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NEW MARINE ALGAE FROM SOUTH AFRICA: I

BY

GEORGE F. PAPENFUSS

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THIS IS the first of a series of papers in which South African marine algae new to science will be described. The present article deals with four species which are of ecologic importance and the validation of their names is consequently of particular interest to Professor T. A. Stephenson (University College of Wales, Aberystwyth; formerly of the University of Cape Town), who for ten years was engaged in an ecological survey of the South African intertidal belt and is now publishing the concluding accounts of that investigation. All but a few of the specimens reported in this paper were collected by Professor Stephenson and his collaborators, and they are listed under the numbers assigned to them by the Ecological Survey of the University of Cape Town. The specimens are deposited in the Herbarium of the University of California. The study was made, in part, during the tenure of a Fellowship granted by the Carnegie Corporation of New York. Mr. T. T. McCabe kindly prepared the Latin diagnoses.

Hypnes rosea Papenfuss, sp. nov.

(Pl. 1, fig. 1; pl. 2, figs. 5–8)

Phyca nexa laxa rosea super algis aliis ad vel vix sub aeguum demissum gesti maritimi, inaequaliter ramulosa, rami praecipui axes percurrentes efficere pertinentes. Rami teretes, usque ad 1.5 mm. diametro, ramuli brevibus echiniformibus, determinatis, 0.5–2 mm. longis vestitis. Acies ramuli praecipui aut circinati-uncati aut direct et attenuati. In sectura transversa rami cellulam centralem proponent circulo 6–7 cellularis medullaris circumdata, illi fere minor sed aliquando aequi cellula centrali. Cellulis medullaris aliae (illes corticem perimetri contigui exceptis) maiores 2–4 magnitudinibus. Crassitudines lenticulares parietibus cellularum medullarum absunt. Chromatophores cellularum medullarum externarum fere moniliformes sed angustiae aliquando inaequaliter disponitae.

Tetrasporangiae 15–27 × (47–) 53–63 (–68) μ in ramulis determinantis, superficies fertilis zona ramularum circumdans. Generatio sexualis ignotus.

Plants forming entangled, reddish pink growths on other algae at or just below the low-tide level, irregularly branched, with the main branches tending to form percurrent axes. Branches terete, to 1.5 mm. in diameter, beset with short, 0.5–2 mm. long, determinate, spiniform ramuli. Tips of the main branches crozier-hooked or straight and attenuate. In transverse section, the branches showing a central cell which is surrounded by a circle of 6–7 medullary cells, which are usually smaller but occasionally as large in diameter. The medullary cells farther toward the periphery, except those adjoining the cortex, 2–4 times larger, as seen in transverse section. Lenticular thickenings absent in the walls of the medullary cells. Chromatophores of the outer medullary cells usually moniliform, but the constrictions at times unevenly spaced.

Tetrasporangia 15–27 × (47–) 53–63 (–68) μ, formed in the determinate branchlets, with the fertile area girdling the branchlet. Sexual reproductive organs unknown.

Type: Umtwalumi, December 26, 1938, Ecol. Surv. Univ. Cape Town M7B (tetrasporic). Other collections: Umpangazi, May 2, 1939, Ecol. Surv. Univ. Cape Town G3C (sterile).

Known range: Natal Coast.

This species seems to be closely related to *Hypnea japonica* Tanaka (1941, p. 236), from which it differs, however, not only in general habit but also in

having shorter fertile branchlets, fewer of the small medullary cells in the center of the branches, and no lenticular thickenings in the walls of the medullary cells.

Hypnea viridis Papenfuss, sp. nov.

(Pl. 1, fig. 2; pl. 2, figs. 9–11; pl. 3, fig. 14)

Phyca tegetæ virides 1–1.5 cm. alta efficientes inaequaliter impliciteque ramulosa. Rama cylindratae, ad 1 mm. pervenientes, in acie minuentes, nunquam in unco terminantes, infrequenter ramuli laterales, determinantas, echiniformes, proferentes. Ramuli in sectura transversa cellulam centralem proponent, 5–6 cellulis medullaris in circulo circumdata. Hae diametro 1.5–3 magnitudinibus maiores sunt cellulis alteris medullaris, quae ad corticem perimetri in magnitudine minuent. Crassitudines lenticulares aliquando parietibus cellularis medullaris adsunt. Chromatophores cellularum medullarum externarum fasciae angustae sunt ad intervalles inaequales angustissime contractae.

Tetrasporangiae (17–) 22–28 × (29–) 34–46 μ in ramulis brevibus lateralibusque incrassatis, superficies fertilis zona ramulam circumdans. Generatio sexualis ignotus.

Plants forming green, matted growths, 1–1.5 cm. high, in the intertidal belt. Fronds irregularly and intricately branched, the branches cylindrical, to 1 mm. in diameter, tapering to a point, never ending in a hook, rarely producing lateral, determinate, spiniform ramuli. In transverse section, the branches showing a central cell which is surrounded by a circle of 5–6 medullary cells, which are 1.5–3 times as large in diameter. The other medullary cells progressively decreasing in size toward the peripheral cortex. Lenticular thickenings occasionally present in the walls of the medullary cells. Chromatophores of the outer medullary cells in the form of narrow bands with constrictions at frequent but irregular intervals.

Tetrasporangia (17–) 22–28 × (29–) 34–46 μ, formed in short, somewhat enlarged, lateral branchlets, with the fertile area girdling the branchlet. Sexual reproductive organs unknown.

Type: Umhlali Beach, December 21, 1938, Ecol. Surv. Univ. Cape Town U8C (tetrasporic). Other collections: Umpangazi, May 2, 1939, Ecol. Surv. Univ. Cape Town G2F (tetrasporic); Port Edward, May 16, 1939, Ecol. Surv. Univ. Cape Town WW1D (tetrasporic).

Known range: Natal Coast.

Hypnea viridis belongs to the section Pulvinatae. So far as it is possible to tell from published accounts, and from a comparison with the material of certain species which are represented in Herb. Univ. Calif., none of the known species of this section shows a close relationship to the plant from South Africa.

Gigartina paxillata Papenfuss, sp. nov.

(Pl. 1, fig. 3; pl. 3, fig. 15; pl. 4)

Phyca caespitosa, frondibus stipitatis usque ad 20 cm. longitudinis et 4 cm. latitudinis. Stipes teres aut leviter compressus, usque ad 1.5 cm. longitudinus et 2 mm. diametro. Frondes 750–1,250 μ crassitudinis, simpleces, vel 1–3 (vel plus?) furcatae, simplex. Fere cum ramulis marginalis, bene auctis, simplicibus aut furcatis et semper cum proliferationibus marginalibus vel superficialibus, simplicibus aut divisis, usque ad 1.3 cm. longitudinis et 1.2 mm. diametro, teretibus ad leviter compressus, papilloidiis ad elongates paxillatisque.

Cystocarpi cum pericarpo proprio 0.5–1.5 (–2) × 1–2 mm., terminantes aut laterales super ramuli paxillati, unus plusve super ramulo quisque.

Sori tetrasporangiales breviter extans, 150–5,000 μ diametro, et super ramulis paxillatis et super superficiebus frondum effecti.

Plants caespitose, with stipitate, to 20 cm. long and 4 cm. broad fronds. Stipe terete to slightly compressed, to 1.5 cm. in length and 2 mm. in diameter. Fronds 750–1,250 μ thick, simple or 1–3 (or more?) times forked, usually with well developed, simple or forked, marginal branchlets and always with simple or divided, to 1.3 cm. long and 1.2 mm. diameter, terete to slightly compressed, papilloid to elongated and peglike superficial and marginal proliferations.

Cytocarps with a proper pericarp, 0.5–1.5 (–2) × 1–2 mm., terminal or lateral on the peg-like branchlets, one or more per branchlet.

Tetrasporangial sori projecting slightly, 150–5,000 μ in diameter, formed on both the peg-like branchlets and the faces of the fronds.

Type: Storms River Mouth, January 25, 1940, Ecol. Surv. Univ. Cape Town TT1O (cystocarpic) and TT1Oa (tetrasporic). Other collections: Knysna, April 6, 1939, Ecol. Surv. Univ. Cape Town Kn1B (tetrasporic); Kleinmond, March 19, 1939, Ecol. Surv. Univ. Cape Town X1E (tetrasporic).

Known range: Knysna to Kleinmond, which lies about twenty miles northeast of Port Alfred.

Gigartina paxillata belongs to the subgenus *Chondracanthus* (Kütz.) Setchell and Gardner (1933, pp. 257, 261, 294). In addition to the seventeen species which were listed by Setchell and Gardner (*op. cit.*, pp. 294–295), new species have been added to this subgenus by Dawson (1944). *G. paxillata* is very different from all of them. Sexual plants with narrow fronds show some slight resemblance to the South African *G. stiriata,* but a comparison with that species at best is forced. Asexual plants of *G. paxillata,* like the sexual ones, are provided with marginal and superficial peglike branchlets and in this respect are very different from those of *G. stiriata,* which entirely lack such proliferations. The sporangial sori of *G. paxillata* occur on both the faces of the fronds and the superficial and lateral outgrowths; and if the characterization of the subgenus *Chondracanthus* by Setchell and Gardner (*op. cit.*, p. 257) is based on accurate observation, *G. paxillata* would be the only species of this subgenus that shows this feature. It does not seem unlikely, however, that in certain of the Pacific North American species, as for example *G. armata,* the sori may likewise be found to occur on the faces of the fronds as well as on the papillae. But this question could be best determined by observations upon living specimens.

In this connection, it is of interest to note that Setchell and Gardner (*op. cit.*, p. 257) characterize *Chondracanthus* as having " . . . tetrasporic sori on short leaflets or papilloid branchlets, marginal or superficial," and (on page 261, where they briefly discuss the characters of the subgenus) they also refer to "fertile branches" or "fertile branchlets." Although this may be true of the majority of Pacific North American species of this subgenus, there are several austral species, including *G. stiriata, G. angulata, G. macrocarpa, G. marginifera,* and *G. protea,* in which the tetrasporic plants are entirely devoid of papilloid growths and the sporangial sori occur directly on the faces of the fronds. It seems likely that, when composing the diagnosis of *Chondracanthus,* Setchell and Gardner had momentarily overlooked the condition that obtains in these species from the Southern Hemisphere. In such species the asexual plants are very different in appearance from the sexual ones; and in at least one of them, the South African *G. stiriata,* the asexual generation had for a long time passed as an autonomous species, *G. Burmanni* (Ag.) J. Ag. It is not inconceivable that this group of austral species will, upon further study, be found to constitute a geographic race which could be segregated into a distinct subgenus.

Dictymenia Stephensonii Papenfuss, sp. nov.
(Pl. 1, fig. 4; pl. 2, figs. 12, 13)

Phyca hapteris cylindratis fixa, erecta, compressa, usque ad 20 cm. altitudine, bilaterales, libere ramulosa. Pars basalis axium praecipuorum in stipite minor 1 cm. longitudine commutatus. Rami in helice torquere inclinati, bilaterali compressique, usque ad 5 mm. in latitudine, costati in partibus vetustis, ramulis brevibus, terminalis, 1–3 furcatis, determinatis, spiniformis, vestiti, qui alternatim distichouseque ex quoque segmento quarto emanant et versus axem flectunt. Haec flexio incremento cellularum plurium et maiorum in latere abaxiali quam adaxiali affecta est. Ramuli determinati fere ramum determinatum evanescentemque ordinis secundi prope basim ad laterem adaxialem generant. Rami indeterminati fere alternati sunt et ramulis determinatis ad intervallum incerta substituent. Rami determinati indeterminatique ad basim cum ramo parentale funditi ramisque sororibus. Axis monopodialis est. Incrementum ex cellula initiale segmenta cuja in cellula initiale cellulaeque pericentralibus sex divisae sunt. Cellula pericentralis una lateralis utrimque et duae superficialis utrimque. Cellulae pericentrales laterales maiores quam pericentralibus superficialibus sunt, et pericentralis quisque ad instar initialis ordinis lateralis cellularum magnorum primarum agit. Thallus totalis mature corticatus partitionibus periclinalibus omnium cellularum pericentralium et corporibus harum derivatis.

Tetrasporangiae in ramulis communibus lateralibus generant. Apparatus sexualis ignotus.

Plant erect, to 20 cm. (or more?) high, freely branched, attached by cylindrical haptera. The basal part of the main axes modified into a stalk of less than 1 cm. in length. Branches tending to twist in a helical spiral, bilateral, compressed, to 5 mm. broad, costate in older parts, beset with short, terminally 1–3 times furcate, determinate, spiniform branchlets, which issue alternately and distichously from every fourth segment and curve toward the axis. This curvature is owing to the formation of larger and more cells on the abaxial than on the adaxial side. The determinate branches usually form an evanescent determinate branch of the second order near the base and on the adaxial side. Indeterminate branches usually alternate and replacing the determinate branchlets at indefinite intervals. All branches fused at their base with the mother branch and adjoining sister branches. Axis monopodial. Growth by means of an initial cell, the segments of which divide into a central and 6 pericentral cells, one pericentral cell on each of the lateral sides and two on each surface. The lateral pericentral cells larger than those on the surfaces and each functioning as the initial of a lateral row of large, primary cells. Entire thallus becoming corticated at an early stage by periclinal division of all pericentral and other primary cells. Trichoblasts rarely formed.

Tetrasporangia formed in ordinary lateral branches. Sexual reproductive organs unknown.

Type: Port Shepstone, July 27, 1938, Papenfuss 1002. Other collections: Umhlali Beach, Dec. 23, 1938, Ecol. Surv. Univ. Cape Town U19A; Port St. Johns, Jan. 6, 1939, Ecol. Surv. Univ. Cape Town J4C, and July 30, 1938, Papenfuss 1088; Bashee River Mouth, Sept. 27, 1939, Pocock 1771b.

Known range: Umhlali Beach (about 50 miles north of Durban) to Bashee River Mouth (about 100 miles northeast of East London).

All the material of this species was sterile, except some of that secured at Port Shepstone on July 27, 1938, which contained tetrasporangia.

This is one of the few records of the occurrence of a member of the genus *Dictymenia* outside of Australia and Tasmania. As in other species of the genus, the thallus of *D. Stephensonii* is areolate in appearance. This condition, as has been pointed out by Falkenberg (1901), is owing to the fact that the medulla consists of a single layer of large, regularly arranged cells, the outlines of which show through the small-celled cortical tissue and consequently impart a netlike effect to the tissues of the thallus as seen under low magnification.

The general habit of *Dictymenia Stephensonii* is illustrated in plate 1, figure 4, and the structure of the apex is shown in plate 2, figure 12 (the transverse pericentral cells are not indicated in the proximal part of the main axis and the older branch to the right). As will be seen from figure 12, the branches issue alternately from every fourth segment. A branch is formed as the result of an oblique division of the apical cell of the axis (which ordinarily divides by transverse walls), and the higher side of the segment thus formed is then cut off and functions as a branch initial (fig. 12). The position of the six pericentral cells is shown in plate 2, figure 13. It will be seen from figures 12 and 13 that the two lateral pericentral cells are larger than the transverse pericentral cells. Figure 12 also shows that the lateral pericentral cells on the abaxial side of a branch, as seen in surface view, are larger than those on the adaxial side and undergo more divisions than they. This results in a bending of the branches toward the axis. The central cells remain distinct throughout the thallus; and, owing to more extensive cortication along the course of these cells, older parts become costate (plate 1, fig. 4).

Dictymenia Stephensonii seems to be more closely related to *D. Harveyana* than to any of the other known species of *Dictymenia*. As in *D. Harveyana*, the tetrasporangia are formed in ordinary vegetative branches. A striking distinction between the two species lies in the fact that in *D. Harveyana* the branches issue from every other segment whereas in *D. Stephensonii* they arise from every fourth segment. Consequently, *D. Harveyana* is a much more profusely branched plant than *D. Stephensonii*.

PLATE 1

Hypnea rosea

Fig. 1. Part of thallus of tetrasporic plant from Umtwalumi (Ecol. Surv. Univ. Cape Town M7B). × 2.

Hypnea viridis

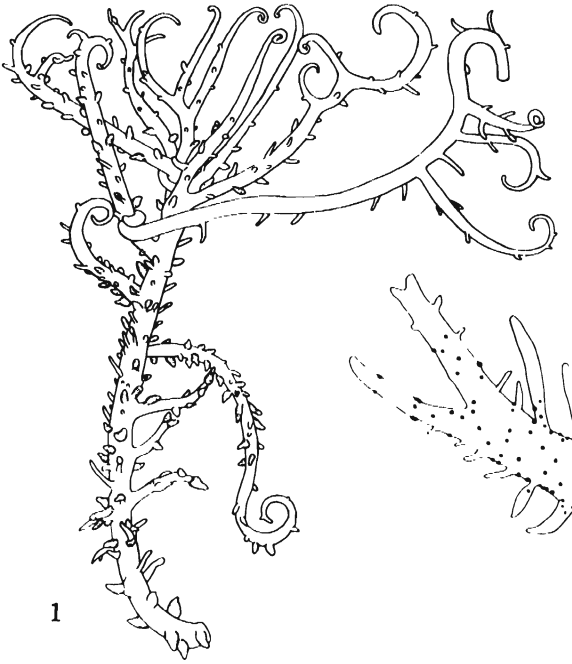
Fig. 2. Part of thallus with tetraspore-bearing branchlets (Ecol. Surv. Univ. Cape Town G2F). × 5.

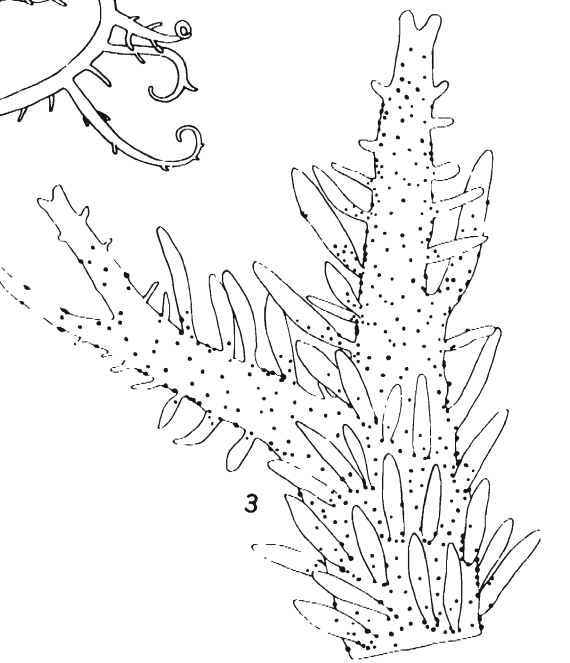
Gigartina paxillata

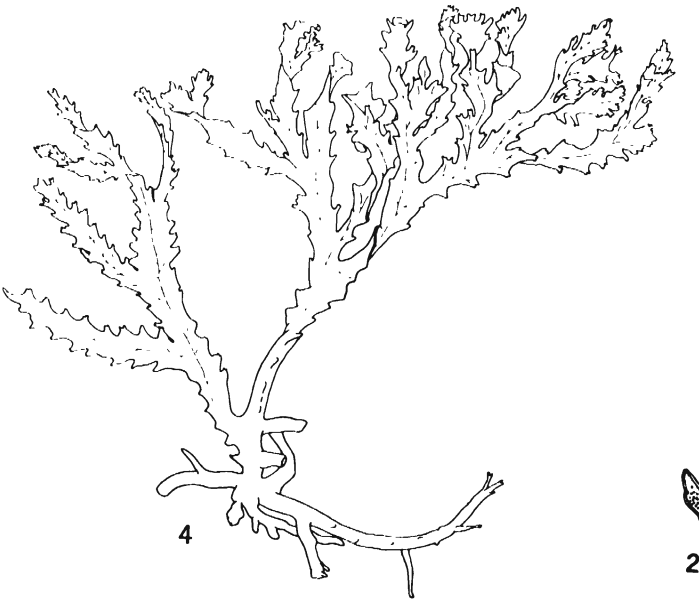
Fig. 3. Part of thallus of tetrasporic plant from Storms River Mouth (Ecol. Surv. Univ. Cape Town TT10a). × 2.

Dictymenia Stephensonii

Fig. 4. Habit of plant from Port St. Johns (Ecol. Surv. Univ. Cape Town J4C). × 1½.


1


3


4


2

PLATE 2

Hypnea rosea

Fig. 5. Transverse section of a branch of a plant from Umtwalumi. × 145. C.C., central cell.

Figs. 6 and 7. Chromatophores from two cells, respectively, in the outer part of the medulla of the same section of a plant from Umtwalumi. × 960.

Fig. 8. Two tetrasporangia from a plant from Umtwalumi. × 320.

Hypnea viridis

Fig. 9. Transverse section of a branch of a plant from Umhlali Beach. × 145. C.C., central cell.

Fig. 10. Chromatophores from a cell in the outer part of the medulla of a plant from Port Edward. × 960.

Fig. 11. Three tetrasporangia from a plant from Umpangazi. × 320.

Dictyomenia Stephensonii

Fig. 12. Apex of an indeterminate branch, showing the formation of lateral branches alternately from every fourth segment. The transverse pericentral cells are not indicated in the proximal part of the main axis and the older side branch to the right. × 625.

Fig. 13. Transverse section through the younger part of a branch, showing the two large lateral pericentral cells and the four smaller transverse pericentral cells, and the cortical cells which develop on either surface. × 70. L.P.C., lateral pericentral cells; T.P.C., transverse pericentral cells.

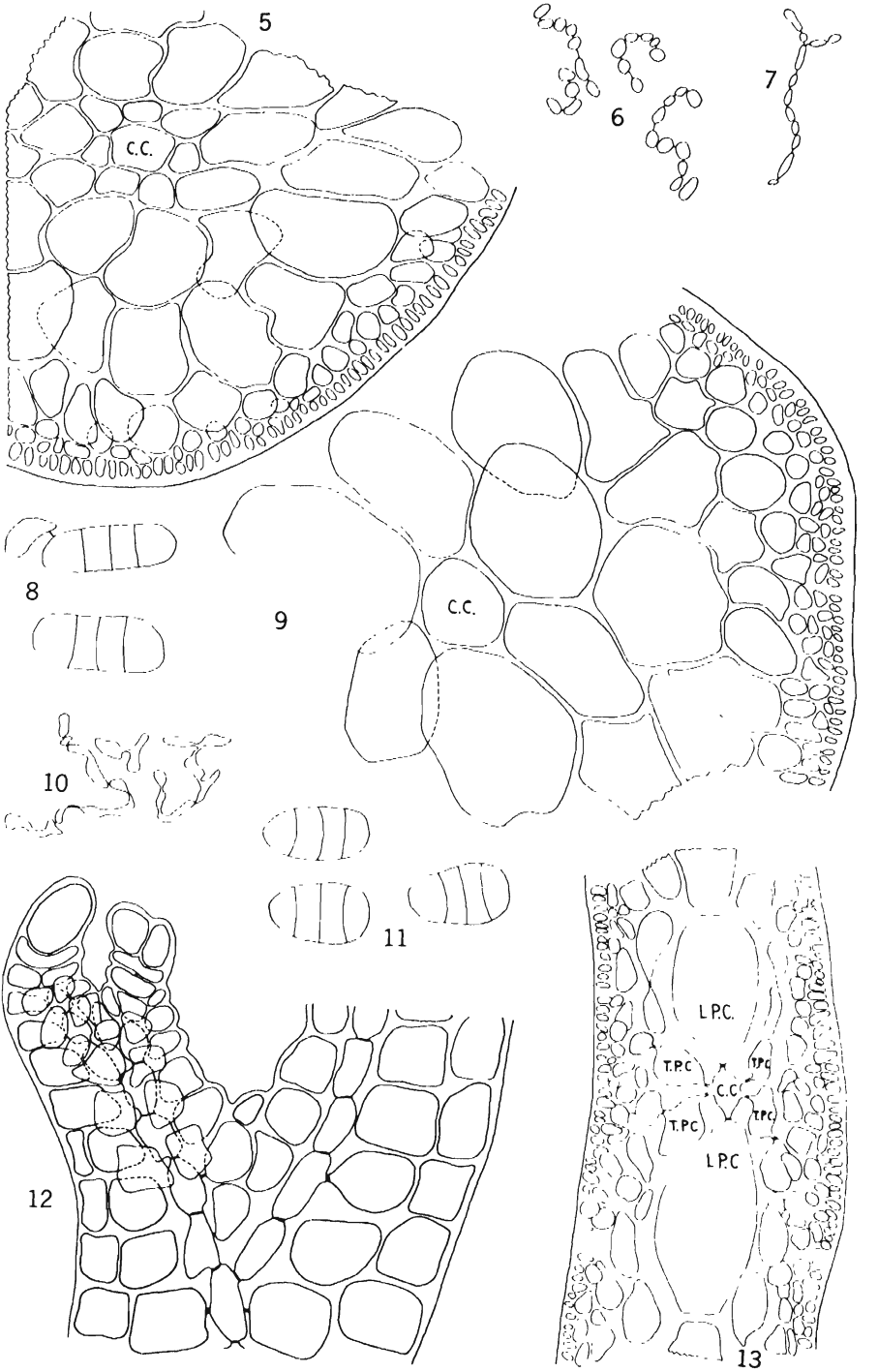

5
C.C.
6
7
8
9
C.C.
10
11
12
L.P.C.
T.P.C.
T.P.C.
C.C.
T.P.C.
T.P.C.
L.P.C.
13

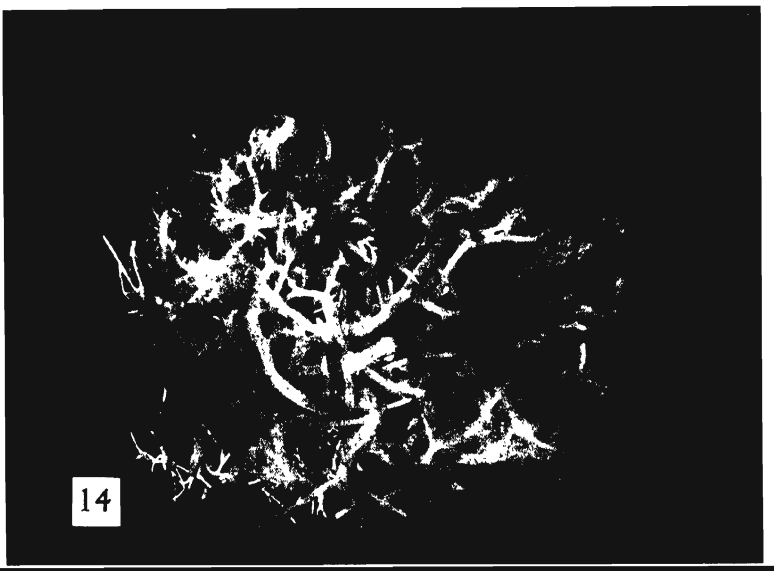
PLATE 3

Hypnea viridis

Fig. 14. Habit of thallus of a plant from Umhlali Beach (type, Ecol. Surv. Univ. Cape Town U8C). × 2.

Gigartina pasillata

Fig. 15. Part of thallus of a cystocarpic plant from Storms River Mouth (type, Ecol. Surv. Univ. Cape Town TT1O). Nat. size.


14

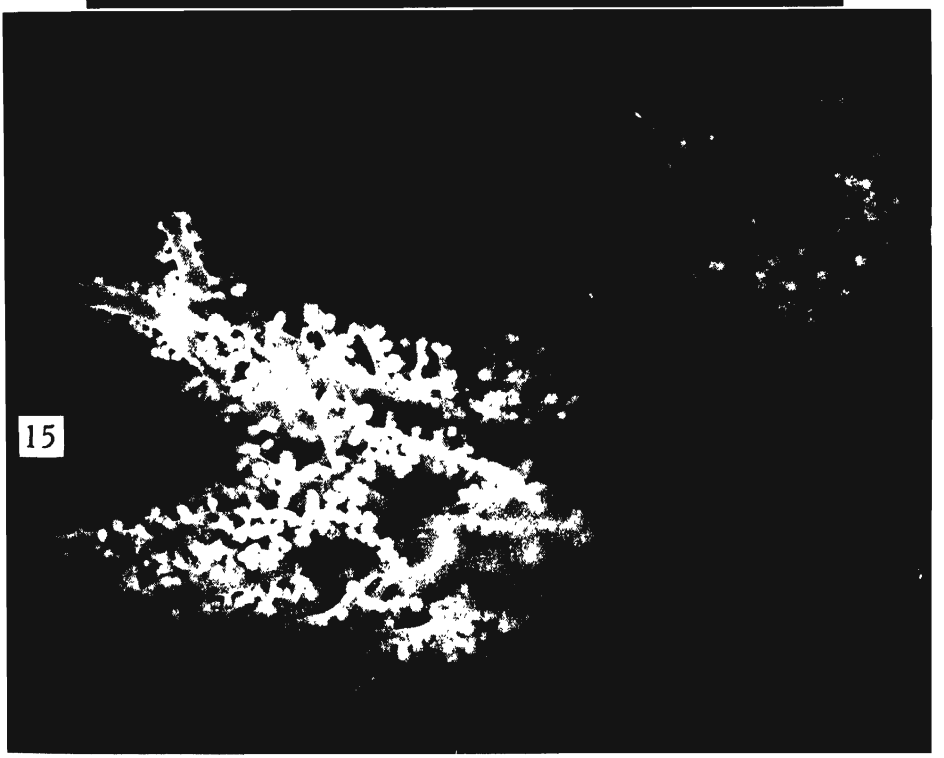

15

PLATE 4

Gigartina paxillata

Fig. 16. Part of frond shown in figure 15. × 3⅓.


16

THE PTERIDOPHYTES OF THE ADMIRALTY ISLANDS

BY

WARREN H. WAGNER, JR., and DAVID F. GRETHER

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THE PTERIDOPHYTES OF THE ADMIRALTY ISLANDS

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WARREN H. WAGNER, JR., AND DAVID F. GRETHER

OUR KNOWLEDGE of the natural history of the Admiralty Islands is very limited compared to that of many of the island groups of the Pacific. Few expeditions of a scientific nature have visited the Admiralties, although the islands were discovered by Schouten as early as 1615. Until very recently the most important contribution to our knowledge of the flora was made by the expedition of H.M.S. *Challenger* in 1875. Unfortunately, the botanical specimens collected by the naturalist, H. N. Moseley, molded so badly that many of them were dust when brought back to England. The Germans established a settlement on Manus Island in 1913, but in 1914, after the outbreak of World War I, the Admiralty group became an Australian possession. During World War II the strategic value of these and other Melanesian islands concentrated Allied servicemen in the areas, and the attention of many naturalists was focused upon the biota of these hitherto obscurely known tropical islands. It was our good fortune to be able to visit the Admiralty Islands a number of times and to accumulate a large number of specimens and notes on their little-known pteridophyte flora. The purpose of this paper is to present brief notes, with keys, on all of the species known to us from these islands—a total of 173 species of ferns and other plants traditionally termed pteridophytes.

We made our first trips to the Admiralties in November, 1944. On each of these and several subsequent trips during 1945, we remained for several days, collecting on Los Negros Island and on the eastern tip of Manus. During November, 1945, we had an opportunity to visit the islands of Lou and Tawi and the summit of Mount Tjajiak in south-central Manus. A collecting trip along "Number One Road" in Manus was made during July, 1946. The organization of our notes and specimens was accomplished by the senior author at the herbarium of the University of California, Berkeley, during the spring and summer of 1946.

Previous study of the pteridophytes of the Admiralty Islands has been slight, the only paper dealing specifically with this group of plants being J. G. Baker's article, "On the Polynesian Ferns of the 'Challenger' Expedition" (Jour. Linn. Soc. Bot. 15: 104–112, 1877). Baker reported thirty-eight species collected by Moseley in the Admiralties. The "Flora der deutschen Schutzgebiete in der Südsee," by Schumann and Lauterbach (Leipzig, 1901), merely republishes these earlier records of Baker. In "Beiträge zur Flora von Papuasien VII" (Bot. Jahrb. von Engler 56: 31–250, 1920), Lauterbach included a few fern records from the Admiralties and from the Bismarck Archipelago. The present paper records a very large addition to the pteridophyte flora of the Admiralties. Collections are referred to by our field numbers, with few exceptions. We key and list these briefly, giving localities and our

collection numbers, known range, data on occurrence and abundance, and a brief discussion when necessary. Each collection will be deposited in the University of California Herbarium unless otherwise indicated, and duplicates have been distributed to the United States National Herbarium, the Botanic Gardens at Sydney, Australia, the Bernice P. Bishop Museum at Honolulu, Hawaii, and other herbaria.

In making this study we have had the kind assistance of Dr. Edwin B. Copeland, and we are especially indebted to him for his sympathetic advice and criticism. We also acknowledge the kindness of the United States Naval authorities and local representatives of the Australian government, especially Commodore C. F. Martin, U.S.N., Lieutenant H. C. Riker, Captain Giles, Lieutenant W. G. Thomas, and the authorities of Naval Air Transport, for permitting us to carry out this work. Without their help the project would have been impossible. A number of native Admiralty Islanders, especially Oti Maikara, were very helpful. Dr. William R. Maxon and Dr. Austin H. Clark, of the United States National Museum, are also given our thanks for their many encouraging communications.

The Admiralty group is situated west of New Ireland and northeast of New Britain in the Bismarck Archipelago, at approximately 2° to 3° south of the equator, and 146° to 148° east longitude. The land mass of New Guinea lies about one hundred and fifty miles to the south. There are numerous small islands in the Admiralty group clustering about the main island of Manus, which is fifty-five miles long by sixteen miles wide and lies east and west. The Mount Dremsel area, the highest point in the Admiralties (2,359 ft.), is in the south-central part of Manus. Mount Tjajiak is an adjoining peak. All of the islands are forested except where they have been burned or cleared for coconut groves and villages. Los Negros is a small island just east of Manus and separated from it by a narrow channel. Lou Island lies twenty miles to the south of Los Negros. Tawi is a tiny, grass-covered islet one mile off the south coast of Manus. Our most fruitful collecting trips were made on Los Negros Island; in the river valley near Lorengau, Manus, particularly at the first large waterfall; on the wooded slopes and summit of Mount Tjajiak; and on the island of Lou. The *Challenger* Expedition collected only in the vicinity of Nares Bay at the opposite, extreme northwestern end of Manus.

The Admiralties have an average temperature of about 80° Fahrenheit and as much as 154 inches of rain annually, half of the sky usually being covered with cloud; their forests are therefore damp and luxuriant, and cleared areas soon become overgrown. As observed from the air, Manus Island is hilly and richly forested. Native trails, especially the Number One Road in the eastern part, stand out conspicuously along the ridges. Many river valleys can be seen, opening usually into shallow inlets that appear mottled light green from the air because of the development of coral. The dark green deep water is usually close to the shore and forms a definite line in sharp contrast to the shallow, pale green, coastal-reef belt. Where the mangrove swamps do not encroach into the shallow water, white beaches are developed. On Lou Island, the beaches appear dark gray because of volcanic sand.

Flying along the southern coast of Manus on a clear day, one sees a series of peaks around Mount Dremsel. White cumulus clouds may be observed along the uppermost ridges even on the clearest days. Here, in the damp summit forests of Mount Tjajiak, we collected in one day twenty-six species of pteridophytes which we found nowhere else. This strongly suggests that the richest floristic area of the Admiralties lies in the forests of the Mount Dremsel region and in the rolling, thickly wooded, high country to the northeast.

Coastal mangrove swamps are poor in species of pteridophytes. The bothersome projecting "knees" of some of the species of mangrove and the danger of sinking to one's waist in smelly black mud combine to make travel through these swamps most unpleasant. Only one fern, *Acrostichum aureum,* is common here, although a number of epiphytic species can be found. Where fresh water seeps into the upland edges of these swamps, however, a varied fern flora, resembling that of fresh-water swamps, is found. The upland freshwater swamps are dominated by sago palms and are more easily traversed. The largest of these swamps observed by us from the air is south of the western part of the Number One Road, but many similar swamps occur along the coasts at the openings of river valleys. In these places *Helminthostachys zeylanica, Craspedodictyum quinatum, Lindsaea sagincola, Cyclosorus glandulosus, Stenochlaena palustris,* and a curious dwarf form of *Ophioglossum pendulum* are especially characteristic, although many other species of pteridophytes are common.

The upland forest is rich, luxuriant, and, as a rule, easily penetrable, except where old clearings have become overgrown with bamboo. The woods above Lorengau River Falls typify the upland forest and illustrate the wealth of pteridophytes in the Admiralty Islands. In the damp, black soil, especially along streams and river banks, such contrasting forms as *Marattia fraxinea, Schizaea dichotoma, Cephalomanes Boryanum, Cystodium sorbifolium, Lindsaea decomposita, Cyathea propinqua, Bolbitis Quoyana, Tectaria menyanthidis,* and *Cyclosorus vestigiatus* are all common. Climbing at the bases of trees are *Lomagramma sinuata, Lygodium circinnatum,* and *Lindsaea Macraeana.* The most numerous epiphytic ferns in these upland woods are *Ophioglossum pendulum, Crepidopteris humilis, Crepidomanes bipunctatum, Davallia epiphylla, Nephrolepis persicifolia, Asplenium nidus, A. cuneatum, Microsorium punctatum, Vittaria elongata, Lycopodium carinatum,* and *L. phlegmaria.* Many other species occur here less commonly.

Wooded limestone cliffs, such as those in the Tauwi Hills of the island of Los Negros, deserve special mention, because *Cyclopeltis novoguineensis, Ctenitis sagenioides, Stenosemia aurita, Tectaria Barclayi, T. ferruginea,* and *Selaginella longiciliata* show particular preference for the shaded bases of the roughly eroded, vertical rock surfaces. On the more exposed limestone faces occurs an unusually dwarfed form of *Asplenium falcatum.*

Pteridophytes characteristic of second-growth fields and woods comprise about one-fifth of the known species. In cleared, grassy marshes and damp meadows are found large stands of *Lygodium scandens, Ceratopteris siliquosa,*

Cyclosorus goggilodus, Athyrium esculentum, and *Selaginella ciliaris.* In old coconut groves, especially in the vicinity of Mokerang, Los Negros, *Nephrolepis exaltata, N. hirsutula,* and *Cyclosorus unitus* are abundant on the ground, and *Davallia solida, Pyrrosia adnascens,* and *Microsorium scolopendria* climb the coconut trunks (pl. 25).

The burned-over, rocky fields on the island of Tawi contain *Ophioglossum petiolatum* (a narrow-leaved form), *Lindsaea ensifolia, Cheilanthes tenuifolia, Blechnum orientale,* and *Lycopodium cernuum.* The resemblance of the ferns of Tawi to those of the savannas of Guam, in the Marianas Islands, is very striking. The dry, limestone fields near Momote, Los Negros, are characterized by the abundant *Cyclosorus unitus,* the two common terrestrial species of *Nephrolepis, Pteris vittata,* and, much less commonly, by *Cyclosorus invisus, Ophioglossum nudicaule,* and *O. petiolatum.*

A large number of ferns are especially characteristic of second-growth, brushy areas and newly developed woods. The most abundant are *Pteris tripartita* and *Selaginella caudata* (and species closely resembling *S. caudata*). Also common are *Ophioglossum reticulatum, Sticherus hirtus, S. laevigatus, Dicranopteris linearis, Microlepia speluncae, Pteris ligulata, Cyathea scaberula, C. contaminans, Cyclosorus truncatus, C. dentatus, Sphaerostephanos polycarpa,* and *Microsorium sylvaticum.* These and less numerous species characteristic of secondary woods are also frequent along native trails.

Areas opened by cutting trees or burning are soon filled with dense growth. In November, 1944, we found *Pteridium aquilinum,* the common bracken fern, near Momote; but a year later the area was so densely covered with new growth that we could not relocate the plant. Occasionally, however, species that normally occur in open, disturbed places persist until the surrounding vegetation approaches a forest condition. Here may be found such unusual environmental forms as very large, lax plants of *Lycopodium cernuum,* which are quite unique in appearance. A most remarkable example of this phenomenon is shown in the huge climbing masses of *Dicranopteris* and *Sticherus,* which grow 150 feet high in the forest of the Lorengau River valley. Both of these plants have probably long persisted here, presumably since the time when this area was cleared or burned. They are characteristic plants of destroyed woods, usually found in upland clearings, often in company with a low, secondary growth of bamboo.

Ferns and fern allies are extremely common in the Admiralties and display diverse habits. The tiny bryophyte-like *Microgonium* species are contrasted with such giant species as *Cyathea contaminans* and *Tectaria Leuzeana.* Of the known species, 67 per cent are terrestrial; the remainder are epiphytic. Some with terrestrial roots, including the three *Lygodium* spp., *Lindsaea Macraeana, Stenochlaena palustris,* and *Selaginella Hieronymiana,* have a marked scandent or liane habit. *Sticherus laevigatus* and *Dicranopteris linearis,* as remarked above, may occasionally develop a similar habit. A most interesting group of ferns is that of the ground creepers which produce fertile fronds only when the rhizome climbs a tree trunk. *Lomariopsis cochinchinensis, Lomagramma sinuata,* and *Microsorium logissimum* are the best examples

of this type of growth; their fertile fronds, however, are very difficult to find. Of *Lomariopsis* we never succeeded in finding fertile specimens, and only once did we discover fertile material of *Lomagramma,* although both species are common. The terrestrial creeping form of the abundant *Microsorium longissimum* bears smaller fronds than the fertile climbing plants, and the stipes are much shorter. It appears certain that the sterile plant from the Admiralties which Baker described as *Polypodium rampans* was merely this terrestrial creeping form of *Microsorium longissimum.*

Aquatic or semiaquatic conditions provide abodes for a number of species of ferns and fern allies. *Ceratopteris siliquosa, Athyrium esculentum,* and *Cyclosorus goggilodus* usually grow where their rootstocks are at least periodically submerged. Several species, notably *Microsorium pteropus* and *Cyclosorus cataractorum,* occur on the banks of streams and rivers, where they are frequently submerged or washed over by the current. Among the families of pteridophytes not yet recorded from the Admiralties are three aquatic families which should be sought: Marsileaceae, Isoëtaceae, and Salviniaceae.

Adaptations of the epiphytic ferns are most interesting. Some of these, like *Weatherbya accedens* and *Microsorium acutifolium,* are vigorous climbers, growing in garlands almost to the tips of the branches of forest trees. The nest epiphytes are exemplified by the abundant and conspicuous *Asplenium nidus* and *Microsorium punctatum. Drynaria rigidula, Microsorium linguaeforme,* and *Merinthosorus drynarioides* are "bracket epiphytes" (Holttum, R. E., "The Ecology of Tropical Pteridophytes," Verdoorn's Manual of Pteridology, p. 431, 1938)—species which collect humus at the sessile bases of the bracket leaves. Many of the epiphytes, such as *Merinthosorus, Pyrrosia, Lycopodium* spp., and *Humata* spp., are found very high in forest trees; many others, including most of the epiphytic Hymenophyllaceae, occupy only the shaded bases of tree trunks near the forest floor. The appearances and adaptations of many of the species of epiphytic ferns are often so unique that the uninitiated might consider them utterly unlike ferns. Thus, *Microgonium omphalodes* is a perfect replica of a liverwort, and *Schizaea Wagneri* looks like a tiny, hairlike moss sporophyte.

Thirty-five of the local pteridophytes are generally abundant, and some even attain near dominance. Selaginellas may cover acres of the ground story in second-growth wooded areas, and *Nephrolepis* spp., together with *Cyclosorus unitus,* form extensive patches in old coconut groves (see pl. 25). In the valleys northwest of Mount Dremsel, Cyatheas may be seen from the air, growing in great profusion. A large number of the ferns listed here, however, are known to us only from single, small localities. Each new place we visited yielded a number of additional species. These facts indicate that the ferns and fern allies of the Admiralties are still far from being completely collected.

Of the species now known here, only 10 per cent are pantropical. Fourteen per cent range as far west as Madagascar. The largest group of the local species, 45 per cent, ranges as far west as Malaya or tropical Asia; 3 per cent do not extend as far as the East Indies, but do occur also in the Philippine Islands. Twenty-four per cent are confined to the area, continental and insu-

lar, lying east of and including the Moluccas; one-third of these are known so far only from New Guinea. Only 4 per cent of the species of the Admiralties are considered here to be endemic to the island group.

Our interpretation of species is comparatively broad. It is suspected that, when more field studies and more ample collections have been made, many of the species of pteridophytes now considered to be restricted to the New Guinea area will prove to be varieties and forms of wide-ranging species. The variation of certain species within a single locality, as in the Admiralties, is often very great, as will be discussed in the ensuing list. Over wide ranges, little-known and rarely collected ferns all too frequently have received several specific names on the basis of differences too trivial, or material too scanty. The description of a sterile *Polypodium* from the Admiralties is an example of the unfortunate creation of unwarranted names. *Stenochlaena Milnei* Underwood may be only a giant form of the abundant and variable *S. palustris*. It is our conviction that an accurate separation of closely related species, subspecies, and varieties can be accomplished only after much more thorough exploration and study of this remote part of the world.

Key to the Families

A. Sporangia borne on fronds or in spikes. *Filicineae.*

B. Sporangia large, the walls many cells thick, opening by slits or pores. *Eusporangiatae.*

C. Sporangia in spikes.....I. Ophioglossaceae

CC. Sporangia in groups on the dorsal surface of unmodified pinnules
II. Marattiaceae

BB. Sporangia small, the walls only 1 cell thick, opening by means of an elastic ring (annulus). *Leptosporangiatae.*

D. Sporangia without stalks or with short stalks, the annulus not interrupted by the stalk.

E. Sori borne variously, but not on specialized free ends of veins; lamina many cells thick.

F. Sporangia in spikes at tip of the frond or marginal on the pinnules; annulus just below the apex of the sporangium...III. Schizaeaceae

FF. Sporangia in sori on the dorsal surface of the frond; annulus medial.

G. Sorus with only 4–10 sporangia, the annulus transverse
IV. Gleicheniaceae

GG. Sorus with more numerous sporangia, the annulus oblique
IX. Cyatheaceae

EE. Sori marginal on free ends of veins (receptacles), with tubular or valvate involucres; lamina usually 1 cell thick.....V. Hymenophyllaceae

DD. Sporangia long-stalked, the annulus usually interrupted by the stalk (formerly considered one family, the Polypodiaceae).

H. Sporangia covering the dorsal surface of the lamina, not in distinct sori.

I. Fronds simple.

J. Rootstock short-creeping; fronds monomorphic. X. Aspidiaceae (*Elaphoglossum*)

JJ. Rootstock long-creeping; fronds dimorphic
XIII. Polypodiaceae (*Selliguea*)

II. Fronds lobed or pinnate.

K. Fertile pinnae confined to the upper part of the frond.
L. Frond lobed and oak-leaf-like; fertile pinnae very contracted; epiphytic
XIII. POLYPODIACEAE
(*Merinthosorus*)
LL. Frond pinnate; fertile pinnae like the sterile; salt marshes
VI. PTERIDACEAE
(*Acrostichum*)
KK. Fertile pinnae borne the entire length of the fertile frond.
M. Plants not climbing, terrestrial.
N. Veins anastomosing generally.
O. Frond pinnate, the pinnae thick and entire.....VI. PTERIDACEAE
(*Taenitis*)
OO. Frond bipinnatifid or more dissected; lamina herbaceous
X. ASPIDIACEAE
(*Bolbitis, Stenosemia*)
NN. Veins free, except along costa.....XI. BLECHNACEAE
(*Blechnum*)
MM. Plants climbing on tree trunks.
P. Veins anastomosing.....X. ASPIDIACEAE
(*Lomagramma*)
PP. Veins free, except along costa.....XI. BLECHNACEAE
(*Stenochlaena*)
HH. Sporangia in distinct sori.
Q. Sori marginal or submarginal.
R. Fronds linear and grasslike, simple; sori in a continuous marginal groove
XIV. VITTARIACEAE
(*Vittaria*)
RR. Fronds of other shapes, simple to decompound; sori mostly discontinuous, not in a groove.
S. Stipes articulate; epiphytic.
T. Rootstock long-creeping, sori indusiate.....VIII. DAVALLIACEAE
TT. Rootstock short and erect; sori without true indusia
XIII. POLYPODIACEAE
(*Prosaptia*)
SS. Stipes not articulate; terrestrial or aquatic.
U. Fronds monomorphic; terrestrial.....VI. PTERIDACEAE
UU. Fronds dimorphic; aquatic.....VII. PARKERIACEAE
QQ. Sori dorsal, not confined to the margin.
V. Sori linear.
W. Sori free, parallel, not irregular along anastomosing veins.
X. Sori elongate parallel to costa, one on each side.
Y. Plant large; sori superficial.....XI. BLECHNACEAE
(*Blechnum*)
YY. Plant small; sori in a groove.....XIII. POLYPODIACEAE
(*Scleroglossum*)
XX. Sori oblique to costa, several to numerous.
Z. Paleae clathrate; mainly epiphytic.....XII. ASPLENIACEAE
ZZ. Paleae not clathrate; terrestrial.....X. ASPIDIACEAE
(*Athyrium*)
WW. Sori anastomosing.
a. Sori anastomosing generally.....XIV. VITTARIACEAE
(*Antrophyum*)
aa. Sori anastomosing only along margins.....VI. PTERIDACEAE
(*Craspedodictyum, Syngramma*)

VV. Sori orbicular to elliptic.
b. Fronds simple.
c. Sori indusiate ..... VIII. DAVALLIACEAE (*Oleandra*)
cc. Sori exindusiate ..... XIII. POLYPODIACEAE
bb. Fronds lobed to decompound.
d. Sori indusiate; stipe not articulate to the rhizome.
e. Pinnae not articulate ..... X. ASPIDIACEAE
ee. Pinnae articulate and deciduous ..... VIII. DAVALLIACEAE (*Nephrolepis*)
dd. Sori exindusiate; stipe articulate to the rhizome XIII. POLYPODIACEAE

AA. Sporangia borne in the axils of scalelike appendages or microphylls.
f. Stems with numerous microphylls; true roots present. *Lycopsida.*
g. Plants homosporous; leaves eligulate; no rhizophores ..... XV. LYCOPODIACEAE
gg. Plants heterosporous; leaves ligulate; rhizophores present XVI. SELAGINELLACEAE
ff. Stems naked except for tiny scalelike "leaves"; no true roots. *Psilopsida.* XVII. PSILOTACEAE

I. OPHIOGLOSSACEAE

Sterile segments palmately divided; venation free ..... 1. *Helminthostachys*
Sterile segments usually simple; venation reticulate ..... 2. *Ophioglossum*

1. *Helminthostachys* Kaulfuss

1. *Helminthostachys zeylanica* (Linnaeus) Hooker, Genera Filicum, pl. 47b, 1840.

Manus: Swamp at Lorengau, no. 4015; along muddy path, sago-palm swamp near coast, Watani River, no. 4159.

Los Negros: Swamp along road near Lombrom Point, no. 4012.

Australasia.

Terrestrial, in damp soil in wooded swamps and flats along streams. Locally frequent.

2. *Ophioglossum* Linnaeus

Plant epiphytic; fronds pendent; fertile spike borne some distance above the base of the sterile segment ..... 1. *O. pendulum*
Plant terrestrial; fronds erect; fertile spike borne at base of the sterile segment.
Blade cordate at base ..... 2. *O. reticulatum*
Blade cuneate at base.
Roots fibrous, not proliferous; blade ovate, apiculate at tip ..... 3. *O. nudicaule*
Roots fleshy, often proliferous; blade lance-ovate, acute at tip ..... 4. *O. petiolatum*

1. *Ophioglossum pendulum* Linnaeus, Sp. Pl. (2d ed.) 2:1518, 1763; Baker, Jour. Linn. Soc. Bot. 15:111, 1877.

This species differs extremely in size according to habitat. Our collections contain two very different forms:

a) Typical (pl. 5).

Large, lax, pale green, 40–120 cm. or more long, the fertile spikes 10–30 cm. long.

Manus: Badlock, alt. 1,000 ft., No. 1 Road, no. 4556; Sabon, No. 1 Road, no. 4568.

Los Negros: Hanging from roots of *Asplenium nidus*, near Momote Field, no. 3270; epiphytic near Momote Field, nos. 3489 and 3538; near Mokerang, no. 4099.

Paleotropics.

Epiphytic, usually from the humus-collecting roots of nest ferns, 10–40 feet above the ground in rather open woods. Frequent.

b) Dwarf form (pl. 6).
Small, stiff, dark green, 6–30 cm. long; fertile spike 1–4 cm. long.
Los Negros: In moss at base of sago palm in swamp, western Los Negros, no. 4145; swamp near Lombrom Point, no. 4011.

Epiphytic in moss near the bases of *Metroxylon* palms, deep in shaded swamps. The small, dark green, stiff fronds are characteristic. Similar forms are frequent in New Guinea and Australia, and our material seems to be merely a peculiar ecological variant of *O. pendulum* ssp. *typicum* Clausen.

2. *Ophioglossum reticulatum* Linnaeus, Sp. Pl. 2: 1063, 1753.
Lou: Shady, grassy places along native trail, no. 4023.
Pantropical.

Terrestrial in humid soil in woods. Very local, but in large colonies where it occurs. The color of the living frond is a dull, pale green. The native name on Lou Island for a little fern such as this one is "tenbang."

3. *Ophioglossum nudicaule* Linnaeus f. var. *tenerum* (Mettenius) Clausen, Mem. Torrey Bot. Club 19: 146, 1938.
Los Negros: Grassy place in poor coral-limestone soil near beach, Momote Field, no. 4217.
Pantropical.

Terrestrial in very poor soil. Very rare. Leaves several, shiny green, and arranged in a nearly flat rosette which is distinctive in the field.

4. *Ophioglossum petiolatum* Hooker, Exotic Flora 1: 56, 1823. (Pl. 7.)
Lou: Shady, grassy place along native trail, one stand, no. 4067.
Tawi: Abundant in burned-over, grassy area, no. 4157.
Los Negros: Grassy place in poor, limestone soil near beach, Momote Field, no. 4216.
Pantropical.

Terrestrial in a variety of habitats, but always in grassy places. Frequent. Leaves usually single, pale green or gray-green; variable, the Tawi specimens which were growing in a dry, exposed situation are narrow, and the specimens from Lou, which were growing along a woodland native trail, have wide, sterile segments. The roots are often proliferous, bearing plants at intervals of 3–5 cm.

II. MARATTIACEAE

Sporangia fused into synangia.....1. *Marattia*
Sporangia contiguous, not fused.....2. *Angiopteris*

1. *Marattia* Swartz

Synangia submarginal.
Veins numerous, 1.5 mm. apart; synangia 1.9 mm. long; lamina dark green above
1. *M. fraxinea*
Veins fewer, 1.8 mm. apart; synangia 2.2 mm. long; lamina pale green above
3. *M. attenuata*
Synangia nearly medial.....2. *M. Smithii*

1. *Marattia fraxinea* J. E. Smith, Plant. Icones ined. 2, pl. 48, 1790.
Manus: Woods above Lorengau River Falls, no. 4132; falls of an eastern tributary of the Lorengau River, no. 4116; second-growth forest along path, Lundrit, alt. 600 ft., no. 4511.
Los Negros: Along stream near Chaporowan Point, no. 4103.
Paleotropics.

Terrestrial in rich woods, often along streams. Common. The pinnules are dark green above and are variable in size and in scaliness.

2. *Marattia Smithii* Mettenius, in Kuhn, Verh. zool.-bot. Ges. Wien 19: 584, 1869.
Manus: Lorengau River Falls, no. 4130.
Polynesia.

Terrestrial in rich woods. A single collection. The pinnules are, similarly, dark green above and are larger than those of *M. fraxinea;* the synangia are much farther from the margin, almost medial.

3. *Marattia attenuata* de Labillardière, Sert. Austro. Caled., p. 9, pls. 13 and 14, 1824.
Manus: Lorengau River Falls, no. 3990; Tingau No. 1, alt. 1,000 ft., No. 1 Road, no. 4526.
New Caledonia and Solomon Islands.

Terrestrial in rich woods. Frequent. The pinnules of this species differ from those of the last two species in being pale green and shiny. The synangia are large, and the veins rather distant.

2. *Angiopteris* Hoffman

1. *Angiopteris evecta* (Forster) Hoffman, Comment. Soc. Reg. Gotting. 12: 29, pl. 5, 1796.
Lou: Stream valley, no. 4040.
Los Negros: Along stream near Chaporowan Point, no. 4104.
Paleotropics.

Terrestrial in deep woods, usually along streams. Frequent.

III. SCHIZAEACEAE

Fronds small and rushlike, erect but not scandent.....1. *Schizaea*
Fronds very long when fully developed, scandent.....2. *Lygodium*

1. *Schizaea* J. E. Smith

Fronds dichotomously branched.....1. *S. dichotoma*
Fronds simple.
Plant terrestrial; fronds 12 cm. tall; sporangiophores more than 3.....2. *S. digitata*
Plant epiphytic; fronds 6 cm. tall; sporangiophores only 3.....3. *S. Wagneri*

1. *Schizaea dichotoma* (Linnaeus) J. E. Smith, Mem. Accad. Turin 5: 422, pl. 9, fig. 9, 1793.
Manus: Summit of Mount Tjajiak, alt. *ca.* 2,000 ft., no. 4175; falls of an eastern tributary of the Lorengau River, no. 4120.
Los Negros: Woods ½ mi. SSW of Lombrom Bay, no. 4109.
Madagascar, tropical Asia, to Polynesia.

Terrestrial in deep woods, usually in company with the next species. Common but inconspicuous. All of the specimens of our collection are of the smaller form, usually 15–20 cm. (rarely 30 cm.) tall.

2. *Schizaea digitata* (Linnaeus) Swartz, Syn. Fil., pp. 150 and 380, pl. 4, fig. 1, 1806.
Manus: Summit of Mount Tjajiak, no. 4176.
Los Negros: On a little, wooded, limestone hill in center of mangrove swamp, western Los Negros, no. 3996.
Ceylon to New Guinea, and Bonin Islands.

Terrestrial, usually in deep woods. Common. All of the specimens seen had spiral leaves 8–16 cm. long.

3. *Schizaea Wagneri* Selling, Svensk Bot. Tidsk. 40: 278, figs. 8–11, 1946.
Manus: Summit of Mount Tjajiak, no. 4177.
Endemic.

Epiphytic in mosses on stumps and on bases of trees in mountaintop forest; abundant at one place, but exceedingly inconspicuous. This tiny plant is discussed in detail by Dr. O. F. Selling (*op. cit.*), who describes it as "closely related to *S. intermedia* Mett. of New Caledonia, though externally reminiscent of *S. Germani* Fée of tropical America." The epiphytic habit and the filiform fronds, with sporangiophores numbering only three, readily distinguish this species from the two other species of *Schizaea* known in the islands.

2. *Lygodium* Swartz

Pinnules pinnate, the segments ovate.....1. *L. scandens*
Pinnules palmate, the segments narrowly oblong.
Bases of sterile pinnules cuneate; fertile pinnules not deeply dissected..2. *L. circinnatum*
Bases of sterile pinnules semihastate; fertile pinnules much dissected..3. *L. trifurcatum*

1. *Lygodium scandens* (Linnaeus) Swartz, Jour. Bot. Schrad. 2: 106, 1801.
Manus: Forest path, Sabon, No. 1 Road, no. 4571.
Los Negros: In grassy, open marsh with *Acrostichum*, Momote Field, no. 3290.
Paleotropics.

Climbing, usually in open marshes. Uncommon.

2. *Lygodium circinnatum* (Burmann) Swartz, Syn. Fil., p. 153, 1806.
Lygodium dichotomum Swartz; Baker, Jour. Linn. Soc. Bot. 15: 111, 1877.
Los Negros: Climbing on ginger plants, near Momote Field, no. 3493; in brackish marsh, western Los Negros, no. 3998.
Tropical Asia to Australia.

Climber in marshes, brushy places, and woods. Abundant.

3. *Lygodium trifurcatum* Baker, Syn. Fil., p. 437, 1868. (Pl. 8.)
Los Negros: Brackish marsh, western Los Negros, no. 3997.
New Guinea and Melanesia.

Swamps and woods. Common, but the plants are very often sterile. The fertile fronds vary widely in the amount of dissection and lamina.

IV. GLEICHENIACEAE

Sori with 3–4 sporangia; veins once-forked.....1. *Sticherus*
Sori with 6–10 sporangia; veins twice-divided.....2. *Dicranopteris*

1. *Sticherus* Presl

Fronds not scandent; lamina thicker, glaucous below; divisions more regular, at angles averaging 30°.....1. *S. hirtus*
Fronds often scandent; lamina thin, not glaucous below; divisions irregular, at angles averaging 50° or more.....2. *S. laevigatus*

1. *Sticherus hirtus* (Blume) Copeland, Philippine Jour. Sci. Bot. 75: 353, 1941.
Manus: Opening in woods near the summit of Mount Tjajiak, no. 4195.
Tropical Asia to New Guinea.

Terrestrial in second-growth area in woods. Only one large colony was found. The natives place the pinnae in their hair as plumes.

2. ***Sticherus laevigatus*** (Willdenow) Presl, Tent. Pterid., p. 52, 1836.
Manus: Banks of the Lorengau River below the Falls, no. 4150.
Tropical Asia to New Guinea.

A vigorous climber among the riverside trees and bushes. Abundant along the lower Lorengau in company with the next species.

2. *Dicranopteris* Bernhardi

1. ***Dicranopteris linearis*** (Burmann) Underwood, Bull. Torrey Bot. Club 34: 250, 1907.
Manus: Woods near Lorengau River Falls, no. 3977; overgrown coconut groves, 2 mi. SE of Lorengau, no. 4112; terrestrial, Sabon, alt. 600 ft., no. 4565.
Pantropics.

A climber along rivers and in old coconut groves. Frequent. In such damp river valleys as that in the vicinity of the Lorengau River Falls, this plant and *Sticherus laevigatus* climb very high in the trees, forming great tangles. Such vigorous growth is remarkable for these species.

V. HYMENOPHYLLACEAE

A. Involucre valvate.
B. Margins entire ..... 1. *Mecodium*
BB. Margins toothed ..... 3. *Meringium*
AA. Involucre tubular or obconic.
C. Rhizome creeping; fronds not clustered.
D. Lamina with false veinlets.
E. Frond pinnate ..... 7. *Crepidomanes*
EE. Frond simple or lobed ..... 8. *Microgonium*
DD. Lamina without false veinlets.
F. Fronds with elongate marginal cells ..... 6. *Crepidopteris*
FF. Fronds without elongate marginal cells.
G. Axes of fronds proliferous ..... 5. *Gonocormus*
GG. Axes not proliferous.
H. Fronds dichotomous, segments more than 1 mm. wide 2. *Microtrichomanes*
HH. Fronds pinnately decompound, segments less than 1 mm. wide 4. *Vandenboschia*
CC. Rhizome erect; fronds clustered.
I. Fronds once pinnate ..... 10. *Cephalomanes*
II. Fronds more divided.
J. Segments extremely narrow ..... 12. *Macroglena*
JJ. Segments broader.
K. Fronds harsh, segments more than 1 mm. broad ... 11. *Selenodesmium*
KK. Fronds soft, segments less than 1 mm. broad ..... 9. *Nesopteris*

1. *Mecodium* Presl

1. ***Mecodium polyanthos*** (Swartz) Copeland, Philippine Jour. Sci. Bot. 67: 19, 1938.
Manus: Summit of Mount Tjajiak, no. 4168B.
Pantropical.

This and the following four species occur epiphytically on mossy trunks in mountainside woods. This species is locally common.

2. *Microtrichomanes* (Mettenius) Copeland

1. ***Microtrichomanes digitatum*** (Swartz) Copeland, Philippine Jour. Sci. Bot. 67: 1, 36, 1938.
Manus: Summit of Mount Tjajiak, no. 4169.
East African Islands to Samoa.

Common around mountaintop.

3. *Meringium* Presl

Stipe and rachis hairy; segments less than 1 mm. wide; cell walls deeply toothed
1. *M. Meyenianum*
Stipe and rachis almost glabrous; segments 1.2–1.5 mm. wide; cell walls at most shallowly toothed ..... 2. *M. holochilum*

1. *Meringium Meyenianum* Presl, Hymen., p. 116, pl. 8, fig. B, 1843.
? Hymenophyllum (*Leptocionium*) *polyodon* Baker, Jour. Linn. Soc. Bot. 15: 105, 1877.
Manus: Summit of Mount Tjajiak, nos. 4166 and 4170; wet epiphyte, dark woods, Tingau No. 2, alt. 1,400 ft., no. 4538.
Philippines to New Guinea.

Abundant at the top of Mount Tjajiak. The variation shown by our large series of this plant is very wide. The commonest form, and the most typical, has a narrow, slightly hairy rootstock, bearing lax, dull brown-green fronds, 6–12 cm. long. The pinnae have numerous narrow segments, less than 1 mm. broad. The stipe is 2–5 cm. long, terete, and slightly hairy, as is the rachis, which is unwinged below. The cell walls are deeply toothed, and the cell contents are dark, occupying most of the cell space in dried specimens. The shape of the involucre varies remarkably, especially in the length of the rather short tube, some of the involucres being cleft almost to the base. The lips are more or less pointed, and the receptacle in undamaged specimens is long exserted. Collection no. 4166B differs from this description in its compact, shiny green fronds, which are more hairy on the rhizome, stipe, and somewhat more zigzag rachis, and more rounded lips of the involucre. Another collection (no. 4170) is so distinct from the typical that it appears on first observation to be a different species. It is, however, merely a dwarf form with small, compact, oval-deltoid fronds 2 cm. (1–4 cm.) long, 1–2 cm. broad, and nearly sessile to stipitate, with stipes up to 1.5 cm. long, winged above. The cell walls agree in structure, and the hairiness and compactness are found also in no. 4166B. The rootstock is very hairy, as are the stipes, rachises, and minor axes. The involucre is almost 2 mm. long, with nearly entire rounded lips, the tube almost half as long as the involucre, and the receptacle exserted up to one and one-half times the length of the involucre. The small size, the shiny green color, the somewhat zigzag rachis, the sturdy and hairy rootstock, and the rounded lips would seem to distinguish this plant as a species were it not that we have a long series with intermediate specimens which show the affinity. The last is a beautiful example of reduction in *Meringium* and of the taxonomic problem imposed by such dwarfs. The whole material of *M. Meyenianum* from Mount Tjajiak averages somewhat smaller than Philippine material, approaching *M. Bakeri* more closely in size.

2. *Meringium holochilum* (van den Bosch) Copeland, Philippine Jour. Sci. Bot. 67: 41, 1938.
Manus: Summit of Mount Tjajiak, nos. 4167, 4168, and 4168B; Drano, alt. 1,000 ft., No. 1 Road, no. 4521.
Malaya to Java and Papua.

In the field this species casually resembles a small stage of *Mecodium polyanthos* rather than its nearer ally, *Meringium Meyenianum*, and part of the material was confused with the former species when collected. This plant is

most distinct from the other *Meringium,* differing from it in its narrower, usually smaller frond, fewer and broader segments, and cell walls that are, at most, shallowly toothed, the marginal ones not at all. The rootstock is very thin, with sparse hairs, and bears stipitate fronds 2–6 cm. long, dull gray-green, and translucent. The stipe and rachis are nearly glabrous, the rachis entire-winged above. Lower pinnae are slightly reduced, with usually two or three segments 1.2–1.5 mm. broad, shortly dentate. The involucres have somewhat pointed, shallowly dentate tips. The tube is provided with a few hairs below. This plant belongs to a group of intricately related and poorly characterized small species of *Meringium,* and this identification is *sensu lato.*

4. *Vandenboschia* Copeland

1. *Vandenboschia aphlebioides* (Christ) Copeland, Philippine Jour. Sci. Bot. 67: 54, 1938.
Manus: Slopes of Mount Tjajiak, alt. *ca.* 1,500 ft., no. 4174.
Sumatra to Fiji.

Epiphytic on mossy trunks. Only a single collection.

5. *Gonocormus* van den Bosch

1. *Gonocormus minutus* (Blume) van den Bosch, Hymen. Javan., p. 7, pl. 3, 1861.
Lou: Epiphytic, no. 4077.
Manus: Slopes of Mount Tjajiak, alt. *ca.* 1,500 ft., no. 4173; wet epiphyte, Warrabi, alt. 500 ft., No. 1 Road, no. 4513; Tingau, alt. 1,000 ft., No. 1 Road, no. 4524.
Los Negros: Tree trunk in deep, hilly woods, northern Los Negros, no. 3679.
Africa to Polynesia and Japan.

Epiphytic on tree trunks in slightly drier places than those in which most of the local filmy-ferns grow. Frequent. The specimens collected on the slopes of the mountain were considerably larger than typical.

6. *Crepidopteris* Copeland

1. *Crepidopteris humilis* (Forster) Copeland, Philippine Jour. Sci. Bot. 67: 58, 1938.
Trichomanes humile Forster; Baker, Jour. Linn. Soc. Bot. 15: 105, 1877.
Lou: On rocks near coast, no. 4066.
Manus: On tree trunks in deep, hilly woods, east end of Manus, no. 3677; on rocks and tree trunks, Lorengau River Falls, no. 4018; wet epiphyte, Warrabi, alt. 500 ft., no. 4512.
Los Negros: Thick, dark woods, along road to Manus, western Los Negros, no. 3686; epiphytic in damp woods, no. 3517.
Sumatra to Tahiti.

Epiphytic, and on damp rocks, in shady, rich woods. Very common.

7. *Crepidomanes* Presl

1. *Crepidomanes bipunctatum* (Poiret) Copeland, Philippine Jour. Sci. Bot. 67: 59, 1938.
Trichomanes Filicula Kaulfuss; Baker, Jour. Linn. Soc. Bot. 15: 105, 1877.
Manus: Epiphytic in woods along the Drangot River, no. 4062; Lorengau River Falls, no. 4019.
Los Negros: no. 3555; epiphytic in wet woods, no. 3516.
Madagascar to Tahiti (with a gap in Malaya).

Epiphytic, and rarely on rocks, in shady woods. Common.

8. *Microgonium* Presl

Frond peltate ..... 1. *M. omphalodes*
Frond stipitate at base, not peltate.
Fronds less than 1 cm. long, entire ..... 2. *M. Beccarianum*
Fronds more than 1 cm. long, lobed ..... 3. *M. mindorense*

1. *Microgonium omphalodes* Vieillard, in Fournier, Ann. Sci. Nat. Bot., ser. 5, 18: 255, 1873.
Trichomanes peltatum Baker, Jour. Linn. Soc. Bot. 15: 105, 1877.
Lou: Tree trunk in forest, no. 4078.
Manus: Eastern end of island, no. 3676.
Los Negros: Epiphytic in wet woods, nos. 3515 and 3553.
Java to Tahiti.

Epiphytic on rather exposed tree trunks in woods. Frequent.

2. *Microgonium Beccarianum* (Cesati) Copeland, Philippine Jour. Sci. Bot. 67: 63, 1938.
Trichomanes Motleyi Baker, Jour. Linn. Soc. Bot. 15: 105, 1877; not van den Bosch, 1861.
Los Negros: Woods 1 mi. W of Pitilu Lake, no. 4143; wet woods, nos. 3557 and 3487.
Ceylon to Formosa and the Solomons.

Epiphytic, often on smooth-barked trees. Frequent.

3. *Microgonium mindorense* (Christ) Copeland, Philippine Jour. Sci. Bot. 67: 61, 1938.
Manus: Deep woods, east end of island, no. 4013.
Los Negros: Very damp woods, road to Lombrom Bay, no. 3514.
Mindoro and Admiralties.

Epiphytic in mats at bases of trees in deep woods. Rare.

9. *Nesopteris* Copeland

1. *Nesopteris intermedia* (van den Bosch) Copeland, Philippine Jour. Sci. Bot. 67: 66, 1938.
Manus: Along stream, slopes of Mount Tjajiak, no. 4165.
Papua and Polynesia.

Terrestrial, growing on rocks along a mountain stream. Only a single collection.

10. *Cephalomanes* Presl

Pinnae narrow, ascending, with conspicuous, sharp projections; sori usually not congregated at tip ..... 1. *C. Boryanum*
Pinnae broader, spreading, without sharp projections; sori usually congregated at tip
2. *C. oblongifolium*

1. *Cephalomanes Boryanum* (Kunze) van den Bosch, Nederl. Kruidk. Arch. 4: 351, 1859.
Trichomanes javanicum Baker, Jour. Linn. Soc. Bot. 15: 105, 1877; not Blume 1828.
Lou: Along small stream, no. 4075.
Manus: Lorengau River Falls, no. 4131; falls of an eastern tributary of the Lorengau River, no. 4121; wet stream bank, Bowat, alt. 800 ft., No. 1 Road, no. 4585.
Los Negros: ½ mi. SSW of Lombrom Bay, nos. 4111 and 3554; wet woods, no. 3508.
Polynesia.

Terrestrial, usually along rocky streams. Very common.

2. *Cephalomanes oblongifolium* Presl, Epim. Bot., p. 19, pl. 10, 1849.
Los Negros: ½ mi. SSW of Lombrom Bay, no. 4110.

Terrestrial in damp, limestone woods, in company with the preceding, but in much larger numbers. Apparently rare in the islands as a whole. This species has a very distinctive appearance in life; the leaves are broader and paler than the leaves of *C. Boryanum,* and the sori are fewer, congregated at the tip on the more than a hundred plants observed. This species lacks the conspicuous, sharp projections of *C. Boryanum.*

11. *Selenodesmium* Copeland

1. *Selenodesmium dentatum* (van den Bosch) Copeland, Philippine Jour. Sci. Bot. 67: 82, 1938.
   Manus: Near the summit of Mount Tjajiak, no. 4196.
   Los Negros: Woods ½ mi. SSW of Lombrom Bay, no. 3507.
   Polynesia.

Terrestrial in rich woods. Occasional, but usually abundant where it occurs.

12. *Macroglena* Copeland

1. *Macroglena meifolia* (Bory) Copeland, Philippine Jour. Sci. Bot. 67: 83, 1938.
   Manus: Near summit of Mount Tjajiak, no. 4172.
   Madagascar to Malaya to Samoa.

Epiphytic at bases of trees. At our single locality this species was very common.

VI. PTERIDACEAE

A. Sori dorsal, not marginal or inframarginal.
  B. Sporangia confluent.
    C. Fronds dimorphic; medium-sized[1] plant; creeping rootstock.....8. *Taenitis*
    CC. Fronds monomorphic; large, coarse plant; erect rootstock..14. *Acrostichum*
  BB. Sporangia in distinct linear sori.
    D. Fronds simple.....9. *Syngramma*
    DD. Fronds palmately divided.....10. *Craspedodictyum*

ÂA. Sori marginal or inframarginal.
  E. Indusium formed by reflexed margin.
    F. Pinnae dimidiate; sori strongly curved.....16. *Adiantum*
    FF. Pinnae not dimidiate; sori not strongly curved.
      G. Veins free; plants small.....15. *Cheilanthes*
      GG. Veins joined by marginal soriferous vein; plants medium-sized to large.
        H. Rootstock long-creeping; fronds coriaceous; sorus continuous.
          I. Segments usually less than 4 mm. broad; veins forking, anastomosing only at tips.....11. *Pteridium*
          II. Segments over 5 mm. broad; veins anastomosing copiously 12. *Histiopteris*
        HH. Rootstock short; fronds chartaceous; sorus interrupted at sinus and tip of segment.....13. *Pteris*
  EE. Indusium opening toward the margin.
    J. Indusium linear, or if not linear, not attached at the sides.
      K. Frond decompound, the pinnules cuneiform.....7. *Sphenomeris*
      KK. Frond at most bipinnate, the pinnules deltoid or oblong.....4. *Lindsaea*
    JJ. Indusium other than linear, attached both basally and laterally.
      L. Rootstock with copious, fine, golden hair.....1. *Cystodium*
      LL. Rootstock hair or scales not golden.
        M. Sori inframarginal; lamina soft and dull pale green..3. *Microlepia*
        MM. Sori marginal; lamina chartaceous and shiny darker green.

[1] The term medium-sized as used here means averaging from 40 to 90 cm. tall.

N. Indusium longer than broad.....5. *Orthiopteris*
NN. Indusium as broad as or broader than long.
O. Plant large, hairy.....2. *Culcita*
OO. Plant of moderate size, glabrous.....6. *Tapaenidium*

1. *Cystodium* J. Smith

1. *Cystodium sorbifolium* (J. E. Smith) J. Smith, in Hooker, Genera Filicum, pl. 96, 1842.
Manus: Lorengau River Falls, no. 3972.
Los Negros: Wet woods, no. 3513.
Malaya to New Guinea.

Terrestrial in rich woods, and especially along stream banks. Common. Apparently the rootstock has not been previously described. It is large, erect to decumbent, with the fronds fascicled at the tip. Our Manus specimen has a rootstock 10 cm. long, decumbent but curved upwards at the tip; the rhizome itself at the center is only 2.5 mm. thick, of dark color, but the persistent stipe bases, 1–2 cm. long, separated by abundant, fine, golden hair, give the rootstock an apparent diameter of 2–3 cm.

2. *Culcita* Presl

1. *Culcita straminea* (de Labillardière) Maxon, Jour. Wash. Acad. Sci. 12: 457, 1922.
Manus: Lorengau River Falls, no. 4137; Bulihot, alt. 500 ft., No. 1 Road, no. 4516.
Construed broadly, this species occurs from Australia to Polynesia and Formosa.

Terrestrial on exposed muddy banks in second-growth thickets. Not common. The fronds are very large, 2–3 m. tall, and the stipe is covered with fine hair, which brushes off easily. Fertile specimens were few in the Lorengau River colony, and these had very sparse sori—sometimes only one sorus to an entire pinna!

3. *Microlepia* Presl

1. *Microlepia speluncae* (Linnaeus) Moore, Ind. Fil., p. xciii, 1857.
Manus: Lorengau River Falls, no. 3989; Bowat, alt. 800 ft., No. 1 Road, no. 4587.
Los Negros: Banks along road to Lombrom Point, no. 4008.
Pantropical.

Terrestrial in second-growth woods and on weedy banks along roads. Frequent. Large plants in shady places have a very different appearance from plants of exposed situations, being much larger and more divided.

4. *Lindsaea* Dryander

Epiphytic.
Medium-sized, robust plant with close, oblong pinnae, often overlapping; rootstock 2.5–3.0 mm. thick; scales dark.....2. *L. Macraeana*
Small, delicate, pale green plant with more remote, deltoid pinnae; rootstock 0.5–1.5 mm. thick; scales light.....3. *L. sagincola*
Terrestrial.
Fronds simply pinnate.
Pinnae not dimidiate, long and narrow.....1. *L. ensifolia*
Pinnae dimidiate, short.
Frond lanceolate, the pinnules more than 1.2 cm. long, dark green, not deeply cut 5. *L. decomposita*
Frond linear, the pinnules less than 1.0 cm. long, light green, more deeply cut 4. *L. brevipes*

Fronds bipinnate.
Veins anastomosing; plant 15–50 cm. tall.
Pinnae crenate ..... 5. *L. decomposita*
Pinnae lobed half-way to costa ..... 6. *L. davallioides*
Veins free; plant 65–90 cm. tall ..... 7. *L. Kingii*

1. *Lindsaea ensifolia* Swartz, Jour. Bot. Schrad. 2: 77, 1801.
Manus: Swamp at Patusi, no. 4155; Kwaliop, alt. 1,400 ft., No. 1 Road, no. 4542.
Africa to Polynesia.

We made our first discovery of this elsewhere often abundant species in a deep sago-palm swamp, where a colony was growing in mud. On the island of Tawi, however, it occurs in a more usual situation for this species: in dry, rocky (nonlimestone) soil, in an open, grassy field. It is apparently not common.

2. *Lindsaea Macraeana* (Hooker and Walker-Arnott) Copeland, Bishop Mus. Bull. 59: 70, 1929.
Manus: Lorengau River Falls, no. 3993; woods along Drangot River, no. 4054; Lundrit, alt. 600 ft., No. 1 Road, no. 4575.
Paleotropics.

Climbing on tree trunks. Frequent. The thick rootstock and large fronds (30–60 cm. long), with numerous approximate dark green pinnae, characterize this plant locally. It may be found also in drier situations than those in which the species next described is found. The local form resembles that in the Hawaiian Islands.

3. **Lindsaea sagincola**, sp. nov. (Pl. 9.)
Lindsaea tenuis epiphytica, gregis L. Macraeanae; rhizomate late repente, 0.5–1.5 mm. crasso, paleis aureis linearibus attenuatis 2–3 mm. longis instructo; frondibus pinnatis membranaceis 9 (5–23) cm. longis, 2 (1.5–3.0) cm. latis, attenuatis, pallidis viridibus non nitidis; pinnis breviter petiolatis, 15 (9–33) paribus, inaequaliter cuneatis, plerumque acuminatis, crenatis, 10 (7–13) mm. longis, basi 4 (3–8) mm. latis; stipitibus 0.5–1.5 cm. longis, brunneis; rhachi superne sulcata pallida; soris a margine remotis; venulis remotis infra sōros liberis.
Type: Univ. Calif. Herb. no. 701238, Grether and Wagner no. 4010.
Manus: Growing with *L. Macraeana* at bases of trees, in wet woods along the Drangot River, no. 4055; bases at sago palms with *L. Macraeana*, 2 mi. E of Lorengau, no. 4128.
Los Negros: Mossy base of sago, swamp near Mokerang, no. 4100; swamp along road near Lombrom Point, no. 4010 (type).

This species differs from the local representative of *L. Macraeana* in being smaller and in having pale golden scales, much more delicate texture, more slender rhizome, differently shaped pinnules, fewer and more widely spaced veins, and broader crenations. Even when it occasionally grows side by side with *L. Macraeana*, *L. sagincola* can immediately be distinguished by these characters. There are, however, specimens of *L. Macraeana*, possibly juvenile, from elsewhere, that somewhat resemble the present species. *L. Foersteri* Rosenstock from New Guinea differs in having smaller, more deeply cut pinnae, thicker texture, and stouter rootstock. *L. Havicei* Copeland differs in that its sori are marginal.

This fern is a climber in mosses at bases of tree trunks, often in association with the small form of *Ophioglossum pendulum* and with *Lindsaea Macraeana*.

The much larger plants of *L. Macraeana* may be entirely sterile, though plants of *L. sagincola* on the same tree trunk are fertile. This species is common in sago-palm swamps, always at the bases of old trees.

4. *Lindsaea brevipes* Copeland, Philippine Jour. Sci. Bot. 6: 83, 1911.
Los Negros: On rocks in woods near Chaporowan Point, no. 4106.
New Guinea.

Only one station for this species was found, on rocks along a stream in company with *L. decomposita.* Our specimens agree with the type of *L. brevipes,* except that the pinnae of adult specimens are more or less crenate. The juvenile specimens are rather deeply lobed. *L. brevipes* is in the group of *L. concinna* J. Smith, but differs in having very short stipes.

5. *Lindsaea decomposita* Willdenow, Sp. Pl. 5: 425, 1810.
Lindsaea lobata Poiret, Baker, Jour. Linn. Soc. Bot. 15: 106, 1877.

There are at least two distinctive local forms of this plant:

a) Fronds dark green, broader, pinnate or bipinnate, the segments not long-attenuate at tips, shallowly crenate; pinnules shallowly crenate, 1.2 cm. or more long.
Manus: Wet woods along Drangot River, no. 4049; Tingau No. 1, No. 1 Road, no. 4532.
Los Negros: No. 3506; rocks along stream near Chaporowan Point, no. 4105; stream bank, no. 3524.
A variable species extending from tropical Asia to Australia and Polynesia.

This, the typical form, is very common generally, occurring terrestrially in woods, often along streams.

b) Fronds pale green, bipinnate, the divisions narrower, long-attenuate at tips; pinnules almost entire to shallowly lobed, up to 1 cm. long, but usually less.
Manus: Lorengau River Falls, nos. 4021 and 4129; No. 1 Road at Bowat, no. 4588.

Common on rocks along streams above Lorengau River Falls and also found on banks of man-made ditches. It often occurs with the ordinary form, from which it is poorly differentiated but apparently distinct locally.

6. *Lindsaea davallioides* Blume, Enum. Plant. Jav., p. 218, 1828.
Manus: Woods at eastern end of island, no. 3674.
Los Negros: Wet woods along road to Lombrom Point, no. 3280.
Malaya, Philippines, New Guinea, Micronesia.

Terrestrial in damp woods. This species is closely related to *L. decomposita,* but is apparently much less common than that species. Distinguished by more deeply lobed and shinier pinnae and usually larger and bipinnate fronds.

7. *Lindsaea Kingii* Copeland, Philippine Jour. Sci. Bot. 6: 83, 1916.
Manus: Woods at summit of Mount Tjajiak, no. 4160.
New Guinea.

Terrestrial in mountaintop woods. Locally common. Recognizable by its large size.

5. *Orthiopteris* Copeland

1. *Orthiopteris minor* (Hooker) Copeland, Genera Filicum, p. 50, 1947.
Manus: Summit of Mount Tjajiak, no. 4161.
Samoa to Malacca.

Terrestrial in rich, mountainside woods. Locally common. The large, firm, dark green, compound fronds, with numerous, rather close pinnules, make this fern distinctive in the field. *Culcita straminea* resembles it somewhat, but differs by its thinner texture, longer pinnules, and very different sori.

6. *Tapaenidium* (Presl) C. Christensen

Plant usually 1 m. tall; ultimate segments more than 1 mm. wide; stipe and rachis brown ..... 1. *T. moluccanum*

Plant 0.5 m. tall; ultimate segments narrow, less than 1 mm. wide; stipe and rachis shiny purple ..... 2. *T. stenolobum*

1. *Tapaenidium moluccanum* (Blume) C. Christensen, Gard. Bull. Straits Settlem. 4: 399, 1929. (Pl. 10.)
Manus: Summit of Mount Tjajiak, no. 4188.
Molucca to New Guinea.

Growing with *Orthiopteris* and the following species. Local. The fronds are 70–120 cm. or more tall, tripinnate, dull green, and paler than those of the following species, with fewer and coarser segments, which are rounded at the tips and mostly more than 1 mm. broad. The stipes and rachises are dull brown.

2. **Tapaenidium stenolobum** (Baker), comb. nov. (Pl. 11.)
Davallia stenoloba Baker, in Beccari, Malesia 3: 35, 1886; C. Christensen, Ind. Suppl. III, p. 69, 1934.
Tapaenidium moluccanum (Blume) C. Christensen var. *stenolobum* (Baker) C. Christensen, Ind. Suppl. III, p. 176, 1934.
Manus: Woods along Drangot River, no. 4057; summit of Mount Tjajiak, in company with *T. moluccanum*, no. 4189; Lorengau River Falls, no. 3978; Tingau No. 1, alt. 1,000 ft., No. 1 Road, no. 4527.
Amboina, ? New Guinea.

Terrestrial in damp woods, usually on shaded hillsides. Frequent and generally distributed, at least on Manus. This is a lacier and more delicate species than the preceding. The fronds are 30–60 cm. tall, tripinnate, dark green above, and lighter below, and the ultimate segments are more numerous, pointed, and narrower, usually less than 1 mm. broad. The stipe and rachis are shiny purple.

Christensen (Ind. Suppl. III, p. 176, 1934) placed *Davallia stenoloba* Baker and *Tapaenidium stenocarpum* v. A. v. R. under *T. moluccanum*. *T. stenocarpum* has indusia much longer than wide, but Christensen considered this plant equivalent to *T. moluccanum* var. *stenolobum*. Since our plant has sori about as broad as they are long, thus agreeing with Baker's description, and since we very clearly have two distinct species in the Admiralties, we identify our plant with Baker's as a separate entity.

7. *Sphenomeris* Maxon

1. *Sphenomeris retusa* (Cavanilles) Maxon, Contr. U. S. Natl. Herb. 17: 159, 1913.
Manus: Lorengau River Falls, no. 3970.
Malaya to Melanesia.

Terrestrial in gravelly soil in shaded brushy places along river. Uncommon.

8. *Taenitis* Willdenow

1. ***Taenitis Requiniana*** (Gaudichaud) Copeland, Univ. Calif. Publ. Bot. 16: 85, 1929.
Manus: Wet woods along Drangot River, no. 4047; ground in forest, Bowat, alt. 600 ft., No. 1 Road, no. 4509.
Los Negros: Woods along the road to Lombrom Point, no. 3510.
Malaya to Melanesia.

Terrestrial in damp woods. Frequent. A peculiar frond (Univ. Calif. Herb. no. 697071) was found, which has contracted, fertile pinnae on one side only, the other half of the frond being entirely sterile.

9. *Syngramma* J. Smith

1. ***Syngramma borneensis*** (Hooker) J. Smith var. ***major*** Baker, Jour. Bot. 17: 299, 1879.
Manus: Summit of Mount Tjajiak, no. 4185; growing on bank, No. 1 Road, Pundrau, no. 4501.

Epiphytic on mossy trunks, and terrestrial on dirt banks. Very local. This is the eastern representative of *S. borneensis* (Hooker) J. Smith of Borneo and Celebes.

10. *Craspedodictyum* Copeland

1. ***Craspedodictyum quinatum*** (Hooker) Copeland, Philippine Jour. Sci. Bot. 6: 85, 1911.
Manus: Watani River, near coast in swamp, no. 4195.5.
Los Negros: Swamp along road, western Los Negros, no. 4146.
Malaya to Melanesia.

Terrestrial in sago-palm swamps. Frequent.

11. *Pteridium* Gleditsch

1. ***Pteridium aquilinum*** (Linnaeus) Kuhn, in v. d. Decken, Reisen in Ost-Afrika 3[3] (Bot.): 11, 1879.
Los Negros: Brushy place near Momote Field, no. 3269 (U. S. Natl. Herb. no. 1860262).
Cosmopolitan.

Terrestrial in dry, brushy place. Evidently rare. Our only collection was identified by Dr. W. R. Maxon as *P. aquilinum* var. *yarrabense* Domin. Within a year, the places where this species had been collected on November 17, 1944, were covered with such dense vegetation that we could not relocate the plant in the tall undergrowth.

12. *Histiopteris* (Agardh) J. Smith

Pinnules usually narrow, deeply lobed ..... 1. ***H. incisa***
Pinnules broad, entire ..... 2. ***H. integrifolia***

1. ***Histiopteris incisa*** (Thunberg) J. Smith, Hist. Fil., p. 295, 1875.
Manus: Tingau No. 2, alt. 1,400 ft., No. 1 Road, no. 4536.
Pantropical.

Our one collection was growing on an old, moss-covered stump. This species is extremely variable, and the following very different-looking plant may possibly be an unusual form.

2. ***Histiopteris integrifolia*** Copeland, Philippine Jour. Sci. Bot. 7: 63, 1912.
Manus: Tingau No. 2, alt. 1,400 ft., No. 1 Road, no. 4537.
Sumatra and Borneo.

Found growing near the preceding species, in a brushy marsh. The single plant was 8 feet tall. The coarse, entire divisions, 1.8–2.0 cm. broad and 8–12 cm. long, are very distinctive.

13. *Pteris* Linnaeus

Pinnae entire or dentate, not lobed.
  Fronds 0.5 m. tall, the pinnae dull pale green, 0.5 cm. broad.....1. *P. vittata*
  Fronds 2 m. tall, the pinnae dark lustrous green, 2 cm. broad.....2. *P. moluccana*
Pinnae lobed.
  Veins free except in sori.
    Sterile and fertile pinnae dimorphic, their segments few.....3. *P. ensiformis*
    Pinnae monomorphic, their segments numerous.
      Lamina thin, shiny dark green; tips of pinnae short, 1.5 cm. long.....4. *P. pacifica*
      Lamina thick, dull pale green; tips of pinnae 4 cm. long.....5. *P. ligulata*
  Veins copiously anastomosing.....6. *P. tripartita*

1. *Pteris vittata* Linnaeus, Sp. Pl. 2: 1074, 1753.
  Los Negros: Momote Airfield, no. 4101.
  Paleotropics.

Terrestrial on dry, exposed, limestone banks along the edge of Momote Airstrip, and along dirt roads in secondary woods near by. Not common.

2. *Pteris moluccana* Blume, Enum. Plant. Jav., p. 208, 1828.
  Lou: No. 4033.
  Malaya to the Solomon Islands.

Only a single, large colony in damp woods on a hillside near the coast of Lou Island. This is a very striking fern, with pinnate frond 2.0–2.5 m. tall. The shiny stipe and rachis, the silky luster of the pinnae, and the bright red-brown, marginal sori make this one of the most beautiful ferns in the Admiralties.

3. *Pteris ensiformis* Burmann, Flora Indica, p. 230, 1768.
  Lou: Coastal cliff, no. 4076.
  Tropical Asia to Polynesia.

Terrestrial in damp soil in woods on steep, rocky hillside, with *Adiantum philippense*. Only one station seen.

4. *Pteris pacifica* Hieronymus, Hedwigia 55: 355, 1914.
  Manus: Lorengau River Falls, no. 3991.
  Los Negros: No. 3621.
  Celebes to the Solomons and Samoa.

Terrestrial in shady places in woods. Frequent. This plant is little more than a subspecies of the wide-ranging and variable *P. quadriaurita* Retzius.

5. *Pteris ligulata* Gaudichaud, Freyc. Voy. Bot., p. 385, 1827.
  Lou: Banks along native trail, no. 4024.
  Manus: Lorengau River Falls, no. 3988.
  Moluccas and Borneo to New Guinea.

Terrestrial in disturbed soil on banks. Frequent.

6. *Pteris tripartita* Swartz, Jour. Bot. Schrad. 2: 67, 1801.
  Manus: Lorengau River Falls, nos. 3981 and 3995.

Los Negros: Nos. 3941 and 3554; edge of woods, no. 3482.
Africa through tropical Asia to Tahiti.

Terrestrial in fields, brushy areas, and second-growth woods. Abundant throughout, and variable in size according to habitat. On dry banks we have found fertile, dwarfed plants, only 10–17 cm. tall.

14. *Acrostichum* Linnaeus

1. *Acrostichum aureum* Linnaeus, Sp. Pl. 2: 1069, 1753.
Los Negros: No. 3939; swamp, no. 3551; salt marsh, west end of Los Negros, no. 3959.
Pantropical.

Terrestrial in coastal swamps and in weedy swamps with slow drainage in low, limestone areas. Abundant. In Moseley's report of his botanical observations in the Admiralties (Jour. Linn. Soc. Bot. 15: 80, 1877) it was stated that the natives eat "the fertile fronds of a large *Acrostichum* (*A. aureum ?*)." Of the three species, *Stenochlaena palustris, Bolbitis Quoyana,* and *Acrostichum aureum,* the last-named is the largest and, of Admiralties plants then placed in the genus *Acrostichum,* is most likely to be the one to which he referred. The other two are very different from *A. aureum.* We can find no other reference to the use of this species as food, and we do not know whether or not the custom of eating it prevails today.

15. *Cheilanthes* Swartz

1. *Cheilanthes tenuifolia* (Burmann) Swartz, Syn. Fil., pp. 129 and 332, 1806.
Tawi: No. 4158.
Tropical Asia to Australia and Polynesia.

Terrestrial around rocks in burned-over, open, grassy field. Rare, probably because there are so few exposed places in nonlimestone areas suitable to this inhabitant of dry, xeric situations. The plants were small at Tawi Island, most of them being less than 15 cm. tall.

16. *Adiantum* Linnaeus

1. *Adiantum philippense* Linnaeus, Sp. Pl. 2: 1094, 1753.
Lou: No. 4072.
Paleotropics and Central America.

Growing luxuriantly in damp soil on wooded coastal cliff. A single collection.

VII. PARKERIACEAE

1. *Ceratopteris* Brongniart

1. *Ceratopteris siliquosa* (Linnaeus) Copeland, Philippine Jour. Sci. Bot. 56: 2, 107, 1935.
Manus: Swamp 2 mi. SE of Lorengau, no. 3967.
Los Negros: In pond in swampy place, no. 3288; in ditches, no. 3494.
Paleotropics.

Aquatic in fresh-water marshes and swamps. Frequent, but very local.

VIII. DAVALLIACEAE

Sori marginal.
Indusium attached at base and sides ..... 1. *Davallia*
Indusium attached only at base ..... 2. *Humata*

Sori dorsal.
Fronds simple, from a long-creeping rootstock.....3. *Oleandra*
Fronds pinnate, from a short rootstock.....4. *Nephrolepis*

1. *Davallia* Smith

Indusium longer than broad, truncate.....1. *D. solida*
Indusium as long as broad, pointed.....2. *D. epiphylla*

1. *Davallia solida* (Forster) Swartz, Jour. Bot. Schrad. 2: 87, 1801.
Los Negros: Edges of Pitilu Lagoon, no. 3944; epiphytic, no. 3522; epiphytic and terrestrial, no. 3264.
Malaya to Polynesia and Australia.

Epiphytic in exposed situations, especially on old coconut trees, and also occasionally terrestrial in coconut groves and along the shores of Pitilu Lagoon, with *Nepenthes* and with *Davallia epiphylla*. The local form of the variable plant has fronds less dissected and with broader segments than usual over much of its range.

2. *Davallia epiphylla* (Forster) Sprengel, Jour. Bot. Schrad. 2: 271, 1799.
Davallia elegans Swartz; Baker, Jour. Linn. Soc. Bot. 15: 106, 1877.
Manus: Epiphytic along logging road near Lorengau River Falls, no. 4213; Lorengau River Falls, no. 3992.
Los Negros: Epiphytic on stumps in wet woods, no. 3519; Pitilu Lagoon, no. 3943.
Tropical Asia to Polynesia and Australia.

Epiphytic in a wide variety of situations and rarely terrestrial. It tends to occur in more shady places than *D. solida* and is the commoner in deep woods.

2. *Humata* Cavanilles

Fronds dimorphic, the sterile entire, the fertile lobed.....1. *H. nervosa*
Fronds uniform, pectinate, oblong-lanceolate.....2. *H. Banksii*
Fronds uniform, or slightly dimorphic, 2- to 3-pinnate, deltoid.
Fronds 6 (2–16) cm. tall; stipe and rachis with scattered scales beneath; rhizome more than 1 mm. thick, the scales broader, their bases more conspicuously dark; sori submarginal between short projections of the lamina.....3. *H. alpina*
Fronds 1.5–3 (1–6) cm. tall; stipes and rachises without scattered scales beneath; rhizome 1 mm. or less thick, the scales narrower, their bases not as dark; sori marginal between long projections of the lamina.
Fronds 1.5 (1–2.5) cm. tall, with short stipes, somewhat dimorphic, the sterile with broad segments, the fertile with narrow segments.....4. *H. pusilla*
Fronds 2.5 (1.5–6.0) cm. tall, with long stipes, monomorphic, both sterile and fertile fronds with very narrow segments.....5. *H. parvula*

1. **Humata nervosa** (Baker), comb. nov. (Pl. 12.)
Davallia heterophylla Smith var. *nervosa* Baker, Jour. Linn. Soc. Bot. 15: 105, 1877.
Manus: High on coconut tree, Pundrau, alt. *ca.* 1,500 ft., No. 1 Road, no. 4502; Tingau No. 1, alt. 1,000 ft., No. 1 Road, no. 4506.
Los Negros: High up on tree trunks, no. 3497; on fallen tree trunk, 50 ft. from base, no. 3968; Pitilu Lagoon, no. 3690.

Epiphytic, usually high on tree trunks. We have also found it completely covering a coconut trunk, from bole to crown, in secondary woods. Apparently by typographical error, Baker (*loc. cit.*) did not give the type locality of his *Davallia heterophylla* var. *nervosa*, but it was probably the Admiralties. This plant is frequent in woods, especially along the coast. Of the derivatives

of the wide-ranging *Humata heterophylla,* this plant is most distinctive, as it has thick, blue-green fronds, subcordate at their bases, and crisped, with conspicuous, raised veins. It is locally very uniform, and its appearance in nature is different from that of *H. heterophylla* in the Marianas Islands.

2. *Humata Banksii* Alston, Philippine Jour. Sci. Bot. 50: 176, 1933.
Los Negros: High up on tree branches in deep woods, no. 3499; epiphytic on tree overhanging the water, along the coast north of Momote Field, nos. 3252 and 4203.
New Guinea to Polynesia.

Epiphytic in coastal woods. Uncommon.

3. *Humata alpina* (Blume) Moore, Ind. Fil., p. xcii, 1857. (Pl. 13.)
Manus: Summit of Mount Tjajiak, no. 4181.
Malaya to Polynesia.

Epiphytic on mossy trunks in mountaintop woods. This plant is often treated as a more dissected variety of *H. repens* (L.) Diels and is a variable fern here. Our mass collection shows very divergent frond forms: the sterile fronds range from small, compact, short-stipitate, 2–5 cm. long with wide segments, to fronds 10–16 cm. tall, with long stipes and narrower segments. A similar variation occurs in the fertile fronds.

4. *Humata pusilla* (Mettenius) Carruthers in Seemann, Flora Vitiensis, p. 335, 1873.
Manus: Lorengau River Falls, no. 3986b; on mossy trunks, slopes of Mount Tjajiak, alt. *ca.* 1,500 ft., no. 4182; wet epiphyte, near Sabon, No. 1 Road, no. 4560.
Melanesia.

A local epiphytic creeper in deep, wet woods.

5. *Humata parvula* (Wallich) Mettenius, Fil. hort. bot. Lips., p. 102, pl. 27, figs. 7 and 8, 1856.
Manus: Epiphytic in damp woods along the Drangot River, no. 4052; Lorengau River Falls, no. 3986a; Buyang No. 1, alt. 1,400 ft., No. 1 Road, no. 4547.
Malaya to New Guinea.

Habit similar to that of the above species, with which it can be easily confused. Our specimens compare well with a cotype, Wallich no. 247 from Singapore, in the University of California Herbarium.

3. *Oleandra* Cavanilles

1. *Oleandra Werneri* Rosenstock, Fedde Repert. Sp. Nov. 5: 40, 1908.
Manus: Summit of Mount Tjajiak, no. 4194.
New Guinea.

A vigorous climber in mountaintop woods. The dimorphic, dull green fronds and long, straight, brittle rhizome are unique among local ferns.

4. *Nephrolepis* Schott

Bases of pinnae cuneate; plants mostly very large, epiphytic in forest trees ..... 1. *N. persicifolia*
Bases of pinnae subtruncate; plants of medium size, usually terrestrial.
Sori marginal or submarginal.
Fronds glabrous ..... 2. *N. exaltata*
Fronds scaly ..... 3. *N. hirsutula*
Sori medial ..... 4. *N. biserrata*

1. ***Nephrolepis persicifolia*** Christ, Nova Guinea 8: 159, 1909. (Pl. 14.)

Manus: On tree overhanging the beach, mouth of Watani River, no. 4197; Tingau No. 1, alt. 1,000 ft., No. 1 Road, no. 4529.

Los Negros: Epiphytic, western Los Negros, no. 3958; epiphytic (juvenile) Pitilu Lagoon, no. 3942; edge of woods, no. 3501.

New Guinea.

Epiphytic in forest trees. Abundant. This is one of the most characteristic and beautiful ferns of the Admiralties. The fronds vary in size from 1 to 3 m. normally, and occasionally, in damp woods along rivers, sprays of fronds 4 or more m. long may be found, growing from the crotches of overhanging trees. The pendent fronds are pinnate, with short-stalked linear pinnae, 15–30 cm. or more long, and 1.3–1.7 cm. or more wide, chartaceous, cuneate at the base, slightly dentate in the outer half, and attenuate at the tips. The pinnae lie at an angle of about 45°–55° to the dull straw-colored rachis. The sori are exactly medial and are served by a single vein. Juvenile plants are membranous, with lanceolate-attenuate pinnae. Our fern agrees well with Christ's description of the plant collected by Versteeg along the Noord River in New Guinea in 1907. If our plant is identical, it is curious that this species has been so little collected, for it is a very common and conspicuous fern in the forest trees of the Admiralties.

2. ***Nephrolepis exaltata*** (Linnaeus) Schott, Genera Filicum, pl. 3, 1834; Baker, Jour. Linn. Soc. Bot. 15: 108, 1877.

Lou: Woods (large form), no. 4027.

Los Negros: No. 3938; at base of tree in brushy woods, Tauwi Hills, no. 4205; coconut groves near Mokerang Airfield, no. 4209.

Pantropical.

Terrestrial in secondary woods and fields and on limestone cliffs. Abundant. In the Admiralty Islands, this plant is apparently always distinct from the one next described. The fronds are essentially glabrous, with the sori located near the margin. The fertile pinnae are crenate and are somewhat narrowed in the local form, whereas the sterile pinnae are practically entire. This and the following two sword-ferns are conventionally considered pantropical, with a profusion of local slightly different forms.

3. ***Nephrolepis hirsutula*** (Forster) Presl, Tent. Pterid., p. 79, 1836.

Los Negros: No. 3940; exposed, sandy fields, Momote Airfield, C. P. Maciel no. 3669; shores of Pitilu Lagoon, no. 3689; brushy woods, Tauwi Hills, no. 4204.

Pantropical.

Terrestrial in open fields, coconut groves, and secondary woods, and occasionally on the boles of coconut trees. It occurs very often with the preceding species, from which it is easily distinguished by the presence of more or less numerous, fine, red-brown scales. Very abundant.

4. ***Nephrolepis biserrata*** (Swartz) Schott, Genera Filicum, pl. 3, 1834.

Los Negros: Woods on the south end of the island, no. 3541.

Pantropical.

This species is apparently less common than the other sword-ferns. We have found this plant growing terrestrially in shady woods, as it does in the Philip-

pines and in the Marianas. In the absence of scales and in having the medial sori, this plant differs from the two other terrestrial sword-ferns. From the epiphytic *N. persicifolia* it differs in its thinner texture, smaller sori, and pinnae with crenate margins and subtruncate bases. Baker (Jour. Linn. Soc. Bot. 15:108, 1877) recorded *N. acuta* Presl and *N. acuta* var. *rufescens* Presl from the Admiralty Islands. The former may have been what is here treated as *N. biserrata,* and the latter, as *N. hirsutula.*

IX. CYATHEACEAE

1. *Cyathea* J. E. Smith

(NOTE: Specimens of *Cyathea* should include stipe-bases.)

A. Frond bipinnate to subtripinnate.
  B. Scales at stipe bases very dark brown and closely appressed; segments 3 mm. wide, nearly entire; indusium persistent.....1. *C. propinqua*
  BB. Scales at stipe bases lighter, not closely appressed; segments usually less than 3 mm. wide, toothed; indusium fugacious.
    C. Scales at stipe base castaneous; pinnules becoming more remote toward pinna tip; segments acute.....5. *C. media*
    CC. Scales at stipe base pale; pinnules equidistant; segments blunt.
      D. Stipes with a "peppered" appearance, with numerous tiny spines, and chaff, hairs, and scales.....3. *C. scaberula*
      DD. Stipes shiny, with fewer and somewhat larger spines, the scales at base unmixed with hairs.....4. *C. contaminans*
AA. Frond tripinnate.
  E. Scales pale, very narrow with entire margins, occurring at stipe-base only; ultimate segments 2 mm. wide, entire or slightly undulate, glabrous.....2. *C. arachnoidea*
  EE. Scales very dark, setiform with toothed margins, occurring throughout the stipe and rachis; ultimate segments 3 mm. wide, deeply lobed, beset with pale, jointed hairs.....6. *C. pulcherrima*

1. *Cyathea propinqua* Mettenius, in Miquel, Ann. Mus. Lugduno-Batavi, Bot. 1: 56, 1863.
Cyathea Moseleyi Baker, Jour. Linn. Soc. Bot. 15:104, 1877.
Manus: Wooded ravine, Lorengau River Falls, no. 4022; Lundrit, alt. 600 ft., No. 1 Road, no. 4510.
Los Negros: No. 3512; dark woods along road, west end of Los Negros, no. 3684.
Fiji and Samoa; similar species elsewhere.

