913).
V. retroflexa Blake in Contrib. Gray Herb. 54: 146 (1918).

Villanova oppositifolia Lag. Nov. Gen. \& Spec. 31 (1815).
Wedelia brachycarpa Baker in Mart. Fl. Bras. 6(3): 181 (1884).
W. Holwayi Blake in Bot. Gaz. 74: 420 (1922).
W. isolepis Blake in Bot. Gaz. 74: 421 (1922).

Werneria apiculata Sch. Bip. in Bonplandia, 4: 52 (1856).
W. aretioides Wedd. Chlor. And. 1: 86 (1856).
W. boraginifolia O. Ktze. Rev. Gen. 3(2): 184 (1898) = W. strigosissima.
W. caespitosa var. Haenkei Wedd. Chlor. And. 1: 83 (1856).
W. caulescens (Wedd.) Rusby in Bull. N. Y. Bot. Gard. 4: 398 (1907).
W. ciliata Wedd. ex Sch. Bip. in Linnaea, 34: 530 (1866), in synon. $=$ W. pectinata.
W. ciliolata A. Gray in Proc. Am. Acad. 5: 140 (1861).
W. dactylophylla Sch. Bip. in Bonplandia, 4: 53 (1858).
W. dactylophylla forma glabriuscula Rockhausen in Engler, Bot. Jahrb. 70: 286 (1939).
W. digitata Wedd. Chlor. And. 1: 86, t. 17D (1856).
W. heteroloba Wedd. Chlor. And. 1: 88, t. 16A (1856).
W. Knocheae Perkins in Engler, Bot. Jahrb. 49: 230 (1913) $=$ W. pectinata.
W. Mandoniana Wedd. ex Klatt in Ann. Naturh. Hofmus. Wien, 9: 367 (1894) $=\mathrm{W}$. Orbignyana.
W. melanandra Wedd. Chlor. And. 1: 88 (1856).
W. nubigena HBK. Nov. Gen. \& Spec. 4: 193 (1820).
W. Orbignyana Wedd. Chlor. And. 1: 85 (1856).
W. pectinata Lingelsh. in Fedde, Repert. Spec. Nov. 8: 6 (1910).
W. plantaginifolia Wedd. ex Klatt in Ann. Naturh. Hofmus. Wien, 9: 367 (1894).
W. pygmaea Gill. ex Hook. \& Arn. in Journ. Bot. 3: 348 (1841).
W. setosa Wedd. ex Sch. Bip. in Linnaea, 34: 530 (1865-66), in synon. $=$ W. strigosissima.
W. solivaefolia Sch. Bip. in Bonplandia, 4: 53 (1856).
W. spathulata Wedd. Chlor. And. 1: 85, t. 17A (1856).
W. staticaefolia Sch. Bip. in Bonplandia, 4: 53 (1856).
W. strigosissima A. Gray in Proc. Am. Acad. 5: 140 (1861).
W. villosa A. Gray in Proc. Am. Acad. 5: 139 (1861).

Wulffia baccata (L. f.) O. Ktze. Rev. Gen. 3(2): 184 (1898).
Xanthium orientale L. Sp. Pl. (ed. 2) 2: 1400 (1763).
X. spinosum L. Sp. Pl. 987 (1753).

Zexmenia foliosa Rusby ex W. W. Jones in Proc. Am. Acad. 41: 162 (1905).
Z. Herzogii Hassl. in Fedde, Repert. Spec. Nov. 7: 357 (1909).
Z. mikanioides (Britton) Blake in Journ. Bot. 53: 200 (1915).

Zinnia pauciflora L. Sp. Pl. (ed. 2) 2: 1269 (1763).


[^0]:    ${ }^{1}$ Looser, G. "El 'Notholaena’ en Chile," Darwiniana 7: 62. 1945.

[^1]:    ${ }^{2}$ Weatherby, C. A. Contrib. Gray Herb. 124: 19. 1939.
    ${ }^{3}$ Hicken, C. M., Rev. Mus. La Plata 15: 256. 1908.

[^2]:    5c. var. cochisensis.

[^3]:    ${ }^{6}$ Weatherby, C. A. Contrib. Gray Herb. 124: 21. 1939.