Terrestrial in ravines along streams and in deep woods. Common. The dark green fronds, narrow trunk, and black stipes, with large, appressed, dark scales at the bases, are characteristic.

2. *Cyathea arachnoidea* Hooker, Syn. Fil., p. 24, 1865.
Manus: Slopes of Mount Tjajiak, no. 4163.
Ternate, Queensland, and similar species elsewhere.

Terrestrial in mountainside forest. Only several trees found. This species belongs in the same variable group as does *C. truncata* (Brackenridge) Copeland. The tripinnate fronds, with shiny, dark green ultimate pinnules, and the dark, closely chaffy rachises distinguish it from the other local species.

3. *Cyathea scaberula* (Christ) Domin, Pteridophyta, p. 263, 1929.
Manus: Eastern tip, no. 3672.
Los Negros: No. 3527; swamp along road, west end of island, nos. 3681 and 4147.
New Guinea, and similar species elsewhere.

Terrestrial in brackish swamps, second-growth areas, and along streams. Common. Quickly distinguishable from the following very similar species by the rough, pale stipes provided with tiny black spines, and by a combination of chaff, hairs, and straggly, narrow, light scales.

4. *Cyathea contaminans* (Wallich) Copeland, Philippine Jour. Sci. Bot. 4: 60, 1909.
Manus: Tingau No. 1, alt. 1,000 ft., No. 1 Road, no. 4534; Tingau No. 2, alt. 1,400 ft., No. 1 Road, no. 4539.
Los Negros: Along road, western Los Negros, nos. 3550 and 4148.
Malaya to New Guinea, with many forms.

Terrestrial, often in company with the species last described. Common. The stipe-base scales are pale straw-colored. The brownish to pale, shiny stipes and rachises are mucronate and are more spiny to the touch than are those of the preceding species.

5. **Cyathea media**, sp. nov. (Pl. 15.)
Arbor caudice 3–4 m. alto; fronde subtripinnata, elliptica, 1.5 m. longa; stipite 20 cm. alto, atropurpureo, squamulis minutis vestito et spinis brevibus acutis paucis aspero, paleis atrocastaneis linearibus attenuatis 1.5 mm. latis ad basim, 0.9–1.7 cm. longis vestito; pinnis alternis lanceolatis, majoribus 48 cm. longis, 16 cm. latis, breviter stipitatis, infimis 8 cm. longis, 3 cm. latis; costis atrobrunneo-pubescentibus et paleis paucis angustis fulvis 2–4 mm. longis adspersis; pinnulis 20–25 paribus, breviter stipitibus vel sessilibus, lanceolatis attenuatis, profunde pinnatifidis, alternis, praesipue versus apicem caudatem remotis; lamina glabra, papyracea, supra atroviride, infra pallida; segmentis 15–18 paribus, oblongi-lanceolatis, dentatis, acutis, 6 mm. longis, 2.5 mm. latis; venulis furcatis; costulis infra squamulis brunneis sparsis praeditis; soris medialibus; ? indusio nullo; receptaculo pilifero.
Manus: Slopes of Mount Tjajiak, Grether and Wagner no. 4162 (type: Univ. Calif. Herb. no. 701237).

Terrestrial in mountain-slope woods. Only one collection. This species is distinguished from the other local *Cyathea* spp. by the spiny, dark purple stipe-base covered with low, dark tomentum and castaneous scales; by the dark brown pubescence of the costa, with scattered, straggly, narrow, brown scales above; by the lamina, dark green above and glaucous beneath; by the remote, spreading to ascending, caudate-tipped pinnules, becoming more distant toward the end of the pinna; and by the rather pointed segments.

6. *Cyathea pulcherrima* Copeland, Univ. Calif. Publ. Bot. 18: 219, 1942.
Manus: Kwaliop, alt. 1,000 ft., No. 1 Road, no. 4504.
New Guinea.

This very striking fern is apparently rare. The long, very dark brown, setiform scales which clothe the stipe and rachis are very distinctive. This specimen agrees closely with the type, differing from it in being smaller and more immature, in having more chaff on the axes, and particularly in having pale down on the costae and costules above. We know of but a single station.

X. ASPIDIACEAE

A. Sporangia confluent.
B. Fronds simple ..... 5. *Elaphoglossum*
BB. Fronds pinnate, strongly dimorphic.
C. Veins free ..... 3. *Lomariopsis*

CC. Veins anastomosing.
D. Rhizome short.
E. Frond deltoid; plant rather small ..... 7. *Stenosemia*
EE. Frond lanceolate; plant of medium size ..... 2. *Bolbitis*
DD. Rhizome long-creeping ..... 4. *Lomagramma*
AA. Sporangia in distinct sori.
F. Sori linear.
G. Sori indusiate; veins free or 1–1.5 pairs of veinlets anastomosing. 12. *Athyrium*
GG. Sori exindusiate; 5–12 pairs of veinlets anastomosing
FF. Sori round to elliptic. 10. *Cyclosorus triphyllus*
H. Veins free.
I. Pinnae lobed or pinnate; bases not semicordate.
J. Hairs jointed (several cells) ..... 6. *Ctenitis*
JJ. Hairs unjointed (single cells) ..... 9. *Lastrea*
II. Pinnae entire; the bases semicordate ..... 1. *Cyclopeltis*
HH. Veins anastomosing only below sinuses.
K. Sori elliptical; indusium densely golden-glandular. 11. *Sphaerostephanos*
KK. Sori orbicular; indusium not densely glandular ..... 10. *Cyclosorus*
HHH. Veins anastomosing elsewhere ..... 8. *Tectaria*

1. *Cyclopeltis* J. Smith

1. *Cyclopeltis novoguineensis* Rosenstock, Fedde Repert. Sp. Nov. 10: 329, 1912.
Los Negros: Tauwi Hills, no. 3956.
New Guinea.

Terrestrial at bases of limestone cliffs. Apparently limited to these places, where it is frequent. In the field this species has a very different appearance from that of *C. Presliana* (J. Smith) Berkeley, which we have collected both in the Philippines and in Biak. The large fronds, with numerous, dull green, narrow pinnae, of *C. novoguineensis* contrast strongly with the usually smaller fronds and with the less numerous and wider, shiny, blue-green pinnae of *C. Presliana.*

2. *Bolbitis* Schott

1. *Bolbitis Quoyana* (Gaudichaud) Ching, in C. Christensen, Ind. Suppl. III, p. 49, 1934.
Acrostichum (*Gymnopteris*) *repandum*, var. *Quoyanum* Gaudichaud; Baker, Jour. Linn. Soc. Bot. 15: 111, 1877.
Lou: Woods, no. 4036.
Manus: Bowat, alt. 800 ft., No. 1 Road, no. 4583.
Los Negros: Tauwi Hills, no. 3277.
Malaya to the Solomons.

Terrestrial in woods. Very common and variable in size.

3. *Lomariopsis* Fée

1. *Lomariopsis cochinchinensis* Fée, Mém. sur la Fam. des Foug. 1 (Acrost.): 66, pl. 26, 1845.
Manus: Near the Lorengau River Falls, no. 4211.
Tropical Asia to New Guinea.

Terrestrial along stream banks. Common, but, although hundreds of plants were examined, none were fertile.

4. *Lomagramma* J. Smith

1. *Lomagramma sinuata* C. Christensen, Svensk Bot. Tidsk. 16: 98, fig. 5, 1922.
Manus: 1 mi. E of Lorengau (sterile), no. 4041; woods along the Drangot River, no. 4056.
Celebes, Borneo, and New Guinea.

A creeper along the ground and at the bases of trees. Rarely the plants climb high upon tree trunks and there produce fertile fronds. The sterile form (bathyphyll) is abundant in woods. In the Admiralties *Lomagramma* is by no means confined to rocks, being found in abundance also in completely non-rocky soil. Our mass collections combine the features of several described species, all of which seem to be very poorly defined.

5. *Elaphoglossum* Schott

1. *Elaphoglossum* sp.
Manus: Summit of Mount Tjajiak, no. 4183.

Epiphytic in mountaintop woods. Our only specimen, collected for us by a native, is sterile, and was growing about 20 feet high on the branch of a tree. It is one of the many closely related forms in the group of *Elaphoglossum conforme* (Swartz) Schott. The rootstock is short-creeping, covered with pale red-brown, lanceolate scales; the fronds are narrowly ovate-lanceolate; the stipes pale, 12–15 cm. long, with a few scales; the lamina somewhat fleshy, glabrous, 20–24 cm. long, 4.5–5.0 cm. wide in the middle; the rachis is stout, pale, glabrous; the margins have very few straggly scales; and the veins are parallel and once-forked, usually toward base.

6. *Ctenitis* C. Christensen

1. *Ctenitis sagenioides* (Mettenius) Copeland, Genera Filicum, p. 124, 1947.
Los Negros: Bases of limestone cliffs near road, western Los Negros, no. 4123.
Malaya, Philippine Islands, and New Guinea.

Terrestrial at bases of limestone cliffs. Infrequent, but in small areas abundant. This fern is variable over its range, and the specimens of this species which we collected on Biak Island in similar situations are smaller and slightly thicker in texture than our Admiralty Islands material. Locally it is a medium-sized plant, with oblong, thin, herbaceous fronds, the pinnae deeply pinnate and having oblong, shallowly crenate segments. The stipe and rachis are reddish and shiny, and the rootstock is erect and large, up to 10 cm. long and 3 cm. thick. Growing plants suggest a peculiar form of *Tectaria ferruginea*.

7. *Stenosemia* Presl

1. *Stenosemia aurita* (Swartz) Presl, Tent. Pterid., p. 237, pl. 10, fig. 24, 1836.
Los Negros: Tauwi Hills, no. 3957.
Malaya to the Solomons.

Terrestrial at the wooded bases of limestone cliffs with *Cyclopeltis novo-guineensis* and *Tectaria ferruginea*. Uncommon. This plant differs greatly in appearance, both in the field and in the herbarium, from the much larger *S. pinnata* Copeland, which we have found in Guam, and which has fronds of different shape.

8. *Tectaria* Cavanilles

A. Frond deeply ternately lobed.....5. *T. christovalensis*
AA. Frond pinnate.
  B. Pinnate at base only.
    C. Plant usually small; rootstock short; terminal pinna much larger than the lateral; limestone cliffs.....6. *T. Barclayi*
    CC. Plant of moderate size; rootstock long; terminal pinna similar in size and shape to lateral; terrestrial.....8. *T. menyanthidis*

BB. Pinnate throughout.
D. Mature plant less than 1 m. tall; pinnae few, up to 3–4 pairs.
E. Pinnae lanceolate, entire to slightly undulate.....8. *T. menyanthidis*
EE. Pinnae triangular, deeply lobed.....2. *T. Cesatiana*
DD. Mature plant 1 m. or more tall; pinnae numerous.
F. Indusium present; pinnae entire to undulate, thin, dark green
5. *T. crenata*
FF. Indusium absent; pinnae deeply crenate, rather thick, pale green
4. *T. irregularis*
AAA. Frond tripinnate.
G. Plant 0.5 m. tall; veins anastomosing generally.....3. *T. ferruginea*
GG. Plant 3 m. or more tall; veins anastomosing only along the costa..1. *T. Leuzeana*

1. *Tectaria Leuzeana* (Gaudichaud) Copeland, Philippine Jour. Sci. Bot. 2: 417, 1907.
Manus: Below Lorengau River Falls, no. 4151.
China to Polynesia.

Terrestrial in rich woods along river banks. Rare. This huge fern is very striking, the decompound fronds being 3 m. tall, with thick, shiny, mahogany-colored stipes rising from a massive rootstock, 50 cm. in diameter, clothed in narrow, dark brown scales 2 or more cm. long.

2. *Tectaria Cesatiana* (C. Christensen) Copeland, Philippine Jour. Sci. Bot. 6: 76, 1911.
Manus: Buyang No. 2, alt. 1,000 ft., No. 1 Road, no. 4550.
New Guinea.

The only stand of this fern found was on the wet banks of a stream, growing near the water in dark woods; individual plants were rather widely scattered.

3. *Tectaria ferruginea* (Mettenius) Copeland, Philippine Jour. Sci. Bot. 6: 76, 1911.
Manus: Ground in forest, Warrabi, alt. 500 ft., No. 1 Road, no. 4573; falls of an eastern tributary of the Lorengau River, no. 4118.
Los Negros: No. 3552; woods, no. 3281; Tauwi Hills, no. 4007.
New Guinea.

Terrestrial at wooded bases of limestone cliffs and on rocky stream-banks in rich woods. Frequent.

4. *Tectaria irregularis* (Presl) Copeland, Philippine Jour. Sci. Bot. 2: 416, 1907.
Manus: Lorengau River Falls, no. 3994.
Malaya to New Guinea.

Terrestrial in rich woods. Occasional. The living plant has a pale green color and a rather thicker texture than most *Tectariae* have.

5. *Tectaria christovalensis* (C. Christensen) Alston, Jour. Bot. 77: 290, 1939.
Manus: Falls of an eastern tributary of the Lorengau River, no. 4121.
New Guinea and the Solomons.

Terrestrial along rocky stream banks. Very local. This species is unique among *Tectariae* in being tripartite but never pinnate, and in showing practically no tendency to develop lateral lobes on the large terminal segment. The fronds sometimes become 50 cm. long, with the terminal segments as much as 11 cm. in width. One very old frond which we collected had had the two lateral lobes destroyed, and at the junction of the lobes, at the top of the stipe, a young plant had developed, with massed roots 12 cm. long and four simple fronds 10–12 cm. long. The color of the living plant is dark green.

6. *Tectaria Barclayi* (Carruthers) C. Christensen, Ind. Suppl. III, p. 177, 1934.
Los Negros: Limestone cliffs, Tauwi Hills, nos. 3549, 3509, and 3682.
New Ireland, New Guinea.

Common on limestone cliffs, growing on the rock itself. The plant grows gregariously and often forms large groups on the vertical, leached limestone surfaces, the fronds mostly pointing downward. The living plant is light green.

7. *Tectaria crenata* Cavanilles, Descr., p. 250, 1802.
Lou: Damp, rocky, wooded hillside, along coast, no. 4035.
Malaya to Polynesia.

Only one stand of this species, elsewhere usually common, was found. The sterile leaves were 1–1.5 m. tall and very lax; the pinnae, 3–5 cm. in breadth. The fertile fronds were of the same height, but the pinnae were barely more than half as broad as the sterile ones. In being thus dimorphic, our specimens contrasted strongly with the typical plant of Guam, but the species as a whole is polymorphic and has numerous local variants. New Guinea plants also show this dimorphism. The American *T. incisa* Cavanilles is very similar and is even more variable.

8. *Tectaria menyanthidis* (Presl) Copeland, Philippine Jour. Sci. Bot. 2:414, 1907.
Manus: Bowat, alt. 800 ft., No. 1 Road, no. 4581.
Los Negros: Woods along the road to Lombrom Point, no. 3952; near Pitilu Lagoon, no. 3548.
Philippines and Melanesia.

Terrestrial in rich woods, especially along shaded stream banks. Very common generally.

9. *Lastrea* Bory

Frond pinnate, oblong-lanceolate; rachis without scales.....1. *L. Harveyi*
Frond tripinnate; deltoid, rachis with white scales.....2. *L. leucolepis*

1. *Lastrea Harveyi* (Mettenius) Carruthers in Seemann, Flora Vitiensis, p. 359, 1873.
Lou: Woods, no. 4026.
Los Negros: Mouth of limestone cave, western Los Negros, no. 4154; Tauwi Hills, no. 4201.
Polynesia.

Terrestrial, often on or around limestone cliffs in woods and brushy places. Common.

2. *Lastrea leucolepis* Presl, Epim. Bot., p. 39, 1849.
Lou: Edge of old garden, no. 4039.
Malaya and Polynesia.

Terrestrial. This species was found several times, but always in or near gardens. It very likely occurs indigenously here, however, as the species is common and wide-ranging.

10. *Cyclosorus* Link

A. Pinnae lobed, the lobes cut ¼–⅔ of the way to costa.
B. Fronds coriaceous; plants of exposed places.
C. Sori marginal, confined to the lobes, the basal pinnae not reduced; open marshes
1. *C. goggilodus*
CC. Sori medial, extending to the costa, the basal pinnae reduced; dry places.

D. One pair of veinlets anastomosing below sinus; reduced pinnae usually only one pair, and these rather large and deltoid, the normal pinnae cut ½ way to costa; sporangia setose ..... 2. *C. invisus*

DD. 2.5–5 pairs veinlets uniting below sinus; reduced pinnae usually numerous and very small or abortive, the normal pinnae cut ⅓ or less to costa; sporangia glabrous ..... 3. *C. unitus*

BB. Fronds chartaceous to membranous; plants of shady places.

E. Rootstock strictly erect.

F. Segments narrow, very oblique, the terminal pinna like the lateral pinnae in size and shape, the basal pinnae not reduced; 1 pair of veins connivent below sinus; plant rather small; river margins ..... 6. *C. cataractorum*

FF. Segments broad, slightly oblique, terminal pinna larger than lateral pinnae and differently shaped, basal pinnae much reduced; 1.5–2 pairs of veinlets united below sinus; medium-sized to large plants; woods and swamps.

G. Rachis and pinnae hirsute; sori medial; segments rounded; plants of medium size ..... 4. *C. hispidulus*

GG. Rachis and pinnae glabrous; sori usually inframedial; segments usually truncate; large plants ..... 5. *C. truncatus*

EE. Rootstock oblique, decumbent, or creeping.

H. Pinnae narrow (less than 1 cm. across at base), numerous (25–30 pairs), lobed ⅔ of the way to costa, the segments narrow ..... 7. *C. vestigiatus*

HH. Pinnae broader (more than 1 cm. across at base), fewer (usually 12–16 pairs), lobed half or less to costa, the segments broad.

I. Pinnae 2–2.5 cm. broad in the middle (rarely only 1 cm. broad), 14–20 cm. long, the terminal pinna larger than, but similar to, the lateral pinnae ..... 11. *C. megaphylloides*

II. Pinnae 1.5 cm. broad in middle, 6–12 cm. long, the terminal pinna deeply pinnatifid at base and unlike the lateral pinnae.

J. Pinna cut ½; 1–1.5 pairs of veins anastomosing; lower pinnae not strongly reduced; membranaceous.

K. Fronds only sparsely hairy; indusium with very short hairs; segments closest to rachis not enlarged; sori borne the length of each segment ..... 8. *C. dentatus*

KK. Fronds hairy; indusium beset with long hairs; lobes of basal pinnae closest to rachis usually enlarged; sori often only a pair at bases of segments ..... 9. *C. parasiticus*

JJ. Pinnae cut only ¼; 2–3 pairs of veins anastomosing; lower 1–3 pairs of pinnae much reduced; chartaceous. 10. *C. subpubescens*

AA. Pinnae shallowly crenate to entire, never cut more than ⅛ to rachis.

L. Frond with only 3 nearly entire pinnae; many (8–10 pairs) veinlets anastomosing; rootstock long-creeping; sori linear ..... 13. *C. triphyllus*

LL. Frond with numerous shallowly crenate pinnae, the basal reduced; 3 pairs of veins anastomosing; rootstock erect; sori orbicular ..... 12. *C. glandulosus*

1. *Cyclosorus goggilodus* (Schkuhr) Link, Hort. Berol. 2: 128, 1833.
Los Negros: Near Momote Field, no. 4006.
Pantropical.

Terrestrial in open marshes, in company with *Lygodium scandens, Acrostichum aureum,* and various marsh grasses. Very local, and apparently rare. The form here lacks the characteristic scales on the costa beneath, but this condition is found in New Guinea and elsewhere.

2. *Cyclosorus invisus* (Forster) Copeland, Genera Filicum, p. 142, 1947.
Los Negros: Along road in second-growth woods, western Los Negros, no. 4124.
Polynesia.

This species may easily be confused with the species next described; it grows in very similar situations, but is much rarer.

3. *Cyclosorus unitus* (Linnaeus) Ching, Bull. Fan Mem. Inst. Biol. 8: 192, 1938.
Los Negros: No. 4005; edges of woods, no. 3492; Momote Field, C. P. Maciel no. 3690.
Tropical Asia to Polynesia.

Terrestrial in open fields, along roads, and on the edges of woods. Extremely abundant. Forms found in shady places are usually much larger and more lax.

4. *Cyclosorus hispidulus* (Decaisne) Copeland, Genera Filicum, p. 142, 1947.
Los Negros: Swamp along road, western Los Negros, no. 4000.
Malaya to New Guinea.

Terrestrial in brackish marshes and in brushy, second-growth woods. Not common, but locally abundant. The numerous, erect fronds, borne on an erect, large rootstock, make this species very distinctive in the field.

5. *Cyclosorus truncatus* (Poiret) Farwell, Amer. Midl. Naturalist 12: 259, 1931.
Nephrodium truncatum Presl; Baker, Jour. Linn. Soc. Bot. 15: 108, 1877.
Lou: Woods, no. 4030.
Manus: Lorengau River Falls, no. 4215; sago-palm swamp, 2 mi. W of Lorengau, no. 4127; Pundrau, alt. 1,000 ft., No. 1 Road, no. 4551; Bulibat, alt. 500 ft., No. 1 Road. no. 4572; Bowat, alt. 800 ft., No. 1 Road, no. 4580.
Los Negros: Tauwi Hills, no. 4206; brushy spots, no. 3618; marshes near Momote Field, no. 4004; along road in second-growth woods, western Los Negros, no. 4125.
Oriental tropics.

Terrestrial in woods, swamps, and brushy places. Common. A variable, large, terrestrial fern with erect rootstock and with fasciculate, usually tall, lanceolate fronds; its pinnae are pinnatifid, with round-truncate segments, and it has several pairs of reduced lower pinnae. In open marshes and in sunny places in woods occurs a shiny, pale green form, with closer and narrower, falcate and pointed lobes (nos. 4127 and 4215), which we keep under this species because of local intermediates. In deep woods is found the usual more herbaceous, dark green form with wider, truncate lobes. This form occasionally reaches great size, the fronds 1.7 m. or more tall, the pinnae 25 cm. long, the stipes thick, up to 0.8 cm. in diameter, and the rootstock massive. In brushy, second-growth areas we have found plants which represent the juvenile stage of the latter, with thin, herbaceous fronds only 50 cm. tall, yet soriferous (no. 4206).

6. **Cyclosorus cataractorum,** sp. nov. (Pl. 16.)
Cyclosorus, C. aquatili affinis; rhizomate amplo erecto vel decumbente, 1.5–2.0 cm. crasso, 3.0–10.0 cm. longo; fronde oblonga, atroviridi, 15–30 cm. longa, 6–16 cm. lata; stipite 5–10 cm. alto, nudo, pallido; rachi superne hirsuta; pinnis linearibus lanceolatis, 5–14 cm. longis, 4–10 mm. latis, acuminatis, angustis, oblique patentibus; venulis infimis solummodo infra sinus anastomosantibus; soris medialibus, parvis, 2–4 paribus; indusio persistente.
Manus: Along river banks, Lorengau River Falls, Grether and Wagner no. 3971 (type: Univ. Calif. Herb. no. 701117); Buyang No. 1, alt. 1,400 ft., No. 1 Road, no. 4545.
Bamler no. R-14 (Univ. Calif. Herb. no. 392002), collected on Rook Island and labeled by Rosenstock "prope D. aquatilem Copel.," is also this species.

A riverside fern, this species occurs in great abundance along the flood plains and banks of the Lorengau River, both above and below the Falls. It resembles *C. aquatilis* Copeland in habit, but differs from that species in

having a thin texture, sharply toothed, ascending pinnae with narrow, attenuate bases, and a terminal pinna which has the form of the lateral pinnae and is but little longer. *C. riparius* Copeland is much closer to *C. aquatilis* than to the present species.

7. *Cyclosorus vestigiatus* Copeland, Genera Filicum, p. 143, 1947.
Manus: Brushy, open spots, east tip of Manus, no. 3616; Drano, alt. 1,000 ft., No. 1 Road, no. 4592; near Sabon, No. 1 Road, no. 4561; Lundrit, alt. 600 ft., No. 1 Road, no. 4577; Kwaliop, alt. 1,400 ft., No. 1 Road, no. 4544.
Los Negros: Brushy edges of woods, no. 3502; muddy creek bank, no. 3529; woods along road to Lombrom Point, no. 4202.
New Guinea.

Terrestrial in rich soil in woods and along streams. The most common *Cyclosorus* in the woods. Our plant agrees very well with typical *C. vestigiatus*, differing from it only in having somewhat more setose costules and slightly narrower segments.

8. *Cyclosorus dentatus* (Forskål) Ching, Bull. Fan Mem. Inst. Biol. 8: 206, 1938.
Nephrodium molle Desvaux; Baker, Jour. Linn. Soc. Bot. 15: 107, 1877.
Manus: Forest at Sabon, No. 1 Road, no. 4567.
Los Negros: Second-growth woods, 1 mi. W of Pitilu Lagoon, no. 4142.
Pantropical.

Terrestrial in secondary woods. Apparently not common.

9. *Cyclosorus parasiticus* (Linnaeus) Farwell, Amer. Midl. Naturalist 12: 259, 1931.
Manus: Lundrit, alt. 600 ft., No. 1 Road, no. 4576.
Tropical Asia, Japan, to the Pacific Islands.

Our only collection of this species was growing along a path in a disturbed place. The hairy fronds, enlarged anterior basal lobes, and common occurrence of mere pairs of sori at the bases of the segments serve to separate this from the closely allied *C. dentatus*.

10. *Cyclosorus subpubescens* (Blume) Ching, Bull. Fan Mem. Inst. Biol. 8: 211, 1938.
Los Negros: Woods along road to Lombrom Point, no. 4009.
India to Polynesia.

Terrestrial in brushy, old, second-growth woods. A single collection. This species differs from *C. dentatus*, according to Ching, in that the pinnae are cut only one-third or a little more of their length; also in that the lower several pairs of pinnae are reduced into mere butterfly-like auricles, there are two or three pairs of anastomosing veins, and the leaf-surfaces are glabrous or subglabrous. Our specimens agree very well with this differentiation.

11. *Cyclosorus megaphylloides* (Rosenstock) Copeland, Genera Filicum, p. 143, 1947.
Lou: Woods, no. 4025.
Manus: Lorengau River Falls, no. 4136; Bowat, alt. 800 ft., No. 1 Road, no. 4582.
New Guinea.

Terrestrial in rich woods. Not common. The apical pinna of this plant resembles the lateral pinnae, and young fronds may be almost simple and resemble the tips of fully grown fronds. Several of our specimens have pinnae

with stalks almost 2 mm. long; others have almost sessile pinnae. No. 4582 is an unusually narrow form, the pinnae only 1.0–1.6 cm. broad. Except for stalked pinnae and narrow pinnae in some individual specimens and a generally sparser hairiness in all of the specimens, our material agrees well with Keysser no. 120, collected at Sattelberg, New Guinea, at an altitude of 800–1,000 m. (Univ. Calif. Herb.).

12. *Cyclosorus glandulosus* (Blume) Ching, Bull. Fan Mem. Inst. Biol. 8: 227, 1938.
Los Negros: Marshes near Momote Field, no. 4003.
Malaya, † Philippines, New Guinea, and Solomons.

Terrestrial in shaded marshes and sago-palm swamps. Found in only two places, both on the island of Los Negros. Our specimens agree rather closely with a specimen collected by Kajewski in Guadalcanal at an altitude of 1,200 m. (Univ. Calif. Herb.); they differ from this one, however, in having slightly fewer pinnae and far fewer globular glands. The glands on our specimens are very few, and all of the indusia appear to have been shed. *C. firmula* (Baker) C. Christensen appears to be the same species, to judge from a specimen in the E. B. Copeland Herbarium collected by Mjöberg in Sarawak, Borneo, so identified, apparently in Christensen's handwriting. We could find no glands at all on this specimen.

13. *Cyclosorus triphyllus* (Swartz) Copeland, Genera Filicum, p. 143, 1947.
Manus: Woods above Lorengau River Falls, no. 4133.
Los Negros: ½ mi. SSW of Lombrom Bay, no. 3504.
India to Queensland.

Terrestrial in deep woods. Frequent.

11. *Sphaerostephanos* J. Smith

1. *Sphaerostephanos polycarpa* (Blume) Copeland, Univ. Calif. Publ. Bot. 16: 60, 1929.
Los Negros: Second-growth woods, 1 mi. W of Pitilu Lagoon, no. 4141.
Malaya to New Guinea.

Terrestrial in second-growth woods. A single collection. In the field it resembles the ostrich-fern (*Pteretis*) of the north temperate zone.

12. *Athyrium* Roth

A. Frond pinnate; upper part of rachis bearing bud.
B. Pinnae entire, 3–5 pairs, very large and coarse, 6 cm. broad, 15 cm. long ..... 4. *A. fraxinifolium*
BB. Pinnae crenate to lobed, not so large.
C. Frond broad, the pinnae few (5–9 pairs), crenate to shallowly lobed, 3–4 cm. broad ..... 3. *A. novoguineensis*
CC. Frond narrow, the pinnae numerous (10–20 pairs), lobed, 1.5–3 cm. broad.
D. Lower pinnae lobed about ⅓ of way to costa ..... 1. *A. bulbiferum*
DD. Lower pinnae lobed almost to costa ..... 2. *A. sorzogonense*
AA. Frond bipinnate to subtripinnate; rachis not proliferous.
E. Veinlets free; shady woods.
F. Ultimate segments 4–6 mm. wide, entire or very shallowly dentate, fronds bipinnate to subtripinnate, axes usually dark ..... 5. *A. sylvaticum*
FF. Ultimate segments 3–4 mm. wide, deeply dentate, fronds subtripinnate to tripinnate, axes above base of stipe usually pale ..... 6. *A. Huttoni*
EE. 1–1.5 pairs of veinlets anastomosing below sinus; usually in open marshes ..... 7. *A. esculentum*

1. *Athyrium bulbiferum* (Brackenridge) Copeland, Bishop Mus. Bull. 59: 53, 1929.
Asplenium (*Diplazium*) *Brackenridgei* Baker, Jour. Linn. Soc. Bot. 15: 107, 1877.
Manus: 2 mi. SE of Lorengau, no. 3964.
Los Negros: Wet woods, road to Lombrom Point, nos. 3272 and 3505.
Africa to Samoa.

Terrestrial in damp, rich woods. Generally frequent.

2. *Athyrium sorzogonense* (Presl) Milde, Bot. Zeit. 28: 354, 1870.
Manus: Woods along logging road near Lorengau River Falls, no. 4214; rich woods above Lorengau River Falls, no. 4135.
Tropical Asia to New Guinea.

Terrestrial in woods. Rare. Distinguishable from *A. bulbiferum* by its broader fronds and deeply truncate-lobed pinnae.

3. **Athyrium novoguineensis** (Rosenstock), comb. nov.
Diplazium silvaticum (Bory) Swartz var. *novoguineensis* Rosenstock, Hedwigia 56: 351, 1915.
Diplazium novoguineensis (Rosenstock) Hieronymus, Hedwigia 59: 327, 1917.
Manus: Damp woods along Drangot River, no. 4060.
New Guinea.

Terrestrial in very damp, rich woods. Rare, but where we found it there was a large colony. In the field the appearance of this fern is exactly intermediate between that of *A. bulbiferum* and *A. fraxinifolium*. Our specimens agree closely with a type specimen in the University of California Herbarium: Bamler no. 56, Sattelberg, found at an altitude of 600 m., in New Guinea, and labeled by Rosenstock, "*Diplazium silvaticum* (Bory) Sw. v. *novoguineensis* v. nov."

4. *Athyrium fraxinifolium* (Presl) Milde, Bot. Zeit. 28: 353, 1870.
Manus: Slopes of Mount Tjajiak along path, alt. *ca.* 1,500 ft., no. 4190.
Malaya to Japan and New Guinea.

Terrestrial in woods. Rare. This species is quickly recognizable by its very coarse, large, simple pinnae.

5. *Athyrium silvaticum* (Blume) Milde, Bot. Zeit. 24: 376, 1866.
Lou: Forest, no. 4074.
Manus: Woods along the Drangot River, no. 4061.
Los Negros: Mouth of limestone cave, western Los Negros (small specimens), no. 4153.
Java and Celebes to New Guinea.

Terrestrial in woods. Frequent. The name is used here in the broad sense. The large, bipinnate fronds and thin, herbaceous texture distinguish it from the other, more common local *Athyria*.

6. **Athyrium Huttoni** (Baker) Copeland, ined., comb. nov.
Manus: Kwaliop, alt. 1,000 ft., No. 1 Road, no. 4546.
"Malay Islands" to New Guinea.

This fern is evidently rare. From the rather similar *A. silvaticum* it may be distinguished by the more dissected and slightly thicker fronds, and by the numerous, narrow, ultimate segments, which are sharply dentate.

7. *Athyrium esculentum* (Retzius) Copeland, Philippine Jour. Sci. Bot. 3: 295, 1908.
Asplenium (*Anisogonium*) *esculentum* (Presl) Baker, Jour. Linn. Soc. Bot. 15: 107, 1877.

Manus: 2 mi. SE of Lorengau, no. 3966; terrestrial in forest, Bulihot, alt. 500 ft., No. 1 Road, no. 4515.

Tropical Asia to Polynesia.

Terrestrial in grassy places and in fresh-water marshes. Along the Drangot River in brushy areas near paths this species is abundant, and individual plants become very large, 1–1.5 m. tall. We were told there by the natives that this plant is used by them as food—a situation which was to be expected, as this species is, throughout its range, the most widely eaten fern. The native word for fern on Lou Island is "pokpok" and in Manus is "kumu."

In our specimens, one to one and one-half pairs of veinlets anastomose at the sinus, and in this respect the local form lies between the western and easternmost forms. In the Philippines and farther west the veinlets anastomose more, but east of the Admiralties the veinlets become free.

XI. BLECHNACEAE

Rhizome short and thick, not climbing.....1. *Blechnum*
Rhizome long and narrow, climbing.....2. *Stenochlaena*

1. *Blechnum* Linnaeus

Fronds dimorphic.
Plant 2–3 m. tall, fronds coriaceous.....1. *B. capense*
Plant 0.4–0.5 m. tall, fronds chartaceous.....2. *B. dentatum*
Fronds monomorphic.....3. *B. orientale*

1. *Blechnum capense* (Linnaeus) de Schlechtendal, Adumbratio Filicum, p. 34, p. 18, 1825.

Manus: Summit of Mount Tjajiak, no. 4180.

Africa, ? Borneo, Melanesia, Polynesia.

Terrestrial in rich mountaintop woods. Only one collection.

2. *Blechnum dentatum* (Kuhn) Diels in Schum. and Laut., Fl. deutschen Südsee, p. 130, 1901.

Manus: Ground in forest, Bulibat, alt. 500 ft., no. 4514; Sabon, No. 1 Road, no. 4562.

Los Negros: Damp woods, ½ mi. SSW of Lombrom Bay, no. 3503.

Bismarck Archipelago and New Guinea.

Terrestrial in rich woods. Not common.

3. *Blechnum orientale* Linnaeus, Sp. Pl. (2d ed.) 2: 1535, 1763.

Tawi: Grassy field, no. 4156.

Manus: Along rocky stream, eastern end of island, no. 3612; Lorengau River Falls, no. 3987; wooded area, Sabon, alt. 600 ft., No. 1 Road, no. 4559.

Tropical Asia to Australia and Polynesia.

This species is frequent in second-growth areas, often in rocky places (not limestone). In the dry, rocky field at Tawi Island the plants grow only 35–45 cm. tall, but in damp places along rivers, plants may become 2.5 m. high.

2. *Stenochlaena* J. Smith

Plant scandent, originating terrestrially, rhizome usually stouter than stipes, pinnae cuneate at base, 10–15 cm. long.....1. *S. palustris*
Plant epiphytic on pandan trees, rhizome much-branched and of approximately same thickness as stipes, pinnae rounded at base, 3.5–7 (rarely 9) cm. long.....2. *S. areolaris*

1. *Stenochlaena palustris* (Burmann) Beddome, Suppl. Ferns Brit. Ind., p. 26, 1876.
Acrostichum (*Stenochlaena*) *scandens* J. Smith; Baker, Jour. Linn. Soc. Bot. 15: 111, 1877.
Manus: Tingau River bank, no. 4558.
Los Negros: Edge of Pitilu Lagoon, no. 3693; climbing on coconut trees at Momote Field, no. 3273.
Asia to Polynesia.

Climber in marshes, coconut groves, and woods. Abundant and variable in size. It is possible that a specimen of *Stenochlaena Milnei* Underwood (Bull. Torrey Bot. Club 33: 38, 1906), cited from the Admiralty Islands, is merely a very broad form of *S. palustris*.

2. *Stenochlaena areolaris* (Harrington) Copeland, Philippine Jour. Sci. Bot. 2: 406, 1907.
Manus: Screw of screw pine, Badlock, No. 1 Road, no. 4557; Tingau No. 2, No. 1 Road, no. 4535.
Luzon and New Guinea.

This peculiar fern was originally described from Luzon as growing at the bases of leaves of pandan trees. It is entirely epiphytic, growing at the bases of the pandan leaves, where its roots are wet and soggy. From the preceding species it is most quickly separable in the field by this habit, by its smaller size, and by the differently shaped pinnae.

XII. ASPLENIACEAE

1. *Asplenium* Linnaeus

Fronds simple.
Fronds more than 50 cm. tall, not proliferous; rootstock erect; nest-ferns.
Sori short (1–2 cm.), closely spaced, and confined to a narrow band along midrib; high epiphyte ..... 1. *A. nidus*
Sori longer, widely spaced, extending almost to margin; low epiphyte.. 2. *A. phyllitidis*
Fronds less than 50 cm. tall, often proliferous; rootstock creeping..... 3. *A. amboinense*
Fronds compound.
Fronds simply pinnate..... 4. *A. falcatum*
Fronds 2- to 3-pinnate..... 5. *A. cuneatum*

1. *Asplenium nidus* Linnaeus, Sp. Pl. 2: 1079, 1753; Baker, Jour. Linn. Soc. Bot. 15: 106, 1877.
Lou: Epiphytic, no. 4032.
Manus: Woods, east end of island, no. 3673; 2 mi. SE of Lorengau, no. 3962.
Los Negros: Nos. 3256 and 3536.
Paleotropics.

High epiphyte in forest trees. This is one of the commonest and most conspicuous ferns in the Admiralties. In addition to the usual strap-shaped specimens, there are also elliptic forms exemplified in our collections by no. 3536, which is 85 cm. long and 23 cm. broad at the widest point. The dimensions vary greatly.

2. *Asplenium phyllitidis* D. Don, Prodromus Fl. Nepal., p. 7, 1825.
Los Negros: Low epiphyte, woods near Momote Field, no. 3268; low epiphyte, woods along road to Lombrom Point, no. 3955.
Construed broadly, this species extends from India to Polynesia.

Epiphyte, usually within 10 feet of the ground in shady woods. Frequent. This plant has the same general aspect as *A. nidus*, from which, however, it

may be distinguished in the field, not only by its tendency to grow nearer to the ground, but also by the more widely spaced and much longer sori, originating farther from the midrib and extending much nearer to the margin. In the Admiralties our field experience has shown that the present species is evidently always distinct from *A. nidus*.

3. *Asplenium amboinense* Willdenow, Sp. Pl. 5: 303, 1810.
Manus: Woods above Lorengau River Falls, no. 4139.
Malaya to Polynesia.

A climber at bases of trees in rich, dark woods along river banks. Rare. The creeping rootstock, simple frond, thin texture, and proliferous tips are characteristic.

4. *Asplenium falcatum* Lamarck, Enc. 2: 306, 1786; Baker, Jour. Linn. Soc. Bot. 15: 107, 1877. (Pl. 17.)
Lou: Woods, no. 4068.
Manus: Woods along the Drangot River, no. 4049; on rocks, Drano, alt. 1,000 ft., No. 1 Road, no. 4591.
Los Negros: Nos. 3488 and 3251; wet woods, western Los Negros, no. 4002; dry limestone cliffs, no. 4144; epiphytic, no. 3530.
Africa to New Zealand and Polynesia.

Epiphytic in forest trees and also on limestone cliffs. Common. On dry cliffs we have found specimens (such as no. 4144) which are about one-fourth the size of the ordinary plants of the forest. The fronds are 15 (10–22) cm. long and have four to seven pairs of short, dentate pinnae, 25 (20–30) mm. long and 9 (8–13) mm. broad. The rachis is mostly green, except for the dark streak below, running from the dark stipe to, at most, about half the length of the rachis. The forest form has sixteen to twenty (normally, eighteen) pairs of larger, more entire, and relatively narrower pinnae, 10 (8–16) cm. long by 21 (19–25) mm. broad; the fronds average 65 (46–145) cm. long, the rachises being dark on both sides in the lower half, and dark below almost to the tip.

5. *Asplenium cuneatum* Lamarck, Enc. 2: 309, 1786; Baker, Jour. Linn. Soc. Bot. 15: 107, 1877. (Pls. 18 and 19.)
Manus: Lorengau River Falls, no. 4016; woods along Drangot River, nos. 4050 and 4051; Sabon, No. 1 Road, no. 4566.
Los Negros: No. 3257; epiphytic near Momote Field, no. 3285; woods along road to Lombrom Point, No. 3953.
Pantropical.

Epiphytic in forest trees. Common. There is wide variation in the length of the sori, in the degree of cutting, and in the size of the plant. It is our conclusion, after observing many hundreds of plants, that *A. laserpitiifolium* Lamarck is merely a large form of *A. cuneatum*. There is apparently in the Admiralty Islands a steady progression from small, bipinnate, but fully fertile specimens, which agree very well with South American material of *A. cuneatum*, to huge, tripinnate individuals, which fall under *A. laserpitiifolium*. It seems neither natural nor convenient to separate these extremes in the Admiralties, when much of the material lies between.

XIII. POLYPODIACEAE

A. Sporangia in definite sori.
  B. Sori dorsal.
    C. Sori orbicular to elliptic.
      D. Veins free.
        E. Fronds pectinate, glabrous, 15 (8–20) cm. long; sori elliptic, parallel to costa ..... 11. *Ctenopteris*
        EE. Fronds ligulate, hairy, 5 (3–9) cm. long; sori orbicular .. 9. *Grammitis*
      DD. Veins anastomosing.
        F. Scales stellate ..... 2. *Pyrrosia*
        FF. Scales other than stellate.
          G. Fronds simple or lobed, not pinnate.
            H. Fronds small, usually 5 (3–10) cm. long; rootstock 0.5 mm. thick ..... 1. *Weatherbya*
            HH. Fronds larger; rootstock 1.5 mm. or more thick.
              I. Sori orbicular, fronds glabrous ..... 3. *Microsorium*
              II. Sori elliptic, fronds hairy ..... 5. *Aglaomorpha*
          GG. Fronds pinnate, the pinnae articulate.
            J. Fronds uniform, sterile and fertile alike. 4. *Goniophlebium*
            JJ. Fronds dimorphic, the sterile fronds lobed and brown, modified for humus-collecting ..... 7. *Drynaria*
    CC. Sori linear, in a groove on each side of midrib ..... 10. *Scleroglossum*
  BB. Sori marginal in cavities on the tips of the lobes ..... 12. *Prosaptia*
AA. Sporangia usually confluent.
  K. Fronds simple, long-stipitate, usually much less than 50 cm. long ..... 8. *Selliguea*
  KK. Fronds deeply lobed below and pinnate above, sessile, more than 50 cm. long 6. *Merinthosorus*

1. *Weatherbya* Copeland

1. *Weatherbya accedens* (Blume) Copeland, Genera Filicum, p. 191, 1947.
  Manus: Falls of an eastern tributary of the Lorengau River, no. 4119.
  Malaya to Polynesia.

A delicate climber on mossy branches and twigs of trees, growing in moisture-laden air near a waterfall. Rare.

2. *Pyrrosia* Mirbel

1. *Pyrrosia adnascens* (Swartz) Ching, Bull. Chinese Bot. Soc. 1: 45, 1935.
  Polypodium (*Niphobolus*) *adnascens* Swartz; Baker, Jour. Linn. Soc. Bot. 15: 108, 1877.
  Lou: No. 4031.
  Manus: Lorengau, no. 3671; Sau, No. 1 Road, no. 4554.
  Los Negros: Northern Los Negros, no. 3696; Tauwi Hills, no. 4199.
  Tropical Asia to Polynesia.

Climber on coconut palms and forest trees. Abundant, especially in coconut groves. Fertile fronds vary from 10 to 35 cm. in length and from 0.4 to 1.8 cm. in breadth.

3. *Microsorium* Link

A. Fronds usually simple (Nos. 3, 4, and 5 may occasionally have lobes).
  B. Fronds sessile.
    C. Sori less than 1 mm. in diameter; fronds ligulate, 60–120 cm. or more long; a high nest-epiphyte ..... 1. *M. punctatum*

CC. Sori more than 1 mm. in diameter; fronds oblong, 20–40 cm. long; a low bracket epiphyte ..... 2. *M. linguaeforme*

BB. Fronds stipitate.

D. Sori not impressed; terrestrial creepers.

E. Stipe and rachis glabrous; creeping on forest floor and at bases of trees 3. *M. longissimum*

EE. Stipe and rachis scaly; producing mats on edges of shaded rocky streams 4. *M. pteropus*

DD. Sori in pits; epiphytic creeper ..... 5. *M. acutifolium*

AA. Fronds normally lobed.

F. Sori sunken and rather large.

G. Sori in one to several rows, in broad, shallow pits; usually thick-textured 6. *M. scolopendria*

GG. Sori in a single row, in very deep pits; herbaceous ..... 7. *M. alternifolium*

FF. Sori superficial and smaller ..... 8. *M. sylvaticum*

1. *Microsorium punctatum* (Linnaeus) Copeland, Bishop Mus. Bull. 93: 73, 1932.
Polypodium (Phymatodes) irioides Lamarck; Baker, Jour. Linn. Soc. Bot. 15: 109, 1877.
Lou: No. 4037.
Los Negros: Near Momote Field, no. 3255.
Paleotropics.

Epiphytic in forest trees. Very common.

2. *Microsorium linguaeforme* (Mettenius) Copeland, Univ. Calif. Publ. Bot. 16: 116, 1929.
Polypodium (Phymatodes) linguaeforme Mettenius; Baker, Jour. Linn. Soc. Bot. 15: 109, 1877.
Manus: Woods 2 mi. W of Lorengau, no. 4126; Drano, alt. 1,000 ft., No. 1 Road, no. 4593.
Los Negros: Woods near Momote Field, no. 3283; tree trunks, nos. 3491 and 3535.
Malaya to Melanesia.

Epiphytic climber, low on tree trunks in shady forest. Frequent. No. 4593 is unusually large, the frond being 68 cm. in length. The clasping, cordate bases of the fronds are characteristic.

3. *Microsorium longissimum* Fée, Genera Filicum, p. 268, pl. 20B, fig. 2, 1850–1852.
Polypodium (Phymatodes) rampans Baker, Jour. Linn. Soc. Bot. 15: 109, 1877.
Manus: Woods 2 mi. SE of Lorengau, no. 3961; Lundrit, alt. 600 ft., No. 1 Road, no. 4579.
Los Negros: Bases of tree trunks, deep woods, nos. 3496 and 3546; Tauwi Hills, no. 3619.
Tropical Asia, Philippines, Amboina.

A creeper along the ground, in humus, upon various types of rocks, and most commonly at the bases of trees. Very numerous in woods, and variable both in size of fronds and in relative length of stipes. Occasional fronds have long, lateral lobes near the base. Plants creeping along the ground have small leaves, with stipes 1 cm. or less long; but the fertile fronds, borne when the plant climbs a tree trunk, are much larger and have stipes 3–12 cm. long.

4. *Microsorium pteropus* (Blume) Copeland, Univ. Calif. Publ. Bot. 16: 112, 1929.
Manus: Falls of an eastern tributary of the Lorengau River, no. 4114.
Tropical Asia to Melanesia.

Terrestrial, growing in mats on rocks submerged in and bordering streams. Not common. The fronds are much crinkled when alive, but flatten entirely when pressed. This characteristic and the aquatic habit, the scaly stipe and rachis, and the abundance of fertile fronds distinguish it easily from *M.*

longissimum. Also, the present species occasionally has fronds with one or two long, lateral lobes. In the water some fronds bear young plants in the sori.

5. *Microsorium acutifolium* (Brause) Copeland, Genera Filicum, p. 197, 1947.
Manus: Deep woods, east tip of island, no. 3615; rich forest above Lorengau River Falls, no. 4138; Sabon, No. 1 Road, no. 4564.
New Guinea.

A vigorous climber on branches of trees in shady forests. Infrequent. Occasional specimens have large, lateral lobes (no. 4564). This plant may be distinguished from simple forms of the following species by its very long rootstock, which is only 1.5 mm. thick, and by the broad elliptic fronds with acute tips.

6. *Microsorium scolopendria* (Burmann) Copeland, Univ. Calif. Publ. Bot. 16: 112, 1929.
Polypodium (*Phymatodes*) *phymatodes* Linnaeus; Baker, Jour. Linn. Soc. Bot. 15: 110, 1877.
Los Negros: Nos. 3253 and 3543; near Pitilu Lagoon, no. 3692; coconut trunks near Momote Field, no. 3500.
Paleotropics.

Usually epiphytic on rather exposed trees, but occasionally terrestrial. Common.

7. *Microsorium alternifolium* (Willdenow) Copeland, Genera Filicum, p. 197, 1947. (Pls. 20 and 21.)
Polypodium (*Phymatodes*) *nigrescens* Blume; Baker, Jour. Linn. Soc. Bot. 15: 110, 1877.
Manus: Woods along Drangot River, no. 4048; Lorengau River Falls, no. 3979; Kwaliop, alt. 1,400 ft., No. 1 Road, no. 4543.
Los Negros: Growing in tussocks along shores of Pitilu Lagoon, no. 3691; bole of coconut tree along beachside road, western Los Negros, no. 3617; woods near Mokerang, no. 4080.
India to Polynesia.

Epiphytic in forests, but occasionally found on the boles of coconut trees and terrestrially. Frequent. At Pitilu Lagoon, on little grassy "islands" along the shores (pl. 20), occurs a curious, very narrow, leathery form, with numerous pinnae (thirty pairs) only 1–1.5 cm. wide. In deep woods the fronds of this species become membranaceous and have fewer pairs of pinnae, six to twenty (usually eight), which average 3.5 (2.4–4.5) cm. wide (pl. 21). The largest frond in our collection is 175 cm. long.

8. *Microsorium sylvaticum* (Brackenridge) Copeland, Genera Filicum, p. 196, 1947.
Manus: Lorengau River Falls, no. 3980.
Los Negros: Dry, sandy woods near Momote Field, no. 3481; open, marshy spot, Mokerang, no. 4210; along road in woods N of Momote, no. 3937.
India to Polynesia.

This species is apparently always terrestrial. It is almost as variable in appearance, according to habitat, as the two preceding species, than which it is less common.

4. *Goniophlebium* (Blume) Presl

1. *Goniophlebium percussum* (Cavanilles) Wagner and Grether, Occ. Pap. Bishop Mus. 19: 88, 1948.

Manus: Tingau No. 1, alt. 1,000 ft., No. 1 Road, no. 4507.
Tropical Asia to Samoa.

Epiphytic. Not common.

5. *Aglaomorpha* Schott

1. *Aglaomorpha Ledermanni* (Brause) C. Christensen, Ind. Suppl. III, p. 20, 1934.
Manus: Coconut grove, 2 mi. SE of Lorengau, no. 3965; Sau, No. 1 Road, no. 4555.
New Guinea.

Epiphytic climber on coconut trunk, 5–15 feet from the ground. Rare.

6. *Merinthosorus* Copeland

1. *Merinthosorus drynarioides* (Hooker) Copeland, Philippine Jour. Sci. Bot. 6: 92, 1911. (Pl. 24.)
Manus: On *Ficus* tree, 30 ft. up, eastern tip of island, no. 3680; base of tree in woods, 2 mi. SE of Lorengau (sterile), no. 3968; Lorengau River Falls, no. 3973; epiphyte, Tingau No. 1, alt. 1,000 ft., no. 4533.
Los Negros: On fallen tree, *ca.* 50 ft. from base of trunk, northern Los Negros, no. 3697.
Malacca to the Solomons.

Epiphytic, usually high in forest trees. Frequent. Fertile fronds are uncommon. No. 3968 is unusually long, 190 cm. when dried.

Acrostichum (*Photinopteris*) *Thomsoni* Baker (Jour. Linn. Soc. Bot. 15: 111, 1877) was described from the Admiralties as differing from the present plant in being much smaller and in having membranous texture.

7. *Drynaria* (Bory) J. Smith

1. *Drynaria rigidula* (Swartz) Beddome, Ferns Brit. Ind., pl. 314, 1869.
Manus: 20 ft. high in coconut tree, 1 mi. E of Lorengau, no. 4045; Pundrau, alt. 1,000 ft., No. 1 Road, no. 4553.
Tropical Asia to Polynesia.

High epiphyte in trees. Not common. Seen also about 50 feet high on a huge forest tree in company with *Merinthosorus,* on the slopes of Mount Tjajiak.

8. *Selliguea* Bory

1. **Selliguea costulata** (Cesati), comb. nov. (Pl. 22.)
Acrostichum costulatum Cesati, Rend. Accad. Napoli 16: 27 and 30, 1877.
Grammatopteridium costulatum (Cesati) C. Christensen, Dansk Bot. Arkiv 6, no. 3: 80, 1929.
Manus: Summit of Mount Tjajiak, no. 4184.
Sumatra and New Guinea.

Locally common, epiphytic climber in trees in mountaintop woods. The shape of the shiny, dark green, leathery, sterile fronds varies considerably: the stipes extend from 3.5 to 22 cm. in length, and the lamina from 12 to 21 cm. in length and from 2.5 to 10 cm. in breadth. The ratio of breadth to length of the laminae of sterile fronds varies from 1 : 2 to 1 : 6, averaging 1 : 2½ locally. The rather rare fertile fronds vary from 24 to 60 cm. in length and from 3 to 8 mm. in breadth. On broader specimens the sporangia beneath may be separated into very close, slightly oblique sori, 11 mm. long and 2 mm. wide, but in the more common narrow fronds the sporangia are entirely confluent.

9. *Grammitis* Swartz

1. ***Grammitis Reinwardtii*** Blume, Enum. Plant. Jav., addend., 1828.
Manus: Summit of Mount Tjajiak, no. 4186.
Java and New Guinea.

Epiphytic on tree trunks in mountaintop woods. Fertile fronds vary from 2.8 to 9.0 cm. in length and the stipes from 2 to 20 mm.

10. *Scleroglossum* van Alderwerelt van Rosenburgh

1. ***Scleroglossum pusillum*** (Blume) van Alderwerelt van Rosenburgh, Bull. Jard. Bot. Buitenzorg, 2d ser., no. 7: 37, pl. 5, figs. 1–2, 1912.
Manus: Summit of Mount Tjajiak, no. 4187.
Malaya to New Guinea.

Epiphytic on tree trunks in mountain woods. Locally frequent. In our collections the fronds vary from 2.5 to 5.7 cm. in length and from 2 to 3 mm. in breadth.

11. *Ctenopteris* Blume

1. **Ctenopteris blechnoides** (Greville), comb. nov.
Grammitis blechnoides Greville, Ann. Mag. Nat. Hist., 2d ser., 1: 328, pl. 17, 1848.
Polypodium decorum Brackenridge; Baker, Jour. Linn. Soc. Bot. 15: 108, 1877.
Manus: Summit of Mount Tjajiak, no. 4178.
Malaya to Polynesia.

Epiphytic on mossy trunks. Abundant on Mount Tjajiak, but Moseley's specimens probably came from a much lower altitude.

12. *Prosaptia* Presl

1. ***Prosaptia contigua*** (Forster) Presl, Tent. Pterid., p. 166, 1836.
Manus: Woods along Drangot River, no. 4058; slopes of Mount Tjajiak, no. 4179; Lorengau River Falls, no. 3982; wet trunks, Buyang No. 2, alt. 1,000 ft., No. 1 Road, no. 4503; Bowat, alt. 600 ft., No. 1 Road, no. 4508.
Tropical Asia to Polynesia.

Epiphytic on mossy tree trunks. Frequent in rich woods.

XIV. VITTARIACEAE

Frond oblanceolate or elliptic, sori dorsal along reticulate veins ..... 1. *Antrophyum*
Frond linear and grasslike, sori in marginal grooves ..... 2. *Vittaria*

1. *Antrophyum* Kaulfuss

Fronds sessile ..... 1. *A. alatum*
Fronds stipitate ..... 2. *A. plantagineum*

1. ***Antrophyum alatum*** Brackenridge, U. S. Expl. Exped. 1838–1842, 16: 64, 1854.
Lou: Woods, no. 4071.
Manus: Eastern tip of island, no. 3678; Lorengau River Falls, no. 3969; falls of an eastern tributary of the Lorengau River, no. 4115; Buyang No. 2, alt. 1,000 ft., No. 1 Road, no. 4549.
Los Negros: Deep woods along road to Lombrom Point, nos. 3518 and 3950.
Philippines to Polynesia.

Epiphytic in deep woods. Rather common.

2. ***Antrophyum plantagineum*** (Cavanilles) Kaulfuss, Enum. Fil., p. 197, 1824.
Lou: Woods, no. 4070.

Los Negros: Woods near Momote Field, nos. 3287 and 3490.
India to Polynesia.

Epiphytic in coastal forests. Infrequent.

2. *Vittaria* J. Smith

1. *Vittaria elongata* Swartz, Syn. Fil., pp. 109 and 302, 1806; Baker, Jour. Linn. Soc. Bot. 15: 111, 1877. (Pl. 23.)
Manus: East end, no. 3675.
Los Negros: Northern part of island, no. 3695; western Los Negros, no. 3683; near Momote, no. 3284; woods along road to Lombrom Point, nos. 3486 and 3954.
Tropical Asia to Polynesia.

Epiphytic in woods. Abundant. According to exposure and humidity the plants vary widely in appearance, from small specimens with short rootstocks and stiff fronds 10–20 cm. long and 2–4 mm. broad to lax plants with long, creeping rootstocks and fronds 50–80 cm. long and 4–12 mm. broad.

XV. LYCOPODIACEAE

1. *Lycopodium* Linnaeus

Sporophylls undifferentiated from the vegetative leaves.
Leaves linear, 1 mm. wide, spreading ..... 1. *L. squarrosum*
Leaves lanceolate, 2–3 mm. wide, ascending ..... 2. *L. carinatum*
Sporophylls grouped into pendent strobili, or tassels, sharply distinct from the vegetative leaves.
Branches 1 cm. or more in diameter, leaves more than 1 mm. wide; epiphytes.
Leaves lanceolate, 1.5–2.5 mm. broad.
Spike usually 1 mm. or less in diameter, several times forked ..... 3. *L. phlegmaria*
Spike 2 mm. or more in diameter, simple or once forked ..... 4. *L. apiculatum*
Leaves ovate, 3–6 mm. broad ..... 5. *L. nummularifolium*
Branches 0.5 cm. or less in diameter, leaves very narrow, less than 1 mm. wide; terrestrial 6. *L. cernuum*

1. *Lycopodium squarrosum* Forster, Prodromus, p. 86, 1786.
Manus: Lorengau River Falls, no. 3985.
India to Polynesia.

Epiphytic in rich forest. Uncommon.

2. *Lycopodium carinatum* Desvaux, in Poiret, Enc. Bot. Suppl. 3: 555, 1823.
Lou: Woods, no. 4034.
Los Negros: Woods along road to Lombrom Point, no. 3285; tree trunks, 40 or more ft. high, no. 3520; northern Los Negros, no. 3694; western Los Negros, no. 4113.
Tropical Asia to Polynesia.

Epiphytic in woods. Common, but often very high in the trees.

3. *Lycopodium phlegmaria* Linnaeus, Sp. Pl. 2: 1101, 1753.
Manus: Lorengau River Falls, no. 3983 (juvenile); Tingau No. 1, alt. 1,000 ft., No. 1 Road, no. 4523; Warrabi, alt. 600 ft., No. 1 Road, no. 4578.
Los Negros: Woods near Momote Field, no. 3495; thick woods, western Los Negros, no. 3687; near Chaporowan Point, no. 4107.
Paleotropics.

Epiphytic in woods. Common, but, like the preceding species, often growing at a great distance above the ground. The sporophylls vary considerably: the sporangia in no. 3687 are barely surpassed by the tips of the sporophylls,

but in our other specimens the sporophylls extend beyond, two to three times the length of the sporangia. No. 3495 is proliferous at the ends of the spikes, bearing eight young plants, the largest 2 cm. long.

4. *Lycopodium apiculatum* Spring, Plant. Junghuhn., p. 272, 1851.
Manus: Lorengau River Falls, no. 3984.
Malaya to Polynesia.

Epiphytic in dark woods. Rare. Our material agrees well with specimens so named from Fiji. The species is in the intricate group of *L. pinifolium* Blume, and van Alderwerelt van Rosenburgh considered it hardly more than a form of that species (Malayan Fern Allies, p. 42, 1915). From the common local representative of *L. Phlegmaria* our plant is most distinct: the simple or once-divided quadrate spike is slightly more than 2 mm. thick and 3–5 cm. long; the vegetative leaves are smaller, paler green, and more approximate than those of the common forest form of *L. phlegmaria.*

5. *Lycopodium nummularifolium* Blume, Enum. Plant. Jav., p. 263, 1828.
Manus: Tingau No. 1, alt. 1,000 ft., No. 1 Road, no. 4522.
Malaya to New Guinea.

The single find of this beautiful club moss was growing in damp woods in a tree-crotch, 30 feet above the ground. The shiny, broadly ovate leaves are entirely unlike those of any other species known in the Admiralties.

6. *Lycopodium cernuum* Linnaeus, Sp. Pl. 2: 1103, 1753; Baker, Jour. Linn. Soc. Bot. 15: 111, 1877.
Manus: Lorengau River Falls, no. 4108; Sabon, No. 1 Road, no. 4563.
Los Negros: Lombrom Point, no. 3974.
Pantropical.

Terrestrial in open, brushy places and along dry banks. Frequent.

XVI. SELAGINELLACEAE

1. *Selaginella* Beauvois

(Note: The following list of *Selaginellae* is based upon preliminary identifications of our collections made by Dr. A. H. G. Alston.)

1. *Selaginella caudata* (Desvaux) Spring, Monogr. Lycopod. 2: 139, 1849.
Selaginella inaequalifolia Baker, Jour. Linn. Soc. Bot. 15: 112, 1877; not (Hooker and Greville) Spring.
Lou: Woods, no. 4028.
Los Negros: No. 3533; near Momote Field, no. 3271.
Melanesia.

Terrestrial in woods and in shaded, brushy places. This and/or the following species are abundant. Dr. Alston has informed us that Moseley's specimens were of this species. The native name for *Selaginella* on Lou Island is "sisir" and in Manus is "kamkam." Near the Drangot River was a little native boy who was naked except for a *Selaginella* hanging in front, in lieu of a "lap-lap."

2. *Selaginella Durvillei* (Bory p. p.) A. Braun, in Kuhn, Verh. zool.-bot. Ges. Wien 19: 585, 1869.
Los Negros: Tauwi Hills, no. 4198.
Melanesia.

Very similar in general aspect to the preceding species, and confused with it in the field by us.

3. *Selaginella Volkensii* Hieronymus (?), Bot. Jahrb. 52: 1, 1914.
Manus: Slopes of Mount Tjajiak, no. 4191.
Yap Island.

Terrestrial in mountainside woods in company with *S. quadrivenulosa*. The present plant is "near *S. Volkensii*," a Yap endemic, and, if identical, represents a considerable extension of range.

4. *Selaginella deliculata* (Desvaux) Alston, Jour. Bot. 70: 282, 1932.
Lou: Brushy places, no. 4029.
Manus: 2 mi. SE of Lorengau, no. 3963.
Los Negros: Tauwi Hills, no. 4200.
India to the Moluccas and Admiralties.

Terrestrial on damp limestone rocks, on stream banks, and in brushy places. Common. In aspect, the pink stems, the pale green of the fronds, and the decumbent habit distinguish this species from the abundant *S. caudata*.

5. *Selaginella Muelleri* Baker, Jour. Bot. 23: 122, 1885.
Manus: Lorengau River Falls, no. 4134.
Los Negros: No. 3960; Tauwi Hills, no. 4208.
New Guinea.

Terrestrial in shady woods. Frequent. The glossy appearance of the plants in nature is distinctive.

6. *Selaginella quadrivenulosa* van Alderwerelt van Rosenburgh, Nova Guinea 14: 65, 1924.
Manus: Slopes of Mount Tjajiak, no. 4192.
New Guinea.

Terrestrial in rich, rocky soil along path in mountain woods. Found only once. The broad, pale green branches are unique.

7. *Selaginella suffruticosa* van Alderwerelt van Rosenburgh, Bull. Jard. Bot. Buitenzorg, 2d ser., no. 1: 22, 1911.
Manus: Lorengau River Falls, no. 3975; wet woods, Bowat, No. 1 Road, no. 4586.

Terrestrial in very rich, dark woods. Locally common. The branches are broad, dark green above, and pale below.

8. *Selaginella nana* (Desvaux) Spring (?), Monogr. Lycopod. 2: 240, 1849.
Los Negros: Western end, no. 4001.
Melanesia.

Terrestrial in muddy swamp. No. 3613, collected along rocky stream at the eastern tip of Manus, may also be this species. No. 4020, a common plant along rocky river banks below the Lorengau River Falls, is similar in size and habit, but probably represents a new species.

9. *Selaginella Hieronymiana* van Alderwerelt van Rosenburgh, Bull. Jard. Bot. Buitenzorg, 2d ser., no. 6: 31, 1912.
Manus: Lorengau River Falls, no. 3976; Buyang No. 1, alt. 1,400 ft., No. 1 Road, no. 4548.
Moluccas and New Guinea.

A tall climber on forest trees; on one tree, seen to have climbed about 50 feet. Locally common. The climbing stems are very brittle.

10. *Selaginella Zahnii* Hieronymus, Bot. Jahrb. 50: 37, 1913.
Manus: Summit of Mount Tjajiak, no. 4193.
New Guinea.

Epiphytic on mossy tree trunks in company with various species of Hymenophyllaceae. A very mosslike plant.

11. *Selaginella ciliaris* (Retzius) Spring, Bull. Acad. Sci. Belg. 10: 231, 1843.
Lou: Grassy, open place, no. 4065.
Manus: East end, nos. 4046 and 3614; Drangot River, no. 4053.
India to northern Australia.

Terrestrial in open, grassy meadows. Frequent.

12. *Selaginella longiciliata* Hieronymus, Bot. Jahrb. 50: 33, 1913.
Los Negros: Mouth of limestone cave, western Los Negros, no. 4152.
New Guinea.

Terrestrial on horizontal rock surfaces under limestone cliffs in shade, the "fronds" borne obliquely to catch the rays of sunlight. Frequent. Nos. 4107 and 3275 from limestone cliffs in Tauwi Hills, Los Negros, are probably the same species. No. 4069, from damp banks in woods on Lou Island, may also be the same.

XVII. PSILOTACEAE

1. *Psilotum* Swartz

Branches triangular, the ultimate branches 1 mm. or less thick.....1. *P. nudum*
Branches flattened, 1–3 mm. broad.....2. *P. complanatum*

1. *Psilotum nudum* (Linnaeus) Grisebach, Ges. wiss. Göttingen, Abhandl. 7: 278, 1857.
Psilotum triquetrum Swartz; Baker, Jour. Linn. Soc. Bot. 15: 112, 1877.
Manus: Eastern tip of island, no. 4014.
Los Negros: Woods near Momote Field, nos. 3483 and 3540; western Los Negros, no. 3688.
Pantropical.

Epiphytic on stumps and in crotches of trees, sometimes in rather exposed places. Common.

2. *Psilotum complanatum* Swartz, Syn. Fil., pp. 188 and 414, pl. 4, fig. 5, 1806; Baker, Jour. Linn. Soc. Bot. 15: 112, 1877.
Los Negros: Mangrove swamp, western end of island, no. 3999.
Pantropical.

Epiphytic, usually in shady forests. Frequent.

PLATE 5

Ophioglossum pendulum Linnaeus, typical, a rather small specimen.



FERNS OF THE ADMIRALTY ISLANDS

D. E. Gardner del.

PLATE 6

Ophioglossum pendulum Linnaeus, dwarf form. Growing in moss at base of sago palm in swamp, western Los Negros, no. 4145.


MILLIMETER

PLATE 7

Ophioglossum petiolatum Hooker. Upper row: plants from exposed, grassy field, Tawi Island, no. 4157. Lower row: plants from shady woods, along native trail, Lou Island, no. 4067.


MILLIMETER

PLATE 8

Lygodium trifurcatum Baker, showing variation in degree of dissection of fertile pinnae on one frond. Los Negros, no. 3997.



PLATE 9

Lindsaea sagittcola Wagner and Grether, sp. nov. (type).


MILLIMETER

PLATE 10

Tapeinidium moluccanum (Blume) C. Christensen. Woods at summit of Mount Tjajiak, no. 4188.

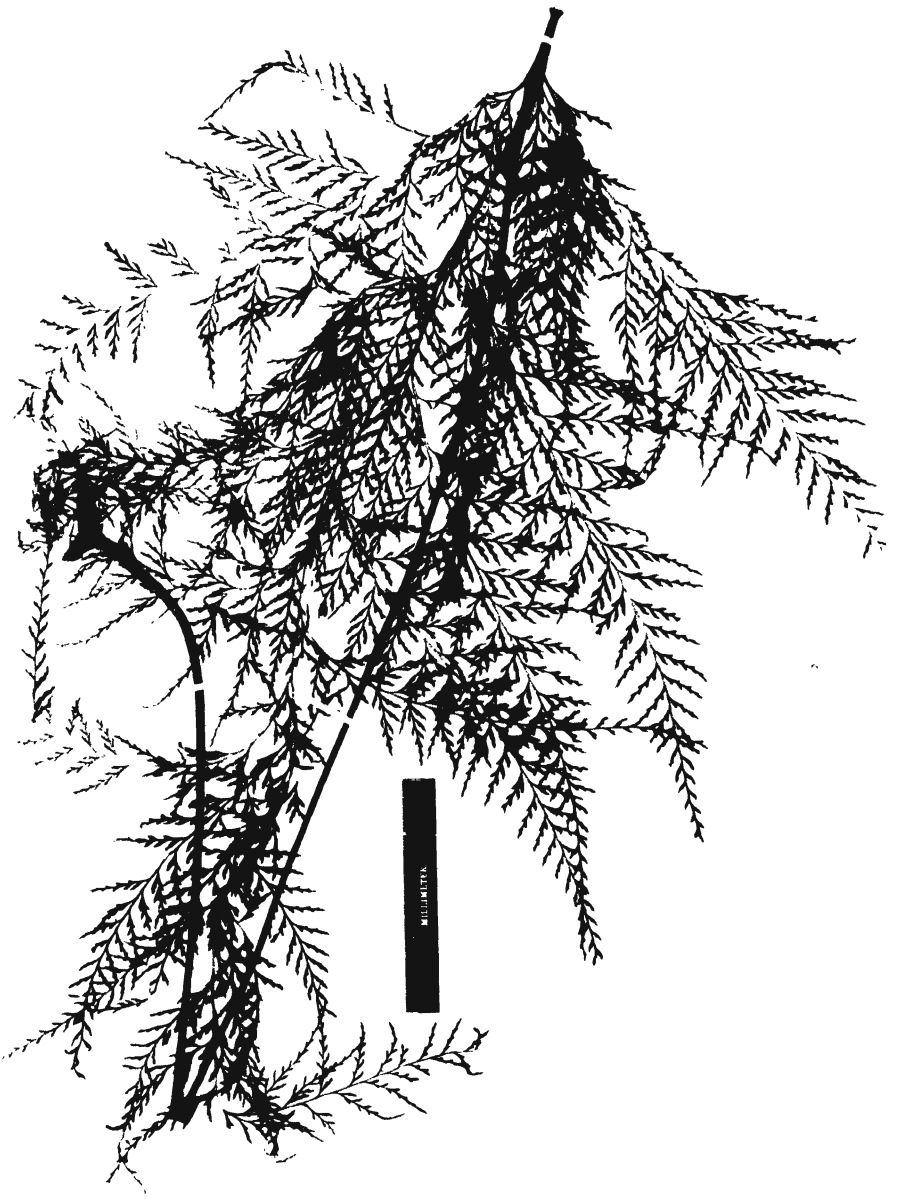


PLATE 11

Tapacuidium stenolobum (Baker) Wagner and Grether, comb. nov. Lorengau River Falls, Manus, no. 3978.


MILLIMETER

PLATE 12

Humata nervosa (Baker) Wagner and Grether, comb. nov. Los Negros, no. 3968.



PLATE 13

Hamata alpina (Blume) Moore, forms. Abundant on trees at summit of Mount Tjajiak, no. 4181.


MILLIMETER

PLATE 14

Nephrolepis persicifolia Christ. Epiphyte, western Los Negros, no. 3958.


MILLIMETER

PLATE 15

Cyathea media Wagner and Grether, sp. nov. (type). Slopes of Mount Tjajiak, no. 4162.



FERNS OF THE ADMIRALTY ISLANDS

PLATE 16

Cyclosorus cataractorum Wagner and Grether, sp. nov. (type). River banks, Lorengau River Falls, Manus, no. 3971.



FERNS OF THE ADMIRALTY ISLANDS

PLATE 17

Asplenium falcatum Lamarck. Large frond: epiphytic in woods, Lou Island, no. 4068. Small plant: dry, exposed limestone cliffs, Los Negros Island, no. 1144.


MILLIMETER

PLATE 18

Asplenium cuneatum Lamarck, small form. Woods along Drangot River, Manus, no. 4051.


MILLIMETER

PLATE 19

Asplenium cuneatum Lamarck, large form. Woods along Drangot River, Manus, no. 4050.



PLATE 20

Microsorium alternifolium (Willdenow) Copeland, narrow form. Pitilu Lake, Los Negros, no. 3691. (Lower part of stipe removed.)


MILLIMETER

PLATE 21

Microsorium alternifolium (Willdenow) Copeland, broad form. Woods along Drangot River, Manus, no. 4048.


MILLIMETER

PLATE 22

Selliguea costulata (Cesati) Wagner and Grether, comb. nov. Epiphytic climber, summit of Mount Tjajiak, Manus, no. 4184, showing variation in fertile fronds.

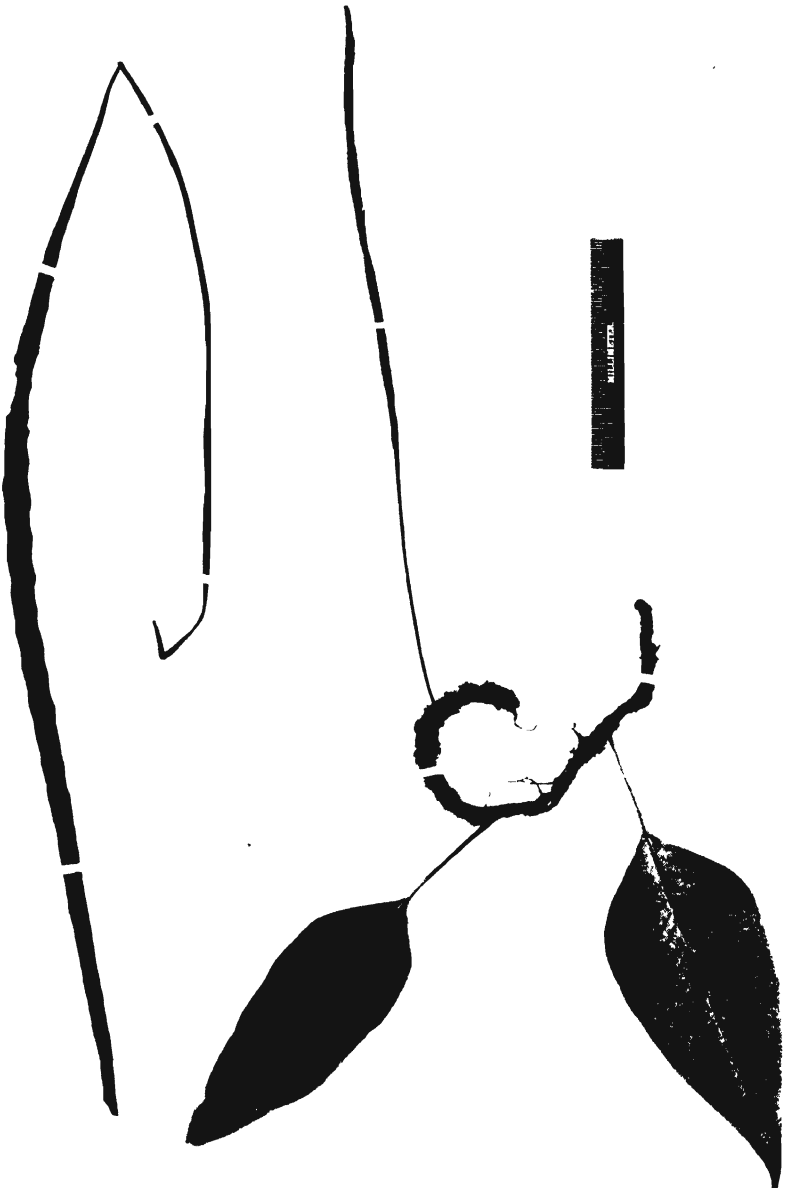


PLATE 23

Vittaria elongata Swartz. Large specimen, no. 3954, and small specimen, no. 3683, show variation in size of plants with different conditions of light and humidity.



PLATE 24

Merinthosorus drynarioides (Christ) Copeland. Growing on a coconut trunk, Sau Plantation, Manus.



PLATE 25

A characteristic second-growth coconut grove, Sau Plantation, Manus.



THE GENUS OSMORHIZA (UMBELLIFERAE)

A Study in Geographic Affinities

BY

LINCOLN CONSTANCE AND REN HWA SHAN

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THE GENUS OSMORHIZA (UMBELLIFERAE) A STUDY IN GEOGRAPHIC AFFINITIES

BY

LINCOLN CONSTANCE AND REN HWA SHAN

OSMORHIZA was one of ninety-two genera included by Mathias and Constance in their taxonomic account of the Umbelliferae for the "North American Flora." The present authors, Constance and Shan, thought it might prove worthwhile to investigate one of these genera more intensively, to see what flesh might be found to clothe the bare bones of the formal keys and descriptions. It has long been realized by thoughtful botanists that many taxonomic treatments are published with an air of embalmed finality that completely fails to reflect the inherent difficulties of pigeonholing species populations. We suspect that the conventional rigid taxonomic format frequently conceals fully as many problems as the treatment pretends to solve. *Osmorhiza* was selected as a test case.

None of the "newer techniques" has been employed in this expanded study of the genus, not because we fail to recognize the desirability of utilizing all such approaches, but only because limited time forced us to confine ourselves to traditional methods. We have, in fact, only examined the genus as a whole and attempted to see as much critical material as possible. Plate 26 represents a tentative excursion into comparative anatomy of the fruits. Although, between us, we have had field experience with a fair proportion of the species of the genus, we have conducted little special field work during the course of the present study.

We have attempted to map the distribution of all members of the genus because we are especially interested in the geographic relationships they show. Some of these relationships have been remarked before. Asa Gray (1859) stressed the affinity of the Asiatic with the eastern American plants; Clarke (1871) regarded them as conspecific. Reiche (1902) and Coulter and Rose (1895) hinted at a relationship between certain of the North American species with those of South America. Fernald (1925), in the development of his Nunatak theory, recognized two of the western American forms as part of his Western Cordilleran Element in the presumably unglaciated areas of the Great Lakes and eastern North America. Finally, Skottsberg, Stebbins, and others have drawn attention to the suitability of some *Osmorhiza* fruits for epizoötic dispersal.

The distribution of species is stressed because we find that the world occurrence of most genera of Umbelliferae is insufficiently well known, and we suspect that the same holds true for most other families of flowering plants. We are very much intrigued by the causes underlying these distributions, but we think it most important to record the actual distributions. Much plant-geographical discussion has been based upon so little concrete evidence as to make its conclusions essentially worthless. The distributional patterns mani-

fested by *Osmorhiza* can scarcely be explained satisfactorily until those of many other genera showing partly similar ones have been carefully detailed. Hence, we present maps (figs. 1–5) showing the distribution, for each species, of all the specimens seen by us, to serve as a standard of comparison with other genera. We have a very inadequate representation from Asia and Latin America, and increased collecting in these areas may be expected to fill out and extend the ranges indicated. We have cited a fairly large number of collections (although these represent only a very small fraction of the several thousand specimens studied) because, as every taxonomist knows, a distribution map not backed up with cited specimens is likely to be completely valueless. In order to obviate crowding of symbols, and because more than one species frequently occur in the same locality, we have omitted from the maps a number of collections and have been unable to avoid some lateral displacement of symbols. Within the limits of convenient representation, however, the distributional patterns are as accurate as we could make them in the light of our present knowledge.

In the following treatment it may be noted that no "formae," and only one variety, are accorded taxonomic status—not that such units have not been proposed, most of them as species, nor that none are recognizable; but we are primarily interested in delineating the major natural populations that comprise *Osmorhiza*, and feel that the recognition of one-character entities accomplishes little in this regard. Such segregates can easily be delimited on the basis of leaf form, pubescence, pedicel length, flower color, fruit size, and the like, perhaps within all the better-collected species. Inasmuch as such variants usually show little community of characters and do not form discrete populations, we have not given them special recognition. If taxonomic designation were to be restricted to natural populations, plant classification would be freed from a ponderous burden of formal categories which, by their nature, may be as few or as numerous as the taste and the industry of the describer dictate. At least within the Umbelliferae, there appear to be very few "uniform" species: most manifest a degree of polymorphism sufficient to afford interminable activity for the devotee of minor entities.

NATURAL DIVISIONS OF THE GENUS

Osmorhiza's generic distinctness is not in doubt except for its close relationship to the monotypic European *Myrrhis*, with which it has been wholly or partly united by some authors. Although the affinity of *Osmorhiza occidentalis* and *O. glabrata* with *Myrrhis* appears to be strong, *Myrrhis* may be satisfactorily maintained as a distinct genus by its pinnately decompound leaves, scarious involucels, marginally zygomorphic (radiant) flowers, prominently winged fruit ribs, larger seeds, and involute seed face (pl. 26, figs. 1, 2, 3). *Myrrhis odorata* and the two species of *Osmorhiza* which have been investigated cytologically (Wanscher 1931, 1932), *O. aristata* and *O. longistylis*, are all reported to have eleven pairs of chromosomes.

The species of *Osmorhiza* appear to fall into four groups, which may be designated the Glycosmae (*Glycosma* Nutt.), the Mexicanae, the Aristatae,

and the Nudae. Nuttall, Asa Gray, Rydberg, and some others treated the species with caudate fruits as comprising *Osmorhiza* and those with unappendaged mericarps as a separate genus, *Glycosma;* Bentham and Greene assigned the latter to *Myrrhis.* Drude, followed by Coulter and Rose, placed both groups of species in *Osmorhiza* (*Washingtonia*), but recognized the subgenera *Euosmorrhiza* (*Osmorhiza*) and *Glycosma.* Later in this paper, evidence will be offered that the principal distinction between the two subgenera may be less profound than has been commonly supposed.

The Glycosmae embrace two species, *O. occidentalis* and *O. glabrata.* Their unappendaged mericarps strongly suggest those of *Chaerophyllum* and *Myrrhis,* and may reflect the primitive condition of the *Osmorhiza* fruit. The Mexicanae and Aristatae, with usually appendaged mericarps and bracteolate involucels, differ from each other primarily in the length of their styles; each of these groups contains three species. The lack of appendages in *O. bipatriata* and their brevity in *O. brachypoda* suggest a relationship between the Mexicanae and the Glycosmae. The Nudae, also comprising three species, are regarded as the most specialized in fruit structure, a suggestion strengthened by their almost complete lack of involucels. Because the caudal appendages are not found in related genera, it is believed that these represent a specialized, derived development.

There is very little evidence upon which to postulate a phylogenetic progression for the species of *Osmorhiza.* Emphasis upon different characters will produce quite different arrangements. If we can assume that *Osmorhiza* arose somewhere in the Chaerophylloid Umbelliferae (Ammineae-Scandicineae of Bentham, Apioideae-Scandicineae-Scandicinae of Drude), we would expect the generic prototype to possess well developed involucels, a conical stylopodium, unappendaged fruits with evident vittae (oil tubes), and a sulcate seed face. No known species of *Osmorhiza* possesses all these characters, and the vittae appear to have become obscure before the development of the modern species. Unappendaged fruits and a sulcate seed face are characteristic of the Glycosmae, and one of the Mexicanae wholly or almost wholly lacks appendages; an involucel is a conspicuous feature of the Mexicanae and Aristatae; only the Aristatae manifest a sharply conical stylopodium. The Nudae, with highly developed fruit appendages, small fruits, reduced stylopodia, an almost complete loss of involucels, and a slightly concave seed face, would appear to be the most specialized members of the genus. Thus, the supposedly primitive characters seem to have been assorted more or less at random among the different sections. The Glycosmae appear to have retained the lion's share of primitive features and the Nudae the fewest, with the Mexicanae and Aristatae occupying an intermediate position. Such an arrangement may appear too tenuous to be worth attempting, but it has an important bearing on the interpretation of the geographical distribution of the species.

GEOGRAPHICAL DISTRIBUTION

The present distribution of *Osmorhiza* appears to reflect a series of migrations, involving all the sections of the genus. The present pattern of distribution may be summarized as follows (figs. 1–5).

GLYCOSMAE: One species in western North America, another in temperate Chile, and a relatively close relationship to the Eurasian *Myrrhis*.

MEXICANAE: One species known only from the Davis Mountains of western Texas and the Sierra Madre Oriental of Nuevo León; a second extending from Chihuahua southward through Mexico to Guatemala and Costa Rica, reappearing in Colombia and reaching into northwestern Argentina; a third in central and southern California and local in Arizona.

ARISTATAE: Two species widespread in the eastern United States and adjacent Canada; a third extending from Sakhalin and Siberia through Japan and China to the Himalayas of northwestern India.

NUDAE: Two species primarily of western North America, but reappearing in the Great Lakes region, New England, the Maritime Provinces, Newfoundland, and southern South America; a third extending from northern Montana and northwestern California to Alaska.

Thus, the Glycosmae suggest the necessity of migration lanes connecting North and South America, and perhaps Eurasia to account for *Myrrhis*. In the case of the Mexicanae, the connection between northern Mexico and northern Argentina appears to be nearly intact, perhaps as intact as it ever was; the California-Arizona and Texas–Nuevo León species distributions afford no special migrational problems. The Aristatae demand a "bridge" between eastern Asia and eastern North America. The Nudae would seem to require migration routes connecting western and extreme eastern North America, probably through the Great Lakes region, and also a route to temperate South America. This last connection is now interrupted by some sixty degrees of latitude.

The existence of an American-Eurasian migration route, through Beringia, has been so fully documented that it appears to need no bolstering by evidence from *Osmorhiza*. The fact that *O. aristata, O. longistylis,* and *O. Claytoni* are so similar morphologically as to have been frequently regarded as conspecific suggests that this connection must have been intact at a relatively recent date, or that differentiation of these species must have proceeded very slowly. The North–South American bridge rests on less well authenticated pillars. Johnston (1940), dealing primarily with woody desert plants, has postulated a desert connection between the two continents, but *Osmorhiza* species are mesophytic woodland herbs. As he remarks, "the distributional behavior and general relationships of the herbs . . . are remarkably different from those of the trees and shrubs. Practically all of these rather numerous herbs belong to genera appearing to have had an origin and relatively modern evolution in North America." Since both the purportedly least and most advanced sections of the genus show the same north-south link, but at different taxonomic levels, a long-persisting or intermittent connection is suggested. It is tempting to fall back upon occasional long-distance fruit dispersal by birds or other agents to account for the wanderings of the Nudae, with their small, appendaged mericarps. However, the Glycosmae appear to have followed the same route, although their larger and heavier fruits are without obvious dispersal mechanisms. It should be pointed out, also, that *Osmorhiza* species are not culti-

vated nor are they in any sense "weedy," and the activities of man (which have permitted the renaissance and spread of so many other plants) tend to restrict their distributions rather than to advance them.

It may be noted that all the sections are represented in North America, and that all but two of the eleven species occur there. Hence, this continent would appear to be the locale for most of the development of the genus. Where the same species occurs in both North and South America, the southern representation appears to be considerably poorer in biotypes, again suggesting a derivation, with losses, from North America.

ACKNOWLEDGMENTS

The writers are grateful to the curators of the following herbaria for the privilege of examining the material of *Osmorhiza,* or at least certain critical specimens in their care. The name of each institution is followed by its symbol in the citation of specimens (Lanjouw 1939, 1941).

University of Arizona Herbarium (ARIZ)
Ira W. Clokey Herbarium, deposited at the University of California (CLOKEY)
Dudley Herbarium, Stanford University (DS)
Chicago Natural History Museum (F)
University of Georgia Herbarium (GA)
Botanical Garden, Göteborg (GB)
Gray Herbarium, Harvard University (GH)
Royal Botanic Gardens, Kew (K)
Missouri Botanical Garden (MO)
National Research Council, Academia Sinica, Nanking (NAC)
New York Botanical Garden (NY)
Naturshistoriska Riksmuseet, Stockholm (S)
University of Texas Herbarium (TEX)
University of California Herbarium (UC)
United States National Museum, Smithsonian Institution (US)
Rocky Mountain Herbarium, University of Wyoming (WYO)

Transverse sections of mericarps illustrated in plate 26 were prepared, from dried herbarium material, by Mr. Ernest Gifford, a teaching assistant in the Department of Botany, University of California.

SYSTEMATIC TREATMENT

Osmorhiza Raf. Jour. de Phys. 89 : 257. 1819.

Osmorhiza Raf. Am. Mo. Mag. 2: 176. 1818. (Nomen nudum.)
Washingtonia Raf. Am. Mo. Mag. 2: 176. 1818. (Nomen nudum.)
Gonatherus Raf. Am. Mo. Mag. 2: 176. 1818 (Nomen nudum.)
Uraspermum Nutt. Gen. 1: 192. 1818. Not *Urospermum* Scop. 1777.
Spermatura Reichenb. Consp. 141. 1828.
Glycosma Nutt.; T. & G. Fl. N. Am. 1: 639. 1840.
Myrrhis § *Glycosma* A. Gray, Proc. Am. Acad. 7: 346. 1868.
Osmorrhiza subgen. *Euosmorrhiza* Drude in Engl. & Prantl. Pflanzenfam. 3[8]: 153. 1897.
Washingtonia subgen. *Osmorhiza* Coult. & Rose, Contr. U. S. Nat. Herb. 7: 61. 1900.
Washingtonia subgen. *Glycosma* Coult. & Rose, Contr. U. S. Nat. Herb. 7: 62. 1900.
Uraspermum § 1. *Osmorhiza* Kuntze, Lexicon 582. 1904.
Scandix § *Aporhynchus* K.-Pol. Bull. Soc. Nat. Moscou II. 29: 142. 1916.
Scandix § *Urascandix* K.-Pol. Bull. Soc. Nat. Moscou II. 29: 143. 1916.

Slender to rather stout, erect or decumbent at the base, herbaceous, caulescent, branching, pubescent to glabrate perennials from thick fascicled roots. Leaves petiolate, membranaceous, ternate or ternate-pinnate, the leaflets lanceolate to orbicular, serrate to pinnatifid, with mucronate teeth or lobes. Petioles sheathing. Inflorescence of loose compound umbels; the peduncles terminal and lateral, usually exceeding the leaves. Involucre wanting, of a single foliaceous bract, or of several, narrow, foliaceous bracts. Involucel of several narrow foliaceous reflexed bractlets or wanting. Rays few, slender, ascending to divaricate and reflexed, unequal. Pedicels spreading to divaricate. Flowers white, purple, or greenish yellow, the petals spatulate to obovate with a narrower inflexed apex; calyx teeth obsolete; styles slender to obsolete, their tips spreading or divaricate, the stylopodium conic. Carpophore 2-cleft less than one-half of its length. Fruit linear to oblong, cylindric to clavate, obtuse, tapering, beaked or constricted at the apex, rounded or caudate at the base, flattened laterally, bristly-hispid to glabrous; ribs filiform, acute, often bristly; oil tubes obscure or wanting; seed subterete in cross section, the face concave or sulcate.

Type species, *Myrrhis Claytoni* Michx. (*Osmorhiza Claytoni* Clarke).

The most recent treatment of the North American part of the genus left the validity of the generic name in doubt, but this question may be quickly settled. in the "North American Flora" *Osmorhiza* was listed as a "nomen conservandum propositum," because it was believed that *Uraspermum* Nutt. (1818) clearly antedated the first valid publication of *Osmorhiza* Raf. (1819). It has since been established, however, that *Uraspermum* Nutt. is a later homonym of *Urospermum* Scop. (1777), of which it is to be considered an orthographic variant. *Osmorhiza* thus becomes the first eligible name for the genus, as indicated in the full synonymy, listed above.

KEY TO THE SPECIES

Fruit base obtuse and without appendages, or these rudimentary, the fruit glabrous or rarely sparsely bristly at base.
  Fruit 10–20 mm. long; style and stylopodium about 1 mm. long; involucel inconspicuous or lacking.
    Petals yellow; leaflets serrate to lobed, not dissected ..... 1. *O. occidentalis*
    Petals white; leaflets laciniate or pinnatifid ..... 2. *O. glabrata*
  Fruit 10–12 mm. long; style and stylopodium less than 0.5 mm. long; involucel conspicuous ..... 3. *O. bipatriata*
Fruit base attenuate into prominent appendages, the fruit conspicuously bristly at least at the base.

Involucel conspicuous.
Style and stylopodium usually less than 1 mm. long, the latter low-conic, the disc often conspicuous; pedicels 1–6 mm. long.
Fruit linear-oblong; pedicels spreading-ascending, 4–6 mm. long: flowers greenish white ..... 4. *O. mexicana*
Fruit oblong-fusiform; pedicels ascending, 1–3 mm. long; flowers greenish yellow ..... 5. *O. brachypoda*
Style and stylopodium 1–4 mm. long, the latter conic, the disc inconspicuous; pedicels 5–30 mm. long.
Pedicels 5–12 mm. long; fruit oblong-fusiform, strongly acute at apex.
Style and stylopodium 2–4 mm. long; plants anise-scented..... 6. *O. longistylis*
Style and stylopodium 1–1.5 mm. long; plants not anise-scented... 8. *O. Claytoni*
Pedicels 10–30 mm. long; fruit linear-clavate, abruptly acute or obtuse at apex.
Leaflets incised and pinnately lobed to pinnatifid at base..... 7. *O. aristata*
Leaflets coarsely serrate to sparsely lobed at base..... 7a. *O. aristata* var. *laxa*
Involucel lacking or rudimentary.
Rays and pedicels spreading-ascending; fruit cylindric, beaked.
Stylopodium depressed, the disk conspicuous; fruit constricted below the apex, 8.5–13 mm. long..... 9. *O. purpurea*
Stylopodium conic, the disk inconspicuous; fruit tapering at the apex, 12–27 mm. long .....10. *O. chilensis*
Rays and pedicels divaricate; fruit clavate, obtuse.....11. *O. obtusa*

1. *Osmorhiza occidentalis* (Nutt.). Torr. Bot. Mex. Bound. Surv. 71. 1859

Glycosma occidentalis Nutt.; T. & G. Fl. N. Am. 1: 639. 1840.
Myrrhis Bolanderi A. Gray, Proc. Am. Acad. 7: 346. 1868. Based upon *Bolander 6525*, "Lamberts Lake, Mendocino County, California."
Glycosma Bolanderi A. Gray, Proc. Am. Acad. 8: 386. 1872.
Glycosma ambiguum A. Gray, Proc. Am. Acad. 8: 386. 1872. Based upon *E. Hall 217*, "foot of Cascade Mountains [Silver Creek, Marion County], Oregon."
Osmorhiza occidentalis var. *Bolanderi* Coult. & Rose, Rev. N. Am. Umbell. 119. 1888.
Osmorhiza ambigua Coult. & Rose, Rev. N. Am. Umbell. 119. 1888.
Myrrhis ambigua Greene, Fl. Fran. 332. 1892.
Washingtonia occidentalis Coult. & Rose, Contr. U. S. Nat. Herb. 7: 67. 1900.
Washingtonia Bolanderi Coult. & Rose, Contr. U. S. Nat. Herb. 7: 68. 1900.
Washingtonia ambigua Coult. & Rose, Contr. U. S. Nat. Herb. 7: 69. 1900.
Glycosma maxima Rydb. Bull. Torrey Club 40: 67. 1913. Based upon *Rydberg & Carlton 7585*, "Mt. Nebo, Utah."
Osmorrhiza Bolanderi Jepson, Madroño 1: 120. 1923.

Plants rather stout, 3–12 dm. high, villous at the nodes and hirtellous to glabrate throughout; leaf blades oblong or ovate, 1–2 dm. long, 6–15 cm. broad, 1–3-ternate or ternate-pinnate, the leaflets oblong-lanceolate to ovate, 2–10 cm. long, 0.5–5 cm. broad, acute or acutish, serrate and usually incised or lobed, the rachis and sheath finely pilosulous or glabrate; petioles 5–30 cm. long; peduncles 6–20 cm. long; involucre usually wanting; involucel usually wanting; rays 5–12, stiffly ascending to spreading-ascending, 2–13 cm. long; pedicels spreading to ascending, 3–8 mm. long; flowers yellow, the styles and stylopodium 0.8–1.2 mm. long, the latter low-conic, the disc conspicuous; carpophore cleft one-fourth to one-third of its length; fruit linear-fusiform, 12–20 mm. long, constricted below the apex, obtuse at the base, glabrous.

Type locality—Western side of the Blue Mountains of Oregon," *Nuttall.*

Distribution—Alberta to Colorado, west to British Columbia and central California.

This is an easily differentiated species, characteristic primarily of mountainous areas in the western United States and southwestern Canada. Varia-

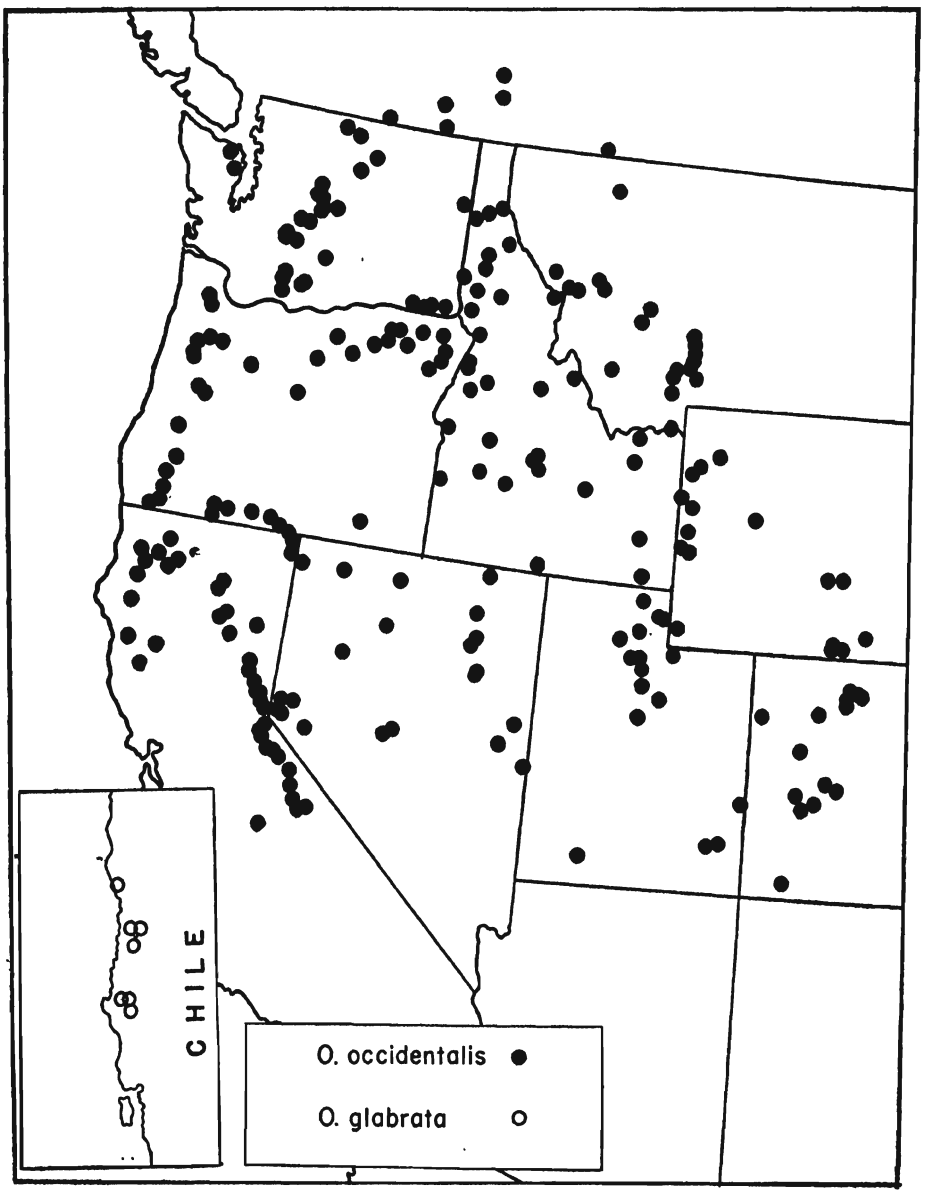


Fig. 1. Distribution of *Osmorhiza occidentalis* (North America) and *O. glabrata* (South America)

tion in the form and division of the leaves, pubescence, and size of fruit is considerable, but apparently not such as to permit the delimitation of tenable subspecific entities. The spreading rays and resultant lax umbels which led Asa Gray to describe *Myrrhis Bolanderi* and *M. ambigua* are most common among relatively low-altitude plants of western California, Oregon, and Washington, but the same condition occurs elsewhere over the range. The

supposed complementary fruit differences were apparently based upon insufficient material.

Representative specimens.—ALBERTA. Waterton Lake, *J. Macoun 10,678* (GH,NY,US); 5 miles W of Pincher Creek, *E. H. Moss 106* (GH,US); W of Beaver Mines, *E. H. Moss 325* (GH,US). MONTANA. Midvale, Glacier Co., *L. M. Umbach 508* (NY,WYO); Grant Creek, Missoula, Missoula Co., *J. E. Kirkwood 1229* (GH,MO,UC), *1230* (CLOKEY, GH,MO,UC); Mt. Stuart, Missoula, Missoula Co., *J. E. Kirkwood 1228* (DS,GH,MO,UC); Summit, Great Northern Railway, Gallatin Co., *R. S. Williams 196* (NY,US,WYO); Bridger Mountains, Gallatin Co., *Rydberg & Bessey 4597* (GH,NY,US,WYO); Mt. Bridger, Gallatin Co., *J. W. Blankinship 214* (F,MO,US); Spanish Basin, Madison Range, Madison Co., *J. H. Flodman 688* (MO,NY,US). IDAHO. Near Stevens Peak, Shoshone Co., *J. B. Leiberg 1444* (GH,MO, NY,UC,US,WYO); Clearwater River, Nez Perce Co., *Sandberg, MacDougal & Heller 108* (GH,NY,US); Forest, Nez Perce Co., *Heller & Heller 3451* (DS,MO,NY,UC,US); Henry Lake, Fremont Co., *Payson & Payson 2010* (GH,MO,NY,WYO); Boulder Creek Canyon, Blaine Co., *J. W. Thompson 14,092* (DS,F,GH,MO,NY,S,UC,US); Martin, Blaine Co., *Macbride & Payson 3086* (DS,GH,MO,NY,UC,US,WYO); Ketchum & Guyer Hot Springs, Blaine Co., *Nelson & Macbride 1280* (DS,GH,MO,NY,UC,US,WYO). WYOMING. Battle, Carbon Co., *F. Tweedy 4521* (NY,US); Teton Pass, Teton Co., *A. Carter 1656* (GH,NY, UC), *Merrill & Wilcox 1250* (GH,US,WYO); Grand Teton Natl. Park, *L. O. Williams 1142* (GH,MO,S); Teton Mountains, Uinta Co., *A. & E. Nelson 6472* (GH,MO,NY,US,WYO). COLORADO. Rabbit Ears, Larimer Co., *L. N. Goodding 1563* (GH,MO,NY,UC,US,WYO); Cerro Summit, Montrose Co., *C. F. Baker 413* (DS,GH,MO,NY,UC,US,WYO); Ruby, Mesa Co., *C. F. Baker 723* (GH,MO,NY,UC,US,WYO); Bob Creek, La Plata Mountains, Montezuma Co., *Baker, Earle & Tracy 177* (CLOKEY,GH,MO,NY,UC,US,WYO). UTAH. West Fork of Bear River, Summit Co., *Payson & Payson 4936* (DS,GH,MO,UC,US,WYO); Logan Canyon, Cache Co., *M. Burke 3640* (GH,UC,WYO); Horse Creek, Wasatch Co., *E. H. Graham 9229* (GH,MO,US); Provo, Utah Co., *M. E. Jones 5581* (MO,NY,UC,US,WYO); Mt. Nebo, Juab Co., *Rydberg & Carlton 7585* (NY: type of *Glycosma maxima* Rydb., WYO); N slope of Abajo Mountains, San Juan Co., *Goodman & Hitchcock 1399* (MO,NY, WYO); Alta, Wasatch Mountains, Salt Lake Co., *M. E. Jones 1184* (DS,F,GB,NY); central Utah, 1875, *C. C. Parry 22* (GH,MO,NY). NEVADA. Allegheny Creek, Elko Co., *Nelson & Macbride 2174* (GH,MO,S,US,WYO); Big Spring, Cave Creek, Elko Co., *H. L. Mason 4735* (MO,NY,UC); Jarbidge, Elko Co., *Nelson & Macbride 2013* (GH,US,WYO); Humboldt Mountains, *J. Torrey 172* (GH,NY,US); Hunter Creek, Washoe Co., *P. B. Kennedy 1861* (DS,GH,MO,NY,UC,US,WYO); King's Cañon, Ormsby Co., *C. F. Baker 1200* (GH,MO,NY,UC,US).

BRITISH COLUMBIA. 13 miles W of Kaslo, *T. T. McCabe 6572* (UC); mountains near Ainsworth, Kootanie Lake, 1890, *J. Macoun* (F,NY); boundary between Kettle and Columbia rivers, *J. M. Macoun 64,628* (F,GH,NY,US). WASHINGTON. Mt. Carleton, Spokane Co., *F. O. Kreager 282* (CLOKEY,GH,NY,US); Peshastin, Okanogan Co., *Sandberg & Leiberg 502* (GH,NY,UC,US); Tumwater Canyon, Leavenworth, Chelan Co., *J. W. Thompson 8451* (DS,MO,NY,UC); Stuart Ridge, Chelan Co., *J. W. Thompson 11,713* (CLOKEY, DS,GH,MO,NY,US); Mt. Stuart, Chelan Co., *J. W. Thompson 7787* (DS,GH,MO,S,UC); Teanaway Creek, Kittitas Co., *J. W. Thompson 9483* (DS,GH,MO,NY); Bald Mt., Kittitas Co., *J. W. Thompson 14,799* (CLOKEY,DS,GH,MO,NY); Goat Mountains, Lewis Co., *O. D. Allen 256* (DS,GH,MO,NY,UC,US); Mt. Aix, Yakima Co., *J. W. Thompson 15,056* (GH,MO,NY); Mt. Adams, Yakima Co., 1882, *L. F. Henderson 377* (F,GH,MO), *W. N. Suksdorf 760* (MO,NY,UC,US); Blue Mountains, Walla Walla Co., *C. V. Piper 2334* (GH, NY,US); Godman Springs, Columbia Co., *Constance et al. 1189* (MO,UC); Mt. Angeles, Clallam Co., *J. W. Thompson 7470* (DS,GH,MO,UC). OREGON. Wallowa River, Wallowa Co., *Constance & Jacobs 1307* (UC); Powder River (Eagle Creek) Mountains, *W. C. Cusick 1819* (DS,UC,US); Blue Mountains, *T. Nuttall* (GH,NY: type collection of *Glycosma occidentalis* Nutt.); stream banks, eastern Oregon, *W. C. Cusick 1817* (DS,MO,UC,US); Rhea Creek, Morrow Co., *J. B. Leiberg 99* (GH,S,UC,US); Klamath River, Keno, Klamath Co.,

M. E. Peck 9426 (DS,GH,MO,NY); Crane Mt., Lake Co., *J. W. Thompson 13,236* (MO, NY); foot of Cascade Mountains [Silver Creek, Marion Co.], *E. Hall 217* (GH: type of *Glycosma ambiguum* A. Gray, F,MO,NY); Oakland, Douglas Co., 1881, *T. J. Howell* (NY, S,US); Siskiyou Mountains near Waldo, Josephine Co., 1887, *T. J. Howell* (DS,F,MO, NY,UC); Grants Pass, Josephine Co., 1884, *T. J. Howell* (GH,NY,US). CALIFORNIA. Shackleford Creek, Siskiyou Co., *G. D. Butler 1668* (ARIZ,DS,MO,UC,US,WYO); Buck Mt., Humboldt Co., *J. P. Tracy 8810* (DS,GH,MO,NY,UC); Cahto, Mendocino Co., *Kellogg & Harford 312* (GH,MO,NY,US); Lamberts Lake, Mendocino Co., *H. N. Bolander 6525* (GH: type of *Glycosma Bolanderi* A. Gray, MO); Deer Park, Lake Tahoe region, *A. Eastwood 430* (GH,NY,US); S of Donner Pass, Nevada Co., *A. A. Heller 7183* (DS,GH,MO, NY,UC,US,WYO); Soda Springs, Nevada Co., *M. E. Jones 2511* (DS,GB,US,WYO); Big Trees road, Calaveras Co., *W. H. Brewer 1954* (GH,UC); Mono Pass, Mono Co., *H. N. Bolander 6342* (GH,UC).

2. *Osmorhiza glabrata* Phil. Linnaea 28: 653. 1856. (Pl. 27, fig. 1)

Myrrhis odorata sensu Hooker, Clos, etc. as to Chilean plants. Not *M. odorata* Scop. 1772.
Uraspermum glabratum Kuntze, Rev. Gen. 1: 270. 1891.
Myrrhis Renjifoana Phil. Anal. Univ. Chile, Santiago, 85: 725. 1894. Based upon *Philippi*, "in Valle Nevularum prope Therma de Chillan," Chile.
Elleimataenia Renjifoana K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 164. 1916.

Plants rather stout, 1–4 dm. high, villous or hirsutulous throughout to glabrate except on the sheaths; leaf blades deltoid, 0.5–1 dm. long and broad, ternate-bipinnate, the leaflets ovate, 0.7–2 cm. long, 0.5–1.5 cm. broad, acute or acuminate, laciniately lobed or pinnatifid with linear ultimate divisions, the rachis hirsutulous to glabrate, the sheaths strongly ciliate; petioles 4–13 cm. long; peduncles 4–14 cm. long; involucre wanting; involucel of one or two minute bractlets, or wanting; rays 1–7, rather stiffly ascending, 1–6 cm. long; pedicels ascending, 2–5 mm. long; flowers white, the styles and stylopodium about 1 mm. long, the latter conic; carpophore cleft about one-third of its length; fruit linear-fusiform, 10–16 mm. long, acute at both apex and base, but without appendages, or these rudimentary, glabrous or rarely sparsely bristly at very base.

Type locality.—"In subandinis provinciae Concepcion ad St. Barbara," Chile, *Gay 1514.*
Distribution.—Central Chile, from Santiago to Ñuble, at 3,000 to 8,000 feet altitude.

This species is remarkable for its close similarity to *O. occidentalis* (pl. 26, figs. 2 and 3), an affinity long concealed by the South American plant having been generally regarded as a *Myrrhis*. Even as late as 1926, Thellung remarks of *Myrrhis*, "Die Gattung umfast wahrscheinlich nur eine einzige Art, da die zweite, aus Chile beschriebene Spezies (*M. Renjifoana* Phil.) vermütlich dort nicht einheimisch, sondern nur eine durch das stark abweichende Klima hervorgerufene Aberration der Hauptart ist." It agrees, however, in all the characteristics but flower color in which *O. occidentalis* differs from *Myrrhis odorata*. The occurrence of "a *Glycosma*" in South America has not previously been recognized, and it has no known close relatives in that continent.

The single specimen which caused the most trouble in our study was *Pennell 12,487*, from Baños de Chillan, Chile. This plant has the ascending rays and long styles of *O. glabrata*, but combines these characteristics with appendaged, bristly fruits and subentire leaflets. We can only suggest that the plant in question may be the result of interbreeding between *O. glabrata* and either *O. chilensis* or *O. obtusa*, all three of which occur in this area. If this interpretation should prove to be correct, some light might thereby be thrown on the breadth of the genetic gulf between the Glycosmae and the Nudae.

Representative specimens.—CHILE. "Chile austral. andin.," 1829, *E. Poeppig* (MO). Santiago: Maipo, *Bro. Claude-Joseph 2964* (US); Valdes-Tal (Volcantal), Cordillera de Santiago, 1936, *C. Grandjot* (US). Colchagua: Cordillera de Colchagua, *A. Pirion 159* (GH). Ñuble: Termas (Baños) de Chillan, *R. Philippi* (F, GH, UC: photos), *F. Jaffuel 3715* (GH), *3717* (GH), *E. Werdermann 1571* (NY,S), *C. Deltor 2035* (GH).

3. *Osmorhiza bipatriata* Constance & Shan, sp. nov. (Pl. 27, fig. 2)

Plants slender, 2–6 dm. high, sparsely hirsutulous throughout; leaf blades ovate, 4–12 cm. long and broad, ternate-pinnate, the leaflets ovate or ovate-oblong, 0.8–4 cm. long, 0.5–3 cm. broad, lacinately lobed to pinnatifid, pilose especially on the veins beneath; petioles 4–12 cm. long; peduncles 3–18 cm. long; involucre wanting; involucel of several linear, ciliate bractlets, 1–3 mm. long; rays 2–5, spreading-ascending, 15–35 (10–80) mm. long; pedicels spreading, 3–6 (2–12) mm. long; flowers white, tinged with green or rose; styles and stylopodium 0.2–0.4 mm. long, the latter low-conic; carpophore cleft about one-fourth of its length; fruit linear-fusiform, 10–12 mm. long, tapering into a short beak at the apex, acute or with rudimentary appendages at base, glabrous, or with a few bristles at the very base.

Plantae sparsim hirsutulae; folia ovata, ternato-pinnata, foliola laciniato-lobata usque ad pinnatifida; involucellus pluribus bractulis linearibus ciliatisque; radii expandentes-ascendentes; pedicelli expandentes; flores albi; styli et stylopodium 0.2–0.4 mm. longi; fructus linearis-fusiformis, 10–12 mm. longus, apice rostrum brevis attenuatus, acutus vel ad basim appendiculis inchoatis, glaber vel sparsissime setosus ad basim ultimam.

Type locality.—West branch of Madera Canyon, Mount Livermore, Davis Mountains, Jeff Davis Co., Texas," about 7,000 feet altitude, July 26, 1937, *L. C. Hinckley* (NY: type, ARIZ, GH).

Distribution.—Known only from Mount Livermore in southwestern Texas and Cerro Potosi in the Sierra Madre Oriental of Nuevo León, Mexico, 7,000–10,000 feet altitude.

This species was not included in the "North American Flora," because only the Mexican specimens had come to the attention of Mathias and Constance at the time that account was published, and these had been regarded as somewhat aberrant representative of *O. mexicana*. Mr. L. C. Hinckley of Marfa, Texas, sent a flowering specimen for identification in 1945; this led to a careful search for more and better material.

On the basis of its fruit, the Texas material would have to be referred to the Glycosmae, but the involucel and the very short style and stylopodium are those of the Mexicanae. Two of the Cerro Potosi specimens, *Schneider 1108* and *Mueller 2231*, possess rudimentary appendages and some bristles on the bases of the fruits, marking a transition to *O. mexicana* and *O. brachypoda*. This species stands squarely on the boundary between *Glycosma* and *Osmorhiza*, and would necessitate submergence of the former if that disposition had not already been generally accepted upon other grounds.

The specific epithet is an intentional *double entendre*, referring to the distribution of the entity, which is not likely to be found outside of the United States and Mexico, and also to the different nationalities of the authors, who have combined their common interest but very different associations with the Umbelliferae in the present study.

Representative specimens.—TEXAS. Madera Canyon, Mt. Livermore, Jeff Davis Co., *L. C. Hinckley 408* (F, TEX), 1937 (ARIZ, GH, NY), *3489* (UC). NUEVO LEÓN. Hacienda La Jolla, Cerro Potosi, Municipio de Galeana, *R. A. Schneider 1108* (F); Cerro Potosi, Municipio de Galeana, *R. A. Schneider 1043* (F); cañon below Las Canoas, Cerro Potosi, Municipio de Galeana, *C. H. Mueller 2231* (GH).

4. *Osmorhiza mexicana* Griseb. Abh. Ges. Wiss. Gött. 24: 147. 1879

Osmorrhiza brevistylis sensu Weddell, Hemsley, etc. Not *O. brevistylis* DC. 1830.

Uraspermum aristatum var. *brevistyle* Kuntze, Rev. Gen. 1: 270, as to Costa Rican plants. 1891.

Washingtonia mexicana Rose, Contr. U. S. Nat. Herb. 8: 337. 1905.

Plants slender, 4–8 dm. high, hirsutulous throughout; leaf blades ovate-deltoid, 5–15 cm. long, ternate-pinnate, the leaflets ovate, 1.5–4 cm. long, 15–25 mm. broad, coarsely serrate,

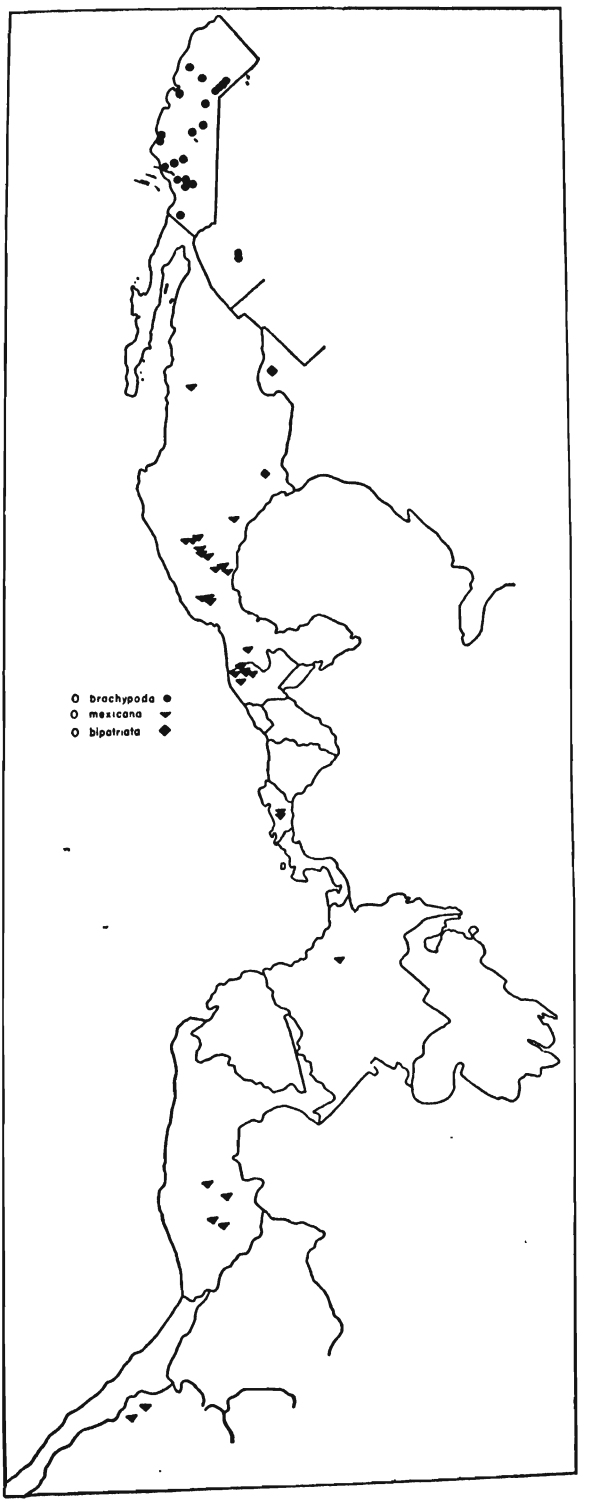


Fig. 2. Distribution of *Osmorhiza brachypoda* (North America), *O. mexicana* (North and South America), and *O. bipartriata* (North America).

incised and pinnately lobed toward the base, pilose especially beneath; petioles 8–20 cm. long; peduncles 7–14 cm. long; involucre wanting; involucel of several linear, ciliate bractlets, 2–6 mm. long; rays 3–4, spreading-ascending, 25–75 mm. long; pedicels spreading-ascending, 4–6 mm. long; flowers white or greenish white, the styles and stylopodium 0.5–11 mm. long, the latter low-conic, the disc often conspicuous; carpophore cleft about one-fourth of its length; fruit linear-oblong, 13–18 mm. long, tapering into a short beak at the apex, caudate at the base, the appendages 3–5 mm. long, bristly on the ribs and densely so on the appendages.

Type locality.—Mexico, *Schaffner.*

Distribution.—Chihuahua, south to Guatemala and Costa Rica; Colombia, Bolivia, Peru, and northwestern Argentina, 4,000–12,000 feet altitude.

This entity is so well marked that it narrowly escaped being described twice under the same name, the second time by Coulter and Rose (1895). The only problem involving this species has been the extent of its geographic distribution. Rose gave an herbarium name to a specimen from Colombia, *Pennell 3101,* but never published it. Grisebach, however, had recognized that plants from Bolivia (*Mandon 594*) and Argentina were conspecific with Mexican material; we have been able to confirm the correctness of his interpretation.

Representative specimens.—MEXICO. Chihuahua: Mt. Mohinora, *E. W. Nelson 4864* (GH,US). San Luis Potosi: Alvarez, Sierra Madre Oriental, *F. W. Pennell 17,883* (UC, US), 1902, *E. Palmer 127* (US). Mexico: Forêt de la Desérta Vieja, Vallée de Mexico, *M. Bourgeau 781* (GH,K,S,US); Vallée de Mexico, *J. G. W. Schaffner 164* (K); Sierra de las Cruces, *C. G. Pringle 5208* (MO,US); Crucero–Agua Blanca, Temascaltepec, *G. B. Hinton 8324* (ARIZ,F,GH,MO,NY,UC); Méson Viejo, Temascaltepec, *G. B. Hinton 1308* (F,GH,US); Vaqueria del Jacal, *F. M. Liebmann 12,240* (F,US). D. F.: Sierra de Ajusco, *C. G. Pringle 6615* (DS,GH,MO,NY,S,UC,US,WYO). Puebla: Mt. Orizaba, *F. M. Liebmann 12,241* (F,GH,UC,US), *F. Müller 1722* (GH,NY), *H. E. Seaton 195* (F,GH,US); Popocatepetl, *Rose & Hay 6249* (NY,US); Esperanza, *C. A. Purpus 7456* (MO,NY,UC,US). Oaxaca: Sierra de San Felipe, *C. G. Pringle 5547* (US); Sierra de Clavellinas, *C. L. Smith 896* (MO); Cordillera of Oaxaca, *H. Galeotti 2751* (K). Chiapas: near San Cristobal, *E. W. Nelson 3188* (US). GUATEMALA. Quezaltenango: Volcan Santo Tomas, *J. A. Steyermark 34,714* (F,UC). Huehuetenango: "Chancol," Sierra Cuchumatanes, *A. F. Skutch 1210* (F,GH); mountains near Hacienda of Chaucol, *E. W. Nelson 3545* (GH,NY,US). Solola: Volcan Toliman, *J. A. Steyermark 47,581* (F). COSTA RICA. Irazu, 1874, *Costurno* (GH), *H. Pittier 200* (US), *4273* (US); Cerro de las Vueltas, Prov. de San Jose, *Standley & Valerio 43,592* (US), *43,669* (US).

COLOMBIA. Forest below Paramo de Ruiz, Dept. Tolima, *F. W. Pennell 3101* (NY,US); Paramo de Ruiz, Cauca, *F. C. Lehmann 3074* (K,US); Paramo de Heruco, *J. Goudot* (K). BOLIVIA. Nord-Yungas, Cochabamba, *O. Buchtien 659* (GH,NY,US); viciniis Sorata, La Paz, *G. Mandon 594* (GH,K,NY,S); Pongo, Cordillera Real, *G. H. H. Tate 194* (NY). PERU. Cuzco: Cachu-pampa–Chile-chile, *C. Vargas 1352* (F) *9697* (UC); Ollantaitambo, *Cook & Gilbert 747* (US). ARGENTINA. Catamarca: Comne Euquina Grande, Dept. Andalagala, *P. Jörgensen 1812* (GH,MO,US); Alemania, Dept. Guachipas, *S. Venturi 9810* (GH,MO).

5. ***Osmorhiza brachypoda*** Torr.; Durand, Jour. Acad. Phila. II. 3: 89. 1855

Myrrhis brachypoda Greene, Fl. Franc. 332. 1892.

Washingtonia brachypoda A. Heller, Cat. N. Am. Pl. 5. 1898.

Scandix brachypoda K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 143. 1916.

Osmorhiza brachypoda var. ***fraterna*** Jepson, Fl. Calif. 2: 670. 1936. Based upon *Peirson 415a,* "Arroyo Seco, San Gabriel Mts. 2000 feet," Los Angeles Co., Calif.

Plants rather stout, 3–8 dm. high, hirsutulous to villous throughout; leaf blades ovate or deltoid, 8–25 cm. long, 10–18 cm. broad, ternate-pinnate, the leaflets ovate, 2–6 cm. long, 1–4 cm. broad, acute or obtuse, coarsely serrate, incised and pinnately lobed toward the base, hirsutulous especially beneath; petioles 5–20 cm. long; peduncles 9–20 cm. long; involucre wanting, or occasionally of a foliaceous bract; involucel of several linear or lanceolate, acute, ciliate bractlets, 2–10 mm. long, spreading or reflexed, exceeding the pedicels; rays 2–5, spreading-ascending, 2.5–10 cm. long; pedicels ascending, 1–3 mm. long; flowers greenish yellow, the styles and stylopodium 0.5–1 mm. long, the latter low-conic, the disc often conspicuous; carpophore cleft about one-third of its length; fruit oblong-fusiform, 12–20 mm. long, 3–4 mm. broad, tapering into a narrow beak at the apex, caudate at the base, the appendages 1–5 mm. long (sometimes obsolete), the ribs very bristly and prominent.

Type locality.—"Near the banks of Deer Creek," Nevada City, Nevada County, California, *Henry Pratten.*

Distribution.—Central to southern California, and Arizona.

Although the type of the species was supposedly obtained in Nevada County, California, and Bigelow purportedly made his collection even farther north, in Sierra County, we have seer no recent collection from north of Tuolumne County in the Sierra Nevada nor Mount Diablo in the Coast Ranges. Local collectors should see if they can extend this distribution and verify the location of the type locality. The reappearance of predominantly southern Californian species in the mountains of Arizona is now a well-documented phenomenon.

The transverse section of the fruit (pl. 26, fig. 6), notable for its very prominent ribs, is somewhat reminiscent of that of the Glycosmae, and the brevity of the appendages suggests the same relationship. Thus, *O. brachypoda* and *O. hipatriata* appear to connect closely the Glycosmae to the Mexicanae, and thence to the Aristatae and the Nudae. One might regard the Mexicanae as the oldest group of the genus, which could have given rise to *O. occidentalis* and *O. glabrata* by abortion of fruit appendages and involucel. Since the Mexicanae nearly bridge the gap between the present area of *O. occidentalis* and *O. glabrata,* this hypothesis could explain the origin of this pair of species. This assumption would necessitate regarding the fruit appendages as a primitive characteristic of the genus, which seems unlikely in view of their complete absence from related genera, and it would not explain the similarity in styles and stylopodia and in fruit between the two species of the Glycosmae. Finally, the discontinuities in the ranges of *O. chilensis* and *O. obtusa* would remain unsolved.

Representatve specimens.—ARIZONA. Mazatzal Mountains, Gila Co., *Mrs. R. E. Collom 866* (UC), *G. J. Harrison 7830* (US).

CALIFORNIA. Downieville, Yuba River, *J. M. Bigelow* (GH,NY); Rattlesnake Ridge, Placer Co., 1909, *W. R. Dudley* (DS); Eldorado Co., 1866, *V. Rattan* (DS); Hetch-Hetchy trail, Yosemite, *Hall & Babcock 3379* (ARIZ,DS,NY,UC,US,WYO); Yosemite Valley, *L. R. Abrams 4529* (DS,GH,NY,UC); Tuolumne River below Hetch-Hetchy, *R. Bacigalupi 1420* (DS,GH,NY); Pine Ridge, Fresno Co., *Hall & Chandler 229* (MO,NY,US); Sherlock's, Mariposa Co., 1883, *J. W. Congdon* (DS,US); Keene Station, Tehachapi Mountains, Kern Co., 1931, *Hastings & Darland* (CLOKEY,MO,NY,S,UC); vicinity of Bisses Station, Kern Co., *W. R. Dudley 473* (DS,NY,UC,US); Kern Canyon, Kern Co., *L. Benson 3342* (DS,NY, WYO); Mt. Diablo, Contra Costa Co., *M. L. Bowerman 3650* (UC); Alum Rock Park, Santa Clara Co., *A. A. Heller 8481* (F,GH,MO,NY,US); Tassajara Hot Springs, Monterey

Co., *A. D. E. Elmer 3378* (DS,MO,US); Santa Lucia Mountains, Monterey Co., *E. S. Ferris 3288* (DS,GH,UC); Santa Barbara, Santa Barbara Co., *A. D. E. Elmer 3879* (DS,F,GH, MO,NY,US); Sulphur Mountain Springs, Ventura Co., *Abrams & McGregor 24* (DS,GH, NY,US); southern California, *Parry & Lemmon 146* (F,GH,NY); Tuna Canyon, Verdugo Hills, Los Angeles Co., *F. A. MacFadden 2608* (NY,UC,WYO); Old Wilson trail, Sierra Madre, Los Angeles Co., *G. B. Grant 1371* (ARIZ,F,UC,WYO); Silverado Canyon, Santa Ana Mountains, *Munz & Harwood 3722* (DS,NY,WYO,US); vicinity of San Bernardino, San Bernardino Co., *Parish & Parish 985* (F,GH,MO), *S. B. Parish 4165* (GH,MO,NY, UC,US); hills near Claremont, Los Angeles Co., *C. F. Baker 4730* (MO,NY,S,UC,US); Cuyamaca, San Diego Co., *L. R. Abrams 3838* (DS,F,GH,MO,NY,UC,US); near Julian, San Diego Co., 1889, *C. R. Orcutt* (F,MO,US).

6. *Osmorhiza longistylis* (Torr.) DC. Prodr. 4: 232. 1830

Uraspermum Claytoni Nutt. Gen. 1: 193. 1818. Not *Myrrhis Claytoni* Michx. 1803.
Myrrhis longistylis Torr. Fl. U. S. 310. 1824.
Osmorhiza cordata Raf. Med. Fl. 2: 249. 1830.
Osmorhiza vilosa Raf. Med. Fl. 2: 249. 1830.
Myrrhis Claytoni D. Dietr. Syn. Pl. 2: 984. 1840. Not *Myrrhis Claytoni* Michx. 1803.
Uraspermum aristatum Kuntze, Rev. Gen. 1: 270, in part. 1891. Not *Chaerophyllum aristatum* Thunb. 1784.
Uraspermum aristatum var. *longistyle* Kuntze, Rev. Gen. 1: 270. 1891.
Myrrhis aristata MacM. Metasp. Minn. Valley 398. 1892. Not *Chaerophyllum aristatum* Thunb. 1784.
Washingtonia longistylis Britton in Britt. & Brown, Ill. Fl. 2: 530. 1897.
Washingtonia longistylis var. *villicaulis* Coult. & Rose, Contr. U. S. Nat. Herb. 12: 443. 1909. Based upon *Heller*, "On limestone on the Conestoga near Binkley's Bridge," Lancaster County, Pennsylvania.
Scandix longistylis K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 143. 1916.
Uraspermum aristatum var. *villicaulis* Farwell, Papers Mich. Acad. 1: 96. 1923.
Osmorhiza longistylis var. *brachycoma* Blake, Rhodora 25: 110. 1923. Based upon *Blake 6902*, "slope in woods, Cabin John, Montgomery County, Maryland."
Washingtonia longistylis var. *brachycoma* House, Bull. N. Y. State Mus. 254: 529. 1924.
Osmorrhiza villicaulis Rydb. Brittonia 1: 93. 1931.

Plants rather stout, 6–10 dm. high, villous or hirsutulous throughout, the stems densely long-villous to glabrate; leaf blades orbicular, 8–25 cm. long, biternate or ternate-pinnate, the leaflets ovate or oblong-lanceolate, 3–10 cm. long, 1–5 cm. broad, acute, coarsely serrate, incised or pinnately lobed toward the base, sparingly hirsutulous, especially on the veins and margins; petioles 5–16 cm. long; peduncles 5–13 cm. long; involucre of 1 – several, linear or lanceolate, foliaceous, ciliate bracts, 5–15 mm. long; involucel of several bractlets like the bracts, 5–10 mm. long, sharply reflexed; rays 3–6, spreading-ascending, 1.5–5 cm. long; pedicels spreading-ascending, 5–8 mm. long; flowers white, the styles and stylopodium 2–4 mm. long, the later high-conic; carpophore divided about one-third of its length; fruit oblong-fusiform, 15–20 mm. long, acute at the apex, caudate at the base, the appendages 4–6 mm. long, sparingly bristly on the ribs.

Type locality.—"In wet meadows near Albany," New York, *Tracy.*

Distribution.—Quebec to Alabama, west to Alberta, Montana, Colorado, New Mexico, and Texas.

This and the two following species are evidently closely related, and were combined by Clarke, but they appear to represent natural and distinct populations. If there were no genetic barriers between *O. longistylis* and *O. Claytoni*, it is difficult to see how the two entities could have retained any distinctness. They appear to grow together over most of their ranges, and

are so often collected at the same time and place that their respective symbols frequently appear in pairs on our map (fig. 3). Nevertheless, with the exception of very immature specimens, there are none among the several hundred examined which could not be referred to one species or the other with reasonable confidence.

The two pubescence variants described are not accorded taxonomic status here because we regard them as one-character segregates of sporadic occurrence. The pubescent forms do appear, however, to be more numerous in the southern and western parts of the species' range. It is tempting to imagine that this pubescence may somehow have been derived from *O. Claytoni,* but we have no corroborative evidence.

Representative specimens.—QUEBEC. Baie Girard (Lac Temiscamingue), Temiscaming-Abitibi, *M.-Victorin 8546* (GH,NY); Restigouche River, Matapedia, Bonaventure Co., 1904, *Collins & Fernald* (GH); Caughnawaga, vicinity of Montreal, *M.-Victorin 24,818* (GH). NOVA SCOTIA. Clay, Green Bay, Cumberland Co., *A. E. Roland 41,583* (GH). NEW BRUNSWICK. Joe's Point–St. Andrews, *M. O. Malte 843/29* (GH,US); Woodstock, St. John River valley, Carleton Co., *Fernald & Long 14,235* (GH). MAINE. Fort Fairfield, Aroostook Co., *M. L. Fernald 2020* (GH); Vassalboro, Kennebec Co., 1902, *E. B. Chamberlain* (GH). NEW HAMPSHIRE. Lebanon, Grafton Co., 1890, *G. G. Kennedy* (GH); Walpole, Cheshire Co., *M. L. Fernald 417* (GH). VERMONT. Hancock, Addison Co., 1914, *D. L. Dutton* (GH,MO); Connecticut River, Westminster, Windham Co., *B. L. Robinson 7* (GH). MASSACHUSETTS. Boston, Suffolk Co., *Biltmore Herb. 674c* (GH,NY,US); New Bedford, Bristol Co., 1890, *E. W. Hervey* (MO); New Marlboro, Berkshire Co., 1919, *J. R. Churchill* (GH,MO). RHODE ISLAND. Cumberland near Lonsdale, Providence Co., *E. S. Reynolds 069* (GH,NY); Warwick, Kent Co., 1870–77, *J. W. Congdon* (DS,MO,NY). CONNECTICUT. Berlin, Hartford Co., 1870, *T. S. Brandegee* (UC); vicinity of Green's Farms, Fairfield Co., *C. L. Pollard 37* (US).

NEW YORK. Hermon, St. Lawrence Co., *O. P. Phelps 1615* (GH,US); Mohawk River E of Crescent, Saratoga Co., 1906, *S. H. Burnham* (GH); North Harpersfield, Delaware Co., *D. L. Topping 166* (US); Cold Spring Harbor, Suffolk Co., *H. J. Banker 2850* (NY); Buffalo, Erie Co., 1827, *Kinnicutt* (NY). PENNSYLVANIA. Osterhout P. O., Wyoming Co., *G. E. Osterhout 7134* (WYO); Conestoga near Binkley's Bridge, Lancaster Co., 1901, *A. A. Heller* (GH: type of var. *villicaulis* Fernald, F,US); Benezett, Elk Co., *H. A. Wahl 612* (GH); Bellevue-Westview, Allegheny Co., *L. K. Henry 596* (CLOKEY,F,US). NEW JERSEY. Vincentown, Burlington Co., *B. Long 9790* (GH); Riddleton, Salem Co., *B. Long 16,774* (GH). DELAWARE. Mt. Cuba, 1875, *A. Commons* (MO,NY); Mill Creek one mile W of Stanton, Newcastle Co., *Randolph & Randolph 94* (GH). MARYLAND. Mt. Washington, Baltimore, 1910, *J. R. Churchill* (GH,MO); vicinity of Cabin John, Montgomery Co., *S. F. Blake 6902* (US: type of var. *brachycoma* Blake, GH), *9377* (GH, WYO). WEST VIRGINIA. Snowy Mt., Pendleton Co., *P. A. Rydberg 9122* (NY); Upshur Co., 1897, *W. M. Pollock* (MO,US); Wheeling, Ohio Co., 1878–79, *H. N. Mertz* (NY, US); McCreery, Raleigh Co., *J. P. Tosh 823* (US). VIRGINIA. Dead Run, Fairfax Co., *M. E. Mathias 1392* (DS,GH,MO,NY,UC,US); Tobacco Row Mt., Amherst Co., 1903, *M. A. Coe* (GH); James River, Claremont Wharf, Surry Co., *Fernald & Long 8386* (GH,MO,NY,US); Middle Holston Valley near Marion, Smyth Co., 1892, *J. K. Small* (F,GH). KENTUCKY. Elk Lick Falls, *F. T. McFarland 118* (MO,S,US); "Big Woods," Grecnup Co., *Smith, Hodgdon, Gilbert & McCoy 3581* (GH, NY,US); Lexington, Fayette Co., 1837–53, *C. W. Short* (GH,UC); McCotrey School, Union Co., *H. T. Shacklette 376* (GH,NY). NORTH CAROLINA. 5 miles W of Blowing Rock, Watauga Co., 1891, *Small & Heller* (F); French Broad River near Biltmore, Buncombe Co., *Biltmore Herb. 674b* (F,MO,NY,US,WYO). TENNESSEE. Near Knoxville, Knox Co., *A. Ruth 426* (NY), *429* (US); Nashville, Davidson Co., 1886, *A. Gattinger* (F,US); Memphis, Shelby Co., *E. J. Palmer 17,458* (MO). GEORGIA. Shell Bluff, Burke Co., *Pyron & McVaugh 2494* (GA). ALABAMA. Jasper, Walker Co., 1941, *Harper, Brown & Morgan* (CLOKEY,GH);

Warrior River above Hurricane Creek, Tuscaloosa Co., *E. M. Harper 144* (F,GH,MO, NY,US).

ONTARIO. S of Little Current, Manitoulin Island, *Fernald & Pease 3448* (GH,US); near St. Thomas, *J. Macoun 81,729* (F); Kingston, 1901–02, *J. Fowler* (GH,US). MICHIGAN. Calumet, Houghton Co., 1882, *S. Minns* (GH); Hubbardstown, Ionia Co., 1877, *E. F. Smith* (GH); Belle Isle, Detroit, Wayne Co., *O. A. Farwell 1365* (GH). OHIO. Hiram, Portage Co., *R. J. Webb 110* (GH); Cedar Point, Sandusky Co., 1917, *L. H. Pammel* (GH); Friendship, Scioto Co., *D. Demaree 10,647* (DS,GH,MO,UC); Cincinnati, Hamilton Co., *C. G. Lloyd* (GH,MO). INDIANA. 56th Street, Marion Co., *R. C. Friesner 16,672* (GH,NY); Cogg Lake, Lagrange Co., *C. C. Deam 20,129a* (NY); Bedford, Lawrence Co., *R. M. Kriebel 1879* (GH). ILLINOIS. Riverdale, Cook Co., *J. M. Greenman 2627* (GH,MO); Peoria, Peoria Co., 1900–03, *F. E. McDonald* (GH,NY,WYO); Bluff Lake, St. Clair Co., 1878, *H. Eggert* (MO,NY,UC, US,WYO); Mounds, Pulaski Co., *E. J. Palmer 14,880* (MO). WISCONSIN. Green Bay, Brown Co., 1878, *J. H. Schuette* (F); Fond du Lac, Fond du Lac Co., 1902, *J. H. Schuette* (F,NY); Madison, Dane Co., 1877, *J. M. Johnson* (MO).

MANITOBA. Fort Ellice, *Macoun & Herriot 77,116* (NY); Winnipeg Valley, 1859, *E. Bourgeau* (GH). SASKATCHEWAN. Cypress Hills, *J. Macoun 72* (GH); Moose Jaw Creek, *J. Macoun 858* (NY). MINNESOTA. Grand Portage, Cook Co., *Pease & Bean 26,329* (GH); Center City, Chisago Co., 1892, *B. C. Taylor* (NY,UC,US,WYO); Bear Point, Clearwater Co., *J. B. Moyle 207* (GH,NY,UC,US); Glenwood, Pope Co., 1891, *B. C. Taylor* (UC). NORTH DAKOTA. Walhalla, Pembina Co., *L. E. Waldron 1617* (WYO); peninsula of Lake Ibsen, Benson Co., 1908–09, *J. Lunell* (NY,US,WYO), 1899 (F,GH); Abercrombie, Richland Co., *H. F. Bergman 1769* (MO,UC,WYO). SOUTH DAKOTA. Sioux River, Brookings, Brookings Co., 1894, *J. J. Thornber* (ARIZ,MO,UC); West Short Pines, Harding Co., *S. S. Visher 459* (F); Whitewood, Lawrence Co., *H. E. Hayward 1257* (F,WYO); Elk Cañon Hot Springs, Black Hills, *P. A. Rydberg 725* (GH,NY,US). IOWA. Estherville, Emmet Co., *A. Hayden 9426* (MO); Grinnell, Poweshick Co., 1876–77, *M. E. Jones* (DS,NY,UC,WYO); Decatur Co., 1896–97, *Fitzpatrick & Fitzpatrick* (F,GH,NY), 1903, *J. P. Anderson* (MO,WYO). NEBRASKA. Weeping Water, Custer Co., 1887, *H. J. Webber* (MO); Barada, Richardson Co., *H. C. Reynolds 3035* (MO,UC); Red Cloud, Webster Co., *J. M. Bates 3218* (GH). MISSOURI. Glenwood, Schuyler Co., *B. F. Bush 10,473* (MO,US); Courtney, Jackson Co., *B. F. Bush 4954* (GH,MO,NY,US); Cedar Gap, Wright Co., *J. A. Steyermark 23,671* (F,UC); Bradleyville, Taney Co., *J. A. Steyermark 22,949* (F,MO). KANSAS. Riley Co., *J. B. Norton 700* (GH,MO,NY,US,WYO); Arkansas City, Cowley Co., *Rydberg & Imler 486* (NY). ARKANSAS. Sulphur Springs, Benton Co., *D. Demaree 4974* (GH,MO); Magazine Mt., Logan Co., *D. Demaree 22,889* (GH,MO,NY); Dripping Springs, Hot Springs Co., *F. J. Scully 938* (UC,US). OKLAHOMA. Sapulpa, Creek Co., *B. F. Bush 1059* (MO,NY); Hinton, Caddo Co., *G. W. Stevens 932* (DS,GH,US), *D. Demaree 12,325* (MO,NY,UC) TEXAS. Near Trinity, Tarrant Co., *A. Ruth 601* (NY,US).

ALBERTA. Medicine Hat, *J. M. Macoun 858* (GH). MONTANA. Lower Falls of the Missouri, *R. S. Williams 275* (US); Bozeman, Gallatin Co., *J. W. Blankinship 704* (F,US). WYOMING. Sundance, Crook Co., *A. Nelson 2130* (MO,WYO); Sheridan Co., *F. Tweedy 2436* (NY); Horse Creek, Laramie Co., 1889, *J. E. Bodin 6* (F). COLORADO. Horsetooth Gulch, Larimer Co., *C. S. Crandall 1446* (NY,US,WYO); Buckhorn Creek, Larimer Co., *G. E. Osterhout 1034* (US,WYO); Spring Cañon, Larimer Co., *G. E. Osterhout 344* (F,WYO). NEW MEXICO. Johnson's Mesa, Colfax Co., 1910, *E. O. Wooton* (US).

7. *Osmorhiza aristata* (Thunb.) Makino & Yabe, Bot. Mag. Tokyo 17: 14. 1903

Chaerophyllum aristatum Thunb. Fl. Japon. 119. 1784.

Myrrhis aristata Spreng. Umbell. 133. 1813.

Osmorhiza japonica Sieb. & Zucc. Abh. Akad. Münch. IV. 2: 203. 1843. Based upon *Chaerophyllum aristatum* Thunb.

Osmorhiza amurensis F. Schmidt ex Maxim. Prim. Fl. Amur. 129. 1859. Based upon *Maximowicz*, "Am untern Amur, in der Nähe der Dondon-Mündung, bei Dshare."

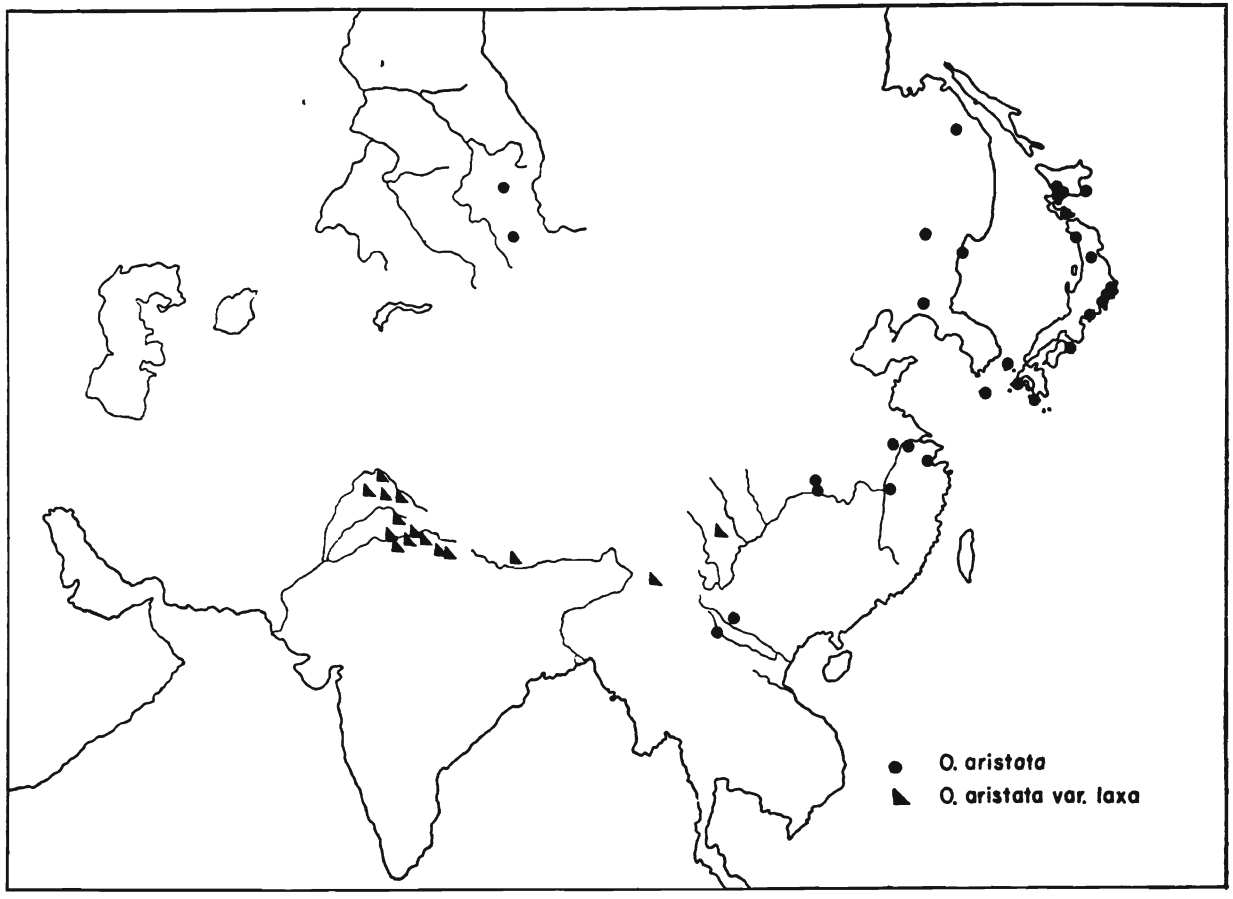


Fig. 3. Distribution of *Osmorhiza aristata* (Asia).

Uraspermum aristatum Kuntze, Rev. Gen. 1: 270. 1891.
Scandix Claytonii K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 143. 1916, in part.
Scandix aristata K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 143. 1916.
Scandix amurensis K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 143. 1916.
Osmorhiza aristata var. ***montana*** Makino, Jour. Jap. Bot. 2: 7. 1918. Based upon ***Makino,*** "Nikkô, Prov. Shimotsuka."
Washingtonia Claytonii sensu K.-Pol. ex Fedtsch. Fl. Asiat. Russ. 15: 51. 1920, in part. Not ***Myrrhis Claytoni*** Michx. 1803.
Washingtonia amurensis K.-Pol. ex. Fedtsch. Fl. Asiat. Russ. 15: 52. 1920, as synon.
Osmorhiza montana Makino, Jour. Jap. Bot. 5: 28. 1928. Based upon ***Osmorhiza aristata*** var. ***montana*** Makino.
Osmorhiza longistylis sensu A. Gray, Forbes & Hemsl., etc., as to Asiatic plants. Not ***Myrrhis longistylis*** Torr. 1824.
Osmorhiza Claytoni Clarke ex Hook., etc., as to Asiatic plants in part. Not ***Myrrhis Claytoni*** Michx. 1803.

Plants rather stout, 3–8 dm. high, the foliage hirsutulous, the older stems glabrate; leaf blades deltoid to orbicular, 7–20 cm. long, ternate-pinnate or biternate, the leaflets oblong-oval to ovate-deltoid, 1.5–9 cm. long, 1–6 cm. broad, obtuse to acuminate, coarsely serrate, incised, and pinnately lobed or pinnatifid toward the base, the leaflets of the first leaves conspicuously more dissected, hirsutulous especially on the veins; petioles 5–26 cm. long; peduncles 3.5–25 cm. long; involucre usually wanting; involucel of 1 – several, linear or lanceolate, foliaceous, ciliate or hirsutulous bractlets, 3–18 mm. long, sharply reflexed; rays 3–6, spreading to spreading-ascending, 3.5–14 cm. long; pedicels spreading, 10–30 mm. long; flowers white, the styles and stylopodium 1.5–2.5 mm. long, the latter conic; carpophore cleft about to the middle; fruit linear-clavate, 10–22 mm. long, about 2 mm. broad, obtuse or abruptly acute at the apex, caudate at the base, the appendages 5–8 mm. long, sparingly bristly on the ribs, densely so on the appendages.

Type locality.—Japan, *Thunberg.*

Distribution.—Southern Siberia, Sakhalin, and Manchuria, throughout Japan, to eastern and southwestern China, 2,000–10,000 feet; in the varietal phase to Tibet and northwestern India.

Our study indicates that all the Asiatic representatives of *Osmorhiza* are conspecific, despite the several names under which they have been known. The only significant variations appear to be in the degree of the cutting of the leaves, which shows something of a geographical trend (cline) from north to south. The plants of Sakhalin and Siberia, which have been designated *O. amurensis,* show the maximum of dissection, those of Japan are intermediate in this respect, and those of the Himalayan area are the least divided. The Chinese material, however, presents such a mixture of foliar characters supposedly typical of the Siberian and Japanese regions, respectively, as to preclude even subspecific separation of these two leaf phases. The Himalayan population is tentatively retained as a variety, because of the constancy of its foliage characters.

The relationship among *O. longistylis, O. aristata,* and *O. Claytoni* is so close that the three were regarded as conspecific by Clarke, and have been badly confused by others. The Asiatic plants are intermediate between *O. longistylis* and *O. Claytoni* in the length of style and stylopodium, but are readily separable from either by a combination of small differences. There can be little doubt, however, that the three have had much of their history in common.

Representative specimens.—SAKHALIN. Insula Sachalin, 1860, *F. Schmidt* (GH,K). JAPAN. "Japan," 1881, *Dickins* (K), *J. Peterson* (S). Hokkaido: Forêt du Saruru, *U. Faurie 10,488* (MO); Sorachi, 1898, *U. Faurie* (K); Hakodate, 1861, *C. J. Maximowicz* (GH,K,S,US), 1861, *Albrecht* (K,MO), 1853–56, *C. Wright* (GH), 1860, *C. P. Hodgson* (K); Ishyama, 1884, *W. P. Brooks* (UC); Mokomonai woods, 1884, *W. P. Brooks* (UC); southern Hokkaido, 1884, *W. P. Brooks* (UC); Poronai, 1884, *W. P. Brooks* (UC); Sapporo, 1889, *Y. Tokubuchi* (MO), 1891, *E. Tokubuchi* (GH,MO,NY), 1903, *S. Arimoto* (GH,MO); Nopporo, *T. Tanaka 255* (NY,US). Honshu: Simoda, 1855, *C. Wright* (GH,NY), 1854, *J. Small* (US), *Williams & Morrow* (GH); Tokyo, 1879, *J. Matsumura* (US), 1906, *T. Terasaki* (K); Akabana, 1926, *H. Migo* (NAC); Nagamachi, Rikuzen, 1926, *E. Iishiba* (S,UC); Yokobori, Ugo, 1905, *K. Yushun* (NY); Yokohama, 1862, *C. J. Maximowicz* (K), 1876, *J. Bisset* (K); Nagasaki, *R. Oldham 299* (K), *606* (K); central mountains of Japan, *Maries* (K); Hondo, *K. Shiota 2167* (GH), *2168* (GH), *8652* (GH). Shikoku: Nanokawa, Tosa, 1888, *K. Watanabe* (GH). Kyushu: Prov. Satsuma, 1923, *G. Masamune* (NY). Tsushima, Strait of Korea, *C. Wilford 765* (GH,K).

SIBERIA. Amur, *C. J. Maximowicz* (K); Possiet District, South Ussuri, 1929, *Saberkin* (NY); Kuznetski Alatau, Lipovski Island between the rivers Kondoma and Kundelem, 1890, *P. Krylof* (S); Altay, Teletskoe Ozero Tulkuy, 1927, *Koshurnikova & Vishniovskya* (GH,NY). KOREA. Quelpaert Island, *Taquet 881* (K), *2901* (S). CHINA. Manchuria: ad. fl. Yalu ad pay Szi-sydagou, *V. Komarov 1158* (K); ad plat. Czan-lin. Prov. Kirin, *V. Komarov 1158* (GH). Kiangsu: Bau Hua Shan, *Chiao & Cheo 3541* (NY); Kuyung, Pao Hwa Shan, *Chen & Teng 162* (NAC), *Y. Tsiang 9762* (NAC); I-hing, Lung-ge, *C. L. Tso 473* (NAC); Lungjushan, Changtsu, *C. Y. Luh 1045* (NAC). Anhwei: Wu Yuan, *R. C. Ching* (NAC). Chekiang: Mt. Hsi-tienmu-shan, 1935, *H. Migo* (NAC); West Tien-mu, *H. [illegible] 1654* (UC). Hupeh: S Wushan, *E. H. Wilson 1044* (K,NY); Chienshih, *A. Henry* [illegible] (K,US). Kiangsi: Lushan Mountains, *Chung & Sun 295* (NY). Yunnan: Mengtze, *A. [illegible] 223* (K,MO,NY); Kira-chi-ling, *J. Cavalerie 2961* (K).

7a. *Osmorhiza aristata* var. *laxa* (Royle) Constance & Shan, comb. nov.

Osmorhiza laxa [illegible] Bot. Himal. 233, pl. 52, f. 1. 1839.

Osmorhiza brevistylis [illegible] Royle, A. Gray, etc. Not *Osmorhiza brevistylis* DC. 1830.

Washingtonia laxa K.-[illegible] ex Fedtsch. Fl. Asiat. Russ. 15: 52. 1920.

Washingtonia longistylis [illegible] Pol. ex Fedtsch. Fl. Asiat. Russ. 15: 52. 1920, as synon.

Osmorhiza Claytoni Clarke ex Hook., etc., as to Asiatic plants in part. Not *Myrrhis Claytoni* Michx. 1803.

Leaves biternate, the leaflets coarsely serrate to sparsely lobed at the base.

Type locality.—"Sirmore [Sirmur], in the Himalayan Mountains," Punjab, India, *Royle.*

Distribution.—Kashmir to Kumaon, United Provinces, northern India, to Tibet and southwestern China, 6,000–10,000 feet elevation.

Representative specimens.—CHINA. Sikang: Kangting (Tachienlu) distr., Cheto, *H. Smith 10,963* (GB). Yunnan: Yungning, *H. Handel-Mazzetti 7049* (NAC). Tibet: Rongshar Valley, *R. W. G. Hingston 183* (K). INDIA. United Provinces: Lahur, Kumaun, *Strachey & Winterbottom* (GH,K); near Burhi, Bians, Kumaun, *J. F. Duthie 5595* (K); side of Tyne Deba, Garhwal, *Falconer* (K); Garhwal, *T. Thomson 1254* (K); near Kinani Pani, Jaunsar-Bawar, Dehra Dun, *J. S. Gamble 1136* (K); Chaelipur, Jaunsar-Bawar, *J. S. Gamble 23,539* (K). Punjab: "N. W. India [Sirmur]," *Royle* (K: type collection); Tila Lotui, Kulu-Lahul, *J. R. Drummond 23,131* (K,UC); Pulga, Kulu-Lahul, *J. R. Drummond 23,122* (K); Jibhi, Kulu-Lahul, *J. R. Drummond 23,132* (UC); Swajani Maidan, Parbati Valley, Kulu-Lahul, *M. Nath 123* (NY); Raiengarh Mut, *J. S. Gamble 26,799* (K); Jangla, *Dudgeon & Kenoyer 386* (MO); Narkanda, Simla Hills, 1849, *T. Thomson* (GH,K). Kashmir & Jammu: Jammu Hills, *1848, T. Thomson (GH,K); Pahlgam, R. R. Stewart 9271 (NY); Keran, Kishenganga Valley and road to Nanga Parbat via Gangabal Lakes, Stewart & Stewart 17,544* (NY); Sharda-Kel, Kishenganga Valley and road to Nanga Parbat, *Stewart & Stewart 17,800* (NY).

8. ***Osmorhiza Claytoni*** (Michx.) Clarke in Hook. f. Fl. Brit. Ind. 2: 690, as to name only. 1879

Myrrhis Claytoni Michx. Fl. Bor. Am. 1: 170. 1803.
Chaerophyllum Claytoni Pers. Syn. Pl. 1: 320. 1805.
Scandix dulcis Muhl. Cat. 31. 1813.
Uraspermum hirsutum Bigel. Fl. Bost. ed. 2. 112. 1824.
Osmorhiza brevistylis DC. Prodr. 4: 232. 1830.
Osmorhiza dulcis Raf. Med. Fl. 2: 249. 1830.
Myrrhis brevistylis D. Dietr. Syn. Pl. 2: 984. 1840.
Chaerophyllum dulce Fisch.; Steud. Nom. Bot. ed. 2. 1: 339. 1840.
Uraspermum aristatum var. *brevistyle* Kuntze, Rev. Gen. 1: 270, in part. 1891.
Osmorrhiza aristata Rydb. Bot. Surv. Nebr. 3: 37. 1894. Not *Chaerophyllum aristatum* Thunb. 1784.
Washingtonia Claytoni Britton in Britt. & Brown, Ill. Fl. 2: 530. 1897.
Scandix Claytonii K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 143. 1916.
Uraspermum dulce Farwell, Am. Midl. Nat. 9: 273. 1925.
Uraspermum dulce var. *laevicaule* Farwell, Am. Midl. Nat. 9: 273. 1925. Based upon *Farwell 5267*, "Near Pontiac," Michigan.

Plants rather stout, 4–10 dm. high, densely villous or hirsutulous throughout to rarely glabrate; leaf blades orbicular, 1–3 dm. long, ternate-pinnate, the leaflets ovate to lanceolate, 3–7 cm. long, 2–3 cm. broad, acute or acuminate, serrate to incised or pinnately lobed toward the base, more or less densely pilose; petioles 5–12 cm. long; peduncles 5–13 cm. long; involucre wanting or occasionally of 1 or 2 foliaceous bracts; involucel of several linear, attenuate, ciliate bractlets, 3–8 mm. long, sharply reflexed; rays 3–5, spreading-ascending, 1.5–8 cm. long; pedicels spreading-ascending, 5–12 mm. long; flowers white, the styles and stylopodium 1.0–1.5 mm. long, the latter high-conic; carpophore cleft about one-fourth of its length; fruit oblong-fusiform, 15–22 mm. long, tapering into an attenuate beak at the apex, caudate at the base, the appendages 5–7 mm. long, sparsely bristly on the ribs, more densely so below.

Type locality.—"In montibus Alleghanis," *Michaux.*

Distribution.—Nova Scotia and Quebec to North Carolina and Alabama, west to Manitoba, Missouri, and Nebraska.

Although the ranges of *O. Claytoni* and *O. longistylis* are largely coincident, the former is more abundant to the north and east, the latter to the south and west. *Osmorhiza Claytoni* appears to be remarkably uniform, and our studies have not revealed any significant variations.

The attributing of *O. Claytoni* to Asia by Clarke and others is based upon the assumption that *O. aristata, O. aristata* var. *laxa, O. longistylis,* and *O. Claytoni* were all phases of the same species. Under the name of *O. brevistylis,* this species was also made to include representatives of *O. mexicana* from Mexico, Central America, and South America.

Representative specimens.—QUEBEC. Grand Cascapedia River, Bonaventure Co., 1905, *Williams, Collins & Fernald* (GH); Mt. Nicolabert, Joffre, Matane Co., *Fernald & Pease 25,208* (GH); St. Francois, Montmorency Co., *Victorin, Germain, Michel & Meilleur 43,675* (CLOKEY,GH); Lac Mead, Ottawa, *Bro. Rolland 6183* (GH,US); Lac Ouimet, St. Jovite, Terrebonne Co., 1922, *J. R. Churchill* (GH,MO); Cleveland, Richmond Co., 1923, *Chamberlain & Knowlton* (GH,MO). PRINCE EDWARD ISLAND. Bear River, Kings Co., *Fernald & St. John 11,140* (GH,UC,US). NOVA SCOTIA. George River, Cape Breton Co., *Bissell & Linder* (GH, S), *22,050* (GH,S); Mabou, Cape Breton, Inverness Co., *C. B. Robinson 229* (NY). NEW BRUNSWICK. Grand Manan, Charlotte Co., *Weatherby & Weatherby 7327* (GH,US).

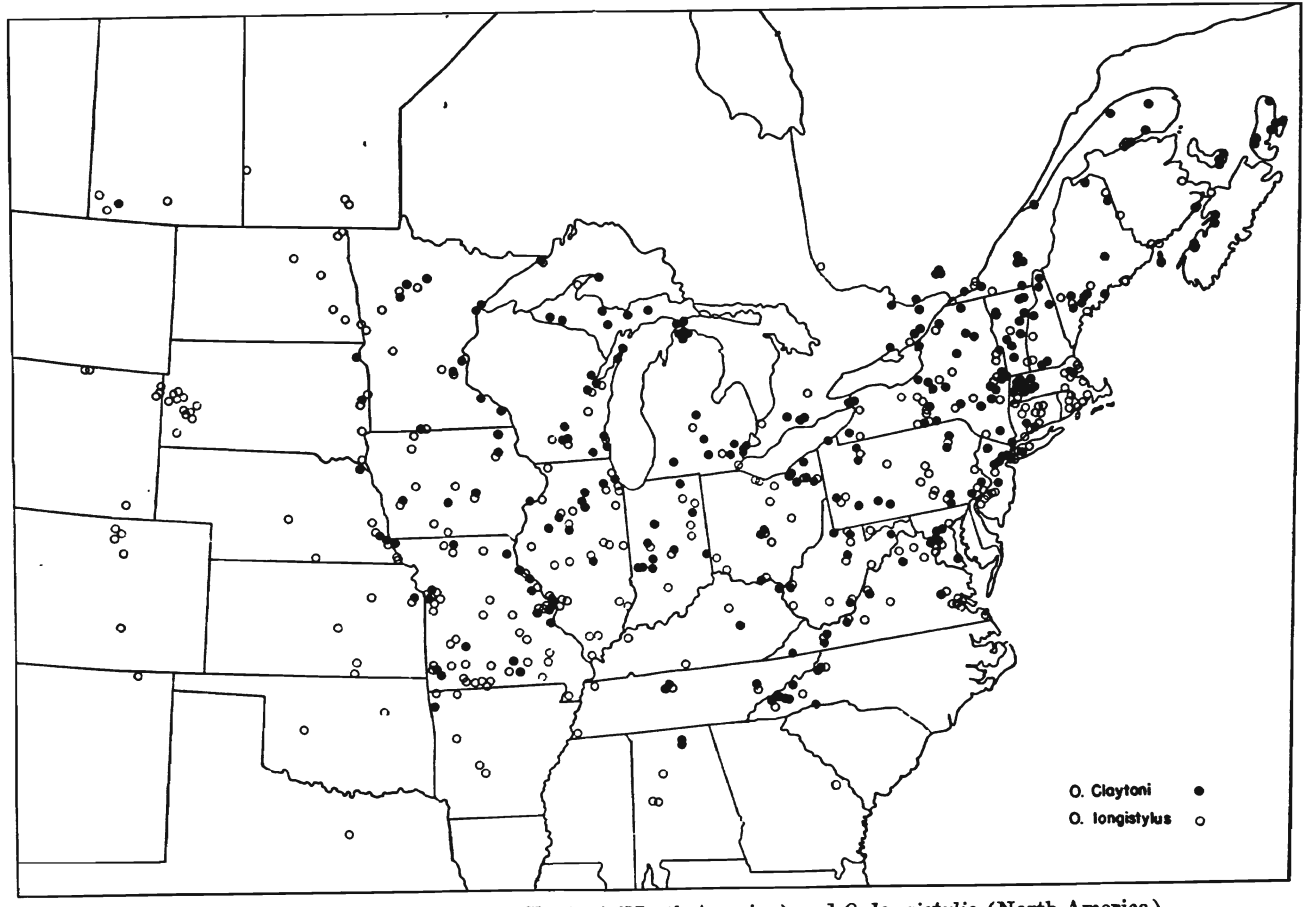


Fig. 4. Distribution of *Osmorhiza Claytoni* (North America) and *O. longistylis* (North America).

MAINE. Fort Kent, Aroostook Co., 1904, *M. L. Fernald* (GH,NY,WYO); Fort Fairfield, Aroostook Co., *M. L. Fernald 51* (GH,MO,UC,US); Camden, Knox Co., 1902, *G. G. Kennedy* (GH); Canton, Oxford Co., *J. C. Parlin 2065* (GH). NEW HAMPSHIRE. Pittsburg-Clarkesville, Coos Co., *A. H. Moore 3720* (GH); North Woodstock, Grafton Co., *M. L. Fernald (Pl. Exsic. Gray. 386)* (DS,GH,MO,NY,S,UC,US,WYO); Peterborough, Hillsboro Co., 1931, *C. F. Batchelder* (MO). VERMONT. Peacham, Caledonia Co., 1892, *F. Blanchard* (F-part,MO,NY,WYO); Charlotte, Chittenden Co., 1879, *F. H. Horsford* (F); Bromley Mt., Bennington Co., *Moldenke & Moldenke 9973* (MO,NY). MASSACHUSETTS. Near Boston, Suffolk Co., *Biltmore Herb. 1362c* (GH,US); Mt. Toby, Leverett, Franklin Co., 1909, *S. C. Brooks* (UC); Florida, Deerfield River, Berkshire Co., *Fernald & Long 10,088* (GH). RHODE ISLAND. "Rhode Island," *G. Thurber* (GH-part). CONNECTICUT. Southington, Hartford Co., *L. Andrews 542* (GH); New Haven, New Haven Co., *D. C. Eaton* (MO,S).

NEW YORK. Newcomb, Essex Co., *H. F. Heady 377* (UC); Brunswick, Rensselaer Co., *H. D. House 26,381* (MO,TEX); South Bay, Wellesley Island, Jefferson Co., *Robinson & Maxon 25* (GH,NY,US); Niagara, Niagara Co., 1874, *O. Kuntze 2609* (NY); New York, *J. Torrey* (GH,NY); Forest Home, Tompkins Co., *Muenscher & Bechtel 384* (CLOKEY, MO). PENNSYLVANIA. "In montibus Alleghenis," *Michaux* (GH: type photograph); Osterhout P. O., Wyoming Co., *G. E. Osterhout 7133* (WYO); North Warren, Warren Co., *H. N. Moldenke 15,678* (NY,UC); Little Conestoga, Lancaster Co., 1891, *Small & Heller* (F,US); Belleville-Westview, Allegheny Co., *L. K. Henry 594* (CLOKEY,F,US). NEW JERSEY. Sparta Glen, Sussex Co., *K. K. Mackenzie 4243* (MO); Watchung, Somerset Co., *H. N. Moldenke 1626* (NY); 1 mile S of Arneytown, Burlington Co., *B. Long 27,649* (GH). MARYLAND. Howard Co., 1881, *J. Donnell Smith* (F,US); Chesapeake Beach, Calvert Co., *H. D. House 764* (NY); Little Falls Brook, *Maxon & Standley 315* (US); Cumberland, Allegheny Co., 1894, *H. Shriver* (NY). WEST VIRGINIA. Wheeling, Ohio Co., *H. N. Mertz 1042* (F); Upshur Co., 1897, *W. M. Pollock* (F,MO,US); White Sulphur Springs, Greenbrier Co., 1914, *F. W. Hunnewell, 2nd* (GH); Pleasant Valley, Cabell Co., *Williams & Gilbert 445* (F,GH,MO,NY). VIRGINIA. Dead Run, Fairfax Co., *M. E. Mathias 1394* (DS,GH, MO,NY,UC,US,WYO); Shenandoah Park, *W. H. Camp 1176* (NY); Hot Springs, Bath Co., 1917, *F. W. Hunnewell, 2nd, 4754* (GH); Richmond, Henrico Co., 1881, *J. R. Churchill* (MO); Chatham Hill Gap, Smyth Co., 1892, *J. K. Small* (F,GH,MO,UC); 11 miles NW of Bristol, Scott Co., *H. A. Gleason 8785* (NY). KENTUCKY. "Big Woods," Greenup Co., *Smith, Hodgdon, Gilbert & McCoy 3580* (F,GH,NY,US); Big Hill, Berea, Madison Co., *McFarland & Lyle 4294* (MO). NORTH CAROLINA. Paint Rock, Madison Co., *Biltmore Herb. 1362* (MO, US,WYO); Hot Springs, Madison Co., *Biltmore Herb 1362b* (GH,NY,US); Melrose, Polk Co., *D. C. Peattie 698* (F). TENNESSEE. Great Smoky Park, *Camp & Jennison 1734* (NY); Lane's Creek, Knox Co., *Sharp & Hester 584* (NY); Joelton, Davidson Co., *H. K. Svenson 93* (GH). ALABAMA. Montesano, Madison Co., 1897, *C. F. Baker* (NY,US,WYO); Huntsville, Madison Co., 1897, *C. F. Baker* (MO,NY).

ONTARIO. Near High Falls, Manitoulin Island, *Pease & Ogden 25,065* (GH); Stokes Bay, Bruce Peninsula, *P. V. Krotkov 9273* (GH,NY,US); Britannia, 1911, *J. Macoun* (F); Battersea, 1898, *J. Fowler* (F,US); Aylmer, *E. T. Anderson 9296* (S,WYO). MICHIGAN. Monroe Lake, Cheboygan Co., *J. H. Ehlers 374* (GH,MO,US); Riggsville, Cheboygan Co., *Gleason & Gleason 21* (GB,GH,NY); Burt Lake, Cheboygan Co., *Gates & Gates 10,631* (F,MO,WYO); Turin, Marquette Co., 1901, *B. Barlow* (GH,NY,US); Gogebic Lake, Gogebic Co., *N. C. Fassett 19,868* (F,MO,NY); W of Pellston, Emmet Co., *Gates & Gates 10,310* (F,MO,WYO); near Pontiac, Oakland Co., *O. A. Farwell 5267* (GH: isotype of *Uraspermum dulce* var. *laevicaule* Farwell). OHIO. Shaker Pond near Cleveland, Cuyahoga Co., *J. M. Greenman 710* (GH,MO); Lancaster, Fairfield Co., *J. M. Bigelow* (US); Friendship, Scioto Co., *D. Demaree 10,648* (DS,GH,MO). INDIANA. Lancaster Township, Wells Co., 1905, *C. C. Deam* (US); Crawfordsville, Montgomery Co., 1887, *J. N. Rose* (F); Cataract Falls, Owen Co., *R. C. Friesner 5578* (UC,WYO). ILLINOIS. Starved Rock, La Salle Co., *Greenman, Lansing & Dixon 27* (GH,NY,UC); Peoria, Peoria Co., 1900–03, *F. E. McDonald* (GH,NY,WYO); Decatur, Macon Co., *H. A. Gleason 9159* (NY). WISCONSIN. Egg

Harbor, Door Co., 1883, *J. H. Schuette* (F); Milwaukee, Milwaukee Co., *H. E. Hasse* (NY); Madison, Dane Co., 1887, *W. Trelease* (MO).

SASKATCHEWAN. Crane Lake, Assinboia, *J. Macoun 4970* (GH). MINNESOTA. Near Mineral Center, Cook Co., *Rosendahl & Butters 4590* (GH,NY); Lindstrom, Chisago Co., 1892, *B. C. Taylor* (F,WYO); Floating Bog Bay, Clearwater Co., *M. L. Grant 2885* (MO,NY, UC); Mississippi River, 1888, *J. H. Schuette* (F,GH,NY). SOUTH DAKOTA. Brookings, Brookings Co., *A. G. Johnson* (MO); Big Stone Lake, Roberts Co., *W. H. Over 14,409* (US). IOWA. Rice Lake, Worth Co., *L. H. Pammel 122* (GH); Fayette Co., 1894, *B. Fink* (US); Grinnell, Poweshiek Co., *M. E. Jones* (NY); Shelby Co., 1894, *Fitzpatrick & Fitzpatrick* (WYO). NEBRASKA. L'Eau qui Court, 1853–54, *F. V. Hayden* (MO); Ponca, Dixon Co., *F. Clements 2564* (US); Nehawka, Cass Co., *G. D. Swezey* (NY); Nebraska City, Otoe Co., 1900–01, *J. J. Thornber* (ARIZ). MISSOURI. Little River, Saline, Mercer Co., *Palmer & Steyermark 41,324* (MO,NY); Watson, Atchison Co., *B. F. Bush 141* (GH,MO); Burge Park, Jackson Co., *Bush & Mackenzie 867* (MO,NY,US); Mill Creek, Silex, Lincoln Co., *J. A. Steyermark 25,981* (F,MO); near Hematite, Jefferson Co., 1893; *H. Eggert* (F, MO,NY,US,WYO). KANSAS. Leavenworth Co., *A. S. Hitchcock 701* (GH,NY,WYO—not MO,US!). ARKANSAS. Siloam Springs road, 1927, *J. F. Normand* (TEX).

9. *Osmorhiza purpurea* (Coult & Rose) Suksd. Allg. Bot. Zeits. 12: 5. 1906

Washingtonia Leibergi Coult. & Rose, Contr. U. S. Nat. Herb. 7: 66. 1900. Based upon *Sandberg & Leiberg 666*, "Nason Creek, branch of Wenatchee River, Kittitas County, Washington."

Washingtonia purpurea Coult. & Rose, Contr. U. S. Nat. Herb. 7: 67. 1900.

Osmorrhiza Leibergi Blankinship, Mont. Agr. Coll. Stud. 1: 93. 1905.

Plants slender, 2–6 dm. high, the herbage almost glabrous to sparingly hirsutulous; leaf blades deltoid or orbicular, 3–10 cm. long, 1–3-ternate, the leaflets lanceolate to ovate, 1.5–7 cm. long, 5–40 mm. broad, acute or acuminate, coarsely serrate to incised or lobed, usually sparingly hirsutulous on the veins and margins; petioles 5–12 cm. long; peduncles 3–10 cm. long; involucre wanting; involucel wanting; rays 2–6, spreading-ascending, 2–7.5 cm. long; pedicels spreading-ascending, 5–20 mm. long; flowers purplish or greenish white, the styles and stylopodium 0.3–1.1 mm. long, the latter depressed-conic, the disc conspicuous; carpophore cleft about one-fourth of its length; fruit linear-fusiform, 7–10 mm. long, constricted below the short-beaked apex, caudate at the base, the appendages 1.5–3 mm. long, bristly toward the base.

Type locality.—Sitka, Alaska, *Coville & Kearney 796.*

Distribution.—Northern Montana and Idaho to Alaska and northwestern California.

Although sometimes uncomfortably close to glabrate phases of *O. chilensis* (*O. divaricata*), the species is usually readily distinguishable by the subapically constricted small fruits and the depressed stylopodium. The development of a conspicuous disc is an additional earmark. The flower color does not appear to be correlated with any other morphological variant. We have been able to extend considerably the known range of this entity as given in the "North American Flora."

This is the only member of the Nudae not discovered also in the Great Lakes area, the Maritime Provinces, and in South America as well as in western North America. The fruits appear to be fully as well "adapted" to dispersal as those of *O. chilensis* and *O. obtusa*, so its restriction can scarcely be explained on this basis. Perhaps it is significant that it usually occurs either at high elevations or high latitudes, or in areas with abundant rainfall.

Representative specimens.—MONTANA. Blackfoot Glacier, Flathead Co., 1909, *M. E. Jones* (DS,MO); Glacier Camp, Glacier Co., *J. W. Blankinship* (GH); Midvale, Glacier Co., *L. M.*

Umbach 249 (F,WYO—not NY,US!); vicinity of Lake McDermott, Glacier Natl. Park, *P. C. Standley 15,333* (US). IDAHO. Packsaddle Peak, Kootenai Co., *Sandberg, MacDougal & Heller 845* (NY,US); near Sohons Pass, Shoshone Co., *J. B. Leiberg 1427* (DS,GH,NY, UC,WYO).

ALASKA. Port Wells, Prince William Sound, *Coville & Kearney 1264* (US); Sitka, *C. V. Piper 4290* (US), *Coville & Kearney 796* (US: type of *Washingtonia purpurea* Coult. & Rose); Yakutat, *C. V. Piper 4281* (US); Juneau, *J. P. Anderson 6322* (GH,WYO); Deer Mt., Revillagigedo Island, *T. T. McCabe 8644* (UC); Douglas Island, *W. Trelease 4527* (GH, US); Mt. Harris, *H. C. Cowles 1402* (F,MO); Ketchikan, 1934, *F. W. Went* (GB), BRITISH COLUMBIA. Calvert Island, *T. T. McCabe 4383* (UC); Queen Charlotte Islands, *F. Boas 112* (NY); mountains near Ainsworth, Kootanie Lake, *J. M. Macoun* (F,US); Big Bend district, *C. H. Shaw 992* (GH,NY); Illecillewaet Valley, Glacier, *S. Brown 273* (GH,MO,NY, US); Laggan, *H. C. Cowles 187* (F,MO); Chilliwack Valley, *J. M. Macoun 44,490* (NY, US); first summit W of Skagit River, *J. M. Macoun 79,439* (F,NY); Swanson Bay, Graham Reach, *T. T. McCabe 3524* (UC); Mt. Arrowsmith, Vancouver Island, *W. R. Carter 836* (GH). WASHINGTON. Grouse Ridge, Mt. Baker, Whatcom Co., *H. L. Mason 3853* (GH, MO,NY,UC); Perry Creek trail, Snohomish Co., *J. W. Thompson 14,712* (GH,MO,NY); Nason Creek, Okanogan Co., *Sandberg & Leiberg 666* (US: type of *Washingtonia Leibergii* Coult. & Rose, (GH,MO,NY,S,UC); Three Brothers, Okanogan Co., *J. W. Thompson 10,854* (DS,MO,NY,US); Stevens Pass, Chelan Co., 1893, *Sandberg & Leiberg* (MO,NY,S,US); Mt. Stuart region, Chelan Co., *J. W. Thompson 7787½* (DS,GH,MO); Paradise Park, Mt. Rainier, *H. C. Cowles 667* (F,MO); Mt. Paddo [Adams], Yakima Co., *W. N. Suksdorf 2651* (DS,F,MO,US), *2759* (DS,F,MO,UC,US); Chiquash Mountains, Skamania Co., *W. N. Suksdorf 8164* (UC); Mt. Angeles, Clallam Co., *J. W. Thompson 7487* (GH,MO); Sawtooth Ridge, Mason Co., *F. G. Meyer 1704* (GH,MO,UC); Colonel Bob Peak, Grays Harbor Co., *F. H. Lamb 1382* (DS,MO,NY), *J. W. Thompson 7275* (DS,GH,MO,UC). OREGON. Mt. Hood, Hood River Co., 1924, *L. F. Henderson 632* (MO); Crater Pass, Klamath Co., *J. S. Newberry* (GH,US); Wilson River, Tillamook Co., *J. W. Thompson 4111* (DS,K,MO); Brown's Cabin, Jackson Co., *E. I. Applegate 5951* (DS). CALIFORNIA. Wilson Creek, Del Norte Co., *Abrams & Bacigalupi 8323* (DS,WYO); Requa, Del Norte Co., 1921, *E. A. McGregor* (DS).

10. *Osmorhiza chilensis* Hook. & Arn. Bot. Beechey Voy. 26, 1830; Hook. Bot. Miscel. 3: 355. 1833. (Pl. 28)

Osmorhiza Berterii DC. Prodr. 4: 232. S 1830. Based upon *Bertero*, "in sylvis umbrosis propre Tagua-Tagua Chilensium."

? Osmorhiza brevistylis Bong. Mem. Acad. St.-Petersb. VI. 2: 142. 1832. Not *Osmorhiza brevistylis* DC. 1830.

Osmorhiza divaricata Nutt.; T. & G. Fl. N. Am. 1: 639. 1840. (Nomen nudum.). Based upon *Nuttall*, "Columbia woods," Oregon.

Myrrhis Berterii D. Dietr. Syn. Pl. 2: 984. 1840.

Osmorhiza nuda Torr. Pacif. R. R. Rep. 4[1] : 93. 1857. Based upon *Bigelow*, "Shady woods, Napa Valley," California.

Uraspermum Berterii Kuntze, Rev. Gen. 1: 270, 1891.

Uraspermum nudum Kuntze, Rev. Gen. 1: 270. 1891.

Myrrhis nuda Greene, Fl. Franc. 333. 1892.

Osmorrhiza depauperata Phil. Anal. Univ. Chile, Santiaga 85: 726. 1894. Based upon *Philippi*, "In 'Valle de las Nieblas' haud procul a thermis chillanensibus," Chile.

Osmorrhiza Berterii var. *gracilior* Phil. Anal. Univ. Chile, Santiago 85: 726. 1894. Based upon *O. Philippi*, "in andibus provinciae Valdiviae l. d. Chihuim," Chile.

Washingtonia divaricata Britton in Britt. & Brown, Ill. Fl. 2: 531. 1897.

Washingtonia nuda A. Heller, Cat. N. Am. Pl. 5. 1898.

Washingtonia intermedia Rydb. Mem. N. Y. Bot. Gard. 1: 289. 1900. Based upon *Rydberg & Bessey 4595*, "Bridger Mountains, Montana."

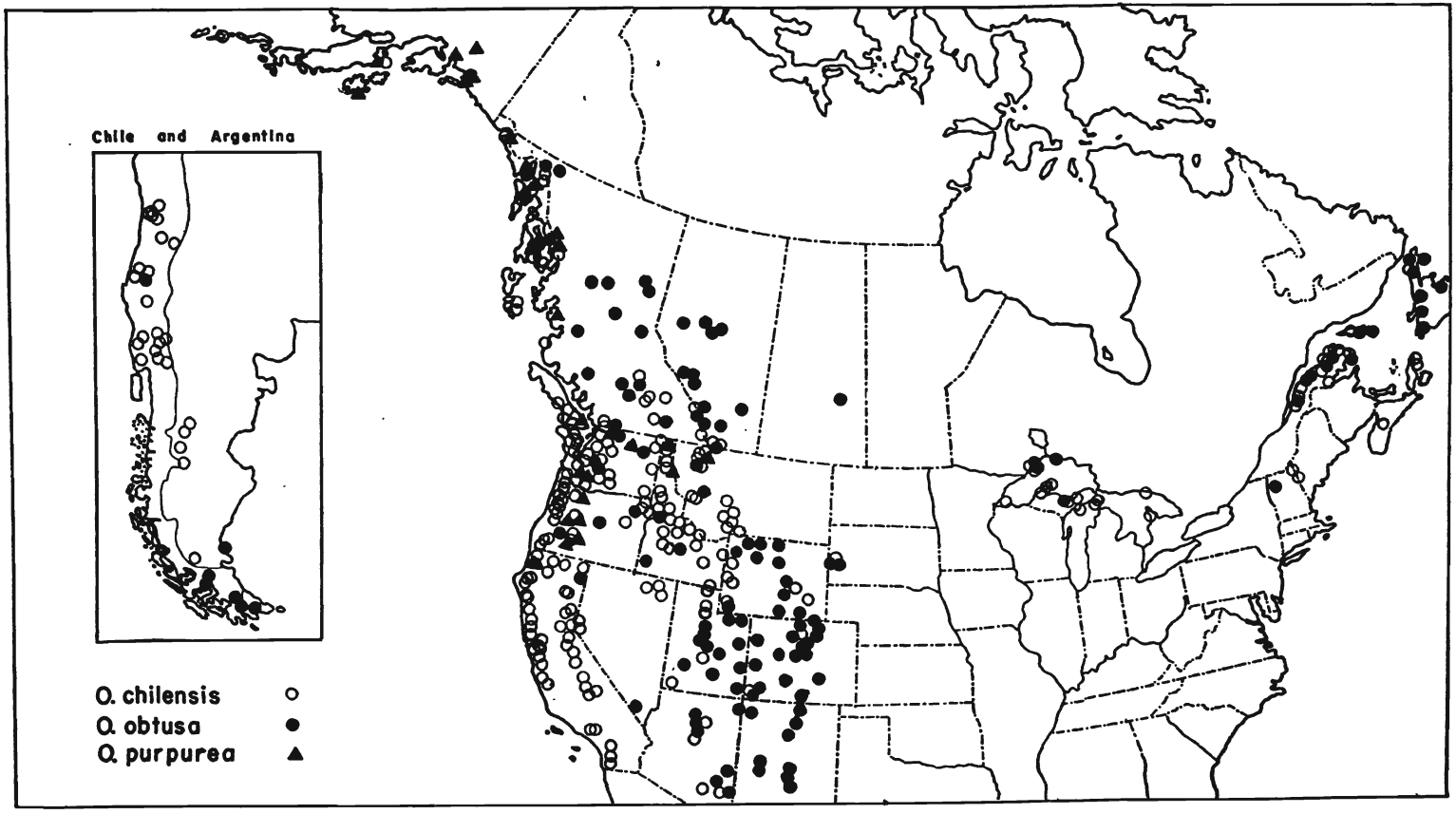


Fig. 5. Distribution of *Osmorhiza chilensis* (North and South America), *O. obtusa* (North and South America), and *O. purpurea* (North America).

Washingtonia brevipes Coult. & Rose, Contr. U. S. Nat. Herb. 7: 66. 1900. Based upon *Palmer 2481*, "Mount Shasta and vicinity, Siskiyou Co., Calif."
Osmorrhiza brevipes Suksd. Allg. Bot. Zeits. 12: 5. 1906.
Osmorhiza divaricata var. *nuda* M. E. Jones, Bull. Univ. Mont. Biol. 15: 42. 1910.
Scandix nuda K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 143. 1916.
Scandix divaricata K.-Pol. Bull. Soc. Nat. Mosc. II. 29: 143. 1916.
Osmorrhiza nuda var. *brevipes* Jepson, Madroño 1: 119. 1923.
Osmorrhiza nuda var. *divaricata* Jepson, Madroño 1: 119. 1923.
Urasper[m]um brevipes Farwell, Am. Midl. Nat. 12: 70. 1930.
Uraspermum divaricata Farwell, Am. Midl. Nat. 12: 70. 1930.
Uraspermum barbatum Farwell, Am. Midl. Nat. 12: 70. 1930. Based upon *Farwell 8490*, "Copper Harbor, Michigan."

Plants slender, 3–10 dm. high, the herbage hirtellous to hirsutulous or villous; leaf blades orbicular, 5–15 cm. long, biternate, the leaflets ovate-lanceolate to orbicular, 2–6 cm. long, 1–4 cm. broad, obtuse or acute, coarsely serrate, incised or lobed, appressed-hispid or hispidulous especially on the veins and rachis; petioles 5–16 dm. long; peduncles 5–25 cm. long; involucre usually wanting; involucel wanting, rarely vestigial; rays 3–8, spreading-ascending, 2–12 cm. long; pedicels spreading-ascending, 5–30 mm. long; flowers greenish white, rarely pinkish, the styles and stylopodium 0.3–1 mm. long, the latter conic; carpophore divided about one-fourth of its length; fruit linear-oblong, 10–20 mm. long, tapering toward the apex into a slender beak, caudate at the base, the appendages 2–7 mm. long, densely hispid at the base.

Type locality.—"Concepcion," Chile, *Lay & Collie.*

Distribution.—Newfoundland and Quebec to New Hampshire; Ontario to northern Michigan and Wisconsin; Alberta to Arizona, west to Alaska and California; southern Argentina and Chile.

Osmorhiza chilensis is the most variable of all the species of the genus and has, accordingly, been denominated in its various phases as *O. nuda, O. divaricata, O. brevipes, O. intermedia, O. Berterii,* and *Uraspermum barbatum.* Although the species population apparently differs considerably in biotype content from place to place, we have been unable to discover any tenable subspecific entities. In general, the less pubescent forms with pedicels longer than the fruits, which occur most frequently in the northern part of the range, have been regarded as *O. divaricata,* and were so mapped by Fernald (1925), who did not consider the relationship of this entity to *O. nuda.* Torrey (1874), however, remarked: "I was not aware when the description of *O. nuda* was published that it was identical with the plant of Oregon . . . or I should have adopted Nuttall's manuscript name [*O. divaricata*]." *Osmorhiza nuda* was founded upon an immature, pubescent specimen with unusually elongate pedicels. The pubescent forms with pedicels shorter than the fruits, most common from western-central Oregon through northwestern California, have been known as *O. brevipes.* These two phases, regarded by Jepson (1923) as varieties of *O. nuda,* are abundantly connected by plants combining pubescence with slender pedicels and lack of pubescence with short pedicels. The type of *O. intermedia* is an immature specimen of *O. chilensis,* but Rydberg assigned to this segregate, judging by his annotations on specimens, representatives also of *O. purpurea* and *O. obtusa,* so the unit became truly "intermediate!"

The interpretation of the South American *O. chilensis* and *O. Berterii* as

conspecific with North American plants has not previously been made. Reiche (1902) suggested that they greatly resembled each other, and Coulter and Rose (1895) remarked that "A western Cordilleran type seems to extend through North and South America, which is *O. nuda* in the United States, *O. mexicana* in Mexico, and *O. Berterii* in South America." In general, however, the North and South American plants appear to have been kept in separate folders in herbaria and never compared. With the exception of some details of leaf dissection, every variation observed in the South American material can be readily matched in the North American (pl. 28). It is noteworthy that the phases designated in North America as *O. divaricata* and *O. brevipes* occur also in South America. Some of the North American variations have not been found in South America, suggesting that the Chilean-Argentine population may have fewer biotypes. This suggests, in turn, that the South American population may have been derived from the North American, rather than the reverse.

The question of the priority of specific epithets apparently cannot be finally solved, despite the generous efforts of Mr. George Taylor of the British Museum and Dr. H. W. Rickett of the New York Botanical Garden. It is definitely established that *O. chilensis* and *O. Berterii* were both published in 1830, the latter very probably in September, but the month of the appearance of the former is apparently unascertainable. Because Hooker and Arnott (1833), Hooker (1846), and Asa Gray (1854) accepted *O. chilensis* and put *O. Berterii* in its synonymy, we feel justified in assuming that this procedure is to be followed. Study of an isotype of *O. Berterii* and a cotype of *O. chilensis* leaves no doubt that both names apply to the same entity. The identity of *O. depauperata* Philippi remains uncertain; from the original description the name might apply equally well to either *O. chilensis* or *O. obtusa*, and both species occur in the vicinity of the type locality. Reiche's use of this name for specimens from "Estrecho de Magellanes" would suggest the latter interpretation, but neither Philippi nor Reiche evoked any of the characters which distinguish the two species. We are unwilling to abandon *O. obtusa* in favor of *O. depauperata* unless some conclusive evidence can be found to demonstrate that these names were originally applied to the same entity.

An additional name that has appeared in the synonymy of this species is the obscure *Scandix chilensis* Molina, Saggio 398. 1788 (*Schudia chilensis* Molina; Hook. f. Fl. Antartica 2: 288, 1846, as synon; *Chaerophyllum chilense* Poir. in Lam. Encycl. 5: 145. 1804.). The original description consists of only the following phrase, "semin. rostro longissimo, foliolis integris ovato-lanceolatis," and no type locality is cited. According to Reiche (1902), *Scandix chilensis* Molina = *Erodium cicutarium!* Whatever its identity, there is nothing to indicate that the name applies to any species of *Osmorhiza*.

Specimens examined.—NEWFOUNDLAND. N of Doctor Hill, St. John Bay, *Fernald & Long 28,771* (GH,US). QUEBEC. Percé, Gaspé Co., *Collins & Fernald 119* (GH,NY,UC,US); Rivière-aux-Renards, Gaspé Co., *Victorin, Brunel, Germain & Rousseau 17,319* (GH,MO, NY,US); Bic, Rimouski Co., 1904, *Collins & Fernald* (GH); Rivière du Loup, Temiscouata Co., 1902, *Williams & Fernald* (GH,US), *W. W. Eggleston 2981* (MO,NY-part,US—not

DS!). NOVA SCOTIA. Aspy Bay, Cape Breton, 1909, *J. R. Churchill* (GH,MO); Port Bevis, Victoria Co., *Fernald & Long 22,052* (GH); North Mt., N of Middleton, Annapolis Co., *B. Long 22,051* (GH). NEW BRUNSWICK. Morris Rock, Bass River, 1873, *J. Fowler* (MO). MAINE. Fort Kent, Aroostook Co., *K. K. Mackenzie 3358* (MO,NY,US), *3509* (MO,NY). NEW HAMPSHIRE. Alpine Cascade, Gorham, Coos Co., *A. S. Pease 16,432* (GH); Carter Notch, 1900, *F. F. Forbes* (GH).

ONTARIO. Talus Lake, Thunder Bay district, *Taylor, Losee & Bannan 1146* (CLOKEY, GH); Little Current, Manitoulin Island, *Fernald & Pease 3449* (GH); Stokes Bay, Bruce Peninsula, Bruce Co., *P. V. Krotkov 9272* (GH,US), *Victorin, Germain & Dominique 46,125* (GB,WYO). MICHIGAN. Near Cliff, Keweenaw Co., *F. J. Hermann 7647* (F,NY,WYO), *Fernald & Pease* (GH,US); Copper Harbor, Keweenaw Co., *O. A. Farwell 8490* (GH: isotype of *Uraspermum barbatum* Farwell); near Carp Lake mine, Porcupine Mountains, Ontonagon Co., *N. C. Fassett 10,412* (GH); above Miner's Falls near Minising, Alger Co., *Fernald & Pease 3450* (GH,NY). WISCONSIN. E of Sand Bay, Bayfield Co., *L. S. Cheney 6414* (GH); Port Wing, Bayfield Co., *N. C. Fassett 9830* (GH).

SOUTH DAKOTA. Deadwood, Lawrence Co., *W. P. Carr 130* (F,GH,MO,NY,WYO); Lead City, Lawrence Co., *P. A. Rydberg 724* (NY,US).

ALBERTA. 8 miles W of Pincher Creek, *E. H. Moss 86* (GH,US); Cameron Creek, Waterton, *E. H. Moss 497* (GH,US). MONTANA. Big Fork, Flathead Co., 1904, *W. W. Jones* (DS, UC,US); Columbia Falls, Flathead Co., 1894, *R. S. Williams* (MO,NY,US,WYO); Helena, Lewis & Clark Co., 1887–91, *F. D. Kelsey* (F,US); Paddy Creek, Missoula Co., *F. H. Rose 205* (UC); Bridger Mountains, Gallatin Co., *Rydberg & Bessey 4595* (NY: type of *Washingtonia intermedia* Rydb., US); upper Madison River, Madison Co., 1899, *J. W. Blankinship* (US,WYO); Red Lodge, Carbon Co., *J. N. Rose 30* (GH,NY,US). IDAHO. Priest River Experiment Station, Bonner Co., *C. Epling 6041* (F,MO); Lake Waha, Nez Perce Co., *Heller & Heller 3385* (MO,NY,UC,US); Lewiston, Nez Perce Co., *Heller & Heller 3137* (DS,MO, NY,UC,US); Hatwai Creek, Nez Perce Co., *Sandberg, MacDougal & Heller 168* (DS,GH, MO,NY,US); 4 miles below Lowell, Idaho Co., *Constance & Rollins 1608* (MO,UC); near Josephus Lakes, Custer Co., *Macbride & Payson 3596* (GH,MO,US,WYO); Salmon, Lemhi Co., *Payson & Payson 1884* (GH,MO,NY,WYO); Big Springs, Fremont Co., *A. Cronquist 1578* (MO,NY); Hillyard Creek, Franklin Co., *R. J. Davis 3963* (UC); South Mt., Owyhee Co., *P. Train SM8* (S,US). WYOMING. Sheridan Co., *F. Tweedy 2435* (NY); Casper Mt., Casper, Natrona Co., *F. J. Hermann 4609* (MO); Bear Creek, Laramie Co., 1899, *C. Schuchert* (US); Mammoth Hot Springs, Yellowstone Natl. Park, *E. A. Mearns 1611* (DS,NY, US); Teton Mountains, Uinta Co., *A. & E. Nelson 6473* (GH,MO,NY,US,WYO-part). COLORADO. Rocky Mountains, latitude 39°–41°, 1862, *Hall & Harbour* (F,GH); Glenwood Springs, Garfield Co., *G. E. Osterhout 2120* (NY,WYO); Aldrich Lake, Rio Blanco Co., *Ramaley & Johnson 760* (UC). UTAH. Logan Canyon, Cache Co., *B. Maguire 3637* (GH, UC,WYO), *3639* (GH,UC,WYO); City Creek Canyon, Salt Lake Co., *M. E. Jones 1852* (DS,F,GB,NY,US,WYO), *P. A. Rydberg 6144* (NY,US,WYO); Forest Camp, Washington Co., *F. W. Gould 1846* (ARIZ,CLOKEY,GH,NY). ARIZONA. Mt. Lemmon, Pima Co., *Peebles, Harrison & Kearney 2581* (US); Mt. Graham, Graham Co., *Peebles, Harrison & Kearney 4483* (US); Pyles Ranch, under Mogollon Rim, Gila Co., *Mrs. R. E. Collom 753* (MO,US). NEVADA. La Moille Canyon, Elko Co., *A. H. Holmgren 1354* (NY,UC); Little Valley, Washoe Co., *C. F. Baker 1363* (GH,MO,NY,UC,US,WYO).

ALASKA. Unalaska, Aleutian Islands, *W. J. Eyerdam 2256* (S); Yakutat, *C. V. Piper 4283* (US), *4280* (US); Sitka, 1865–66, *F. Bischoff* (F,GH), *A. Kellogg 172* (US); Shaw Island, *J. P. Anderson 1382* (US); Hyder, *T. T. McCabe 8462* (UC); Glacier Bay, *Cooper & Andrews 233* (F). BRITISH COLUMBIA. Louise Island, Queen Charlotte Islands, 1900, *W. H. Osgood* (US); Bella Coola, *T. T. McCabe 1402* (UC); Observatory Inlet, *J. Scouler 139* (NY); Nanaimo, Vancouver Island, *C. O. Rosendahl 1885* (GH,MO,NY,US), *J. Macoun 78,610* (NY,US); Carbonate, *R. T. Shaw 219* (GH,MO,NY,S,US,WYO); Revelstoke, *C. H Shaw 860* (GH,MO,NY,US); Chilliwack Valley, *J. M. Macoun 44,491* (GH,NY), *4489* (US); near Emerald Lake, *C. H. Shaw 87b* (GH,MO,NY,S,US); Douglas *W. Spread-*

borough 79,445 (F,NY); Kootenai Lake, 1860, *D. Lyall* (K). WASHINGTON. Barnaby Creek, Ferry Co., *H. T. Rogers 568* (DS,GH,MO,NY,UC); Sherman Creek, Ferry Co., *Boner & Wildert 240* (DS,GH,MO,NY,WYO); Clarks Springs, Spokane Co., *F. O. Kreager 44* (CLOKEY,GH,NY,US); Tumwater Canyon, Chelan Co., *J. W. Thompson 8458* (DS,GH, MO,NY,UC,US); Falcon Valley, Klickitat Co., *W. N. Suksdorf 2115* (GH,MO,UC,US); Bingen, Klickitat Co., *W. N. Suksdorf 10,037* (DS,GH,MO,NY,UC,US), *5662* (DS,MO, NY,US); Godman Springs, Columbia Co., *Constance et al. 1162* (DS,GH,MO,UC); Friday Harbor, San Juan Co., *Zeller & Zeller 768* (GH,MO,NY); Seattle, King Co., *C. V. Piper 110* (DS,MO,US); upper valley of the Nisqually, Pierce-Lewis Cos., *O. D. Allen 34* (DS, MO,NY,UC,US); Olympic Mountains, Clallam Co., *A. D. E. Elmer 2774* (DS,MO,NY,US); Montesano, Grays Harbor Co., *Heller & Heller 3975* (GH,MO,NY,UC,US), 1919, *J. M. Grant* (K,MO,NY); Quiniault, Grays Harbor Co., *H. S. Conard 219* (GH,NY,US). OREGON. Oregon woods, *T. Nuttall* (GH,NY: type collection of *Washingtonia divaricata* Britton); Wallowa River, Wallowa Co., *Constance & Jacobs 1304* (MO,UC); Dixie Mt., Grant Co., *L. F. Henderson 5687* (DS,GH,MO); Fort Klamath, Klamath Co., *J. B. Leiberg 681* (GH,NY,S,UC,US); Portland, Multnomah Co., *Kellogg & Hartford 311* (MO,NY,US); Big Creek, Clatsop Co., *Constance & Beetle 2663* (GH,MO,NY,UC,US,WYO); Silver Creek, Marion Co., *E. Hall 216* (F,GH,MO,NY,US); Eight Dollar Mt., Josephine Co., *L. F. Henderson 6056* (DS,MO,WYO; Sykes Creek, Wimer, Jackson Co., *E. W. Hammond 157* (MO, NY,US), *157a* (MO,NY,US,WYO), *158* (MO,NY,US). CALIFORNIA. NE base of Mt. Eddy, Siskiyou Co., *A. A. Heller 12,467* (CLOKEY,DS,GH,MO,NY,US); Quartz Valley, Siskiyou Co., *G. D. Butler 1453* (DS,MO,UC,US,WYO); Mt. Shasta and vicinity, Siskiyou Co., *E. Palmer 2481* (US: type of *Washingtonia brevipes* Coult. & Rose); Shasta Springs, Siskiyou Co., *A. A. Heller 7978* (GH,MO,NY,US); Hatchet Creek, Shasta Co., *L. Benson 2210* (MO,NY,US); Eureka, Humboldt Co., *J. P. Tracy 2464* (DS,UC,US,WYO); Summit Lake, Lake Co., *A. A. Heller 5879* (DS,GH,MO,NY,UC,US,WYO); Napa Valley, Napa Co., 1853–54, *J. M. Bigelow* (NY: type of *Osmorhiza nuda* Torr.,GH,MO-photograph); Ukiah, Mendocino Co., *H. N. Bolander 4649* (F,GH,MO,US); Noyo, Mendocino Co., *L. Constance 2518* (DS,GH,MO,NY,UC,US,WYO); Petrified Forest, Sonoma Co., *A. A. Heller 5737* (DS,GH, MO,NY,US,WYO); Tiburon Peninsula, Marin Co., 1902, *A. A. Heller* (GH,MO,NY,US); Diamond Mt., Lassen Co., 1897, *M. E. Jones* (DS,MO,US); Nevada City, Nevada Co., *A. Eastwood 522* (GH,NY,US); Jonesville, Butte Co., *E. B. Copeland* (*Univ. Calif. Exsic. 391*) (ARIZ,DS,GH,MO,NY,S,UC,US,WYO); Emigrant Gap, Placer Co., *M. E. Jones 2734* (CLOKEY,MO,NY,US); "The Iceberg," Tuolumne Co., *I. L. Wiggins 9497* (DS,GH,NY, WYO); Pescadero, San Mateo Co., *A. D. E. Elmer 4285* (DS,MO,NY,US); W of Los Gatos, Santa Clara Co., *A. A. Heller 7430* (DS,F,GH,MO,NY,UC,US); Santa Lucia Mountains, Monterey Co., *E. A. Plaskett 52* (GH,NY,US); New York Falls, Agricultural Station, Amador Co., *G. Hansen 331* (DS,MO,NY,US); Yosemite Valley, Mariposa Co., *L. R. Abrams 4395* (DS,GH,NY,UC,US); Farewell Gap trail, Mineral King, Tulare Co., *Hall & Babcock 5667* (DS,UC); Sequoia Natl. Forest, Tulare Co., *Bacigalupi, Wiggins & Ferris 2605* (DS,GH,UC); Prairie Fork of San Gabriel River, Los Angeles Co., *I. M. Johnston 2084* (DS,UC); Lost Creek, San Bernardino Co., *Munz & Johnston 8562* (GH,NY); Palomar Mt., San Diego Co., *Epling, Darsie, Knox & Robison* (DS,MO,UC); Stonewall Mine, Cuyamaca Mountains, San Diego Co., *S. B. Parish 4421* (DS,GH,MO,NY,US).

ARGENTINA. Nequén: Polcahue, *H. F. Comber 461* (K). Rio Negro: Puerto Nuevo, Llaollao, *E. Ljungner 254* (GB), *377* (GB); El Cröhol, *R. de Barba 95* (UC); Puerto Blest–Laguna Frias, *J. West 4808* (GH,UC); Puerto Liu Nombre, *I. R. Cordini 92* (US); San Carlos de Bariloche, 1905, *O. Buchtien* (US), *L. R. Parodi 11,433* (GH). Chubut: Valle de la Laguna Blanca, *J. Koslowsky 85* (S). Santa Cruz: Valle 16 [-de-Octubre], 1882, *F. P. Moreno* (NY); Rio Jeinemeni, *Von Platen & Greiner 150* (MO).

CHILE. Aconcagua: Los Ojos de Agua, *T. Bridges 475* (K). Valparaiso: "Chili," 1830, *C. G. Bertero 74* (F,GH,UC, photographs); Linachi [Limache], 1828, *C. G. Bertero* (NY); Tagua Tagua, *C. G. Bertero 446* (GH: isotype of *Osmorhiza Berterii* DC); Valparaiso, *H. Cuming 335* (K); 8 km. from La Dormida, *J. L. Morrison 16,823* (GH,MO,UC). Santiago:

Quebrada del Manzano, Valle del Maipo, *A. Pirion 1233* (GH); Santiago. *Bro. Claude-Joseph 721* (US). Concepcion: Concepcion, *E. W. D. Holway 139* (GH,NY,US), *F. Jaffuel 3976* (GH), *1380* (GH); Gualpen (Parque Pedro del Rio), *H. Gunskel 9980* (GH). Cautin: Volcan Llaima, *E. Werdermann 1246* (F,GH,MO,NY,S,UC,US); Termas de Tolhuaco–Curacautin, *Morrison & Wagenknecht 17,486* (GH,UC); Temuco, *Bro. Claude-Joseph 1928* (US). Valdivia: "Los Canellos," *T. Bridges 768* (K); Valdivia, *H. Gunckel 2498* (GH), 1896–98, *O. Buchtien* (GH,US); Panguipulli, *Bro. Claude-Joseph 2568* (US). Chiloé: Ancud, Chiloé Island, *MacMillan & Erlanson 11* (S,US). Llanquihua: Puella, Lago Todos los Santos, *Holway & Holway 194* (US). Magellanes: 50 km. NW of Puerto Natales, *Eyerdam, Beetle & Grondona 24,181* (GH,MO,UC). "Chile," *E. C. Reed* (K).

11. *Osmorhiza obtusa* (Coult. & Rose) Fernald, Rhodora 4:154. 1902. (Pl. 29)

Scandix clavata Banks & Solander; Hook. f. Fl. Antartica 2: 288. 1846, as synon. Based upon *Banks & Solander*, "Good Success Bay," Tierra del Fuego.

Washingtonia obtusa Coult. & Rose, Contr. U. S. Nat. Herb. 7: 64. 1900.

Plants slender, 15–65 cm. high, the herbage sparsely, or rarely densely, hirsutulous to glabrate; leaf blades orbicular, 4–11 cm. long, biternate or ternate-pinnate, the leaflets broadly lanceolate to ovate, 1.5–5 cm. long, 1–3 cm. broad, obtuse or acute, coarsely serrate, incised or lobed, the leaflets and rachis sparingly hispid or hispidulous; petioles 3–20 cm. long; peduncles 5–15 cm. long, often divergent; involucre wanting, or often of a foliaceous bract; involucel wanting, or of one or more caducous bractlets; rays 2–5, widely divergent or some reflexed, 2–7 cm. long; pedicels 2–5, widely divergent, 10–30 mm. long; flowers greenish white, the styles and stylopodium about 0.5 mm. long, the latter low-conic or depressed; carpophore cleft about one-third of its length; fruit clavate, 8–15 mm. long, obtuse or abruptly acute at the apex, caudate at the base, the appendages 3–5 mm. long, densely hispid at the base.

Type locality.—"Ishawood [Ishawooa] Creek," northwestern Wyoming, *Rose 476.*

Distribution.—Labrador and Newfoundland to Vermont; Ontario and northern Michigan; Saskatchewan and Alberta to New Mexico, west to Alaska, south to northeastern California; extreme southern Argentina and Chile.

Although Banks and Solander apparently had prepared a plate of this entity, as *Scandix clavata,* it was never formally published. So far as we can learn, the species was not properly distinguished and described until 1900, and then from North American material. Indeed, the South American material of the species was apparently never distinguished from *O. chilensis,* although adequate collections were available to Hooker, Asa Gray, and others. Wildeman (1905) illustrated it beautifully under the name of *O. chilensis.* From the fact that Reiche referred to *O. depauperata* Philippi specimens from southernmost Chile, it may be suspected that he perceived a difference between *O. chilensis* (*O. Berterii*) and the plants from the Strait of Magellan, but he mentioned none of the characters by which *O. chilensis* and *O. obtusa* may be separated, and the actual identity of *O. depauperata* remains uncertain.