[^4]:    Uruguay: Commerson. Montevideo (TYPE, P; fragment, F). Commerson, Montevideo (Photograph of probable Isotype, in Madrid: F, us). Commerson, Montevideo (type of S. prustrata Cav., p). Herter 96563. Eifler, Dept. San José (mo). Kuntze, Nov. 1892, Sierra de Locy (F, Ny). Rosenguil B 467, Rio Yi and Matanzas, Dept. Flores (GH). Rosengurtt B 725. Cerro Colorado, Dept. Florida (us). Rosengurtt et al. PE 596 1/2, Juan Jackson, Dept. Soriano (us). St. Hilaire, "Pâturages près de Salto Grande" Uruguay (rype of S. intermedia; p)

    Argentina: Bartlett 20183, Rosario, Sierra de Córdoba, Prov. Córdoba (US). Krapolickas 2919. Tandil, Prov. Buenos Aires (mo). Kuntze, Dec. 1891, Córdoba (Ny). Montero 522, Loreto. Dep. Candelaria, Gob. Misiones (US) Pedersen 1221, Est. Herradura, Dep. Boca del Bermejo, Gob. Formosa (us).

    Without definite locality: Née, "Chile" (Photograph of specimen in 1: F). Née, "Colonia de Sacramento" (Fragment from Madrid: F).

[^5]:    Chile: Atacama: Gigoux. March 1886, vicinity Copiapó, Dept. Copiapó (Gh). Johnston 4984. vicinity Copiapó, Dept. Copiapó (GH). Coqumbo: Joseph 5439, La Serena (us). W'erdermann 130. Coquimbo (UC, F. GH, Mo). W'orth \& Morrison 16445. east Fray Jorge Forest. Dept. Ovalle (gh, mo, uc). Santiago: Joseph 969. Cartagena (us). Joieph 16-1. Santiago (us). Without definite locality: Joseph 1216. 4 Nov. 1920 (US). Bebn, 4 Feb. 1934, Coucou (vc). Gay, "Prov. de ......" (GH).

    Argentina: Buenos Aires: Altures 446, "Km. 54 - F. C. S." (us). Burkart 8510, Baradero. Rio Parana (Ny, F). Eyerdam et al. 23605, 7 kilometers east Mar del Plata (GH, UC). Eyerdap: et al. 23731. Dept. Coronel Dorego, Sauce Chico Rio, 120 kilometers west Bahia Blanca ( $\mathrm{GH}, \mathrm{uC}$ ). Parker 3, Buenos Aires (GH). Jujuy: Lorentz \& Hieronymus, 13 May 1873, El Volcan (ny). Venturi 6914. Tilcara, Dept. Tilcara (cs). Venturi 10075, Tres Cruces, Dept. Humahuaca ( gh ). Mendoza: Gillies 105, Mendoza, (isotype or type fragment of Malva sulphurea Gillies: Gh). Rio Negro: Fischer 210, vicinity General Roca (ny, mo, Us, F, GH). Meyer 7242, Salcheta (us). W'ilkes Exped. 1838-42, "Rio Negro, north Patagonia" (GH, us). Salta: Venturi 6911, San Carlos, Dept. San Carlos (us). Tucumina: Venturi 445, Chanar Pazo, Dept. Leales (us). Without

[^6]:    Fig. 1. Graphs prepared from hybrid index numbers derived from sooring plants of four different hybrid populations and one population each of $I$.. Lescturii and I. densipila. The number of plants scored to produce each graph is as follows: 53128-129 plants: 53129-95 plants: 53131-50 plant:: 53133-159 plant: : 53135-25 plants: 53140-50 plants: Map 1 ,hows the lecation of each population.

[^7]:    *Reciprocal pollinations were made for all combinations. Since there were no instances where significant differences in the data from reciprocal combinations occurred, these data were merged.

[^8]:    ${ }^{3}$ Fruits developed in many pollinated flowers involving crosses with L.. grandiflora but they were empty of viable seeds. Parthenocarpy was more commonly observed in L. grandiflora than in the other species. Incompatibility studies in lesquerella should definitely take parthenocarpy into account, if fruit swelling is used as an indication of a successful pollination.

[^9]:    ${ }^{4}$ The genetics of self-incompatibility in lesquerella was included as part of his the is work by Dr. Iexter Sampson (Harvard Unisersity thesis, 1956). Up) to the present, this work has not been published.

[^10]:    ${ }^{5}$ I am indebted to Dr. W. H. Anderson of the U. S. National Museum for

[^11]:    ${ }^{2}$ Condensed and revised from a dissertation submitted to the Department of Botany in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the (iraduate School of Arts and Sciences. Duke L'nivervity, June 11555.

[^12]:    ${ }^{2}$ Darlington. William. 18ty. Memorials of John Bartram and Humphrey Marshall. Philadelphia, Linsay and Blakiston. pp. 576-57.

[^13]:    "I beg leave to inform you, that the new edition of Genera Linnaei is safely arrived. The first volume is only bound in paper. I am happy to see that the editor, my friend D. Schreber, has done what I required from him. He has given your name to a hitherto undescribed plant, that belongs to the Syngenesia, Polygamia aequalis, which he names Marshallia."