The angle of the rays and pedicels is slightly less in all the South American specimens examined than in some of the North American, but the fruits appear to be identical, and the foliar variations found on the two continents can be matched in detail (pl. 29). Some of the North American plants show a caducous involucel bractlet or two in the flowering stage, a feature which sometimes helps to separate them from *O. chilensis* and *O. purpurea.*

Several specimens available in herbaria give an apparently erroneous idea of the distribution of *O. obtusa,* and should perhaps be mentioned with a word

of caution. Two collections purportedly from the "summit of Mt. Angeles, Clallam Co." *J. B. Flett 3311* and *E. B. Webster 21,* are the sole indication of the occurrence of the species in Washington west of Mount Rainier. In view of the fact that Mount Angeles has been visited repeatedly by collectors, it is very doubtful that the species would have been obtained so infrequently if it actually occurs there. The two sheets were both obtained in August, 1911, and probably represent the same collection, but there has doubtless been a confusion of locality. Two sheets supposedly from "Sierra Co., Calif.," 1883, *J. G. Lemmon,* are to be questioned as to locality, since Lemmon's data are notoriously unreliable. The 1946 collection cited from the Warner Mountains of Modoc County is probably the only authentic record to date of the occurrence of this species in California.

Representative specimens.—LABRADOR. Capitan Island, *A. C. Waghorne 25* (GH); Forteau, 1893, *A. C. Waghorne* (MO). NEWFOUNDLAND. Nameless Cove–Mistaken Cove, Straits of Belle Isle, *Wiegand, Pease, Long & Hotchkiss 28,767* (GH,US); 4 miles NE of Port a Port, *Mackenzie & Griscom 10,362* (GH,US); Dildo Run, Notre Dame Bay, *Fernald, Wiegand & Bartram 5952* (GH,NY,US); Frenchman's Cove, Bay of Islands, *A. C. Waghorne 15* (GH,MO); Romaine Brook, *R. B. Kennedy 419* (GH,S). ANTICOSTI ISLAND. Rivière Vaureal, *Victorin, Germain & Marie 21,762* (GH,MO,US); Rivière au Fusil, *Victorin & Germain 27,340* (GH,MO,S,US); Rivière du Renard, *Victorin & Germain 27,139* (F,GH, MO,S). QUEBEC. Rivière du Loup, *W. W. Eggleston 2981* (DS,NY-part—not MO,US!); Grand River, Gaspé Co., 1904, *M. L. Fernald* (GH-part,NY,US); Mt. Albert, Gaspé Co., *Collins & Fernald 120* (GH,NY,S,UC,US), *Victorin, Brunel, Germain & Rousseau 17,592* (F,GH,MO,NY,US); Mt. Lyall, Gaspé Co., *Victorin, Germain & Jacques 33,546* (GB,GH, NY); Little Metis, 1906–08, *J. Fowler* (GH,MO,US); Bic, Rimouski Co., 1905, *F. F. Forbes* (DS,WYO); Bonaventure River, Bonaventure Co., *Collins, Fernald & Pease 5920* (GH). NEW BRUNSWICK. St. Francis, 1904, *Knowlton & Eaton* (GH). VERMONT. Mt. Mansfield, *J. M. Greenman 691* (MO).

ONTARIO. Thunder Bay district, *Taylor, Losee & Bannan 1142* (GH), *1143* (GH), *1144* (CLOKEY), *1145* (DS); Copper Island, *Hosie, Losee, & Bannan 2187* (UC), *2189* (GH). MICHIGAN. Isle Royale, *W. S. Cooper 123* (GH); Negaunee, Marquette Co., 1902, *P. A. Rydberg* (NY).

SASKATCHEWAN. Wallwort, *A. J. Breitung 651* (MO). SOUTH DAKOTA. Savoy, Black Hills, Lawrence Co., *H. E. Hayward 296* (F,NY); Roundhouse Gulch, Deadwood, Lawrence Co., *J. Murdoch 4195* (F,NY); Harney Peak region, Pennington Co., *H. E. Hayward 1986* (F,WYO).

ALBERTA. Stony Squaw Mt., Banff, *M. E. Moodie 1239* (F,US); Elbow River valley, Calgary, *M. E. Moodie 1056* (CLOKEY,DS,F,GH,NY,US); Saskatchewan River, Edmonton, *W. C. McCalla 3569* (UC); Atauwau Cabin, Slave Lake District, *A. H. Brinkman 4335* (NY); Rocky Mountains, 1858, *E. Bourgeau* (GH); Maligne Lake, Jasper Natl. Park, *E. Scamman 2658* (GH). MONTANA. McDougal Peak, Flathead Lake, *M. E. Jones 8603* (US); Midvale, Glacier Co., *L. M. Umbach 249* (NY,US—not F,WYO!); Swiftcurrent Creek, Glacier Natl. Park, *P. C. Standley 15,528* (US); Spanish Basin, Madison Range, *J. H. Flodman 687* (NY,US); Mystic Lake, Bozeman, Gallatin Co., *J. W. Blankinship 220* (F,MO,S,US). IDAHO. Near Sohons Pass, Shoshone Co., *J. B. Leiberg 427* (US); Papoose Creek, Idaho Co., *R. J. Davis 2398* (CLOKEY,UC); Henry Lake, Fremont Co., *Payson & Payson 1946* (GH,MO,NY,WYO); Mackay, Custer Co., *Nelson & Macbride 1485* (DS,GH, MO,WYO); Stanley Lake, Custer Co., *J. W. Thompson 14,029* (DS,F,GH,MO,NY,UC,US); Challis Creek, Custer Co., *Macbride & Payson 3332* (DS,GH,MO,NY,UC,US,WYO). WYOMING. Happy Jack Canyon, Albany Co., *L. O. Williams 1718* (GB,MO,S,WYO); Tie City, Albany Co., *A. Nelson 7661* (GH,MO,NY,US,WYO); 1 mile N of Centennial, Albany Co., *E. C. Rollins 940* (GB,MO,NY,UC); Centennial Valley, Albany Co., *A. Nelson 1722*

(GH,MO,US,WYO); Black Hills, *A. Nelson 9457* (DS,GH,NY,US,WYO); Bridger Peak, Carbon Co., *L. N. Goodding 1969* (GH,MO,NY,UC,US,WYO); 10–15 miles E of Kane, Big Horn Co., *Williams & Williams 3030* (GB,GH,MO,NY,UC,WYO); Ishawooa Creek, Park Co., *J. N. Rose 476* (US: type of *Washingtonia obtusa* Coult. & Rose); Crazy Woman Creek, Park Co., *Williams & Williams 3511* (GB,GH,MO,NY); Bradley Creek, Grand Teton Natl. Park, *L. O. Williams 1128* (GB,MO,S,WYO); Teton Pass, Teton Co., *Merrill & Wilcox 1021* (GH,NY,US,WYO). COLORADO. Pennock's Mt. Ranch, Larimer Co., *C. S. Crandall 1442* (MO,NY,US,WYO); Upper Clear Creek Valley, Jefferson Co., 1874, *G. Engelmann* (GH,MO); Georgetown, Clear Lake Co., *M. E. Jones 514* (DS,GB,NY,UC); Trapper's Lake, Garfield Co., *F. J. Hermann 5459* (GH,MO,US); Jack Brook, El Paso Co., *Clements & Clements 236* (DS,GH,MO,NY,US,WYO); vicinity of Mt. Carbon, Gunnison Co., *W. W. Eggleston 5814* (GH,NY,US); Cedar Edge, Delta Co., *C. F. Baker 240* (GH,MO,NY,UC, US,WYO); Sierra Mojada, Fremont Co., *T. S. Brandegee 555* (F,MO,UC); San Francisco Canyon, Las Animas Co., *R. C. Rollins 1844* (GH,MO,NY,UC); Sangre de Christo Creek, Costilla Co., *Rydberg & Vreeland 5829* (NY,US,WYO); near Pagosa Peak, Mineral Co., *C. F. Baker 510* (GH,MO,NY,US,WYO); La Plata P. O., La Plata Co., *Baker, Earle & Tracy 849* (GH,MO,NY,US,WYO); Upper West Mancos Cañon, Montezuma Co., *Baker, Earle & Tracy 188* (GH,MO,NY,US,WYO). UTAH. Wasatch Mountains, Uintahs, *S. Watson 446* (GH,NY,US); Chain Lakes trail, Duchesne Co., *F. J. Hermann 5249* (GH,MO,US); Cottonwood Canyon, Salt Lake Co., *A. O. Garrett 1621* (GH,NY,US,WYO); Rock Creek 10 miles E of Sunnyside, Carbon Co., *E. H. Graham 9599* (CLOKEY,F,GH,MO); Middle Forks Park, San Pete Co., *B. Maguire 20,035* (GH,NY,UC); Slate Canyon, Provo, Utah Co., *M. E. Jones 5580* (MO,NY,UC,US,WYO); LaSal Mountains, Grand Co., *Payson & Payson 3951* (DS,GH,MO,UC,WYO); Marysvale, Piute Co., *M. E. Jones 5893t* (MO,NY, US); Abajo Mountains, San Juan Co., *Goodman & Hitchcock 1437* (MO,NY,WYO), *Rydberg & Garrett 9821* (NY,US,WYO). NEW MEXICO. Santa Fe Cañon, 9 miles E of Santa Fe, Santa Fe Co., *Heller & Heller 3822* (DS,GH,MO,NY,US); Apache Peak, Taos Co., *W. W. Eggleston 19,249* (US); Navajo Indian Reservation, Tunitcha Mountains, *P. C. Standley 7668* (US); Winsor Creek, Pecos River Forest, *P. C. Standley 4041* (GH,MO, NY,US,WYO); Ruidosa Creek, White Mountains, *L. C. Hinckley 726* (ARIZ,F,GH,NY, TEX,UC); Cloudcroft, Sacramento Mountains, Otero Co., 1899, *E. O. Wooton* (MO,NY, US,WYO); Hillsboro Peak, Black Range, Grant Co., *O. B. Metcalfe 1206* (F,GH,MO,NY, US). ARIZONA. Humphrey's Peak, San Francisco Mountains, *D. T. MacDougal 397* (ARIZ, GH,NY,UC,US,WYO); Luka-Chukai Mountains, Apache Co., *Goodman & Payson 2816* (CLOKEY,GH,MO,NY); Rustler Park, Chiricahua Mountains, Cochise Co., *R. S. Ferris 9950* (CLOKEY,DS,GH,TEX); Soldiers Camp, Santa Catalina Mountains, *Goodman & Hitchcock 1253* (MO,NY,WYO). NEVADA. Little Falls, Charleston Mountains, Clark Co., *I. W. Clokey 8050* (DS,GH,MO,NY,US,WYO), *5547* (CLOKEY,GH,NY,UC,US,WYO).

ALASKA. Coopers Landing, *J. P. Anderson 6882* (GH,WYO); Valdes, *C. V. Piper 4288* (US); Point Gustavus, Glacier Bay, *Coville & Kearney 726* (US). BRITISH COLUMBIA. Peace River valley, vicinity of Hudson Hope, *Raup & Abbe 3640* (F,NY,S); Wicked River near the Peace, *Raup & Abbe 3878* (F,GH,NY,S); 15 miles SW of Kleena Kleena, *T. T. McCabe 606* (UC); 3 miles N of Takla Landing, *T. T. McCabe 7916* (UC); Upper Hat Creek, Marble Mountains, *Thompson & Thompson 523* (MO,NY,UC,US); Lake Bootahnie, Marble Mountains, *Thompson & Thompson 112* (MO,NY,UC,US); Sheep Mt., 34 miles N of Natal, *W. A. Weber 2373* (GH,NY,UC). WASHINGTON. Ashnola River, Okanogan Co., *W. W. Eggleston 13,385* (US); Natches Pass, Yakima region, 1882, *F. Tweedy* (NY); Wenatchie region, *T. S. Brandegee 794* (GH,UC). OREGON. S of Prairie City, Grant Co., *Ferris & Duthie 831* (DS,WYO); Upper Paulina Creek, Crook Co., *J. B. Leiberg 555* (NY,S,UC,US); near Garden of the Gods, Crater Lake, Klamath Co., *A. A. Heller 13,469* (DS,MO,NY,US). CALIFORNIA. Deep Creek, Warner Mountains, Modoc Co., *L. Constance 3104* (UC).

ARGENTINA. Santa Cruz: Cape Fairweather, *Capt. King* (K). Tierra del Fuego: Estancia la Esperanza, 80km. inland from Rio Grande, *Y. Mexia 7925* (F,GB,GH,MO,NY,UC,US);

Orange Harbor, 1838–42, *Wilkes Exped.* (GH,NY,US); Mt. Susanna, 1933, *P. Jordan* (GH); Ushuaia, *C. Skottsberg 134* (S); Tierra del Fuego, *M. Gusinde 48* (GB); †Rosvig, *A. Donat 348* (F,GH,NY).

CHILE. Ñuble: Termas de Chillan, *F. Jaffuel 3765* (GH). Magellanes: 15 km. NW of Punta Arenas, *Eyerdam, Beetle & Grondona 24,105* (GH,UC); Punta Arenas, 1872, *J. H. Blake* (GH), *P. Dusén 153* (S), 1866–67, *R. O. Cunningham* (GH,K,NY), *W. Lechler 1186* (K,S), *W. E. Safford 26* (NY); Paso Famine, 1869, *R. O. Cunningham* (K); Laredo Bay, 1888, *L. A. Lee* (US); Fretum magellanicum, 1851–53, *N. J. Andersson* (NY,S,US); Magalhaens Land, *N. J. Andersson 310* (S).

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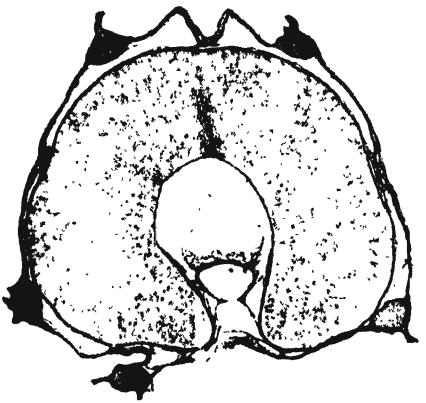
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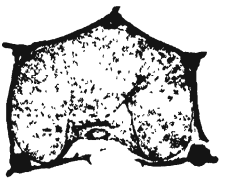
PLATE 26

Transverse sections of *Myrrhis* and *Osmorhiza* mericarps. × 17.

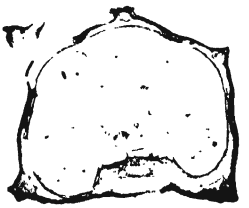
1. *Myrrhis odorata* (pericarp collapsed); Kyrkslätt, Nyland, Finnland, 1907, *H. Lindberg* (MO,UC).
2. *Osmorhiza occidentalis;* Teton Pass, Teton Co., Wyoming, *A. Carter 1656* (GH,NY,UC).
3. *O. glabrata;* Valdes-Tal, Cordillera de Santiago, Chile, 1936, *C. Grandjot* (US).
4. *O. bipatriata;* Mt. Livermore, Davis Mountains, Jeff Davis Co., Texas, 1937, *L. C. Hinckley* (ARIZ,GH,NY).
5. *O. mexicana;* Esperanza, Puebla, Mexico, *C. A. Purpus 7456* (MO,NY, UC,US).
6. *O. brachypoda;* Laguna Mountains, San Diego Co., California, 1904, *T. S. Brandegee* (UC).
7. *O. longistylis;* Bluff Lake, St. Clair Co., Illinois, 1878, *H. Eggert* (MO, NY,UC,US,WYO).
8. *O. aristata* var. *laxa;* Keran, Kishenganga Valley, Kashmir, India, *Stewart & Stewart 17,544* (NY).
9. *O. Claytoni;* Lac Ouimet, St. Jovite, Terrebonne Co., Quebec, 1922, *J. R. Churchill* (GH,MO).
10. *O. purpurea;* Sohons Pass, Shoshone Co., Idaho, *J. B. Leiberg* (DS,GH, NY,UC,WYO).
11. *O. chilensis;* Mad–Trinity rivers, Trinity Co., California, *L. R. Abrams 6222* (DS,NY).
12. *O. chilensis;* Termas de Tolhuaco–Curacautin, Cautin, Chile, *Morrison & Wagenknecht 17,486* (GH,UC).
13. *O. obtusa;* Luka-Chukai Mountains, Apache Co., Arizona, *Goodman & Payson 2816* (CLOKEY,GH,MO,NY).
14. *O. obtusa;* Tierra del Fuego, Argentina, *Y. Mexia 7925* (F,GB,GH,MO, NY,S,UC,US).



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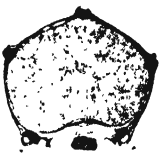
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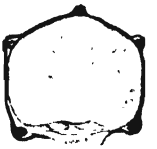
11



12



13



14

PLATE 27

Typical specimens of *Osmorhiza glabrata* and *O. bipatriata*

1. *O. glabrata;* Valdes-Tal (Volcantal), Cordillera de Santiago, 1936, *C. Grandjot* (US).
2. *O. bipatriata;* Mt. Livermore, Davis Mountains, Jeff Davis Co., Texas, 1937, *L. C. Hinckley* (NY: type).



[1]



[2]

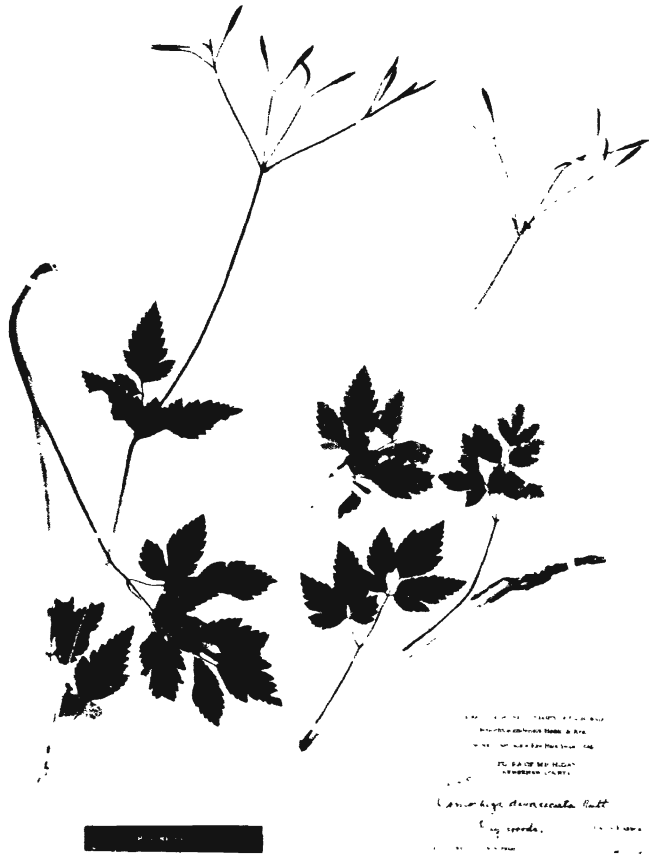
PLATE 28

Typical specimens of *Osmorhiza chilensis*

1. Panguipulli, Valdivia, Chile, *Bro. Claude-Joseph 2568* (US).
2. Eagle Harbor, Keweenaw Co., Michigan, *Fernald & Pease 4453* (NY).



[1]



[2]

PLATE 29

Typical specimens of *Osmorhiza obtusa*

1. Estancia la Esperanza, Tierra del Fuego, Argentina, *Y. Mexia 7925* (S).
2. Rivière du Renard, Anticosti Island, Quebec, *M.-Victorin & R.-Germain 27,159* (GH).



[1]



[2]

STUDY IN THE EVOLUTION OF THE SUNFLOWER SPECIES HELIANTHUS ANNUUS AND H. BOLANDERI

BY

CHARLES B. HEISER, JR.

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STUDY IN THE EVOLUTION OF THE SUNFLOWER SPECIES HELIANTHUS ANNUUS AND H. BOLANDERI*

BY

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IN RECENT years, important contributions to systematic botany have been made by the use of disciplines new to the taxonomist. These newer approaches combined with the stand-bys of comparative morphology and geographical distribution are shedding light on problems of both inter- and intraspecific relationships. The works in this country of Babcock, Anderson, and Clausen, Keck, and Hiesey provide good examples of the application of the new techniques. In the present study of two annual species of *Helianthus* in California, an attempt has been made to employ certain of the newer approaches. The usual field and herbarium studies have been supplemented by field and greenhouse plantings and cytogenetical investigations.

The common sunflower, *H. annuus,* occurs as a weed throughout the greater part of the United States and adjacent parts of Canada and Mexico, and domesticated forms of it are cultivated throughout most of the world. This species is extremely variable. Part of the observed variation is due to ecological modification of the phenotype, but a great deal of true genetic diversity exists within the species.

The wide distribution of *H. annuus* in the United States is probably a direct result of its weedy tendencies and its introduction by man into many regions. It is extremely doubtful if the species occurs in any area undisturbed by man. In many parts of the Middle West and occasionally in the eastern United States, the sunflower is found in railroad yards, about waste places, and to a lesser extent along roadsides. Throughout most of the western United States the sunflower is particularly common along roadsides and railroad rights of way. The race occurring in the western United States is in general much smaller than the eastern race and has fewer rays, a smaller disk, and leaves which may be truncate rather than cordate. The two races appear to intergrade freely in many regions and it is difficult to determine to which form a single herbarium specimen should be referred. However, when whole populations are examined or when the two forms are grown together in the experimental

* This paper embodies a portion of a thesis entitled "Hybridization and Variability in the Sunflower Species, *Helianthus annuus* and *H. Bolanderi* in California" submitted in partial fulfillment of the requirements for the degree Doctor of Philosophy at the University of California in 1947. The writer wishes to express his thanks to Drs. H. L. Mason, G. L. Stebbins, Jr., and Lincoln Constance for their helpful suggestions and criticisms. During the study, specimens have been consulted from several herbaria, the Arnold Arboretum and Gray Herbarium of Harvard University, the University of California, the California Academy of Sciences, the Dudley Herbarium of Stanford University, the Missouri Botanical Garden, the University of Oregon, Pomona College, and Willamette University. The writer expresses his appreciation to the curators of these herbaria for making specimens available for study. Thanks are also due the writer's wife and many colleagues who have made collections of plants and seeds or read portions of the manuscript.

garden the differences are frequently striking. Both races occasionally may cross with the cultivated sunflower.

Hybridization with other species of annual sunflowers resulting in introgression has greatly increased the variability of this species. Reciprocal introgression between *H. annuus* and *H. petiolaris* is known to occur (Heiser, 1947) and, judging from circumstantial evidence, hybridization between *H. annuus* and *H. debilis* var. *cucumerifolius* in Texas also takes place. A successful cross between these two species has been reported by Cockerell (1915) and has also been made by the writer.

In all probability *H. annuus* was not introduced into California until fairly recently. The early botanists in California did not consider it indigenous (Greene, 1897, Parish, 1920). It may well have been introduced by Indians. It is known that sunflower seeds were an important item in the diet of many Indians, and moreover, the "flowers" often had ceremonial usage. Blankinship (1905), Castetter (1935), Chamberlin (1911), Coues (1893, 1897), Dodge (1870), Gilmore (1919), Havard (1895), Newberry (1887), Palmer (1878), Pickering (1848), and Stephens (1936) have reported the use of wild sunflowers by Indians of the western United States. Pickering listed an annual species of *Helianthus* as being recently introduced into northwestern America. He mentioned this as being the only weed which he saw growing around the native villages of interior Oregon and stated that it was, perhaps, aboriginally introduced from the south. He added, "I met the same plant however, at the California settlements." He was probably speaking of either *H. annuus* or *H. Bolanderi,* the former being the more likely.

The use of sunflowers by the Indians of California has been noted by a number of authors (Kroeber, 1925; Sparkman, 1908; Stewart, 1933; and Voegelin, 1938). Kroeber and Sparkman list *H. annuus* among the food plants of the Luiseño Indians of southern California. No particular species is given by Voegelin for the sunflowers used by the Indians of the Kern River Valley, and *H. Bolanderi* is listed by Stewart for the Owens Valley Paiutes. Since the latter locality is completely outside the known range of *H. Bolanderi,* this reference is probably incorrect; *H. annuus* would be much more probable. Although there is no absolute proof, the view held here is that *H. annuus* was introduced into California by the Indians. Little or no evidence supports the reverse hypothesis that *H. annuus* was native to California and subsequently moved eastward. Dr. Marion Ownbey in a letter to the writer expresses the feeling that *H. annuus* is not native to Washington. He writes, "... there are vast areas in which it does not appear even as a weed.... Physiologically, it appears to be out of adjustment with (1) our very dry summers, and (2) our very wet winters." The latter statement would also apply very well to California. The probable reason for the successful invasion of large areas of California by *H. annuus* as a weed occupies a rather important part of this paper and will be dealt with in later sections.

With the coming of the white man, *H. annuus* was probably repeatedly introduced into California and it has now attained a rather wide distribution

in the state (fig. A, p. 164). It is found along roadsides and railroad tracks, and occurs also as a weed in cultivated fields. The cultivated form of *H. annuus* is grown in the state as a field crop and is also very common as a garden plant.

Helianthus Bolanderi, a native annual sunflower of California and Oregon, comprises two races, the first apparently confined to serpentine outcrops of foothill regions and the second as a ruderal or weed in the central and northern valleys of California in much the same situations as *H. annuus.* The blooming periods of *H. Bolanderi* and *H. annuus* overlap, and hybridization between the two may occur.

Two other annual species, *H. petiolaris* Nutt. and *H. Jaegeri,* are known to occur in California. Gray (1876) reports the sparse occurrence of *H. petiolaris* in the eastern and southern parts of the state and adds that it "seemingly passes into depauperate forms of the preceding" (*H. annuus*). Parish (1920) lists *H. petiolaris* as an introduction, and says it is found in certain areas in the southern half of the state. In the Los Angeles region *H. annuus* and *H. petiolaris* grow in close proximity and hybrids between them may be expected, although as yet none have been reported. Certain specimens from a population sample of *H. petiolaris* var. *canescens* collected by Stebbins in San Joaquin County strongly suggest that introgression with *H. annuus* has taken place.

Helianthus Jaegeri has only recently been described (Heiser 1948). Thus far it is known from only one locality in San Bernardino County. Four perennial species of *Helianthus* occur in California, but they do not enter into the present problem and will not be discussed here.

TAXONOMY

The genus *Helianthus* dates from 1753, when Linnaeus described *H. annuus.* The most complete early treatment of the genus is that of Asa Gray in the Synoptical Flora (1884). The California species treated in the present paper were, of course, included in the floras of Brewer and Watson by A. Gray (1876), Greene (1897), and Jepson (1925). The nearest approach to a monographic treatment is E. E. Watson's "Contributions to a monograph of the genus *Helianthus*" (1929), which is valuable chiefly because it is the sole work of its kind. His treatment is unsatisfactory in that he does not divide the genus into sections, his key is cumbersome and essentially unusable, he fails to include an index to either species or synonyms, and he cites few specimens. However, inasmuch as he attempts to treat over one hundred species in his work, some of these shortcomings are understandable. His work has been criticized previously by Cockerell (1929) who himself made many contributions to our knowledge of the genus.

The common sunflower, since shortly after its introduction into Europe, has been described and named many times. The earliest descriptions were made by the herbalists, who usually figured the plant rather prominently despite its lack of medicinal value. Both Cockerell (1915) and Watson (1929) have gone into the matter of the synonymy to some extent. Cockerell states that Linnaeus based his type on the large cultivated form. The plant may

have been cultivated, but the type is certainly not the same as the giant monocephalic cultivated form discussed in this paper. I have had the privilege of examining a photograph of the type from the Arnold Arboretum. Only the upper portion of the plant is available, but it is clearly branched and the head appears to be much smaller than that of the typical cultivated sunflower. The nomenclatorial type appears to be very similar to the form common about towns and cities in the Middle West and found occasionally more eastwardly. In the present paper this race will be referred to as the ruderal sunflower, because of its apparent affection for rubbish heaps and dumps.

The name *H. lenticularis* Dougl. (1829) has received considerable usage for the western races of *H. annuus,* and Cockerell (1914) assigns it subspecific rank under *H. annuus.* I have not seen the type but the original description is accompanied by an excellent drawing which had been reproduced here as plate 30. The text states that the number of rays is 36, but the illustration clearly shows 22. According to the original publication the distribution of *H. lenticularis* is the interior and west coast of North America, and the description, except for the high ray number given, is fairly typical of the western races as a whole. This assemblage of plants is to be referred to here as the western race.

No formal subspecific categories have been erected for the various races of *H. annuus* discussed here. Although there are slight morphological differences, it is very difficult, if not impossible, always to distinguish the two from herbarium material. Very broad geographical ranges have been used in discussing the races (western *vs.* ruderal) for their distribution has not yet been worked out in detail. Both are weeds, which complicates any study of their exact relationship, for in weeds man has frequently obliterated any geographical distinction that may have existed among subspecies. It is not surprising, therefore, to find the western race cropping up in the Middle West or the ruderal in the West. Much further study will have to be devoted to the problems of morphology, geographical distribution, and ecological preferences before the races can be dignified with scientific names.

Helianthus Bolanderi was first described by Bentham in 1844 as *H. scaberrimus* from Bodega. I have not examined the type, but the description agrees fairly closely with that of *H. Bolanderi.* However, the name *H. scaberrimus* had been applied earlier to a perennial species of the genus by Elliott, hence Bentham's name is a later homonym. The next published name, *H. Bolanderi* A. Gray, thus becomes valid. Both *H. Bolanderi* and *H. exilis* were published simultaneously by A. Gray (1865). Watson (1929) adopted the name *H. Bolanderi,* and according to the International Rules this must be followed.

I have examined the types of *H. Bolanderi* (*Bolander 3958*)[1] and *H. exilis* (*Bolander 2623*) from the Gray Herbarium (pls. 31 and 32) and isotypes in the Herbarium of the University of California. The two described entities appear to be quite distinct. The specimens of *H. Bolanderi* have large heads and

[1] The italicized citations used throughout this paper refer to collections of sunflower species. When the number is used alone, the collections are those of the writer.

large (13.5 × 7.5 cm.) crenate-serrate lower leaves. The two specimens of *H. exilis* have much smaller heads and smaller (5.3 × 1.2 cm.) entire lower leaves. There is no locality given on the type of *H. Bolanderi,* but the University of California specimen has the data, "At the Geysers, Lake Co."[2] The locality for the plants of *H. exilis* is given as Clear Lake (Lake Co.). On the type sheet of *H. exilis* are three specimens; these are from left to right: (1) "*H. petiolaris,* Van Horn at Owens Valley,"—this poor specimen is either a depauperate *H. annuus* or a hybrid derivative; (2) undetermined, bearing a lightly penciled, "Siskiyou Co.—Greene," and is the valley weed form of *H. Bolanderi;* (3) the actual type.

From a mere examination of the types, one would be inclined to follow Asa Gray in regarding *H. Bolanderi* and *H. exilis* as distinct species. If a larger series of specimens is examined, however, it will be found that the two so overlap morphologically that they cannot be delimited satisfactorily by any one character or any series of characters. Although there is little doubt that two entities are involved, only one can be maintained as a species; Watson was the first to regard them as parts of the same species.

Of the entities comprising *H. Bolanderi,* the one Gray designated *H. exilis* appears to be confined almost exclusively to areas of serpentine outcrops in many of the foothill regions of California, whereas true *H. Bolanderi* occurs in the valleys as a weed. The former generally has smaller stature, leaves, and achenes, fewer rays, smaller disks, and occasionally a slightly different pubescence (table 1, pp. 162–163). Growing the two entities in the greenhouse and the experimental garden has revealed that many of these differences are genetically controlled.

The two races of *H. Bolanderi* conform to the definition of the "ecotype" of the experimental taxonomist. Only a few crosses have been made between the two races, and from the limited data obtained it appears that the offspring of such crosses may either be as fertile as the parents or may show a high degree of sterility similar to that observed when crossing species of annual sunflowers.

The valley weed race of *H. Bolanderi* appears to have originated wholly or in part through interspecific hybridization between *H. annuus* and the serpentine form of *H. Bolanderi* in a manner which will be discussed later. The application of a name here may be justified after further study, for this race—although highly variable—does have slight morphological distinction and ecological preference different from the serpentine form. But until more experimental work can be undertaken, it would not appear wise to give formal taxonomic recognition to the two races.

[2] The writer has not visited the type locality of *H. Bolanderi.* However, a visit was made to the Sonoma Geysers in northern Sonoma County. The specimens found there were growing in abundance in the warm soil near or in the seepage from the hot springs. The plants varied greatly in size from about a foot high (corresponding more or less to "*H. exilis*") to nearly six feet in height (corresponding to "*H. Bolanderi*"). The plants here were in bloom on May 17, nearly a month earlier than either race of *H. Bolanderi* in other localities. Seeds from these plants have not yet been grown. It is possible that they may constitute a distinct ecotype of *H. Bolanderi.*

TABLE 1

COMPARISON OF MORPHOLOGICAL FEATURES OF HELIANTHUS ANNUUS, H. BOLANDERI AND THEIR HYBRID

	1 *H. Bolanderi* (serpentine, foothill race)	2 *H. Bolanderi* (valley weed race)	3 *H. annuus* × *H. Bolanderi*	4 *H. annuus* (western)	5 *H. annuus* (ruderal)
Height	3–10 dm.	6–13 dm.	6–15 dm.	8–18 dm.	12–24 dm.
Leaf Shape	Linear-lanceolate to ovate-lanceolate, cuneate at base	Ovate-lanceolate to ovate, cuneate, rarely truncate at base	Ovate-lanceolate to ovate, cuneate to truncate at base	Ovate-lanceolate to ovate, truncate to cordate at base	Ovate, rarely ovate-lanceolate, cordate, rarely truncate at base
Margin	Entire to shallowly irregularly serrate	Rarely entire, usually regularly to irregularly serrate	Shallowly to deeply serrate	Regularly deeply serrate	Regularly deeply serrate
Involucre Shape	Convex	Convex	Low convex	Low convex	Low convex to nearly flat
Bracts	3.0–4.0 mm. broad, oblong to lanceolate, gradually attenuate, equaling or exceeding head	3.5–4.5 mm. broad, otherwise much as in 1	5.0–7.0 mm. broad, lanceolate to ovate, more abruptly attenuate than in 1 and 2, less so than in 4 and 5, equaling heads	5.0–7.0 mm. broad, lanceolate-ovate to ovate, abruptly attenuate, equaling head	6.0–10.0 mm. broad, ovate to lanceolate-ovate, otherwise as in 4
Pubescence	Hirsute or hirsute-villous	Hirsute, rarely somewhat hispid	Hirsute to hispid	Hispid	Hispid
Diameter of disk	1.5–2.0 cm.	1.7–2.5 cm.	2.0–3.0 cm.	2.5–3.5 cm.	3.0–5.0 cm.

Middle cusp (awn) of the chaff	Erect, long and slender, glabrous at tip, exceeding disk flowers	As in 1	Semierect, long and fairly slender, glabrous at tip, exceeding disk flowers	Curved over disk flowers, broad, hispid almost to tip, less than or equaling disk flowers	As in 4
Ray					
Apex	Deeply bifid	Deeply bifid	Bifid to entire	Entire or shallowly bifid	As in 4
Number	10–13	12–17	14–20	17–24	21–35
Size					
(length	1.3–1.9 cm.	1.4–1.9 cm.	1.8–3.7 cm.	2.5–3.9 cm.	3.0–4.0 cm.
×					
width)	0.7–0.9 cm.	0.7–0.9 cm.	1.0–1.6 cm.	0.9–1.3 cm.	1.0–1.3 cm.
Disk–corolla length	4–6 mm.	5–7 mm.	6–7 mm.	6–8 mm.	7–8 mm.
Achenes, length	3.0–4.0 mm.	3.5–4.5 mm.	About 4 mm.	4.0–5.5 mm.	4.5–7.0 mm.

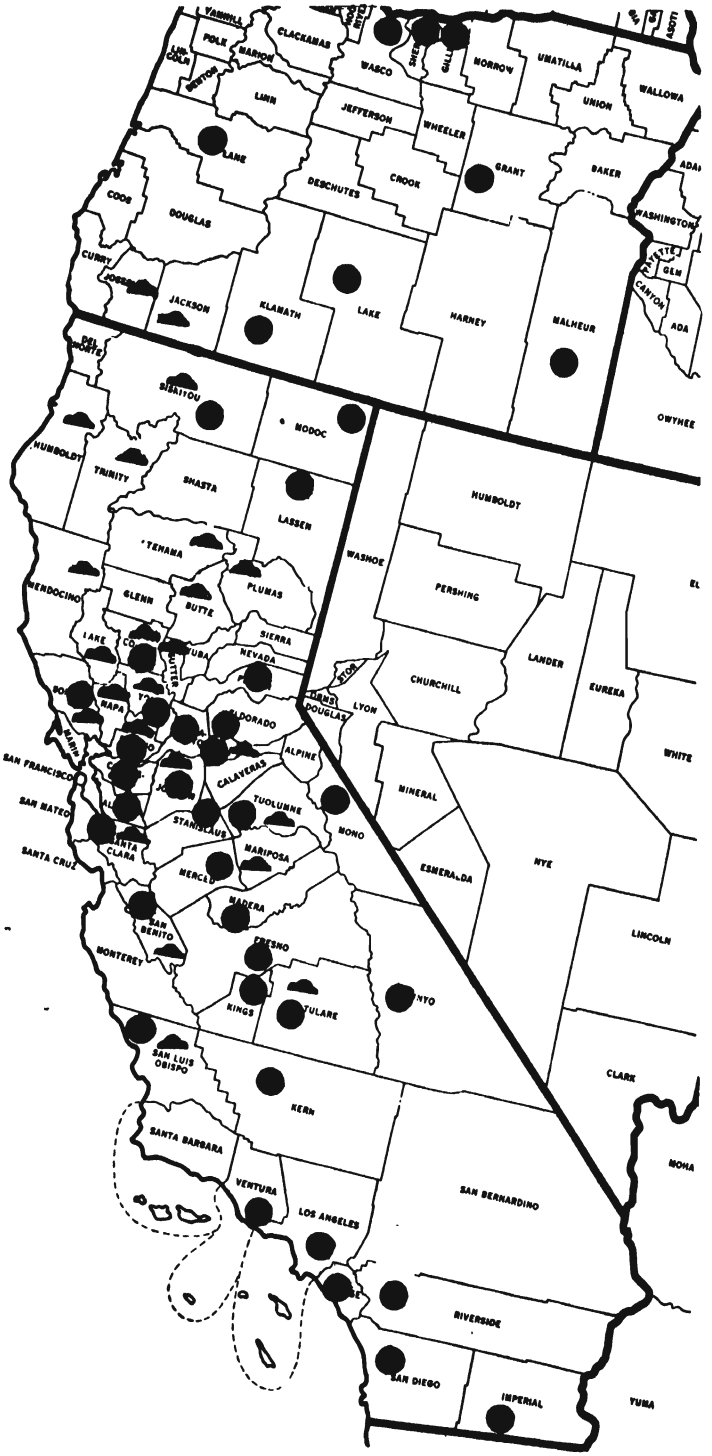


Fig. A. Map showing the distribution of *Helianthus annuus* (large dots) and *H. Bolanderi* (small designs) in California and Oregon by counties. (Distribution of *H. annuus* in neighboring states not shown.)

The taxonomic status of the hybrids requires some discussion. The International Rules provide for a formular treatment or the assignment of a distinct specific name to hybrids between two species. Following these recommendations, the hybrid *H. annuus* × *H. Bolanderi* is recorded by the use of a formula.

The matter of the naming of hybrids has received the consideration of Allan, Sprague, and Uittien in *Chronica Botanica* (1939). The suggestion of Allan's, with which Sprague agrees, that it is wisest to remain content with a formular treatment and that each author must evolve a method best suited to his needs, appears sound. Uittien suggests that the words "hybrid" and "half-breed" be suppressed and adds that "It is undesirable to introduce genetical methods into taxonomy and to use genetical terms in descriptive botany." In another place he says that when there is occasion to distinguish different "hybrid" forms of the same parentage, each of these may be designated by a separate specific or varietal name.

It is this writer's opinion that nothing would be gained by suppressing the familiar words "hybrid" and "half-breed" for they have entered the language and continue to constitute a serious problem. Moreover, in regard to the introduction of genetical methods into taxonomy, it is becoming more and more evident that many great advances in taxonomy today are coming about through the introduction of genetical and cytological methods; consequently the need for genetical terms in taxonomy will probably increase. And to distinguish different "hybrid" forms of the same parentage by separate names is hardly justified. It would probably be possible to distinguish 25 or more "forms" from a hybrid swarm of *H. annuus* × *H. Bolanderi*. Perhaps the most significant statement to come out of the symposium on names for hybrids was Allan's remark that "more intensive studies of wild hybridism are necessary before we can assess its full significance for taxonomy." Anderson and Hubricht (1938) in one such study concluded that the effects of introgressive hybridization in *Tradescantia* were too slight to merit nomenclatorial recognition.

GEOGRAPHICAL DISTRIBUTION IN CALIFORNIA

The broad distribution of *H. annuus* and its probable introduction into California has already been discussed (p. 157); *H. annuus* has now acquired a rather wide distribution in California (fig. A). The common sunflower is rather abundant in southern California except in the Mojave Desert region, and is widespread in most of the Great Valley, ranging into northern California and the Sierras.

Helianthus Bolanderi is restricted to central and northern California and southern Oregon, as shown in fig. A. As previously stated, it is not always possible to distinguish the two races in herbarium material. Plants which appear to belong to the foothill race of *H. Bolanderi* have been collected in Siskiyou, Trinity, Humboldt, Plumas, Tehama, Mendocino, Colusa, Lake, Napa, Amador, Tuolumne, and San Luis Obispo counties; those of the valley

weed race in Siskiyou, Butte, Sutter, Colusa, Lake, Yolo, Sonoma, Amador, Solano, Tuolumne, San Joaquin, Santa Clara, Mariposa, San Benito, Tulare, and San Luis Obispo counties. This does not agree entirely with the distribution given by Jepson (1925) for the two entities.

A comparison of the distribution of *H. Bolanderi* with the Geologic Map of California (Jenkins, 1938) reveals that (although certain areas are unmapped) most specimens of the foothill race of *H. Bolanderi* occur in areas marked "Jurassic ultra-basic intrusives," which include serpentine. From field experience, it has been found that this race definitely occurs on or near serpentine outcrops in Lake, Colusa, and Napa counties. Additional field work will be necessary to determine whether this relationship holds throughout California. The valley race of *H. Bolanderi* occurs mainly in the valleys of northern and central California.

It is apparent from an examination of the map that the distributions of *H. annuus* and *H. Bolanderi* overlap considerably in central California, and provide opportunities for hybridization in this region. Hybrids have been found in Colusa, Solano, and Yolo counties (*Stebbins* and *Heiser 5, Heiser 1857, 1859, 1864, 1865, 1866, 1867, 1868, 1869, 1870* and *1954*). This is the area in which the writer has collected most extensively.

Hybrids between cultivated *H. annuus* and weed *H. annuus* have also been found in California (not shown on map; *Heiser 1856, 1860*). Mackie (oral communication) reports that they are not uncommon in southern California. This hybrid has also been found in other parts of the United States.

The map (fig. A) has been compiled from the specimens in the herbaria of the California Academy of Sciences, the Missouri Botanical Garden, the University of Oregon, Pomona College, Stanford University, and Willamette University, in addition to those in the Herbarium of the University of California and the writer's personal collection; most of the latter is to be deposited in the Herbarium of the University of California.

MORPHOLOGY

The chief morphological criteria which have been employed here to distinguish the various entities are listed in table 1. Although descriptions of the two species will be found in Watson (1929, pp. 348, 357) it is necessary to discuss the more important morphological features used in this study. It is chiefly through the study of morphology, supplemented by cytogenetical investigation, that the conclusions concerning introgression have been reached. Certainly a thorough understanding of the morphology of the parent species is necessary before any consideration can be given to the effects of hybridization.

The measurements used in the table show the approximate normal ranges found in the various entities. Generally the measurements, with the exception of those of the rays, are based on dried material. The size and number of rays have proved to be very important, but these characters are frequently of little value in herbarium specimens. Depauperate plants, deprived of the necessary water, light, or soil for good growth, are very common among the

annual sunflowers and their identification from herbarium material is very difficult. A great many herbarium specimens of sunflowers consist of only the upper part of the plant, and frequently the disks are so mounted that it is impossible to examine both the disk flowers and the involucral bracts. For these reasons it is difficult to score herbarium material and hence it has been necessary to depend almost entirely upon the writer's own collections, but supplemented, of course, with study of herbarium specimens. Mass collections (population samples) of the annual sunflowers, in which each collection includes a branch with two or three heads from a plant in fruit and flower (if possible) and one or two of the larger lower leaves, have proved adequate.

The morphology of the hybrids has been drawn up from both the experimentally produced F_1's and from plants collected by the writer in central California (*1857, 1866*). The small amount of good pollen (0–8 per cent) of the latter plants, their occurrence in the regions where both parent species are found, and their comparison with the artificial F_1's suggest that these plants may be first-generation hybrids between *H. annuus* and *H. Bolanderi*. The variability of these plants as shown in the table is rather great, but this is not unexpected since different genetic strains of the parents have been involved.

All leaf measurements have been of larger lower leaves, and the descriptions of shape, size, and decurrence are to be considered as applying to them. The size of the leaf seems to be extremely modified by the environment and consequently shows great variability. The following very broad ranges of length and width give, however, some indication of the leaf size in nature: *H. Bolanderi* (foothill serpentine) 6–13 × 3–7 cm.; *H. Bolanderi* (valley, weed) 6–15 × 4–12 cm.; *H. annuus* (western) 9–22 × 6–18 cm.; *H. annuus* (ruderal) 14–24 × 10–22 cm. In addition to the difference in serration given in table 1, the serration in *H. annuus* is usually crenate, but noncrenate serrations are not uncommon; the reverse appears true for *H. Bolanderi*. The serration may be in part simply an expression of the size differences. In *H. annuus* the petiole is usually naked or there is a slight decurrence of the blade onto the petiole; in *H. Bolanderi* the petiole is either naked or frequently the blade is decurrent onto the petiole, so that the leaves quite often appear to be nearly sessile. There also appears to be a slight difference in the color of the leaves: those of *H. Bolanderi* are generally light green, whereas those of *H. annuus* are dark green. Illustrations of various leaf shapes are given in fig. B.

The various terms used to describe pubescence are so elusive that it is difficult to give precise definition to the differences. In general, the hairs of *H. Bolanderi* are long and slender with a slightly enlarged base; the hairs of *H. annuus* are relatively broad and much enlarged at the base (fig. C). The pubescence of the stem of the foothill serpentine form of *H. Bolanderi* and, to a lesser extent, of the valley weed *H. Bolanderi*, consists of long, spreading or deflexed hairs rather soft to the touch. The pubescence of the stem of *H. annuus* consists of afflexed or somewhat appressed hairs which are harsh to the touch. The pubescence of the leaves of *H. Bolanderi* also is generally

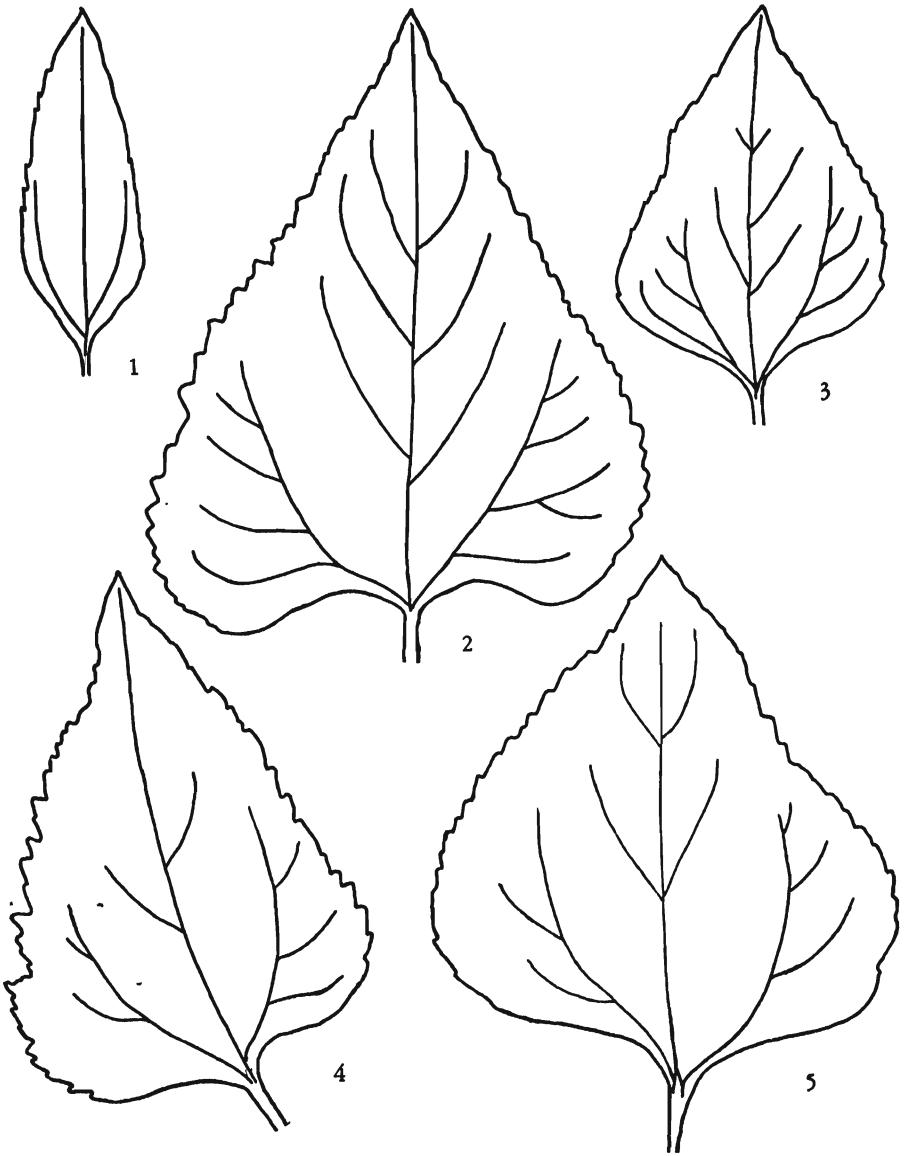


Fig. B. Leaves, × ⅔. 1, *Helianthus Bolanderi* (*1854*) (extreme type found in foothill serpentine race); 2, *H. annuus* (*1791*) (common type in ruderal race); 3, *H. annuus* × *H. Bolanderi* (*1857*); 4, *H. annuus* (*1846*) (common type in western race); 5, *H. Bolanderi* (*1853*) (extreme type found in valley weed race).

softer to the touch than in *H. annuus,* although some plants of the valley weed *H. Bolanderi* are exceptional in this respect. The pubescence of the latter is quite variable, rarely approaching that of *H. annuus.* The pubescence of the first-generation hybrids is best described as somewhat intermediate, but more nearly approaching *H. Bolanderi.* The pubescence of the involucral bracts and chaff is treated sufficiently in the table. In his key to *Helianthus,* Jepson

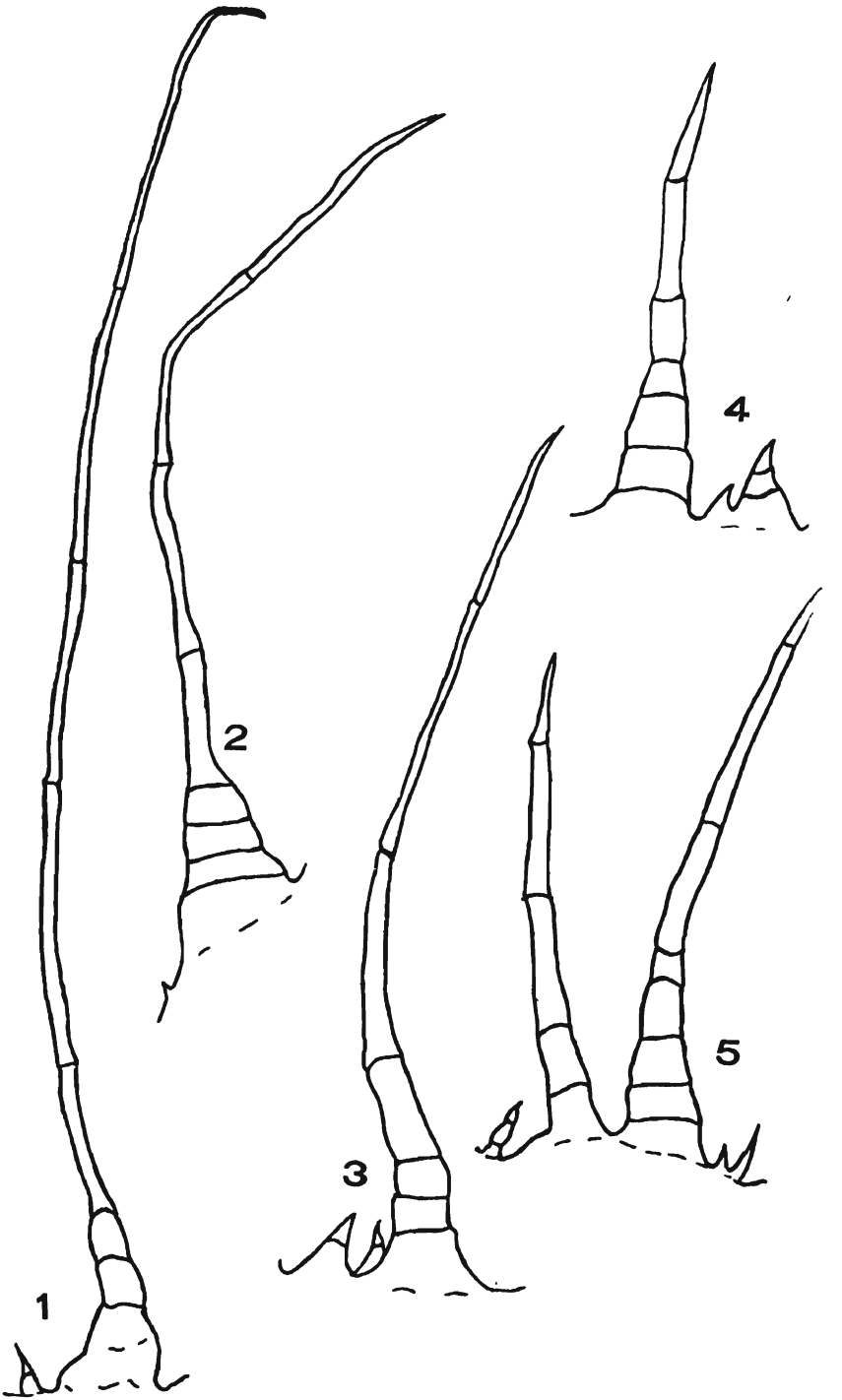


Fig. C. Hairs from involucral bracts, × 60. 1–2, *Helianthus Bolanderi;* 3, *H. annuus* × *H. Bolanderi;* 4–5, *H. annuus.*

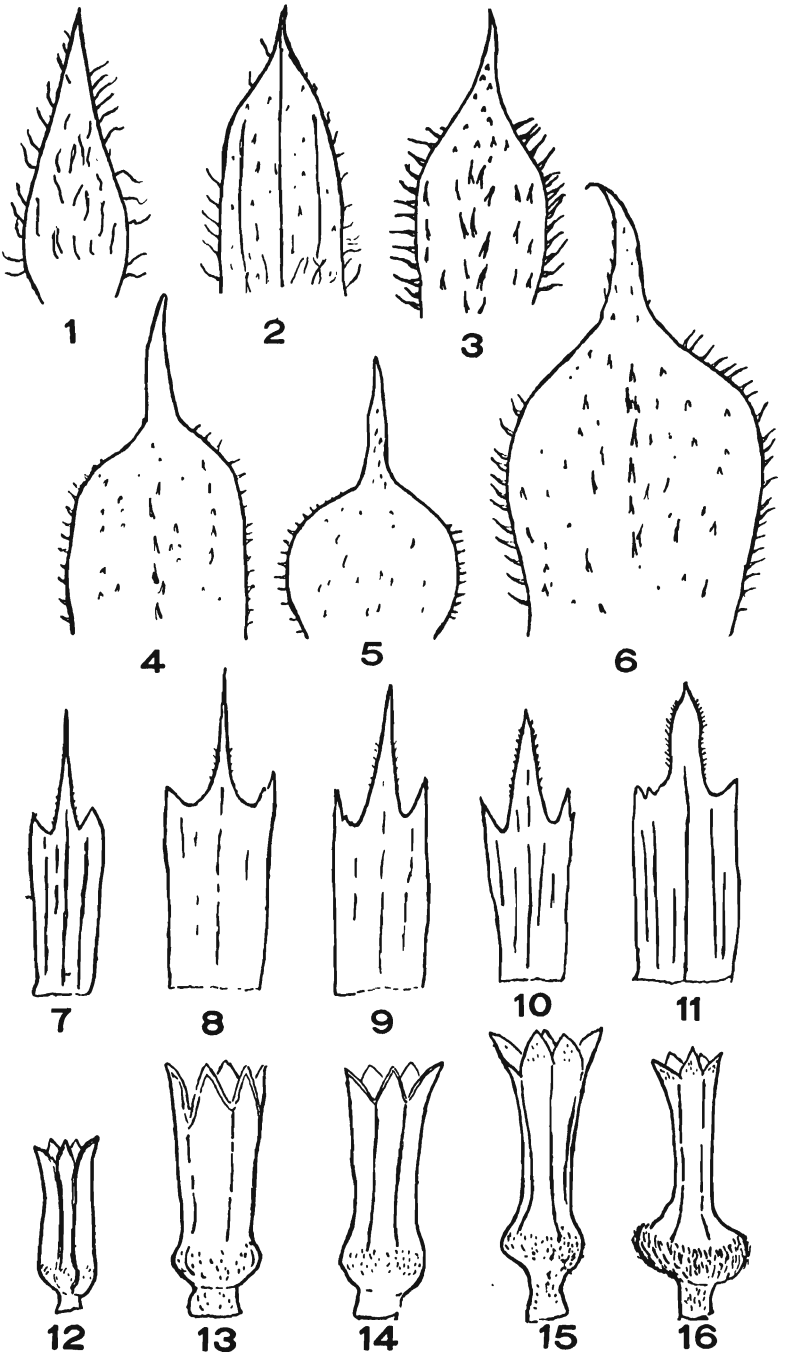


Fig. D. 1–6. Involucral bracts, × 3⅕. 1, *Helianthus Bolanderi (1854)*; 2, *H. Bolanderi (1853)*; 3, *H. annuus* × *H. Bolanderi (1857)*; 4–5, *H. annuus (1846)*; 6, *H. annuus (1791)*. 7–11. Pales of the receptacle, × 3⅕. 7, *H. Bolanderi (1854)*; 8, *H. Bolanderi (1853)*; 9, *H. annuus* × *H. Bolanderi (1857)*; 10, *H. annuus (1846)*; 11, *H. annuus (1791)*. 12–16. Disk flowers, × 5. 12, *H. Bolanderi (1854)*; 13, *H. Bolanderi (1853)*; 14, *H. annuus* × *H. Bolanderi (1857)*; 15, *H. annuus (1846)*; 16, *H. annuus (1791)*.

(1925) separates *H. Bolanderi* from *H. exilis,* partly on the basis of the pubescence of the stem: *H. Bolanderi* is described as having scabrous stems and *H. exilis,* stems often hirsute. Although this distinction is quite often valid, it is by no means universal.

The size of the disk is extremely variable in both species depending upon both environmental modifications of the phenotype and genetical differences. The primary head in all sunflowers is generally the largest, and there is a gradual diminution in size until heads produced late in the season are comparatively small. This difference in size between early and late heads is most strongly developed in the ruderal *H. annuus.* In all measurements in this paper there has been an attempt to use only the larger heads in field studies and only the primary heads in the plants grown in the experimental garden.

The nature of the involucral bracts of *H. annuus* is one of the chief characters used to distinguish this species from other members of the genus. Both the shape and size (table 1) are characteristic of this species. In addition to the differences of the bracts of the two species which are given in the table it should be pointed out that the outermost bracts of *H. Bolanderi* at times tend to be very leaflike.

H. Bolanderi is most readily distinguished from other species of the genus by the long, slender, glabrous-tipped, middle cusp (awn) of the chaff (fig. D), and this has long been used as an important "key" character. In *H. Bolanderi* these awns are erect from the time the involucral bracts open, whereas the awns of *H. annuus* are at first appressed and become erect only when the flowers open. This difference is striking in living plants but obscure in herbarium material. In some instances, however, an intermediate condition is found, as in the F_1 hybrids and in most plants of the greenhouse population *646,* which, on the sum total of characteristics, must be identified as *H. annuus.* In these plants the awns are best described as semierect. On the whole, the awns of the hybrids are much more like those of *H. Bolanderi* than like those of *H. annuus* except for their slightly greater breadth and pubescence. In their treatment of *H. Bolanderi* and *H. exilis,* Greene (1897) and Jepson (1925) distinguish *H. Bolanderi* as having the chaff equaling the disk flowers and *H. exilis* having the chaff surpassing the disk flowers. This difference does not hold true for the two races as recognized here; in both, the awns generally surpass the disk flowers.

The rays in *H. annuus,* which are rather long and narrow, are generally entire or only shallowly bifid at the apex; in *H. Bolanderi* the rays are short, broad, and rather deeply once or twice forked. Plants of *H. annuus* (*1858*) with deeply forked rays have been collected in California, however. The rays are rather few in *H. Bolanderi* and more numerous in *H. annuus* (table 1), and *H. Bolanderi* has fewer veins to the ray. The color of the rays varies from light yellow to deep orange in both species, and in addition a great many cultivated forms of *H. annuus* are known with variously colored rays.

The difference in the shape of the disk flowers is shown in figure D. The presence of a very large "bulb" on the florets seems to be distinctive of *H.*

annuus. This enlarged basal portion of the tube continues to grow even after the top of the flower begins to wither (Anderson *et al.*, 1946). However, the bulb becomes aborted early if the flower is not pollinated.

In both species the tube of the disk flowers is yellow and the lobes are either yellow or various shades of red or purple. Both mixed and pure populations have been found in regard to the color of the lobes of the corolla. However, it has been observed that yellow lobes are rare among the western race of *H. annuus* and that they are quite common in the ruderal race. The colors of the corolla lobes, the stigma, the stamens, and the chaff show some correlation. In *H. annuus* all of these parts may be red or purple; or the lobes, stigma, and chaff may be yellow and the stamens black. In *H. Bolanderi* three general conditions are found as regards the pigmentation of these parts. The stamens may be red and all of the other parts yellow; or more commonly the stamens and the lobes may be red or purple and the stigma and chaff yellow; or all of the parts may be purple. The hybrids generally show the same variations of colors as observed in *H. Bolanderi*.

The difference in the achenes of the two species is principally one of size. The color and mottling of the achenes vary greatly, even within the same population. In *H. Bolanderi* the achenes are usually gray to reddish brown (rarely purple) and usually speckled. In *H. annuus* the color varies from gray to reddish brown in the wild varieties and from blackish purple to white in cultivated forms, and may be speckled, striped, solid colored, or both speckled and striped in wild forms, or either striped or solid colored in cultivated forms.

The morphology of the cultivated sunflower [*H. annuus* var. *macrocarpus* (DC.) Ckll.] has not been included in the table. This variety is most closely related to the ruderal race and differs from it chiefly in its monocephalic habit and the larger size of all parts of the plant.

CYTOLOGY

All of the annual species of *Helianthus* thus far investigated have the haploid count of 17 chromosomes (Heiser, 1948). In the present work, counts of 17 pairs were obtained for *H. annuus* from both the wild races and cultivated material. Counts of 17 pairs were also obtained for both races of *H. Bolanderi* (fig. E).

The method employed for the chromosome study was the smearing of microsporocytes in acetocarmine. There was no great difficulty in determining the chromosome number of the parent species, but in the hybrid material there was difficulty in making smears suitable for a detailed study of the configurations present. This difficulty was particularly marked in material from greenhouse plants.

Microsporocytes from a number of known F_1 hybrids were examined but only those from four greenhouse plants (*726-2, 3, 10,* and *731-2*) and the three spontaneous garden hybrids (*D3B-1, 2, 4*) were suitable for study. Approximately 25 cells were studied in each case. In all of the plants there was a

variable number (7–12) of bivalents present at metaphase I, and the remainder of the chromosomes were associated in one to three (generally two) chains or rings; rarely two univalents were present. Fragments were observed after telophase II in some cells and occasionally chromatid bridges were still evi-

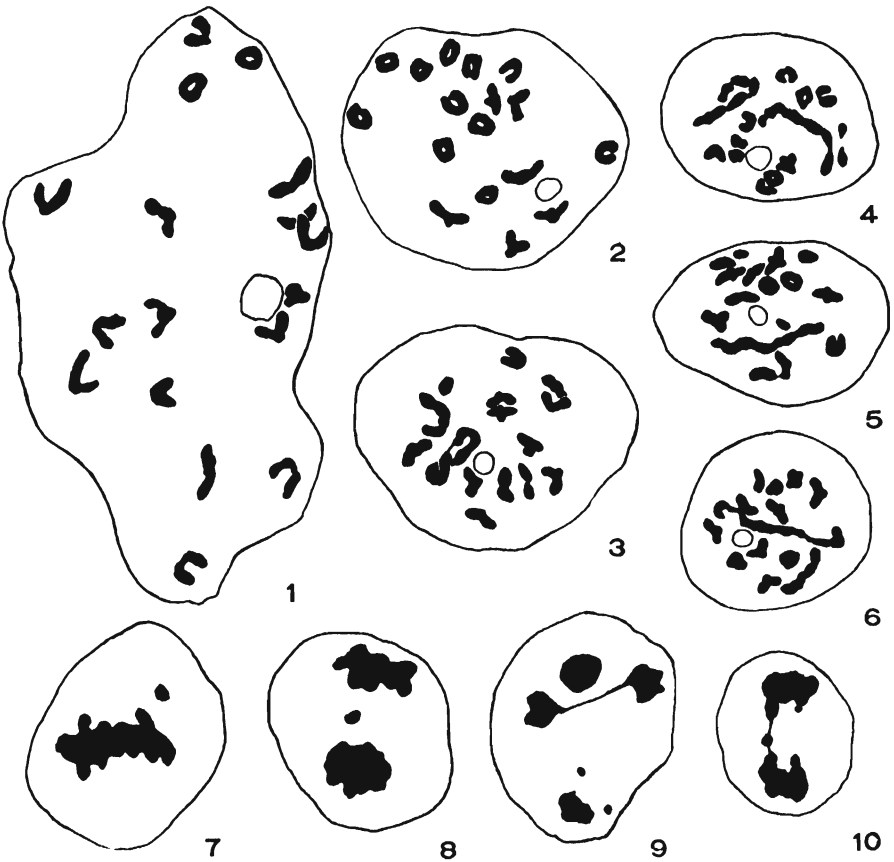


Fig. E. Camera lucida drawings of meiotic configurations of *Helianthus annuus, H. Bolanderi,* and hybrids, × approximately 1000. 1, *H. annuus (655)*, 17 II's; 2, *H. Bolanderi (642)*, 17 II's; 3, *H. annuus* × *H. Bolanderi (D3B)*, 1 I, 12 II's, 1 III, 1 VI; 4, *H. annuus* × *H. Bolanderi (731)*, 2 I's, 10 II's, 2 VI's; 5, *H. annuus* × *H. Bolanderi (1866)*, 2 I's, 11 II's, 1 IV, 1 VI; 6, *H. annuus* × *H. Bolanderi (1866)*, 11 II's, 1 IV, 1 VIII; 7–8, *H. annuus* × *H. Bolanderi (1859)*; 9, *H. annuus* × *H. Bolanderi (726)*; 10, *H. annuus* × *H. Bolanderi (1857)*.

dent. The material on the whole was unfavorable for cytological investigation and did not lend itself to a statistical analysis.

Three natural hybrids (*1857, 1866,* and a single plant from *1859*) whose morphology and lack of fertility suggest that they may be F_1 hybrids have been studied cytologically. From five to eleven bivalents and from two to three chains (or rarely rings) of several chromosomes each were observed (fig. E). Univalents were rare in *1857* and *1866,* but as many as four were observed in a few cells. In *1859,* univalents were observed in over three-fourths of the 150 cells examined. In most cells a single univalent was present, but as

many as four were observed in about 5 per cent of the cells. At telophase I, chromatid bridges and acentric fragments were observed in a few cells.

Although the cytological analysis is somewhat fragmentary, there appears to be strong evidence for structural differences between the chromosomes of the two parent species. The presence of fragments and chromatid bridges indicates structural hybridity for inversions. The presence of rings or chains, which was observed in every cell of both the artificial and natural hybrids, indicates structural hybridity for interchanges of relatively large chromosomal segments.

Only a few cells were suitable for examination in the plants of *645,* which appear to be the progeny of a natural hybrid. In most instances good pairing

TABLE 2

FERTILITY DATA ON THE PROGENY OF A NATURAL HELIANTHUS ANNUUS × H. BOLANDERI HYBRID

Plant number	Percentage of good pollen	Number of seeds set when crossed with		
		H. Bolanderi	*H. annuus*	Sib
645–2	26	4	3	(*645–6*) 0
645–3	33	11	5	(*645–5*) 4
645–4	55	(Not attempted)	(Not attempted)	(*645–7*) 29
645–5	48	11	1	(Not attempted)
645–6	17	5	4	(*645–2*) 0
645–7	71	11	41	(*645–4*) 31
645–8	56	(Not attempted)	(Not attempted)	(Not attempted)

was observed, but an occasional pair of univalents or an association of four or more chromosomes in the form of a chain appeared. All the plants, however, showed a great reduction in pollen fertility (table 2). Thus there appears to be a reduction of structural hybridity in later generations but, judging from the reduced pollen fertility, perhaps there are still structural differences for smaller segments or cryptic structural hybridity (Stebbins, 1945). The artificial backcrosses have not been studied cytologically as yet.

In the few plants examined which were regarded as introgressants, good pairing was observed, although in a few cells two univalents were observed. The introgressants, on the whole, show little or no reduction from the normal pollen fertility.

The percentage of fertile pollen grains was determined throughout this study by the use of cotton blue in lactophenol. Pollen grains which took a deep blue stain were counted as "good." Except for an exceptional plant which had as low as 60 per cent good pollen, both parent species from a number of localities exhibited 85 per cent or more good pollen. The two natural hybrids (*1857* and *1866*) had pollen fertilities ranging from 0 to 8 per cent. The data pertaining to the pollen of the other hybrid populations are given in the next sections under the individual populations.

ANALYSIS OF POPULATIONS

During the past five years, collections of sunflowers have been made in a number of localities in the United States by both the writer and a number of colleagues. The two species under consideration here, as well as several other annual species of the genus, have been grown in the greenhouse for several winters at Washington University (1944–1945), University of California at Berkeley (1945–1946), University of California at Davis (1946–1947), Indiana University (1947–1948). The majority of the genetic studies have been made from the greenhouse plants. In addition, experimental garden plantings were made at Berkeley in the summer of 1946 and at Davis in 1947 in order to study the variations of the plants when grown under similar field conditions.

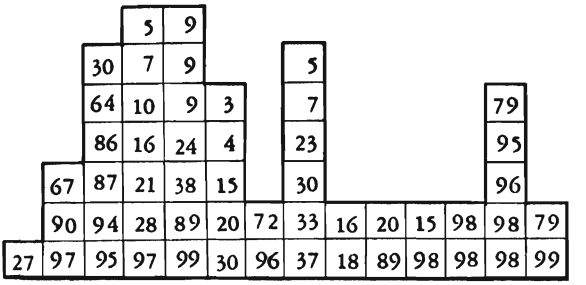
Field collections.—There is always considerable morphological diversity both within and between any populations of *H. annuus* and *H. Bolanderi* which have been studied. There is a slight geographical basis for certain types of variability (i.e., western *vs.* ruderal *H. annuus,* and foothill serpentine *vs.* valley weed *H. Bolanderi*). A convenient method for showing this variation graphically has been devised by Anderson (1936) and has since been employed by a number of students of hybridization. Several natural populations of sunflowers are analyzed by this method (fig. F).

The characters used for scoring the plants and the index values of each are:

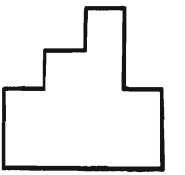
Pubescence
H. Bolanderi-like (0); intermediate (1); *H. annuus*-like (2)
Leaf shape
cuneate (0); cuneate to truncate (1); truncate (2); cordate (3)
Width of involucral bracts
up to 3.9 mm. (0); 4.0–4.9 mm. (1); 5.0–5.9 mm. (2); 6.0–6.9 mm. (3); 7.0 mm. and over (4)
Chaff
H. Bolanderi-like (0); intermediate (1); *H. annuus*-like (2)
Ray number
up to 11 (0); 12–15 (1); 16–20 (2); 21–25 (3); 26–39 (4)
Disk flower shape
H. Bolanderi-like (0); intermediate (1); *H. annuus*-like (2).

The usual method of scoring in previous works has been to assign index values of 0, 1, and 2. The present procedure of giving higher index scores for some characters has been done in an attempt to show the differences between the races of the two species as well as the differences between the two species. The choice of the characters and their index values is arbitrary, and this method is open to criticism for that reason. The use of such methods without adequate genetical information was recently criticized by Baker (1947). Certainly, however, the frequency distributions show, in a very simple and easily understood manner, the differences and similarities among various populations. The frequency distributions should, however, be used merely as a supplement to other methods and not as the sole basis for conclusions.

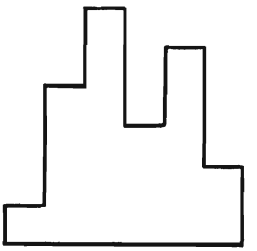
Of the histograms presented, that farthest to the left represents a popula-



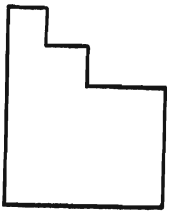
1



2



3



4

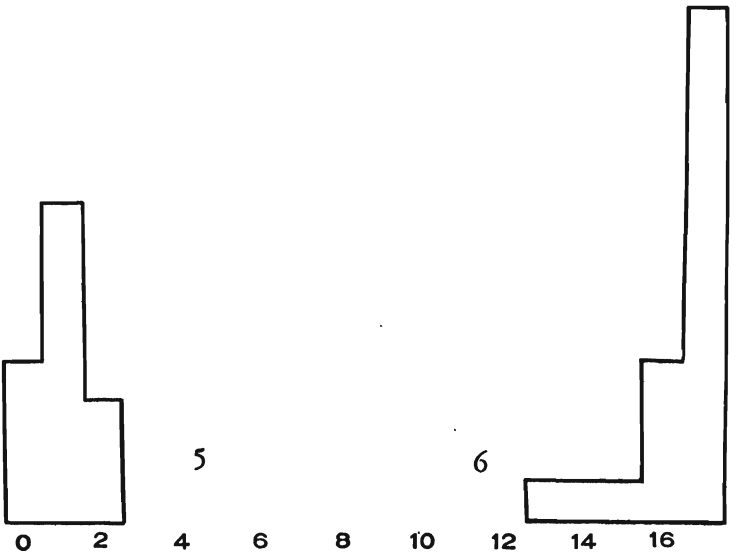


Fig. F. Histograms of natural populations of *Helianthus*. 1, *H. annuus* × *H. Bolanderi* (*1859*); 2, *H. annuus* (*Beetle 4415*); 3, *H. Bolanderi* (*1851 & 1853*); 4, *H. annuus* (*1846*); 5, *H. Bolanderi* (*1854*); 6, *H. annuus* (*1791*). Explanation in text.

tion of *H. Bolanderi* from a serpentine region (fig. F, 5). Other populations of the foothill serpentine race of *H. Bolanderi* show the same range of index values. At first it was thought that the low index value of these populations might merely reflect a dwarfing influence of serpentine on the plants since a large number of size characters are used in scoring. Subsequent study (see Experimental Garden Results) has shown that this is not true. Two small populations of valley weed *H. Bolanderi* have been combined to produce the histogram shown in fig. F, 3, which illustrates the extreme approach of *H. Bolanderi* toward *H. annuus*. Other populations of the valley weed race have index values ranging from 0 to 7, with the mode at 3.

Of the three populations of *H. annuus,* the one from California had the lowest index values (fig. F, 4), a ruderal population from St. Louis the greatest (fig. F, 6), and somewhat intermediate between the two is a small population from Colorado (fig. F, 2).

It is felt that these histograms actually show the relative degree of differences existing between these populations in nature. The valley weed *H. Bolanderi* tends to approach *H. annuus* in certain morphological features, notably size, and *H. annuus* in California tends to approach *H. Bolanderi.* Nevertheless, as shown by the histograms, there is a definite discontinuity between the two species in California. This gap, as will be seen shortly, however, is bridged by hybrid swarms in which the intermediate forms are generally rather highly sterile. Populations (such as *646,* discussed on p. 182) containing a high number of introgressants may narrow the gap but do not completely bridge it.

A large hybrid swarm (*1859*) consisting of over 200 individuals, of which more than 50 plants were collected for study, was found growing along the highway between Sacramento and Davis, California. The plants were crowded, and there was consequently a large number of depauperate individuals. The frequency distribution scores for this hybrid swarm range from 0 to 13; the distribution is probably somewhat to the left of what it would have been if there had been fewer depauperate plants. Pollen counts, as well as records on seed set, were made on all of the specimens collected. The amount of good pollen varied from 3 to 99 per cent and the seed set from as few as one to a head to thirty to fifty seeds or 100 per cent seed set. Most of the plants with a high percentage (80 per cent or better) of good pollen had nearly 75 per cent or better set of seeds. Those with a reduced amount of good pollen usually had the percentage of seed set slightly below that of the amount of good pollen, but there were some exceptions. Six of the plants had a higher percentage of good seeds than of good pollen; two plants with very low seed set had a high percentage of good pollen. The percentages of good pollen are superimposed upon the frequency distribution of this hybrid swarm (Fig. F, 1). There is some correlation of the pollen fertility with the appearance of the plant. The plants with the higher index values, scoring as *H. annuus,* in general have high percentages of good pollen. The plants with the lowest index values, scoring as *H. Bolanderi,* also tend to have high percentages of good pollen,

although this is somewhat variable. The plants with intermediate index values have a low percentage of good pollen; for example, the six plants with index values of 7 have 37 per cent or less good pollen, and the two plants with index values of 8 have less than 20 per cent good pollen. However, there are some significant exceptions to these generalizations. The one plant with an index value of 0 has only 27 per cent good pollen, and two plants with index values of 3 have less than 10 per cent good pollen. If the data from Riley (1938) on *Iris* are treated in the same manner, it is also seen that the hybrid types, in general, have lower percentages of good pollen than do the parent species.

The plants of *1859* probably consist mostly of the parent species, F_1's, and backcrosses. The taxonomy of such plants has already been discussed. It is essential that a permanent record be kept of such plants as Turrill (1938) has previously pointed out, and consequently a large sample of this population is to be deposited in the herbarium of the University of California.

A short distance from the hybrid swarm of *H. annuus* and *H. Bolanderi* a small population (*1856*) was found which appeared to be a hybrid swarm between the giant cultivated and the wild form of *H. annuus*. Cultivated sunflowers were observed in a field nearby, and it was subsequently learned that they have been grown there for a number of years. An analysis of this hybrid swarm will not be undertaken here since it only indirectly concerns the present problem. Hybridization between the cultivated and the wild sunflower, however, is another factor that has to be given some consideration in any study of the variability of *H. annuus*. Such hybridization is of recent origin in California, since the Indians of this region did not cultivate sunflowers. The hybrids insofar as is known at present are fully fertile, and such hybridization can explain the occurrence of occasional individuals of exceptional size among the western race of *H. annuus*. It should also be mentioned that the hybrids between cultivated *H. annuus* and western *H. annuus*, as for example some forms observed in the population *1856*, resemble very closely plants of the ruderal race.

Greenhouse results.—Small populations of up to twenty individuals of both species were grown in the greenhouse of the Division of Genetics of the University of California at Berkeley. The seeds, which came from a number of sources (see table 3), were planted in flats in early December. Germination, even after subjecting the seeds to low temperatures for ten days, was very poor for some of the samples. The seedlings were transplanted to four-inch pots and then again to eight-inch pots, in which they were allowed to mature. Such small pots do not allow either species, particularly *H. annuus*, to attain its maximum size and hence there is no attempt to make direct comparisons with plants in the field. Remarks concerning only a few of these populations will be made here.

Helianthus Bolanderi.—The plants of population number *642* (pl. 35), grown from seed collected in a serpentine region in Lake County, were for the most part small in stature and showed characteristically narrow bracts, small disks and achenes, and few rays. The leaves were rather narrow and

TABLE 3

COLLECTION DATA

I. FIELD

Number	Determination	Collector and date	Locality
1	*H. Bolanderi*	Stebbins & Heiser Nov. 10, 1945	1 mi. NE of Middletown (serpentine), Lake Co., Calif.
2	*H. Bolanderi*	Stebbins & Heiser Nov. 10, 1945	3 mi. NE of Middletown (serpentine), Lake Co., Calif.
3	*H. Bolanderi*	Stebbins & Heiser Nov. 10, 1945	18 mi. W of Williams (serpentine), Colusa Co., Calif.
4	*H. Bolanderi*	Stebbins & Heiser Nov. 10, 1945	4 mi. S of Williams, Colusa Co., Calif.
5	*H. annuus* × *H. Bolanderi*	Stebbins & Heiser Nov. 10, 1945	8 mi. S of Williams, Colusa Co., Calif.
6	*H. Bolanderi*	Stebbins & Heiser Nov. 10, 1945	6 mi. S of Arbuckle, Yolo Co., Calif.
7	*H. annuus*	Stebbins & Heiser Nov. 10, 1945	7.6 mi. S of Arbuckle, Yolo Co., Calif.
9	*H. Bolanderi*	Stebbins & Heiser Nov. 10, 1945	Zamora, Yolo Co., Calif.
11–1	*H. annuus*	Stebbins & Heiser Nov. 10, 1945	3 mi. E of Davis, Yolo Co., Calif.
11–2	*H. annuus* × *H. Bolanderi*		
12	*H. annuus*	Stebbins & Heiser Nov. 10, 1945	3 mi. W of Sacramento, Yolo Co., Calif.
1791	*H. annuus*	Heiser July 3, 1946	St. Louis, Mo.
1825	*H. annuus*	Heiser August 24, 1946	South Gate, Los Angeles Co., Calif.
1837	*H. Bolanderi*	Heiser August 19, 1946	Davis, Yolo Co., Calif.
1846	*H. annuus*	Heiser & Meagher August 24, 1946	1 mi. E of Tracy, San Joaquin Co., Calif.
1850	*H. Bolanderi*	Heiser & Meagher August 24, 1946	8 mi. E of Woodland, Yolo Co., Calif.
1851	*H. Bolanderi*	Heiser & Meagher August 25, 1946	5 mi. N of Yolo, Yolo Co., Calif.
1853	*H. Bolanderi*	Heiser & Meagher August 25, 1946	Between Live Oak and Pennington, Sutter Co., Calif.
1854	*H. Bolanderi*	Heiser & Meagher August 25, 1946	18 mi. W of Williams (serpentine), Colusa Co., Calif.
1856	*H. annuus* (wild × cultivated)	Heiser & Heiser Sept. 4, 1946	4 mi. E of Davis, Yolo Co., Calif.
1857	*H. annuus* × *H. Bolanderi*	Heiser & Heiser Sept. 4, 1946	5.8 mi. E of Davis, Yolo Co., Calif.

TABLE 3—*Continued*

Number	Determination	Collector and date	Locality
1858	*H. annuus*	Heiser Sept. 4, 1946	Under Yolo Causeway, Yolo Co., Calif.
1859	*H. annuus* × *H. Bolanderi* (hybrid swarm)	Heiser & Heiser Sept. 4, 1946	5.4 mi. E of Davis, Yolo Co., Calif.
1864–1870	*H. annuus* × *H. Bolanderi*	Heiser Sept. 18, 1946	Along Putah Creek, Solano Co., Calif.
1954	*H. annuus* × *H. Bolanderi*	Heiser July 8, 1947	Esparto, Yolo Co., Calif.
1450	*H. annuus*	Tucker August 17, 1946	2 mi. SE of Paicines, San Benito Co., Calif.
4415	*H. annuus*	Beetle Sept. 9, 1946	3 mi. W of Fort Collins, Larimer Co., Colo.

II. GREENHOUSE

Number	Determination	Source of seed
619	*H. annuus*	St. Louis, Mo.
634	*H. Bolanderi*	Serpentine meadow, 3 mi. E of Middletown, Lake Co., Calif. (Mason)
637	*H. annuus*	El Centro, Imperial Co., Calif. (Anderson)
642	*H. Bolanderi*	*Stebbins & Heiser 1*
643	*H. Bolanderi*	*Stebbins & Heiser 2*
644	*H. Bolanderi*	*Stebbins & Heiser 4*
645	*H. annuus* × *H. Bolanderi*	*Stebbins & Heiser 5*
646	*H. annuus*	*Stebbins & Heiser 7*
648	*H. annuus*	*Stebbins & Heiser 11-1*
649	*H. annuus* × *H. Bolanderi*	*Stebbins & Heiser 11-2*
655	*H. annuus*	*Stebbins & Heiser 12*

TABLE 3—*Continued*

III. EXPERIMENTAL GARDEN

Number	Determination	Source of seed
D1	*H. Bolanderi*	*Stebbins & Heiser 1*
D2	*H. Bolanderi*	*Stebbins & Heiser 2*
D4	*H. Bolanderi*	*Heiser & Meagher 1854*
D5	*H. Bolanderi*	Same as for greenhouse *634*
D7	*H. Bolanderi*	*Stebbins & Heiser 4*
D8	*H. Bolanderi*	*Stebbins & Heiser 6*
D11	*H. Bolanderi*	*Stebbins & Heiser 9*
D13	*H. Bolanderi*	*Heiser 1837*
D14	*H. Bolanderi*	*Heiser & Meagher 1850*
D15	*H. Bolanderi*	*Heiser & Meagher 1851*
D16	*H. Bolanderi*	*Heiser & Meagher 1853*
D18	*H. annuus*	*Stebbins & Heiser 7*
D20	*H. annuus*	*Stebbins & Heiser 12*
D24	*H. annuus*	*Tucker 1450*
D25	*H. annuus*	*Heiser 1825*
D30	*H. annuus*	Wawawai, Whitman Co., Wash. (Ownbey)
D31	*H. annuus*	Lewiston Grade, Nez Perce Co., Idaho (Ownbey)
D32	*H. annuus*	*Beetle 4415*
D34	*H. annuus*	Near Woonsocket, Sanborn Co., S. Dak. (Nelson)
D36	*H. annuus*	Fargo, Cass Co., N. Dak. (Stevens)
D40	*H. annuus*	Near Delicias, Chihuahua, Mexico (Morley)
D45	*H. annuus*	East St. Louis, St. Clair Co., Ill.

frequently entire. Population number *644* (pl. 36), from a valley region, consisted of larger plants with more numerous rays, broader involucral bracts, etc. The leaves were slightly broader and more often serrate. None of the size differences, however, were statistically significant. A third population (*643*), also from seed collected in a serpentine locality in Lake County, was somewhat intermediate morphologically between the above two. A few of the latter plants were completely sterile, for reasons as yet unknown.

Helianthus annuus × *H. Bolanderi* (*645*, pl. 37).—The parent plant of this greenhouse population was regarded as a hybrid and agrees rather closely with the description of the hybrids given in table 1. The plant had 14 per cent good pollen, and a total of eight achenes was found in twenty heads. The pollen parent is unknown, of course, but the offspring could represent backcrosses to either or both parents or possibly even an F_2. In any event the progeny might be expected to show some segregation. Seedlings were raised from seven of the eight seeds. All the plants reached maturity and were vigorous. Three of the progeny approached *H. annuus* in appearance and the other four approached *H. Bolanderi*. In other words, definite segregation was observed. Size of the leaves of the seven plants varied little, but the serration varied greatly; some of the plants had nearly entire leaves and two plants had deeper serrations than either parent. On the whole, the disks were small and the involucral bracts were narrow, but one plant appeared with rather large measurements in these respects. The rays were few in number on all the plants, but approached the rays of *H. annuus* in size. The color and shape of the awns of the chaff showed considerable variation. Only a few seeds were set when the plants were backcrossed to either parent, except that *645-7*, when backcrossed to *H. annuus*, produced nearly 100 per cent good seed (table 2, p. 174). This plant is also unusual in that it yielded twenty-two seeds to a head when selfed; the parent species are normally rather highly self-sterile.

Helianthus annuus (*646*, pl. 38).—The parents of this population (*Stebbins* and *Heiser 7*) were the most extreme approach of *H. annuus* to *H. Bolanderi*. The very long awns of the chaff, the small heads, and the narrow bracts of the involucre of the parent plants definitely suggest *H. Bolanderi*. A study of the offspring revealed several features of interest. The awns of the chaff of the greenhouse plants were extremely long for *H. annuus* and were semierect when the heads opened; the rays were few in number and their shape and size were those of *H. annuus*. The bract width and the disk diameter were rather small, and the leaves were relatively narrow for *H. annuus*. However, the serration of the leaves was even more pronounced than in *H. annuus*. The number of heads in bud when the first head opened was greater than is typical for *H. annuus*. When all characteristics are considered, however, the plants appear to be closer to *H. annuus* than to *H. Bolanderi*. These plants are regarded as introgressants containing some germ plasm of *H. Bolanderi*.

Crosses of *646* have been made with both *H. annuus* and *H. Bolanderi*. A study of the progeny revealed that in crosses with *H. annuus* as a parent there

is complete fertility, but when *H. Bolanderi* is used as a parent, a high degree of sterility is encountered.

Population *648* (pl. 39), seed for which were collected in the same county as *646,* resembles this population in all particulars. Whole populations like *646* and *648* appear to be rare in nature and then appear only in regions where *H. Bolanderi* occurs. In plants collected near Tracy (*1846*) a few such plants were found, but they were definitely in the minority.

Artificial F_1 *hybrids.*—Reciprocal crosses between *H. annuus* and *H. Bolanderi* were made, using plants from several seed sources as parents. In general, either way the cross is made a large number of seeds are set. The crossing technique employed has been described previously (Heiser, 1947).

Germination of the hybrid seed was poor, although the achenes appeared to be filled. Poor germination, however, is frequently encountered among seeds from both parent species. Seeds from the following crosses germinated: *707* (*637* × *642*), *726* (*637* × *642*), *727* (*642* × *646*), *729* (*644* × *646*), *731* (*H. annuus*—cultivated "Mammoth Russian"— × *634*), *733* (*642* × *619*). The hybrids were vigorous and were generally rather highly sterile with pollen fertility ranging from 2 to 35 per cent. Only two plants had as high as 35 per cent good pollen, all of the remainder having 10 per cent or less good pollen. The seed set in the hybrids, when *H. annuus, H. Bolanderi,* or a sib was used as pollen parent, was very low. No seed at all was set in a few cases and the highest amount obtained was 20 per cent.

Morphologically these F_1 hybrids were more or less intermediate between the two parent plants. The general morphology of the F_1's has been incorporated in table 1, and their cytology has been dealt with in a previous section.

Crosses have also been made between the two races of *H. Bolanderi,* using plants from populations *642* and *644*. The average pollen fertility of the fifteen hybrids obtained was 70 per cent, but there was a wide range from as low as 9 per cent to as high as 100 per cent.

The study of the crosses between plants of *H. annuus* from different regions is still being carried on, but preliminary results indicate that the hybrids are fully fertile, producing as a rule 90 per cent or more good pollen and setting high amounts of good seed.

Backcrosses.—Several backcrosses of the hybrids were made to both parents and good seeds were obtained. Only twelve plants have been raised to maturity, however. The failure of the plants to reach maturity apparently was not due to any inherent weakness but to a severe attack of white flies when the plants were in the seedling stage. The pollen fertilities of these twelve backcross plants varied from as low as that of the F_1 to as high as that of the pure species.

No attempts have been made to grow an F_2 generation. The sterility of the F_1 generation is so great that it is difficult to obtain enough seed to make profitable the growing of an F_2. It is the backcrosses, however, that are probably of greater significance in nature and it is highly desirable that more information be had regarding successive backcrosses to both parents.

Experimental Garden Results.—During the summer of 1946 a number of plants of both *H. annuus* and *H. Bolanderi* were grown for observational purposes in an outdoor garden at Berkeley. Controlled crosses were not made but seed was collected from a number of open pollinated plants. Of particular interest here are those from a plant of *H. Bolanderi*. Of the twenty seeds planted the following summer, four germinated (*D3B*) and were set in the experimental garden. One of the four plants appeared to be pure *H. Bolanderi* and the other three, without much doubt, were hybrids with *H. annuus*. The pollen fertilities of the three hybrids were 5, 11, and 15 per cent and the seed set after open pollination was less than 10 per cent to the plant. Thus it can be seen that the two species will cross naturally if grown in close proximity.

During the summer of 1947 a large number of plants of both species were grown from a number of localities. The seeds from each locality were planted in cans in the greenhouse and were then transplanted to the field in random order. The field was irrigated four times during the season. These garden cultures served as the basis for measurement data on the races of both species when grown under similar conditions.

For analyzing these data the plants have been pooled into the following four categories: *H. Bolanderi* from or near serpentine outcrops in the foothill regions (*D1, D2, D4, D5*); *H. Bolanderi* from valley regions (*D7, D8, D11, D13, D14, D15, D16*); *H. annuus* from California (*D18, D20, D24, D25*); *H. annuus* from localities other than California (*D30, D31, D32, D34, D36, D40, D45*). Plants definitely known to belong to the ruderal race were excluded from the last category. As it stands, the fourth category is still something of a hodgepodge. It is very difficult to draw the distinction between the western and ruderal race at times, and in spite of precautions the fourth category may not represent a valid sample of the western race. The third category, *H. annuus* from California, also is a very heterogeneous assemblage, including plants from both central and southern California. The plants from southern California, where *H. Bolanderi* does not occur, would be expected to show little or no influence of genes from *H. Bolanderi*. However, it is conceivable that there could be a gene flow from central to southern California since there is a continuity in the distribution of *H. annuus* through the Tehachapi Mountains. The ideal would be to compare plants of *H. annuus* from regions in which *H. Bolanderi* occurs with "typical" *H. annuus* plants, but what constitutes a "typical" *H. annuus* plant is somewhat debatable. For these reasons it would appear wise to draw only tentative conclusions from the data to be presented.

Blooming dates of the plants varied greatly, but in general there was a period of over two months overlap between the blooming dates of plants of any of the four categories. In general, plants of *H. Bolanderi* from valley regions came into bloom one to two weeks earlier than plants of *H. Bolanderi* from serpentine regions.

Measurements of certain characters of the plants of the four categories are given in table 4. Measurements of the ray number and disk diameter from primary heads show differences not only between the two species but also

within the species, those of *H. Bolanderi* from serpentine regions being smallest in this respect and those of *H. annuus* from outside of California being largest.

There is, as might be expected (see Charles and Goodwin, 1943, with respect to disk size and ray number in *Solidago*), some correlation between the number of rays and the diameter of the disk, i.e., plants with the larger disks have a greater number of rays. However, the correlation coefficient did not exceed .5 for any of the four categories. Thus it might appear that, although certain

TABLE 4

MEASUREMENTS OF RAY NUMBER; DISK DIAMETER; RAY LENGTH AND WIDTH; AND LEAF LENGTH AND WIDTH OF HELIANTHUS ANNUUS AND H. BOLANDERI FROM THE EXPERIMENTAL GARDEN

Measurements	*H. Bolanderi*				*H. annuus*			
	Serpentine N=34		Valley N=61		Calif. N=35		Non-Calif. N=29	
	$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s
Ray number	12.7	1.2	14.8	3.4	18.2	3.0	20.7	3.4
Disk diam. in cm.	1.70	.18	2.07	.35	2.41	.46	2.98	.39
Ray length in mm.	15.7	2.6	16.7	4.0	29.4	7.7	34.2	6.2
Ray width in mm.	7.5	1.5	8.3	1.7	10 2	2.8	11.3	3.0
Ray index	.48	....	.50	....	.35	....	.33	....
Leaf length in cm.	11.6	2.3	13:3	2.9	16.8	4.8	15.2	4.2
Leaf width in cm.	5.7	1.5	8.9	2.2	13.3	3.6	11.0	3.6
Leaf index	.49	....	.67	....	.79	....	.72	....

genes influence both the size of the disk and the number of rays, other genes work independently in the development of these characteristics.

The measurements of the ray length and width show the same trend observed in the disk diameter and the number of rays, the smallest measurements being found in the foothill serpentine *H. Bolanderi,* the largest in *H. annuus* from outside of California. The ray index (width divided by length) reveals that whereas there are significant differences between the two species in this regard, the differences within each species are hardly significant. In fact, the index of the valley weed *H. Bolanderi* is slightly higher than that of the foothill serpentine race, reversing the usual trend thus far observed. Although there are differences in length and width of the rays within each species, apparently there has been little or no change in the relation of these two figures to one another; the rays of *H. Bolanderi* tend to be broad in relation to their length, and those of *H. annuus* narrow.

The same trend is again observed in the length and width of the leaves of the two races of *H. Bolanderi*. The difference in the index does appear to be significant. The leaf index of the valley weed race approaches the index of *H. annuus*. However, the trend observed in the other size characters is reversed in the leaves of the two categories of *H. annuus*. The leaves of California *H. annuus* are both longer and wider and have a slightly greater index than the leaves of non-California *H. annuus*.

With the exception of the leaves of *H. annuus* and the ray index within the two species, one trend prevails throughout for the characters examined. Data are not presented here but the same trend also holds for the width of the involucral bracts, the length of the achenes, and probably other size differences.

It appears that there may be a genetic coefficient (Anderson and Ownbey, 1939; see also Simpson, 1944: 164–165) determining size. The genetic coefficient in *H. Bolanderi* is one for small size; in *H. annuus* for large size. However, the coefficient apparently has been modified in the valley weed *H. Bolanderi* and in *H. annuus* in California. Hybridization offers a possible explanation for the modification; genes from the one species may have infiltrated the other species and brought about a change in the genetic coefficient.

The exception to the general trend in the leaf of *H. annuus* requires some discussion. The larger leaf size of *H. annuus* in California does not necessarily preclude the assumption that hybridization with *H. Bolanderi* has modified these plants. Assuming that the difference does not merely represent a sampling error, explanations are still possible. In *H. annuus* hybridization between the wild and the cultivated forms occurs. The larger leaf of *H. annuus* in California could possibly be caused by extensive hybridization with the cultivated sunflower. Yet, the plants selected from outside of California might show smaller leaves because introgression from *H. petiolaris* had occurred in their ancestry (Heiser, 1947).

A study of the leaf base of the two categories of *H. annuus* is pertinent here. *Helianthus annuus*, it will be remembered, has predominantly a truncate or cordate leaf base, whereas the leaf base in *H. Bolanderi* is cuneate or, rarely, truncate. Of the 35 *H. annuus* plants from California grown in the experimental garden, 8 had cuneate leaves, 13 had truncate leaves, and 14 had cordate leaves. Of the 29 *H. annuus* plants from outside of California, only 4 had cuneate leaves, 11 had truncate, and 14 cordate. The leaf base of the plants of *H. annuus* from California is more nearly like that of *H. Bolanderi*. A full understanding of the various genetic and environmental factors influencing leaf size and shape will be necessary before an explanation of the facts presented here can be given.

The characters used for analysis here were chosen partly because of ease with which precise measurement could be made. The best in this regard are the ray number and the disk diameter. The diagnostic species characters other than size, such as the middle awn of the chaff, the nature of the pubescence, and the shape of the involucral bracts, defy precise measurement. The two species appear to approach one another in regard to these characters only in

areas where active hybridization is taking place. There are perhaps other genetic coefficients controlling these differences, as well as the ray index, which are not readily broken by hybridization. On the whole, a study of the plants in the experimental garden bore out the previous conclusion that the two species may approach one another in certain characteristics but the species boundary remains distinct.

The preceding analysis provides a beginning toward a statistical study of the differences within and between the two species. More questions have been brought up perhaps than have been answered. Before a more refined analysis is possible, such as Woodson's (1947) study of variation in butterfly weed leaves, it will be necessary to have more information concerning the variability of *H. annuus* throughout its total range, as well as some idea of the factors responsible for the variability. Moreover, it will be desirable to make a more extensive study of the two races of *H. Bolanderi*. Yet from the material presented here, although much of it is of a tentative nature, grounds have been laid for certain theorizing regarding the evolution of the two species in California.

DISCUSSION AND CONCLUSIONS

From the facts presented in the previous sections a hypothesis can be erected to explain the present appearance and distribution of *H. annuus* and *H. Bolanderi* in California.

Before the introduction of *H. annuus* into California, *H. Bolanderi* may have consisted of only a single race restricted to certain foothill regions on or near serpentine outcrops. By the agency of man, *H. annuus* was brought into close contact with *H. Bolanderi* and hybridization occurred between the two species. Both *H. annuus* and the hybrid derivatives originally may have found ecological niches created for them around Indian camp sites, and then with the coming of the white man new areas for colonization were opened through his many activities such as cultivation of land and road building. Through such activities *H. annuus* would have been brought into contact with *H. Bolanderi* many times and have been hybridized in different areas.

The hybridization of the two species is probably of fairly recent origin, perhaps dating back only a few hundred years. The original hybridization according to this hypothesis would have taken place between *H. annuus* and the foothill serpentine race of *H. Bolanderi*. The hybridization that is occurring today, however, and that which has been studied here, is mainly between *H. annuus* and the valley weed race of *H. Bolanderi*.

Perhaps there would have been little chance for the hybrid types to survive because of their high degree of sterility, but as has been shown here the hybrids nearly always produce some good pollen. Thus it would be theoretically possible for genes to pass from one species to another by means of continual backcrossing of the hybrids to the parent species. According to most recent students of evolution (e.g., Sturtevant, 1938), selection would tend to favor the development of sterility barriers between the two species since the hybrids would lead to a decrease in the potential reproductive capacity. How-

ever, no such barrier has yet been erected between the two species. Species which have been differentiated in isolation from one another, as these two presumably were, may hybridize when they come together (Huxley, 1942). No complete sterility barriers have been erected between *H. annuus* and *H. petiolaris,* although it would appear that these two species had been in contact for a fairly long period. Great morphological diversity (such as that in *H. annuus* and *H. Bolanderi*) may develop, however, without the erection of sterility barriers. Other examples could be mentioned, chiefly that of *Platanus* (Sax, 1933).

As a result of this hybridization, *H. annuus* within California may have changed since its original introduction there. The experimental garden results show that *H. annuus* within California is slightly smaller in many respects than *H. annuus* from without California. There can be little doubt that many populations of *H. annuus* are modified morphologically in areas where hybridization is known to be taking place with *H. Bolanderi.* Probably more important than the slight morphological changes are the physiological adaptations that the species would have to make to become widely distributed in California with its varied climatic conditions. Such an adjustment could come about either through gene mutation, or by the assimilation of genes from a species already adapted to California—*H. Bolanderi*—through hybridization, backcrossing, and selection of the favorable recombinations. *Helianthus petiolaris,* another annual species introduced into California, has not made the successful exploitation of the whole state that *H. annuus* has, nor has it come into contact with *H. Bolanderi.*

The interchange of genes between *H. annuus* and *H. Bolanderi* appears to have changed the latter species even more than the former. Although one would expect selection against the hybrid derivatives on or near serpentine in the foothills, there may have been a selection for certain of the recombination products in newly disturbed areas in the valleys. Although the exchange of genes may have been slight, it would be significant if in some way the genes derived from *H. annuus* had some selective value. A weed race of *H. Bolanderi* might make advantageous use of characteristics from the weedy *H. annuus.* Earlier blooming might be pointed to as one such example, for which there is some evidence. The weedy *H. Bolanderi* of the valleys is larger in size than its counterpart of the foothill serpentine regions. The difference in size could easily have been derived from genes of *H. annuus.*

Hybridization might have aided these species by introducing genes which (1) directly better adapt the plants to a new environment and (2) increase the variability thus providing more raw materials for natural selection. Hybridization accounts for a large part of the "reservoir of variability" of these sunflowers, and recombination has exposed the variation to the action of selection (Mather, 1942). Hybridization followed by selection appears to have led to the formation of the slightly different forms of both species in California.

In addition to hybridization with *H. Bolanderi,* hybridization also occurs between the cultivated and wild forms of *H. annuus* in California. Crossing

of this type is not uncommon in plants. The so-called "degeneration" of *Brassica* is the result of hybridization between weeds and cultivated forms of the same species. Such crossing also occurs between the citron and watermelon (*Citrullus vulgaris*) much to the displeasure of seed growers, and from the observations of both Dr. Marion Ownbey and the writer it appears that crossing takes place between cultivated lettuce (*Lactuca sativa*) and the weed *L. serriola,* which biologically belong to the same species.

Hybridization between the two forms of *H. annuus* could further increase the diversity of *H. annuus* in California. It has been suggested in the previous section that the large size of the leaves of the wild species in California might owe its origin to such a process. From an evolutionary standpoint this hybridization, however, does not appear to be important in California (although it may prove to be elsewhere throughout the range of *H. annuus*). The cultivated sunflower, a man-selected entity, apparently has little of selective value to offer to the wild forms in California.

The preceding account of the appearance and distribution of the two species in California seems to be the most plausible one. Gene mutations, of course, could also be used for an explanation, but it would be difficult to accept these as the only explanation, because hybridization definitely occurs and the variation is always in the direction of the other species. Much of what has been called mutation in nature may very well be segregation following such wide crosses. It has been fortunate that the present study was made at a time when the actual hybridization could be witnessed. A few thousand or even a few hundred years hence the role of hybridization might have become obscured.

The exchange of genes between *H. annuus* and *H. Bolanderi* as a result of hybridization may be termed reciprocal introgression. Anderson and Hubricht (1938) introduced the term "introgressive hybridization" ("introgression" is now generally used) to describe the transfer of genes by means of hybridization from one species of *Tradescantia* to another. This phenomenon has now received the attention of several biologists and has been observed in a number of genera. This work is to be reviewed in another paper (Heiser, in press, 1949), and therefore will not be treated in detail here. Allan (1937) has reviewed some of the earlier work on natural hybridization.

Before discussing the mechanism and consequences of introgression, it might be well to point out some of the possible types of species hybrids that may occur in plants: (1) completely sterile hybrids, the so-called "mule plants," in which introgression cannot occur; (2) allopolyploids in which the sterility is overcome by a doubling of the chromosomes; (3) the special class of hybrids found in *Oenothera,* in which special cytological mechanisms have developed for the perpetuation of the hybrid; (4) those hybrids that are not completely sterile; within this group backcrossing to the parent species may occur and introgression may take place. The introgression may be (a) of minor importance and its effects purely local, or (b) the gene exchange may take place on a fairly large scale. Through the latter process superior genotypes may emerge which are better adapted to certain available environments; this

seems to be happening in the annual sunflowers. The introgression that takes place may go only in one direction or it may proceed toward both species, as in hybridization between *H. annuus* and *H. Bolanderi.*

Exactly how introgression comes about is worth consideration. It is possible that great variability in the F_2 generation or backcrosses could arise by whole chromosomes passing from one species to another and the introduction of a whole series of genes. On the whole this is probably uncommon, since the genome of the species is in a finely balanced physiological adjustment, and the introduction of a foreign chromosome would probably lead to very severe upsets, particularly at low chromosome levels. Gordon (1946) has concluded that the W chromosome in domesticated stocks of the fish *Platypoecilus maculatus* may represent a *Xiphophorus helleri* sex chromosome, the transfer having come about through introgression.

It is more probable that in most introgressions there has simply been an exchange of relatively small segments of chromosomes. Experimental evidence has been obtained for this by Hiorth (1933). In the cross between the species *Collinsia bicolor* and *C. bartsiaefolia* it was possible by repeated backcrossing to transfer genes from one species to another, and moreover a section of a *C. bartsiaefolia* chromosome could be introduced into *C. bicolor.* This is probably what happens during introgression. In the annual sunflowers it is probable that gene exchange occurs through crossing over. The fact that in all hybrids of *H. annuus* and *H. Bolanderi* a high number of bivalents are observed lends support to this view.

An explanation of where hybridization takes place requires only brief discussion. It has been pointed out in several studies that hybridization occurs most frequently in areas in some way disturbed by man. Brainerd (1906) suggests that the spread of species of *Viola* and the opportunities for hybridization followed the removal of the forests by man. Disturbance of the environment by man may not only bring species together but may also create new intermediate types of habitats which would be necessary for the success of the hybrid derivatives or introgressants, as has been suggested by Hubricht and Anderson (1941) and Anderson (1948). It should be pointed out that disturbance of the environment could be created through agencies other than man, so that introgression is not necessarily of recent origin. However, the conspicuous changes occurring at present in the vegetation of the earth are in a large measure due to the activities of man (Stebbins, 1947).

It is quite clear that the hybridization in the annual species of *Helianthus* owes its origin to man. *Helianthus annuus* has been so influenced by man that it is doubtful if the species occurs in any areas undisturbed by him.

The evolutionary potentialities of introgression have been considered previously by Anderson and Hubricht (1938). A few remarks in that direction are in order here, however. It is possible that hybridization might lead to the creation of a new species on a homoploid level (with or without introgression). Epling and Lewis (Epling, 1947) have suggested the origin of a *Delphinium* species by such a process. *Euchlaena* is thought to have arisen as a "by-

product" of hybridization between *Zea* and *Tripsacum* (Mangelsdorf and Reeves, 1939; Mangelsdorf, 1947). The artificial production of a "new species" which is partially sterile when backcrossed to either parent has been obtained through hybridization by Lamprecht (1941). Babcock (1947) points out that hybridization has been of importance in the origin of species of *Crepis,* although of secondary importance when compared to reciprocal translocations and gene mutations.

It is possible that the valley weed race of *H. Bolanderi* could become a distinct species in time, if by some means it could be isolated from the races with which it crosses. At present there is little doubt that the two races should be considered as belonging to the same species. The two are made up of the same materials which are put together in almost the same fashion, whereas *H. annuus,* although made up of the same materials, has the emphasis placed differently.

During the course of this paper it has been maintained that in spite of hybridization there has been no tendency for an amalgamation of the two species into a single highly variable species. Apparently a swamping of distinct species through hybridization does not take place in nature. Epling (1947) discusses the failure of a swamping of species following hybridization and cites several excellent examples. One explanation for the failure of swamping may be found in Anderson's (1939) study of recombination in species crosses. The failure of swamping depends upon several factors, chief among them hindrances imposed by linkage and the environment (Anderson, 1948).

Lotsy (1916, 1925), who attempted to explain all evolution in terms of hybridization, maintained that new characters can arise on crossing, presumably by an interaction of genes. But Anderson (1939) stated that the novelty of hybrids will be due to new combinations of parental characters and not to the appearance of new characters, the only exceptions being tetralogical upsets in physiologically ill-adjusted hybrids. If nothing new is created by hybridization, it is difficult to imagine that it is an important evolutionary process. If hybridization between species were found to influence mutability, however, perhaps hybridization then might be pointed to as a very important evolutionary process. Harland (1937) has shown that hybridization influenced the mutability of certain genes in crosses between *Gossypium purpurascens* and *G. hirsutum.*

In conclusion it may be stated that rapid evolution appears to be occurring in the annual species of *Helianthus.* They enjoy the ability to exchange genes, which allows for great flexibility and a great array of types for selection to act upon. Groups such as these may attain wide geographical distribution and be able to adapt themselves to changing conditions, as Clausen, Keck, and Hiesey (1945) have pointed out. *Helianthus annuus* is a marked example of a species which is extremely variable and as a weed has been able to invade wide areas with different climates. Introgression has probably played a prominent role in its development.

There may be some doubt as to whether one is justified in considering *H. annuus* and *H. Bolanderi* as distinct species. If by definition species are always intersterile when crossed and if intermediates between them do not occur, then these are not entitled to specific ranking. If the assumptions made here are correct these two entities were geographically separated before man entered the scene, and today the two species hybridize as a result of man's interference and intermediates are produced. However, there is only a slight blurring effect on the specific boundary produced by introgression and the specific lines have not been obliterated.

An attempt has been made here to explain some of the many problems connected with the evolution of *H. annuus* and *H. Bolanderi* in California. Any such explanation at present, of course, involves much speculation. How and when the two species originated are questions that remain unanswered. Many years of detailed work, involving field, cytogenetic, and statistical analyses, would be required to attempt a more precise definition of the evolutionary processes at work.

SUMMARY

Helianthus annuus L., a widespread weed in the United States, is an extremely variable species. Two main races are recognized, in addition to the monocephalic cultivated sunflower. There is circumstantial evidence that *H. annuus* was introduced into California by the American Indian in fairly recent times.

Helianthus Bolanderi A. Gray, native to Oregon and California, comprises two races or ecotypes; one occurs in foothill regions on or near serpentine outcrops (*H. exilis* of A. Gray); the second occurs as a weed in valley regions.

The two species hybridize in California. Several natural hybrids and one large hybrid swarm have been found in nature. The artificial F_1 hybrid between the two species has been produced and some backcrosses have been made.

The chief morphological criteria used to distinguish the various entities are discussed. Important taxonomic distinctions between the two species are found principally in the shape of the involucral bracts, the nature of the chaff, and the overall size of the plants.

Both *H. annuus* and *H. Bolanderi* have the haploid chromosome number of seventeen. The hybrids, both natural and artificial, show certain meiotic irregularities in the development of the pollen, resulting in a high degree of sterility.

Population samples of both species and hybrids from natural, greenhouse, and experimental garden populations are analyzed. A statistical study of the experimental garden plants revealed size differences in the various entities under consideration.

It is concluded that reciprocal introgression has occurred between the two species, and that perhaps the exchange of genes has enabled both species to become successful weeds in California. The introgression may have produced a slightly larger form of *H. Bolanderi* and a slightly smaller form of *H. annuus* in California. The introgression has caused a great increase in the variability of the two species but has not resulted in their fusion into a single highly variable species.

Some of the consequences of introgression are discussed briefly. Introgression takes place through the backcrossing of hybrids to one or the other or both of their parental species; it occurs chiefly in areas which have been disturbed in some way by man. No definite conclusions can be reached as yet in regard to the general evolutionary significance of introgression, although it can readily be seen that introgression creates great variability which provides raw material for the action of natural selection.

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Helianthus lenticularis Dougl. (illustration from Bot. Reg. 15: pl. 1265).



Type of *Helianthus Bolanderi* A. Gray (from Gray Herbarium of Harvard University



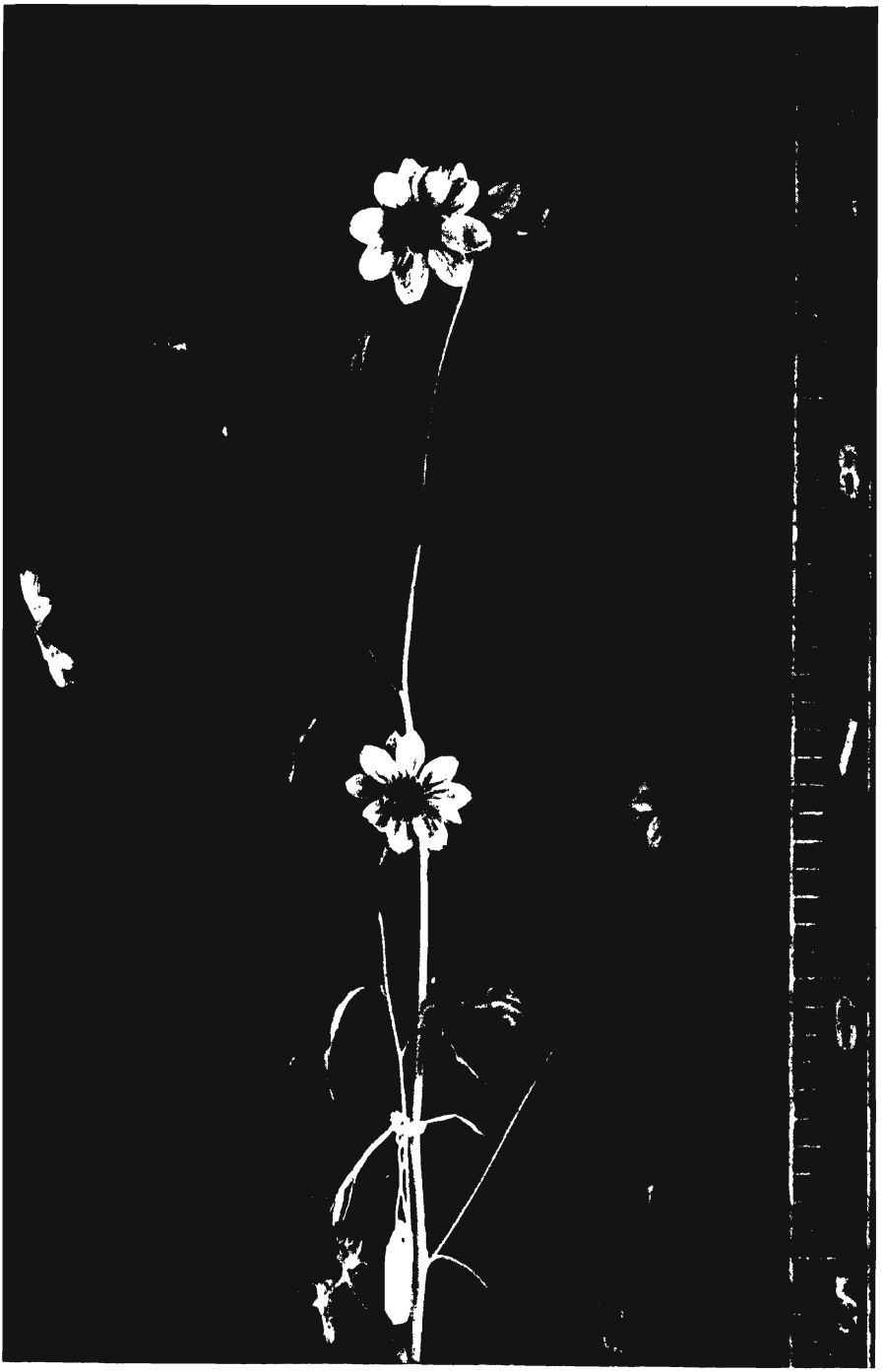
Type of *Helianthus exilis* A. Gray (on right) (from Gray Herbarium of Harvard University).



Helianthus annuus × *H. Bolanderi* (natural hybrid).



Helianthus annuus × *H. Bolanderi* (natural hybrid). (The label on the sheet should read "Solano County" for "Yolo County").



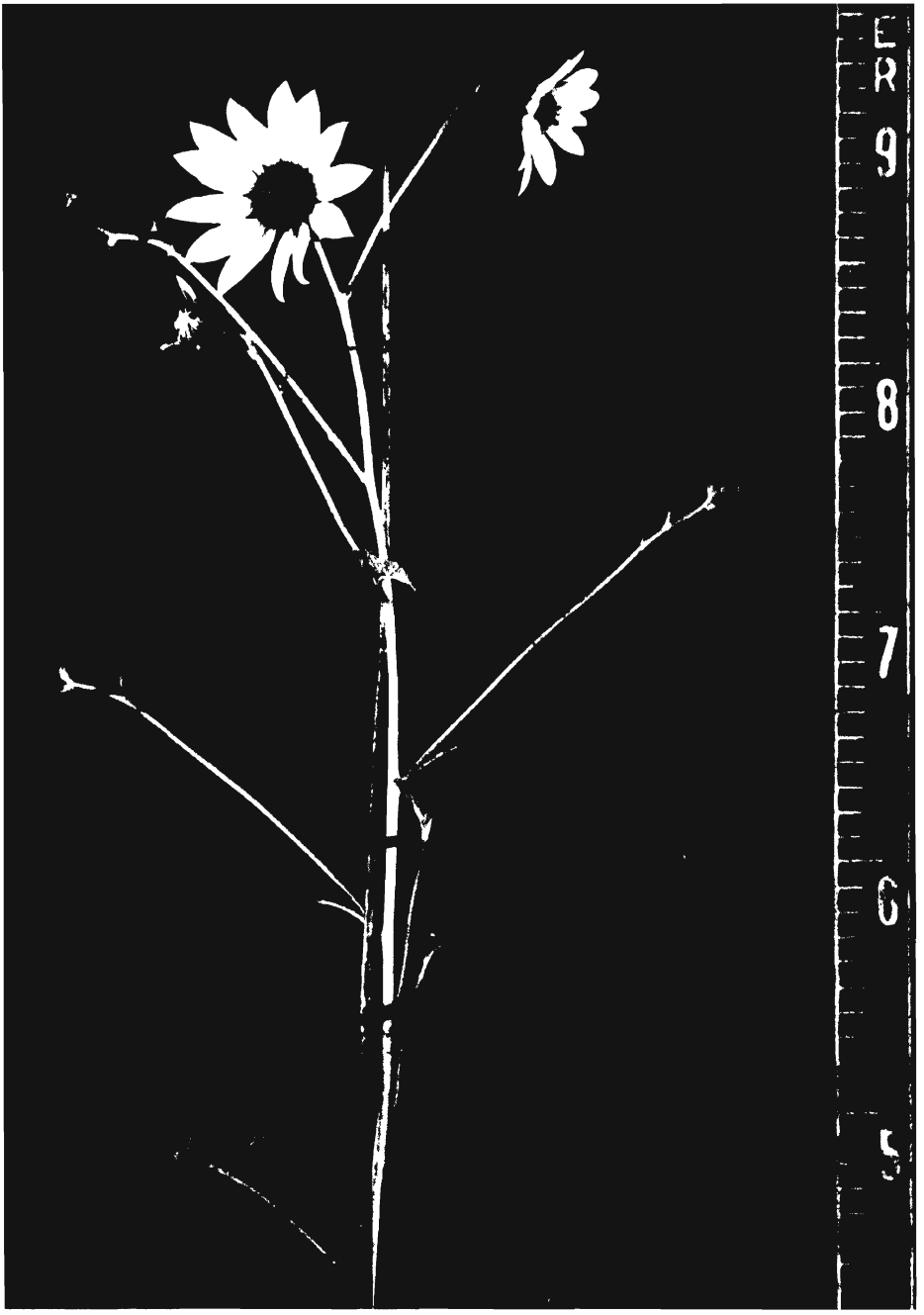
Helianthus Bolanderi A. Gray "foothill serpentine form" *Heiser 642* (from greenhouse).



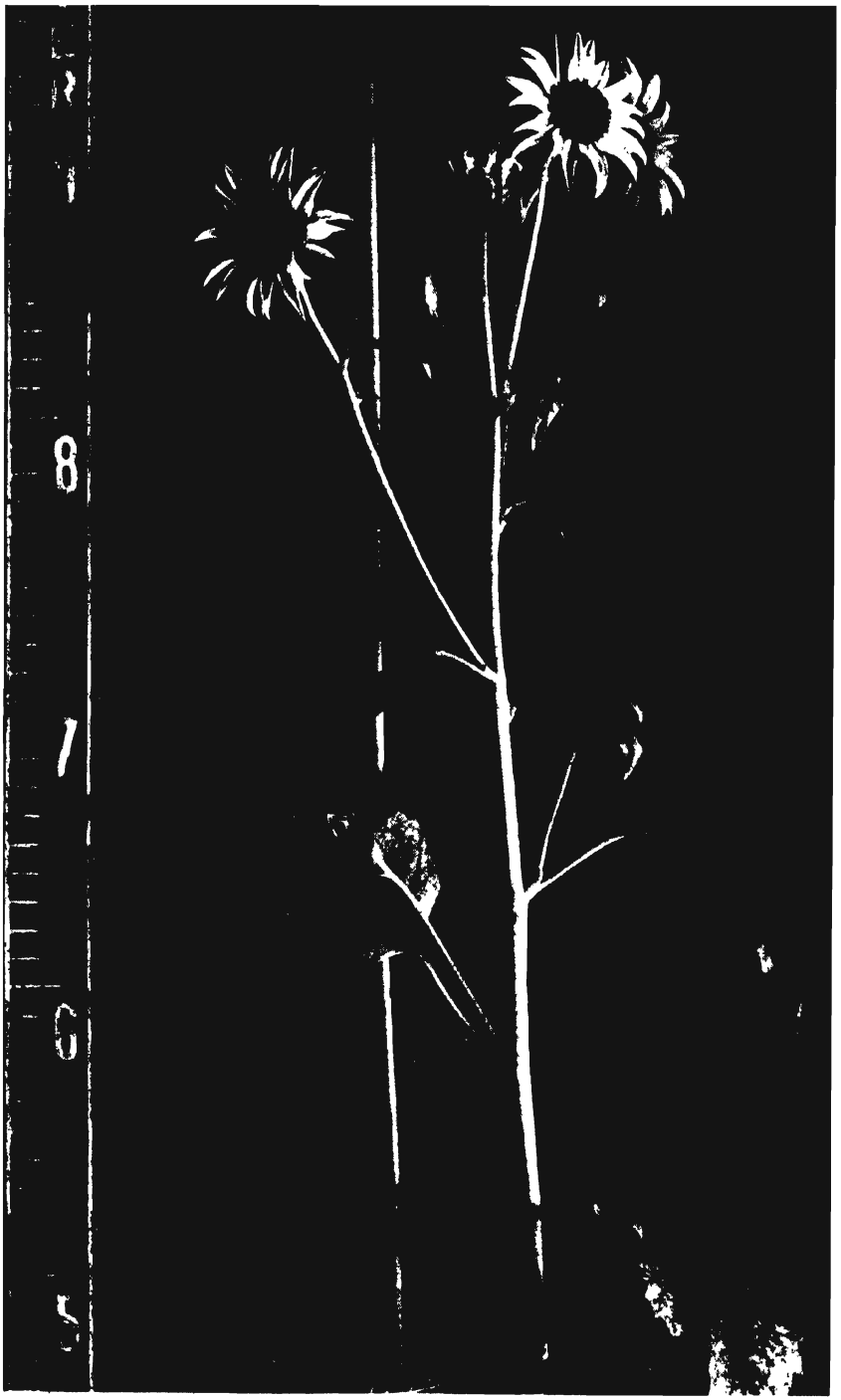
Helianthus Bolanderi A. Gray "valley weed form" *Heiser 644* (from greenhouse).



Helianthus annuus × *H. Bolanderi Heiser 645* (from progeny of a natural hybrid grown in greenhouse).



Helianthus annuus L., *Heiser 646* (introgressant form from California grown in greenhouse).



Helianthus annuus L., *Heiser 648* (introgressant form from California grown in greenhouse).

THE GENUS POLEMONIUM [TOURNEFORT] L.

BY

JOHN F. DAVIDSON

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THE GENUS POLEMONIUM [TOURNEFORT] L.

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IN 1830 LINDLEY remarked upon the "miserable state of confusion" in the genus *Polemonium,* a statement which Asa Gray later (1853) also endorsed. After a lapse of over one hundred years one can only reiterate Lindley's remark, with even greater emphasis. However, increased knowledge and larger accumulations of material facilitate a new attack upon the problem. The present paper, although not pretending to solve all the enigmas of interrelationship within the genus *Polemonium,* does strive to remove some of the existing confusion through a reëvaluation of specific concepts and the banishing of certain purely nomenclatural difficulties that have long obscured affinities within the group.

The genus has been discussed by Bentham (1845), and Gray (1870), and monographed by Brand (1907). The latter treatment includes a number of categories, based upon purely morphological grounds and limited material, many of which seem to be untenable in the light of present knowledge. Wherry (1942) published a tentative key to the American perennial species which had the virtue of eliminating Brand's polynomials, but which included neither specific descriptions nor citations of specimens, and was apparently based largely upon type specimens and type descriptions. At present there is no treatment of the genus by which even a trained harbarium worker can accurately identify specimens.

The present work on the genus *Polemonium* was undertaken because the group lends itself to study from various approaches. Apart from the classical comparative morphological and distributional studies possible in the herbarium, the members of the genus respond readily to cultivation, and thus cytological and genetic material can be easily procured once seed is available. Flowers for genetic or cytological work may be produced from seed in as short a time as four months, whereas root tips may be produced in a week or ten days. The chromosomes of all the species examined are moderately large and may be seen and sometimes counted under a magnification of 100 diameters. The basic number ($n = 9$) is also small enough for facility in counting under rapid smear preparations.

The perennial habit of the majority of the species makes possible the retention of the parent stock for hybridization work, yet, because of early flowering from seed, the perennial habit does not greatly increase the length of time required to produce an F_2 generation. Under artificial illumination, two generations may be be produced per year.

One very definite disadvantage is the inaccessability of the seed of many species. The wide distribution of the genus over many mountain ranges increases the difficulty of establishing a really representative collection of seed at any one point. Since the problem was undertaken, seed has been secured from many sources, but many species are still unrepresented in our collections.

The problem of delimiting species in *Polemonium* is complicated by their predominantly montane habitats. Mountain-top isolation of populations, comparable to insular isolation, favors a certain amount of random fixation of genes. In some such cases speciation may result in narrow endemics restricted to a single peak or mountain range. In other cases the populations on neighboring but isolated mountains are remarkably similar morphologically, a fact which presumably suggests their common origin. If cognizance were taken of the minute differences existing between populations on different mountains, one might eventually delimit as many subspecies as there are populations on isolated mountains. In the light of our present data, such a treatment would necessarily be purely descriptive, and would be of dubious value. Such an undertaking, or indeed the problem of any positive taxonomic evaluation of specific or subspecific relationships, is greatly facilitated when approached from a genetic or cytological basis. However, until the present time, interpretation of genetic and cytological data has been complicated by the confused nomenclature in the genus.

The present paper is therefore an attempt to ascertain and depict the pattern of morphological variation and geographical distribution of the natural populations of the genus, and then to determine the valid name for each of these entities. (Fig. 24.) This should clear the way for more detailed studies of relationships, based upon cytological and experimental data.

The mass of published species of *Polemonium* is rather staggering when compared with the number of discrete entites that can be recognized in nature. Since Asa Gray described *Polemonium confertum* in 1853, and noted the confused state of the genus, botanists have increased that confusion by describing new species based upon extremes or merely minor variations of characters which are very variable in the population as a whole. Yet such "species" have been described more or less consistently for the last century, based upon one or a few specimens which showed such lack of variation that the specific diagnoses were fairly narrowly circumscribed. The present study is directed toward such aggregation of synonomy and clarification of taxonomic concepts as must precede any intensive experimental work.

If all the diagnostic characters of a supposed species are present in the surrounding populations, either singly or in various combinations, such a species has been reduced to synonymy in the present treatment. In North American material, for instance, a natural group of specimens may be readily segregated, ranging from the Aleutian Islands through the Rocky Mountains to Montana. When specimens from the extremes of the range are compared, they may appear dissimilar, but there is a transition or gradient from one form to the other. Also, intergrading expressions of any character or group of characters appear at apparently uncorrelated points throughout the broad range of the species. The whole population stands as a natural group, with possibly more morphological variation than many authors would like to ascribe to one species, but thus far no criteria have been found to subdivide the group into smaller natural species with significant distributional patterns.

Since *Polemonium pulcherrimum* Hook. was the first name applied to a member of this population, it is accepted as the valid designation, and subsequent names have been placed in synonymy. Some of these names may represent subspecies of *P. pulcherrimum*, but confirmation of this will require further evidence. In many cases it is felt that names have been applied to small populations in which some of the genes of the species have become lost through random fixation, or which may be simply nongenetic modifications brought about by different environments. The possibility of the latter interpretation has been demonstrated in the growth studies carried out.

METHODS EMPLOYED

It was concluded that the most complete evaluation of interspecific relationships could be made by the utilization of as many taxonomic tools as possible. Thus, while the majority of the data were obtained from the fields of comparative morphology and plant distribution, facts gleaned from cytology, genetics and growth studies have also been utilized.

Comparative morphology.—This study was based largely upon herbarium materials, supplemented by reference to the growing plants. The usual coordination of specimens with original descriptions and type specimens was undertaken with a view to refining concepts and nomenclature in the light of greater accumulations of materials.

Distribution.—The field source of each herbarium specimen examined has been recorded and plotted as far as is possible on appropriate distribution maps. (See pp. 273–282 below.)

Cytology.—The cytological information was obtained from meiotic configurations of pollen mother cells, although root tips have also been studied. Emphasis was placed upon meiotic behavior because of its greater significance in determining the character of potential specific barriers.

Both buds and root tips were fixed for twenty-four hours in 3:1 alcohol-acetic, and were then washed and stored in 70% ethyl alcohol. Smears were made with iron acetocarmine, and in all cases the slides were made permanent before the camera lucida drawings were made. Except for the first few slides made, all of the cytological preparations are referable to herbarium specimens taken from the same plants which are deposited in the herbarium of the University of California, at Berkeley.

Growth studies.—While growing plants for cytological material, it was thought advantageous to vary the environment somewhat as a check against possible ecological modification. At the same time, seedlings from any one parent were studied for variability, due either to the inherent variability of the plant, or to the segregation of some of the parental types.

Plants were grown outdoors in the Botanical Gardens of the University of British Columbia, at Vancouver, Canada, and on the campus of the University of California, at Berkeley. Plants were also grown in a greenhouse on the Berkeley campus, where facilities were available for employing artificial illumination.

In June, 1946, seed was secured from a collection made by *Alexander and Kellogg 5106* at Eagle Rock, Modoc Co., Calif. This was sown in June, and by September the plants produced flower buds which remained unopened for about two weeks, and which then began to wither. These buds were borne on peduncles subequal in height to the basal leaves, as may be seen on the herbarium sheets under the above number. Since no changes had been made in the cultivation procedure it was considered possible that the bud dormancy might have been due to the shortening of the length of day. Consequently, a 300-watt light, with an automatic switch, was installed about three feet from the plants, to increase the daily illumination from twelve to twenty hours. The response was apparent within a week. The plants not only produced numerous flower buds, but their vegetative characteristics were markedly affected. The flower peduncles attained a length double that of the basal leaves, and the leaflets which had been broadly elliptical previously, developed on the new leaves as narrowly elliptical. The appearance of the plants duplicated specimens from northern British Columbia and Alaska, and served to indicate the possible range of variation in this species in response to change in the length of day.

Another feature of the use of artificial illumination is the advantage obtained in bringing plants into anthesis at the same time for hybridization purposes. The extra illumination mentioned above was not confined to *P. pulcherrimum* alone, and the other species in the plot (notably *P. cæruleum, P. foliosissimum* and *P. pauciflorum*) also responded to the lengthened day by increased growth and flower production.

Genetic work.—The possibility of natural hybridization cannot be overlooked, and the demonstration of definite sterility barriers is an aid to specific delimitation. Thus, hybridization studies should form an integral part of any taxonomic revision. Ostenfeld (1929) has demonstrated that while some interspecific crosses may produce fertile hybrids (*P. mexicanum* × *P. pauciflorum*), other crosses may produce self-sterile hybrids (*P. filicinum* × *P. cæruleum, P. carneum* × *P. cæruleum*). J. Clausen (1931), in his cytological observations in Ostenfeld's material, reported the occurrence of irregularities in meiosis in even the self-fertile *P. mexicanum* × *P. pauciflorum* F_1, with the formation of polysomic chromosome groups.

One of the barriers to hybridization is the difference in time of anthesis, a phenomenon much more marked in Berkeley than in Vancouver. In Vancouver the plants appeared to flower earlier in the season, and the various species tended to flower more concurrently than in Berkeley.

The only two species that flowered simultaneously in Berkeley in 1946 were *Polemonium pauciflorum* and *P. foliosissimum*. A reciprocal cross between these two species was made in the following manner:

P. pauciflorum	*Result*	*P. foliosissimum*	*Result*
Castrated and bagged	no seed	Castrated and bagged	no seed
Castrated and selfed	seed set	Castrated and selfed	seed set
Castrated × *foliosissimum*	no seed	Castrated × *pauciflorum*	no seed
Bagged only	seed set	Bagged only	seed set

Since the above results were obtained from only seven to ten flowers per experiment, complete incompatibility cannot be assumed, but it is evident that the two species are not completely interfertile. The cross must be repeated with larger numbers of flowers before complete incompatibility can be demonstrated. The fact that the bagged flowers produced seeds indicates the ability of these species to perpetuate the genome of the parent, and may help to explain some of the distributional problems. That it is a case of self-pollination rather than apomixis is shown by the fact that the castrated flowers produced no seed, and Ostenfeld's successful hybridization of each of these species eliminates the possibility of pseudogamy. The same self-pollination in bagged flowers has been demonstrated in *Polemonium micranthum,* but *P. pulcherrimum,* on the basis of similar experimental evidence, is not normally self-pollinated. This difference in behavior is correlated with the relative diversity of these two species.

SUMMARY OF TREATMENT

The paucity of cytological and experimental data on interspecific and infraspecific relationships in *Polemonium* hampers the assignment of infraspecific categories. However, it has been considered advisable to reduce a number of previously described species to an infraspecific category in order to stress affinities. These infraspecific entities, where they have been assigned taxonomic rank, have not been named below the subspecific level. Where described species have been reduced to synonomy and no taxonomic name assigned them in the present treatment, they have been submerged in the accepted species for lack of sufficient evidence to warrant according them subspecific status. The author hopes that additional evidence, especially of an experimental nature, will be forthcoming, but believes that at the present time the retention of names for what now appear to be merely variants would serve only to encumber the literature.

The present treatment recognizes 19 species and 5 subspecies entirely confined to the northern hemisphere with the exception of a few scattered individuals of *Polemonium micranthum* Benth., which are to be found in the southern portion of South America. In addition to the above, the genus is found in many latitudes, from the mountains of Mexico (*P. mexicanum, P. grandiflorum*) to the shores of the Arctic Ocean (*P. boreale, P. cæruleum* subsp. *villosum*). In ecological requirements the members of the genus are also variable. Some are found in peat bogs (*P. cæruleum* subsp. *occidentale*), some on alpine crags (*P. viscosum*), and others in semideserts (*P. micranthum*) associated with *Artemisia tridentata* and *Opuntia* spp.

The Polemoniaceæ probably originated in the montane area of western North America, and in the course of development gave rise to two genera, *Polemonium* and *Phlox,* which could withstand the rigors of an alpine habitat. During the Tertiary, or one of the later interglacial periods, representatives of these two genera migrated to Alaska, to Asia, and thence to Europe, where they now constitute the sole members of the family. That this occurred re-

cently is assumed on the basis of the reduced number of species in the Old World in both of these genera, and the close relationship shown between the Eurasian and the North American species.

The closest affinity of *Polemonium* within the family is probably with the genus *Gilia* from which it is separated by its wholly herbaceous and accrescent calyx. The calyces of some of the members of *Polemonium viscosum* (described as *Gilia Brandegei* A. Gray) show traces of scariosity in the sinuses and these occasionally tend to rupture in age.

CITATION OF SPECIMENS

Only those specimens are cited which have duplicates in several herbaria, or which aid in depicting the variation and distribution of the species. The number of specimens examined, shown before each list of citations, is the total number of herbarium sheets examined.

The following abbreviations have been used to denote the corresponding herbaria:

CAN	National Museum of Canada, Ottawa, Ontario.
F	Chicago Museum of Natural History.
GH	Gray Herbarium, Harvard University.
K	Royal Botanical Gardens, Kew, England.
LD	Botanical Museet, Lund, Sweden.
NY	Herbarium of the New York Botanical Gardens.
S	Naturahistoriska Riksmuseet, Stockholm, Sweden.
UC	University of California, Berkeley.
US	United States National Herbarium.
WYO	Rocky Mountain Herbarium, University of Wyoming.

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The kindness of the curators of the above herbaria, in making their *Polemonium* material available is greatly appreciated.

Grateful acknowledgment is hereby accorded Drs. H. L. Mason, Lincoln Constance, G. L. Stebbins, and A. S. Foster for their helpful suggestions and stimulating discussions in the course of these investigations.

Thanks are due also to my father, Professor John Davidson, for his continued interest in this undertaking, and for his coöperation, through the Botanical Gardens of the University of British Columbia, in establishing and maintaining a living collection of the available species and variants of *Polemonium*.

Polemonium [Tournefort] L. Species Plantarum, 162. 1753

Erect, spreading, or decumbent annuals or rhizomatous perennials; stems simple or branched; leaves pinnately divided, the leaflets entire, pinnately or palmately divided, narrowly linear to rotund; flowers in terminal or axillary cymes, solitary to capitately congested, or in a loose sympodial cyme; calyx herbaceous throughout (except in some specimens of *P. viscosum* Nutt.), accrescent, campanulate, the lobes deltoid to acuminate; corolla rotate-campanulate to narrowly funnelform, with no sharp distinction between tube and throat, lobes spatulate to rotund, white, yellow, pink, purple, or blue; stamens normally equally inserted on the tube, the level of insertion varying in some species, the filaments of equal length, included or exserted; style with three stigmas, included or exserted; capsule trilocular, ovoid, each locule 1–10 seeded, the seeds in some species becoming mucilaginous when moistened; embryo orthotropic in evident endosperm.

Named for *Polemon*, a Greek philosoper.

About 20 species, the greatest number occurring in the mountains of western North America. Also occurs in eastern North America, and the mountains of South America, Asia, and Europe. In the northern lattitudes the species are to be found at sea level.

KEY TO THE SPECIES OF POLEMONIUM

Corolla limb exceeding or subequal to the tube, the corolla campanulate to rotate from a short funnelform tube.
- Leaves predominantly cauline.
  - Corolla less than 20 mm. in diameter, or if greater, the plants erect, strict.
    - Leaflets elliptic to broadly ovate.
      - Corolla greatly exceeding the calyx.
        - Leaflets lanceolate to elliptic; capsule sessile.
          - Terminal leaflets discrete; seeds not becoming mucilaginous when moist ..... 1. *P. cæruleum*
          - Terminal leaflets confluent; seeds becoming mucilaginous when moist ..... 2. *P. foliosissimum*
        - Leaflets broadly elliptic; capsule stipitate ..... 3. *P. reptans*
      - Corolla slightly exceeding or shorter than the calyx.
        - Corolla exceeding the calyx, blue ..... 4. *P. mexicanum*
        - Corolla shorter than the calyx, commonly white ..... 5. *P. micranthum*
    - Leaflets narrowly linear ..... 6. *P. pectinatum*
  - Corolla commonly more than 25 mm. in diameter; plants decumbent, spreading.
    - Leaflets 10–25 mm. wide, commonly elliptic ..... 7. *P. carneum*
    - Leaflets less than 6 mm. wide, commonly lanceolate ..... 8. *P. grandiflorum*
- Leaves predominantly basal.
  - Plants erect; peduncles strict.
    - Flowers in condensed subcapitate cymes; leaflets broadly elliptic to subrotund, less than twice as long as broad; calyx densely glandular-pilose ..... 9. *P. boreale*
    - Flowers in lax, elongated cymes; leaflets lanceolate, more than twice as long as broad; calyx sparingly pubescent ..... 1. *P. cæruleum*
  - Plants cæspitose; peduncles branching.
    - Calyx lobes approximately one and one-half times the length of the calyx tube.
      - Leaflets all discrete, but on a narrowly winged rachis ..... 10. *P. delicatum*
      - Proximal leaflets discrete, but at least the terminal three confluent ..... 11. *P. californicum*
    - Calyx lobes equaling the calyx tube.
      - Corolla lobes funnelform; the terminal three leaflets confluent ..... 12. *P. pulchellum*
      - Corolla lobes rotate; all leaflets discrete ..... 13. *P. pulcherrimum*

Corolla limb definitely shorter than the tube, corolla tubular to funnelform, if the limb rotate, the tube elongate.
Inflorescence congested, subcapitate to spicate; leaflets two-ranked or verticillate.
Stamens exserted, longer than the corolla.
Leaflets two-ranked.....14. *P. elegans*
Leaflets verticillate.....15. *P. chartaceum*
Stamens included, shorter than the corolla.
Calyx lobes acute, but rounded at the extreme apex; inflorescence ovoid in fruit, the axis elongating very little.....16. *P. eximium*
Calyx lobes acute to the extreme apex; inflorescence cylindrical in fruit through the elongation of the axis.....17. *P. viscosum*
Inflorescence open, or the flowers borne singly; leaflets two-ranked, never verticillate.
Corolla tubular, not over 12 mm. broad at the apex, yellow tinged with red 18. *P. pauciflorum*
Corolla funnelform, 15–20 mm. broad at the apex, blue.....19. *P. glabrum*

1. **Polemonium cæruleum** L.

P. cæruleum L., Sp. Pl. 1: 162. 1753.

Perennial from a horizontal or descending rootstock; stems solitary, glandular-pubescent, becoming glabrate below, 2–10 dm. tall, the cauline leaves reduced toward the inflorescence; leaves commonly pinnate, occasionally bipinnate (*P. sibiricum* Don, *P. dissectum* Reichb.); leaflets 19–27, lanceolate to elliptic, acute or acuminate at the apex, obliquely rounded at the base, 7–40 mm. long, 2–12 mm. wide; bracts pinnatifid to entire; inflorescence a strict or open corymbose cyme; pedicels commonly shorter than the calyx; calyx campanulate, the acute segments twice as long as wide, exceeding the tube; corolla blue, rarely white, 8–25 mm. long, 10–25 mm. broad, the lobes commonly rotund, often elliptic, about twice the length of the tube; stamens subequal to the corolla or exserted, inserted commonly at or below the middle of the corolla tube, their basal pubescence apparently occluding the tube when viewed from above; style subequal to the corolla to one and one-half times as long, often exserted in bud; seeds not mucilaginous when wet. Flowering from June to August.

Type locality.—"Europe," Linnæus.

Distribution.—From the mountains of North America, Asia, and Europe to the Arctic coast.

It is not without some misgiving that the present treatment of the *P. cæruleum* complex is proposed. However, the validity of retaining specific rank for the proposed subspecies is even more questionable.

During their trip through the Rocky Mountains, Hooker and Gray did not question the identity of the American "*P. cæruleum*," a plant with which Gray was familiar in the eastern states, and with which Hooker was undoubtedly familiar in Europe. Later, in sending Gray what was destined to become the type specimen of *P. carneum*, Greene wrote on his collection label, "I have not myself seen much of *P. cæruleum* except under the forms known in the Rocky Mountain region. If this is that species it ought to get a new *name* to bring it into *fame!* It is a beauty!" (The italics are Greene's.) Eight years later, Green "brought into fame" the Rocky Mountain form by "defining it as a probable species" based upon a rootstock character which is constant in neither the New nor the Old World specimens. The inclusion of the eastern American representatives in *P. occidentale* Greene drew from the east the immediate rebuttal of *P. VanBruntiæ* Britton. Britton was quite justified in

separating his *P. VanBruntiæ* from *P. occidentale,* since in the majority of cases they may be distinguished on the basis of stamen exsertion. However, a fact ignored by both authors was that neither entity was adequately distinguished from the variable *P. cæruleum.* It has not been found possible, on the basis of herbarium material and growing plants, to separate consistently *P. occidentale* or *P. VanBruntiæ* from Eurasian representatives of *P. cæruleum* without referring to the collection data. This situation has been rendered especially acute by the introduction of European *P. cæruleum* into the eastern United States and western Canada. More significantly, the combination of characters which gives distinctiveness to the American subspecies occurs also, but sporadically, in Eurasia.

Stebbins' (1942, p. 256–257) concept that species with a restricted distribution are genetically homogeneous, and that those with a widespread distribution are genetically more diverse, affords a reasonable explanation of the present situation. If the ancestors of the present Eurasian populations of *P. cæruleum* originated in North America, as seems probable because of the greater diversity of the genus in the New World, it is also possible that several species, or at least genetic strains, contributed genes to this ancestral *P. cæruleum* stock. The migration of such ancestral populations across the Behring "bridge" would increase the possibility of interbreeding through increased geographical proximity, and would be expected to produce a genetically diverse population. Then too, the area occupied by the American subspecies, as well as the probable number of individuals in these groups, is much less than in the total Eurasian population. Thus the more constant pattern of the American representatives may be explained by either of two postulations, both of which support the subspecific status proposed. Either the North American subspecies were more or less distinct before the production of the Eurasian *P. cæruleum,* and were in part ancestral to the latter; or the North American subspecies were at one time as diverse as the Eurasian, and have subsequently become somewhat genetically and morphologically depleted as a result of habitat selection. The possibility that the North American subspecies may represent a return to North America after the establishment of the Old World *P. cæruleum* is hardly tenable since the Eurasian population would then be the older and, through having as great a range of selective forces operating upon it for a longer period of time, would presumably be broken into as discrete subspecific populations as the younger inhabitants of the New World.

In its range across Europe and Asia, *P. cæruleum* exhibits remarkable morphological and genetic (Ostenfeld, 1923) diversity. The form with bipinnate leaves (*P. sibiricum, P. dissectum*) may appear and disappear in normal *P. cæruleum* subsp. *vulgare* stock, as the writer learned in his growth studies in Vancouver. Height, rootstock, pubescence, foliage, flower size, stamen insertion and exsertion, and style exsertion are all more variable than in the American populations. Specimens which may be regarded as typical of subsp. *occidentale* (*J. G. Leefe* 1838; *Gereke 998; I. Dabkowska* 1937; *Huter 2128;*

Warodell 1876; *G. Forrest 10390*) and subsp. *VanBruntiæ* (*E. B. Wilson 3187; J. F. Rock 12919; E. Liant* 1930) occur in Europe and Asia, apparently as isolated individuals. This leads to the conclusion that the genes present in the American populations are present also in the Eurasian stock, although usually masked by others. Under fortuitous circumstances the phenotypic expression of these genes results in a specimen identical with those of the New World.

However, subsp. *occidentale* is characterized by its strict habit, greatly exserted styles, and included stamens; whereas subsp. *VanBruntiæ* is characterized by its stamen exsertion. While these characters occur in the Eurasian plants, the Eurasian diversity does not occur in the American specimens. It is upon this reduced genetic and morphological variability of the New World populations that the author accords subspecific recognition to these entities, rather than recommending their complete submergence within the variable *P. cæruleum.*

Brand's recognition of a single subspecies in the temperate regions of the Old World is followed here.

KEY TO THE SUBSPECIES OF POLEMONIUM CÆRULEUM L.

Stamens exceeding the corolla; style slightly exceeding the stamens.
  Corolla lobes glabrous, obtuse at the apex.
    Stamens slightly exceeding the corolla.....1a. subsp. *vulgare*
    Stamens one and one-half times the length of the corolla.....1b. subsp. *VanBruntiæ*
  Corolla lobes ciliate, acute at the apex.....1c. subsp. *villosum*
Stamens shorter than the corolla; style twice the length of the stamens . 1d. subsp. *occidentale*

1a. **Polemonium cæruleum** L. subsp. **vulgare** (Ledeb.) Brand

P. cæruleum L., Sp. Pl. 1: 162. 1753.
P. valerianæfolia Gilib., Fl. lithuan. 1: 145. 1781.
P. elatum, Salisb. Prodr. 125. 1789.
P. vulgare S. F. Gray, Nat. Arr. Brit. Pl. 2: 341. 1821.
P. sibiricum Don, Edinb. Philos. Journ. 7: 287. 1822.
P. dissectum Reichb., Icon. Fl. Germ. 4: 38. 1840.
P. lacteum Lehm., Sem. Hort. Hamp. 17. 1845.
P. cæruleum α *vulgare* Ledeb., Fl. Ross. 3: 83. 1847.
P. campanulatum Fries, Not. Sellsk. Faun. Fl. Fenn. 13: 288. 1871.
P. cæruleum subsp. *vulgare* Brand, in Engler, Pflanzenr. 4^{250}: 38. 1907.

Very obviously, in the light of the preceding discussion, it has been found impossible to write a satisfactory diagnosis for this subspecies which would include the range of variation to be found, and at the same time exclude the remaining subspecies. However, for the majority of specimens, the characters outlined in the key to the subspecies are typical.

The specimens from northern North America which have previously been referred to this subspecies, are more probably the expression of characters intermediate to subsp. *occidentale* and subsp. *villosum.* (Fig. 1; map 1.)

Specimens examined (total: 177).—AUSTRIA. "Bei Altenmarkt," *Krebs* (1897), F; "Tyrol near Trafoi," *Pease* (1911), GH; "Southern Tyrol, Mt. Roen," *Huter* 2128, NY; "Albula, Rhætic Alps," *Muhlenbeck,* NY; "Fohrenbez," *Braun Blanquet* 181, GH.

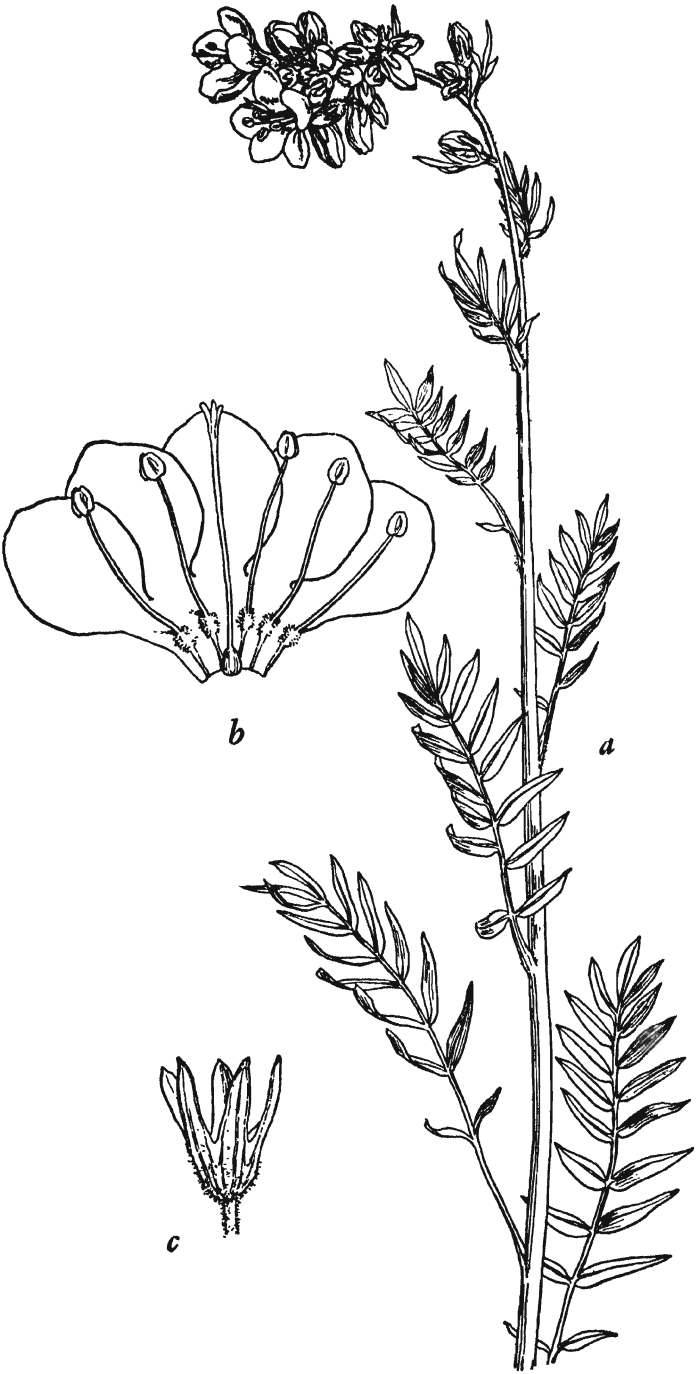


Fig. 1. *Polemonium cæruleum* L. subsp. *vulgare* (Ledeb.) Brand. *a*, Habit, × ⅔. *b*, Dissection of flower, × 2⅓. *c*, Calyx, × 2⅓.



Fig. 2. *Polemonium cæruleum* L. subsp. *VanBruntiæ* (Britt.), comb. nov.
a, Habit, × ⅔. *b*, Dissection of flower, × 2. *c*, Calyx, × 2.

CHINA. "Yunnan," *Forrest* 10390, GH; "Sungpan-hsien," *Fang* 4296, GH; "Western Hupeh," *Wilson* 3187, GH, 2289, NY; Kansu: "Toul Ping near Lichen," *Ching* 414, GH; "Tao River, Toyube, S.E. Choni," *Rock* 12574, GH, NY; Shansi: "Tsiliyu, Wo Shan Mts.," *Licent* (1935), GH; "Fung-ya-ti, Lin shih Hsien," *Tang* 974, NY; Hopi: "Hsiao Wu Tai Shan," *Liu* 2344, NY; "Po Hua Shan," *King* 19, NY.

ENGLAND. "Dib Scar, Grassington," Edmondson 268, NY.

GERMANY. "Weisen bei Bufow on Hinterspommern," *Doms* (1861), F; "Munich," *Woerlein* (1882), F; "Bei Königsberg," *Gereke* 998, GH.

HUNGARY. "Szepes, Montis Fishberg ad balneas Iglofüred," *Filarsky & Szurák*, 394, GH, WYO; "In monte hohe Tatra Carpathorum," *Ullepitsch* 2867, GH; "Near Hohenfulth on Moldau," *Schott* (1899), GH.

INDIA. "Parbatti Valley, Kulu," *Stewart* 124, GH, NY; "Near Bhagtaur," *R. R. & I. D. Stewart* 17930, GH; "Mt. Kolahoi," *Stewart* (1931), GH; "Sonnemarg," *Stewart* 3486, 13278, NY; "above Tola," *Strachey & Winterbottom*, NY; "Shipting Nulla," *Koelz* 884, NY; "Kolang," *Koelz* 9881, NY.

ITALY. "Longobardia, Prov. Sondrio," *Longa* 1333, GH.

JAPAN. "Hamanaka, Kusuri," *Miyabe* (1884), GH; "Sapporo," *Arimoto* (1903), GH.

MANCHURIA. "Turga Rock, 'Lac Hanka' Prairies, Chaffangoi Mission," *Bohnhof* 90, 130, NY; "Buchedo," *P. H. & J. H. Dorsett* 3584, NY; "W. Thingen Mts., near Trekte," *Litvinov* 532, NY; "Er tieng tien tse," *P. H. & J. H. Dorsett* 3045, GH, NY; "Heng Tao Hotze," *P. H. & J. H. Dorsett* 3212, GH, NY.

MONGOLIA. "Kentei Mts., at headwaters of Mesa, Tola and Iro Rivers," *Ikonnikov-Galitsky* 2333, NY; "Iro River," *Kidd & Douglas* (1901), GH; "Khangai on Khalzyngin near Zain-gegen," *Pavlov* 1183, NY.

NORWAY. "Kantskino Maa Arjovarre," *Dahl* (1913), GH; "Davre," *Moe* (1888), NY, *Ahlberg & Axell* (1864), NY.

POLAND. "Olszow distr. Swieciany," *Dabkowska*, F.

RUSSIA. "Distr. Mychajlowsky, Prov. south Ussuriensis," *Mykova* 147, NY; "Krasnojarsk ad fl. Kas," *Schipczinsky* 116, GH; "Transbaicalense ad fl. Angara superiore," *Sukaczew* 224, NY; "Altai Sibir. orient.," *Adrianow* (1883), NY.

SWEDEN. "Norrbottens, O. Torneå, Matarengi," *Hellberg* (1903), NY; "Värmland, Philipstad," *Larson* (1869), NY; "Jämtland, Frösön," *Warodell* (1876), NY; "Hammensone," *Lindström* (1882), GH; "Dalarne, Hedemora," *Ringselle*, GH, *Fredricsson* (1893), WYO.

TURKESTAN. "Ad fl. Naryn," *Fetissow* (1882), NY.

1b. **Polemonium cæruleum** L. subsp. **VanBruntiæ** (Britt.), comb. nov.

P. VanBruntiæ Britt., Bull. Torr. Bot. Club 19: 224. 1892.

This subspecies is characterized by the almost invariable exsertion of the stamens as well as the style, and its rounded corrola lobes which are quite glabrous as contrasted with the acute, ciliate, or erose corolla lobes of subsp. *villosum*. It flowers from June to August. (Fig. 2.)

Type locality.—"Balsam Lake, Catskill Mts.," Mrs. C. Van Brunt (1890).

Distribution.—Restricted to the Allegheny plateau, from Vermont to Maryland and West Virginia. (Map 1.)

Specimens examined (total: 90).—VERMONT. "Abby Pond, Ripton," *Brainerd* (1879), NY, US, WYO; "Green Mts., Ripton," *Brainerd* (1879), GH, NY, US (1880), GH, NY.

NEW YORK. Herkimer Co. "Swamp near Warren," *House* (1917), GH, *Denslow* (1928), NY; Madison Co. "Peterboro," *House* (1916), NY (1917), UC, WYO (1918), GH; Chenango Co. "East McDonough, east side of Bowman Creek," *Edwards & Clausen* 2588, NY; Delaware Co. "Delhi," *Gilbert* (1865), GH; Greene Co. "Balsam Lake, Catskill Mts.,"



Fig. 3. *Polemonium cæruleum* L. subsp. *villosum* (Rud.) Brand. *a*, Habit, × ⅔. *b*, Single flower, × 1. *c*, Single leaf, × ⅔. *d*, Stamen insertion, × 2.

C. Van Brunt (1888), NY (1890), NY, US; Ulster Co. "Beaverskill River, east of Turnwood," *Gleason* 9942, NY; Sullivan Co. "Sucker Brook above Mongaup Pond, Rockland," *Jones, Phillips & Stebbins* 30, NY.

PENNSYLVANIA. Sullivan Co. "Shady Nook," *Stewardson Brown* (1901), GH, NY; Somerset Co. "Glade Run, near Peck's School," *Lisi* (1934), WYO.

NEW JERSEY. Warren Co. "N. of Washington," *Porter* (1867), F, (1868), NY, US; "Sphagnous swamp," *Porter* (1867), GH.

MARYLAND. Garrett Co. "Oakland," *Smith* (1879), F, GH, NY, US; "Near Oakdale," *Smith* (1879), NY, US.

WEST VIRGINIA. "Cranberry Summit," *Guthenberg* 2139, F (1878), NY, *Mertz* (1877), NY; "Canaan," *Core* (1931), NY.

1c. **Polemonium cæruleum** L. subsp. **villosum** (Rud.) Brand

P. villosum Rud. ex Georgi, Beschr. Russ. Reichs. (3) 4: 771. 1800.
P. acutiflorum Willd. ex R. & S., Syst. Veget. 4: 792. 1819.
P. cæruleum, Hook. Fl. bor.-amer. 2: 71. 1838.
P. cæruleum var. *acutiflorum* Ledeb., Fl. Ross. 3: 84. 1847.
P. cæruleum var. *ovatum*, Fl. Ross. 3: 84. 1847.
P. cæruleum subsp. *villosum* (Rud.) Brand, in Engler, Pflanzenr. 4[250]: 38. 1907.

This subspecies is characterized by its much reduced cauline leaves, and the acute corolla lobes which are commonly ciliate, or at times erose at the apex. It flowers from June to August. It is morphologically less diverse than either subspecies *occidentale* or subspecies *vulgare* as might be expected under the more severe selective influence of the Arctic climate. This more evident homogeneity lends support to Hulten's acceptance of subsp. *villosum* as a distinct species. It is felt, however, that the subspecific category best expresses its relationship in the *P. cæruleum* complex without detracting in any way from its recognition as a naturally occurring entity. The intergradation of subsp. *villosum* with subsp. *occidentales* in Alaska, Yukon, and northern British Columbia produces plants which are normally referred to subsp. *vulgare*. Subsp. *villosum* occurs sporadically, often in association with subsp. *vulgare*, as far west as Finland. (Fig. 3.)

Type locality.—In the western region of North(ern) America, collected by Pallas.

Distribution.—The distribution is centered around the Behring Sea, but representatives are found through Kamchatka, Siberia, Russia to Finland in the west, and through Alaska, the Yukon, and the northwest territories of Canada in the east. (Map 1.)

Specimens examined (total: 327).—FINLAND. "Lapponia kemensis, Sattanen," *Asplund* (1935), WYO; "Vesterelven in Naesseby," *Sommerfelt*, GH.

RUSSIA. "Unterlauf des Jenissei," *Nilsson* (1898), GH, NY, US; "Cape Vankarem, Siberia," *Muir* 202, GH; "South shore Anadyr River, Primorsk Region," *Jochelson* 70, NY; "Plover Bay, gravel spit," *Dall* 338, F, GH, NY; "Kamchatka, Savoiko," *Eyerdam* (1928), GH, NY, US.

ISLANDS OF BEHRING SEA. "Little Diomede Is." *A. E. & R. T. Porsild* 1721, CAN, GH, US; "Behring Island," *Gwbitchy* (1891), GH; "Hall Island," *Coville & Kearney* 201, NY; "St. Matthew Island," *Gabrielson* (1940), GH; "Gambell, St. Lawrence Island," *Chambers* 24, US; "St. Paul Island," *Coville & Kearney* 1814, F, GH, NY, US; "St. George Island," *True & Prentiss* 55, GH, NY, US; "Akutan Island," *Norberg* 413, NY, S; "Unimak Island," *Eyerdam* 1887, NY, S.

ALASKA. "King Cove, Alaska Peninsula," *Eyerdam* 1672a, CAN, NY, S; "Kodiak Island," *Harrington* (1871–2), GH; "Port Hobron, Sitkalidak Island," *Eyerdam* 145, NY,

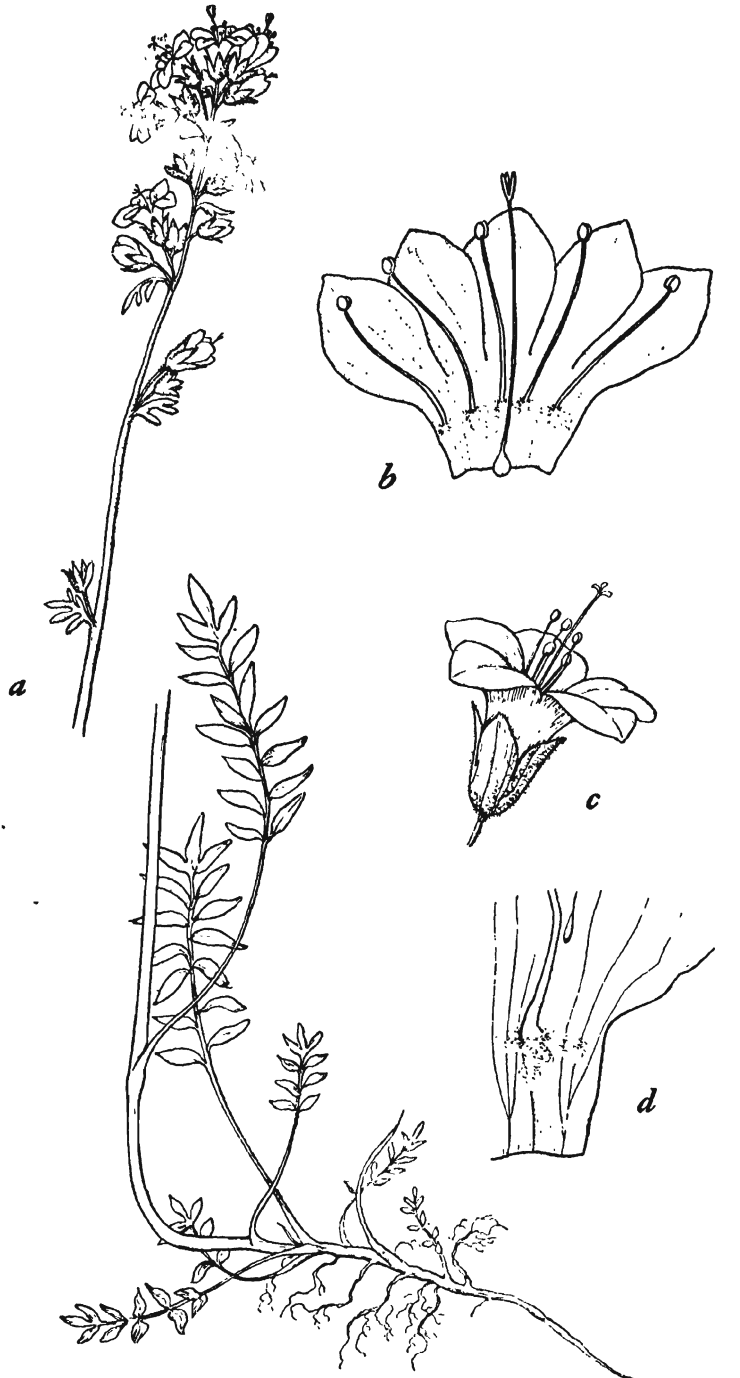


Fig. 4. *Polemonium cæruleum* L. subsp. *occidentale* (Greene), comb. nov. *a*, Habit, × ⅔. *b*, Dissection of flower, × 2⅓. *c*, Single flower, × 2. *d*, Stamen insertion, × 4.

S; "Kuichak, Bristol Bay," *Jones* 9302, GH, S; "Mt. McKinley, around Park headquarters," *E. A. & A. Nelson* 3682, NY, US, WYO; "Hope," *Anderson* 6661, GH, S, WYO; "Kokrines Mts., Melozitna River," *A. E. & R. T. Porsild* 793, CAN, GH, S, US; "Dillingham," *Martel* 213, GH, NY, S.

BRITISH COLUMBIA. "South Fork, Stikine River, 120 miles from mouth," *Preble & Mixter* 579, 586, US; "Mountains near head of Iskut River, Cassiar District," *Preble & Mixter* 630, US.

YUKON. "Herschell Island," *Dutilly* 257, GH, *Stringer* 62247, CAN, *Lindström* (1), NY; "Dawson," *Eastwood* 135, CAN, GH, UC, US; "Lake Kluane to Don Jek River," *Müller* (1920), CAN, GH; "White River," *Cairns* (1911), CAN, NY; "Branch Valley," *Gorman* 1170, CAN, NY.

NORTHWEST TERRITORIES. "Northwest Territory near Yukon Border, 62° 30′ N.–129° W.," *Goodwin* 8, 9, 10, 15, NY; "Slave Lake District, Martin Cabin," *McBean* 4551, NY; "Fort Resolution," *Kennicott* (1861–2), NY; "Liard River, between Nahanni Butte and Simpson," *Crickmay* 100, CAN; "Shingle Point," *Porsild* 6909, 7112, CAN.

1d. **Polemonium cæruleum** L. subsp. **occidentale** Greene, comb. nov.

P. occidentale Greene, Pittonia 2: 75. 1890.
P. Helleri Brand, in Engler, Pflanzenr. 4[250]: 32. 1907.

This subspecies is characterized by its strict inflorescence; small corolla, commonly less than 15 mm. long; included stamens; exserted style, often one and one-half times the length of the corolla; and a horizontal rootstock. (Fig. 4.)

The range extends from the Yukon, where it intergrades with subsp. *villosum*, southward through the Rocky Mountains to Utah, and to the Sierra Nevada range in California and Nevada. It is usually associated with a high water table, either in marshes or along streams, which may account for the horizontal rootstock which is commonly but not invariably present. It flowers from June to September.

P. Helleri Brand is not here considered a valid species since the isotypes (*Heller 7190*) are typical *P. cæruleum* subsp. *occidentale*, and do not exhibit the diagnostic features cited by the author. The very short filaments mentioned by Brand may occur in any portion of the range of the species and has been reported from Europe by Ostenfeld (1923). It is assumed that Brand's name refers only to an aberrant individual in the Berlin Herbarium which was unavailable to the present author.

While Greene designated "the Rocky Mountains of Colorado" as the type locality, he did not cite any specimens. However, Brand's citation of specimens includes *Baker 365* from Gunnison, Colorado, and this material was determined by Greene. Thus it is deemed appropriate to designate this collection as the lectotype of Greene's *Polemonium occidentale*, the type specimen being filed in the herbarium of the University of California.

Type locality.—"Rocky Mountains of Colorado." No collection cited by Greene. "Gunnison, Colorado, 7680′." *C. F. Baker* 365, July 7, 1901, as lectotype.

Distribution.—In damp ground from the Yukon southward through the Rocky Mountains to Utah. Also in the Cascade Mountains of Washington and Oregon, in the Wallowa Mountains of Oregon, and in the Sierra Nevada range of California and Nevada. (Map 1.)

Specimens examined (total: 344).—YUKON. "Above Hunker Creek," *Macoun* (1902), CAN.

BRITISH COLUMBIA. "Head of Dease Lake," *McCabe* 8810, UC; "Mouth of Salmon River," *Macoun* 66622, CAN, NY; "Anahim Lake, Chilcotin," *Cornwall* 12397, CAN.

ALBERTA. "Sunbeam Cabin, Nordegg River," *Brinkman* 3753, NY; "Elbow River," *Macoun* 23765, GH, NY, US; "Dixonville, north of Grimshaw," *Moss* 6146, GH; "Elbow Divide, swamps and bogs," *Macoun* (1897), CAN; "Elbow River," *Dawson* (1884), CAN.

IDAHO. "Santianne Creek," *Leiberg* 1045, F, GH, NY, US, WYO; "Big Creek, 13 mi. east of Cascade," *Jones* 5081, GH, NY; "Cape Horn," *Macbride & Payson* 3514, GH, NY, US, WYO; "Mackay, Pass Creek," *Macbride & Payson* 1411, F, GH, WYO; "Stanley Lake, Challis Forest," *Thompson* 14032, F, GH, NY, US; "Above Clear Creek, 7 mi. north of Lowman," *Hitchcock & Muhlick* 9751, GH, NY, WYO; "Trinity Lake region," *Macbride* 669, F, GH, NY, US, WYO; "Henny Lake," *E. B. & L. B. Payson* 2004, GH, NY, WYO.

MONTANA. "Lolo, near Woodman," *Kirkwood* 1247, GH; "Fish Creek, near mouth of Cache Creek, Lolo Nat. For.," *Hitchcock* 1717, GH, WYO; "Fish hatchery, Bozeman," *Mrs. Henshall* (1901), WYO; "Dwelles," *A. & E. Nelson* 6792, GH, NY, US, WYO.

WYOMING. "North Park, in edge of Wyoming, Hiltons," *Osterhout* 1715, WYO; "Twin Lakes," *Williams* (1888), NY, WYO; "Moran, Jackson Hole, vicinity Jackson Lake," *Yuncker* 5382, F; "Wind River Mountains," *J. C. Fremont*, NY; "Vicinity Green River Lakes," *E. B. & L. B. Payson* 4461, WYO; "Bailey Lake, Grand Canyon of the Snake River," *Williams* 822, GH, NY, WYO; "Head of Wood's Creek," *A. Nelson* 8034, GH, NY, US, WYO.

COLORADO. "Route 131 along Yampa River, below Yampa," *Parnell & Shaeffer* 22338, WYO; "North Park, on North Fork," *Osterhout* 5177, WYO; "Walden," *Gooding* 1495, GH, NY, US, WYO; "Empire," *Tweedy* 5672, NY, WYO; "Breckenridge," *Shear* 4562, NY, UC, WYO; "Middle Park, wet places," *Parry* (1864), GH; "Twin Lakes," *Clokey* 3528, F, GH, NY, UC, WYO; "Gunnison," *Baker* 365, GH, NY, UC, US, WYO; "Ironton Park, 9 mi. south of Ouray," *Underwood & Selby* 366, NY; "Near Trout Lake, San Miguel Co.," *E. B. & L. B. Payson* 4118, GH, WYO; "Goose Creek, Rio Grande Nat. For.," *Murdoch* 4777, F, NY, UC, US; "Headwaters, Sangre de Cristo Creek," *Rydberg & Vreeland* 5719, NY.

UTAH. "Logan Canyon," *Maguire* 3679, GH, WYO; "Goodman Ranch, near Bear River," *E. B. & L. B. Payson* 4835, GH, NY, US, WYO; "Parley's Park," *Watson* 932, GH, NY; "Wolf Creek Pass," *Garrett* 8340, UC; "American Fork Canyon," *Jones* 1884, F, NY, US, WYO; "Big Cottonwood Canyon, below Silver Lake," *Carleton & Rydberg* 6604, NY; "Fish Lake, around Twin Creeks," *Carleton & Rydberg* 7501, NY, US, WYO; "Six miles west of Panguitch Lake," *Goodman & Hitchcock* 1574, F, GH, NY, WYO.

WASHINGTON. "Wet meadows, Marshall Junction," *Piper* 2251, GH, NY; "Cheney," *Tucker* 27, GH, UC; "Dartford," *Turesson* (1913), WYO.

OREGON. "Wet soil, Summit Prairie, Blue Mts.," *Cusick* 2647, F, GH, NY, UC, US, WYO; "Near head of Metolius River," *Hitchcock & Martin* 4878, NY; "Marshy ground, Diamond Lake," *Thompson*, NY, S; "Creek, 30 mi. south of Crescent," *Abrams* 9672, WYO.

CALIFORNIA. "Sisson," *Eastwood* (1895), GH; "Jonesville," *Copeland* 392, GH, NY, UC, US, WYO; "Genessee Valley near Genessee," *Heller & Kennedy* (1907), F, NY, US; "Truckee," *Heller* 7190, GH, NY, UC, US, WYO; "Tuolumne Meadows, banks of brook," *Munz* 7541, GH, UC, WYO; "Mono Pass," *Bolander* (1866), GH, US; "Wet meadow, south fork of Santa Ana," *Munz & Johnston* 8577, GH.

NEVADA. "Ruby Range, 2 mi. north of Lamoille," *Maguire & Holmgren* 22036, GH, NY, UC; "North east of Mt. Rose Pass," *Hitchcock & Martin* 5535, NY, WYO; "Divide, 1 mi. south of Marlette Lake," *Train* 3256, GH, NY; "Spring at headwaters of Cory Creek, Wassuk Range," *Archer* 7052, NY, UC.

2. Polemonium foliosissimum A. Gray

P. foliosissimum A. Gray, Syn. Fl. 2: (1), 151. 1884.

P. filicinum Greene, Pitt. 1: 124. 1887.

P. Archibaldæ A. Nels., Bot. Gaz. 31: 397. 1901.

P. pterospermum Nels. & Cock., Proc. Biol. Soc. Wash. 16: 45. 1903.
P. albiflorum Eastw., Bot. Gaz. 37: 437. 1904.
P. robustum Rydb., Bull. Torr. Bot. Club 31: 635. 1904.
P. grande Greene, Leafl. Bot. Observ. 1: 153. 1905.
P. molle Greene, Leafl. Bot. Observ. 1: 153. 1905.
P. dasyphylla Brand, in Engler, Pflanzenr. 4^{250}: 80. 1907.
P. decurrens Brand, Repert. Spec. Nov. Reg. Veget. 17: 316. 1921.

Stems erect from a usually descending rootstock, 2–8 dm. tall, leafy, the cauline leaves not much reduced; leaflets 11–25, elliptic and obtuse to narrowly lanceolate and acute, at least the terminal five commonly confluent on the rachis, 5–35 mm. long (the mean about 25 mm.), up to 10 mm. broad; inflorescence a corymbose cyme; pedicels, at least on some flowers, shorter than the calyx; calyx campanulate, 5–10 mm. long, glandular-pubescent, the elliptic segments acute and equaling or exceeding the tube; corolla (according to Gray commonly white or cream color, sometimes violet) white, cream, blue or violet, 10–15 mm. broad, about the same in length, the lobes elliptic to rotund, almost twice as long as the tube; stamens inserted about the middle of the corolla tube, shorter than the corolla; style variable in length, either included or exserted even in bud; the seeds becoming mucilaginous when moistened. Flowering from June to August. (Fig. 5.)

Type locality.—"Rocky Mountains of New Mexico, Colorado and Wyoming." No type designated by Gray. "Headwaters of Clear Creek, Colorado," *Parry* 275, 1861. Lectotype (*Wherry* 1942, p. 746).

Distribution.—In the Rocky Mountains of Idaho, Wyoming, Colorado, Utah, and New Mexico, and in the White and Pinaleno Mountains of Arizona, and in the East Humboldt and Ruby Mountains of Nevada. (Map 2.)

The present *P. foliosissimum* complex appears to be a series of variable populations, from which many individuals have been selected and assigned specific names. Despite the number of named segregates, many specimens must still be considered intergrades. In the following discussion, the specific names within quotations refer to above-mentioned segregates, which are for the present submerged in synonymy under *P. foliosissimum* A. Gray.

The existence of aberrations in this group first became apparent in the study of meiotic configurations in the pollen mother cells of *"P. robustum"* Rydb. Meiosis was found to be irregular, with some chromosomes segregating at random toward either pole, or remaining at the equator when the division was completed. In the latter case they formed micropollen grains, the smallest being about one-third the diameter of the normal. Plants from seed exhibited a wide range of morphological variability, and a very high mortality. Since the material studied had been grown from seed from the Botanical Garden, Champex, Switzerland, it was thought that the seed had been contaminated through hybridization in the botanical garden. However, pollen of *"P. robustum"* from herbarium sheets, including that of the type specimen, was also found to exhibit the same size variation when studied in lactophenol mounts.

The pollen of authentic material of *"P. grande"* Greene and *"P. molle"* Greene also shows sufficient variability in size to call into question the regularity of meiosis in these "species."

In 1945, seed of *"P. filicinum"* Greene was received from Champex, Switzerland. Plants grown from this seed agreed with Greene's type material,

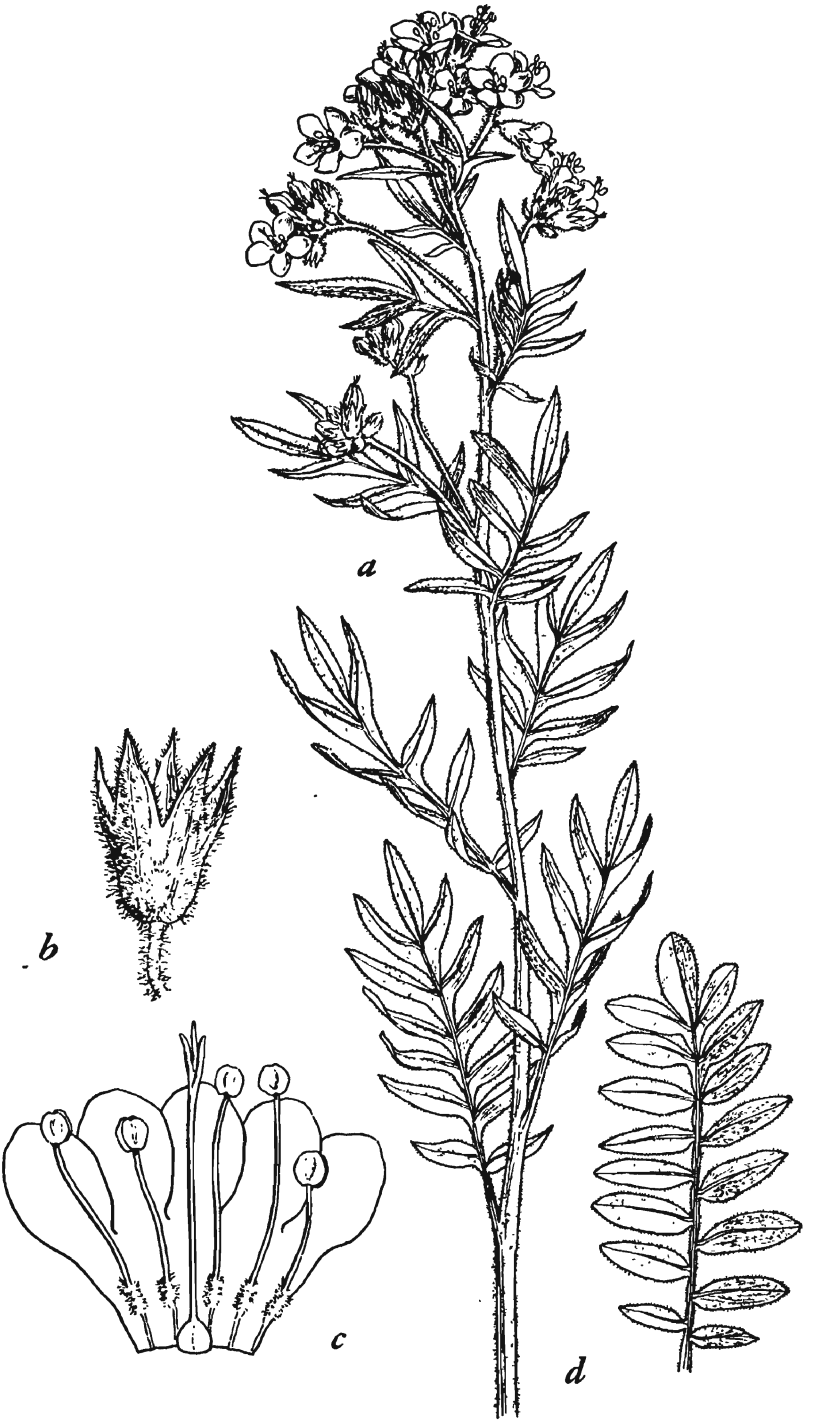


Fig. 5. *Polemonium foliosissimum* A. Gray. *a*, Habit, × ⅔. *b*, Calyx, × 2⅓. *c*, Dissection of flower, × 2⅓. *d*, Leaf to show variation, × ⅔.

meiosis was regular (n = 9), and the plants when selfed bred true. However, the individuals studied were extremely close to authentic material of "*P. foliosissimum*" A. Gray, and the possibility of their being conspecific cannot be overlooked.

While "*P. foliosissimum*" and "*P. filicinum*" are close enough to suggest conspecificity, "*P. Archibaldæ*" is an intermediate form. Brand placed "*P. Archibaldæ*" under "*P. foliosissimum*," and Wherry placed it under "*P. filicinum*."

"*Polemonium albiflorum*" Eastw. may be distinct, but the occurrence of white flowers, commonly used as a distinguishing character from "*P. foliosissimum*" is generally not a specific or even subspecific character in the genus. Ostenfeld (1923) has shown that in *P. cæruleum* the blue coloration is a simple dominant; it may well be here also. However, there is a tendency toward geographical separation in Eastwood's species, which may denote ecological or other differences, or which may be simply a demonstration of the fact that the recessive factor for white corolla has been successfully isolated from the genes for the dominant blue coloration.

The present nomenclatural status of "*P. filicinum*" and "*P. albiflorum*" is uncertain. While many specimens were examined which appeared to be intergrades between these two entities, there was very little evidence of poor pollen formation. Thus these may later be considered subspecies of *P. foliosissimum*, but additional evidence, particularly of an experimental nature, would be desirable.

Until such data are available, it is considered advisable to recognize this complex as a single variable species, to stress the interrelationships of the component populations. As such, the earliest name applied to a member of the population, *P. foliosissimum* A. Gray, is retained.

Specimens examined (total: 335).—IDAHO. "Star Valley Dugway near Montpelier," *A. Nelson* 9105, WYO; "Caribou Mt., Bonneville Co.," *Payson & Armstrong* 3539, GH, WYO.

WYOMING. Lincoln Co. "Sagebrush, south end Star Valley," *Porter* 3813, WYO; "Narrows, Swift Creek Canyon, Star Valley," *Rollins* 228, GH; "Hills east of Afton," *Payson & Armstrong* 3377, GH, WYO.

COLORADO. Weld Co. "Windsor," *Osterhout* 4933, WYO; Routt Co. "Willow Creek, moist timbered slopes," *Gooding* 1682, GH, NY, US, WYO; Grand Co. "Berthoud Pass," *Tweedy* 5669, NY, US, WYO; Gilpin Co. "Eldora to Baltimore," *Tweedy* 5867, NY, WYO; Boulder Co. "S. fork, Vrain River," *Dodds* 1873, WYO; Archuleta Co. "Piedra, along Piedra River," *Schmoll* 1127, WYO; *Baker* 545, F, GH, NY, UC, US, WYO; Conejos Co. "Los Piños," *Barnhart* 2918, NY; Mineral Co. "Near Pagosa Peak," *Baker* 544, F, GH, NY, UC, US, WYO; "Pass Creek," *Bethel, Milley & Clokey* 4252, NY, UC, WYO; Costilla Co. "Meadow 1 mi. west of La Veta Pass," *Ownbey* 1382, GH, NY, WYO; Las Animas Co. "North slope, Raton Mesa, head of San Francisco Canyon," *Rollins* 1845, GH, NY; La Plata Co. "Bob Creek, W. La Plata Mts.," *Baker* 274, F, GH, NY, US, WYO; Hinsdale Co. "Near Pole Creek, 7 mi. n.w. Rio Grande Reservoir," *Rollins* 1501, GH; El Paso Co. "Stream valley near Woodland Park," *Ehlers* 7756, GH; Pueblo Co. "Pueblo," *Horner* (1898), GH; Custer Co. "Custer County," *Cockerell* (1889), F; Rio Blanco Co. "Burro Mts., north Elk Canyon," *Sturgis* (1902), GH; Garfield Co. "Hills south of Rifle," *Osterhout* 7441, WYO; Saguache Co. "Sargents," *Clements* 136, NY; Gunnison Co. "Keblar Pass," *Baker* 798, GH, NY, UC, US, WYO; Mesa Co. "Mountain between Loma and Vernal Hiway," *Cottam* 5791, F; Delta Co. "Oak Mesa," *Cowen* (1892), NY; "Top of Mesa," *Purpus* 301, F;



Fig. 6. *Polemonium reptans* L. *a*, Habit, × ⅔. *b*, Dissection of flower, × 2⅓. *c*, Calyx dissected to show mature capsule, × 2⅓.

Montrose Co. "Uncompahgre Divide," *E. B. & L. B. Payson* 3900, GH, WYO; Ouray Co. "Chatanooga," *Schmoll* 1531, WYO; San Miguel Co. "Near Trout Lake," *E. B. & L. B. Payson* 4902, NY; Larimer Co. "Estes Park," *Osterhout* 2207, NY, WYO; Clear Creek Co. "Clear Creek Canyon at Dumont," *Paterson* 104, F, GH, NY, US; Summit Co. "In wash near Dillon," *A. & R. A. Nelson* 142, GH, WYO; Jefferson Co. "Foothills near Golden," *Jones* 299, F, NY; Teller Co. "Dry soil, Cripple Creek," *Clokey* 3839, F, GH, NY, S, UC, US, WYO.

UTAH. Wasatch Co. "Soldier Summit," *Jones* 5601, NY, US, WYO; Emery Co. "Mts. southeast of Silver Lake, near headwaters of Big Cottonwood Creek," *Rydberg & Carleton* 6551, GH, NY, WYO; San Pete Co. "Black Mountain, Manti," *Jones* (1895), GH; Sevier Co. "Ireland's Ranch, Salina Canyon," *Jones* 5441ae, GH, NY, US, WYO; Wayne Co. "Wayne Wonderland," *Milner* 7238, F; Carbon Co. "Scofield," *Jones* (1904), GH; Cache Co. "Logan," *Shear* (1895), NY; Rich Co. "Mountain valleys and canyons," *Linford* (1898), US; Morgan Co. "Banks of streams," *Linford* (1895), US; Summit Co. "Sagebrush slopes, Bear River," *E. B. & L. B. Payson* 4842, GH, NY, US, WYO; "Uintah Mts., west fork Bear River," *Goodman & Hitchcock* 1550, GH, NY, WYO; Salt Lake Co. "Alta, Wasatch Mts.," *Jones* 1114, F, GH, NY; "Red Butte Canyon," *Mrs. J. Clemens* (1909), NY, UC, WYO; Utah Co. "Provo," *Jones* 3589d, NY, US; Juab Co. "Mt. Nebo," *Rydberg & Carleton* 7762, NY, WYO; San Juan Co. "Kilgalia Ranger Station, Elk Ridge," *Holmgren & Hanson* 3477, GH, NY, UC; "N. slope Abajo Mts.," *Goodman & Hitchcock* 1440, F, NY, WYO.

NEW MEXICO. San Juan Co. "Hematite," *Berg* (1897), NY; Taos Co. "Penasco, Santa Barbara Canyon," *Marceline* 2001, F; Colfax Co. "Half-mile north of Elizabethtown," *Bacigalupi* 596, GH, UC; "Raton," *Tracy & Evans* 79, NY; Mora Co. "Mora River," *Fendler* 645, GH; San Miguel Co. "Rio Pecos, above Windsor's Ranch," *Standley* 4071, GH, NY, US; Bernalillo Co. "Sandia Mts.," *Ellis* 96, NY, US, *Castetter* 1286, WYO; Sandoval Co. "Valle Grande," *A. & R. A. Nelson* 246, WYO; Lincoln Co. "White Mts.," *Wooton* 289, GH, NY, US, WYO; Otero Co. "Cloudscroft," *Wooton* (1899), WYO; Socorro Co. "Water Cañon, Magdalena Mts.," *C. J. & R. Herrick* 219, F; Catron Co. "Mogollon Mts.," *Metcalfe* 500, GH, NY, UC, US, WYO; Sierra Co. "Lookout Mines," *Metcalfe* 1078, F, GH, NY, UC, US; Grant Co. "Pinos Altos Mts.," *Greene* 377, F, GH, NY; Santa Fe Co. "Aspen Ranch, vicinity of Santa Fe," *Arsène* 23584, US; Rio Arriba Co. "Vicinity of Champa," *Standley* 6674, 6758, US.

ARIZONA. Coconino Co. "Canyon of Clear Creek, 50 mi. from Rio Verde," *Mearns* 160, NY; Apache Co. "Head of White River, White Mts.," *Gooding* 672, GH, NY, US, WYO; "Thompson's Ranch, Black River, White Mts.," *Gooding* 563, GH, NY, US, WYO; Graham Co. "Pinaleno Mts.," *Kearney & Peebles* 14111, NY, US, *Clark* 9169, WYO, *Barrow* (1943), UC; Cochise Co. "Head of Chaperone Canyon," *Blumer* 1614, F, GH, NY, US, WYO; "Carr Peak, Huachua Mts.," *Gooding* 215, NY.

NEVADA. Elko Co. "Ridge, north side of Lamoille Canyon," *Heller* 9375, NY; "Seventy miles northwest of Elko, on Jack Creek," *Nicholls & Lund* 185, GH, NY.

3. Polemonium reptans L.

P. reptans L., Syst. Nat. 2: 925. 1759.

P. humile, Salisb. Prodr. 125. 1796. (non Willd.)

P. quadriflorum Raf., Atlantic Journal 1: (6), 177. 1835.

P. reptans var. *macrophyllum* Brand, in Engler, Pflanzenr. 4^{250}: 33. 1907.

P. reptans var. *villosum* E. L. Braun, Rhodora 42: 50. 1940.

Perennial from a woody caudex subtended by a fibrous root system; stems solitary to several, erect, pubescent or glabrous, 1.5–5 dm. high, leafy; leaflets 7–19, broadly ovate to lanceolate, acute, 10–50 mm. long, 3–20 mm. broad, commonly bearing three prominent longitudinal veins; inflorescence a lax corymbose cyme, the pedicels slender, subequal to or exceeding the calyx; calyx campanulate, 3–8 mm. long, the deltoid segments subequal to the tube; corolla campanulate, 10–15 mm. long, the blue obovate lobes slightly exceeding

the tube; stamens subequal to the corolla, or shorter, inserted below the middle of the corolla tube; style commonly longer than, at times equal to the corolla; capsule obovoid, stipitate from a basal disc. Flowering from April to June. (Fig. 6.)

Type locality.—Uncertain. The type is Plate 209 in Miller, Fig. Pl. Gard. Dict. 2: 1758. According to Wherry (1942, p. 753) the plant portrayed therein came from Virginia.

Distribution.—Fairly common in moist woods and damp meadows from the Atlantic Coast to the Great Lakes, but it is not common west of the Mississippi River. (Map 3.)

This slender-stemmed species is fairly common in moist locations from the eastern Mississippi Basin to the Atlantic coast, ranging from the Great Lakes south to Alabama and Georgia. Its large, ovate to broadly elliptic leaflets, stamens subequal to the corolla, and stipitate capsule distinguish it readily from its nearest geographical associate, *P. cærulcum* subsp. *VanBruntiæ.*

Seed from both the glabrous and pubescent forms was very kindly supplied by Dr. E. T. Wherry, and plants were raised in Berkeley from this material. The plants grown from the two lots of seed were all quite glabrous, and the advisability of according taxonomic recognition to such an evanescent character is considered doubtful, even in the category of "forma."

Specimens examined (total: 323).—VERMONT. "Ripton," *Kennedy* (1908), GH; "Peacham," *Blanchard* (1883), NY.

NEW HAMPSHIRE. "Bethlehem," *Bean* 1477, GH; "Hanover," *Chivers* (1903), GH; "Franklin," *Clark* (1919), GH.

CONNECTICUT. "New Fairfield," *Eames* 10150, GH; "Wilton," *Eames* 11604, GH.

NEW YORK. "Tioga County, Barton," *Feuno* 288, NY; "Valley of Chemung River," *Lucy* 482, WYO, 7298, NY, US; "Allegheny State Park," *Alexander & House* 12908, GH; "Alluvial woods, Cattaraugus Creek," *Johnson* 1316, NY; "Rushford," Baxter (1907), UC.

NEW JERSEY. "Major's Run, Sharptown," *Long* 15974, GH, *Mackenzie* 7635, GH.

PENNSYLVANIA. "Selinsgrove," *Moldenke* 2309, NY; "Little Conestoga," *Bitner* (1893), WYO, *Heller* (1889), GH; "Edison," *Fritz* (1896), GH; "Wissahickon Ravine, Philadelphia," *Lang* 351, GH; "Gouglersville," *Wilkens* 5461, GH; "Crum Creek, Swarthmore," *Schaeffer* 1445, GH; "Thorn Creek, McBride," *Bright* 18950, UC; "Natrona," *Shafer* 260, UC, US.

MARYLAND. "Near Baltimore," *LeRoy* (1866), GH, NY; "Woods, Summerfield," *Churchill* (1910), GH; "Stone Run," *Carter* (1907), NY.

DISTRICT OF COLUMBIA. "Bob Creek, Washington," *Chickering* (1879), GH (1875), NY.

VIRGINIA. "E. Williamsburg," *Grimes* 3361, NY; "Lexington," *Churchill* (1891), GH; "Near Christiansburg," *Mossbach & Hodgson* 7017, GH; "About falls of Holston," *Small* (1892), GH; "River knobs, Fort Holston," *Carr* 593, GH.

WEST VIRGINIA. "Russel Creek," *Williams* 435, F, GH, NY, US; "Huntington," *Gilbert* 33, GH, 420 F, NY, US; "Pocahontas Co.," *Pollock* (1895), WYO.

MINNESOTA. "Rice Lake," *Sheldon* (1874), GH, WYO; "Winona," *Holzinger* (1901), NY, WYO; "Spring Grove," *Rosendahl* 335, GH.

WISCONSIN. "Reedsburg," *Thompson* (1907), UC; "Mt. Vernon," *Fassett* 8140, GH; "Ashwanberron," *Schuette* (1882), GH, US; "Boscabel," *Sylvester* 77, NY; "Bethel," *Fassett, Drescher & Silker* 14108, GH; "Poynette," *Russell* (1886), GH; "Fort Howard," *Schuette* (1890), NY.

IOWA. "Near Decorah," *Tolstead* (1933), UC; "Peterson township," *Hayden* 945, GH; "Pine Creek Park, Eldora," *Pammel* 51, NY; "Grinnell," *Jones* (1877), GH, WYO; "East of Mediapolis," *Goodman* 2999, GH, NY, UC.

MICHIGAN. "Manchester," *Spofford* (1890), GH.

ILLINOIS. "Augusta," *Mead* (1847), GH; "Rockford," *Goddard* (1879), NY; "Chicago, woods," *Moffatt* 176, 42, WYO; "Beecher," *Moore* (1897), WYO; "Urbana," *Gleason* 536,

GH, 999, UC; "Decatur," *Clokey* 978, UC; "Near Muncie," *Jones* 11336, NY; "Near Christopher," *Jones* 12133, GH.

INDIANA. "Valparaiso," *Lansing* 806, F; "Penn. R.R. west of Woodland," *Loughbridge* 112, WYO; "Marion Co.," *Bartlett* (1904), GH; "Three miles southwest of Avon," *Friesner* 16656, NY; "Woods near Greencastle," *Welch* 5965, UC; "Greencastle," *Banker* (1904), NY; "Four miles southwest of Fairbanks," *Deam* 22651, NY; "Four miles east of Washington," *Deam* 27270, GH.

OHIO. "Geauga Lake," *Jones* (1892), UC; "Garrettsville," *Webb* (1905), GH; "Mansfield," *Wilkinson* 359, NY, US; "Columbus," *Sullivant* (1840), GH; "Near Portsmouth," *Roth* (1937), GH; "Beaver Pond," *Braun* (1939), GH.

KENTUCKY. "Hazel Branch," *Braun* 2178, GH; "Robards," *Anderson* 4, GH; "W. B. Threlkeld woods, Union Co.," *Shacklette* 269, GH, NY; "Lexington," *Short* (1840), GH, NY, US; "Kuttawa," *Eggleston* 4760, NY; "Mammoth Cave," *Allen* (1900), NY.

TENNESSEE. "Near Knoxville," *Ruth* 159, GH, US; "Near Dyersburg," *Palmer* 17269, GH; "Jackson," *Bain* 32, GH, NY; "Bears Creek," *Svenson* 9984, GH.

MISSOURI. "Grain Valley," *Bush* 95, GH, NY, US, *Mackenzie* (1899), NY, WYO; "Near Columbus," *Palmer* 36683, GH; "St. Louis," *Eggert* (1879), NY, WYO; "Silica," *Eggert* 7298, US, WYO; "Knox's Cave," *Shepard* (1879), GH; "Pontiac," *Bush* 13379, NY, S.

KANSAS. "Woods, Doniphan Co.," *Clothier* 1093, GH, NY, US.

OKLAHOMA. "Spavinaw State Park," *Van Valkenburgh* 113, GH, UC; "Broken Bow," *Ward* 106, UC.

ARKANSAS. "Benton County," *Plank* (1899), NY; "Marion Co., springy places," *Bush* 13407, S.

ALABAMA. "Northeast Sheffield," *Harper* 3219, GH, NY; "Simpson Creek," *Morgan* 100, GH, UC, US; "Near Jasper," *Harper & Morgan* (1941), GH, UC; "Rocky Branch," *Harper* 3489, GH, NY, US.

GEORGIA. "Rome," *Chapman*, NY; "Dry Rocks, Floyd Co.," *Chapman* (1883), US.

4. **Polemonium mexicanum** Cerv. ex Lag.

P. mexicanum Cerv. ex Lag., Gen. et Sp. Plant. 10. 1816.

Perennial, erect, 2–6 dm. high, the stems branching and leafy; rachis of the leaf commonly winged, and the terminal seven leaflets commonly confluent; leaflets ovate to elliptic, subacute at the apex, 6–20 mm. long, 2–6 mm. wide; inflorescence cymose; pedicels slender, commonly shorter than the calyx at anthesis, often much longer in fruit; calyx short-campanulate, 5–10 mm. long, the deltoid segments one-half the length of the tube; corolla blue, short-campanulate, little exceeding the calyx, 7–13 mm. long, about the same in breadth, the ovate lobes subequal to the tube; stamens shorter than the corolla, inserted from one-fourth to halfway up the corolla tube; style shorter than the corolla, slightly exceeding the stamens. Flowering from July to October. (Fig. 7.)

Type locality.—"Mexico." Collector unknown.

Distribution.—Thus far reported only from Mexico in a restricted area around the Federal District, and including the states of Puebla and Mexico. (Map 4.)

This quite discrete species is characterized by its small corolla which scarcely exceeds the calyx. It has affinities in both floral and foliar morphology with *P. foliosissimum* and with *P. micranthum*.

Seed of the species was unavailable, and although the Botanical Register (6 : t 420, 1820) claims the plant to be biennial, it is probable that the species may behave as either an annual or perennial, as do other southern representatives of the genus. Some of the specimens examined appeared to be perennial, while others had apparently flowered the first year.

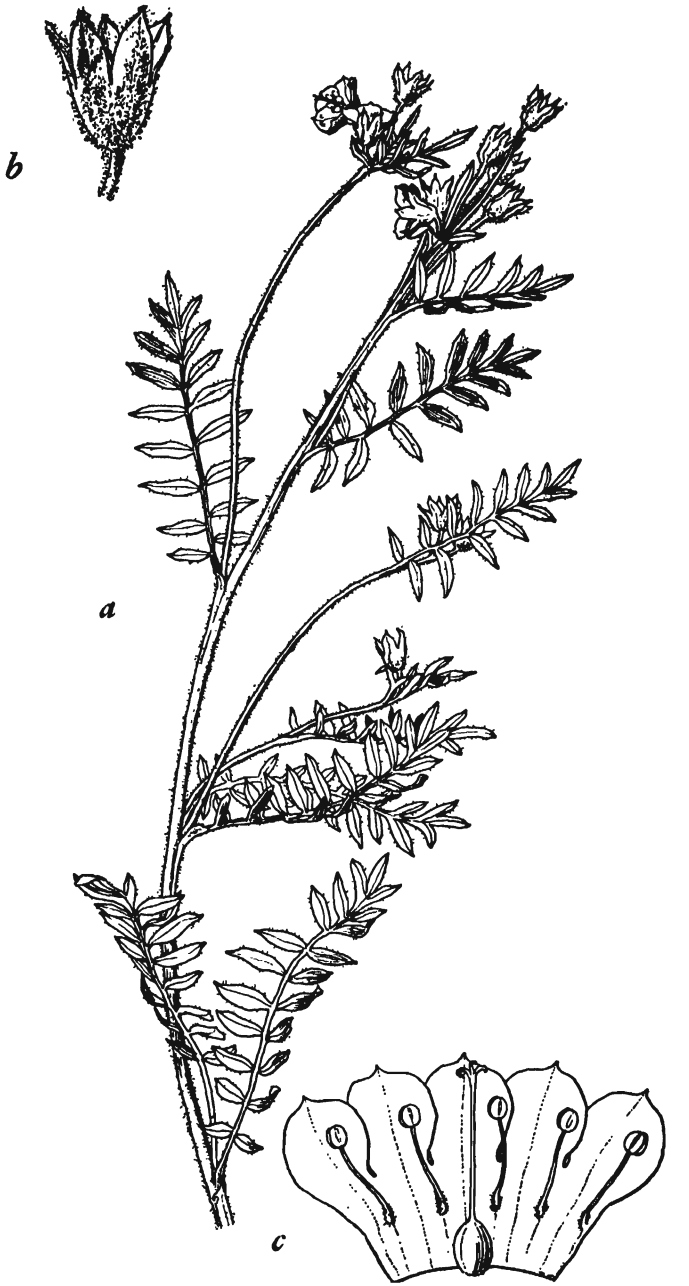


Fig. 7. *Polemonium mexicanum* Cerv. ex Lag. *a*, Habit, × ⅔. *b*, Calyx, × 2. *c*, Dissection of flower, × 2⅓.

Specimens examined (total: 47).—MEXICO. "Mexico," *Consul Woelflin* (1845), NY; "New Spain," *Sessé & Mociño* (1787–1804), F; Mexico: "Sierra de la Cruces," *Pringle* 5283, GH, 9311, GH, US; "Desierto Viejo," *Bourgeau* 878, GH, S, US; "Temescaltepec," *Hinton* 4397, F, GH, NY, US; Federal District: "Serrania de Ajusco," *Pringle* 13799, GH, S, US; "Desierto de los Leones," *Kenoyer* A360, F; Puebla: "Popocatepetl," *Rose & Hay* 6059, GH, NY, US.

5. **Polemonium micranthum** Benth.

P. micranthum Benth., DC Prodr. 9: 318. 1845.
P. antarcticum Griseb., Goett. Abh. 6: 131. 1854.
Gilia Gayana, Wedd. Chlor. And. 2: 82. 1859.
Gilia diffusa Phillipi, Linnæa 30: 197. 1859.
Gilia Johowski Meigen, in Engler, Bot. Jahrb. 16: 291. 1893.
Polemoniella micrantha Heller, Muhlenb. 1: 57. 1904.
Polemonium Gayanum Brand, in Engler, Pflanzenr. 4^{250}: 46. 1907.

Annual; stems 3–25 cm. high, solitary to diffusely branched, slender, glabrate to pilose with glandular hairs; leaflets 7–15, narrowly elliptic to spatulate, 1–5 mm. long, 0.5–2 mm. wide, glandular-pubescent; inflorescence a sympodial cyme, each flower produced terminally on a shoot bearing one leaf, and each succeeding flower shoot developing in turn from the axil of the uppermost leaf, the subtending leaves similar to foliage leaves in shape and pubescence, but somewhat reduced; flowers solitary to many; pedicels up to 13 mm. long, exceeding the calyx; calyx campanulate, 3–7 mm. long, the segments commonly one and one-half times as long as the tube, the whole glandular-pubescent; corolla white, or occasionally blue, shorter than the calyx, 2–6 mm. long, broadly campanulate, the rotund lobes equaling the tube; stamens inserted from one-fourth to halfway up the tube, the bases sparsely pubescent, the dilation of the base of the filaments variable, the stamens shorter than the corolla; style subequal to the corolla; capsule subglobose; seeds becoming mucilaginous when moistened. Flowering from April to May in North America, and from August to January in South America. (Fig. 8.)

Type locality.—"Columbia River," *Douglas* 1829. (!)

Distribution.—In arid regions of the Great Basin, western North America from 40°–50° N., and on either side of the southern Andes 30°–50° S., in Argentina and Chile. (Map 5.)

The reasons for rejecting the genus *Polemoniella* Heller have been discussed in a previous paper (1947) and need not be repeated here. The distinction between *Polemonium antarcticum* and *Polemonium Gayanum* is based upon leaf characters which are duplicated in many North American specimens, and which have been found to vary in North American plants apparently with the amount of water and light available.

The distinction between the North and South American populations is based upon the dilation of the base of the filaments, a character which is variable in both populations. Thus subdivision into two or more species must be predicated solely upon their geographical separation, an unwise basis for segregating species without further supporting evidence. On the other hand, the retention of a single name for the two widely separated populations emphasizes the problem of distribution, a factor which might be overlooked were two or more names perpetuated for morphologically identical populations. The distributional pattern is not novel, but agrees with the distribution of *Osmorhiza chilensis Hook & Arn.* and *O. obtusa* (C. & R.) Fern. (Constance and Shan, 1947) and many other perennial herbs (Johnston, 1940).

Specimens examined (total: 220).—BRITISH COLUMBIA. "Pritchard," *McCabe* 2016, 2020, UC; "Spence's Bridge," *Newcombe* 212, F; "Lytton," *Macoun* 16231, CAN, NY, (1889), GH; "Boston Bar." *McCabe* 832, UC, *Macoun* 16232, CAN; "Penticton," *Spreadborough* 61252, GH, NY; "Five miles south of Oliver," *McCabe* 5835, UC.

WASHINGTON. Whitman Co. "Wawawai," *Piper* 1521, GH, NY, WYO; Stevens Co. "Fort Colville," *Lyall* (1861), GH, S; Lincoln Co. "Keller Ferry," *Rogers et al.* 242, GH, NY;

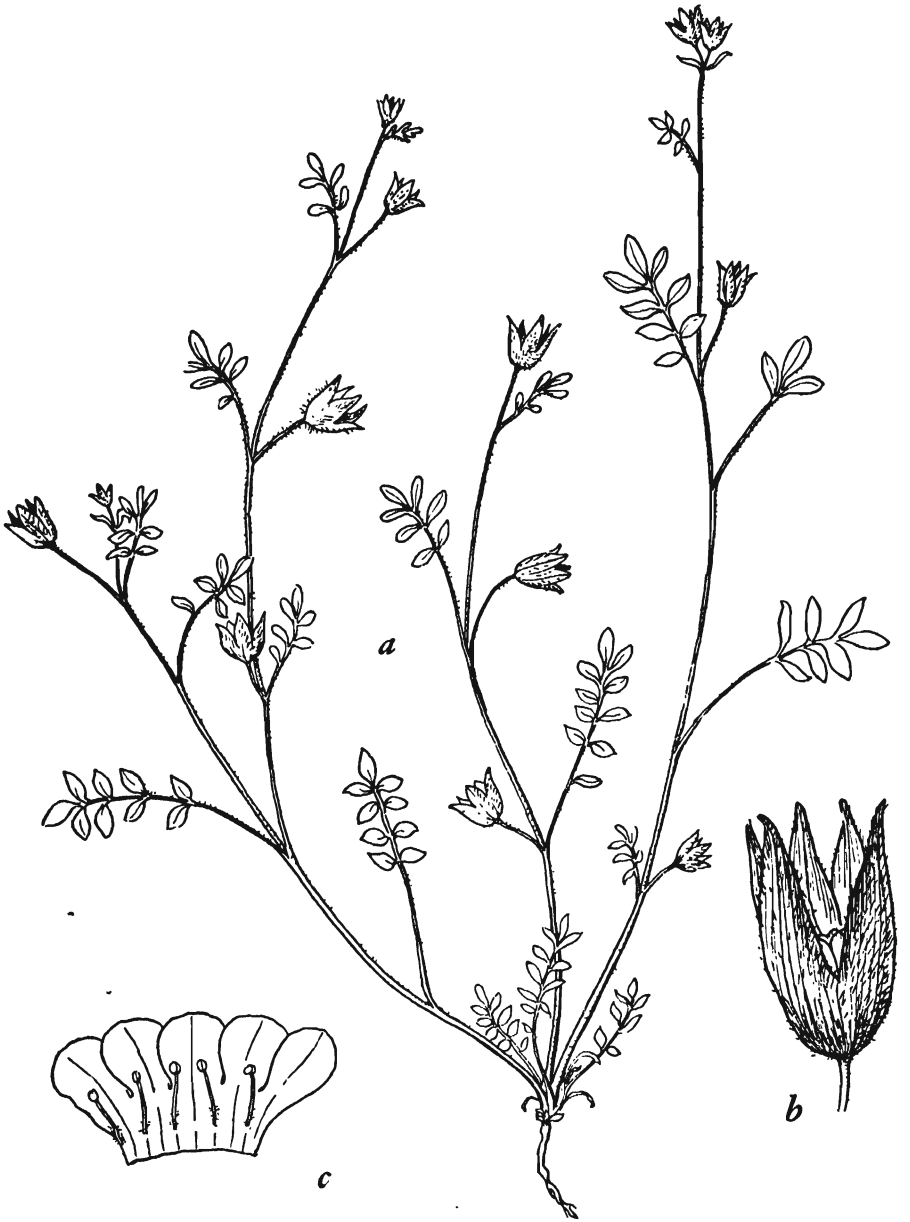


Fig. 8. *Polemonium micranthum* Benth. *a*, Habit, × 7/8. *b*, Single flower, × 7. *c*, Dissection of corolla, × 7.