[^14]:    "I have just received yours of the 9th instant, and am very much pleased to hear of the arrival of the Genera Plantarum. I am very sensible of the
    ${ }^{3}$ (Kew) Bulletin of Miscellaneous Information, Numbers 6. 1.8 \& 9. p. +32. 1935.
    ${ }^{4}$ (Kew) Bulletin of Miscellanerous Information, Number 3, p. 129. 1940.
    ${ }^{5}$ Harshberger, John W. 1894. Botanists of Philadelphia. Philadelphia T. C. Davis \& Sons, pp. 97-107.

[^15]:    ${ }^{6}$ In the introductory enumeration of genera contained in this work (page xxxv) the generic name is spelled Marschallia. This is clearly an orthographic variant of Marshallia, the accepted spelling which appears in the body of the work (page 836).
    ${ }^{7}$ While the generic name Persoonia is attributed by Merrill (Index Rafinesquianus, page 240.1949) to Rafinesque (Med. Repos. II. 5: 353. 1808), the name was actually never proposed by Rafinesque as new. In the reference, Rafinesque merely indicated that Marshallia Schreb. has priority over Michaux's "personia" and that the latter name was already appropriated. Thus the indexing of the name as Merrill has done, tends to misrepresent Rafinesque's intention. The name is clearly an orthographic variant of Persoonia Michx., intentionally decapitalized to denote its synonymous position.
    ${ }^{8}$ Differing only in orthography.

[^16]:    ${ }^{0}$ Cassini, H. Dictionnaire des Sci. Nat., Paris, 1816-1834.
    ${ }_{11}^{10}$ Lessing, C. F. Synopsis Gen. Comp. page 241. 1832.
    ${ }_{12}^{11}$ De Candolle, A. P. Prodromus 5: 680. 1836.
    ${ }^{12}$ Gray. Asa and John Torrey. Flora of North America 2: 390. 1842.

[^17]:    ${ }^{13}$ A meticulous study of the nomenclature of Marshallia Schreb. suggests that the name may have in reality been unnecessarily conserved. The formal action leading to its conservatoon was undertaken by Dr. R. Mansfeld of the Rotanisches Museum. Berlin, a full report of which is given in the Kew Bulletin, page 432, 1935. The basic assumption which forms the crux of the problem is that Marshallia Schreb. (Compositae) (ien. Pl. 2: 810.1791, is considered to be a later homonym of Marshallia J. F. Gmel. (Flacourtiaceae) Syst. Nat. 2: 836. 1-91. Accordingly, Marshallia Schreb. is illegitimate even though the carlier homomem. Marshallia Gmel., has been treated as a synonym on taxonomic grounds (Article 64, International Code of Botanical Nomenclature, 1956). If, on this basis, Marshallia Schreb. were not protected by conservation, Phyteumopsis Juss. ex Poir. would become the valid name.

    As presented by Mansfeld, Marshallia J. F. Gmel. (Flacourtiaceae) Sist. Nat. 2: *36. 1791, is a new name for Lagunezia Scop. Introd. (ien. 216. 17\%, being itself hut a newer name for Racouliea Aubl. 1775. That genus is now recognized as Homulium Jacq. 1760, Section Racoubea Endl. 1839.

    The two homonyms in question have equal priority as to the year of publication, however, both having been validly published in 1791. There is a suggestion in favor of the priority of Marshallia Schreb., inasmuch as this genus (with full reference to cdition and page) is itself catalogued by (imelin in his Systema Naturae, 1791. This would indicate that Schreber's edition of Linnacus' (iencra Planfarum was published, in 1791, prior to Gmelin's Systema Naturae of the same vear. If this is true, all of the names enumerated in the generic synonymy above would thus sutomatically be eliminated from consideration, including Phytermopsis Juss. ex Poir. On the basis of this reasoning, Marshallia Schreb, becomes the legitimate name and there was no real necessity for its conservation. However, the action of conservation by the International Botanical Congress has diminated any ponsibility for confusion.

[^18]:    ${ }^{14}$ Bulletin of the Charleston Muscum. vol. 8. no. 5. May 1912. edited by Paut M. Rea.

[^19]:    ${ }^{15}$ The original spelling with the single " $i$ " is treated in accordance with Recommendation 73c of the International Code of Botanical Nomenclature, 1956.