Spokane Co. "Hangman's Creek," *Sandberg & Leiberg* 13, GH, NY; Yakima Co. "South of Sunnyside," *Cotton* 322, GH, NY, US, WYO; Klickitat Co. "Near Goldendale," *Thompson* 8193, GH, NY, UC, US.

OREGON. Locality uncertain: "Amer. bor. occ." (Columbia River) *Douglas* (1829), K; "Oregon," *Geyer* 463, GH, K; Lake Co. "Paisley, near Chewacan Marsh," *Eggleston* 6784, GH, NY, US; Malheur Co. "Near Harper Ranch," *Leiberg* 2083, GH, NY; Wasco Co. "Near Maupin," *Thompson* 10358, GH, NY; Gilliam Co. "Mouth of John Day River," *Henderson* 5125, GH; Sherman Co. "Moro," *Lloyd* (1894), NY; Morrow Co. "Near Lexington," *Leiberg* 22, GH, NY, US, WYO; Wallowa Co. "Imnaha Canyon," *Peck* 18123, NY.

CALIFORNIA. Siskiyou Co. "Near Yreka," *Greene* 706, GH, F, *Butler* 1137, US, WYO; "Siskiyou Mts.," *Wheeler* 3426, GH, NY, US; Sierra Co. "East of Loyalton," *Stebbins & Jenkins* 2139, GH; Nevada Co. "Hobart Mills," *Drew* (1925), WYO; Ventura Co. "North slope of Pine Mt. Hiway 399," *Davidson* 4625, UC.

IDAHO. Nez Perces Co. "Lapwai Creek, near Culdesac," *Sharsmith* 4004, GH, NY, S, WYO; Idaho Co. "Clearwater, Oregon," *Spalding*, GH, K; Canyon Co. "Falk's Store," *Macbride* 758, F, GH, NY, US, WYO; Ada Co. "Boise," *Clark* 27, F, GH, NY, S, US, WYO.

MONTANA. "Bitterroot Valley, 30 mi. south of Missoula," *Hitchcock* 1566, WYO; "Near Livingston," *Scribner* 164, GH.

NORTH DAKOTA. "Leeds," *Lunell* 20, WYO.

WYOMING. "Near Mammoth Hot Springs," *Burglehaus* (1893), NY, US.

NEVADA. "Carson City," *Watson* 934, GH, NY, US; "South of Vya," *Train* 2863, UC; "Hunter Creek Canyon," *Kennedy* 875, WYO.

UTAH. "Holliday," *Jones* 256, GH; "Fort Douglas," *Clemens* (1909), F; "Provo," *Jones* (1880), NY, US, WYO; "Salt Lake City," *Stokes* (1900), NY, US, *Garrett* 977, GH, NY, 8511, UC.

CHILE. Prov. Coquimbo: "25 KM. south of Vicuna," *Wagenknecht* 18549, GH; "10 KM. east of Matancilla," *Worth & Morrison* 16662, GH; "Near Lagunilla," *Looser* 3675, GH; Prov. Santiago: "Near Las Condas," *Grandjot* 3204, GH; "Cresta de la Prado," *Pirion* 1739, GH; "Termas del Tupungato, Rio Colorado," *Looser* 749, 752, GH.

ARGENTINA. "Capal Cabo negro," *Lechler* 1080, K; "Patagonia," *Moreno & Tonini* 229, NY; "Tehuelches," *Donat* 169, F, GH, NY; "Rio Chico, Chubut," *Riggs* 85, F; "50 KM. north of San Julian," *Eyerdam, Beetle & Grondona* 23956, GH.

6. **Polemonium pectinatum** Greene

P. pectinatum Greene, Cal. Acad. Sci. Bull. 1: 10. 1884.

Perennial, 3.0–7.5 dm. high; stems stout, terete, erect and clustered, glabrous; leaflets 11–21, linear, filiform, up to 30 mm. long, glabrous; inflorescence a cyme, the flowers borne on pedicels 4–10 mm. long, subequal to the calyx; bracts foliaceous; calyx narrowly campanulate, 4–10 mm. long, the segments glandular-pubescent, slightly exceeding the tube; corolla rotate-campanulate, white to cream, up to 20 mm. broad, the obovate lobes three times as long as the tube; stamens inserted two-thirds of the way up the tube, subequal to the corolla in length, pubescent at the base; style subequal to the corolla. Flowering in May and June. (Fig. 9.)

Type locality.—"Eastern part of Washington Territory," *Hilgard*, June, 1882. (!)

Distribution.—Restricted to Spokane and Whitman counties of Washington, in the vicinity of Rock Lake. (Map 7.)

This species, characterized by its narrowly linear leaflets, is restricted to the Rock Lake area of eastern Washington, on the border of the scattered yellow pine formation which was described by Piper (1906, p. 48) as the "scab land area." Whether its closest affinity is with *P. foliosissimum* as Greene suggested, or with its closer geographical associate *P. cæruleum* subsp. *occidentale*, is dubious. This problem, together with the determination of the factors restricting the distribution of the species, may be attacked in the future through experimental studies. At the present time, they remain interesting but unsolved problems.

Specimens examined (total: 23).—WASHINGTON. "Washington Territory," *U. S. South Pacific Exploring Expedition 1838–42*, NY; "Eastern part of Washington Territory," *Hilgard* (1882), GH; "Spokane Co.," *Tucker* 65, GH; "Hangman Creek, Spokane Co.," *Sandberg & Leiberg* 105, NY, S, US; Whitman Co.: "Rock Lake," *Sandberg & Leiberg* 105, GH, NY, US (June, 1893), F, NY; "Near Oaksdale," *Suksdorf* 8863, GH, NY, US.

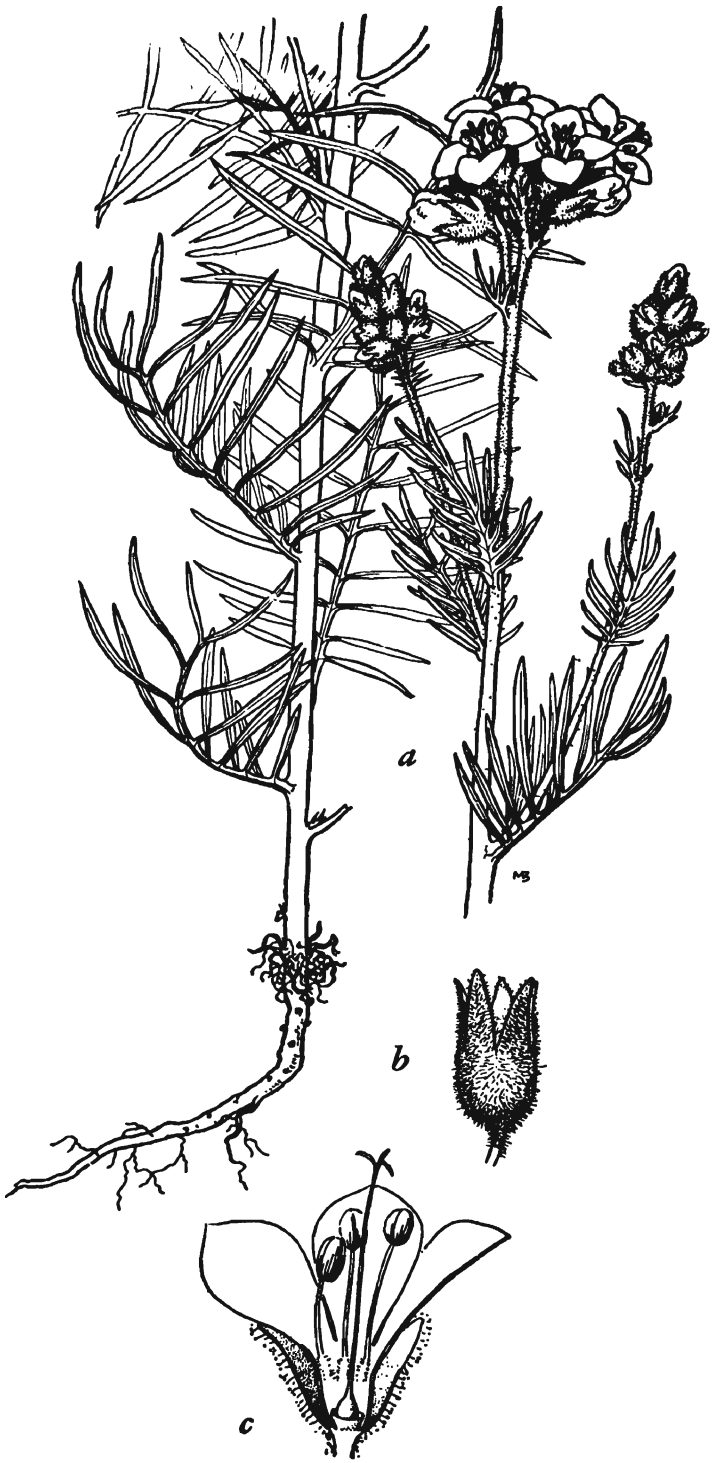


Fig. 9. *Polemonium pectinatum* Greene. *a*, Habit, × ¾. *b*, Calyx, × 3. *c*, Dissection of flower, × 3.

7. Polemonium carneum A. Gray

P. carneum A. Gray, Syn. Fl. 2: (1), 151. 1878.
P. incarnatum A. Gray ex Greene, Bot. Mag. 6965. 1887.
P. amœnum Piper, Erythrea 7: 174. 1899.
P. luteum Howell, Fl. N. W. Amer. 1: 65. 1903. (non Greene)

Perennial, 4–8 dm. high, branching from the base, decumbent in age; stems stoutish, 3–5 mm. in diameter, microscopically pubescent with round-tipped hairs; leaflets 13–21, ovate to oblong-lanceolate, up to 4 cm. in length, the terminal three leaflets often confluent; inflorescence a cyme; pedicels 2–10 mm. long; calyx 7–18 mm. long, the segments slightly exceeding the tube, finely pubescent with round-tipped nonglandular hairs; corolla purple, or salmon or flesh-colored aging purple, rotate-campanulate, 10–25 mm. broad, about the same in length, the lobes broad, rounded, obovate, slightly longer than the tube; stamens inserted slightly below the middle of the tube, 2–5 mm. from the base, subequal to the corolla, the filaments slender, pubescent at the base; style exceeding the corolla, commonly exserted in bud. Flowering from May to September. (Fig. 10.)

Type locality.—"Near Yreka, Siskiyou Co., California," *Greene 796.* (!)

Distribution.—Along the Pacific coast, from the Olympic Peninsula in Washington to the San Francisco Bay region of California. (Map 7.)

Gray's type material (*Greene 796*) with flesh-colored (yellowish-pink) corollas came from the Siskiyou (Klamath) Mountains of northern California, about the center of distribution of the species. Corolla color varies from pink or purple in the San Francisco Bay region, through flesh color in the northern part of the state, to yellow in the Cascade Mountains of Oregon (*P. luteum* Howell, non Greene), and toward the northern limits of distribution seems to interbreed with *P. californicum* Eastw. These intergrading forms comprise *P. amœnum* Piper.

Throughout the southern part of its range, the pubescence of *P. carneum* is characterized by trichomes with a unicellular apex. The following specimens: *Thompson 14602; Grant 3058,* are typical *P. amœnum,* but the trichomes are of two types, those of the southern *P. carneum,* and those of *P. californicum* (which possess a two- or four-celled head). The specimens of "*P. amœnum*" examined seem to be intergrades between *P. carneum* and *P. californicum* in other gross morphological details as well. In most respects however, they more closely resemble *P. carneum.*

Cytological material collected in Stonybrook Canyon, Alameda County, California, showed normal diploid meiosis (n = 9).

Specimens examined (total: 68).—WASHINGTON. Clallam Co. "Obstruction Point Ridge," *Meyer* 1277, GH; Grays Harbor Co. "Humptulips," *Thompson* 14602, GH, S; "Montesano," *Grant* 3058, GH; Skamania Co. "Mt. Prindle," *Suksdorf* 11706, GH, UC, US.

OREGON. Jefferson Co. "Mt. Jefferson," *Nelson* 1190, GH; Linn Co. "Fish Lake Ranger District, Santianne Forest," *Eggleston* 22150, US; Lane Co. "Near Foley Springs," *Collier,* GH; "O'Leary Mt.," *Detling* 3096, UC; Klamath Co. "Summit of Cascade Mts.," *Peck* 9275, GH; Jackson Co. "Western slopes of Cascades," *Cusick* 2869, GH, UC, US; "Siskiyou Mts., near Ashland," *Applegate* 335, GH, UC, US; Josephine Co. "Near Kirby," *Gorman* (1925), UC; Curry Co. "Harbor," *Peck* 8728, GH; "Chetco," *Howell* 208, GH, US.

CALIFORNIA. Del Norte Co. "Between Smith River and Harbor," *Keck & Clausen* 3405, GH, UC; "Mouth of Smith River," *H. E. & S. T. Parks* 24001, GH, UC, US, WYO; Siski-



Fig. 10. *Polemonium carneum* A. Gray. *a*, Inflorescence, × ⅔. *b*, Single flower, × 1⅓. *c*, Calyx, × 2. *d*, Dissection of flower, × ⅓. *e*, Leaf, × ⅔.

you Co. "Near Yreka," *Greene* 796, GH; "McAdam's Creek," *Butler* 1344, UC, US, WYO; Humboldt Co. "Near Big Lagoon," *Tracy* (1911), GH, UC, US; Marin Co. "Sausalito, opposite San Francisco," *Kellogg* (1866), GH (1871), UC; "Angel Island," *Vasey* (1876), GH; San Mateo Co. "Pilarcito Reservoir," *Blake* (1893), UC, *Davey* 1040, UC.

8. **Polemonium grandiflorum** Benth.

P. grandiflorum Benth., DC Prodr. 9: 317. 1845.
P. luteum Greene, Pittonia 4: 100. 1899.
P. Ehrenbergii Brand, in Engler, Pflanzenr. 4[250]: 41. 1907.

Perennial; stem erect and branching, 1.5–5.0 dm. high, leafy; the leaflets 15–23, ovate to lanceolate, 5–20 mm. long, 1.5–5.0 mm. wide; flowers solitary to few on a peduncle, on pedicels subequal to the calyx; calyx campanulate, 10–20 mm. long, the broadly lanceolate acute segments equaling or exceeding the tube; corolla large, blue or yellow (*P. luteum* Greene), broadly funnelform, 25–35 mm. long, the same in breadth, the obovate, often mucronate lobes shorter than the combined tube and evident throat; the stamens slightly shorter than the corolla, inserted at the junction of the tube and throat; style subequal to the corolla or longer. Flowering from June to September. (Fig. 11.)

Type locality.—"Peak of Mt. Orizaba, Mexico," *Linden 325*, 1838.

Distribution.—In the high mountains of Mexico, from the southern portion of Chihuahua to Oaxaca. (Map 4.)

This species has been reported only from Mexico, and the material observed has been collected in two widely separated areas in that country; near Guadalupe y Calvo in Chihuahua, and in the Sierra Madre Oriental north of Mt. Orizaba. The type of *P. luteum* Greene was collected near the center of distribution of the normal violet-colored specimens, and since the only difference appears to be in corolla color, it is here held to be merely a color form of the species. Some of the original collections of Galeotti, while inscribed "corolla violet," have faded to yellow, and are quite indistinguishable from the type of *P. luteum*. The collection data on Balls' specimen notes "dull mauve and yellowish bells." The type specimen of *P. grandiflorum* from the herbarium at Kew shows sufficient variation in the shape of the calyx segments to call into question the advisability of delimiting *P. Ehrenbergii*.

Specimens examined (total: 20).—Mexico. Chihuahua: "15 mi. south of Guadalupe y Calvo," *Nelson* 4821, GH, K, US; Hildago: "El Chico," *Lyonnet* 470, GH, NY, US; "Sierra de Pachuca," *Pringle* 6930, GH, NY, S, US, WYO, 11038, GH, NY, US; Puebla: "Tesmalaquilla, Sierra Negra," *Balls* 4466, US; Vera Cruz: "Mt. Orizaba," *Linden* 325, K, Galeotti 1446, K, US, *Purpus* 2734, NY, US, *Rose & Hay* 5740, NY; Oaxaca: "Prov. de Oaxaca," *Galeotti* 1446, NY—the locality of this specimen is doubtful, since it bears the same number as the Orizaba collection.

9. **Polemonium boreale** Adams

P. lanatum Pallas, Reise Russ. Reich. 3: 33. 1776.
P. prostratum Rud. ex Georgi, Beschr. Russ. Reich. 4: 772. 1800.
P. boreale Adams, Mem. Soc. Nat. Mosc. 5: 92. 1817.
P. Richardsonii Graham, Edinb. Philosoph. Journ. 4: 175. 1827.
P. villosum Sweet, Brit. Fl. Gard. 3: 266. 1828. (non Rud.)
P. humile Willd. ex R. & S., Syst. Veget. 4: 792. 1829.
P. speciosum Fisch. ex Hook., Fl. bor.-Amer. 2: 71. 1838.
P. capitatum Benth., in DC Prodr. 9: 318. 1845.

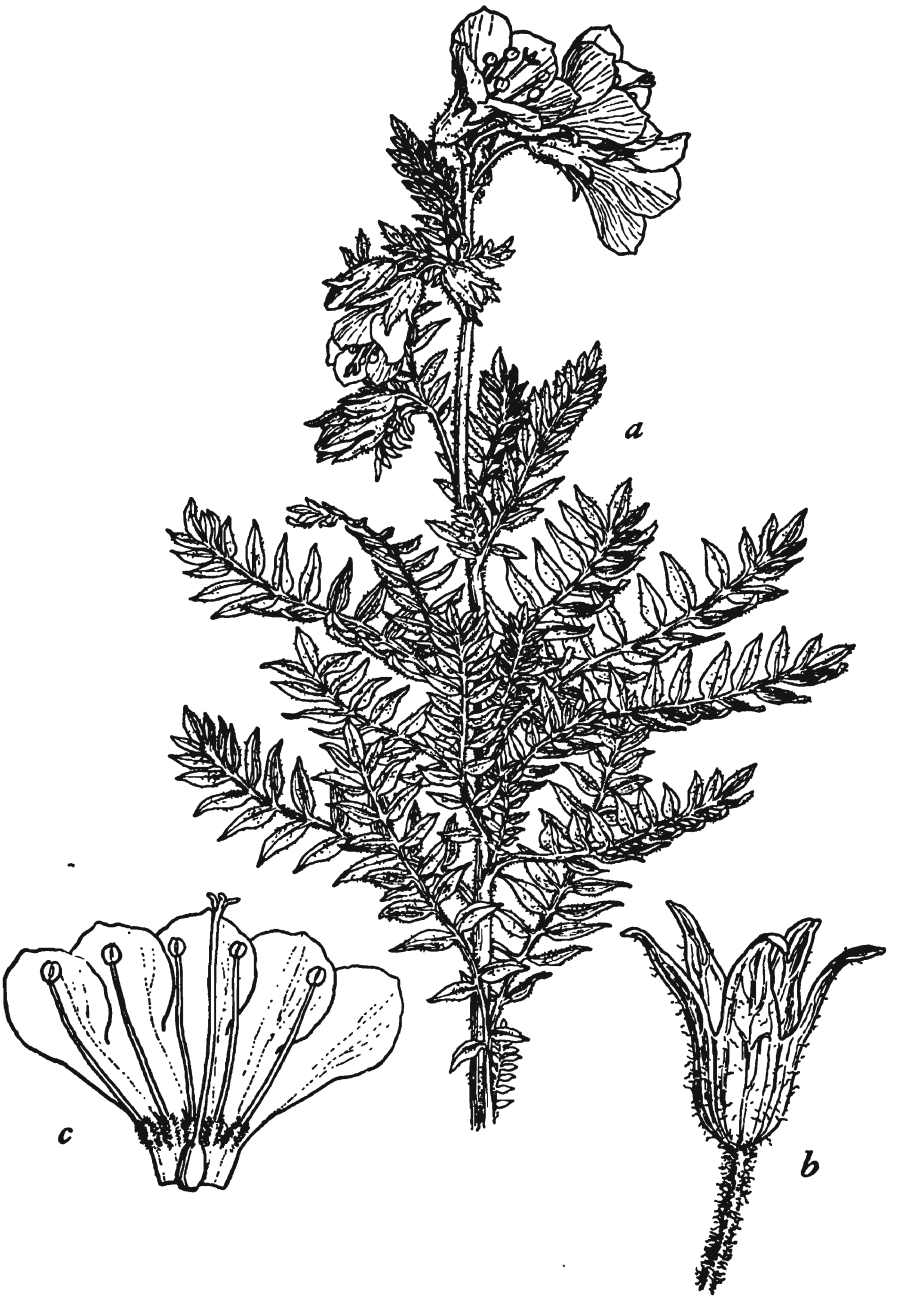


Fig. 11. *Polemonium grandiflorum* Benth. *a*, Habit, × ⅔. *b*, Calyx, × 2. *c*, Dissection of flower, × 1⅓.

P. pulchellum var. *macranthum* Ledeb., Fl. Ross. 3: 85. 1847.
P. arcticum Nyl. & Saell., Herb. Mus. Fenn. 107. 1859.
P. Froloyianum Fisch. ex Herder, Art. Herb. Petropol. 1: 484. 1872.
P. pulchellum Blytt, Norg. Fl. 2: 766. 1874. (non Bunge)

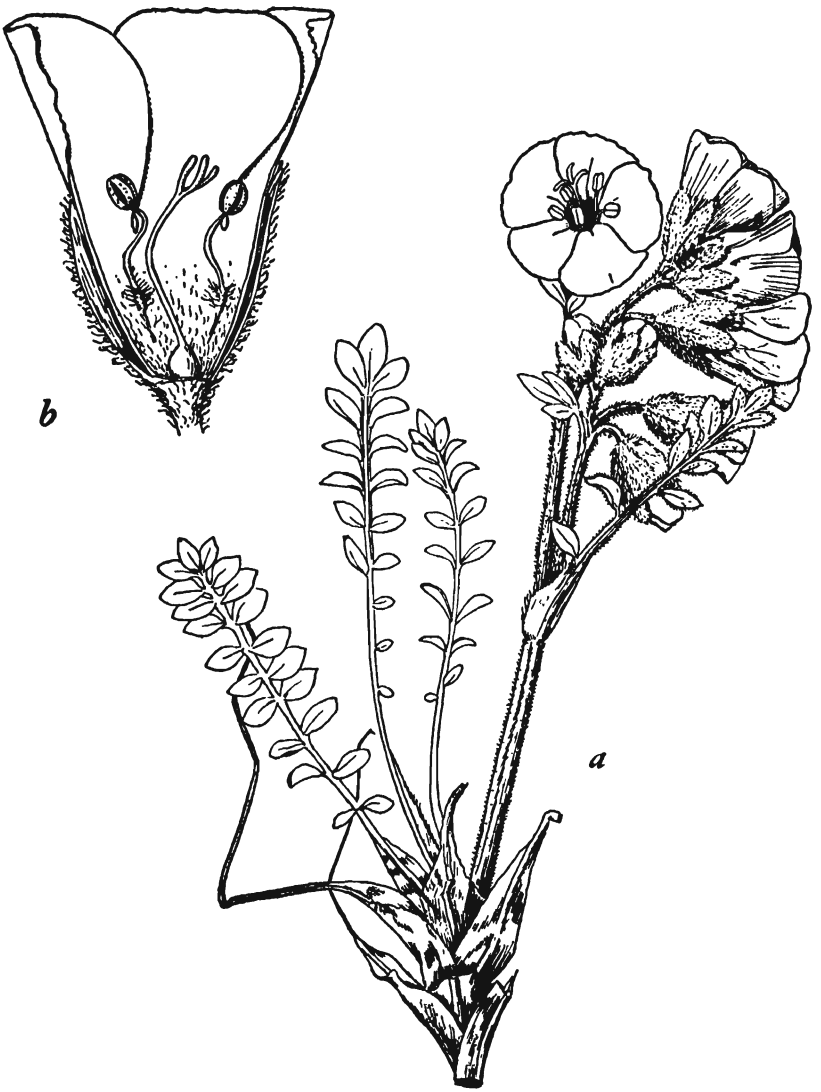


Fig. 12. *Polemonium boreale* Adams. *a*, Habit, × 1⅓. *b*, Longitudinal section of flower, × 2⅔.

P. lanatum subsp. *boreale* Brand, in Engler, Pflanzenr. 4^{250}: 40. 1907.
P. lapponum Gandoger, Soc. Bot. France 65: 59. 1918.
P. samejedorum Gndgr., loc. cit. 65: 59. 1918.
P. hyperborium A. Tolm., Repert. Spec. Nov. Reg. Veget. 23: 15. 1926.

Perennial, commonly under 3 dm. high; peduncles few or solitary, erect from more or less cæspitose basal leaves; mature leaflets 13–23, elliptic to subrotund, on a slightly winged rachis, obtuse at the apex, 2–10 mm. long, 1–5 mm. broad, the young leaflets pubescent, the older glabrous or ciliate; inflorescence commonly subcapitate, the pedicels shorter than the calyx; bracts foliaceous, 0.5–3 mm. long, glandular-pubescent; calyx 5–10 mm. long, glandular-pubescent, often lanate, campanulate, the segments broad, rounded at the apex

and equaling the tube; corolla rotate-campanulate, 15–20 mm. long, 10–25 mm. broad, the lobes rotund, subequal to the corolla tube; stamens inserted halfway up the corolla tube, shorter than the corolla; style subequal to the corolla. Flowering in July and August. (Fig. 12.)

Type locality.—"Mouth of the Lena River." Collector unknown.

Distribution.—Circumboreal, from 60° N. to 80° N., extending slightly farther south in the Behring Sea region. (Map 6.)

Earlier authors can hardly be held accountable for naming and renaming this species, since even today the available collections are somewhat meager. The two earliest names were proposed without the publication of descriptions or figures, and hence must remain *nomina nuda,* validating *P. boreale* Adams for this entity.

The specimens examined, despite an almost completely circumboreal distribution, show a remarkable uniformity which might be attributed to the severity of the selective effect of the Arctic climate in reducing the number of biotypes that can survive (cf. *P. cæruleum* subsp. *villosum*).

In view of the wide acceptance of *P. humile* Willd. ex R. & S., the evidence for the rejection of this name is given herewith: In the type locality of *P. humile* there are only two species which might be confused, *P. pulchellum* Bunge (1829), and the present species. In proposing his *P. pulchellum,* Bunge distinguished it from *P. humile* Willd., and the characters that Bunge applied to *P. humile* are characteristic of Adams' species. Thus the two entities found on the "sandy shores of eastern Siberia" are *P. pulchellum* Bunge and *P. boreale* Adams, the latter being equivalent to the later *P. humile* Willd.

Specimens examined (total: 181).—GREENLAND. "Bowdoin Bay," *Baldwin* (1894), NY; "Green Valley, Clavering Island," *Seidenfaden* 744, GH, NY.

SPITZBERGEN. "Isfiord, Advent Bay," *Ekstam* (1897), F, GH, NY, US, WYO; "Spitzbergen," *Captain Sabine,* K.

NORWAY. "Finmarken, Sydvaranger," *Strøm* (1885), NY; "Ostfinmarken, Sydvaranger, Bügönäs," *Lalin* (1883), GH, *Pleym* (1895), WYO.

RUSSIA. "Kildin," *Hultén* (1927), GH, WYO, *Nylander,* GH; "Ad fl. Kolyma," *Augustinowicz,* K; "Oblastia Jakutsk: Kumach-Sur," *Nilsson* (1898), NY; "Buleen," *Nilsson* (1898), GH, US; NOVA ZEMBLA. "Natotschkin Scharr," *Ekstam* (1891), WYO, *Tolmatchew* 298, GH; "Sukhoi Noss," *Lynge* (1921), GH, *Weber* (1881), F; "Karmakulski Bay," *Ekstam* (1901), NY, WYO.

LITTLE DIOMEDE ISLAND. "Little Diomede Island," *Weyer* (1928), NY.

PRIBILOFF ISLANDS. "St. George's Island," *Gabrielson* (1940), GH; "St. Paul Island," *Hultén* 7251, 7295, 7443, S, *Macoun* 94283, CAN, GH, NY, US, *Langsdorff,* K.

ST. LAWRENCE ISLAND. "Gambel," *Chambers* 18c, 24, 40, US.

ALASKA. "Kodiak Island, Uyak Bay," *Eyerdam* 4, S; "Cape Thompson," *Muir* 120, GH; "Lake Iliamna region," *Gorman* 148, GH, S, US; "Top of MacGonigal Pass, 7000′," *Herning* 4299, GH, US, WYO; "Franklin, Fortymile district," *Anderson and Gasser* 7189, CAN, GH, S, WYO; "Kotzebue Sound," *Beechey,* K.

YUKON. "Herschell Island," *Johansen* 90, CAN, NY, US; "Moosehide Creek, Dawson," *Eastwood* 163, CAN, GH, UC, US; "62° N–141° W, Yukon," *Cairns* (1901), CAN, NY.

NORTHWEST TERRITORIES. "Bear Lake and Arctic sea shore," *Richardson,* K; "British America," *Richardson,* GH, NY; "Carleton House to Bear Lake," *Richardson,* GH; "Slave Lake," *Richardson,* GH; "Arctic sea coast," *Richardson* 43, GH; "Arctic sea coast between Cape Barrow and McKenzie River," *Capt. Pullen* 119, K.

10. **Polemonium delicatum** Rydberg

P. delicatum Rydb., Bull. Torr. Bot. Club 28: 29. 1901.
P. scopulinum Greene ex Rybd., Fl. Colo. 280. 1906.
P. pulcherrimum subsp. *delicatum* Brand, in Engler, Pflanzenr. 4[250]: 35. 1907. (in part)

A small, glandular, often cæspitose perennial with a horizontal or descending rootstock; stem slender, 0.5–2.0 dm. high, scarcely exceeding the basal leaves; leaves chartaceous at the base, sheathing the stem, with 11–23 leaflets, the leaflets thin, ovate-lanceolate to elliptic, 3–15 mm. long, 1–6 mm. wide, on a slightly winged rachis, the terminal three discrete, or occasionally confluent through the dilation of the wing on the rachis; inflorescence cymose; pedicels slender, commonly subequal to the calyx in length; calyx glandular-pubescent, narrowly campanulate, 3–7 mm. long, the segments narrowly lanceolate, acute, exceeding the tube; corolla blue, campanulate with a rotate limb, 5–11 mm. long, about the same in breadth, the obovate lobes commonly exceeding the tube; stamens slightly shorter than the corolla, inserted one-third to two-thirds of the way up the corolla tube; style subequal to the corolla. Flowering from June to August. (Fig. 13.)

Type locality.—"West Spanish Peak, Colorado," *Rydberg & Vreeland 5720*, June 9, 1900.

Distribution.—In the mountains of Colorado, Utah, Arizona and New Mexico, above 2,500 meters. (Map 8.)

Rydberg, in his "Flora of the Rocky Mountains" (1917, p. 681), reduced his original publication of Greene's *P. scopulinum* to synonymy with the earlier *P. delicatum* Rydb. The present author concurs with this reduction, although Wherry (1942, p. 753) states that since *P. scopulinum* is "50% larger in most of its parts," it should be accorded subspecific rank.

Brand included in his subspecies also the northwestern populations of *P. californicum* Eastw., here regarded as distinct. The winged rachis and thin leaflets of *P. delicatum* distinguish it from *P. californicum*, and the narrow, acute calyx segments distinguish it from *P. pulcherrimum*. These morphological characters together with the geographical separation of *P. delicatum* from both *P. pulcherrimum* and *P. californicum* form the basis for classification of the first as distinct species. *P. delicatum* is quite evidently related to *P. pulcherrimum* and may represent a segregate from the original ancestral *P. pulcherrimum* stock. The cytology of *P. delicatum* is at present unknown.

Specimens examined (total: 354).—COLORADO. Locality doubtful: "Canadian," *Dr. James*, NY; Jackson Co. "Cameron Pass," *Baker* (1896), F, NY; Larimer Co. "The Bluffs, Spicer," *Gooding* 1508, GH, NY, US, US, WYO; Clear Creek Co. "Middle Park or Clear Creek," *Parry* 276, GH, NY; "High Mts., about Gray's Peak," *Patterson* 105, F, GH, UC, US; Gilpin Co. "Eldora to Baltimore," *Tweedy* 5670, NY, WYO; Lake Co. "Near Leadville," *Barnhart* 473, NY, *L. M. & N. T. Schedin* 340, 341, WYO; Pitkin Co. "10 mi. west of Independence Pass," *Hitchcock, Rethke, & Raadshooven* 3995, NY, US; Garfield Co. "Mt. Carbon," *Nelson* 64, NY; Boulder Co. "Lake Eldora," *Bethel, Willey & Clokey* 4254, F, S, UC, US, WYO; Grand Co. "Berthoud Pass," *Asa Gray* (1872), GH, *Tweedy* 5671, NY, WYO; El Paso Co. "Bottomless Pit." *F. E. & E. S. Clements* 512, GH, NY, US, WYO; Park Co. "Tarryall," *Hall & Harbour* 452, F, GH, US, WYO; Chaffee Co. "Alpine summit, Cottonwood Cañon Road," *Beetle* 2192, NY, WYO; Gunnison Co. "Carson," *Baker* 305, GH, NY, US, WYO; Delta Co. "Mts. on Bear Creek, Uncompahgre River," *Purpus* 636, F; Saguache Co. "Marshall Pass (?)," *Shear* 5142, NY; Huerfano Co. "West Spanish Peak," *Rydberg & Vreeland* 5720, NY, WYO; Costilla Co. "South fork, Culebra Creek," *Warren* 53, WYO; Hinsdale Co. "Spring Creek Pass," *Hitchcock, Rethke & Raadshooven* 4108,



Fig. 13. ***Polemonium delicatum*** Rydb. *a*, Habit, × ¾. *b*, Calyx, × 4. *c*, Dissection of flower, × 3.

UC, WYO; Mineral Co. "Near Pagosa Peak," *Baker* 546, GH, NY, UC, US, WYO; Ouray Co. "Mt. Abram, Ouray," *Shear* 4814, NY, US; San Juan Co. "Silverton," *Crandall* (1892), NY, US; Dolores Co. "Rico," *Payson* 1112, WYO; Montezuma Co. "Bob Creek," *Baker, Earle & Tracy* 162, F, GH, NY, US, WYO.

UTAH. Grand Co. "La Sal Mts.," *Walker* 286, GH, NY, US, WYO; *E. B. & L. B. Payson* 3953, GH, UC, WYO; San Juan Co. "North slope, Abajo Mts.," *Goodman & Hitchcock* 1394, F, GH, NY, UC; Salt Lake Co. "Little Cottonwood Canyon," *Garrett* 1379, GH, US, WYO; Daggett Co. "Spirit Lake," *Jensen* (1942), NY, UC; Duchesne Co. "Mt. Emmons, Krebs Basin," *Hermann* 5223, GH, WYO; Uintah Co. "Fish Lakes," *Gooding* 1387, GH, NY, UC, US, WYO; Piute Co. "Marysvale," *Jones* 5390, F, NY, UC, US, WYO; Wayne Co. "North face, Aquarius Plateau," *Dixon* 740, F; Iron Co. "Brian Head Ranger District," *Eggleston* 8407, UC; Washington Co. "Three miles east of Pine Valley," *Gould* 1792, GH, UC; Juab Co. "Indian Head Farm Creek," *Holmgren & Maguire* 21944, 21975, GH, NY, UC.

ARIZONA. "Navajo Mt. summit," *Clute* 14, WYO; "Humphrey's Peak, San Francisco Mts.," *MacDougall* 391, F, GH, NY, US; "Fremont Peak," *Clausen & Trapido* 4651, NY; "Mt. Agassiz," *Benson* 9631, UC; "Thomas Peak, White Mts.," *Gooding* 1135, NY, US, WYO.

NEW MEXICO. "Pecos Baldy," *Standley* 4274, NY, US, WYO; "Top of Las Vegas Range," *Cockerell* 22, NY; "Lake Peak, vicinity of Santa Fe," *Arsène & Benedict* 15635, 16157, F.

11. **Polemonium californicum** Eastwood

P. californicum Eastw., Bot. Gaz. 37: 437. 1904.
P. calycinum Eastw., Bot. Gaz. 37: 438. 1904.
P. tricolor Eastw., Bot. Gaz. 37: 439. 1904.
P. Tevisii Eastw., Bot. Gaz. 37: 440. 1904.
P. columbianum Rydb., Bull. Torr. Bot. Club 40: 477. 1913.

Perennial from a slender horizontal rootstock; 1–2 (or occasionally 3) dm. high; stems solitary to subcæspitose, glandular-pubescent; leaflets 11–23, ovate, lanceolate or oblong, mostly acute, the upper three commonly confluent, 3–20 mm. long, 1–8 mm. broad, thin glabrous to glandular-pilose; inflorescence cymose; bracts entire to pinnatifid, glandular-pubescent; flowers many, on slender pedicels subequal to the calyx; calyx narrowly campanulate 5–8 mm. long, the segments commonly twice, but at least one and one-half times as long as the tube, glandular-pubescent; corolla blue with a white tube, throat blue, white or yellow, rotate-campanulate, 8–15 mm. broad, the lobes twice as long as the tube; stamens inserted halfway up the tube, pubescent at the base, subequal to the corolla; style exceeding the corolla by the length of the stigmas. Flowering from June to August. (Fig. 14.)

Type locality.—"Snow Flat, Old Tioga Road, Yosemite National Park," *Eastwood*, July, 1902.

Distribution.—California to Washington, Idaho, and Montana, from 1,000–3,000 meters. (Map 8.)

Polemonium californicum exhibits considerable variability, as may be deduced from the above synonymy. It was found impossible to delimit subspecies upon the basis of Eastwood's descriptions or types, since the proposed diagnostic characters are not consistently linked on the specimens. The situation here is similar to that in *P. pulcherrimum*, in which certain variants in a variable population have been accorded specific names. While relatively constant over most of its range, there is an apparent series of intergrades in Washington between *P. californicum* and *P. carneum* (forming *P. amœnum* Piper), and in Idaho between *P. californicum* and *P. cæruleum* subsp. *occidentale*. This latter series of intergrading forms includes the type of *P. intermedium* Brand.



Fig. 14. *Polemonium californicum* Eastw. *a*, Habit, × ⅔. *b*, Single flower, × 3. *c*, Dissection of flower, × 3.

At least some of the variability may be due to polyploidy. The only cytological material available at the time of writing was a collection from Silver Lake, Sierra Nevada, California (*Constance 3086*), which proved to be a tetraploid (n = 18). Since meiosis is apparently quite regular, with the formation of eighteen bivalents, it is possible that *P. californicum* is an allotetraploid. Of

course, it is also possible that the material examined was aberrant, and only further investigation can prove whether or not the whole species is tetraploid. The situation may be comparable to that in *P. cæruleum* subsp. *VanBruntiæ,* in which tetraploid individuals have been reported to occur in an otherwise diploid population. (Cain, 1944, p. 462.)

The species was included by Brand (1907) under *P. pulcherrimum* subsp. *delicatum* which is not found north of Colorado, nor west of Arizona, and which has leaflets on a narrowly winged rachis, the terminal three not commonly confluent. The corolla of *P. delicatum* is also usually smaller than that of *P. californicum,* the former ranging from 5–11 mm. and the latter from 8–15 mm. in breadth.

Specimens examined (total: 395).—MONTANA. "Yellowstone Park," *Compton* (1883), NY; Ravalli Co. "Blodgett Trail, Hamilton," *Kirkwood* 1558, GH; Mineral Co. "Quales Peak," *Wilson* 158, UC.

IDAHO. Kootenai Co. "High mountains," *Sandberg* (1887), F; Shoshone Co. "Divide between St. Joseph & Clearwater Rivers," *Leiberg* 1205, F, K, NY, UC, US, WYO; Idaho Co. "Dry Diggings Lookout," *A. & E. A. Nelson* 2995, GH, UC, WYO; Valley Co. "Gold Fork Lookout," *Thompson* 13754, F, GH, NY, S, UC, US; Boise Co. "Pilot Peak," *Hitchcock & Muhlick* 9920, GH, NY, WYO; Butte Co. "Craters of the Moon," *Rodenbaugh* 17, WYO; Washington Co. "Cuddy Mts.," *Jones* 6460, US.

WASHINGTON. Okanogan Co. "Angel's Pass," *Thompson* 7041, GH, UC; Chelan Co. "Near Nason Creek," *Sandberg & Leiberg* 680, GH, NY, S, UC, US; Snohomish Co. "Mt. Pugh," *Eyerdam* 1456, UC; King Co. "Slopes of Cascade Mts., Wellington," *Umbach* (1901), F, NY, S; Pierce Co. "Brushy slopes above Chain Lakes," *Benson* 2333, NY, UC, US, WYO; "Goat Mt.," *Allen* 262, GH, NY, UC, US; Kittitas Co. "Lower moist woods, Table Mt.," *Thompson* 9281, GH, NY, UC, US; Yakima Co. "Alpine slopes, Chinook Pass," *Thompson* 9842, GH, NY, UC, US; "Mt. Paddo," *Suksdorf* 2766, F, GH, US, 2767, GH, 5769, F, NY; Skamania Co. "Mt. St. Helens," *Coville* 779, US; Walla Walla Co. "In woods, Blue Mts.," *Piper* 2326, GH, UC; Benton Co. "Mt. between Yakima and Columbia River," *Lyall* 2, K; Columbia Co. "Godman Springs," *Constance et al.* 1161, GH, NY, UC, US; Garfield Co. "Bear Creek Trail," *Peters* 382, UC; Clallam Co. "Mt. Angeles," *Thompson* 7534, GH, NY, UC, US; Jefferson Co. "Marmot Pass," *Thompson* 9885, NY.

OREGON. Crook Co. "North of Tuwale Ranger Station," *Whited* 597, GH; Hood River Co. "Mt. Hood," *Henderson* 850, GH, *Shaw* (1917), UC, *Barber* 223, GH, WYO; Klamath Co. "Southeast slopes, Crater Lake," *Thompson* 12276, GH, LD, NY, UC, US; Douglas Co. "Three miles south of Hershberger Butte," *Hitchcock & Martin* 5107, NY, US, WYO; Jackson Co. "Abbott Butte," *Thompson* 13062, GH, NY, US; Ashland Peak," *Thompson* 12360, NY, UC; Umatilla Co. "Blue Mts., near Meacham," *Brode* 332, UC; Union Co. "Fourteen miles east of Weston," *Peck* 22231, UC; Wallowa Co. "Aneroid Lake," *Pennell* 21067, UC, WYO; Grant Co. "Highest Blue Mts.," *Cusick* 230, F, 1717, UC, US; Baker Co. "Anthony Lakes region," *Thompson* 13457, GH, NY, UC, US.

CALIFORNIA. Siskiyou Co. "Marble Mt.," *Chandler* 1671, GH, NY, UC, US; Shasta Co. "Jason & Stewart's camp," *Eggleston* 7388, NY, US; Sierra Co. "Webber Lake," *Lemmon,* GH, UC, *Kennedy & Doten* 72, WYO, 197, UC; Placer Co. "Mt. Lincoln," *Heller* 12929, F, GH, NY, US; Nevada Co. "Donner Pass," *Heller* 6971, GH, NY, UC, US, WYO; Eldorado Co. "Haypress Meadow," *Heller* 12513, F, GH, UC, US; Alpine Co. "Carson Pass," *Evans* (1919), F, *Yates* 3951, UC; Tuolumne Co. "Long Meadow," *Chestnut & Drew* (1889), UC; Mariposa Co. "Lake Tenaya," *Brewer* 1687, GH, NY, UC, US; Fresno Co. "Meadows near Black Mt.," *Hall & Chandler* 592, NY, UC, US.

NEVADA. Washoe Co. "Divide, south side of Slide Mt.," *Heller* 10918, F, GH, K, NY, UC, US, WYO.



Fig. 15. *Polemonium pulchellum* Bunge. *a*, Habit, × ⅔. *b*, Dissection of flower, × 2.

12. **Polemonium pulchellum** Bunge

P. pulchellum Bunge, Fl. Altaica, 1: 283. 1829.
P. moschatum Wormsk. ex Graham, Edinb. Philos. Journ. 7: 786. 1829.

Perennial; cæspitose from a woody caudex; stems pubescent to glabrous, with many basal and few cauline leaves; leaflets 13–25, broadly elliptic to lanceolate, acute at the

apex, 3–12 mm. long, 1.5–5 mm. wide, the terminal three commonly confluent upon the slightly winged rachis; inflorescence cymose, open, the pedicels subequal to the calyx; calyx campanulate, pubescent, 4–7 mm. long, the elliptic, subacute segments equaling or slightly exceeding the tube; corolla blue, broadly funnelform from a narrowly cylindrical white or cream-colored tube, with a short but distinct throat, the corolla tube three times as long as broad, the lobes obovate to obovate-truncate, not rotate, subequal to the tube and throat combined; stamens inserted at the junction of the tube and throat, shorter than the corolla; style subequal to the corolla or exserted. Flowering from May to September. (Fig. 15.)

Type locality.—"In rocks, Kurai Island, and on the banks of the Tschuja River," *Bunge.*

Distribution.—From the Altai to the Arctic Ocean, and east to the Kamchatka Peninsula. (Map 8.)

In habit and foliage this species resembles *P. delicatum* Rydb. and *P. pulcherrimum* Hook., as is shown in Ledebour's "Icones," table 20. This similarity probably accounts for the persistently recurring records of the species from North America. The corolla of *P. pulchellum* is characterized by its funnelform limbs as contrasted with the rotate limbs of the above-mentioned North American species. Also, the corolla tube in *P. pulchellum* is much more constricted, being only one-third as broad as long, whereas in both *P. pulcherrimum* and *P. delicatum* the corolla tube breadth is subequal to the length. Thus far, no material has been seen from North America which could be referred to *P. pulchellum.* The inclusion of *P. moschatum* Wormsk. in the synonymy of this species is based upon a specimen of Wormskiold's labeled *P. moschatum,* from the Gray Herbarium.

In Kamchatka, *P. boreale* Adams approaches the habit of *P. pulchellum,* but may be distinguished by the rotate limbs, broad corolla tube and obtuse leaflets in *P. boreale.*

Specimens examined (total: 27).—RUSSIA. Altai: "Flora Altaica," *Ledebour,* GH, *Bunge,* GH, NY; "Altai," *Polixow,* NY; "Valley, Sk-kem River," *Laposhnikov* (1897), NY; "Valley, Tarchata River," *Laposhnikov* (1909), GH; "In gravel, Lake Koso Gol," *Turczaninow* (1859), GH. Northern Russia: "Lower Yenissei River, near Goltschicha," *Tolmatchew* 292, GH. Kamchatka: "Kamchatka," *Wormskiold,* GH; "Petropavlovski," *Wright* (1853–56), GH, *Hultén* 790, GH; "Labotchni River," *Komarov,* S.

13. **Polemonium pulcherrimum** Hooker

P. pulcherrimum Hook., Bot. Mag. 57: 2979. 1829.
P. mexicanum Nutt., Journ. Acad. Philad. 17: 41. 1834. (non Cerv.)
P. parvifolium Nutt. ex Rydb., Bull. Torr. Bot. Club 24: 253. 1897.
P. Haydenii A. Nels., Bull. Torr. Bot Club 26: 353. 1899.
P. viscosum Nutt. var. *pilosum* Greenman, Bot. Gaz. 25: 263. 1899.
P. Berryi Eastw., Bot. Gaz. 37: 440. 1904.
P. rotatum Eastw., Bot. Gaz. 37: 441. 1904.
P. fasciculatum Eastw., Bot. Gaz. 37: 442. 1904.
P. shastense Eastw., Bull. Torr. Bot. Club 32: 205. 1905.
P. montrosensis A. Nels., Proc. Biol. Soc. Wash. 17: 174. 1906.
P. orbiculare Gandoger, Soc. Bot. de France 65: 58. 1918.
P. oreades Gandoger, Soc. Bot. de France 65: 58. 1918.
P. oregonense Gandoger, Soc. Bot. de France 65: 58. 1918.
P. pilosum G. N. Jones, Univ. Wash. Publ. Biol. 5: 215. 1936.
P. Lindleyi Wherry, Amer. Midl. Nat. 27: 748. 1942.
P. nevadense Wherry, Amer. Midl. Nat. 34: 375. 1945.

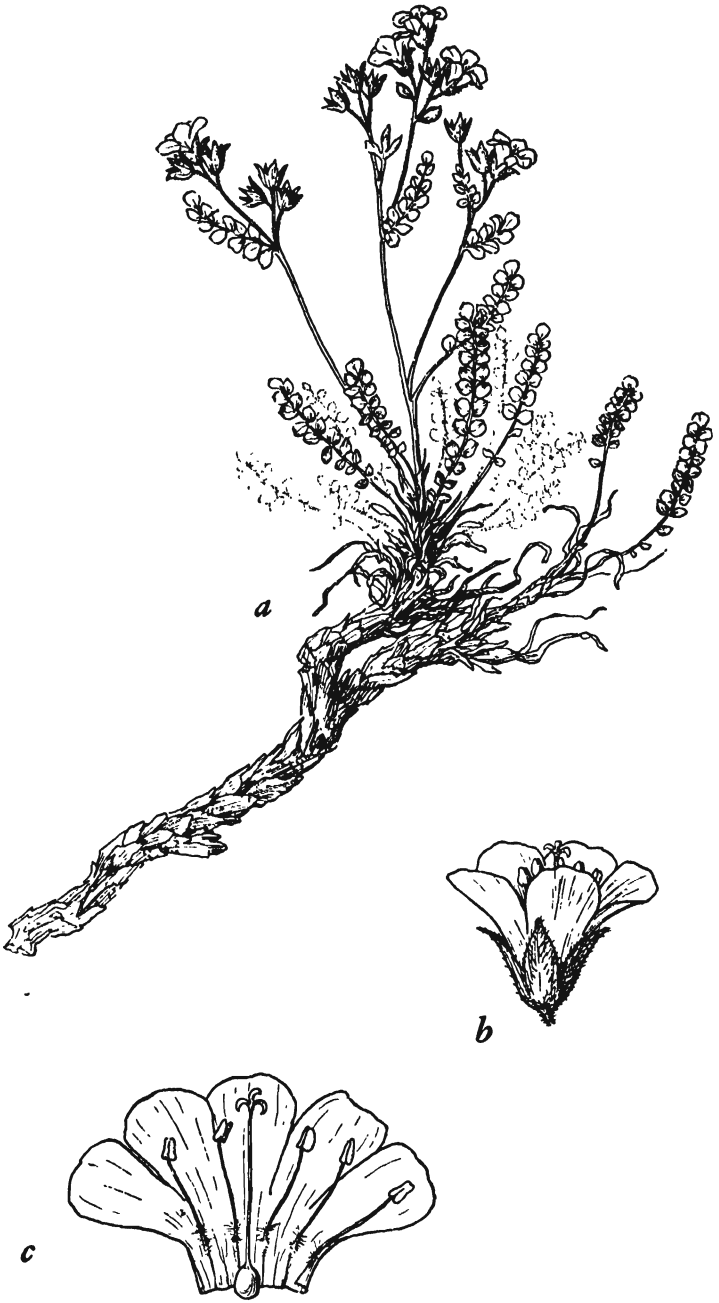


Fig. 16. *Polemonium pulcherrimum* Hook. *a*, Habit of montane plant, × ¾. *b*, Single flower, × 3. *c*, Dissection of flower, × 3.

Perennial; 1–3 dm. high, erect, becoming cæspitose in age; leaflets 11–23, ovate to orbicular, or in the northern representatives elliptical, 2–18 mm. long, 1–5 mm. broad, sparsely pubescent with short glandular hairs, the terminal leaflets discrete; inflorescence a cyme, the pedicels long, slender, exceeding the calyx; bracts entire to pinnatifid, up to 7 mm. long; calyx campanulate, 4–6 mm. long, the segments equaling the tube, glandular-

pubescent; corolla rotate-campanulate, 5–8 mm. long, the same in breadth, the blue, ovate, obtuse lobes subequal to the yellowish tube; stamens inserted below the middle of the tube, subequal to the corolla, the bases pubescent; style subequal to the corolla. Flowering from June to August. (Fig. 16.)

Type locality.—"Highest Rocky Mountains," [southern British Columbia], *Drummond.*

Distribution.—From Alaska and Yukon Territory southward through British Columbia and Alberta to the Rocky Mountains of Idaho, Montana, and Wyoming; also in the Cascade Mountains of Washington and Oregon, in the Olympic Mountains of Washington, and in the Sierra Nevada of California and Nevada. (Map 8.)

Polemonium pulcherrimum Hook. is variable in height; in size, shape, and number of leaflets; in length of peduncles; in size of corolla; in insertion and exsertion of stamens; and in exsertion of the style. Growth studies in Berkeley on seed from California and British Columbia have demonstrated a number of variations in the plants.

While most of the leaves produced on the growing plants were of the normal type with two-ranked leaflets, a few of the plants produced leaves which bore evidences of verticillate leaflets. These leaflets varied from 2 to 5 per node on the rachis, and approximated the foliar appearance of *P. nevadense* Wherry. These specimens bring into question the advisability of stressing the possession of verticillate leaflets as opposed to coplanar leaflets as a sole basis for specific segregation.

Under poor soil conditions, or when crowded, the plants produced small leaves with short, rotund leaflets, and produced no flowers the first season. In contrast, plants grown from the same seed, when transferred to rich soil quickly replaced similar leaves with larger ones bearing long, narrowly elliptical leaflets, and flowered in approximately four months.

Under normal length of day (8–16 hours in Berkeley) the flowering peduncles were subequal in length to the basal leaves, but under illumination of increased duration (16–20 hours) the length of the peduncles was increased to as much as three times the height of the basal leaves. The leaflet shape exhibited the same change under increased illumination as under better soil conditions, namely, the leaves produced under increased illumination bore narrowly elliptical leaflets, whereas those produced under a shorter day were more rotund. With the cessation of the illumination experiment, the new leaflets produced showed a definite tendency to return toward the rotund shape. There was no appreciable change in the width of the leaflets, the change of shape being apparently due only to the increase in length of the leaflets.

The present distribution offers a reasonable explanation of the variability of the species. At the southern limits of its distribution, *P. pulcherrimum* is confined to alpine or subalpine regions, and thus consists of a series of relatively small populations. These small isolated populations favor the possibility of becoming genetically depauperate either through random fixation or through ecological selection. In the northern portion of its range, *P. pulcherrimum* is found in the valleys (British Columbia) or at sea level (Alaska). Here the genetic isolation is reduced to a minimum, and while the species is moderately constant over the northern portion of its range, specimens identi-

cal with various isolated individuals from the southern populations occur *sporadically.*

The effect of the increasing length of day in the higher latitudes is comparable to that observed under experimental circumstances in Berkeley, namely the narrow leaflets and elongated peduncles so characteristic of P. Haydenii.

The names included in the list of synonyms appear to be based upon various combinations of variable characters. An attempt was made to maintain these names upon either a specific or subspecific level, but the diagnostic characters proposed by the authors showed no actual segregation from the main species population.

Cytological materials from Rossland, B.C., and from Eagle Rock, Modoc Co., California, were found to be diploid (n = 9).

Specimens examined (total: 720).—ALASKA. "Hope," *Anderson* 6600, GH, S, WYO; "Franklin, Forty-mile district," *Anderson & Gasser* 7119, CAN, GH, S, WYO; "Hunter," *A. & R. A. Nelson* 3496, GH, NY, US, WYO; "Kodiak, Sitkalidak Island," *Eyerdam* 180a, S, UC.

YUKON. "Dawson," *Eastwood* 135, CAN, GH, UC, US, 138, F, GH, UC, US; "Bear Creek," *Müller* (1920), CAN, GH, NY, US.

NORTHWEST TERRITORY. "Letty Harbour," *Dutilly* 319, GH.

BRITISH COLUMBIA. "Stuart Lake," *Rothrock* 56, F, GH, NY; "Atlin," *Eastwood* 650, GH, UC, US; "Kespiox Indian Village," *McCabe* 6987, UC; "Germansen Landing," *McCabe* 7712, UC; "Limestone Island, Queen Charlotte Islands," *Newcomb* (1912), GH; "Chilcat River, Vancouver Is.," *Newcombe* (1902), F; "Kleena Kleene," *McCabe* 524, UC; "Pavilion, Fraser River," *Dr. Campbell* (1859), K; "Spences Bridge," *Macoun* (1889), NY; "Lake Bootahnie, Marble Mts.," *J. W. & E. M. Thompson* 135, CAN, NY, US; "Ashcroft," *Cowles* 261, F; "Deer Park, Lower Arrow Lakes," *Macoun* 16227, CAN, US; "North of Natal," *Weber* 2283, GH, NY, UC, US, WYO.

ALBERTA. "Jumping Pond Creek," *Macoun* 23766, CAN, GH, NY; "Maligne Lake," *Brown* 1271, GH, NY; "Sheep Mt., Waterton Lake," *Macoun* 11806, CAN, F.

IDAHO. Kootenai Co. "Steep rocky mountain sides," *Sandberg* 139, F; Lemhi Co. "Sandy banks above Silver Creek," *Hitchcock & Muhlick* 9458, GH, NY, WYO; Custer Co. "Challis Creek," *Macbride & Payson* 3318, GH, NY, US, WYO; Elmore Co. "Five mi. east of Featherville," *Hitchcock & Muhlick* 8776, GH, NY, WYO.

MONTANA. Glacier Park: "Mt. Henry, Midvale," *Umbach* 194, F, NY, US, WYO; Flathead Co. "Lake McDonald," *Vreeland* 922, GH, K, NY, US; Sanders Co. "Flathead River, west of Perma," *Hitchcock* 1519, WYO; Mineral Co. "Fish Creek, Superior," *Lamm* 17037, WYO; Missoula Co. "Spring Gulch," *Antonich* 7, F, GH, NY; Ravalli Co. "Hamilton," *Blankenship* 364a, F, US, WYO; Granite Co. "Rock Creek Ranger Station," *Applegate* 6416, UC; Powell Co. "Six mi. south of Helmville," *Hitchcock & Muhlick* 11705, GH, UC; Deer Lodge Co. "Fishtrap, 25 mi. south of Anaconda," *Hitchcock & Muhlick* 9176, GH, NY, WYO; Madison Co. "Spanish Basin," *Flodman* 739, NY, US; Gallatin Co. "Bridger Mts.," *Rydberg & Bessey* 4839, GH, NY, UC, US, WYO; Meagher Co. "Belt Creek," *Anderson* (1884), NY, UC; Park Co. "Sweet Grass Hills," *Kemp* (1918), NY; Stillwater Co. "Haystack Mt.," *Hitchcock & Muhlick* 13453, GH, UC; Sweetgrass Co. "Head of Boulder Creek Valley," *Scribner* 163, US.

WYOMING. Sheridan Co. "Bighorn Mts.," *Mead* 2571, NY; Big Horn Co., "Big Horn County," *Worthley* 44, 46, 93, US, WYO; Park Co. "Stinking Water," *Parry* 243, F, GH, K, NY; Yellowstone Co. "Crescent Hill," *A. & E. Nelson* 6921, GH, NY, US, WYO; "Golden Gate," *A. & E. Nelson* 5526, GH, NY, UC, US, WYO; Teton Co. "Snake River, 6 mi. west of Jackson," *Williams* 3007, GH, NY, WYO; Fremont Co. "Upper Buffalo Fork to head of Du Noir River," *Curtis* (1899), NY.

WASHINGTON. Ferry Co. "Kettle River," *Boner & Weldert* 197, GH, NY, UC, WYO; Okanogan Co. "Muckamuck Lookout," *Thompson* 6977, GH, NY, US; Chelan Co. "Alpine slopes, Three Brothers," *Thompson* 10735, GH, NY, US; Pierce Co. "Goat Mt.," *Allen* 261, GH, NY, US; Kittitas Co. "Head of Beverley Creek," *Thompson* 9496, GH, NY, UC, US; Whatcom Co. "Near Barron," *Muenscher* 8412, GH; San Juan Co. "Olga" [on Orcas Is.], *Engberg* (1905), NY; Clallam Co. "Mt. Angeles," *Thompson* 7440, GH, UC, 8395, GH, NY, WYO; Jefferson Co. "Marmot Pass," *Thompson* 9938, NY; Mason Co. "Mt. Steele," *Meyer* 1146, GH.

OREGON. Lane Co. "South slope, South Sister," *Andrews* 140, UC; Klamath Co. "North Cliffs, mountains of Cycan Valley," *Cusick* 2750, F, GH, NY, UC, US, WYO; Lake Co. "Crane Mt.," *Thompson* 13211, GH, NY, UC, US; Harney Co. "Steen Mt.," *Leiberg* 2519, GH, NY, US.

CALIFORNIA. Siskiyou Co. "Mt. Shasta," *Copeland* 3515, GH, NY; Trinity Co. "Twin Lakes to Thompson Peak," *Alexander & Kellogg* 296, 270c, UC; Lassen Co. "Lassen's Peak," *Lemmon* 960, F, GH; Eldorado Co. "Mt. Tallac," *Eastwood* 1173, GH, NY, UC, US; Butte Co. "Cliff, Big Summit," *Copeland* (1930), UC; Alpine Co. "Ebbett's Pass," *Brewer* 2070, GH, K, NY, UC, US; Calaveras Co. "Summit of Silver Mt.," *Brewer* 2046, US; Tuolumne Co. "White Mt., Mt. Conness Range," *Mason* 11328, UC; Mono Co. "Tioga Crest," *Mason* 11460, UC; Mariposa Co. "Tenaya Creek," *Smiley* 871, GH.

NEVADA. Washoe Co. "Mt. Rose," *Doten* 4, WYO, *Kennedy* 1157, GH, NY, UC, WYO, *Heller* 9863, F, GH, NY, US; Nye Co. "Table Mt.," *Maguire & Holmgren* 25721, GH, UC, WYO; "Toiyabe Dome," *Maguire & Holmgren* 25972, GH, UC, WYO.

14. **Polemonium elegans** Greene

P. viscosum A. Gray, Syn. Fl. 2: (1), 150. 1878. (non Nutt.)
P. elegans Greene, Pittonia 3: 305. 1898.
P. bicolor Greenman, Bot. Gaz. 25: 262. 1898.

Perennial, dwarf, cæspitose, 5–12 cm. high, the basal leaves half as high, densely glandular-pubescent; the leaflets crowded, obovate to rotund, rarely lobed, and then the sinuses not to the base, 2–4 mm. long; inflorescence a subcapitate cyme; pedicels shorter than the calyx; bracts pinnatifid, glandular-pubescent; calyx narrowly campanulate, 5 mm. long, the segments slightly shorter than the tube, densely glandular-pubescent; corolla funnelform, 10–14 mm. long, the obovate, blue lobes rotate, rounded at the apex, and half as long as the yellow tube; stamens inserted halfway up the tube, pubescent at the base, shorter than the corolla; style shorter than the corolla. Flowering in July and August. (Fig. 17.)

Type locality.—"In volcanic sand at 9000′ altitude on Mt. Rainier, Washington," *C. V. Piper* (August, 1895).

Distribution.—On the higher peaks of the Cascade Mountain Range in British Columbia and Washington. (Map 9.)

This species was considered by Brand to be closely related to *P. viscosum* Nutt., particularly the small northern form which Rydberg segregated from Gray's *P. confertum*. The present author agrees with this interpretation of the morphological and distributional data, since *P. viscosum* is found in the Coast Range of British Columbia to the west of *P. elegans*, and in the Rocky Mountains to the east, and *P. eximium* is found in the Sierra Nevada Range in California to the south. In short, in the Cascade Range of British Columbia and Washington, in the regions where *P. viscosum* would be expected, it is replaced by *P. elegans*.

Wherry (1942, p. 743) says of *P. elegans* and *P. bicolor*, "Since not based on the same type specimen, these two names cannot be classed as synonyms; the later published one should be placed in some infraspecific status under the

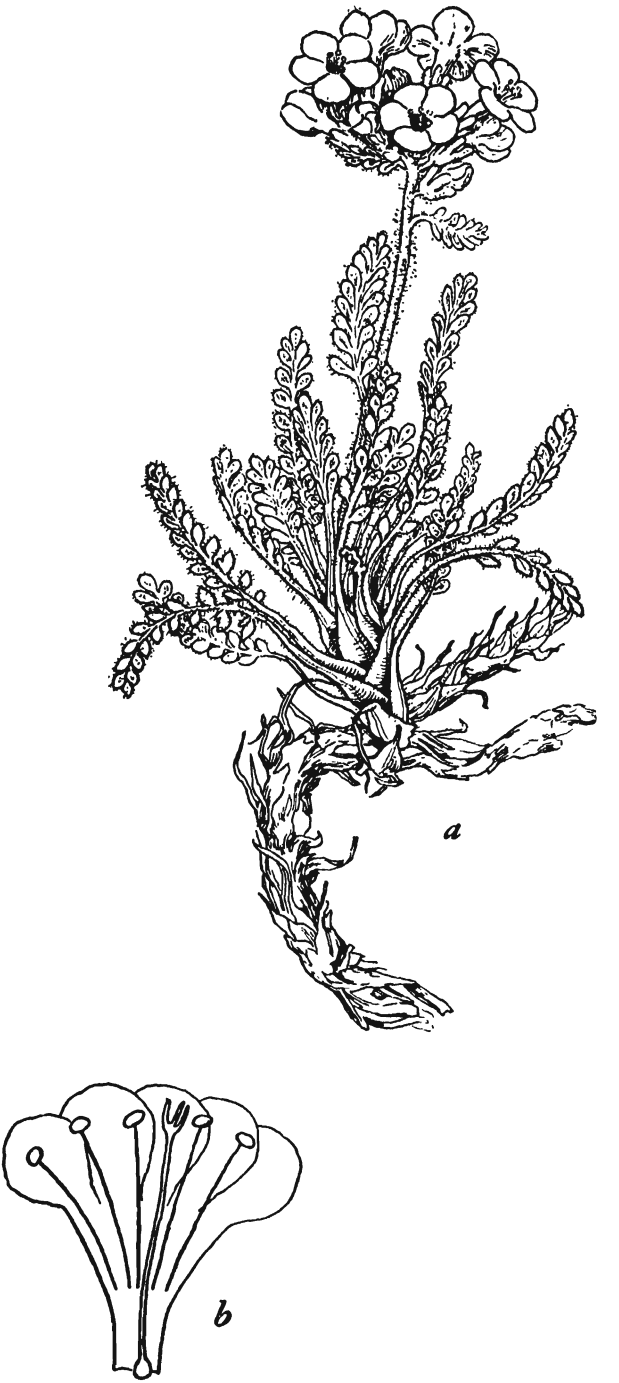


Fig. 17. *Polemonium elegans* Greene. *a*, Habit, × ⅞. *b*, Dissection of flower, × 2½.

earlier. This may well be: *P. elegans* Greene f. *bicolor* (Greenm.) W., stat. nov." The fact that the type and cotype of *P. elegans* were cited as cotypes of *P. bicolor* is surely evidence that the authors had the same entity in mind, and indicates synonymy. It is felt that the elimination of such a name as *P. bicolor* Greenm. will do more to relieve the confusion in the genus than would its perpetuation as a hypothetical form.

Specimens examined (total: 46).—BRITISH COLUMBIA. "Skagit Valley," *Macoun* 68716, F, GH, NY, S.

WASHINGTON. Whatcom Co. "Mt. Baker," ——— (1868), US; Chelan Co. "Indian Head Peak," *St. John* 4821, GH, NY, UC; Pierce Co. "Mt. Rainier," *Piper* 2129, GH, US, *Allen* 294, NY, UC, US, *Jones* 10352, GH, NY; Yakima Co. "Mt. Aix," *Thompson* 15013, GH, NY, S; "Mt. Adams," *Suksdorf*, F, *Gorman* 3281, UC, *Henderson* 2411, GH, *Thompson* 11168, NY.

15. **Polemonium chartaceum** Mason

P. chartaceum H. L. Mason, in Jepson, Man. Fl. Pl. Calif. 725. 1925.

Perennial, 10–30 cm. high, from a woody caudex; stems several, erect, cæspitose, leafy; petioles with a broad sheathing chartaceous base, the rachis not rigid in age; leaflets small, 3–5-lobed, the lobes spatulate, 0.5–3.0 mm. long, glandular-pubescent; inflorescence subcapitate, the pedicels about half as long as the calyx; bracts pinnatifid, glandular-pubescent; calyx narrowly campanulate, 6–8 mm. long, the rounded obtuse segments shorter than the tube, glandular-pubescent; corolla funnelform, 11–13 mm. long, about as broad, the rounded obtuse blue lobes rotate, one-third as long as the white tube; stamens inserted one-quarter of the way up the tube, pubescent at the base, subequal to the corolla, much exceeding (4 mm.) the tube; style subequal to the stamens. Flowering in June and July. (Fig. 18.)

Type locality.—"White Mountain Peak, Inyo Co. Calif." *Jepson 7383.*

Distribution.—Reported thus far only from the type locality and from Mt. Eddy and Mt. Scott in Siskiyou Co., California. (Map 10.)

The occurence of *P. chartaceum* in the Mount Shasta region of northern California (*Heller 13577, Lemmon 10*), midway between the ranges of *P. elegans* Greene and *P. eximium* Greene, focused attention upon the affinities of these species. The description of *P. chartaceum* shows its affinities with *P. eximium* in the corolla and leaflets, but separates it upon the exsertion of the stamens and its chartaceous leaf bases and the fact that the rachis is not rigid in age. The corolla of *P. eximium* is similar to that of *P. elegans*, the main point of distinction being the exsertion of the stamens in the latter. *P. chartaceum* has a closer affinity with *P. elegans* than with *P. eximium* on the basis of floral morphology, and on the character of the sheathing leaf bases and rachis character, but in leaflet character the closest affinity is with *P. eximium*. By reason of the relative importance attached to the possession of verticillate leaflets in previous treatments, the close morphological relationship of *P. chartaceum* and *P. elegans* may have been overlooked.

Further investigation may result in the reduction of *P. chartaceum* to an infraspecific category of *P. elegans*, but for the present it is tentatively retained in specific rank.

Specimens examined (total: 12).—CALIFORNIA. Siskiyou Co. "Scott Mt.," *Lemmon* 10, GH; "Mt. Eddy," *Heller* 13577, F; Inyo Co. "White Mt. Peak," *Duran* 556, GH, NY, S, UC, WYO.

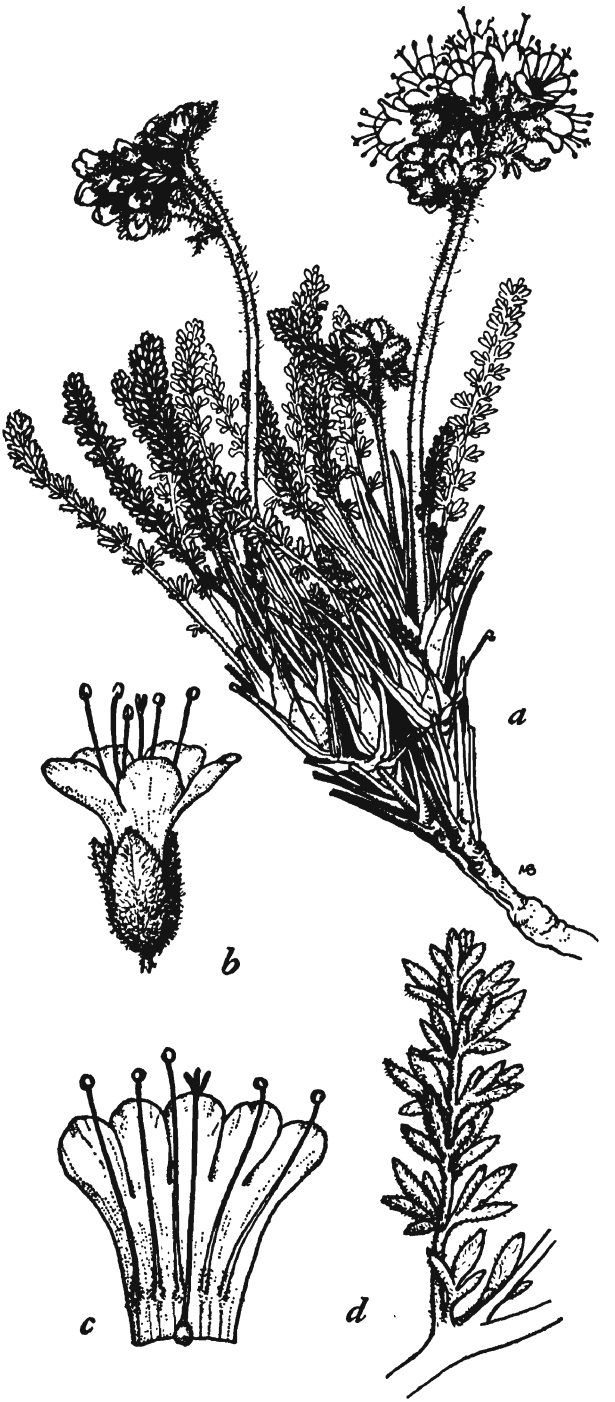


Fig. 18. *Polemonium chartaceum* Mason. *a*, Habit, × ⅔. *b*, Single flower, × 2⅔. *c*, Dissection of flower, × 2⅔. *d*, Single leaf from flowering peduncle, × 3.

16. **Polemonium eximium** Greene

P. eximium Greene, Pittonia 3: 305. 1898.
P. confertum var. *eximium* Jepson, Man. Fl. Pl. Calif. 783. 1925.

Perennial, 10–30 cm. high, cæspitose from a woody caudex; leaves mostly basal, few on the floriferous branches; petioles expanded at the base but not chartaceous, rachis rigid in age; leaflets small, 3–5-parted, from 0.5–5.0 mm. long, the lobes spatulate to oblanceolate, glandular-ciliate; inflorescence subcapitate in flower and in fruit; pedicels shorter than the calyx; bracts lobed to entire; calyx narrowly campanulate, 5–10 mm. long, the segments slightly shorter than the tube, elongate, rounded at the apex, densely glandular-pubescent; corolla narrowly funnelform to cylindrical, with a rotate limb, 12–15 mm. long, 10–15 mm. broad, the blue, spreading, rounded lobes from one-third to one-half as long as the tube; stamens inserted one-quarter of the way up the tube, pubescent at the base, slightly exceeding the tube, but shorter than the corolla; style subequal to the stamens. Flowering in June and July. (Fig. 19.)

Type locality.—"Mt. Conness, Tuolumne Co., Calif.," *Harford.*

Distribution.—Peaks of the Sierra Nevada, California. (Map 10.)

This species is closely related to *P. viscosum* Nutt. (*P. confertum* A. Gray, as synonym) as noted by Jepson, but its inflorescence is consistently more congested, especially in fruit. The calyx characters are quite constant, the extreme apex of the segments being invariably rounded, as contrasted with the acute apex of *P. viscosum.* In the specimens of *P. eximium* examined, there were none that showed any trace of scariosity in the calyx sinuses, a character which may be observed in some specimens of *P. viscosum.*

No specimens have been seen which could be mistaken for *P. viscosum.* That fact, together with the geographical segregation, is the basis for maintaining the species as distinct.

Specimens examined (total: 62).—CALIFORNIA. Tuolumne Co. "Mt. Conness," *Clark* (1898), UC; "Mt. Dana," *Brewer* 1737, GH, NY, UC, US, *Bolander* 6408, F, NY, UC, US; Mono Co. "White Mt.,"*Keck* 4928, GH, NY, UC; Mariposa Co. "Mt. Lyell," *Muir*, GH, *Christenson* 2017, UC; Fresno Co. "Mt. Goddard," *Hall & Chandler* 666, NY, UC; Tulare Co. "Mt. Whitney," *Culbertson* 4542, F, GH, NY, UC; Inyo Co. "Kearsage Pass," *Alexander & Kellogg* 3250, UC.

17. **Polemonium viscosum** Nuttall

P. viscosum Nutt., Journ. Acad. Nat. Sci. Philad. II, 1: 154. 1848.
P. confertum A. Gray, Proc. Amer. Acad. Sci. Philad. 15: 73. 1853.

Perennial, 0.5–5.0 dm. high from a persistent rhizome; leaves mostly basal, few on the floriferous branches, the petioles expanded at the base, chartaceous, the rachis rigid and persistent in age; leaflets occasionally 2-ranked, but commonly 3–5-parted, appearing verticillate, the lobes elliptic to spatulate, 1–10 mm. long, 0.5–4 mm. wide, glandular-ciliate to glabrous on the margin; inflorescence elongated and subspicate to congested subcapitate in anthesis, becoming elongate in fruit; pedicels shorter than the calyx, bracts pinnatifid; calyx narrowly campanulate, 8–16 mm. long, the segments one-third as long as the tube, lanceolate, acute, densely glandular-pubescent; corolla blue, yellow, or occasionally white, narrowly funnelform with a subrotate limb, 17–35 mm. long, 10–20 mm. broad, the rotund lobes about one-third as long as the tube; stamens commonly inserted halfway up the tube (but occasionally this feature is variable), pubescent to glabrous at the base, slightly exceeding the tube, but shorter than the corolla; style subequal to the corolla, slightly exceeding the stamens. Flowering from June to August.

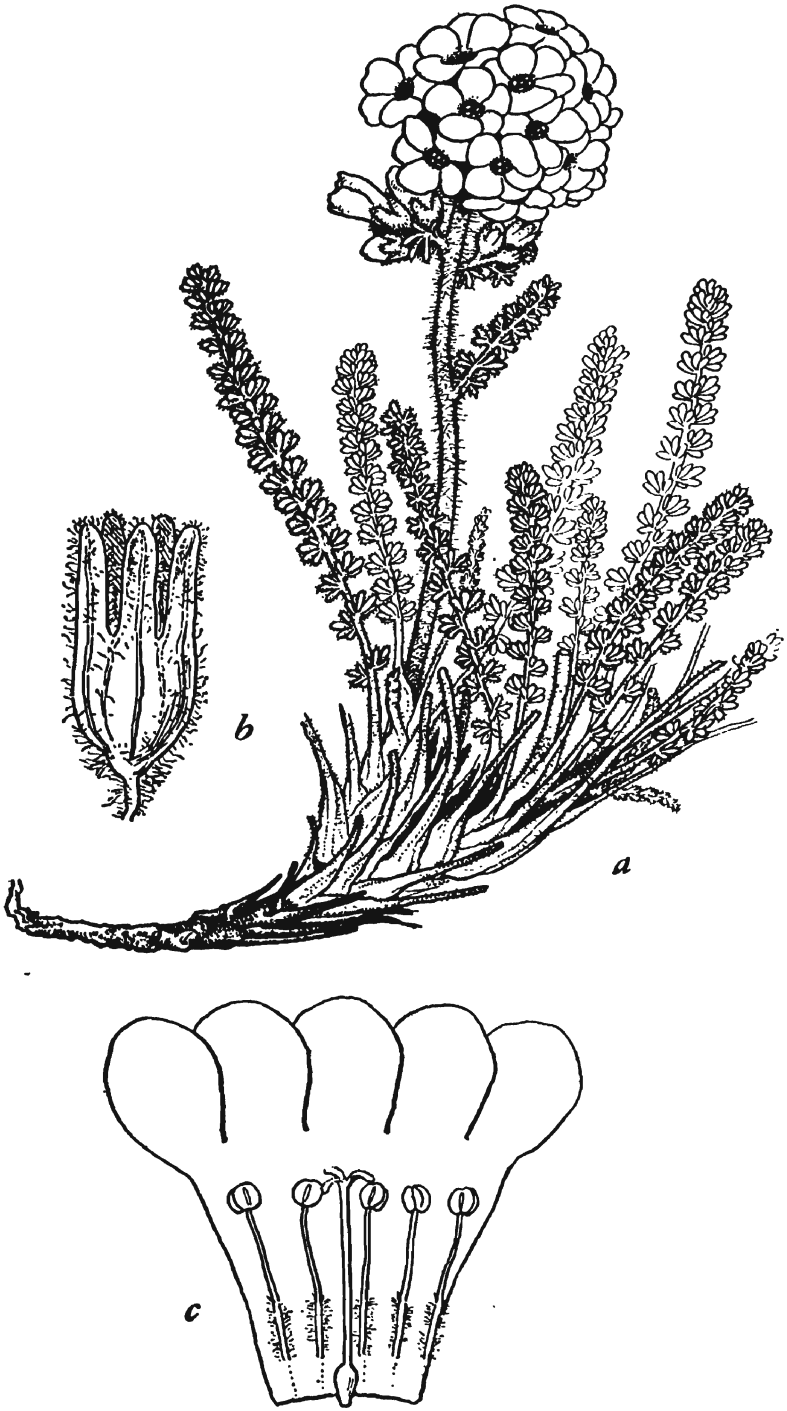


Fig. 19. *Polemonium eximium* Greene. *a*, Habit, × 9/10. *b*, Calyx, × 4. *c*, Dissection of flower, × 4.

Type locality.—"Rocky ridges and ledges toward the headwaters of the Platte," *Nuttall.*
Distribution.—In the Arctic-Alpine zone of high peaks from Arizona and New Mexico north to British Columbia and Alberta along the Rocky Mountains. Also recorded from the Coast Range of British Columbia, from the eastern Cascade Mountains of northern Washington, and from the Wallowa Mountains in northeastern Oregon. (Map 9.)

The *Polemonium viscosum* complex, long characterized by its verticillate leaflets, has been confused by practices current since the time of Asa Gray. Some authors, for example, have separated *P. confertum* A. Gray, or *P. confertum* A. Gray emend. Rydberg, from *P. viscosum* Nutt., yet Gray apparently admitted that Nuttall's type was equivalent to *P. confertum.* Rydberg was apparently unwilling to discard Gray's name, and reapplied it to a larger specimen on the type sheet which had obviously been included in Hall and Harbour's collection to show the range of variation. Other workers, noticing the fine points drawn upon to separate these supposed entities, have described other variations on comparable minutiæ, until at the present time the same worker has frequently assigned two or more specific names to the same collection.

The confusion existing between *Polemonium confertum* A. Gray and *P. viscosum* Nutt. apparently arose from a mechanical error in the disposition of a label. There are two sheets in the Gray Herbarium bearing in Nuttall's writing the name "*Polemonium *viscosum.*" One sheet bears a specimen of a high alpine form of *P. pulcherrimum* Hook. (*P. shastense* Eastw. according to Rydberg, 1897), which obviously does *not* agree with Nuttall's description of *P. viscosum.* The other sheet, which does agree with Nuttall's description, has on Nuttall's label, in Gray's writing, the notation, "This has the flowers of my *P. confertum* ?" Examination of the specimen indicates that the foliage is also that of Gray's description, especially when it is borne in mind that Nuttall commonly collected small specimens. While the exact source of the Hall & Harbour collection is unknown, Parry's collection from the Clear Creek area of Colorado, annotated by Gray as *P. confertum,* is not far from the "headwaters of the Platte," the type locality of Nuttall's species.

Gray proceeded to apply Nuttall's name to the spurious specimens which had 2-ranked leaflets and a rotate corolla, so that *P. viscosum* sensu Gray = *P. pulcherrimum* Hook. in part, and *p. confertum* Gray = *P. viscosum* Nutt. As a further complication, Gray described *P. confertum* var. *mellitum* (1853), and later described the same entity as *Gilia Brandegei* (1875). In the first instance he pointed out the very close relationship between the variety and the typical species, a view in which the present author concurs.

Although Wherry (1942) keys out *P. Grayanum* Rydb. as having coplanar leaflets, Rydberg described the "leaflets of at least the basal leaves more or less verticillate," as is also shown on the type collection. Rydberg's characterization of the species is based upon calyx pubescence, a character which is quite variable in *P. viscosum.* Like other members of the genus, *P. viscosum* is variable in the point of filament insertion on the corolla, which is unlike other members of the Polemoniaceæ. When large numbers of specimens are

plotted for this character, they show a normal curve, with no segregation into two or more populations as would be expected if this character were diagnostic in separating species. Thus separations into subspecies on this character, as Wherry treats *P. Lemmoni* Brand, tend to be purely subjective.

The occurrence of coplanar and verticillate leaflets on the same plants is evidence that this character is also variable, and certainly does not indicate specific status *per se*. *Polemonium speciosum* Rydberg is a form in which only coplanar leaflets are found, and, while common on Mt. Garfield, Colorado, may also occur at random throughout the range of *P. viscosum*.

KEY TO THE SUBSPECIES OF POLEMONIUM VISCOSUM NUTT.

Inflorescence subcapitate; coralla blue, violet or white.....17a subsp. *genuinum*
Inflorescene lax, subspicate; corolla yellow.....17b. subsp. *mellitum*

17a. **Polemonium viscosum** Nuttall subsp. **genuinum** Wherry

P. viscosum Nutt., Journ. Acad. Nat. Sci. Philad. ii, 1: 755. 1848.
P. confertum var. ∝ A. Gray, Proc. Amer. Acad. Nat. Sci. Philad. 15: 73. 1853.
P. confertum A. Gray, emend. Rydb. Bull. Torr. Bot. Club 24: 252. 1897.
P. speciosum Rydb., Bull. Torr. Bot. Club 28: 29. 1901.
P. Grayanum Rydb., Bull. Torr. Bot. Club 31: 635. 1904.
P. Lemmoni Brand, in Engler, Pflanzenr. 4^{250}: 44. 1907.
P. viscosum subsp. *genuinum* Wherry, Am. Midl. Nat. 27: 755. 1942.

This subspecies, based upon Nuttall's description and his specimen in the Gray Herbarium, includes those individuals with a condensed subcapitate inflorescence with blue, or occasionally white, flowers. Since Nuttall's type specimen in the herbarium of the Academy of Natural Sciences, Philadelphia, has become badly fragmented, the more complete specimen in the Gray Herbarium is designated as the lectotype. (Fig. 20.)

Specimens examined (total: 487).—BRITISH COLUMBIA. "Castle Towers Peak, Garibaldi Park," *Davidson* (1913), in herbarium of University of British Columbia; "Summit, south Kootenai Pass," *Dawson* 16221, CAN; "Rocky Mountains," *Lyall* (1861), GH, S.

ALBERTA. "Sheep Mt., Waterton Lakes," *Macoun* 11807, GH, NY, US; "Waterton Carthew Lakes," *Moss* 523, GH, US.

WASHINGTON. Okanogan Co. "Burch Mt.," *Thompson* 10839, GH, US; 10837, WYO.

OREGON. Wallowa Co. "Eagle Cap Peak, Wallowa Mts.," *Sharsmith* 3947, UC; "High alpine ridges, eastern Oregon," *Cusick* 707, F, GH.

MONTANA. Glacier Co. "Mt. Henry, Midvale," *Umbach* 193, F, NY, US, WYO; Deer Lodge Co. "Mt. Powell," *Blankenship* (1918), WYO; Meagher Co. "Long Baldy, Little Belt Mts.," *Flodman* 742, NY; Park Co. "Head of Porcupine Creek, Crazy Mts.," Blankenship (1902), WYO; Gallatin Co. "Bridger Mts.," *Rydberg & Bessey* 4836, GH, NY, US, WYO.

WYOMING. Yellowstone National Park. "Mt. Washburn," *Smith* (1902), F; Park Co. "Subalpine," *Tweedy* (1887), NY; Big Horn Co. "Little Bald Mt.," *Buffman* 621, WYO; Sheridan Co. "Bald Mt., Bighorn Mts.," *Williams* 3055, GH, NY, WYO; Teton Co. "Teton Pass," *E. B. & L. B. Payson* 2083, GH, NY, UC, WYO; Lincoln Co. "Union Pass," *Nelson* 991, GH, NY, WYO; Sublette Co. "Wind River Mts.," *E. B. & L. B. Payson* 2865, F, GH, NY, US; Carbon Co. "Bridger Mts.," *Williams* 1378, S, WYO; Albany Co. "One mile north, University Camp, Medicine Bow Mountains," *Rollins* 893, GH, NY.

COLORADO. Locality unknown: *Nuttall*, GH; "Rocky Mountain Alpine Flora," *Hall & Harbour* 450, F, US; Larimer Co. "The Bluffs, Spicer," *Gooding* 1505, GH, NY, US, WYO;



Fig. 20. *Polemonium viscosum* Nutt. subsp. *genuinum* Wherry. *a*, Habit, × ¾. *b*, Single flower, × 1½. *c*, Dissection of flower, × 1½.

Boulder Co. "Bald Mt.," *Ramaley, Dodds & Robbins* 2978, WYO; Gilpin Co. "James Peak," *Cox* 12, F; Grand Co. "Berthoud Pass," *Tweedy* 5674, NY, WYO; Clear Creek Co. "Gray's Peak," *Rydberg* (1895), NY; Summit Co. "Near Breckenridge," *MacKenzie* 163, NY, WYO; Lake Co. "Mt. Elbert, near Leadville," *Holm* (1899), F, S; Chaffee Co. "Monassas Creek," *Clokey* 3566, F, GH, NY, S, UC, US, WYO; El Paso Co. "Mt. Garfield," *Clements* (1900), NY, 523, GH, NY, WYO; Garfield Co. "Trapper's Peak, White River Plateau," *Hermann* 5613, GH; Ouray Co. "Mt. Abram," *Shear* 4081, NY; San Juan Co. "Mountains of Bear Creek," *Purpus* 477, F; Hinsdale Co. "Carson," *Baker* 290, GH, US, WYO; Mineral Co. "Sa Garita Range, near Halfmoon Pass," *Murdoch* 4689, F, NY, UC, US; Montezuma Co. "Little Kate Basin, La Plata Mts.," *Baker, Earle & Tracy* 521, GH, NY, UC, US, WYO; Conejos Co. "Side of mountain west of Platoro," *Harrington* 1637, WYO; Herfuano Co. "West Spanish Peak," *Rydberg & Vreeland* 5721, NY, WYO.

UTAH. Summit Co. "La Motte Peak," *E. B. & L. B. Payson* 5016, GH, NY, S, US, WYO; Duchesne Co. "Mt. Emmons, Krebs Basin," *Hermann* 5148, GH, NY, US, WYO; Uintah Co. "Bald Mt." *Clements* (1911), UC; Grand Co. "La Sal Mts.," *Rydberg & Garrett* 8718, GH, NY, US, WYO; Wayne Co. "Thousand Lake Mt.," *Dixon* 362, 363, 8, F; Garfield Co. "East side, Aquarius Plateau," *Dixon* 670, F; San Juan Co. "Saddle between Mt. Peale & Mt. Tukuhnikivatz," *Maguire & Redd* 2040, GH, WYO.

ARIZONA. "Aggassiz Peak, San Francisco Mts.," *Mearns* (1887), NY, *Lemmon & wife* (1884), US; "Mt. Humphrey," *Rusby* 727, F, NY, S, US.

NEW MEXICO. "Head of Red River," *Berg* (1897), NY; "Pecos Baldy," *Standley* 4298, NY, US.

NEVADA. Nye Co. "Pine Creek Canyon, Toquima Range," *Maguire and Holmgren* 25795, GH; White Pine Co. "Ely," *Hitchcock* 1419, US.

17b. **Polemonium viscosum** Nuttall subsp. **mellitum** (A. Gray), comb. nov.

P. confertum var. *mellitum* A. Gray, Proc. Acad. Nat. Sci. Philad. 15: 73. 1853.
Gilia Brandegei A. Gray, Proc. Amer. Acad. 11: 85. 1875.
Gilia Brandegei var. *Lambornii* A. Gray, Proc. Amer. Acad. 11: 85. 1875.
P. Brandegei Greene, Pittonia 1: 126. 1887.
P. mellitum A. Nels., Bull. Torrey Bot. Club 26: 354. 1899.

Differing from the nomenclaturally typical phase in its more open racemose inflorescence, and its yellow corolla. The range too, is more restricted, extending from Wyoming and the Black Hills of South Dakota to Utah, New Mexico, and Nevada. (Fig. 21.)

Type locality.—"Rocky Mountains, rocks in Middle mountains," *Hall & Harbour 451.* (!)
Distribution.—High mountains of Wyoming, Colorado, Nevada, Utah, and New Mexico; and in the Black Hills of South Dakota. (Map 9.)

The proposed subspecific status of this entity is admittedly debatable, since the characteristic form of the species occurs over most of the range of this subspecies. The writer first considered subsp. *mellitum* to be a distinct species, and intergrades between it and subsp. *genuinum* were thought to be possible hybrids, but the mapping of the two subspecies tends to corroborate Gray's original concept of close infraspecific relationship.

Specimens examined (total: 95).—SOUTH DAKOTA. "Black Hills," *Greene* 6, GH, 17, NY.

WYOMING. Sheridan Co. "Big Horn Mts.," *Mead* 2570, NY; Big Horn Co. "Head south Paintrock Creek," *L. O & R. Williams* 3148, GH, NY, WYO; Albany Co. "Ragged Top," *Nelson* 8227, GH, NY, S, US, WYO; "Horse Creek," *Nelson* 3881, GH, WYO, 208, NY, US.

COLORADO. Grand Co. "Sulphur Springs," *Osterhout*, GH, NY, WYO; Boulder Co. "Mountains between Sunshine & Ward," *Tweedy* 5116, NY, WYO; Gilpin Co. "Rocky Mountains,

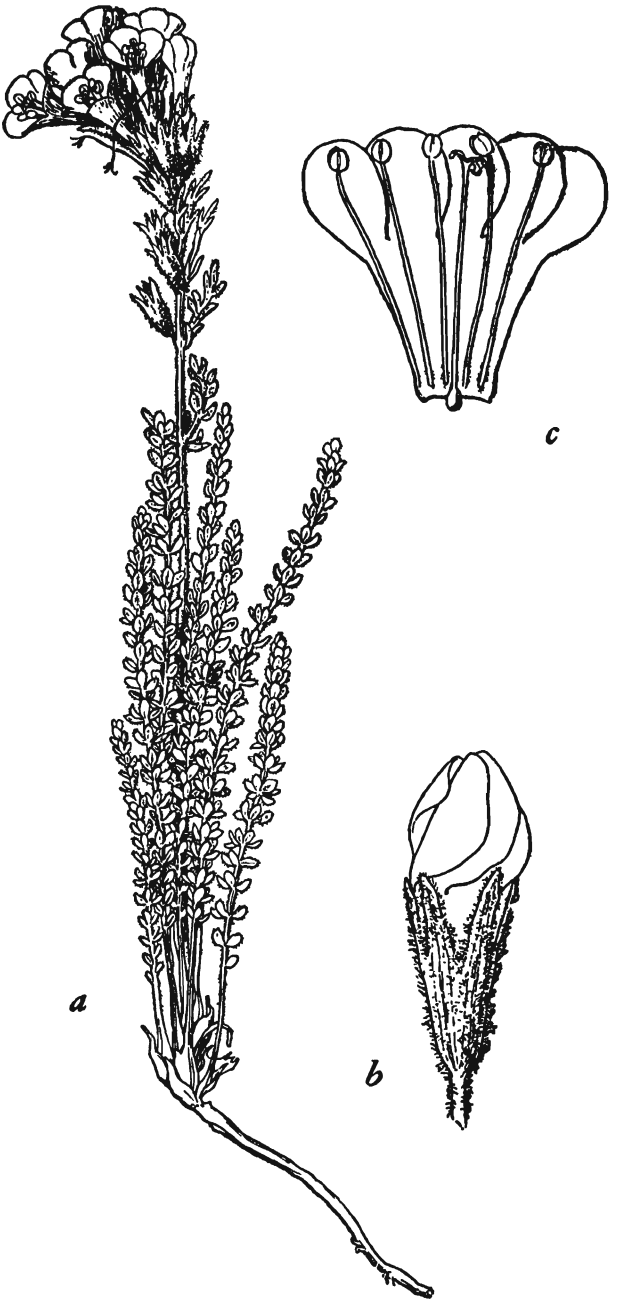


Fig. 21. *Polemonium viscosum* Nutt. subsp. *mellitum* (A. Gray), comb. nov. *a*, Habit, × ¾. *b*, Single flower bud, to show calyx, × 2¼. *c*, Dissection of flower, × 1½.

rocks in Middle mountains," *Hall & Harbour* 451, F, US, WYO; Montrose Co. "Canyon, Gunnison River, near Cimmaron," *Ripley & Barnaby* 5453, NY; Mineral Co. "Alpine Sierra Blanco," *Hooker, Gray & Lamborn* (1877), NY; West Spanish Peak," *Rydberg & Vreeland* 5122, NY, WYO.



Fig. 22. *Polemonium pauciflorum* S. Watson. *a*, Habit, × ⅔. *b*, Calyx, × 2. *c*, Dissection of flower, × 1.

NEW MEXICO. "Near Monument Lake," *A. & R. A. Nelson* 4614, WYO; "Sandia Mts., summit near Via Grande," *Ellis* 93, NY, US.

UTAH. "Marysvale," *Jones* 5942, GH, NY, US.

NEVADA. "East Humboldt Mts.," *Watson* 931, GH, NY, US.

18. **Polemonium pauciflorum** S. Watson

P. pauciflorum S. Wats., Proc. Amer. Acad. 23: 280. 1888.
P. Hinckleyi Standl., Amer. Midl. Nat. 18: 18. 1937.
P. stenocalyx Standl., Amer. Midl. Nat. 18: 18. 1937.
P. pauciflorum subsp. *Hinckleyi* Wherry, Amer. Midl. Nat. 27: 747. 1942.
P. pauciflorum subsp. *stenocalyx* Wherry, Amer. Midl. Nat. 27: 754. 1942.
P. pauciflorum subsp. *typicum* Wherry, Amer. Midl. Nat. 27: 751. 1942.

Perennial (sometimes annual in cultivation, possibly also in nature), 1.5–6.0 dm. high; stems solitary, erect and branching, or branching from the base in older plants, leafy; leaflets 11–25, broadly to narrowly lanceolate, acute at the apex, 9–26 mm. long, 2–5 mm. wide; flowers solitary or few on slender pedicels; calyx narrowly campanulate to funnelform, 9–17 mm. long, with narrowly attenuate to linear segments 1.5–2 times as long as the tube; corolla narrowly funnelform, almost tubular, 25–40 mm. long, about 10 mm. broad at the apex, yellow, tinged with red, the lobes ovate to rotund, about one-fourth as long as the tube; stamens included, commonly unequal in length and insertion, inserted about one-fourth of the way up the tube; style subequal to the corolla, commonly slightly shorter; seeds becoming mucilaginous when moistened. Flowering from June to August. (Fig. 22.)

Type locality.—"Shaded ledges in the Sierra Madre, Chihuahua," *Pringle 1558* (!) October, 1887.

Distribution.—In the Sierra Madre Occidentale and the Sierra Madre Oriental in Mexico, and north into the mountains of Texas and Arizona. (Map 4.)

This species is rendered distinct by its tubular corolla, but the value of attempting to delimit subspecies is doubtful, particularly in view of the fact that the northern area of Mexico is not botanically well known. In all probability there will be a much more intelligent distributional pattern when further exploratory work records new stations and variations of this species. The calyx characters previously used to segregate individuals from the norm of the species are at times variable in individual plants. The pubescence varies with age, and with the amount of available water, and the proportionate length of the calyx tube and segments changes with the age of the flowers.

Specimens examined (total: 43).—MEXICO: "Shaded ledges, Sierra Madre, Chihuahua," *Pringle* 1558, GH, 2011, NY, US; "Colonia Garcia, in Sierra Madre Oriental," *Townsend & Barber* 81, GH, NY, US, WYO; *Nelson* 6143, GH, US; "Below Las Canoas, Cerro Potosi, Galeana," *C. H. & T. M. Mueller* 2216, F, GH.

TEXAS: "Madera Cañon, Mt. Livermore," *Hinckley* 283, F (1936), GH.

ARIZONA: "Chiricahua Mts.," *Kusche* (1927), GH, NY, US; "Chaperone Canyon," *Blumer* 1926, F, GH, NY, US; "South of Rustler Park," *Clausen & Trapido* 5226, NY.

19. **Polemonium glabrum** J. F. Davidson

P. glabrum J. F. Davidson, Madroño 9: 187. 1948.

Perennial; slender, erect, 2–3 dm. high, from a rootstock or horizontal rhizome; leaves 4–8 cm. long with 13–17 leaflets; leaflets 3–11 mm. long, 2–4 mm. wide, elliptical, acute, glabrous or ciliate on a slightly winged rachis, the bases of the distal five leaflets commonly confluent; flowers solitary to few on slender pedicels; calyx glabrous, narrowly campanulate, 10 mm. long, 4 mm. broad, the segments narrow, acute, equaling the tube; corolla blue,



Fig. 23. *Polemonium glabrum* J. F. Davidson. *a*, Habit, × ½. *b*, Calyx, × 1½. *c*, Dissection of flower, × 1. *d*, Dissection of capsule, × 1½. *e*, Leaf apex, × 1½.

truly funnelform in limb as well as in tube, 25–30 mm. long, 15–20 mm. broad, the lobes two-thirds as long as the tube, spatulate and apiculate; stamens inserted 3 mm. from the base of the corolla tube, pubescent at, and slightly above, the point of insertion, 20 mm. long; style slightly exceeding the stamens, shorter than the corolla; capsule ovoid, many-seeded; seeds not becoming mucilaginous when wet. Flowering August and September. (Fig. 23.)

Type locality.—"Mt. Mohinora, Chihuahua, Mexico," ***E. W. Nelson 4865.***
Distribution.—Reported thus far only from the type locality. (Map 4.)

Polemonium glabrum may be readily distinguished from any other naturally occurring *Polemonium* by the shape and size of the corolla, and by its glabrous calyx. The only other record of a similar corolla is found in the report of Ostenfeld's (1929) crosses between *P. pauciflorum* and *P. mexicanum*. The affinities of the present species may well be with these, but neither have been reported from the vicinity of *P. glabrum*. The closest geographical associate is *P. grandiflorum*, and it is conceivable that a cross such as *P. grandiflorum* × *P. pauciflorum* could produce a hybrid resembling *P. glabrum*. The probability that P. *glabrum* is merely a hybrid may be discounted on the grounds that the pollen of *P. glabrum* is perfectly normal, whereas the pollen of known hybrids examined by the author shows irregularity in size. Also, there is apparently no reduction in the number of seeds set, as might be expected in a hybrid plant.

Specimens examined (total: 2).—MEXICO: "Mt. Mohinora, south west Chihuahua," *Nelson* 4865, GH, US.

SPECIES EXCLUDED

Polemonium acaule Schiede ex Mart. & Gal., Bull. Acad. Brux. 2: (2) 276. 1845 = *Phacelia platycarpa* var. *bursifolia* (Spreng.) Const.

Polemonium achilleaefolium R. & S. Syst. Veget. 4: 793. 1819 = *Phacelia platycarpa* (Cav.) Spreng.

Polemonium biflorum O.K. Rev. Gen. Plant. 3: 202. 1898 = *Navarretia biflora* O.K.

Polemonium bursifolium Willd. ex R. & S. Syst. Veget. 4: 793. 1819 = *Phacelia platycarpa* (Cav.) Spreng.

Polemonium campanuloides Thunb. Prod. Pl. Cap. 35. 1794 = *Retzia campanuloides* (Thunb.) Spreng.

Polemonium candidum Sessé & Moc. La Naturaliza 2: 42. 1893 = Gilia sp.

Polemonium capitatum Esch. Mem. Acad. Petersb. 10: 282. 1826 = *Gilia achillaeifolia* subsp. *Chamissonis*.

Polemonium ciliatim Willd. ex R. & S. Syst. Veget. 4: 792. 1819 = *Phacelia Purshii* Buckley.

Polemonium dubium L. Sp. Pl. 1: 163. 1753 = *Phacelia dubia* (L..) Trelease.

Polemonium morenonis Ktze. Rev. Gen. 3: 203. 1898 = *Microsteris* sp. (?)

Polemonium Nycetelea L. Sp. Pl. ed. 2: 231. 1762 = *Ellisia Nycetelea* L.

Polemonium pimpinelloides Willd. ex R. & S. Syst. Veget. 4: 793. 1819 = *Phacelia platycarpa* (Cav.) Spreng.

Polemonium roëlloides Thunb. Prod. Pl. Cap. 34. 1794 = *Retzia roëlloides* (Thunb.) Spreng.

Polemonium rubrum L. Sp. Pl. 1: 163. 1753 = *Navarretia rubra* O.K.

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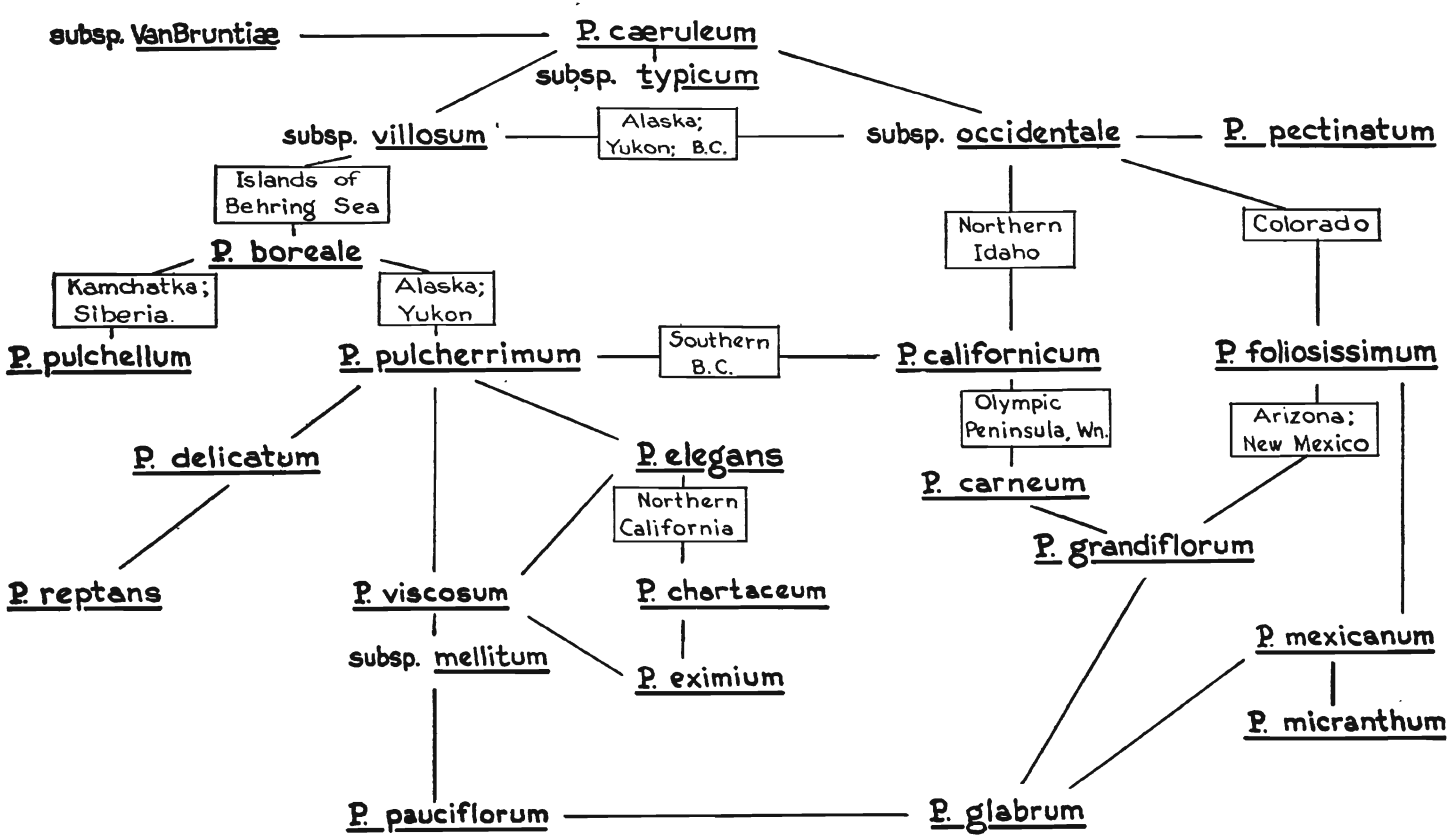
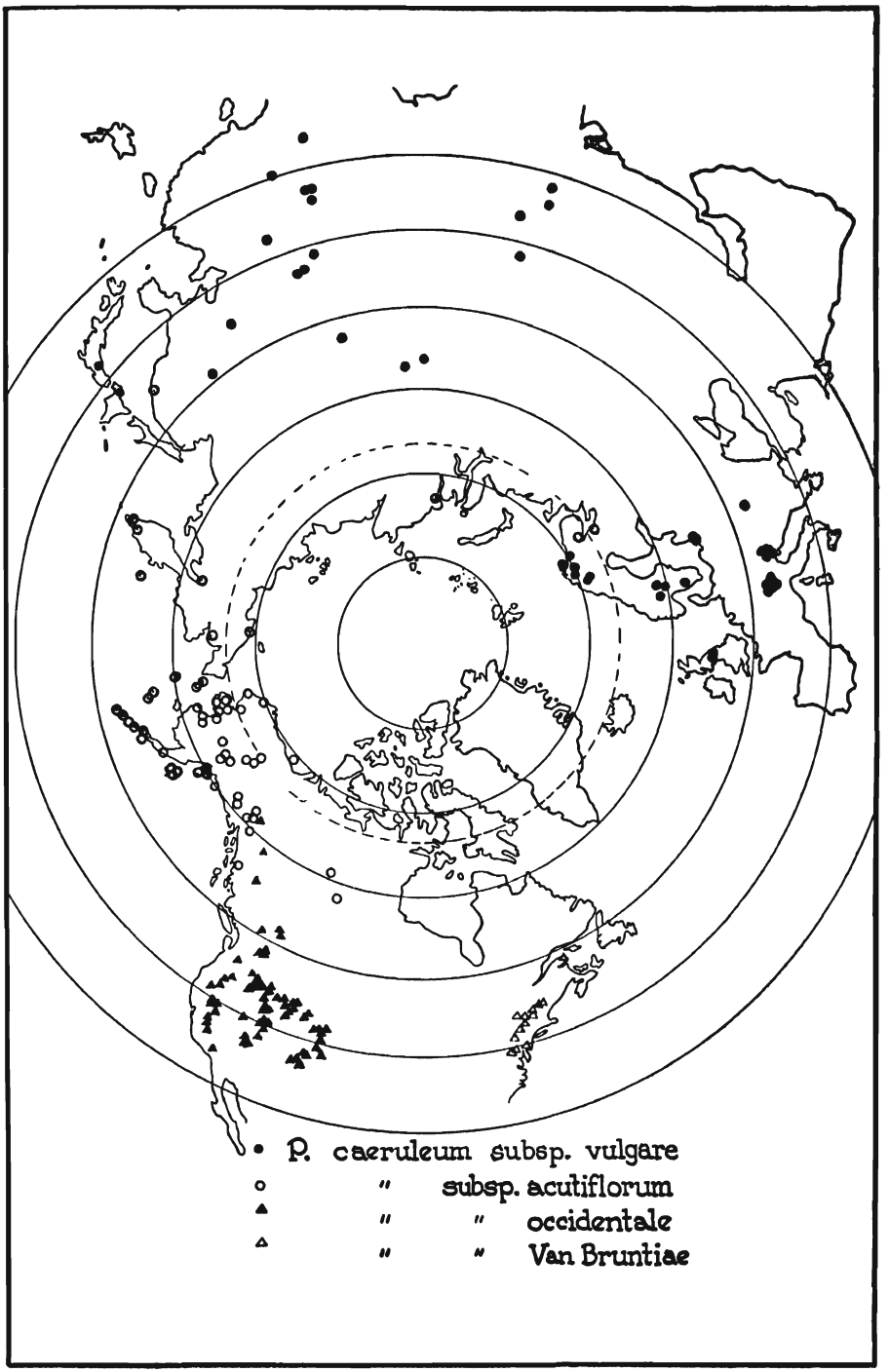
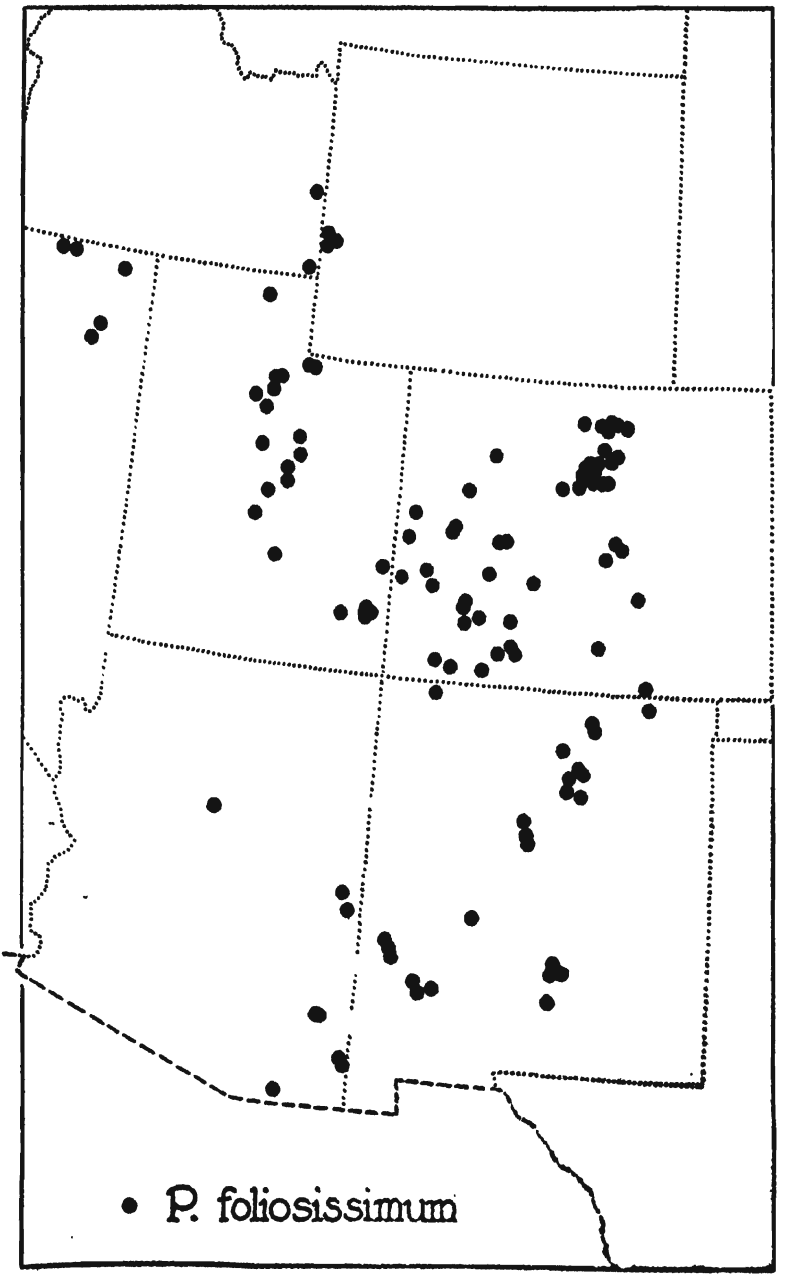


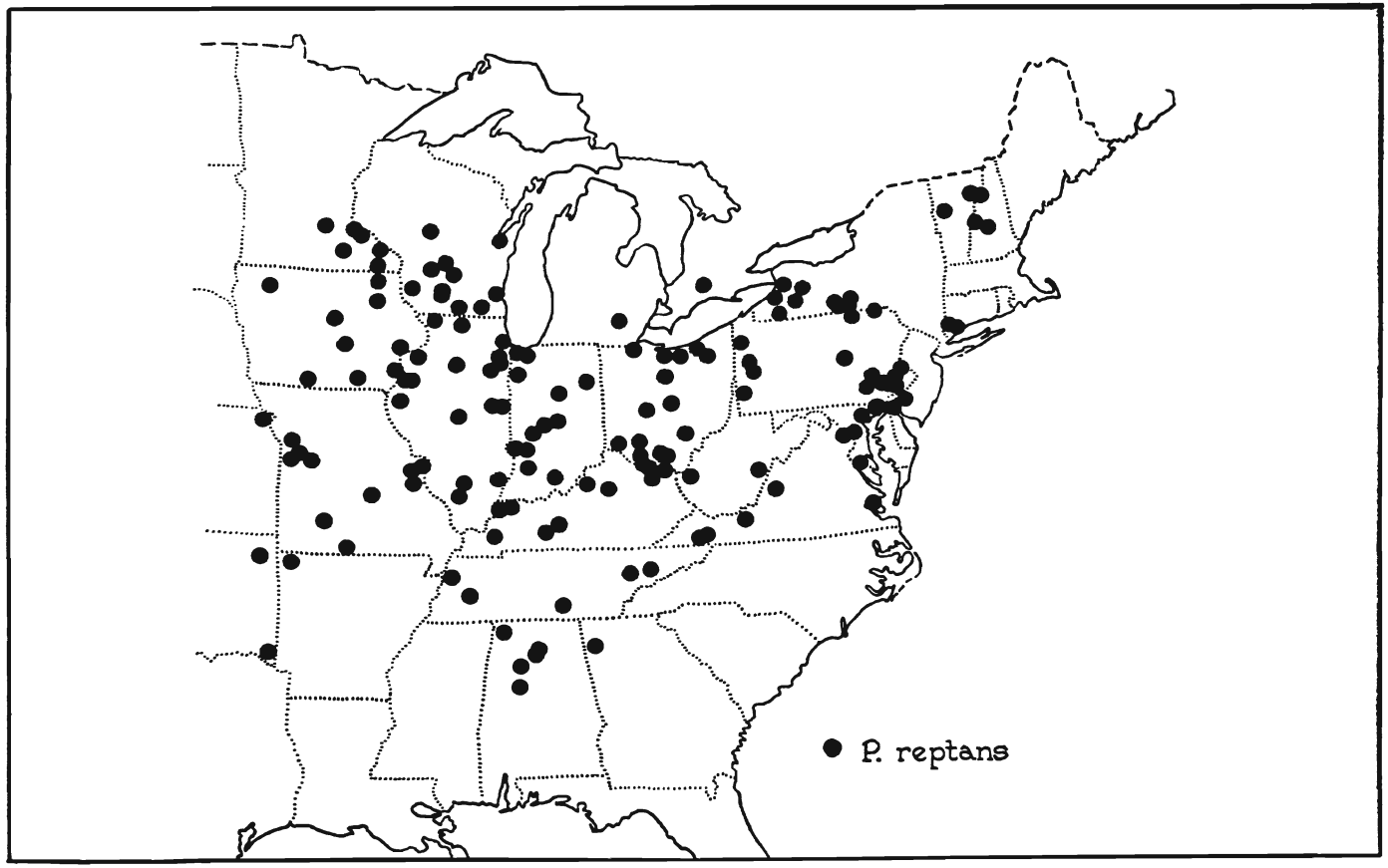
Fig. 24. A chart showing the postulated affinities between the recognized entities in *Polemonium*. The connecting lines indicated possible relationships, and the blocks show areas where intergradation occurs.



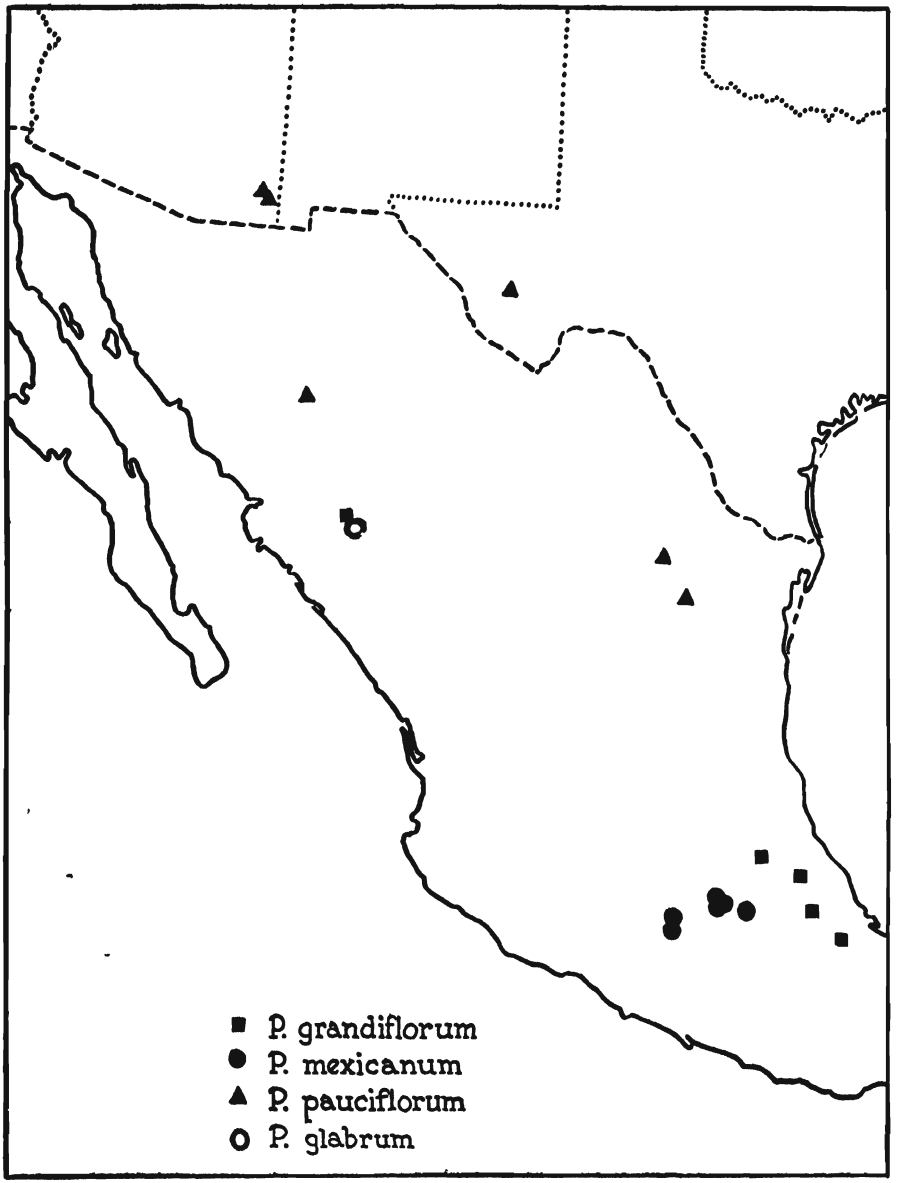
Map 1. The distribution of *P. cæruleum* L., north polar projection.



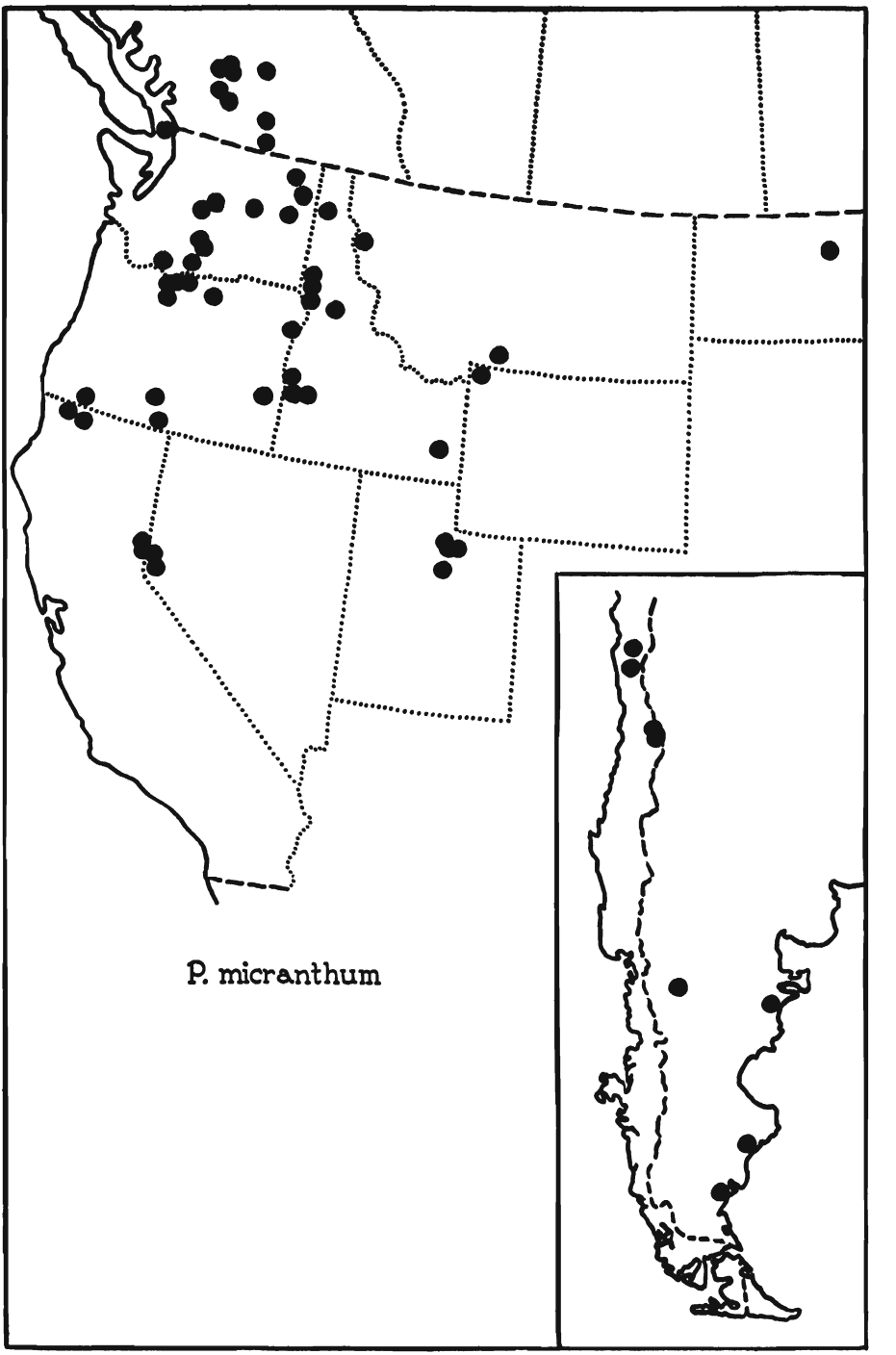
Map 2. The distribution of *P. foliosissimum* A. Gray.



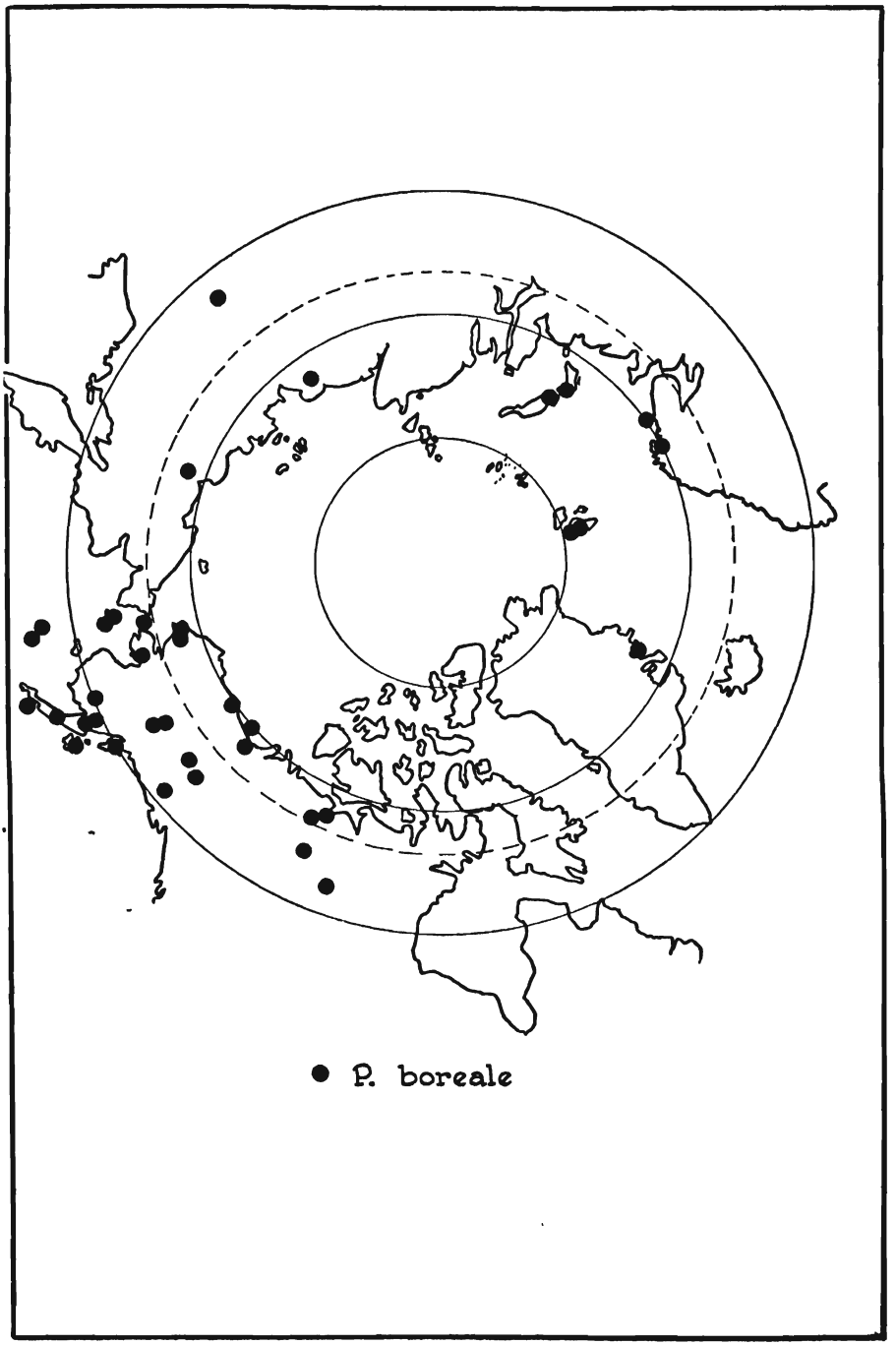
Map 3. The distribution of *P. reptans* L.



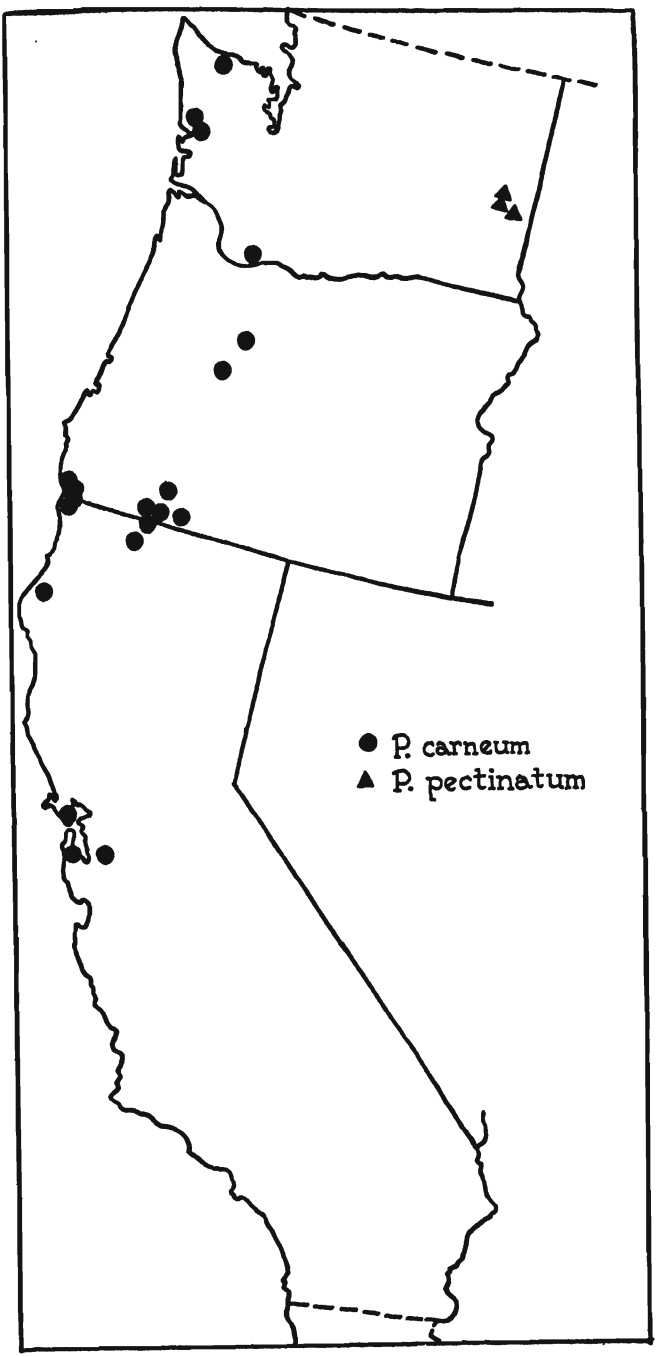
Map 4. The distribution of *P. glabrum* J. F. Davidson, *P. grandiflorum* Benth., *P. mexicanum* Cerv. ex Lag., and *P. pauciflorum* S. Wats.



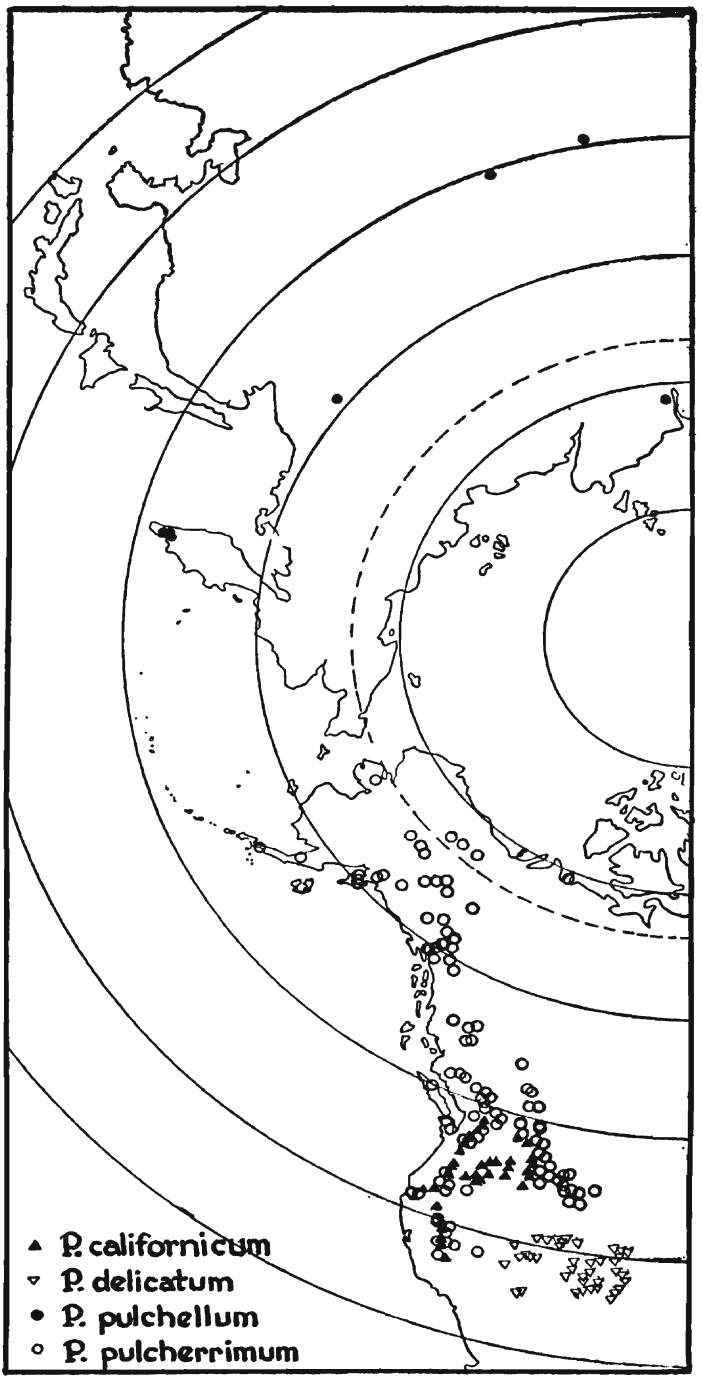
Map 5. The distribution of *P. micranthum* Benth. in western North America and in southern South America.



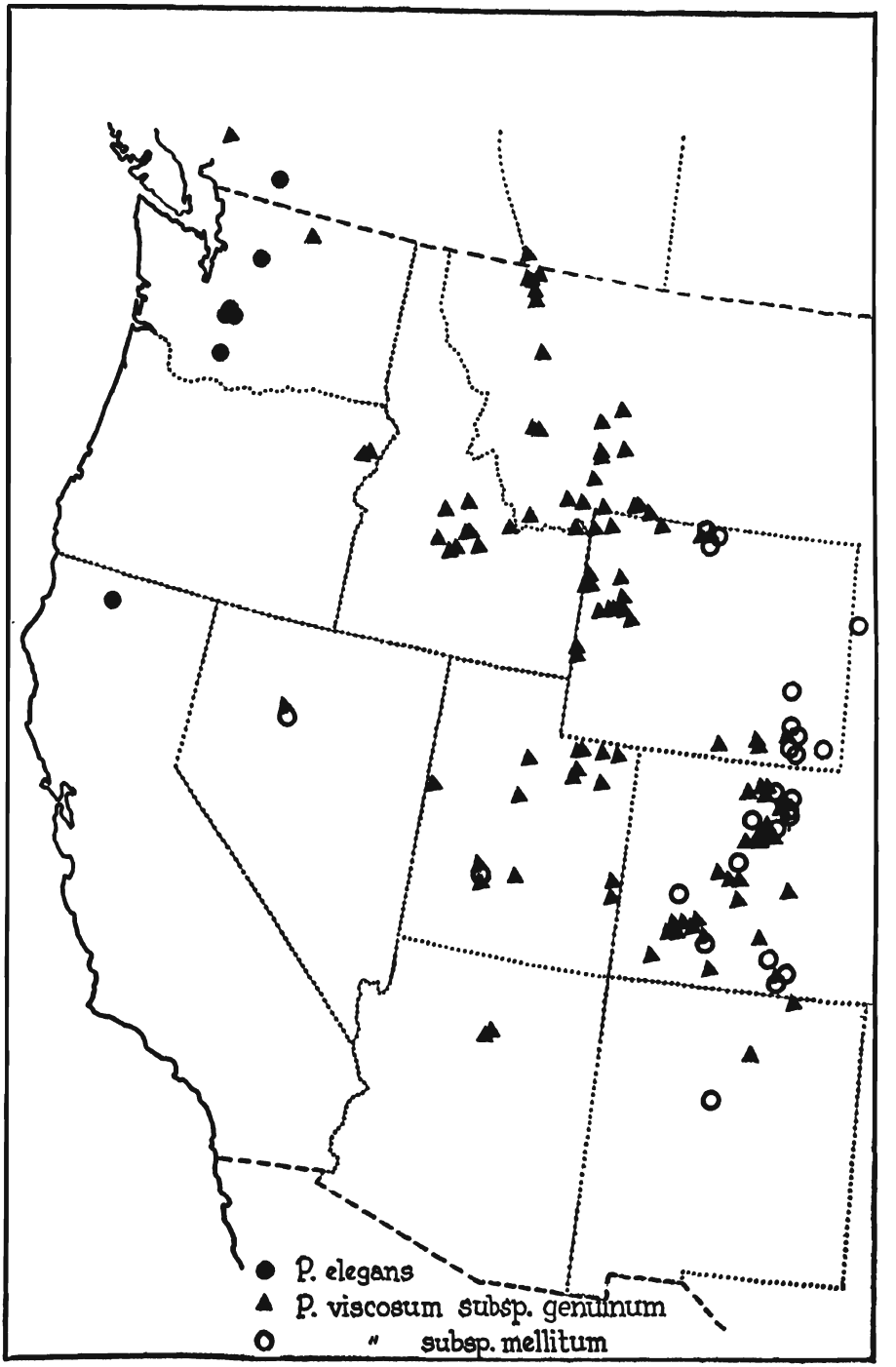
Map 6. The distribution of *P. boreale* Adams, north polar projection.



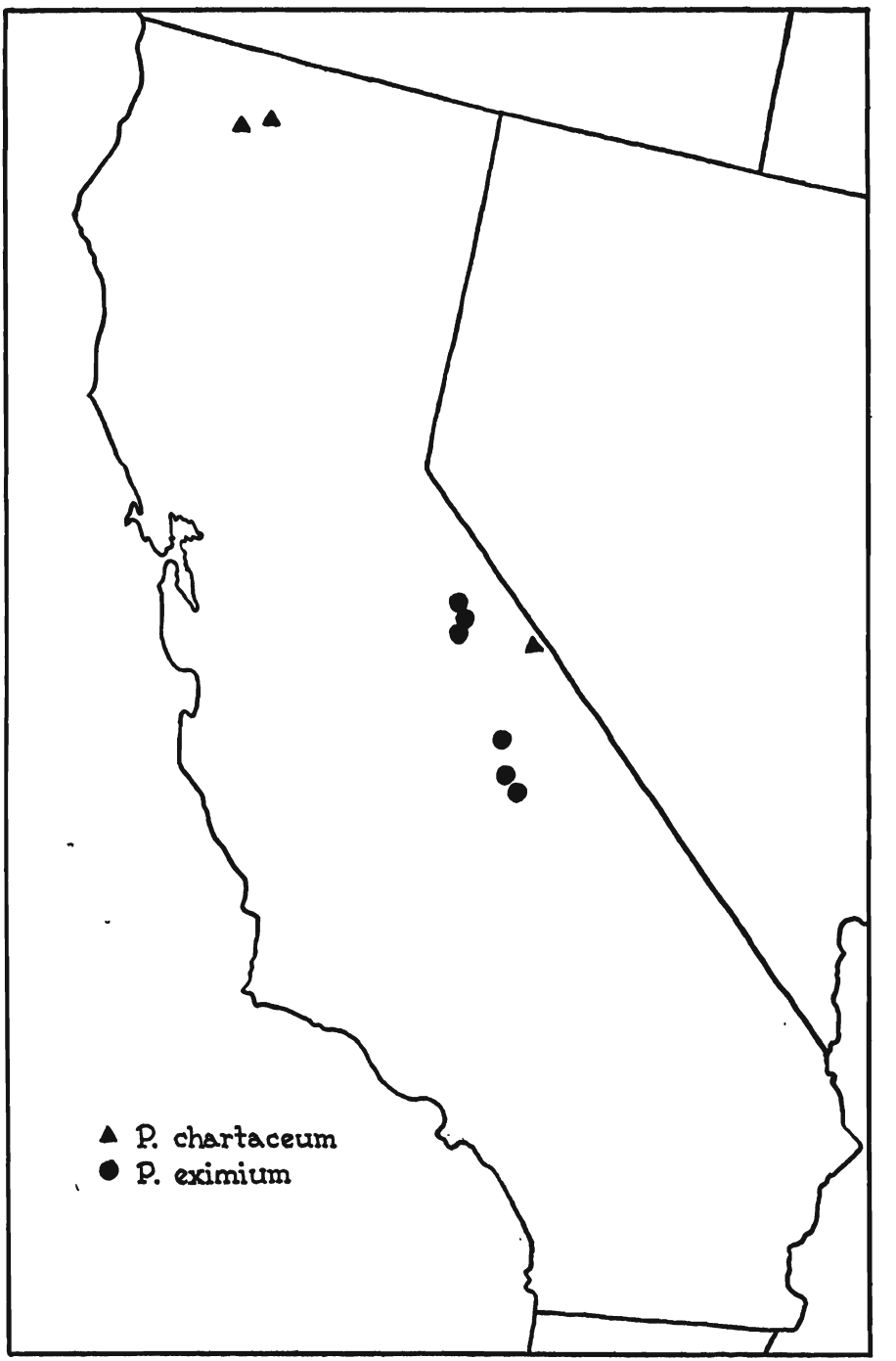
Map 7. The distribution of *P. carneum* A. Gray, and *P. pectinatum* Greene in the western United States of America.



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Map 10. The distribution of *P. chartaceum* Mason and *P. eximium* Greene in California.

CYTOTAXONOMIC STUDIES IN THE GENUS SORGHUM

BY

EDWARD D. GARBER

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CYTOTAXONOMIC STUDIES IN THE GENUS SORGHUM

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INTRODUCTION

Objectives and the Scope of the Problem

The sorghums constitute an important economic crop in the agriculture of many countries. While hybridization and selection have played a major role in the production of new varieties of both grain and forage types, the sorghum breeder has been restricted almost completely to one species, *S. vulgare*. Breeders of such other important commercial species as cotton, tobacco, and wheat, to mention a few, have come to pay greater attention to the potential breeding value of the related wild species. In attempting to produce perennial strains of the forage type, the sorghum breeder has resorted to interspecific hybridization between *S. vulgare* and *S. halepense*. Since other species included in the genus *Sorghum* had not been considered to any great extent in breeding programs involving interspecific hybridization, a cytological investigation was undertaken to determine whether these species provide a future reservoir of germ plasm.

Although the primary objective of the cytological study was to obtain information for a practical purpose, a possible application of the data to the problem of taxonomy of *Sorghum* and its related genera was considered. Since the breeder must accept the results of the taxonomist in considering possible sources of germ plasm, it is important to define the limits of the potential breeding population. Love (1947) has clearly presented the relationship between systematist and plant breeder: "Species and genera are delimitations of populations and groups of populations set up by the taxonomist. Rarely have cytological and genetic studies played an important part in his deliberations. This is not meant to cast any reflection on the systematist, for cytogenetic studies are time-consuming and it is hardly to be expected that the systematic botanist would delay the classification of plants until the pertinent cytogenetic data were forthcoming. Nevertheless, anyone interested in the improvement of forage crops, and particularly the uncultivated grasses, must realize that the delimitations of populations set by the systematist do not always provide an accurate index of the potential hybridization possibilities of the material."

Scope of Study

A cytological survey of chromosome numbers, morphology, and association at diakinesis and metaphase I was first undertaken. For some species, a study of the somatic chromosome morphology was included. A taxonomic study was then conducted, using the cytological data as a foundation. Finally, the cytotaxonomic information was applied to the problems of relationship, phylogeny, and probable centers of origin.

Materials

Seeds of all species studied, except those in the subgenus Eu-Sorghum, were supplied by a number of botanists who also provided much information concerning the distribution of the species found in their region. The author wishes to express his sincere appreciation to the following coöperators: F. W. Andrews, Research Division, Department of Agriculture and Forests, Wad Medani, Sudan; C. A. Gardner, Department of Agriculture, Perth, Western Australia; C. O. Grassl, U. S. Department of Agriculture, Beltsville, Maryland; W. Hartley, Council for Scientific and Industrial Research, Canberra, Australia; C. E. Hubbard, Royal Botanic Garden, Kew, England; S. L. Macindoe, Department of Agriculture, New South Wales, Australia; E. J. Salisbury, Royal Botanic Garden, England; S. Solomon, University of Poona, India; A. S. Thomas, Agricultural Research Station, Kampala, Uganda; J. W. Vickery, National Herbarium, New South Wales, Australia; W. L. Waterhouse, University of Sydney, Australia. W. Hartley was especially helpful in providing seeds of many species from the Northern Territory, Australia; C. E. Hubbard greatly facilitated the identification of dubious classifications by making available through loan from Kew the large collection of herbarium specimens of species of Para-Sorghum and Stiposorghum.

Acknowledgments

I am particularly indebted to Dr. G. Ledyard Stebbins, Jr., Division of Genetics, University of California, Berkeley, under whose supervision this work was done, for his constant interest and advice. I am also much indebted to Dr. Lincoln Constance, Botany Department, University of California, Berkeley, for many suggestions in the preparation of taxonomic descriptions. My wife, Rosalie K. Garber, has made a real contribution by her constant encouragement and efforts in preparing the manuscript for publication.

Procedures

Plants were grown from seed both in the greenhouse and in the field at the University of California, Berkeley. Hybridizations were made in accordance with the technique described by Stebbins and Tobgy (1944) whenever self-fertile species were involved.

For cytological study, immature panicles were fixed in a fresh solution of absolute alcohol and glacial acetic acid (3:1) for 24 hours and then transferred to 70 per cent alcohol for storage. Temporary smears of pollen mother cells were stained with acetocarmine. An alcohol vapor chamber technique was used to make temporary smears permanent. Pollen grains were stained with cotton blue in lactophenol.

Root tips were fixed in Randolph's (1935) "Craf" solution, dehydrated through an n-butyl alcohol series, embedded in paraffin, sectioned at 10 micra, and stained in accordance with Stockwell's (1934) procedure.

Not fewer than 50 florets to a plant were examined in determining the percentage of seed set; not fewer than 200 pollen grains were counted to

determine the percentage of pollen grain abortion for each plant examined. Pollen stainability was considered as a criterion of fertility. Care was exercised to insure random sampling whenever florets were examined for seed.

REVIEW OF PREVIOUS TAXONOMIC AND CYTOLOGICAL STUDIES IN THE SORGHASTRAE

Taxonomy

Since the taxonomic history of the Sorghastrae is detailed on pages 319–332 below, only a brief summary of the essential points will be offered here.

Hackel (1889) assembled the species of *Sorghum* in the subgenus Sorghum of the genus *Andropogon*. Stapf (1917) accorded generic status to *Sorghum* and considered Eu-Sorghum and Sorghastrum as component sections. The species of Eu-Sorghum with bearded nodes and simple panicle branches were specifically mentioned and treated as a unit in Stapf's key to the species of *Sorghum*. Nash (1901), however, had previously considered Sorghastrum generically distinct, a view shared by most American grass taxonomists. Snowden (1935) considered the species of *Sorghum* with bearded nodes, already noted by Stapf (1917), as members of the section Para-Sorghum and the other species as members of the section Eu-Sorghum. Evidence to be presented indicates that the genus *Sorghum* does not merely consist of two sections, but comprises six subgenera! Moreover, the section Para-Sorghum is not homogeneous but includes two distinct groups: Para-Sorghum and Stiposorghum.

While *Cleistachne* was recognized as a genus by Hackel (1889), its affinity to the Hackelian subgenus Sorghum was also noted.

To give concrete expression to the circle of affinity embracing the genera *Sorghum* and *Cleistachne,* Stapf (1917) coined the term "Sorghastrae." In Stapf's taxonomic treatment this term represents a "group" and may be best considered as a supergenus. In view of its convenience for describing this circle of affinity, the term Sorghastrae will be used throughout to include the following genera and subgenera:

1. *Sorghum:* Eu-Sorghum; Chaetosorghum; Heterosorghum; Sorghastrum; Para-Sorghum; Stiposorghum.
2. *Cleistachne.*

Cytology

The cytological study of the Sorghastrae has, in the main, been restricted to the subgenus Eu-Sorghum of the genus *Sorghum,* which includes the agronomically important species *S. vulgare.* Since the species comprising the other groups of the Sorghastrae have comparatively little or no economic value, they have not been the subject of much cytological study. A summary of the reported somatic chromosome numbers of species of the Sorghastrae appears in table 1.

Eu-Sorghum.—Longley (1932), Huskins and Smith (1932, 1934), and Karper and Chisholm (1936) list the chromosome numbers of many species of Eu-Sorghum. Excepting *S. halepense* with a somatic chromosome number

of 40, all the species have a somatic chromosome number of 20. There is reason to believe that there is actually only one species with ten pairs of chromosomes (*S. vulgare*), the other reputed species being only well-defined varieties (Snowden, 1935). Huskins and Smith (1934) have observed quadrivalents in the diploid species, and multivalents, up to hexivalents, in *S. halepense,* but Garber (1944) found only bivalents in the diploid species, and multivalents, up to quadrivalents, in *S. halepense,* the maximum number of quadrivalents in a single pollen mother cell being 5.

TABLE 1

A SUMMARY OF REPORTED SOMATIC CHROMOSOME NUMBERS IN SPECIES OF THE SORGHASTRAE

Species	2n	Authority
Sorghum		
Eu-Sorghum		
S. vulgare	20	Kuwada, 1925
S. halepense	40	Nakajima, 1930
Sorghastrum		
S. nutans	40	Church, 1929
Para-Sorghum		
S. purpureo-sericeum	10	Huskins (Hubbard, 1933)
subsp. dimidiatum	10	Huskins (Hubbard, 1933)
S. versicolor	10	Karper, 1930
S. nitidum	10	Ayyanger and Ponnaiya, 1941
Stiposorghum		
S. intrans	10	Garber, 1948

Sorghastrum.—The somatic chromosome number of only one species of Sorghastrum has been reported: Church (1929) observed 40 chromosomes in root tips of *S. nutans.*

Para-Sorghum.—Snowden (1935) considered all species of *Sorghum* with bearded nodes (pl. 40) and simple panicle branches as members of his section Para-Sorghum of the genus *Sorghum,* presumably on the basis of African species of the subgenus Para-Sorghum (see pp. 319–339 below). The cytological differences between species of the sections Eu-Sorghum and Para-Sorghum seemed to emphasize the distinctness of each section (Stadler in a communication to Hubbard, 1933; Garber, 1944). Karper and Chisholm (1936), in noting the large chromosomes of a species of Para-Sorghum in contrast with those of two species of Eu-Sorghum, reported the following measurements as average chromosome length at somatic metaphase: *S. versicolor,* 4.86 micra; *S. vulgare,* 2.24 micra; and *S. halepense,* 1.98 micra. Actually, all these observations concerned only two of the six subgenera of the genus *Sorghum,* Para-Sorghum and Eu-Sorghum.

The chromosome numbers reported for the subgenus Para-Sorghum have been confirmed by other investigators. Only the observations on *S. nitidum* by Ayyanger and Ponnaiya (1941) are open to doubt. According to their report, a collection from the Western Ghats of India with a *tendency* toward

perenniality had a somatic chromosome number of 10. No other collector has reported this species from western India; the only species of Para-Sorghum found in this area is *S. purpureo-sericeum*. A vigorous plant grown at Berkeley, California, for the last six years indicates that *S. nitidum* is strongly perennial. Moreover, three collections (N603, N7107, N7108) of this species were found to have a somatic chromosome number of 20 with 10 bivalents at diakinesis and metaphase I. Unfortunately, efforts to get a collection of *S. nitidum* from western India have been unsuccessful. A similar situation had existed for *S. purpureo-sericeum* when Longley (1932) reported that this species had a somatic chromosome number of 40. It is possible that *S. laxiflorum* may have been involved. There is no other report of 40 chromosomes for *S. purpureo-sericeum*.

Stiposorghum.—A somatic chromosome number of 10 has been reported for one species, *S. intrans*, of the subgenus Stiposorghum (Garber, 1948).

CYTOLOGY

The Sorghastrae belong to the tribe Andropogoneae, 21 of whose 26 genera listed by Darlington and Janaki Ammal (1945) have somatic chromosome numbers that are multiples of 5. Prior to the discovery of the chromosome number of species of the subgenus Para-Sorghum, 10 had been regarded as the basic chromosome number rather than 5. The lowest haploid chromosome number yet found in the Gramineae is 5. This number has been reported for three other unrelated genera: *Briza, Anthoxanthum,* and *Coix*. The subgenera Para-Sorghum and Stiposorghum contain more species with this haploid chromosome number than any of the three genera mentioned.

Chromosome Number and Association in the Sorghastrae

THE GENUS SORGHUM

Excepting *Cleistachne,* all the known species of the Sorghastrae have chromosome numbers that are multiples of 5. Table 2 summarizes the observed somatic chromosome numbers.

Eu-Sorghum.—While *S. vulgare* appears to be an allotetraploid (pl. 41, *a*) as a multiple of 5, *S. halepense* can only be termed an octoploid, inasmuch as no information is available concerning its origin. The chromosome association at diakinesis and metaphase I of meiosis supplies no conclusive evidence on this point. As previously mentioned, 5 quadrivalents represent the maximum number of multivalents yet observed (Garber, 1944). Whether this number has any significance in view of the basic chromosome number of the Sorghastrae is not yet known. Although interspecific hybridizations between *S. halepense* and *S. vulgare* have been reported, no detailed cytological analyses have been presented. Consequently, the genomic constitution of *S. halepense* is not known. Huskins and Smith (1932) suggest that *S. halepense* may have originated from an interspecific hybridization between a diploid species of Eu-Sorghum and some other member of the Andropogoneae.

TABLE 2

A Summary of Somatic Chromosome Numbers in Collections of Species of the Sorghastrae

Species	Culture	2n	Source
Sorghum			
Chaetosorghum			
S. macrospermum	M791	40	Port Darwin, Northern Territory, Australia
Heterosorghum			
S. laxiflorum	La796	40	Northern Queensland
Sorghastrum			
S. elliottii		20	U. S. A.
S. secundum		20	U. S. A.
S. rigidifolium		60	Ugunda, Africa
Para-Sorghum			
S. versicolor	V601	10	Africa (locality unknown)
	V701	10	Tanganyika
	V707	10	Tanganyika
	V740	10	India (origin unknown)
	V797	10	Tanganyika
S. purpureo-sericeum	P604	10	Sudan
	P702	10	Tanganyika
	P744	10	Southern Sudan
	P745	10	Southern Sudan
	P739	10	India (origin unknown)
Subsp. deccanense	P7100	10	Poona, India
Subsp. dimidiatum	D602	10	Sudan
	D743	10	Sudan
S. leiocladum	L749	20	Canberra, Australia
	L789	20	Glen Innes, New South Wales
S. nitidum	N603	20	Queensland
	N7107	20	Hodel, northern Queensland
	N7108	20	Osborne, northern Queensland
Stiposorghum			
S. intrans	I713	10	Port Darwin, Northern Territory
	I793	10	Katherine, Northern Territory
S. brevicallosum	B792	10	Katherine
S. stipoideum	S790	10	Port Darwin
	S794	10	Katherine
S. plumosum	P1795	20	Katherine
	P17103	20	Home Hill, northern Queensland
Cleistachne			
C. sorghoides	Cs802	36	Uganda

Chaetosorghum.—Sorghum macrospermum, with a somatic chromosome number of 40, has 20 bivalents at diakinesis and metaphase I of meiosis (pl. 41, *b*). One plant displayed a variable number of univalents, always in equal numbers, perhaps owing to a partial asynapsis or desynapsis. This species may be considered an alloöctoploid. Unless the diploid and tetraploid

species have perished, additional species of this subgenus may be expected in northern Australia.

Heterosorghum.—*Sorghum laxiflorum* has a somatic chromosome number of 40 with 20 bivalents at diakinesis and metaphase I of meiosis (pl. 41, *c*). This species may be considered an alloöctoploid. As in the previous subgenus, additional species of Heterosorghum may yet be found in the range of distribution of *S. laxiflorum.*

Sorghastrum.—Excepting *S. rigidifolium,* the chromosome numbers of the species listed in table 2 have been determined from root tips. However, *S. elliottii* and *S. secundum* may be expected to have 10 bivalents at diakinesis and metaphase I. *Sorghum nutans* probably has 20 bivalents at the same stages of meiosis. *Sorghum rigidifolium,* with a somatic chromosome number of 60, has 30 bivalents at diakinesis and metaphase I (pl. 41, *d*). The subgenus Sorghastrum, to which these species belong, has the most extensive polyploid series yet found in *Sorghum* (n = 10, 20, 30).

Para-Sorghum and Stiposorghum.—Within the subgenus Para-Sorghum are found diploid species, an allotetraploid species, and a species that behaves cytologically as an autotetraploid. The subgenus Stiposorghum contains diploid species and a tetraploid species. Five is the basic chromosome number of these two subgenera.

THE GENUS CLEISTACHNE

Only one species, *C. sorghoides,* was examined cytologically and was found to have a somatic chromosome number of 36 with 18 bivalents at diakinesis and metaphase I (pl. 42, *c*). It seems reasonable to assume that 9 is the basic chromosome number in this genus and that *C. sorghoides* is an allotetraploid species. Although no detailed study was made, the bivalents at diakinesis obviously differed in size.

Chromosome Morphology in the Sorghastrae

Since differences in chromosome morphology at pachytene, diakinesis, and metaphase I of meiosis between species of Eu-Sorghum and Para-Sorghum appeared to be more striking than at somatic metaphase (Garber, 1944), chromosome morphology was studied at these meiotic stages for all the available species of the Sorghastrae. Somatic chromosome morphology was studied in only the subgenera Para-Sorghum and Stiposorghum.

Since the species of Para-Sorghum and Stiposorghum received the most attention, the results of this work will be discussed in detail in a later section. Some of the data, however, will be presented here in reference to the comparative cytology of the Sorghastrae.

Differences in the volume and size of the chromosomes at diakinesis and metaphase I were noted although measurements were not taken. On a relative basis, the meiotic chromosomes of the subgenera Eu-Sorghum, Chaetosorghum, Heterosorghum, and Sorghastrum, and the genus *Cleistachne* were the smallest, of the subgenus Stiposorghum intermediate, and of the subgenus Para-Sorghum the largest in dimensions and volume. Other differences in

TABLE 3

A Summary of the Cytological Differences at Meiosis in the Genera and Subgenera of the Sorghastrae

Genera and subgenera	Haploid chromosome numbers	Relative chromosome size at diakinesis and metaphase I	Number of nucleolus chromosomes in the basic complement	Position of the nucleolus organising region at pachytene	Chromosome stainability at pachytene	Chromosome stainability at diakinesis
Sorghum						
Eu-Sorghum	10, 20	Small	1	Intercalary	Differential	Differential
Chaetosorghum	20	Small	(1)	Intercalary	Uniform	Differential
Heterosorghum	20	Small	(1)	Intercalary	Uniform	Uniform
Sorghastrum	10, 20, 30	Small	(1)	Intercalary	Uniform	Uniform
Para-Sorghum	5, 10	Large	1	Terminal, subterminal	Uniform	Uniform
Stiposorghum	5, 10	Intermediate	2, 4	Intercalary, subterminal	Uniform	Differential
Cleistachne	18	Small	(1)	Intercalary	Uniform	Uniform

certain cytological features of the meiotic chromosomes will be considered in the following order (and summarized in table 3):

1. Chromosome stainability at pachytene.
2. Chromosome stainability at diakinesis.
3. Position and morphology of the nucleolus organizing region at pachytene.
4. Number of nucleolus chromosomes at pachytene.

CHROMOSOME STAINABILITY AT PACHYTENE

Except in Eu-Sorghum (pl. 43, *c*), the pachytene chromosomes in the Sorghastrae stained essentially uniformly with acetocarmine, i.e., there was no marked accumulation of stain in any one region of the chromosome. Only *S. rigidifolium* of the subgenus Sorghastrum was available for a study of the meiotic chromosomes. In the subgenus Eu-Sorghum, the centromeres were distinct and the regions immediately adjacent to the centromeres were very heavily stained. The quality of staining decreased noticeably beyond these heavily staining regions until the remainder of the chromosome was almost unstained, especially at the very end of each arm. These observations had been reported for *S. vulgare* by Longley (1937).

CHROMOSOME STAINABILITY AT DIAKINESIS

In species of Eu-Sorghum (pl. 41, *a*) and *S. macrospermum* of Chaetosorghum (pl. 41, *b*), the chromosomes at diakinesis are so highly condensed that internal details are obscured and the nonstaining portions extend beyond the small, heavily stained region. While the internal details of the chromosomes of Heterosorghum, Sorghastrum, and *Cleistachne* are obscured at diakinesis, they do not have the prominent nonstaining ends. Because of their relatively large size and uniform staining with acetocarmine, the chromosomes of Para-Sorghum at diakinesis show internal details clearly (pl. 42, *a*). In Stiposorghum the chromosomes show differential staining at diakinesis but, as does not appear in Eu-Sorghum, there is an accumulation of stain at the ends of the chromosomes (pl. 42, *b*). The differences in stainability may be more fully appreciated by referring to the photomicrographs mentioned.

POSITION AND MORPHOLOGY OF THE NUCLEOLUS-ORGANIZING REGION AT PACHYTENE

The position of the nucleolus-organizing region differs in the different subgenera of *Sorghum:* in Para-Sorghum, it is either terminal or subterminal (pls. 42, *d* and 43, *a*); in Stiposorghum, subterminal or intercalary (pl. 43, *b*); in Eu-Sorghum (pl. 43, *c*), Chaetosorghum, Heterosorghum, and Sorghastrum, intercalary.

Only in Para-Sorghum was the nucleolus-organizing region visibly distinguishable from the rest of the chromosome. In three species of Para-Sorghum, the terminal nucleolus-organizing region was a heteropycnotic ball, clearly distinguishable from the rest of the chromosome (pl. 42, *d*). In the one species, *S. purpureo-sericeum,* with a subterminal nucleolus-organizing region, the region was an irregular, heteropycnotic region, clearly visible.

NUMBER OF NUCLEOLUS CHROMOSOMES AT PACHYTENE

The number of nucleolus chromosomes was obtained from basic diploid species. Since such species were available only in the subgenera Para-Sorghum and Stiposorghum, the data are necessarily incomplete. However, there is reason to believe that only one nucleolus chromosome to a basic complement may be expected in *Sorghum* and *Cleistachne*. *Sorghum vulgare* with 10 pairs of chromosomes has only one nucleolus chromosome in the complement;

TABLE 4

CYTOLOGICAL CHARACTERS DISTINGUISHING THE TWO SUBGENERA, PARA-SORGHUM AND STIPOSORGHUM, AT MEIOSIS AND AT MITOSIS

Character	Para-Sorghum	Stiposorghum
Meiosis		
Number of nucleolus chromosomes	One per complement	Two or 4 per complement
Pachytene chromosomes	Indistinguishable	Distinguishable
Position of the nucleolus organizing region	Terminal or subterminal	Subterminal or intercalary
Stainability of the nucleolus organizing region	Heteropycnotic	Not heteropycnotic
Appearance of chromosomes at diakinesis	Bulky	Thready
Chromosome stainability at diakinesis	Uniform	Differential
Mitosis		
Chromosome morphology at somatic metaphase	V-shape	J- or almost V-shape

Cleistachne sorghoides with 18 bivalents has one bivalent associated with the nucleolus. Stiposorghum, however, is unique in having two nucleolus chromosomes in the basic complement of 5 chromosomes (pl. 43, *b*).

THE SUBGENERA PARA-SORGHUM AND STIPOSORGHUM

MEIOSIS

Differences between the subgenera Para-Sorghum and Stiposorghum were first noted cytologically. These concerned (1) the appearance of the chromosomes at pachytene, (2) the number of nucleolus chromosomes at pachytene, (3) the stainability of the chromosomes at diakinesis, (4) the size of the chromosomes at metaphase I, and (5) the chiasma frequency at diakinesis and metaphase I (tables 4 and 5). By means of these differences, species of one subgenus were completely distinguishable from the other since no species was found with an intermediate condition for even one character. Moreover, it was possible to set up a cytological key to the species of Para-Sorghum and Stiposorghum on the basis of these differences.

APPEARANCE OF THE CHROMOSOMES AT PACHYTENE

The pachytene chromosomes of species of Para-Sorghum are relatively long and so intertwined that it was not possible to obtain any pollen mother cells with clearly defined chromosomes (pl. 42, *d*); in Stiposorghum, however, the pachytene chromosomes are somewhat shorter and many pollen mother cells

TABLE 5

MEAN FREQUENCY OF CHIASMATA PER CHROMOSOME AND THE PERCENTAGE OF BIVALENTS WITH ONE CHIASMA AT DIAKINESIS AND METAPHASE I IN SPECIES OF PARA-SORGHUM AND STIPOSORGHUM

Species	2n	Number of PMC's	Number of chiasmata per bivalent				Mean number of chiasmata per chromosome	Per cent bivalents with one chiasma
			0	1	2	3		
Diakinesis								
Para-Sorghum								
S. versicolor	10	50	0	6	133	111	1.21	2.4
	10	28	0	6	116	18	1.04	3.5
S. purpureo-sericeum	10	30	0	6	133	11	1.02	4.0
subsp. *dimidiatum*	10	30	0	6	136	8	1.00	4.0
S. nitidum	20	30	0	134	156	10	0.79	44.7
Stiposorghum								
S. intrans	10	37	0	146	39	0	0.60	78.9
S. brevicallosum	10	50	1	222	27	0	0.55	88.9
S. stipoideum	10	20	0	87	13	0	0.56	87.0
Metaphase I								
Para-Sorghum								
S. versicolor	10	30	0	6	131	13	1.02	4.0
S. purpureo-sericeum	10	30	0	13	137	0	0.95	8.7
subsp. *dimidiatum*	10	30	0	14	136	0	0.95	9.3
S. nitidum	20	24	5	111	124	0	0.75	46.3
Stiposorghum								
S. intrans	10	30	0	144	6	0	0.52	96.0
S. brevicallosum	10	37	1	164	20	0	0.55	89.0
S. stipoideum	10	50	0	227	23	0	0.55	90.8

had clearly defined chromosomes (pl. 43, *b*). The difference in the general appearance of the pachytene chromosomes is more striking when the two photomicrographs mentioned are compared. This difference in the appearance of the pachytene chromosomes in these subgenera has been paralleled by a recent report of Randolph (1948) on the pachytene chromosomes of *Zea mays*. In this species, a genetic basis was postulated for the occurrence of "excellent" pachytene preparations as compared with the "normal" appearance of the chromosomes at pachytene.

NUMBER OF NUCLEOLUS CHROMOSOMES AT PACHYTENE

The species of Para-Sorghum and Stiposorghum may be separated into two groups, cytologically, on the basis of the number of nucleolus chromosomes at pachytene. The species of Para-Sorghum have 1 nucleolus chromosome per complement; the species of Stiposorghum have 2 or 4 nucleolus chromosomes per complement. This situation in the latter subgenus has no counterpart in the Sorghastrae.

Differences in the morphology and position of the nucleolus-organizing region at pachytene were present in both subgenera. In Para-Sorghum, differences in both morphology and position were found to distinguish *S. purpureo-sericeum* from the other species in the subgenus. In this species, the nucleolus-organizing region is subterminal, heteropycnotic, irregular, and knoblike (pl. 43, *a*). In *S. versicolor, S. leiocladum,* and *S. nitidum* the nucleolus-organizing region is a terminal, heteropycnotic ball (pl. 42, *d*). There did not seem to be any visible difference in the appearance of the nucleolus-organizing region of these three species. In Stiposorghum, two nucleolus chromosomes are associated with the one nucleolus at pachytene in the diploid species (pl. 43, *b*). Differences in the position of the nucleolus organizing region, however, were noted in these species. The position of the nucleolus-organizing regions was not marked in any visible manner, morphologically, except by their attachment to the nucleolus.

In *S. brevicallosum* and *S. stipoideum,* one nucleolus chromosome was associated with the nucleolus at an intercalary position nearer the centromere than the end of the chromosome while the other nucleolus chromosome was associated with the nucleolus at a subterminal position (pl. 43, *d*). No visible difference was noted in the position of association of the two nucleolus chromosomes of these two species. In *S. intrans,* however, both nucleolus chromosomes were associated with the nucleolus at an intercalary position nearer the centromere than the end of the chromosome (Garber, 1948, and pl. 43, *b*). Since *S. intrans* appears to be the most advanced species in Stiposorghum, it seems reasonable to assume that an inversion was responsible for moving a subterminal association to an intercalary association in one of the two nucleolus chromosomes. The difference between both *S. brevicallosum* and *S. stipoideum,* on the one hand, and *S. intrans,* on the other hand, with respect to the position of the two nucleolus chromosomes is paralleled by morphological differences. In *S. plumosum,* however, four nucleolus chromosomes, each associated with the nucleolus at an intercalary position, are present, and occasionally two nucleoli are found with two nucleolus chromosomes each.

If we assume that the two nucleolus chromosomes in diploid species of Stiposorghum originated through a reciprocal translocation in the ancestral stock involving the original nucleolus chromosome with the point of break at the nucleolus organizing region, then it would follow that the species resulting from this progenitor would have two nucleolus chromosomes once the reciprocal translocation became homozygous. McClintock (1934) has reported such a reciprocal translocation induced by X-ray irradiation in *Zea mays.*

One plant of *S. nitidum* (N7108) in Para-Sorghum was found to have two nucleolus chromosomes. Since other reciprocal translocations have been found in this species in nature, it is probable that the two nucleolus chromosomes found in this one plant may have originated in such a manner. Also, the inversion postulated for the situation in *S. intrans* may have occurred after the initial reciprocal translocation had become homozygous.

On the basis of the number of nucleolus chromosomes in Para-Sorghum and Stiposorghum, it seems logical to consider the latter subgenus more homogeneous than the former. This idea is supported by comparing the geographic distribution of the two subgenera. Stiposorghum occupies a compact and rather uniform area compared with the diverse, tricontinental range of Para-Sorghum (fig. 1).

STAINABILITY OF THE CHROMOSOMES AT DIAKINESIS

The chromosomes of Para-Sorghum at diakinesis present a uniform appearance when stained with acetocarmine (pl. 42, *a*); the chromosomes of Stiposorghum, on the other hand, are differentially stained with acetocarmine (pl. 42, *b*). In the latter subgenus, the stain accumulated at the ends of the chromosomes. No comparative study of the extent and exact location of the heavily staining regions in the species of Stiposorghum has been made.

SIZE OF THE CHROMOSOMES AT METAPHASE I

The chromosomes of Para-Sorghum at metaphase I are relatively large and bulky (pl. 44, *b*); the chromosomes of Stiposorghum are somewhat slender and more extended at the same stage (pl. 44, *a*). The real difference in size is best appreciated by referring to the pertinent photomicrographs.

CHIASMA FREQUENCY AT DIAKINESIS AND METAPHASE I

Striking differences in the chiasma frequency of species belonging to different subgenera were noted. Although chiasma frequency at diakinesis and metaphase I is known to be variable and influenced by many factors both internal and external even in a single species, a comparison of the mean chiasma frequency of species of each subgenus suggests that the difference is real and may be used to distinguish members of one subgenus from the other (pl. 42, *a* and *b*). A summary of the mean number of chiasmata to a chromosome in species of Para-Sorghum and Stiposorghum is presented in table 5. The mean number of chiasmata per chromosome at diakinesis ranged from 0.79 to 1.21 in Para-Sorghum and from 0.55 to 0.60 in Stiposorghum. A similar difference was noted at metaphase I where the mean number of chiasmata to a chromosome in Para-Sorghum ranged from 0.75 to 1.02 and in Stiposorghum from 0.52 to 0.55. The difference in chiasma frequency is even more marked if only diploid species of each subgenus are compared. The allotetraploid species in Para-Sorghum, *S. nitidum*, had a mean number of chiasmata per chromosome at diakinesis and metaphase I (0.79 and 0.75, respectively) intermediate between that of the diploid species in this subgenus and those in Stiposorghum. That polyploidy per se may not account for this situation is suggested by

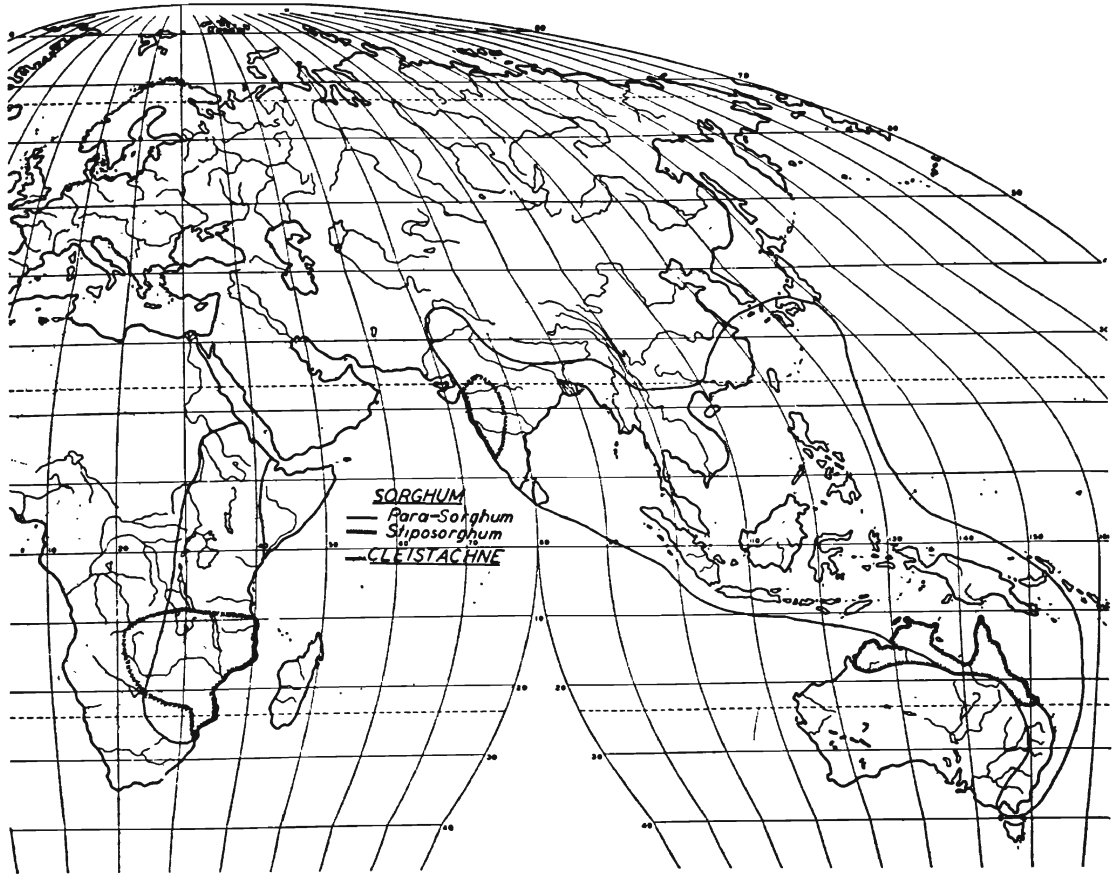


Fig. 1. Distribution of the subgenera Para-Sorghum and Stiposorghum of the genus *Sorghum* and the genus *Cleistachne*.

the mean number of chiasmata per chromosome in *S. leiocladum*, which behaves as an autotetraploid cytologically. In this species, the mean number of chiasmata per chromosome at diakinesis is 0.95. The results of an interspecific hybridization involving *S. nitidum* suggest that the low mean number of chiasmata to a chromosome in this species may be owing to the fact that the segments of chromosome available for the formation of chiasmata are relatively shorter. These results will be presented in a later section.

The mean number of chiasmata per chromosome at diakinesis and metaphase I represents the closest approach to the lowest possible limit on the hypothesis that at least one chiasma is necessary for the formation of a bivalent. In one species, *S. intrans*, 96 per cent of the bivalents at metaphase I (146 of 150 bivalents) had only one chiasma to a bivalent.

The difference in the chiasma frequency per chromosome is made more graphic by treating the same data in a different manner. The percentage of bivalents with only one chiasma was calculated for each species at both diakinesis and metaphase I. The percentage of such bivalents at diakinesis in Para-Sorghum ranged from 2.4 to 44.7 per cent and in Stiposorghum from 78.9 to 88.9 per cent. A similar difference was noted at metaphase I, where the percentage of such bivalents in Para-Sorghum ranged from 2.4 to 46.3 per cent and in Stiposorghum from 89.0 to 96.0 per cent. The difference in the percentage of bivalents with only one chiasma is even more marked if only diploid species of each subgenus are compared.

Cytological Key to the Species of Para-Sorghum and Stiposorghum

Differences in chromosome number, chromosome association at meiosis, and the position of the nucleolus-organizing region, as well as the number of nucleolus chromosomes in Para-Sorghum and Stiposorghum, were found to have cytotaxonomic value and consequently led to the formulation of a cytological key to the species of these subgenera. This key laid the foundation for the construction of another, paralleling, key based on morphological characters (see pp. 319–332 below). In Stiposorghum, cytological data did not distinguish *S. brevicallosum* and *S. stipoideum*, but a distinction was possible on morphological grounds.

A. One nucleolus chromosome per complement ..... Para-Sorghum
  B. Diploid.
    C. Terminal nucleolus-organizing region ..... *S. versicolor*
    CC. Subterminal nucleolus-organizing region ..... *S. purpureo-sericeum*
  BB. Tetraploid.
    D. Allotetraploid, bivalents only ..... *S. nitidum*
    DD. Autotetraploid, multivalents present ..... *S. leiocladum*
AA. Two or four nucleolus chromosomes per complement ..... Stiposorghum
  E. Diploid.
    F. Both nucleolus-organizing regions intercalary ..... *S. intrans*
    FF. One nucleolus-organizing region intercalary .. *S. stipoideum, S. brevicallosum*
  EE. Tetraploid ..... *S. plumosum*

Somatic Chromosome Morphology in Para-Sorghum and Stiposorghum

The nucleolus chromosome at somatic metaphase in species of Para-Sorghum has a subterminal nucleolus-organizing region with a stalked trabant (pl. 44, *d*). Although many somatic metaphase plates of *S. nitidum,* the allotetraploid, were examined, no more than two nucleolus chromosomes were observed. In *S. versicolor, S. nitidum,* and *S. leiocladum* the nucleolus-organizing region at pachytene of meiosis is terminal, but in *S. purpureo-sericeum* it is subterminal; in all four species, however, the nucleolus-organizing region is subterminal at somatic metaphase. Darlington and Thomas (1941) present a photomicrograph of a somatic metaphase in *S. purpureo-sericeum* clearly illustrating the morphology of the nucleolus chromosome with its stalked trabant. There is no evidence to explain the difference in the position of the nucleolus-organizing region at pachytene of meiosis and somatic metaphase in the subgenus Para-Sorghum.

In the diploid species of Stiposorghum, four nucleolus chromosomes were observed at somatic metaphase in contrast to the two nucleolus chromosomes observed in Para-Sorghum. In *S. intrans,* each nucleolus chromosome had an intercalary nucleolus-organizing region near the centromere (pl. 45, *a*). In both *S. brevicallosum* and *S. stipoideum,* two nucleolus chromosomes had an intercalary nucleolus-organizing region near the centromere and two nucleolus chromosomes had a subterminal nucleolus region and stalked trabant (pl. 45, *b*). These observations paralleled the results obtained from the study of pachytene chromosomes. Unfortunately, the somatic chromosomes of *S. plumosum* did not lend themselves to a detailed study of their morphology.

The chromosomes of Para-Sorghum are either V- or nearly V-shaped at somatic metaphase. In the diploid species of Stiposorghum, however, eight of the ten chromosomes are definitely J-shaped and two chromosomes more nearly approach the V shape than the J shape. From these observations, it seems reasonable to assume that the J-shaped chromosomes have their one chiasma almost always in the long arm whereas the chromosomes approaching the V shape may have a second chiasma in the other shorter arm.

Cytological Analysis of an Interspecific Hybrid between S. leiocladum and S. nitidum (Subgenus Para-Sorghum)

The evidence from the position and morphology of the nucleolus-organizing region at pachytene and the results of the attempts to produce interspecific hybrids in the subgenus Para-Sorghum suggested that *S. leiocladum* might be hybridized with *S. nitidum.* Consequently, these species were hybridized using *S. leiocladum* (L749-14) as the seed parent and *S. nitidum* (N603-5) as the pollen parent. Emasculation is not necessary in *S. leiocladum* since this species is self-incompatible.

The somatic chromosome number of the interspecific hybrid (LN13-2) was 21, of which 11 chromosomes were contributed by the seed parent and 10 chromosomes by the male parent. Meiosis in the pollen parent, *S. nitidum,* was regular, the gametes usually having the haploid chromosome number of

10; meiosis in the seed parent, *S. leiocladum* (L749-14), was irregular as compared with meiosis in another plant (L749-9) in the same culture. In plant L749-14, 70 per cent of the pollen mother cells at anaphase I had one or more lagging chromosomes or chromatids; in plant L749-9, less than 5 per cent of the pollen mother cells had any laggards at the same stage. Although no attempt was made to tabulate the frequency of pollen mother cells

TABLE 6

CHROMOSOME ASSOCIATIONS AND THEIR FREQUENCY IN POLLEN MOTHER CELLS AT DIAKINESIS AND METAPHASE I IN TWO PLANTS OF S. LEIOCLADUM

Chromosome association				Number of PMC's	
I	II	III	IV	L749-9	L749-14
1	2	1	3	2	4
1	4	1	2	3	6
1	6	1	1	..	5
1	..	1	4	..	1
2	2	2	2	..	1
2	4	2	1	..	2
2	1	..	4	1	1
2	3	..	3	2	2
2	5	..	2	1	2
2	7	..	1	1	1
2	..	2	3	..	1
3	1	1	3	..	1
3	3	1	2	..	1
3	5	1	1	..	1
4	1	2	2	..	1
..	2	..	4	26	2
..	4	..	3	31	5
..	6	..	2	10	6
..	8	..	1	6	2
..	10	..	..	1	..
..	..	..	5	12	1

in the seed parent with a chromosome distribution of 11 and 9 at anaphase I, such cells were not difficult to find.

Pollen fertility in the seed parent (L749-14) was 37.7 per cent, in excess of 95 per cent in the pollen parent (N603-5), and less than 1 per cent in the interspecific hybrid (LN13-2).

Morphologically, the interspecific hybrid resembles the seed parent more closely than the pollen parent. The midrib at the upper surface of the leaf blade in the hybrid was similar to that found in the pollen parent, *S. nitidum*. In this species, the midrib is always prominent, relatively wide, and white; in *S. leiocladum*, the midrib is usually not prominent, relatively narrow, and dull green in color. The beard at the upper nodes of the culm was longer and more prominent in the hybrid than in either parent.

Univalents, bivalents, trivalents, and quadrivalents were observed at diakinesis and metaphase I in pollen mother cells of the interspecific hybrid,

LN13-2 (pl. 45, *c*). These data are summarized in table 7. Not more than two quadrivalents to a pollen mother cell were seen, and such cells were in the minority at both diakinesis and metaphase I (13 per cent and 3 per cent, respectively). The number of univalents to a pollen mother cell ranged from four (6.4 per cent) to eight (2.1 per cent) at diakinesis and from five (20 per cent) to nine (17.8 per cent) at metaphase I. There was some doubt concerning the observation of four univalents in the three cells noted at diakinesis since a trivalent in each may have been a bivalent and univalent. The number of trivalents to a pollen mother cell at diakinesis and metaphase I ranged from none (35.6 per cent) to four (1.4 per cent).

TABLE 7

CHROMOSOME ASSOCIATIONS AND THEIR FREQUENCY IN POLLEN MOTHER CELLS AT DIAKINESIS AND METAPHASE I IN AN INTERSPECIFIC HYBRID (LN13-2) BETWEEN S. LEIOCLADUM AND S. NITIDUM

Chromosome association				Number of PMC's
I	II	III	IV	
4	4	3	..	1
4	5	1	1	1
4	..	3	2	1
5	3	2	1	10
5	2	4	..	1
5	4	..	2	1
5	5	2	..	6
5	6	..	1	5
5	8	..	..	3
6	1	3	1	1
6	2	1	2	6
6	4	1	1	7
6	3	3	..	1
6	6	1	..	6
7	2	2	1	4
7	4	2	..	6
7	5	..	1	11
7	7	..	..	3
8	3	1	1	3
8	5	1	..	3
9	3	2	..	1
9	4	..	1	4
9	6	..	..	2

A comparison between the frequencies of certain chromosome configurations in the interspecific hybrid and in *S. leiocladum* revealed striking differences (table 9). At metaphase I, the percentage of univalents in the interspecific hybrid was 53.3 per cent, and in L749-14, the seed parent, 12.6 per cent; the percentage of quadrivalents in the interspecific hybrid was 3.8 per cent, and in L749-14, 28.7 per cent. It is interesting to note that none of the chromosome associations in a single pollen mother cell of *S. leiocladum* was observed in any pollen mother cells of the interspecific hybrid (table 7).

TABLE 8

CHROMOSOME ASSOCIATION AT DIAKINESIS AND METAPHASE I IN AN INTERSPECIFIC HYBRID (LN13-2) IN THE SUBGENUS PARA-SORGHUM: S. LEIOCLADUM × S. NITIDUM

Frequency	No. of PMC's	Univalents	Bivalents			Trivalents	Quadrivalents			Mean number of half chiasmata per chromosome
			I	∧	Total	I	□	I	Total	
Diakinesis										
Absolute....	47	270	83	100	183	60	18	24	42	1.11
Mean.....		5.74			3.89	1.28			0.89	
Per cent....		48.7			33.0	10.7			7.6	
Metaphase I										
Absolute....	40	277	56	132	188	35	8	12	20	1.09
Mean.....		6.93			4.70	0.88			0.50	
Per cent....		53.3			36.2	6.7			3.8	

TABLE 9

A Summary of Chromosome Association at Diakinesis and Metaphase I in S. leiocladum (L749-9, L749-14) and an Interspecific Hybrid (LN13-2) between S. leiocladum (L749-14) and S. nitidum

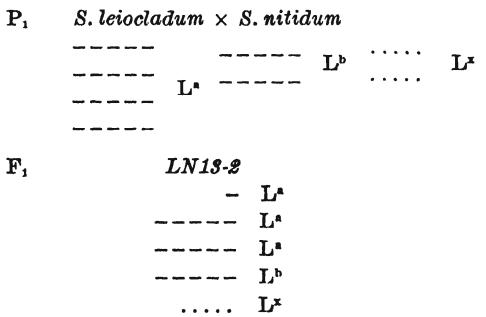
Plant no.	No. of PMC's	Univalents (per cent)	Bivalents (per cent)	Trivalents (per cent)	Quadrivalents (per cent)	Mean no. of half chiasmata per chromosome
Diakinesis						
L749-9	50	1.7	52.6	0.6	45.1	1.89
LN13-2	47	48.7	33.0	10.7	7.6	1.11
Metaphase I						
L749-9	47	3.5	46.4	1.3	48.2	1.88
L749-14	46	12.6	50.8	7.9	28.7	1.50
LN13-2	40	53.3	36.2	6.7	3.8	1.09

In order to interpret the data resulting from the cytological analysis of the interspecific hybrid, it is necessary to consider certain observations. The basic chromosome number in the subgenus Para-Sorghum is 5. *Sorghum leiocladum,* as an autotetraploid, has four homologous genomes on the basis of five chromosomes in each genome. The allotetraploid species, *S. nitidum,* with a somatic chromosome number of 20, has ten bivalents at diakinesis and metaphase I. The four genomes in this species are present in pairs with no apparent homology between the chromosomes of the different genomes. The interspecific hybrid received two homologous genomes plus an extra chromosome from *S. leiocladum* and two genomes from *S. nitidum.* The occurrence of quadrivalents in the interspecific hybrid requires an association involving chromosomes from *S. leiocladum* and *S. nitidum.* In such configurations both autosyndesis and allosyndesis are present. This observation is supported by the presence of more than one trivalent and more than six bivalents in a single pollen mother cell.

The occurrence of allosyndesis in the interspecific hybrid indicates homology between the genome in *S. leiocladum* and one genome, at least, in *S. nitidum.* The degree of homology must be high inasmuch as no configuration in any of the pollen mother cells may be interpreted without invoking allosyndesis (table 7). One pollen mother cell ($4^{I}+3^{III}+2^{IV}$), moreover, had five chromosomes from *S. nitidum* associated with chromosomes from *S. leiocladum.*

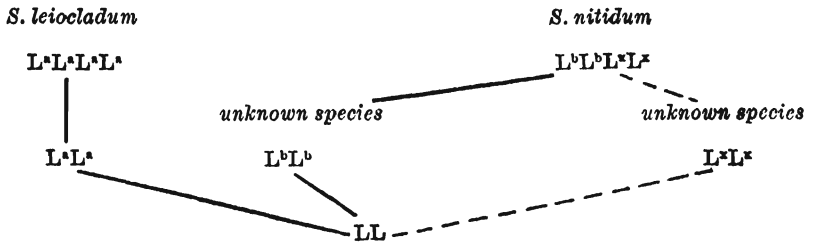
The chromosome configurations in certain pollen mother cells (61 of 87 pollen mother cells) may be interpreted only on the basis of pairing between chromosomes from *S. nitidum* (autosyndesis). The following chromosome configurations are examples: $5^{I}+3^{II}+2^{III}+1^{IV}$, $7^{I}+5^{II}+1^{IV}$, and $6^{I}+4^{II}+1^{III}+1^{IV}$. Although *S. nitidum* appears to be an allotetraploid, the two genomes are somewhat homologous; one of these genomes is closely related to the genome in *S. leiocladum.*

The following diagrams illustrate the genomic constitution of *S. leiocladum, S. nitidum,* and the interspecific hybrid, LN13-2:



The L^a and L^b genomes are closely related to each other, and both are related to the L^x genome. The data do not conclusively indicate whether the L^a and L^b genomes are sufficiently alike to be considered essentially the same or whether these genomes are derived from a common source and have retained

a high degree of homology. The data clearly suggest, however, that the L^x genome, which may have had a common origin with the L^a and L^b genomes, is not closely related to these genomes. Since the degree of homology between the L^a and L^b genomes is unknown, the following diagram illustrates an hypothesis concerning the probable origin of *S. nitidum:*



Although *S. nitidum* appears to behave as a typical allotetraploid (amphiploid), since only bivalents occur, the presence of partly homologous genomes requires a more critical appraisal of the polyploid situation in this species. Stebbins (1947), in a thorough discussion of the types of polyploids, distinguishes the typical allopolyploid from the segmental allopolyploid, listing many examples in each category. Briefly, the typical allopolyploid is characterized, cytologically, by a lack of intergenomal pairing, whereas the segmental allopolyploid is characterized by the occurrence of multivalents in varying numbers. On this basis, *S. nitidum* could be considered an example of a typical allopolyploid, cytologically, in which the partly homologous genomes have become differentiated to such a degree that preferential pairing (L^bL^b and L^xL^x) is the rule. Therefore, this species may have proceeded from a condition of segmental allopolyploidy to typical allopolyploidy although it does not yet possess completely nonhomologous genomes.

Autopolyploidy and Chromosome Association in Para-Sorghum

Autotriploidy in S. purpureo-sericeum

An autotriploid plant (P748-1) of *S. purpureo-sericeum* was found in a collection from India. No evidence is available concerning the origin of this plant. The seed giving rise to the autotriploid plant was extracted from a spikelet which had the constricted glumes characteristic of *S. purpureo-sericeum* subsp. *dimidiatum* but lacked the membranaceous texture of the glume above the constriction characteristic of this subspecies. The original collection was identified as *S. purpureo-sericeum,* and diploid plants from this collection were typical of this species in every detail. Moreover, the subspecies is not reported from India. The spikelets of the autotriploid plant also had constricted glumes.

The autotriploid had strongly pubescent, broad leaves and sturdy tillers. Panicles failed to emerge from the boot, nor were any stainable pollen grains found while the plant was kept in the greenhouse during the winter. Diploid plants from this collection behaved normally under the same conditions inasmuch as panicles emerged from the boot and the percentage of pollen grains

staining with aniline blue in lactophenol exceeded 95 per cent. Once the plant was removed to an outdoor soil bin in the spring, panicles appeared and 66 per cent of the pollen grains were stained. Seed set (open pollinated) was approximately 10 per cent. Whether the peculiar behavior of this plant was due to triploidy cannot be stated definitely.

The seeds from the open pollinated autotriploid were classified for size and degree of plumpness. Four classes were found: large and plump, intermediate and plump, small and somewhat shrunken, and very small and very shrunken. Germination was 100 per cent in the first class, 92 per cent in the second, 92 per cent in the third, and 40 per cent in the fourth. Damping off, however, reduced the number of plants available for a cytological study.

A cytological analysis of chromosome association in the autotriploid at diakinesis and metaphase I revealed univalents, bivalents, and trivalents (pl. 45, *c*) occurring with a mean frequency of 2.52, 2.46, and 2.52, respectively (table 10). A chromosome association of three trivalents, two bivalents, and two univalents at diakinesis in one pollen mother cell occurred most frequently (19 of 48 PMC's) and the same at metaphase I (17 of 42 PMC's).

There was a significant decrease in the mean number of half chiasmata to a chromosome at diakinesis and metaphase I in the autotriploid as compared with the diploid. The autotriploid had 1.40 half chiasmata to a chromosome at diakinesis, while the diploid had 2.03 half chiasmata to a chromosome at the same stage. At metaphase I, the autotriploid had 1.32 half chiasmata to a chromosome and the diploid had 1.91.

AUTOTETRAPLOIDY IN S. LEIOCLADUM

Both collections of *S. leiocladum* (L749, L789) behaved as autotetraploids cytologically in that univalents, bivalents, trivalents, and quadrivalents were observed at diakinesis and metaphase I (pl. 42, *a*). The number of quadrivalents in pollen mother cells ranged from zero to five at both stages. These data are summarized in table 11.

The mean number of half chiasmata per chromosome at diakinesis was 1.89, and at metaphase I, 1.88. Although no diploid race of this species was available, it is possible that the mean number of half chiasmata to a chromosome at diakinesis, at least, could exceed 2.0.

SUPERNUMERARY CHROMOSOMES IN PARA-SORGHUM

Janaki Ammal (1939) first reported supernumerary or B chromosomes in a species of Para-Sorghum, *S. purpureo-sericeum*, and later (1940) presented data on their frequency in a population of 100 plants. No mention was made of any difference in the morphology or pairing relationship of these chromosomes. Darlington and Thomas (1941) reëxamined the same material and found three types of B chromosomes: one similar in length to the "regular" chromosomes, one very short chromosome, and a very long isochromosome. No synapsis was observed between B chromosomes of different morphology or between B and "regular" chromosomes.

TABLE 10

TYPES OF CONFIGURATIONS AND THEIR FREQUENCIES AT DIAKINESIS AND METAPHASE I IN AN AUTOTRIPLOID PLANT (3n = 15) OF S. PURPUREO-SERICEUM

Frequency	No. of PMC's	Univalents	Bivalents			Trivalents				Mean number of half chiasmata per chromosome	
			^ v	| |	Total	| | |	V |	^ v –	Total	3n	2n
Diakinesis											
Absolute	48	121	96	22	118	69	5	47	121	1.40	2.03
Mean		2.52			2.46				2.52		
Per cent		33.6			32.8				33.6		
Metaphase I											
Absolute	42	106	83	20	103	82	5	19	106	1.32	1.91
Mean		2.52			2.46				2.52		
Per cent		33.7			32.6				33.7		

TABLE 11

TYPES OF CONFIGURATIONS AND THEIR FREQUENCIES AT DIAKINESIS AND METAPHASE I IN AN AUTOTETRAPLOID COLLECTION (L749-9) OF S. LEIOCLADUM

Frequency	No. of PMC's	Univalents	Bivalents			Trivalents	Quadrivalents			Mean number of half chiasmata per chromosome
			∧ ∨	| |	Total	| | |	□	Total	
Diakinesis										
Absolute....	50	6	162	20	182	2	26	130	156	1.89
Mean.....		0.12			3.64	0.04			3.12	
Per cent....		1.7			52.6	0.6			45.1	
Metaphase I										
Absolute....	47	11	135	12	147	4	29	126	155	1.88
Mean.....		0.23			3.13	0.09			3.31	
Per cent....		3.5			46.4	1.3			48.2	

Six collections of *S. purpureo-sericeum,* each from a different locality, four from Africa and two from India, were examined cytologically. Of the four African collections, only one (P600), from the Gedaref District, Kassala Province, Sudan, had B chromosomes (pl. 44, *b*); one of the two Indian collections (P7100) had B chromosomes. This one Indian collection was identified as *S. purpureo-sericeum* subsp. *deccanense.*

It is interesting to note that B chromosomes have not yet been found in any other species of Para-Sorghum or Stiposorghum. According to J. G. O'Mara (comm.), B chromosomes are present in *S. purpureo-sericeum* subsp. *dimidiatum.* Since the subspecies is not genetically isolated from the rest of the species (see pp. 317 ff.), B chromosomes may have been introduced into the germ plasm from *S. purpureo-sericeum* subsp. *typicum,* or, as an alternate

TABLE 12

FREQUENCY OF PLANTS WITH A GIVEN NUMBER OF B CHROMOSOMES IN THE P600 COLLECTION OF S. PURPUREO-SERICEUM, COMPARED WITH DATA PRESENTED BY JANAKI AMMAL (1940)

Collection	Number of B chromosomes							
	0	1	2	3	4	5	6	Total
P600	39	12	9	0	2	1	0	63
Janaki Ammal	60	12	20	5	1	1	1	100

hypothesis, *S. purpureo-sericeum* subsp. *dimidiatum* may have been derived from plants of *S. purpureo-sericeum* already carrying B chromosomes.

Although Darlington and Thomas (1941) reported three different morphological types of B chromosomes, only two were found in the P600 collection. The isochromosome was not encountered. As Darlington and Thomas had noted, synapsis did not occur between the long and short B chromosomes. The short B chromosome is approximately half as long as the long B chromosome at metaphase I (pl. 45, *d*). Since five small B chromosomes in a single pollen mother cell were occasionally found as a chain of five at diakinesis, chromosome length does not seem to be a barrier to the formation of, at least, two half chiasmata to a small B chromosome, or, expressed in another way, two chiasmata per small B chromosome pair. Since no information is available concerning a possible genetic homology between the different morphological types of B chromosomes, lack of pairing at diakinesis may be considered an indication of nonhomology, at least in a cytological sense. Whether synapsis had occurred at pachytene is not known since this stage in *S. purpureo-sericeum* does not lend itself to a cytological study. Excepting the report of Darlington and Thomas (1941) and the confirmatory evidence herein reported, the author is not aware of any other report of nonhomologous B chromosomes in any species carrying them. Any hypothesis concerning the origin of these chromosomes must also include an explanation of the lack of homology between B chromosomes.

Of the 100 plants examined by Janaki Ammal (1940), 40 per cent had B chromosomes; of the 63 plants studied in the P600 collection, 38 per cent had B chromosomes (table 12). While Janaki Ammal found a plant with six B's and O'Mara (comm.) found one with seven, the maximum number in a single plant of the P600 collection was five. Not finding any plants with three B

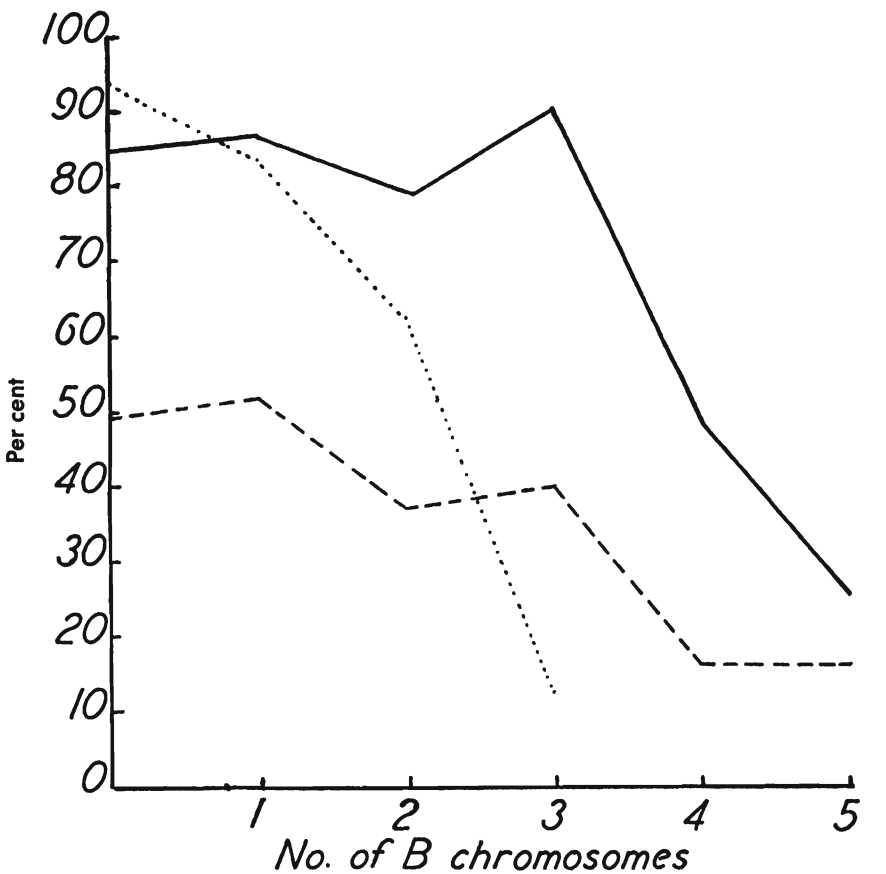


Fig. 2. The relationship between the number of B chromosomes and the percentage of pollen fertility and seed set in *S. purpureo-sericeum*. Solid line, pollen fertility; dotted line, pollen fertility according to Janaki Ammal; broken line, seed set.

chromosomes may have been due to the relatively small sample since such plants were obtained in the progeny of plants carrying two B's.

Janaki Ammal and Darlington and Thomas present data correlating a decrease in the percentage of pollen fertility with an increase in the number of B chromosomes. The indicated correlation suggests a direct proportionality. This proportionality does not seem to hold in the P600 collection although the correlation appears to be valid (fig. 2). Since neither report included the effect of B chromosomes on the percentage of seed set, this information was collected. All the data concerning the percentage of pollen fertility and seed set as they are influenced by B chromosomes are presented in table 14.

In contrast to the material studied by Janaki Ammal and Darlington and Thomas, the data from the P600 collection indicate that B chromosomes do not seem to influence appreciably the percentage of pollen fertility or seed set until four such chromosomes are present. The effect of B chromosomes on both the percentage of pollen fertility and seed set in the P600 collection appears to be of the same order of magnitude.

A considerable range of variation in the percentage of pollen fertility and seed set was found in plants with either no B chromosomes or the same number of B chromosomes. These data are summarized in tables 13, 14, and 15, along with comparable data from Darlington and Thomas. Janaki Ammal did not present information on this point. Since the percentage of seed set in other collections of *S. purpureo-sericeum* lacking any B chromosomes was in excess of 90 per cent, it is difficult to explain the occurrence of plants in the P600 collection carrying up to three B's with such low seed set as 2 per cent. The extreme range of variation in the percentage of pollen fertility and seed set may be an expression of segregating genetic factors affecting gametic fertility superimposed on the effects of the B chromosomes on gametic fertility. Such an explanation may account for the differences observed in the results of Janaki Ammal and Darlington and Thomas and those obtained from the analysis of the P600 collection.

The results of the study of B chromosomes in *S. purpureo-sericeum* may be briefly summarized. One collection from Africa (P600) carried B chromosomes. Whether this collection is the same as the material studied by Janaki Ammal (1939, 1940) and Darlington and Thomas (1941) is not known, but there is reason to believe that it is not. One collection from India (P7100) also had B chromosomes. No other species of Para-Sorghum or Stiposorghum has yet been found to have these chromosomes. Three morphological types of B-chromosomes were observed by Darlington and Thomas; two of these types were found in the P600 collection. One type was twice as long as the other at diakinesis. No pairing was observed at diakinesis either between B and "regular" chromosomes or between different types of B's. Although the previous reports indicated a decrease in the percentage of pollen fertility and seed set proportional to an increase in the number of B chromosomes in a plant, the effect of these chromosomes on the percentage of pollen fertility and seed set in the P600 collection was not found as a regular occurrence until four B's had accumulated in one plant. Considerable variation in the percentage of pollen fertility and seed set was observed in plants carrying a specific number of B chromosomes.

Perhaps the most ingenious explanation of the origin of B chromosomes has been offered by Avdulov and Titova (1933), who considered these chromosomes to have been produced in the course of evolution of the karyotype in the Gramineae. Although this subject is considered in detail further on (pp. 343 ff.), one point should be presented here since it concerns the origin of B chromosomes. The alterations of the karyotype, both in number and morphology, in the Gramineae from one tribe to another proceed along the lines of a lowering of the basic number of chromosomes. According to Avdulov

TABLE 13

MEAN PERCENTAGE OF SEED SET AND POLLEN FERTILITY IN RELATION TO NUMBER OF B CHROMOSOMES IN THE P600 COLLECTION OF S. PURPUREO-SERICEUM, COMPARED WITH DATA PRESENTED BY JANAKI AMMAL (1940) AND DARLINGTON AND THOMAS (1941)

	Number of B chromosomes					
	0	1	2	3	4	5
Seed set	49.8 (13)*	51.4 (10)	37.8 (8)	40.0 (1)	16 (3)	16 (3)
Pollen fertility	84.5 (17)	86.3 (8)	76.9 (7)	90.0 (1)	48 (4)	26 (2)
Pollen fertility:						
Janaki Ammal (1940)	93.6 (6)	83.6 (3)	63.0 (5)	11.5 (2)	.....	.....
Darlington and Thomas (1941)	86.7 (3)	76.7 (2)	62.8 (2)	4.0 (1)	.....	.....

* Number of plants in each category enclosed in parentheses.

TABLE 14

RELATIONSHIP BETWEEN NUMBER OF B CHROMOSOMES AND PERCENTAGE OF POLLEN FERTILITY AND SEED SET IN PLANTS OF THE P600 COLLECTION OF S. PURPUREO-SERICEUM GROWN FROM A BULK COLLECTION OF SEED

No. of B's	Percentage of pollen fertility									
	0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–100
0	..	..	..	..	1	..	2	3	11	9
1	..	..	..	..	1	..	..	1	1	4
2	1	..	..	..	1	..	..	2	1	1
3	..	..	..	..	..	..	..	..	..	..
4	.	..	..	..	2	..	..	..	..	..
5	..	1	..	..	..	..	..	..	..	..
	Percentage of seed set									
0	1	4	4	3	..	..	4	1	2	3
1	1	..	1	..	2	3	1	1	..	..
2	2	..	2	..	1	..	1	..	..	..
3	..	..	..	..	..	..	..	..	..	..
4	2	..	..	..	..	..	..	..	..	..
5	1	..	..	..	..	..	..	..	..	..

TABLE 15

RANGE OF VARIATION IN PERCENTAGE OF SEED SET AND POLLEN FERTILITY WITHIN EACH CATEGORY CONTAINING A GIVEN NUMBER OF B CHROMOSOMES IN THE P600 COLLECTION OF S. PURPUREO-SERICEUM, COMPARED WITH DATA PRESENTED BY DARLINGTON AND THOMAS (1941)

	Number of B chromosomes					
	0	1	2	3	4	5
Seed set	12–94	2–80	2–78	40	4–38	2–30
Pollen fertility	63–94	74–92	70–93	90	40–62	13–39
Pollen fertility:						
Darlington and Thomas	77–94	71–82	42–84	4	.....	.....

and Titova, "One may imagine that in the evolution process connected with the loss of separate chromosomes, the respective chromosomes in some cases lose their hereditary(?) substance before they are eliminated and remain in the set as 'empty' and degraded bodies. . . . In regarding the additional chromosomes (B's) as vestiges of the evolution process, i.e., as empty remainders of a karyotype with a greater number of chromosomes than the given one, we avoid the contradictions in the modern conception of the localization of hereditary factors in the chromosomes."

BREEDING BEHAVIOR

Since the cytotaxonomic work in the Sorghastrae centered on the problem of determining the nature of the differences among the groups of species in this circle of affinity, relatively little attention was given to the problem of crossability among these groups. Hybridizations were limited to the subgenera Para-Sorghum and Stiposorghum, and these, in turn, were limited by the very small populations available in the latter.

Self- and Cross-Pollination in the Sorghastrae

Excepting Para-Sorghum and Stiposorghum, the species of the subgenera of *Sorghum* and the one species of *Cleistachne, C. sorghoides,* set amply sufficient seed when selfed. In Para-Sorghum, however, only the diploid species yielded amply sufficient seed when selfed. *Sorghum nitidum* set relatively few seed when selfed, and cross-pollinating did not seem to increase the percentage of seed set. Occasional plants of *S. purpureo-sericeum* subsp. *dimidiatum* behaved in a similar manner. Since collections of these two species received from their native habitat suggest a high percentage of seed set, it seems reasonable to assume that environmental factors in Berkeley, California, do not always favor seed set. *Sorghum leiocladum,* on the other hand, appears to be completely self-incompatible. Panicles of different plants when bagged together set amply sufficient seed (table 16, *A*). The mechanism operating to produce self-incompatibility is not yet known. In Stiposorghum, moreover, all four known species seem to be completely self-incompatible. Seed set results only from cross-pollination (table 16, *B*). As in *S. leiocladum,* no information is available concerning the mechanism involved in the self-incompatibility.

Seed Germination in the Sorghastrae

The germination of seed in Para-Sorghum and Stiposorghum presents a major handicap since seeds of species of these two subgenera require a resting period of some length—more than six months to insure at least 50 per cent germination. The rate of germination of seeds less than six months old was increased after dry seeds had been treated with concentrated sulphuric acid for five minutes. The germination of seeds of Stiposorghum was especially poor, and almost nine months was required for the resting period. According to W. Hartley (oral comm.), species of this subgenus are found in regions where there is absolutely no rain for eight to nine months. The germination

TABLE 16

A SUMMARY OF HYBRIDIZATION IN THE SORGHASTRAE

Intraspecific hybridizations

Female parent	Male parent	No. of florets	No. of seed
A. Para-Sorghum			
*P745A-1	P703-8	46	31
P703-6	P717-1	13	7
P780-1	P7107-2	36	36
P7100-1	P716A-8	47	32
P702-17	P724-1	30	0
P703-8	P709-2	19	0
P702-4	P728-4	12	0
P703-8	P702-7	9	0
P703-6	P702-5	18	0
D736-1	P728-5	20	12
D736-1	P728-5	20	6
D743-6	P751X-5	..	7
D743-3	P763-8	62	46
V707-3	V701-12	6	1
V732-2	V758-14	22	8
V796-2	V760-2	21	6
N706-5	N603-5	160	15
N603-5	N706-5	37	2
N603-4	N603-5	14	2
N603-5	N603-4	62	6
L749-3	L749-2	52	15
L749-2	L749-3	40	21
L749-9	L749-14	78	31
L749-14	L749-9	103	14
B. Stiposorghum			
I713-2	I713-1	8	6
S790-11	S794-15	16	8
S794-15	S790-11	13	1

Interspecific hybridizations

C. Para-Sorghum			
V701-4	P728-3	11	6
V701-7	P729-2	12	3
P702-4	V707-1	9	0
V796-2	P7100-2	45	0
N706-5	D743-6	50	2
N603-5	P723-1	62	13
N706-4	V753	..	11
S. versicolor	N706-5	38	6
L749-9	P751X-9	48	1
L749-14	N603-5	48	8
L749-15	V753	38	4

* The initials preceding the culture numbers correspond to the first letter, usually, of the specific name (see second column of table 2, p. 288).