[^20]:    ${ }^{16}$ Planta acaulis arte scaposa vel subscaposa cum caule breve (minusquam ${ }^{1 / 4}$ longitudo pedunculi), foliis caulinis paucis; superficies foliorum cum nervis lateralibus obscuris sine amplificationem: foliis, squamulis involucri ac paleis receptaculi plerumque supra glanduliferis, et sparse glandulari-atomiferis; acheniis ad maturitatem turbinatis, ad apicem late truncatis, 10 -costatis, villosis, trichomis longioribus quam spatium inter costas adjacentes: squamis pappi (1-) $1.5-2.5(-3) \mathrm{mm}$. longis, plerumque regulariter serratis sed interdum irregulariter laceratis. (GH-Type, coarse sand, plowed fire lane. 3 miles west of Leland along U. S. Rt. 76. Brunswick County, North Carolina. R. K. Godfrey f918t. 21 May 1949: Isotypes-bm, deke, g, gi, VA, nesc; NCU).

[^21]:    ${ }^{15}$ A Journal of Travels into the Arkansas Territory during the Year 1819. Philadelphia: printed and published by Thos. H. Palmer. 1821. Reprinted as Volume 13 of "Early Western Travels," edited by G. H. Thwaites.

[^22]:    "Marshallia spiralis Raf. smooth subscapose, leaves radical linear lanceolate obtuse uninerve, scape elongate spiraly grooved, pubescent above, perianthe segments linear obtuse smooth-in Arkansas and West Louisiana found by Binder, near to M. lanceolata, but quite distinct, leaves narrower 3 inches long, scape twisted as some Xurides (not so in M. lanceolata) pedal, flower incarnate."

[^23]:    ${ }^{14}$ See discussion under M. graminifolia for the erroneous application of the epithers "angustifolia" and "graminifolia" to $M$. tenuifolia.

[^24]:    Arnold Arboretum (A)
    Allan Hancock Foundation, University of Southern California (AHFH)
    University of Arizona (ARIZ)
    Botanical Museum and Herbarium, Copenhagen (C)
    Chicago Natural History Museum (F)
    Conservatoire et Jardin Botaniques, Genève (G)
    Gray Herbarium (GH)
    Botanische Anstalten der Martin Lüther Universität, Halle (HAL)
    Royal Botanic Gardens, Kew (K)
    Botanische Staatssammlung, Munich (M)
    Instituto de Biología, Mexico (MEXU)
    University of Michigan (MICH)
    Missouri Botanical Garden (MO)
    New York Botanical Garden (NY)
    Muséum National d'Histoire Naturelle, Paris (P)
    Academy of Natural Sciences, Philadelphia (PH)
    Naturhistoriska Riksmuseum, Stockholm (S)
    Botanical Museum and Herbarium, Utrecht (U)
    University of California (UC)
    United States National Museum (US)
    Naturhistorisches Museum, Wien (W)

[^25]:    - 1940. On the phylogeny of the Euphorbiaceae and some of their presumed allies. Rev. Univ., Chile 25: 205-220.

    1. 1941. On the systematic position of Daphniphyllum and its allies. Lingnan Sci. Jour. 20: 79-103.
[^26]:    ${ }^{1}$ Original localities for this material may be found in the Systematic Treatment in the citations of specimens under the various species.
    ${ }_{2}$ Additional chromosome counts in Torensendio will be found in a previous paper (Beaman, 1954).

[^27]:    ${ }^{1}$ Tonenscudia incana (cultures 971, 5, and 802), T. montana var. montana (culture 35 ), and $T$. grandifora (culture 39).
    ${ }^{2}$ Explanation of the culture-series symbols will be found in the text, pp. 28-33.

[^28]:    ${ }^{1}$ Townsendia incana (cultures 6, 17, and 875), T. Parrvi (cultures 8 and 27), and
    T. Rothrockii (culture 798).
    ${ }^{2}$ Explanation of the culture-series symbols will he found in the text, pp. 43-50.

[^29]:    ${ }^{1}$ Explanation of the culture-series symbols will be found in the text, p. 47.
    ${ }^{2}$ Embryos are listed by nuclear rather than cell number because walls do not always develop immediately after the mitotic divisions.

[^30]:    Map 1. Phylogenetic relationships of the species of Tou'nsendia on a geographic basis.

[^31]:    ${ }^{1}$ It should be noted that T. Hookeri has been collected by Marcus Jones near the type-locality of T. mensana var. mensana.

[^32]:    ${ }^{2}$ Heller \& Heller 3547 in mo, mse, and us p.p. is of T. annua; in ND, Ny, and us p.p., this collection is made up of plants of T. Fendleri.

[^33]:    ${ }^{3}$ Nuttall's type material of T. strigosa in American herbaria is rather depauperate. Superficially, his plants do closely resemble T. annua. It is not surprising, therefore, that the two species previously have not been distinguished.

[^34]:    ${ }^{4}$ Unfortunately, the chromosomes of T. annua, a species which shares many reduced features with $T$. mexicana, have not yet been examined.