TABLE 16—*Continued*

Female parent	Male parent	No. of florets	No. of seed
	D. Stiposorghum		
I793-4	B792-1	12	0
B792-1	I793-4	8	0
B792-9	S790-8	24	0
B792-9	S790-12	40	0
B792-9	S790-11	68	0
B792-9	S790-12	25	0
S790-2	B792-1	28	0
S790-8	B792-9	18	0
S790-12	B792-9	29	0
S790-11	B792-9	21	0
I793-2	S790-2	18	0
S790-2	I793-3	10	0
I793-4	S790-11	7	0
I793-10	S794-15	20	0
	Intersubgeneric hybridizations		
B792-1	V800-1	12	0
S790-10	V767-2	21	0
S790-10	P801-6	25	0
N706-4	S. vulgare	170	12

of seed of the other four subgenera of *Sorghum* and *Cleistachne sorghoides* was not dependent on any appreciable resting period.

Crossability in the Sorghastrae

Few data were found in the literature on the crossability of species belonging to different subgenera of *Sorghum,* between any species of *Sorghum* and *Cleistachne,* or within the subgenera of *Sorghum.* In the subgenus Eusorghum, *S. vulgare* and *S. halepense* have been hybridized. Few quantitative data, however, are available concerning the ease with which this hybridization succeeds in either direction, the percentage of seed set, the fertility of the first or subsequent generations, or the cytological analysis of the hybrids or their derivatives. Dr. L. F. Randolph (in a letter to G. L. Stebbins, Jr.) states that the hybridization between autotetraploid *S. vulgare* var. *sudanense* and *S. halepense* (male sterile) is relatively easy to accomplish and that the fertility of the first and subsequent generations is relatively high.

Attempts to hybridize species of Para-Sorghum and *S. vulgare* have been reported by Karper and Chisholm (1936), who failed to hybridize *S. versicolor* and *S. vulgare,* and by Ayyanger and Ponnaiya (1941), who failed to cross *S. vulgare* with *S. versicolor, S. purpureo-sericeum, S. purpureo-sericeum* subsp. *dimidiatum,* or their collection of *S. nitidum* (see pp. 285 ff.

above). C. O. Grassl (comm.) also reported failure in attempting to hybridize *S. vulgare* with either *S. versicolor* or *S. purpureo-sericeum*. No success has followed an attempt to hybridize *S. vulgare* and *S. nitidum* (table 16: intersubgeneric hybridization). Of the 12 seeds obtained, only one germinated and this plant proved to be a self. Considering the cytotaxonomic differences between Eu-Sorghum and both Para-Sorghum and Stiposorghum, it does not seem likely that the latter subgenera offer a potential reservoir of germ plasm for the improvement of *S. vulgare*. No positive decision, however, is possible until every combination of crosses involving *S. vulgare* and species of Para-Sorghum and Stiposorghum has been made.

If Para-Sorghum and Stiposorghum are genetically isolated from Eu-Sorghum, do other sources of germ plasm exist for hybridization with *S. vulgare*? This question may be given an indirect answer. Huskins and Smith (1932) suggest that *S. halepense* may be derived from a hybridization between a diploid species of Eu-Sorghum (*S. vulgare* ?) and some other species in the Andropogoneae, probably the subtribe Andropogoninae. Whether this species or closely related species still exist is problematical. A search for such a species should be conducted in the tropics or semitropics of the Old World, probably in Asia.

The Subgenera Para-Sorghum and Stiposorghum

Intraspecific hybridization: Para-Sorghum (table 16, A).—Excepting *S. leiocladum,* which is self-incompatible, hybridization in Para-Sorghum requires the emasculation of the seed parent as well as removal of the pedicellate, staminate spikelets. Hybridizations between collections of *S. purpureo-sericeum* were usually successful except when the seed parent did not set seed even when selfed. *Sorghum purpureo-sericeum* subsp. *typicum* hybridized with both subspecies *dimidiatum* and *deccanense* (P7100) without difficulty. Plants of different collections of *S. versicolor* were usually crossed with ease. In *S. leiocladum,* using a plant (L749-2) with 19 chromosomes as both seed and pollen parent did not seem to affect the percentage of seed set appreciably.

Intraspecific hybridization: Stiposorghum (table 16, B).—Hybridization in this subgenus was greatly facilitated by the self-incompatibility of all four species. Owing to the very small populations available, intraspecific hybridizations were restricted to two species, *S. intrans* and *S. stipoideum*. Little difficulty was encountered in obtaining seeds from crosses. In the latter species, it was possible to get good seed set when two plants were isolated side by side and subjected to air currents.

Interspecific hybridization: Para-Sorghum (table 16, C).—Sorghum purpureo-sericeum and *S. versicolor* did not hybridize, irrespective of the origin of the collections used in crossing (77 florets emasculated). Whenever seeds were obtained, they proved to be selfs. Although seeds were obtained from interspecific hybridizations involving *S. nitidum* as the seed parent, it was not possible to get more than one mature plant (N706-4 × V753), which was a self (more than 208 florets emasculated). Either seeds failed to germi-

nate or damping off killed the few seedlings that did appear. Consequently, it is not known whether attempts to cross this species with other species, except *S. leiocladum,* in the subgenus were successful. A similar difficulty was encountered in interspecific hybridizations involving *S. leiocladum* as seed parent; it seems fairly certain, however, that interspecific hybridizations resulting in seed set were successful since no seeds are found in selfed plants of this species. One plant (LN13-2), resulting from a hybridization between *S. leiocladum,* as seed parent, and *S. nitidum,* was raised to maturity and proved to be an interspecific hybrid. The cytogenetic analysis of this hybrid is presented above (pp. 298–304).

Interspecific hybridization: Stiposorghum (*table 16, D*).—None of the attempts to obtain an interspecific hybrid between diploid species of Stiposorghum was successful. At first, *S. brevicallosum* was considered a possible variant of *S. stipoideum* since their cytology indicated close relationship (see p. 294). Failure to obtain hybrids between these two species strongly suggests that the specific status of the former species is valid and warranted (253 florets). Unfortunately, mature plants of *S. plumosum* were not available for hybridization. Since none of the diploid species yielded any seed when hybridized, it is difficult to explain the origin of the allotetraploid species, *S. plumosum,* unless we assume that other diploid species are yet to be discovered or have become extinct.

Intersubgeneric hybridization (*table 16, end*).—None of the three attempts to hybridize species of Para-Sorghum with species of Stiposorghum was successful. From the 12 seeds obtained from a hybridization between *S. nitidum* and *S. vulgare* (170 florets), only one plant was raised to maturity, and it proved to be a self. Until a complete series of intersubgeneric hybridizations is made, it is not possible to consider the subgenera of the genus *Sorghum* genetically isolated from each other. However, it does seem reasonable to consider Para-Sorghum and Stiposorghum as genetically isolated from the other four subgenera of the genus *Sorghum.*

Intergeneric hybridization.—No attempt was made to hybridize *Cleistachne sorghoides* with any species of *Sorghum.*

Discussion

The results of hybridization attempts within the subgenera Para-Sorghum and Stiposorghum and between species in each subgenus were interesting for several reasons. Within the subgenus Para-Sorghum, the apparent lack of genetic isolation of the subspecies of *S. purpureo-sericeum* made clear the taxonomic relationship of these subspecies. One subspecies, *S. purpureo-sericeum* subsp. *dimidiatum,* had been considered a species, *S. dimidiatum,* by Stapf (1917). The easily accomplished hybridization between *S. purpureo-sericeum* subsp. *typicum* from Africa and *S. purpureo-sericeum* subsp. *deccanense* from India indicates that geographical isolation has not yet resulted in genetic isolation. In the subgenus Stiposorghum, unsuccessful attempts to hybridize *S. brevicallosum* and *S. stipoideum* emphasized the specific status of the former species, as had been indicated by morphological evidence.

The results of attempted hybridizations between species of Para-Sorghum aided in the formulation of an hypothesis concerning the probable origin of *S. nitidum* (see p. 317). Since *S. versicolor* and *S. purpureo-sericeum* did not yield any interspecific hybrids, *S. leiocladum* was considered either one of the species or closely related to one of the species that may have been involved in the interspecific hybridization that ultimately produced *S. nitidum*. A cytological analysis of an interspecific hybridization (LN13-2) between *S. leiocladum* and *S. nitidum* suggests that this hypothesis may be valid.

Although relatively few attempts to hybridize species of Para-Sorghum and Stiposorghum were made, the results suggest that these two subgenera may be genetically isolated.

Until a systematic program of intersubgeneric hybridization is attempted, the limits of crossability in the Sorghastrae must remain unknown. The results of such a program would certainly determine whether it will be possible to find a source of germ plasm for the improvement of *S. vulgare* in the genus *Sorghum*.

TAXONOMY AND DISTRIBUTION OF THE SORGHASTRAE, WITH SPECIAL REFERENCE TO THE SUBGENERA PARA-SORGHUM AND STIPOSORGHUM

Taxonomy

The morphological characters distinguishing Andropogoninae from other subtribes in the tribe Andropogoneae are considered further on (pp. 339 ff.). The *Sorghum* complex and the related genus *Cleistachne* form a circle of affinity recognized by both Hackel (1889) and Stapf (1917). Hackel included *Sorghum* and Sorghastrum within the same subgenus (Sorghum) of his concept of the genus *Andropogon*. Although *Cleistachne* was set up as a distinct genus, Hackel noted its affinity to the subgenus Sorghum. Stapf made special note of this circle of affinity by creating a group, the Sorghastrae, to include the genera *Sorghum* and *Cleistachne*. Although there is no recognized taxonomic category for the term Sorghastrae, it has been retained for purposes of convenience.

The Sorghastrae are distinguished from other circles of affinity in the subtribe by the espatheate panicles, bifid lemmas awned from the sinus, dorsally compressed flowering spikelets, and the pediceled spikelets, staminate, neuter, or suppressed, including the pedicel, as in *Cleistachne*.

As Hackel remarked, generic boundaries in the Andropogoneae are poorly defined. Consequently, a classification of species into genera must be based on a foundation embracing all possible sources of information. Therefore, the proposed taxonomic treatment of the members of the Sorghastrae has included evidence from cytology, morphology, distribution, and phylogeny. The morphological characters used to distinguish the genera and subgenera were evaluated in terms of their phylogenetic significance (see pp. 339 ff. below). The cytological data are presented on pages 287 ff. above. The morphological and distributional data will be considered in this section.

TABLE 17

MORPHOLOGICAL CHARACTERS DISTINGUISHING THE GENERA AND SUBGENERA OF THE SORGHASTRAE

Genera and subgenera	Bearded nodes	Panicle branch divided	Panicle branches whorled	Prominent pulvinus	Prominent callus	Prominent awn	Pediceled spikelet			Seed shape	No. of nerves, lower glume, sessile spikelet	Ciliate lodicules
							Lemmas	Glumes	Pedicel			
Sorghum												
Eu-Sorghum	−	+	+	+	−	−	+	+	+	Obovoid	10–16	+
Chaetosorghum	−	−	−	+	−	−	−	+	+	Obovoid	15–22	−
Heterosorghum	−	+	+	−	−	−	−	+	+	Obovoid	10–12	+
Sorghastrum	−	+	+	−	−	−	−	−	+	Obovoid	9	−
Para-Sorghum*	+	−	+	−	−	+	+	+	+	Obovoid	6–10	+
Stiposorghum	+	−	+	−	+	+	+	+	+	Broadly subulate	7–10	+
Cleistachne	−	+	+	−	−	−	−	−	−	Obovoid	7–8	+

* *S. trichocladum* is not included since this species seems to be anomalous.

Two genera and six subgenera are recognized in the Sorghastrae:

1. *Sorghum* Pers.
   a. Subgenus Eu-Sorghum (Stapf) comb. nov.
   b. Subgenus Chaetosorghum subgen. nov.
   c. Subgenus Heterosorghum subgen. nov.
   d. Subgenus Sorghastrum (Nash) comb. nov.
   e. Subgenus Para-Sorghum (Snowden) comb. nov.
   f. Subgenus Stiposorghum subgen. nov.
2. *Cleistachne* Bentham.

Although Nash (1901) had elevated Sorghastrum to the rank of genus, a treatment accepted by American grass taxonomists, Stapf (1917) considered this group of species a section of the genus *Sorghum*. Inasmuch as the morphological characters and phylogeny indicated a rather close relationship of the species in *Sorghum*, it seemed illogical and premature to set up each smaller circle of affinity as a distinct genus. Although cytological differences exist in certain subgenera, it has not seemed advisable to elevate any of the subgenera to generic rank.

Snowden (1935) recognized the unique status of the species with the bearded nodes by establishing two sections of the genus *Sorghum:* Para-Sorghum and Eu-Sorghum. Cytological and morphological evidence clearly indicates the presence of two well-defined groups of species in the section Para-Sorghum, and this situation has been recognized by creating two subgenera: Para-Sorghum and Stiposorghum. These two subgenera are closely related, and both may be distinguished morphologically (table 17) from the subgenus Eu-Sorghum by the simple panicle branches, the relatively small pulvinus at the base of the panicle branch, and the number of nerves of the lower glume of the sessile spikelets; from the subgenus Chaetosorghum by the whorled panicle branches, the relatively small pulvinus at the base of the panicle branch, the number of nerves of the lower glume of the sessile spikelets, ciliate lodicules, and the staminate or neuter pediceled spikelets never lacking lemmas; from the subgenus Heterosorghum by its simple panicle branches, the number of nerves of the lower glume of the sessile spikelets, and the staminate or neuter pediceled spikelets never lacking lemmas; and from the subgenus Sorghastrum by the simple panicle branches, ciliate lodicules, and the presence of a pediceled spikelet. In the final analysis, the bearded node appears to be the one morphological character distinguishing Para-Sorghum and Stiposorghum from the other subgenera in the genus *Sorghum*. If any species of either subgenus were found lacking the bearded node but possessing the particular combination characterizing each subgenus, a cytological examination would confirm the conclusion drawn from morphology and distribution. The identification of species of Stiposorghum is facilitated by the unique combination of the pointed callus and the broadly subulate mature caryopsis.

In one species of Para-Sorghum, *S. leiocladum*, at least one plant has been found with several divided panicle branches instead of only simple panicle branches. These aberrant branches were restricted to the lowest whorl. Hub-

bard (1938) described this species as having only simple panicle branches as in the other species of Para-Sorghum and Stiposorghum.

Since no attempt is being made to monograph the Sorghastrae, morphological descriptions given here will be restricted to new categories and species. Complete descriptions of established categories and species may be found in Hackel (1889) and Stapf (1917).

THE GENUS SORGHUM

Stapf (1917) presents an excellent description of the genus *Sorghum,* including those species which are found in Africa. Only two categories, however, are recognized: Eu-Sorghum and Sorghastrum. Specific mention is made of species of the subgenus Para-Sorghum, but they are included in the section Eu-Sorghum. Snowden (1935), however, recognized the peculiar status of the sorghums with the bearded nodes and simple panicle branches by establishing the sections Para-Sorghum and Eu-Sorghum. As previously mentioned, Para-Sorghum has been found to include two distinct groups. Finally, two subgenera, Chaetosorghum and Heterosorghum, were created in order to accommodate two species, *S. macrospermum* and *S. laxiflorum,* which could not be placed in either Eu-Sorghum or Sorghastrum. These new subgenera will be described on the basis of the one known species found in each.

The descriptions of categories already established will be restricted to characters essential to the construction of a key to the subgenera of the genus *Sorghum.* Of necessity, such a key must be artificial since available data do not suffice for an accurate evaluation of the phylogenetic position of each subgenus. However, the affinity of Eu-Sorghum and Chaetosorghum, Heterosorghum and Sorghastrum, and Para-Sorghum and Stiposorghum makes possible the construction of a key representing a compromise between artificiality and naturalness.

KEY TO THE SUBGENERA OF THE GENUS SORGHUM

A. Nodes essentially glabrous or lightly pubescent; panicle branches divided (simple in Chaetosorghum); lower glumes of the sessile spikelets 10–22-nerved (9-nerved in Sorghastrum); awns usually not prominent.
  B. Pulvinus prominent; lower glumes of sessile spikelets 10–22-nerved; glumes of pediceled spikelets approximately equal in length.
    C. Panicle branches whorled, divided; lodicules ciliate; pediceled spikelets never lacking lemmas ..... Eu-Sorghum
    CC. Panicle branches not whorled, simple; lodicules glabrous; pediceled spikelets lacking lemmas ..... Chaetosorghum
  BB. Pulvinus not prominent; lower glumes of sessile spikelets 9–12-nerved; glumes of pediceled spikelets, if present, unequal in length.
    D. Pediceled spikelets present; lodicules ciliate ..... Heterosorghum
    DD. Pediceled spikelets absent; lodicules glabrous ..... Sorghastrum

AA. Nodes, at least the upper, bearded; panicle branches usually simple; lower glumes of sessile spikelets 6–10-nerved; awns usually prominent.
  E. Callus obtuse, never exceeding 0.5 mm.; mature caryopsis obovoid ..... Para-Sorghum
  EE. Callus pointed, 1.0–7.5 mm.; mature caryopsis broadly subulate ..... Stiposorghum

TAXONOMIC DESCRIPTIONS

1. *Sorghum* subgenus Eu-Sorghum (Stapf) comb. nov.

Sorghum § Eu-Sorghum Stapf, Fl. Trop. Afr. 9: 105. 1917.
Sorghum § Eu-Sorghum Snowden, Kew Bull. Misc. Info., No. 5: 221. 1935.

Nodi culmorum glabri; rami primarii verticillati cum ramis secundariis; pulvinus grandis; spicularum sessilium callus obtusissimus aristaque brevis; lodiculae ciliolatae, membranacae; spiculae pedicellatae masculae vel neutrae; fructus obovatus.

Nodes of the culms essentially glabrous; primary branches of the panicle whorled, divided; pulvinus prominent; callus of the sessile spikelets obtuse; awns of the sessile spikelets short; lodicules ciliate, membranaceous; pediceled spikelets staminate or neuter, never lacking lemmas; mature caryopsis obovoid.

Distribution: Africa, eastern Mediterranean basin.

Chromosome numbers: x = 10, 20.

Within this subgenus are found *S. vulgare* and *S. halepense*. A thorough taxonomic treatment of the species of Eu-Sorghum may be found in Snowden's monograph (1936). Parodi (1943) has described a species, *S. almum*, from Argentina.

2. *Sorghum* subgenus Chaetosorghum subgen. nov.

Nodi culmorum glabri; rami primarii solitarii, simplices; pulvinus grandis; spicularum sessilium callus obtusissimus aristaque longa; lodiculae glabrae, cupiliformes, crassae; spiculae pedicellatae cum glumis solum; fructus obovatus.

Nodes of the culm glabrous; primary branches of the panicle not whorled, simple; pulvinus prominent; callus of the sessile spikelets obtuse; awns of the sessile spikelets long; lodicules glabrous, cup shaped, thick; pediceled spikelets lacking stamens, lemmas, and palea, glumes only present; mature caryopsis obovoid.

Distribution: Northern Territory, Australia.

Chromosome number: x = 10.

This subgenus is based on a previously undescribed species, as follows:

Sorghum macrospermum sp. nov.

Planta annua; spicularum sessilium glumae inferiores obovatae, 10–12 mm. longae, 15–22-nervis; pili basilares elongati; spicularum pedicellatarum glumae inferiores lanceolatae, 11–12 mm. longae, 12–17-nervis, glumaeque superiores 8–10 mm. longae, 8–11-nervis; fructus obovatus, 6–7 mm. longus, 2–3 mm. latus; aristae spicularum sessilium 33–48 mm. longae.

Annual; lower glumes of the sessile spikelets obovoid, 10–12 mm. long, 15–22-nerved; basal hairs elongate; lower glumes of the pediceled spikelets lanceolate, 11–12 mm. long, 12–17-nerved and upper glumes 8–10 mm. long, 8–11-nerved; mature caryopsis obovoid, 6–7 mm. long and 2–3 mm. wide; awns 33–48 mm. long.

Distribution: Port Darwin, Northern Territory, Australia.

Chromosome number: 2n = 40 (20^{II}).

The type specimen (Herbarium, University of California 753385) was grown in Berkeley, California, in the spring of 1948, from seed collected by W. Hartley in 1947 near Port Darwin.

3. *Sorghum* subgenus Heterosorghum subgen. nov.

Nodi culmorum glabri; rami primarii verticillati, cum ramis secundariis; pulvinus parvus; spicularum sessilium callus obtusissimus aristaque longa; lodiculae ciliolatae, membranacae; spiculae pedicellatae cum glumis solum; fructus obovatus.

Nodes of the culms glabrous; primary branches of the panicle whorled, divided; pulvinus not prominent; callus of the sessile spikelets obtuse; awns of the sessile spikelets long; lodicules ciliate, membranaceous; pediceled spikelets lacking stamens, lemmas, and palea, glumes only present; mature caryopsis obovoid.

Distribution: Northern Queensland, New Guinea, Philippine Islands.

Chromosome number: x = 10.

This subgenus is based on one species, *S. laxiflorum* F. M. Bailey (Bailey, 1889), which has a somatic chromosome number of 40 with 20 bivalents at diakinesis and metaphase I.

4. *Sorghum* subgenus Sorghastrum (Nash) comb. nov.

Sorghastrum Nash ex Britton, Man. Fl. N. U. S. 71. 1901.

Sorghum § Sorghastrum Stapf, Fl. Trop. Afr. 9: 111. 1917.

Distribution: North, Central, and South America, south and west Africa.

Chromosome numbers: x = 10, 20, 30.

This subgenus had been considered a distinct genus by Nash (1901) but only a section of the genus *Sorghum* by Stapf (1917). Hackel (1889) included species of Sorghastrum within the subgenus Sorghum of the genus *Andropogon*. Nash (1901), Stapf (1917), and Hitchcock (1927, 1930, 1935) present excellent descriptions of Sorghastrum and its species.

The morphological characters of this subgenus, considered in the comparative study of the subgenera of the genus *Sorghum*, are listed in table 17 (p. 320). The following species are included: *S. elliottii, S. secundum, S. nutans, S. stipoides, S. parviflorum, S. minarum, S. trichopus, S. micratherum, S. rigidifolium, S. bipennatum, S. pogonostachyum,* and *S. incompletum.*

5. *Sorghum* subgenus Para-Sorghum (Snowden) comb. nov.

Sorghum § Para-Sorghum Snowden, Kew. Bull. Misc. Info., No. 5: 221. 1935.

Nodi culmorum dense barbati; rami primarii verticillati plerumque simplices; pulvinus parvus; spicularum sessilium callus obtusissimus aristaque plerumque longa; lodiculae ciliolatae, membranacae; spiculae pedicellatae masculae vel neutrae; fructus obovatus.

Nodes of the culms, at least the upper, bearded; primary branches of the panicle whorled, usually simple; pulvinus not prominent; callus of the sessile spikelets obtuse; awns of the sessile spikelets usually long; lodicules ciliate, membranaceous; pediceled spikelets staminate or neuter, lacking lemmas; mature caryopsis obovoid.

Distribution: Africa, Asia, Australia, Mexico, Guatemala.

Chromosome numbers: x = 5, 10.

The following species are included: *S. versicolor, S. purpureo-sericeum, S. nitidum, S. leiocladum,* and the anomalous species *S. trichocladum.* Complete descriptions of these species have been presented by Hackel (1889), Stapf (1917), and Hubbard (1938).

6. *Sorghum* subgenus Stiposorghum subgen. nov.

Nodi culmorum dense barbati; rami primarii verticillati, simplices; pulvinus parvus; spicularum sessilium callus acuminatus aristaque plerumque longissima; lodiculae ciliolatae, membranacae; spiculae pedicellatae masculae; fructus lato subulatus.

Nodes of the culms, at least the upper, bearded; primary branches of the panicle whorled, simple; pulvinus not prominent; callus of the sessile spikelets pointed; awns of

the sessile spikelets usually very long; lodicules ciliate, membranaceous; pediceled spikelets staminate; mature caryopsis broadly subulate.

Distribution: Northern Australia.

Chromosome numbers: x = 5, 10.

The following species are included: *S. intrans, S. stipoideum, S. brevicallosum,* and *S. plumosum.* Complete descriptions of the species in this subgenus, except *S. brevicallosum,* have been presented by Hackel (1889).

Sorghum brevicallosum sp. nov.

Planta annua; spiculae sessiles 7.5–8.5 mm. longae; callus acuminatus 1.0 mm. longus; aristae 38–43 mm. longae; pedicellae cicatrix levis.

Annual; sessile spikelets 7.5–8.5 mm. long; pointed callus 1.0 mm. long; awns of the sessile spikelets 38–43 mm. long; pedicel scar shallow.

Chromosome number: 2n = 10 (5^{II}).

The type specimen (Herbarium, University of California 753384) was grown in Berkeley, California, in the spring of 1948, from seed collected by W. Hartley in 1947 near Port Darwin.

THE SUBGENERA PARA-SORGHUM AND STIPOSORGHUM

Snowden (1935) and Hubbard (1938) assigned the following species to the section Para-Sorghum of *Sorghum:*

S. versicolor J. N. Anderss.
S. purpureo-sericeum Aschers. et Schweinf.
S. dimidiatum Stapf
S. nitidum (Vahl) Pers.
S. leiocladum (Hack.) C. E. Hubbard
S. plumosum (R.Br.) Beauv.
S. stipoideum (Ewart et White) Gardner et Hubbard

Although Hubbard, in listing the species of Para-Sorghum, specifically omits *S. intrans* F. Muell., this species definitely belongs in this group. The nodes are bearded; the primary branches are simple; and other morphological characters of the subgenus Stiposorghum are manifested. Furthermore, cytological data confirm the conclusion drawn from morphological evidence.

Pilger (1940) considers *S. trichocladum* a member of the former section Para-Sorghum of the genus *Sorghum* since this species has bearded nodes and simple panicle branches. No cytological data, however, are available.

No separate treatment of the subgenera Para-Sorghum and Stiposorghum has been published, but the species have been described in detail by several taxonomists (Hackel, 1889, Stapf, 1917, Hubbard, 1938) and have appeared in keys to the species of *Sorghum.* A cytological study (pp. 292–298) of these two subgenera was undertaken before a taxonomic study was inaugurated. Consequently, the taxonomy has been greatly influenced by the cytological data which actually furnish the basis for the classification of the species of both subgenera. Differences in the karyotypes of the species of the former section Para-Sorghum made clearly evident the presence of two distinct groups of species. These cytological differences are paralleled by several

morphological characters which permit the construction of a natural rather than artificial key. The species in each group, which are considered to be subgenera of the genus *Sorghum*, are listed below:

Para-Sorghum	Stiposorghum
S. versicolor	*S. intrans*
S. purpureo-sericeum	*S. stipoideum*
S. nitidum	*S. brevicallosum*
S. leiocladum	*S. plumosum*
S. trichocladum	

The key to the species of Para-Sorghum and Stiposorghum closely follows the cytological key presented on page 297 above. Evidence from cytology, morphology, and distribution was considered in the construction of this key.

TABLE 18

HEIGHT OF TALLEST TILLER AND LENGTH OF AWN IN THREE COLLECTIONS OF S. VERSICOLOR

Culture	No. of plants	Mean height (in.)	Range	No. of awns	Mean length (mm.)	S.E.	Range
V701	12	23.8	15.5–38	100	32.9 ±	0.4	27–38
V740	6	38.8	29.0–46	60	36.2 ±	0.7	30–44
V707	5	65.2	58.0–73	40	47.4 ±	1.3	39–54

The difference in the shape of the callus of the sessile spikelet in each subgenus is correlated with the appearance of the pedicel scar. The obtuse callus in Para-Sorghum appears to be inserted in the apex of the pedicel, and removal of the mature spikelet reveals a hollow as though the callus had been inserted in a socket. The pointed callus in Stiposorghum may be due to an oblique abscission layer. In *S. brevicallosum*, however, the very short, pointed callus may account for the shallow pedicel scar.

The difference in the shape of the mature caryopsis in each subgenus is best appreciated by referring to the camera lucida drawings in figure 3. The broadly subulate, mature caryopsis of species of the subgenus Stiposorghum is unique, not being found elsewhere in *Sorghum*.

Although certain species of Para-Sorghum and Stiposorghum are definitely taller than others, height has not been considered at all in their classification since very great differences were noted in plants of a given species grown in their native habitat and in Berkeley, California. For example, *S. stipoideum* may attain a height of 10 to 14 feet in the Northern Territory, Australia, but only 3 to 4 feet in Berkeley. Three collections of *S. versicolor* from different localities proved to be different in height when grown in Berkeley. Since each collection appeared to be rather uniform, a genetic basis for differences in height is suggested. A correlation between plant height and awn length in *S. versicolor* is indicated by the data in table 18. The tallest tiller of each plant was measured in inches from the crown to the base of the panicle. Awn length is expressed in millimeters.

A summary of the morphological characters and their measurements used in constructing the key to the species of the subgenera Para-Sorghum and Stiposorghum is found in table 19. The measurements represent a sample of not fewer than ten items for each character.

TABLE 19

MORPHOLOGICAL CHARACTERS AND THEIR MEASUREMENTS IN SPECIES OF PARA-SORGHUM AND STIPOSORGHUM

Para-Sorghum*

Character	*S. versicolor*	*S. purpureo-sericeum*	*S. nitidum*	*S. leiocladum*
Callus	Obtuse	Obtuse	Obtuse	Obtuse
Callus length (mm.)	.....	.....	.....	.....
Seed shape	Obovoid	Obovoid	Obovoid	Obovoid
Pedicel scar (sessile spikelet)	Transverse hollow	Transverse hollow	Transverse hollow	Transverse hollow
Sessile spikelet (mm.)	5.0–7.0	7.0–9.0	4.0–5.5	6.0–8.0
Pediceled spikelet (mm.)	2.5–5.0	7.0–8.0	4.5–5.0	5.0–6.0
Awn length (mm.)	28–54	27–34	12.5–18	17–24
Glume color (sessile spikelet)	Brown to black	Reddish purple	Brown	Brown
Growth habit	Annual	Annual	Perennial	Perennial

Stiposorghum

Character	*S. intrans*	*S. plumosum*	*S. brevicallosum*	*S. stipoideum*
Callus	Pointed	Pointed	Pointed	Pointed
Callus length (mm.)	5.0–7.5	1.5–2.5	1.0	3.0–5.0
Seed shape	Subulate	Subulate	Subulate	Subulate
Pedicel scar (sessile spikelet)	Oblique level	Oblique level	Oblique shallow	Oblique level
Sessile spikelet (mm.)	8.0–10	5.5–6.0	7.5–8.5	7.5–11
Pediceled spikelet (mm.)	12–13	6.5–7.5	5.5–8.0	8.0–11
Awn length (mm.)	75–85	28–50	38–43	46–63
Glume color (sessile spikelet)	Straw to brown	Brown	Brown	Brown
Growth habit	Annual	Perennial	Annual	Annual

* *S. trichocladum* was not included since living material was not available.

THE SUBGENUS PARA-SORGHUM

Of the six collections of *S. purpureo-sericeum*, five from India and Africa appear to correspond to the published descriptions of this species and with herbarium specimens. One collection from Poona, India (P7100), however, seems to be distinct from the others. The glumes of the sessile spikelets are extremely hairy and the plants are distinctly more slender than the plants of any other collection. The glume hairs are so dense that it is not possible to see the glume epidermis. According to a communication from S. Solomon, University of Poona, this unusual form of *S. purpureo-sericeum* does not seem to have been introduced into India. A study of the floral structure of

the Poona collection yields no marked differences from the other collections of the species. An examination of the Kew collection of Para-Sorghum reveals that Stapf had considered granting this form specific status but had never published a description. Judging from the specimens, the Poona form is probably not slender in its native habitat. Since hybridization between plants from a Sudan and a Poona collection indicates that no sterility barrier is present (see p. 317), and since no evidence is available concerning the genetic basis of the glume pubescence, it would seem needless to propose a new species here for the Poona collection of *S. purpureo-sericeum*. However, it is desirable to note the presence of so distinct a form by proposing the subspecies *S. purpureo-sericeum* subsp. *deccanense*.* Also, this subspecies appears to be restricted to western India.

Information is available pertaining to the taxonomic relationship between *S. purpureo-sericeum* and *S. dimidiatum*, although no specific mention has been made of this point. Ayyanger and Ponnaiya (1941) reported that the glume constriction characteristic of the latter species was due to a single gene difference, recessive to the wholly indurate glume characteristic of *S. purpureo-sericeum*, but they offered no supporting evidence. J. G. O'Mara (comm.), moreover, found that pairing of chromosomes in a hybrid between the two species was regular and that meiosis appeared to be normal. A monogenic ratio would be expected if the difference between the glume characters were due to a single gene and meiosis were regular. Supernumerary or B chromosomes have been found only in *S. purpureo-sericeum* subsps. *typicum* and *deccanense* and *S. dimidiatum*. The similarity of the position and morphology of the nucleolus-organizing region at pachytene in both *S. purpureo-sericeum* and *S. dimidiatum* indicates a close relation between them. No sterility barriers appear to exist between these two species (see p. 317); however, *S. dimidiatum* seems able to maintain itself in its restricted range even though its distribution adjoins that of *S. purpureo-sericeum* (see fig. 4). Collections of one of these species from regions somewhat removed from the regions of the other have yielded plants resembling the opposite species, i.e., a seed enclosed in glumes characteristic of *S. dimidiatum* and received as an *S. dimidiatum* seed yielded a plant resembling *S. purpureo-sericeum* in having wholly indurate glumes, and vice versa. Whether constricted glumes are associated with some selective advantage in the restricted range of *S. dimidiatum* is not known. Consequently, on the basis of all the evidence presented, *S. dimidiatum* Stapf is here assigned to subspecific rank as *S. purpureo-sericeum* subsp. *dimidiatum* comb. nov. (Stapf, Fl. Trop. Afr. 9:140, 1917). Since the only difference between *S. purpureo-sericeum* subsp. *dimidiatum* and the other subspecies is the constriction of the glumes of the sessile spikelets and the essentially glabrous glumes, a detailed description does not seem necessary.

Although *S. versicolor* superficially resembles *S. purpureo-sericeum*, evidence from cytology (pp. 287 ff.), distribution (pp. 333 ff.), and breeding

* *Sorghum purpureo-sericeum* subsp. *deccanense*. Glumae spicularum sessilium dense pubescentes, omnino induratae.

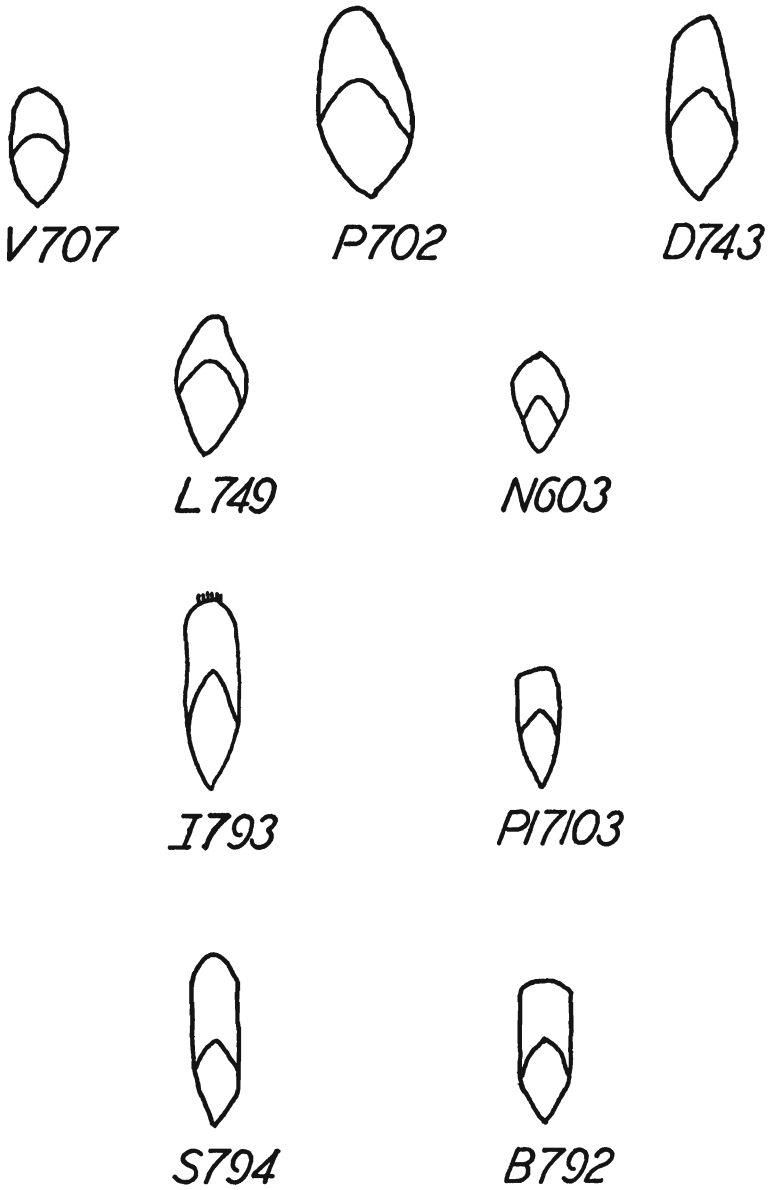


Fig. 3. Camera lucida drawings (*ca.* × 5) of mature caryopses of species of Para-Sorghum and Stiposorghum (*Sorghum*).

behavior (pp. 317 ff.) makes the distinction based on morphology even more convincing. *Sorghum versicolor* is more readily distinguished from the other subspecies than from *S. purpureo-sericeum* subsp. *typicum*, nom. nov.

For the purpose of constructing a key to the species of Para-Sorghum, it was difficult to find stable characters distinguishing the annual from the perennial species. Perenniality versus annuality is not a very useful character to the grass taxonomist examining herbarium specimens. Nevertheless, living

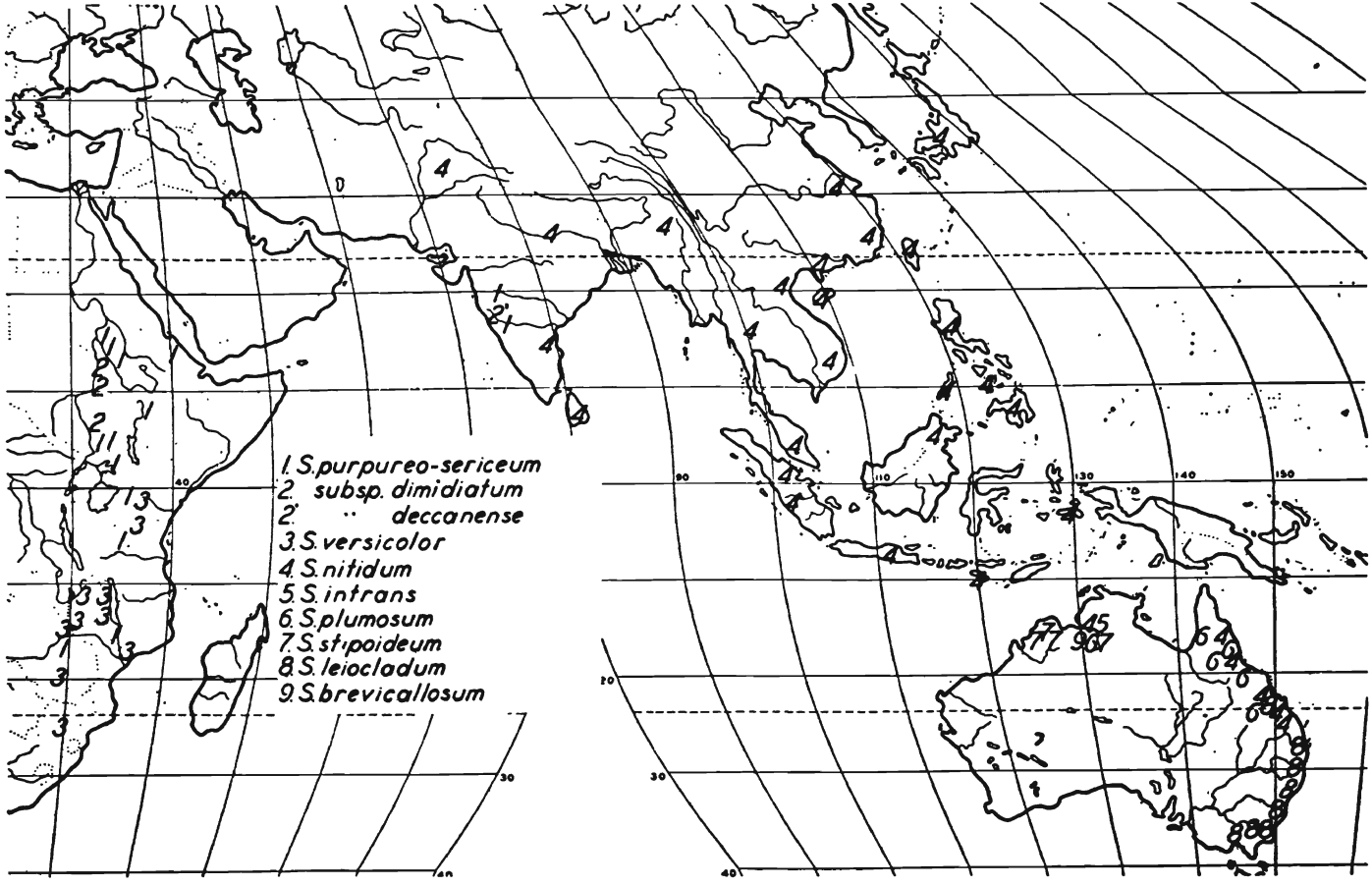


Fig. 4. Distribution of species of the subgenera Para-Sorghum and Stiposorghum (*Sorghum*).

plants of the perennial species are easily distinguished from the living plants of the annual species. Also, field notes would certainly include reference to strong perenniality. Distribution, moreover, would help, inasmuch as the annual species are African, except *S. purpureo-sericeum* subsp. *deccanense* in western India, while the perennial species occur east of central India to Australia (see fig. 4). In general, the leaves of the perennial species are long and narrow whereas the leaves of the annual species are somewhat shorter and broader. A certain amount of overlapping, however, is found, thus making leaf length and width unreliable as a diagnostic character. Awn length proved reasonably reliable and was therefore considered a valuable secondary diagnostic character.

Sorghum leiocladum was formerly confused with *S. plumosum* (Hubbard, 1938). Although these species may have appeared superficially similar since both have long, narrow leaves and are strongly perennial, the former species belongs in Para-Sorghum and the latter in Stiposorghum. In the field, *S. leiocladum* has a growth habit that is somewhat prostrate as compared with the erect appearance of *S. nitidum,* and the difference becomes more marked after the first year of growth.

Two forms of *S. nitidum* have been reported in the literature: *muticum* and *aristatum.* The former lacks awns; the latter is awned. Whether the presence or absence of an awn in this species is due to a single gene or several genes is not known. The awnless phase, moreover, has been reported from diverse regions. Lacking a distinct range of distribution, it would not seem necessary to maintain these names. However, since *S. nitidum* f. *muticum* is the only awnless form of Para-Sorghum or Stiposorghum, it may be retained.

Pilger (1940) has placed *S. trichocladum* in the section Para-Sorghum of the genus *Sorghum.* According to the key to the subgenera of the genus *Sorghum,* this species has been placed in the subgenus Para-Sorghum. Unfortunately, no living material has been available for a morphological and cytological analysis. Morphologically, *S. trichocladum* is distinct from the other species in Para-Sorghum, which form a homogeneous group. Moreover, this species is the only member of Para-Sorghum found in the New World. Whereas the other species have ciliate lodicules and usually staminate pediceled spikelets, *S. trichocladum* has glabrous lodicules and sterile pediceled spikelets. It is not unlikely that a future morphological and cytological study of living material of *S. trichocladum* may led to the establishment of an additional subgenus in the genus *Sorghum.*

THE SUBGENUS STIPOSORGHUM

The annual species, *S. intrans,* is unique among the species of Stiposorghum and Para-Sorghum in having a tuft of erect hairs at the apex of the ovary and mature caryopses. The prominent, pointed callus, longest of all in the species of Stiposorghum, is only a little shorter than the sessile spikelet bearing it. The strongly developed awn is the longest and thickest to be found in the genus *Sorghum.* In the light of all these specialized structures, *S. intrans* appears to be the most advanced species in the genus.

The shorter callus and glabrous ovary and mature caryopsis are common to the remaining species in Stiposorghum. Of these three species, *S. plumosum* is strongly perennial while both *S. brevicallosum* and *S. stipoideum* are annuals. Also, the former species is polyploid and the latter two species are diploid. Such a correlation between polyploidy and perenniality also occurs in the subgenus Para-Sorghum. Although *S. brevicallosum* and *S. stipoideum* may superficially resemble each other morphologically and cytologically, experiments indicate that these species do not hybridize (see pp. 318 ff.).

Sorghum plumosum and *S. brevicallosum* have the shortest callus in Stiposorghum. Whereas the callus of the former species is 1.5–2.5 mm. long, the callus of *S. brevicallosum* is only 1.0 mm. long and hardly noticeable because of the dense, basal glume hairs. *Sorghum brevicallosum* is the only species in the subgenus with a shallow pedicel scar, although a slight depression may be found in the pedicel scar of plants of *S. plumosum* approaching the former species in shortness of the callus.

A KEY TO THE SPECIES OF PARA-SORGHUM AND STIPOSORGHUM

A. Callus obtuse, less than 0.5 mm. long; pedicel scar transverse and hollow; mature caryopsis obovoid ..... Para-Sorghum
  B. Lodicules ciliate; pediceled spikelets usually staminate.
    C. Annual (or weakly perennial); awns longer than 25 mm. long.
      D. Sessile spikelets 5.0–7.0 mm. long, brown-black to black; pediceled spikelets 2.5–5.0 mm. long, often sterile ..... *S. versicolor*
      DD. Sessile spikelets 7.5–9.0 mm. long, reddish purple to red; pediceled spikelets 6.0–8.0 mm. long, always staminate.
        E. Glumes of sessile spikelets wholly indurate, essentially glabrous, except at base ..... *S. purpureo-sericeum*
        EE. Glumes of sessile spikelets wholly indurate, densely pubescent ..... *S. purpureo-sericeum* subsp. *deccanense*
        EEE. Glumes of sessile spikelets constricted, indurate below and membranaceous above the constriction, essentially glabrous, except at base ..... *S. purpureo-sericeum* subsp. *dimidiatum*
    CC. Strongly perennial; awns shorter than 25 mm. long.
      F. Sessile spikelets 4.0–5.5 mm. long; 4–24 panicle branches in a whorl; midrib on upper surface of leaf blade prominent, white ..... *S. nitidum*
      FF. Sessile spikelets 6.0–8.0 mm. long; not more than 6 panicle branches in a whorl; midrib on upper surface of leaf blade more or less obscure, dull green ..... *S. leiocladum*
  BB. Lodicules glabrous; pediceled spikelets never staminate ..... *S. trichocladum*
AA. Callus pointed, 1.0–7.5 mm. long; pedicel scar more or less oblique, level or shallow; mature caryopsis broadly subulate ..... Stiposorghum
  G. Summit of ovary and mature caryopsis pubescent with erect hairs in a tuft; callus 5.0–7.5 mm. long ..... *S. intrans*
  GG. Summit of ovary and mature caryopsis glabrous; callus 1.0–4.0 mm. long.
    H. Sessile spikelets 6.5–7.5 mm. long; strongly perennial ..... *S. plumosum*
    HH. Sessile spikelets 7.5–11.0 mm. long; annual.
      I. Callus 1.0 mm. long; awns less than 50 mm. long ..... *S. brevicallosum*
      II. Callus 3.0–4.0 mm. long; awns 85–90 mm. long ..... *S. stipoideum*

Distribution

The genus Sorghum

Of the six subgenera of *Sorghum,* only Sorghastrum and Para-Sorghum have representatives in the Western Hemisphere. The other subgenera are restricted to the Old World.

Eu-Sorghum.—The subgenus Eu-Sorghum includes the economically important species of *Sorghum, S. vulgare,* cultivated for grain, fodder, and sorghum molasses. According to Brandes (1947): "The recognized wild prototypes of domesticated sorgo (and of all cultivated sorghums) are limited to Africa south of the Sahara, and range far down into the Temperate Zone of South Africa." One species, *S. halepense,* appears to have originated in the eastern Mediterranean regions, but the limits of its range of distribution are not accurately defined (map 1). The species of Eu-Sorghum have been introduced into the agriculture of countries throughout the world.

Chaetosorghum.—The subgenus Chaetosorghum is represented, at present, by only one species, *S. macrospermum,* and this species, in turn, is represented by only one collection, from the Port Darwin–Katherine region of the Northern Territory, Australia (map 1).

Heterosorghum.—The subgenus Heterosorghum is currently represented by only one species, *S. laxiflorum.* This species occurs in northern Queensland, New Guinea, and the Philippine Islands (map 1).

Sorghastrum.—Species of the subgenus Sorghastrum are found in central and western Africa and North, Central, and South America, including the Antilles (map 1). In the Western Hemisphere, Sorghastrum appears to be restricted to the regions of the two continents facing the Atlantic Ocean. The range of distribution of this subgenus would be continuous, in a sense, if the ocean barrier did not exist. In fact, one species of Sorghastrum, *S. incompletum,* has been reported from both hemispheres.

Para-Sorghum.—The range of distribution of Para-Sorghum extends from the Union of South Africa in a discontinuous arc through southern and eastern coastal Asia and the East Indies to Australia (fig. 1, p. 296). In Africa, Para-Sorghum extends from the northern areas of the Union of South Africa through eastern central Africa to Eritrea on the Red Sea. A gap exists between the African range of distribution and the Asiatic-Australian range. This gap includes Arabia, Iran, and the western part of India bordering on Iran. The Asiatic-Australian range extends from the western central provinces of India through coastal tropical and semitropical Asia to Australia. The East Indies serve as a bridge between the Asiatic mainland and Australia. The Australian species of Para-Sorghum are restricted to the coastal regions from northern Australia to Victoria. According to W. Hartley (oral comm.), an extension of the interior desert of Australia reaches the coast in northern Western Australia, constituting a barrier preventing the migration of species of Para-Sorghum westward. Also, the geological history of Australia indicates that the continent is divided into two parts so that the eastern half, containing the species of Para-Sorghum, is not too closely related flo-

ristically to the western half. This division may have supplied the basis for the apparently abrupt ending of the distribution of Para-Sorghum in Victoria. Also, the summer climate of South Australia is extremely dry.

The information concerning the distribution of the Australian species of Para-Sorghum must necessarily be considered incomplete since the range of distribution includes regions that are relatively unexplored or, at least, poorly sampled. Consequently, the apparent restriction of Para-Sorghum to the coastal regions may be a reflection of the inadequate collecting in the more interior areas of Australia, discounting the desert. Almost no information is available concerning the occurrence of species of Para-Sorghum in the islands of the East Indies immediately adjacent to Australia.

Only two species of Para-Sorghum have been reported from Africa: *S. versicolor* and *S. purpureo-sericeum,* including the subspecies *dimidiatum.* Of these two species, only *S. purpureo-sericeum* as the subspecies *deccanense,* found in western India, occurs elsewhere. One collection of *S. versicolor* (V740) was received from India, but no information was supplied concerning the origin of this material. Nothing has been found in the literature nor from personal communications to indicate that it is native to India.

Sorghum versicolor has the most southerly distribution of the African species and has been reported from the Waterberg District of the Union of South Africa, in the Transvaal, Southern and Northern Rhodesia, Nyassaland, Mozambique, Kenya, and Tanganyika. A. S. Thomas (comm.) states that it is not found in Uganda, thus suggesting that Tanganyika may be its northern limit. In general, *S. versicolor* extends from the equator southward through east-central Africa to the Union of South Africa (fig. 4).

Sorghum purpureo-sericeum has been reported from Northern Rhodesia, Nyassaland, Kenya, Uganda, Tanganyika, Sudan, Abyssinia, Eritrea, and India, and only in the southern part of the range does it come in contact with *S. versicolor. Sorghum purpureo-sericeum* has the most northerly distribution of the African species, extending from lat. 15° S to the Red Sea at Eritrea (fig. 4).

Sorghum purpureo-sericeum subsp. *dimidiatum* occupies the most restricted range of distribution in Africa (fig. 4). A. W. Punter, in a communication to Hubbard (1933), reports it to occur only west of the Blue Nile and between the Blue and White Niles as far north as lat. 13° 30′ N in the Jebel Moya District of the Blue Nile Province in the Sudan and as far south as lat. 10° N in the Sudan. This latter limit has been extended to lat. 5° N according to a collection received from C. O. Grassl. Broun and Massey (1929) report both *S. purpureo-sericeum* subsps. *typicum* and *dimidiatum* from El Fung Province of the Sudan, but this province straddles the Blue Nile. It is possible that the former may occur on the eastern side of the river and the latter on the western side. Punter makes a point of mentioning that the subspecies *dimidiatum* does not grow in association with any other wild or cultivated species of *Sorghum.* As previously mentioned, no evidence is available concerning the selective pressure operating to restrict this subspecies to its relatively small range of distribution adjoining that of *S. purpureo-sericeum*

subsp. *typicum* with which it easily hybridizes (see p. 317), nor is there any evidence explaining why the Blue Nile should serve as a boundary between the two ranges of distribution.

Of the African species, only *S. purpureo-sericeum* is found in Asia (fig. 4). As mentioned in the taxonomic discussion, the Indian form is here considered a subspecies, *S. purpureo-sericeum* subsp. *deccanense*. If we assume that the gap between the African and Indian distributions is not a reflection of inadequate collecting, then the present discontinuous range may have formerly been continuous. Cytological and morphological evidence, the absence of sterility barriers between African and Indian collections of this species, and the paralleling situation in the range of distribution of *Cleistachne* (fig. 1) support such a suggestion. There is no information concerning the nature of the factors involved, excepting increased aridity, which led to the elimination of *S. purpureo-sericeum* in the regions comprising the gap (fig. 4).

The other two species of Para-Sorghum, *S. nitidum* and *S. leiocladum*, both polyploids, are restricted to Asia and Australia (fig. 4). The former species occurs on the Asiatic mainland and the neighboring islands, and in the East Indies and Australia; the latter species appears to be restricted to southeastern Australia. According to the available information, the ranges of these two species overlap slightly in Queensland.

Sorghum nitidum, with the most extensive range of distribution of all the species of Para-Sorghum and Stiposorghum, has been reported from India, Malaya, Thailand, Indo-China, China, Japan, Formosa, Philippine Islands, Hainan, Sumatra, Java, British North Borneo, and the Northern Territory and Queensland in Australia (fig. 4). No information has yet been found indicating that this species occurs in New Guinea, even in that part of the island nearest Australia.

Sorghum leiocladum occurs in Queensland, New South Wales, and Victoria (fig. 4). Except for one report from Sarina, Queensland, this species does not seem to extend beyond the Tropic of Capricorn. Since diploid races of this species have not yet been found and may no longer exist, no correlation between diploids and tetraploids and their ranges of distribution may be made.

According to J. R. Swallen, U. S. National Museum (comm.), *S. trichocladum* has been reported from southwestern Mexico in the states of Sinaloa, Nayarit, Michoacan, Mexico, Guerrero, and Oaxaca, and in the department of Chimaltenango, Guatemala (fig. 5). Considering the known distribution of the subgenus Para-Sorghum, the distribution of this species seems anomalous. All the other species are restricted to the semitropical and tropical regions of the Eastern Hemisphere. The subgenus Sorghastrum, however, includes species from Africa and Mexico.

The distribution of the species of Para-Sorghum, excepting *S. trichocladum*, presents an interesting problem inasmuch as the range of distribution of the allotetraploid species, *S. nitidum*, is found between that of the diploid, African species on the west and an Australian species to the east. The combined evidence from cytology, breeding behavior, and distribution

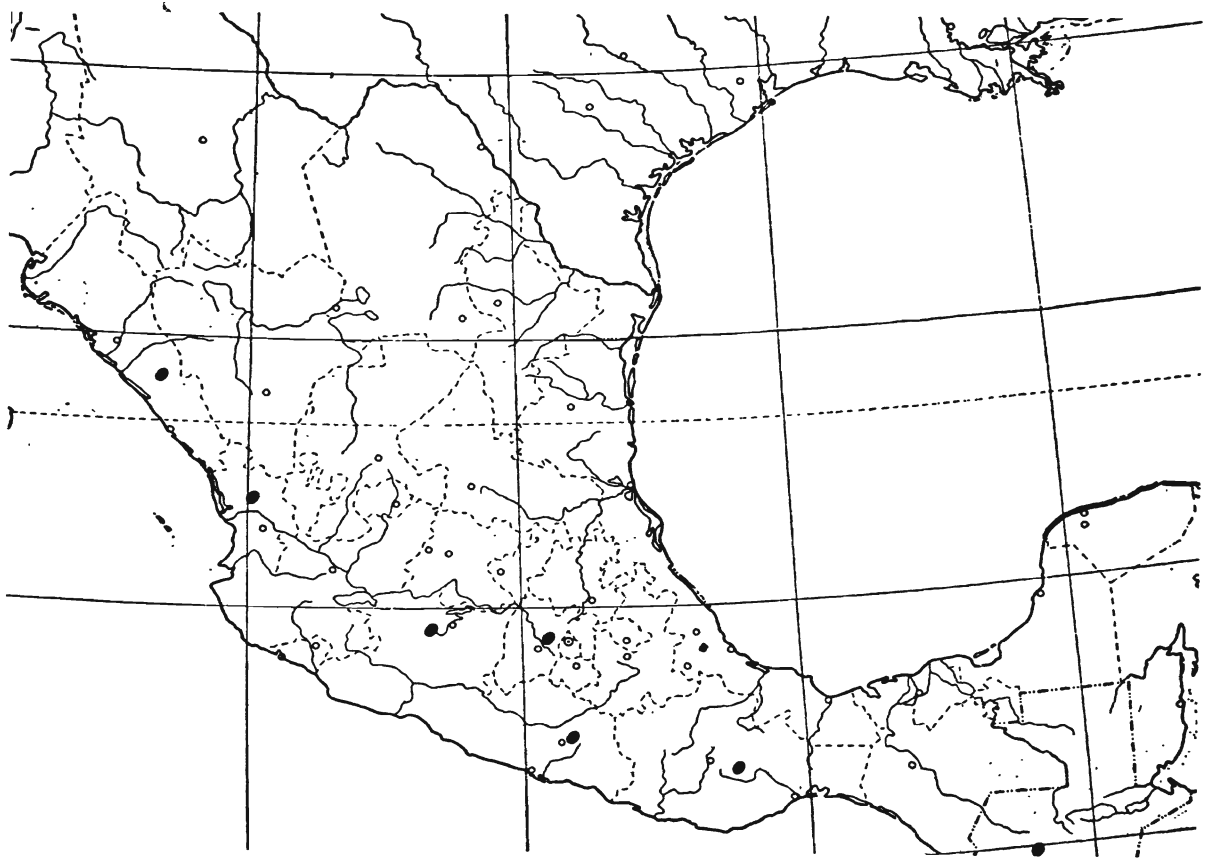


Fig. 5. Distribution of *Sorghum trichocladum* in Mexico and Guatemala by states and not by specific regions of collection.

supplies the basis for a hypothesis concerning the probable origin of *S. nitidum,* the probable center of origin of the subgenera Para-Sorghum and Stiposorghum, and the probable center of origin of the Sorghastrae. This hypothesis considers the following observations:

1. The range of distribution of Para-Sorghum, except *S. trichocladum,* extends from Africa through Asia to Australia.

2. The allotetraploid species, *S. nitidum,* occupies a range of distribution in Asia (and Australia) between that of African, diploid species and an Australian species, *S. leiocladum,* which may still have diploid representatives or may have had them in the past.

3. The nucleolus-organizing region at pachytene in *S. purpureo-sericeum* is subterminal while the nucleolus-organizing region at the same stage in *S. versicolor, S. leiocladum,* and *S. nitidum* is terminal and similar in morphology in all three species (p. 294).

4. *Sorghum versicolor* does not hybridize with *S. purpureo-sericeum* (p. 317).

One of the three continents—Africa, Australia, or Asia—may be considered the center of origin of *S. nitidum.* To assume that Africa may have been the center of origin would require this species and *S. leiocladum* to migrate from one end of the present range to the other; to assume that Australia may have been the center of origin would require the African species to make a similarly long migration. Assuming that the present range of distribution of *S. nitidum* in Asia includes the probable center of origin of this species, then the species involved in the hybridization, which ultimately resulted in the allotetraploid species, must have once had at least overlapping ranges of distribution on this continent. Also, it would follow that the subgenus Para-Sorghum may have had its center of origin in Asia. In response to some unknown change in the environment, the diploid species may have migrated while the allotetraploid species, *S. nitidum,* merely expanded its range. The present distribution of Para-Sorghum suggests a two-pronged path of migration from a center of origin in Asia, probably the southeastern region (fig. 1). The present distribution of the diploid, African species, *S. purpureo-sericeum,* may have been interrupted by some environmental factor after the species had reached Africa, thus accounting for the geographical isolation of *S. purpureo-sericeum* subsp. *deccanense* in India. *Sorghum nitidum* seems to have accompanied *S. leiocladum* in the migration of the latter species to Australia via the East Indies.

According to the hypothesis presented on pages 298–304, *S. nitidum* originated from an interspecific hybridization followed by a doubling of the chromosome number. The cytological data from an analysis of an interspecific hybrid between *S. leiocladum* and *S. nitidum* support the hypothesis that *S. leiocladum* may have been one of the species involved in the origin of *S. nitidum.* Moreover, the other species, as yet unknown, may have been relatively closely related to *S. leiocladum.* Differences in the position and morphology of the nucleolus-organizing region at pachytene make *S. purpureo-sericeum* an unlikely candidate; differences in chromosome size and chiasma

frequency make *S. versicolor* equally unlikely. Nothing is known concerning the cytology of *S. trichocladum*. Consequently, *S. nitidum* may be considered to have resulted from an interspecific hybridization, followed by chromosome doubling, between a perennial diploid species (*S. leiocladum* ?) and an unknown related species, and this interspecific hybridization probably occurred in southeastern Asia.

Stiposorghum.—The species of the subgenus Stiposorghum appear to be restricted to northern Australia and, probably, the immediately adjacent islands of the East Indies (fig. 1). All four known species have been reported from the Port Darwin–Katherine region of the Northern Territory. Since little collecting has been done in the Northern Territory, conclusions drawn from the distribution of these species must be tentative and cautious.

According to all the available information, *S. intrans* appears to be restricted to the Port Darwin–Katherine area (fig. 4). Although this species is too distinct morphologically to be overlooked or misclassified, no representatives have been reported from any other area either to the east or west.

Sorghum brevicallosum is represented by only one collection from the Port Darwin–Katherine area (fig. 4).

Both *S. stipoideum* and *S. plumosum* have relatively wide distributions (fig. 4). The former species extends westward from the Port Darwin–Katherine area to northern Western Australia; the latter species extends eastward from the Port Darwin–Katherine region to northern Queensland.

In general, Stiposorghum seems to have a more homogeneous range of distribution, considering its restriction to northern Australia as compared with the tricontinental spread of Para-Sorghum. The cytological data add weight to this idea of a greater degree of homogeneity among the species of Stiposorghum than among those of Para-Sorghum.

Since Stiposorghum appears to be restricted to northern Australia, this continent may therefore be considered the probable center of origin of this subgenus. No evidence, however, is available for such a hypothesis. As a matter of speculation, the progenitor of Stiposorghum may have migrated to Australia from the Asiatic mainland and then given rise to the species now known.

THE GENUS CLEISTACHNE

According to Bews (1929), species of *Cleistachne* occur in eastern, tropical Africa and western India (fig. 1). This distribution is interesting in view of a similar distribution of a species of Para-Sorghum, *S. purpureo-sericeum.*

PROBABLE CENTER OF ORIGIN OF THE SORGHASTRAE

According to the hypothesis proposed for the probable center of origin of Para-Sorghum, this subgenus may have had its origin in Asia, perhaps in southeastern Asia. The hypothesis may be extended to include the Sorghastrae. The six subgenera of the genus *Sorghum* may be grouped on the basis of morphological affinity so that Eu-Sorghum and Chaetosorghum, Heterosorghum and Sorghastrum, and Para-Sorghum and Stiposorghum constitute smaller circles of affinity. Whereas Eu-Sorghum appears to be

restricted to Africa and the Mediterranean region, Chaetosorghum seems to be restricted to Australia. Comparing the ranges of Heterosorghum and Sorghastrum, the former subgenus probably is restricted to Australia, New Guinea, and the Philippine Islands; the latter, in Africa and the Western Hemisphere. From the hypothesis proposed for the probable center of origin of Para-Sorghum, migration in two directions, southeast and southwest, or both at the same time from a center in southeastern Asia (India, Malaya, Indo-China, southeastern China), offers a logical explanation for the occurrence of related groups of species in the two widely separated regions, Australia and Africa.

On the basis of this hypothesis, the advanced genus *Cleistachne* and the advanced subgenus Stiposorghum may have had their genesis after the migration had started. As a speculation, it is possible that the gap in the range of distribution of Para-Sorghum and *Cleistachne* may have occurred after the migration had extended into Africa on the west. In the east, the land bridge from the Asiatic mainland to Australia may have been broken after the migration had extended into Australia.

RELATIONSHIP AND PHYLOGENY OF THE SORGHASTRAE

Morphology, Relationship, and Phylogeny

The genera of the Andropogoneae fall into two groups: one with the joints and pedicels relatively slender, neither approximate nor fused; the other, with the joints and pedicels more or less stout and approximate or fused to form a receptacle for the sessile spikelet. The former group is considered the more primitive on the basis of the relatively less protection afforded the sessile spikelet. Hackel (1889) recognizes three subtribes in the first group: Dimereae, Sacchareae, and Euandropogoneae. Bews (1929) combined the first two as the Saccharinae and renamed the third the Andropogoninae. In the Saccharinae, the spikelets are usually all alike; in the Andropogoninae, the spikelets of each pair are different in sex, form, or both, or male or neuter should they be alike. This distinction between the subtribes is based on the assumption that the step from a perfect pediceled spikelet to any other condition, including complete absence of the spikelet or even the pedicel, is the basic and most important change possible. In other words, once the spikelets become unlike in some manner, other changes making the paired spikelets still more unlike are secondary. This writer is not aware of any evidence evaluating the relative importance of the different changes which have affected either the sex or form of the pediceled spikelet. However, these subtribes do represent, in a broad sense, circles of affinity within the tribe.

As previously mentioned (p. 319), generic boundaries in the Andropogoneae are poorly defined. Since a single character was considered insufficient for establishing a genus, Hackel (1889) used a combination of morphological characters. Consequently, a very large number of species was included in the single genus *Andropogon*. This extremely unwieldy and essentially artificial genus was divided into numerous subgenera. Subsequent taxonomic work, however, has resulted in the elevation of several subgenera to generic

rank, and sometimes to the creation of new genera. Bews (1929) lists about thirty genera in the subtribe Andropogoninae.

Certain evolutionary trends found in the Sorghastrae merit discussion, since any attempt to understand relationships within this complex of genera must take them into consideration. Although it is possible to set up combinations of morphological characters to delimit one group of species from another, it is very difficult to make these combinations all-inclusive or all-exclusive. Consequently, we are faced with the same dilemma that confronted Hackel. However, the creation of subgenera within one large genus and then the consideration of the subgenus as the unit of classification, following Hackel, may well be the solution. If any subgenus were elevated to generic rank, the entire structure would be suspect. Either all subgenera have equivalent taxonomic meaning or the entire system is open to question. Consequently, each group must be carefully examined to determine its taxonomic status. Although such a procedure may seem straightforward, difficulties in its application soon become apparent. Arranging species on the basis of single characters brings together species obviously unrelated on the basis of the sum total of characters. Consequently, each character will be considered from a phylogenetic point of view in an effort to resolve the problem of classification and relationships within the Sorghastrae. The following morphological characters will be discussed in order: (1) the pediceled spikelet, (2) panicle branching, (3) glume nervation, (4) awn and callus development, and (5) the lodicules. The phylogenetic interpretation of chromosome number and morphology will be considered in detail later.

1. *The pediceled spikelet.*—A clearly defined evolutionary trend is apparent in this organ. Hackel (1889) takes special note of the gradual reduction of the pediceled spikelet from a staminate to a sterile condition to complete suppression of the spikelet and finally of the pedicel. This reduction of the pediceled spikelet takes the following course in the Sorghastrae:

1. Pediceled spikelet present.
   a. Stamens present ..... Eu-Sorghum, Para-Sorghum, Stiposorghum
   b. Stamens absent ..... Eu-Sorghum, Para-Sorghum, Stiposorghum
   c. Lemmas and palea absent ..... Chactosorghum, Heterosorghum
2. Pediceled spikelet absent ..... Sorghastrum
3. Pedicel absent ..... *Cleistachne*

It is interesting to note that both staminate and sterile pediceled spikelets may occur on the same panicle in both Eu-Sorghum and Para-Sorghum. Whenever stamens are absent, the spikelet also lacks a palea but the lemmas are usually present. Consequently, it appears that the presence or absence of stamens is relatively unimportant in the evolutionary trend. Once the lemmas are lacking, however, only the glumes remain. Therefore, categories 1*a* and 1*b* may be considered as one with the following description: lemmas present, stamens present or absent. The following scheme is suggested for the course of this reduction of the pediceled spikelet:

Eu-Sorghum, Para-Sorghum, Stiposorghum → Chaetosorghum, Heterosorghum → Sorghastrum → *Cleistachne*.

A comparison of basic chromosome numbers presents an interesting situation wherein the basic chromosome number of 10, Para-Sorghum and Stiposorghum excepted, is maintained until the terminus of the trend where a basic chromosome number of 9 is found in *Cleistachne* (*C. sorghoides*).

2. *Panicle branching.*—The spreading type of panicle with secondary branching may be considered the more primitive type among the grass inflorescences. Indeed, this character, i.e., panicle branching, plays an important role among the characters used to delimit tribes in the Gramineae. Within the Sorghastrae, only two situations have been observed: (1) divided or (2) simple panicle branches. In the first category are found Eu-Sorghum, Sorghastrum, Heterosorghum, and *Cleistachne;* in the second category, Para-Sorghum, Stiposorghum, and Chaetosorghum. The latter category may be considered more advanced than the former and to have been derived from it.

3. *Glume nervation.*—Although many-nerved versus few-nerved glumes may represent a primitive versus an advanced situation in the Gramineae, little information is available concerning the phylogenetic interpretation of glume nervation in the Andropogoneae, much less the subtribe Andropogoninae. However, differences in the number of nerves in the glumes do have taxonomic significance. There is no essential difference in the number of nerves of the lower glume of the sessile spikelets in Para-Sorghum, Stiposorghum, Sorghastrum, and *Cleistachne* (5–10 nerves). Eu-Sorghum and Heterosorghum may be included in another group with the lower glumes having 10 to 16 nerves. The final category includes Chaetosorghum with 15 to 22 nerves in the lower glume.

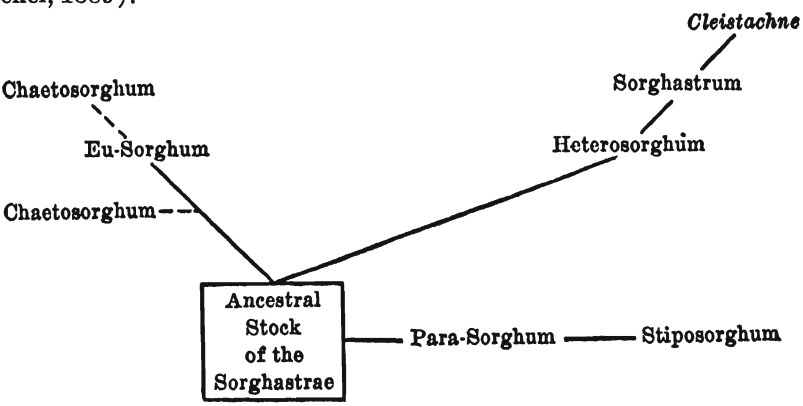
4. *Awn and callus development.*—The production of a well-developed awn and callus is usually considered a mark of advancement, since these structures function for more efficient seed dispersal and to enhance the opportunity for germination. Whereas Eu-Sorghum, Sorghastrum, Heterosorghum, and *Cleistachne* do have awns, these awns never reach the level of development found in Para-Sorghum, Stiposorghum, and Chaetosorghum. Moreover, the callus in the former group is obtuse and extremely short. However, Chaetosorghum with a well-developed awn has an obtuse, very short callus. Consequently, it seems reasonable to assume that awn and callus development, while a mark of advancement, need not be correlated. However, in the subgenus Stiposorghum the development of both awn and callus suggests that this group represents the end point in this evolutionary trend. Within the group of subgenera lacking a well-developed callus, Chaetosorghum marks the end of an evolutionary trend in awn development.

5. *The lodicules.*—While differences in the morphology of the lodicules do not seem to have any phylogenetic meaning, they certainly have taxonomic significance. An outstanding difference concerns the presence or absence of pubescence. Pubescence in the Sorghastrae is usually restricted to tufts of long hairs at the corners of the lodicule. Eu-Sorghum, Heterosorghum, Para-Sorghum, Stiposorghum, and *Cleistachne* have more or less pubescent lodicules; Sorghastrum and Chaetosorghum have glabrous lodicules.

The shape and texture of the lodicules have taxonomic significance. The cup-shaped lodicules in Sorghastrum and Chaetosorghum are thick and glabrous. The membranaceous lodicules of Eu-Sorghum, Heterosorghum, Para-Sorghum, Stiposorghum, and *Cleistachne* are either cup-square, cup-fan, or cup-urn in shape and more or less pubescent.

With respect to relative size of the upper and lower glumes of the pediceled spikelet, in all groups but Heterosorghum the upper glume is only slightly shorter than the lower glume. In Heterosorghum, however, the upper glume never exceeds half the length of the lower glume.

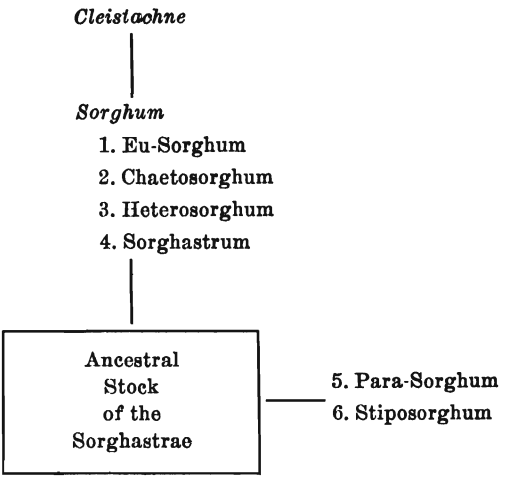
If all the different morphological characters are evaluated in terms of their phylogenetic and taxonomic significance, and if cytological data are considered, it is possible to construct a phylogenetic scheme consistent with all the data; see the accompanying diagram, which represents an elaboration of the simple step from the Hackelian subgenus Sorghum to the genus *Cleistachne* (Hackel, 1889).



Although there is no evidence concerning the position of Chaetosorghum in the phylogenetic scheme, its affinity to Eu-Sorphum is unmistakable. According to this scheme, the simple panicle branches found in Para-Sorghum, Stiposorghum, and Chaetosorghum may be considered an example of parallel evolution. Within Para-Sorghum and Stiposorghum the development of the awn indicates a mark of advance, a situation paralleled in Chaetosorghum relative to Eu-Sorghum. The evolutionary trend of the reduction of the pediceled spikelet is found in the two series: Eu-Sorghum to Chaetosorghum, and Heterosorghum to Sorghastrum to *Cleistachne*. Cytological evidence already presented (see pp. 287 ff.) strongly suggests that Para-Sorghum and Stiposorghum may represent an isolated line of evolution in the Sorghastrae.

The taxonomic status of Chaetosorghum and Heterosorghum must be considered in the light of morphology, cytology, distribution, and phylogeny. Since it was not possible to include *S. macrospermum* and *S. laxiflorum* in either Eu-Sorghum or Sorghastrum, it was necessary to establish new categories for these species. However, there was not evidence enough to permit setting up new genera. Nevertheless, it seems reasonably certain that Chaetosorghum and Heterosorghum warrant equal status with the other subgenera

in the genus *Sorghum*. Since the Hackelian point of view seemed to offer the greatest flexibility within a relatively conservative framework, it was possible to set up a phylogenetic scheme consistent with the taxonomic treatment, as follows:



Cytology, Phylogeny, and the Basic Chromosome Number of the Sorghastrae and the Subtribe Andropogoninae

The results of the cytological study in the Sorghastrae found application in another problem of theoretical importance with phylogenetic implications, namely, the basic chromosome number of the Andropogoneae. The only opinion expressed in the literature concerning this specific problem has been formulated by Avdulov (1931), who considered the taxonomic system proposed by Hackel (1889) in the light of an extensive study of the cytology of the Gramineae.

Since the subtribes Sacchareae and Dimereae were considered the most primitive groups in the tribe Andropogoneae, Hackel sought the most primitive genera within these subtribes. The genera *Dimeria, Miscanthus,* and *Imperata* were deemed to approximate the progenitor of the entire tribe. This conclusion was based on their possession of the greatest number of primitive characters, e.g., spikelets all alike and glumes affording little protection for the spikelets. According to Hackel, however, each genus is independent, and, "These three genera are by no means in any close kinship to one another." *Dimeria* was eliminated as an entirely isolated branch of the tribe which did not develop further. Since *Miscanthus* appeared to have the greatest number of relatively primitive characters, this genus was placed at the source of the tribe as the most primitive and all other genera, including *Imperata,* followed as branches.

Avdulov (1931), in his study of the cytology of the Andropogoneae, followed Hackel's system of classification and concept of phylogeny in this tribe. Of the three most primitive genera, only *Dimeria* was not examined cytologically. Bremer (1924) had already reported a somatic chromosome number

of 20 for a species of *Imperata, I. arundinacea.* The basic chromosome number of this genus, considering subsequent reports for other species, is 10. In the supposedly basic genus of the tribe, Avdulov (1931) examined only one species, *Miscanthus japonicus,* found a somatic chromosome number of 36 and therefore considered 9 the basic chromosome number of the genus *Miscanthus.* Consequently, 9 was considered to be the basic chromosome number for the entire tribe Andropogoneae. The many genera in this tribe with the basic chromosome number of 10 would then represent lines of descent in which a chromosome had been added to the tribal basic complement of 9.

Since Avdulov's report of the chromosome number in a species of *Miscanthus,* other investigators have examined additional species of this genus. Church's (1929) earlier report of 42 chromosomes in *M. sinensis* was discounted by Avdulov but later confirmed by Hunter (1934), who also reported 64 chromosomes in *M. saccharifera.* Moreover, Bremer (1934) observed 38 chromosomes in the same species, *M. japonicus,* studied by Avdulov who had counted 36 chromosomes. Although Avdulov had discounted Church's (1929) report concerning the chromosome number of *M. sinensis,* it is difficult to disregard the independent findings of other investigators. It is also difficult to consider 9 the basic chromosome number in *Miscanthus* as Avdulov does, since no one chromosome number appears to be basic. Unfortunately, meiosis has not been studied in any species of *Miscanthus,* nor has any comparative study been made of chromosome morphology. At any rate, Avdulov's assumptions based on a basic chromosome number of 9 for the Andropogoneae must be viewed in a new light.

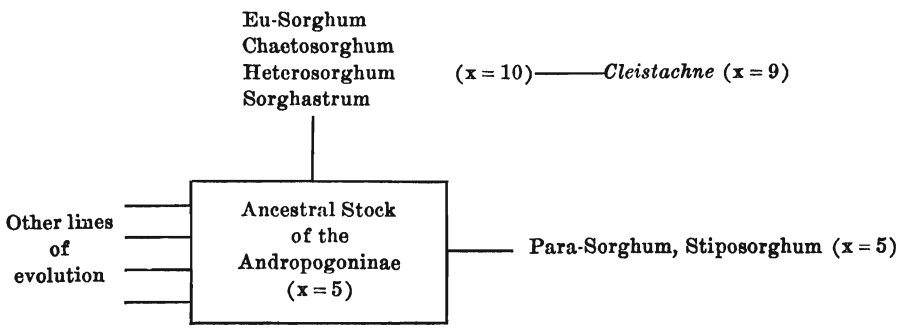
The evidence for the basic chromosome number in the Andropogoneae must result from an examination of chromosome numbers in relatively primitive subtribes, Saccharinae and Andropogoninae, following the example of Avdulov. A survey of the reported basic chromosome numbers of genera in these two subtribes reveals that the predominant basic chromosome number seems to be 10. However, the presence of genera with a basic chromosome number of 5 suggests that this number may be basic for the tribe. The question now arises, whether 5 represents the end point of a descending series of basic chromosome numbers or the starting point of a polyploid series.

Although the tribe Tripsaceae is sometimes considered distinct from the Andropogoneae, it is not yet agreed that the former tribe should be incorporated in the latter as a subtribe, or that it should not. Although their relationship is acknowledged, the crux of the controversy concerns the degree of relationship. Nevertheless, the advanced genus *Coix* in the Tripsaceae has a basic chromosome number of 5 (Mangelsdorf and Reeves, 1939). Within the subtribe Saccharinae of the Andropogoneae, the genus *Narenga* has a basic chromosome number of 5 (Bremer, 1925, Janaki Ammal, 1941). Within the subtribe Andropogoninae, one genus, *Hyparrhenia* (Garber, 1944), and the subgenera Para-Sorghum and Stiposorghum of the genus *Sorghum,* have a basic chromosome number of 5. These subgenera, however, are the only groups in the Andropogoneae now known to contain more than one species with the haploid chromosome number of 5.

The phylogenetic relationship of Para-Sorghum and Stiposorghum to the other genera of the subtribe Andropogoninae as it relates to the broader problem of the entire tribe merits attention. The question whether 5 or 10 is the basic chromosome number of the Andropogoneae may be approached from two points of view: (1) Para-Sorghum and Stiposorghum have a chromosome number representing the end point of a descending series of basic chromosome numbers, or (2) Para-Sorghum and Stiposorghum have a chromosome number representing the starting point of a polyploid series based on a chromosome number of 5. Actually, the question concerns not the subgenus Para-Sorghum or Stiposorghum as the progenitor of the Andropogoneae, but the chromosome number of five found in these groups.

If Para-Sorghum or Stiposorghum is an end point in a descending series of basic chromosome numbers, these groups must be considered an offshoot of the ancestral stock of the Andropogoninae which had a basic chromosome number of 10. However, evidence of the existence of the intermediate steps in this descending series, namely, species with x = 9, 8, 7, 6, is very scanty. Of the 35 genera in the Andropogoninae, 15 genera have been studied cytologically. Thirteen genera have a chromosome number that is a multiple of 5, and only two genera have chromosome numbers that are multiples of 9. On the other hand, if Para-Sorghum or Stiposorghum represents the beginning of a polyploid series, then the genera with the higher chromosome numbers must have resulted from polyploidy based on a chromosome number of 5. The genera with the basic chromosome number of 9 would then result from the loss of a chromosome after polyploidy had occurred.

The subgenera Para-Sorghum and Stiposorghum with the basic chromosome number of 5 may be considered a different line of descent from that of the other groups in the Sorghastrae on cytological and phylogenetic evidence. On purely morphological grounds, Snowden (1935) does not consider Para-Sorghum (the subgenera Para-Sorghum and Stiposorghum) to have taken part in the production of the species of Eu-Sorghum. If the basic chromosome number of the ancestral stock were 5, then Para-Sorghum and Stiposorghum could have been the product of a series of mutations, primarily, rather than polyploidy followed by a series of mutations. Such a line of reasoning makes possible the construction of a diagram illustrating a hypothetical course of evolution in the Andropogoninae, at least, with possible application to the entire tribe itself:



RELATIONSHIP AND PHYLOGENY OF THE SUBGENERA PARA-SORGHUM AND STIPOSORGHUM

The subgenera Para-Sorghum and Stiposorghum are more closely related to each other, morphologically, than either is to any of the other four subgenera of *Sorghum*. Moreover, both subgenera have the basic chromosome number of 5 not found elsewhere in the genus. Of the two subgenera, Para-Sorghum may be considered the less advanced and more closely related to the subgenus Eu-Sorghum. As previously mentioned, Para-Sorghum and Stiposorghum represent a different line of evolution from that giving rise to the other subgenera in *Sorghum*.

Although the morphological evidence, when considered broadly with respect to the entire genus, indicates a close relationship between Para-Sorghum and Stiposorghum, the cytological data suggest that these two subgenera are each more distinct than any of the other four subgenera. Stiposorghum is the most distinct group both cytologically and morphologically. However, all the subgenera share a number of morphological characters of phylogenetic and taxonomic significance great enough to make difficult the establishment of genera on a cytological basis alone. It is entirely possible that Para-Sorghum and Stiposorghum represent incipient genera. Whether the latter subgenus is an offshoot of Para-Sorghum or a parallel line of descent closely related to Para-Sorghum is not yet apparent, although the former hypothesis appears the more likely one.

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PLATE 40

Bearded node. *S. purpureo-sericeum* subspecies *dimidiatum.*



PLATE 41

a. *S. vulgare* (Eu-Sorghum). 2n = 20 (10^{II}). Diakinesis. *Ca.* × 850.

b. *S. macrospermum* (Chaetosorghum). 2n = 40 (20^{II}). Diakinesis. *Ca.* × 850.

c. *S. laxiflorum* (Heterosorghum). 2n = 40 (20^{II}). Diakinesis. *Ca.* × 850.

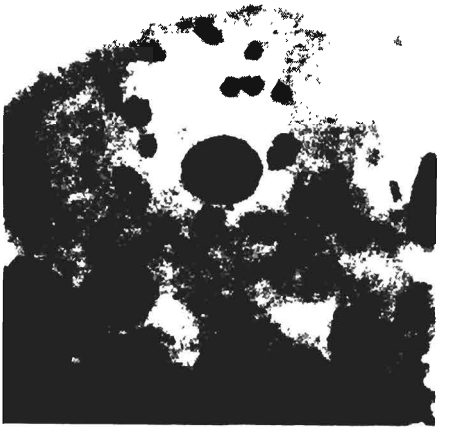
d. *S. rigidifolium* (Sorghastrum). 2n = 60 (30^{II}). Diakinesis. *Ca.* × 450.



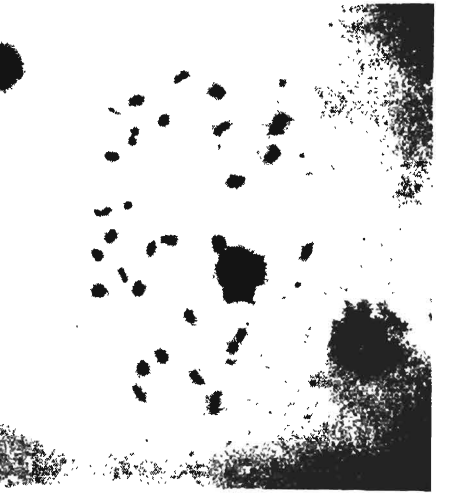
a



b



c



d

PLATE 42

a. *S. leiocladum* (Para-Sorghum). 4n = 20. Diakinesis. $4^{II} + 3^{IV}$. *Ca.* × 375.

b. *S. stipoideum* (Stiposorghum). 2n = 10 (5^{II}). Diakinesis. *Ca.* × 375.

c. *Cleistachne sorghoides*. 2n = 36 (18^{II}). Diakinesis. *Ca.* × 575.

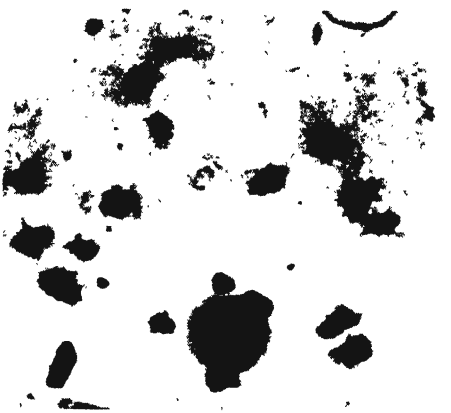
d. *S. versicolor* (Para Sorghum). Pachytene. The terminal, heteropycnotic knob at "12 o'clock" is the nucleolus-organizing region. *Ca.* × 725.



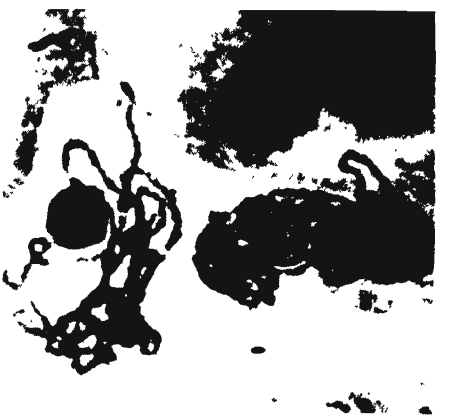
a



b



c



d

PLATE 43

a. *S. purpureo-sericeum* (Para-Sorghum). Pachytene. The subterminal association of the nucleolus organizing region is at "12 o'clock." *Ca.* × 650.

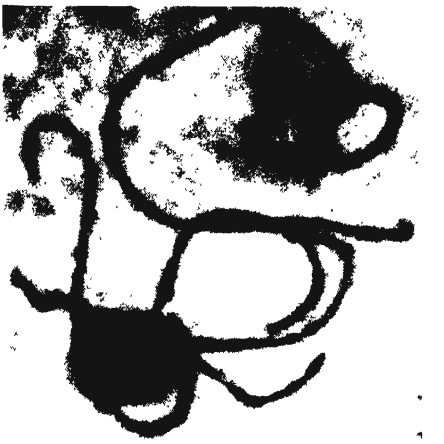
b. *S. intrans* (Stiposorghum). Pachytene. Note the two chromosomes associated with the nucleolus at an intercalary position on each chromosome (3 and 12 o'clock). *Ca.* × 1550.

c. *S. vulgare* (Eu-Sorghum). Pachytene. *Ca.* × 850.

d. *S. brevicallosum* (Stiposorghum). Pachytene. Note the two chromosomes associated with the nucleolus, one with a subterminal point of attachment (12 o'clock) and one with a subterminal point of attachment (9 o'clock). *Ca.* × 850.



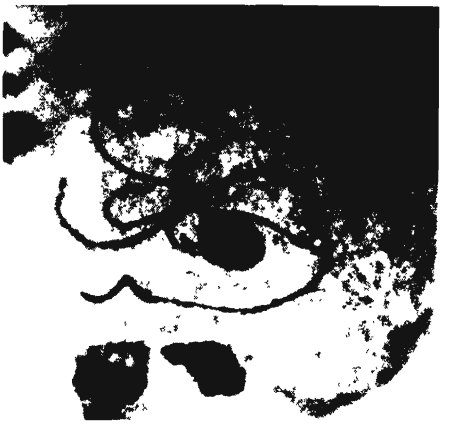
a



b



c



d

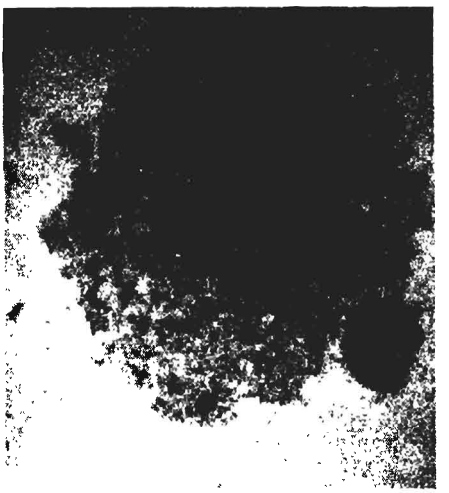
PLATE 44

a. *S. stipoideum* (Stiposorghum). Metaphase I. Four bivalents with one chiasma each and one bivalent with two chiasmata. *Ca.* × 675.

b. *S. purpureo-sericeum* (Para-Sorghum). Metaphase I. $5^{II} + 2I^{II}$. *Ca.* × 450.

c. *S. purpureo-sericeum*. 3n = 15. Metaphase I. $2^{I} + 2^{II} + 3^{III}$. *Ca.* × 450.

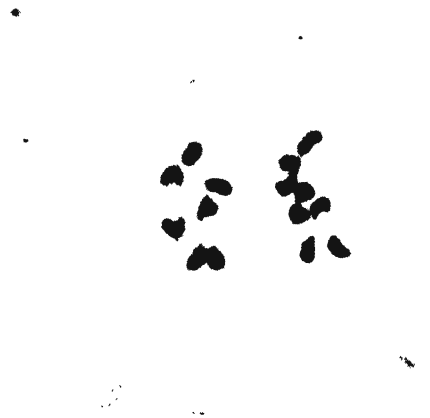
d. *S. purpureo-sericeum*. 2n = 10. Somatic metaphase. Root tip. *Ca.* × 850.



a



b



c



d

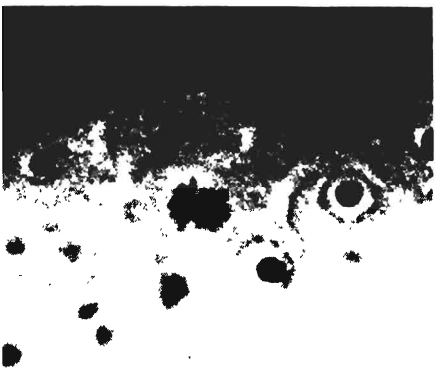
PLATE 45

a. *S. intrans* (Stiposorghum). 2n = 10. Somatic metaphase. Root tip. *Ca.* × 725.

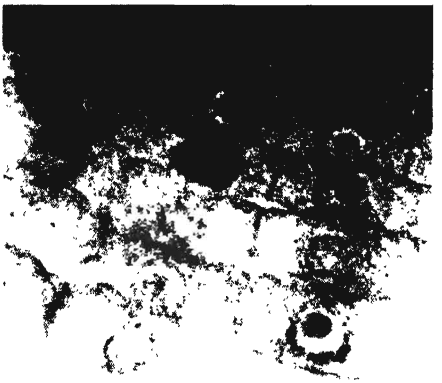
b. *S. stipoideum* (Stiposorghum). 2n = 10. Somatic metaphase. Root tip. *Ca.* × 725.

c. LN13-2. (*S. leiocladum* × *S. nitidum*). Diakinesis. 2n = 21. $7^{I} + 2^{II} + 2^{III} + 1^{IV}$. *Ca.* × 375.

d. *S. purpureo-sericeum*. Telophase 1. Note the two laggard B bivalents of different sizes at the metaphase plate. *Ca.* × 375.



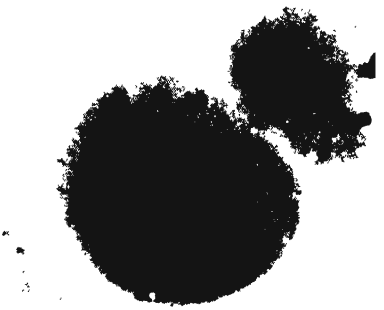
a



b



c



d

CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE: IV

BY

MARION S. CAVE AND LINCOLN CONSTANCE

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CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE: IV

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MARION S. CAVE AND LINCOLN CONSTANCE

IN THE THREE previous papers of this series,* chromosome counts were published for some one hundred and sixteen species and varieties of the Hydrophyllaceae, in the genera *Draperia, Ellisia, Emmenanthe, Eriodictyon, Eucrypta, Hydrophyllum, Miltitzia, Nama, Nemophila, Phacelia, Pholistoma, Romanzoffia, Turricula,* and *Wigandia.* The present paper includes one correction, "new" counts for approximately fifty-six species and varieties, and additional counts for some ten entities already reported upon in earlier papers, but from different geographical populations. Reports are made here for the first time on the genera *Hesperochiron* and *Lemmonia;* we have, as yet, no data on the genera *Codon, Hydrolea,* and *Tricardia.*

A solution composed of four parts chloroform, three parts absolute alcohol, and one part glacial acetic acid (Bradley, 1948) has proved a very good fixative and has the significant advantage that it does not require changing. In practice we have mixed the chloroform and alcohol in advance and added the acetic acid in the field. This technique is exceedingly convenient for field work, but it may be less suitable for some other groups of plants.

The generosity of the American Academy of Arts and Sciences, Southern Methodist University, and the Texas Research Foundation in sponsoring a field trip to Texas in the spring of 1948 is gratefully acknowledged. This excursion made possible not only the acquisition of considerable cytological and herbarium material but also the completion of two papers on *Phacelia* subgenus *Cosmanthus* (Constance, 1949, 1950) in which cytological information played an important role. Clarence R. Quick, Bureau of Entomology and Plant Quarantine, United States Department of Agriculture, has germinated a number of seed samples for us in connection with his studies of seed germination in native plants (Quick, 1947). To all persons who have generously furnished us with cytological materials or seed we are greatly indebted; most of them are listed by name in table 1.

Eucrypta.—We previously reported (1942) a count of nine for *E. micrantha* on the basis of poor and scanty material. The excellent preparation obtained by Dr. Bowerman necessitates our repudiation of this earlier report, for her material clearly shows that the correct number is six rather than nine. We assume that the original bud sample may have become mixed with material of a species of *Nemophila,* which was collected in quantity on the same trip.

Nemophila.—On the basis of counts on eight out of the eleven species, we have assumed that all members of this genus would prove to have nine pairs of chromosomes. It occasioned considerable surprise, therefore, that *N. phacelioides* of the Southwest, type species of the genus, proved to have only seven pairs, and these nearly twice as large as any chromosomes thus far

* University of California Publications in Botany, vol. 18, nos. 9, 13, and 20.

found in the family. Some material showed an additional paired fragment. This discovery reëmphasizes the folly of generalizations about chromosome number in advance of the actual data. The cytological characteristics of *N. microcalyx* of the Southeast are therefore of heightened interest.

Phacelia subgenus *Cosmanthus*.—We remarked earlier (1947) that the lack of any eleven-paired chromosome complement in this group and the possession of nine rather than eleven pairs by the only perennial *Cosmanthus* counted suggested "that Cosmanthus may not be closely related to the rest of the genus." At that time we had information on only five of the fourteen species comprising the group (Constance, 1949). We now have counts on thirteen species, which show the chromosome numbers five (two annual species), eight (one annual species), nine (one perennial, one biennial, and seven annual species), and fourteen (one annual species). The number eleven is still lacking, and morphological criteria have been found to confirm our original observation as to the discrete character of this subgenus.

Phacelia magellanica-californica-heterophylla polyploid complex.—Dr. Alan A. Beetle has made a very thorough survey for us of the representatives of this group occurring in Wyoming, and we have accumulated a number of other records from Arizona, California, Colorado, Oregon, and Utah. At present, however, we are reporting only the additional diploids discovered. These have been obtained from the Cuyamaca Mountains of San Diego County, California, the Kaibab Plateau of Arizona, and the Grand Tetons of Wyoming. The last, seemingly referable to *P. Piersoniae* L. Williams, is apparently nearly identical with *P. virgata* Greene from Siskiyou County, California, and with diploid material of *P. heterophylla* Pursh.

Phacelia section *Euglypta* (*Microgenetes*).—In his recent revision of this section (1946), Howell suggested that, "The essential characters of both flowers and fruits in *P. Leibergii* and *P. glandulifera* emphasize a relationship so close that it might almost be treated varietally if the flowers of the two did not look so different and if each species did not have such highly characteristic geographic ranges. In fact, the more restricted range of *P. Leibergii* completely within the more extended range of *P. glandulifera* and immediately to the north of the range of *P. bicolor* strongly suggests that *P. Leibergii* may have originated long ago through hybridization between small-flowered *P. glandulifera* and large-flowered *P. bicolor*." The possession of thirteen pairs of chromosomes by each of the three species alluded to in this hypothesis provides considerable substantiation.

Miltitzia.—Howell has repeatedly expressed the view (1944*a*, 1944*b*) that *Miltitzia* A. DC. is not closely related to *Emmenanthe* Benth. but is, instead, a section of *Phacelia* coördinate with and related to section *Euglypta*. In addition to the morphological and ecological evidence adduced by Howell to support this disposition, the cytological evidence, also, is corroborative. The species of *Miltitzia* thus far counted have either twelve or thirteen pairs of chromosomes, those of *Phacelia* section *Euglypta* have eleven, twelve, or thirteen, and those of *Emmenanthe* have eighteen—a number thus far unique in the family.

Wigandia.—Drs. H. Emery Moore, Jr., and Carroll E. Wood, Jr., made an especial effort on their fruitful Mexican collecting trip in the summer of 1948 to obtain cytological material of this interesting genus. It was scarcely anticipated, however, that they would reveal the existence of polyploidy, polyploid complexes having previously been reported in the family only for *Phacelia* and, possibly, *Nama*. It seems impossible to attempt identifications in *Wigandia* until the genus has been thoroughly revised. The 38-paired *Wigandia*, however, has the largest number of chromosomes known for any species in the family.

Lemmonia.—The occurrence of seven pairs of chromosomes in this monotypic genus confirms its close affinity with *Nama*, a relationship which has long been suspected on the basis of gross morphology.

Nama.—Further counts in this genus have continued to reveal only either seven or fourteen pairs. The Hawaiian *N. sandwiciense*, the sole extra-American species, proves to be cytologically like the American plants. Section *Zonolacus*, comprising only *N. stenocarpum*, completes the roster of sections in this genus, all of which thus far show the same numerical plan.

Hesperochiron.—The single species of this anomalous small genus (once referred to the Gentianaceae!) which has been counted and shown to have eight pairs of chromosomes, indicates that the group is as unique cytologically as it is morphologically.

Although our work has progressed to a point where the chromosomal data on hand provide a useful tool for taxonomic purposes, we are desirous of making our tabulation as complete as possible. Many species of *Phacelia* and *Nama* are still entirely unknown cytologically. Even in those genera where most of the species have been counted, our experience with *Nemophila* serves as a warning that nothing may safely be taken for granted. We are therefore hopeful that the continued interest of friends and colleagues will make it possible to extend our survey of the family.

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TABLE 1

CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE

(Numbers reported by us for the first time are indicated in boldface type)

Name	n or 2n number	Locality	Collector
Ellisia Nyctelea L.	10	La Prele Reservoir, Converse Co Wyo.	*A. A. Beetle* 4486
	10	La Prele Reservoir, Converse Co., Wyo.	*A. A. Beetle* 4491
Eucrypta micrantha (Torr.) Heller	**6**	Black Mts., Inyo Co., Calif.	*M. L. Bowerman* 4228
Hydrophyllum			
virginianum L.	**9**	Gray Gardens, Cambridge, Mass.	*Constance* 3258
Fendleri (S. Wats.) A. Gray	9	Happy Jack, Albany Co., Wyo.	*A. A. Beetle* 4732
Nemophila			
phacelioides Nutt.	**7**	San Felipe, Austin Co., Tex.	*Constance and Lundell* 3213
	7	Victoria, Victoria Co., Tex.	*Constance and Lundell* 3215
	7	Bastrop, Bastrop Co., Tex.	*Constance and Lundell* 3242
maculata Benth.	**9**	Soda Springs road, Nevada Co., Calif.	*H. L. Mason*
	9	Oregon House, Yuba Co., Calif.	*Constance* 3279
Phacelia			
Subgenus Cosmanthus			
platycarpa (Cav.) Spreng.			
var. *platycarpa*	9	San Marcos, Guatemala	*T. Morley* 728
	9	Quezaltenango, Guatemala	*T. Morley* 730
	9	Patzcuaro, Michoacán, Mexico	*Moore and Wood* 3994
	9	Real del Monte–El Chico, Hidalgo, Mexico	*Moore and Wood* 3706
strictiflora (E. & G.) A. Gray			
var. *strictiflora*	**9**	Lincoln, Lee Co., Tex.	*Constance and Lundell* 3243
var. *Lundelliana* Const. (TYPE)	**9**	Abilene, Taylor Co., Tex.	*Constance and Cory* 3249
	9	Anson, Jones Co., Tex.	*Constance and Cory* 3250
var. *Robbinsii* Const. (TYPE)	**9**	Tishomingo, Johnston Co., Okla.	*G. T. Robbins* 3063

var. *connexa* Const. (TYPE)	9	Grapevine, Tarrant Co., Tex.	*Constance* 3252
	9	Athens, Henderson Co., Tex.	*R. McVaugh* 8382
	9	Carrollton, Dallas Co., Tex.	*Constance* 3251
	9	Mexia, Limestone Co., Tex.	*Constance and Cory* 3244
patuliflora (E. & G.) A. Gray			
var. *patuliflora*	9	Columbus, Colorado Co., Tex.	*Constance and Cory* 3247
	9	Austwell, Refugio Co., Tex.	*Constance and Lundell* 3217
	9	Rockport, Aransas Co., Tex.	*Constance and Lundell* 3219
	9	Nueces River, San Patricio Co., Tex.	*Constance and Lundell* 3221
	9	Encino, Brooks Co., Tex.	*Constance and Lundell* 3231
	9	San Benito, Cameron Co., Tex.	*Constance and Lundell* 3234
	9	Bastrop, Bastrop Co., Tex.	*Constance and Lundell* 3241
var. *teucriifolia* (Johnst.) Const.	9	Sonora, Sutton Co., Tex.	*V. L. Cory* 41,473
	9	Pecos River, Val Verde Co., Tex.	*R. McVaugh* 7709
	9	Menard, Menard Co., Tex.	*Constance and Cory* 3248
laxa Small	9	Alice, Jim Wells Co., Tex.	*Constance* 3223
	9	Ganado, Jackson Co., Tex.	*Constance and Lundell* 3214
	9	Victoria, Victoria Co., Tex.	*Constance and Lundell* 3216
	9	Sinton, San Patricio Co., Tex.	*Constance and Lundell* 3220
hirsuta Nutt.	9	Whitesboro, Le Flore Co., Okla.	*G. T. Robbins* 2359
	9	Tishomingo, Johnston Co., Okla.	*G. T. Robbins* 2407
	9	Mexia, Limestone Co., Tex.	*Constance and Cory* 3245
	9	Arthur City, Lamar Co., Tex.	*Constance and Lundell* 3256
	9	Paris, Lamar Co., Tex.	*Constance and Lundell* 3257
gilioides Brand	9	Caledonia, Washington Co., Mo.	*H. H. Iltis* 4084
maculata Wood	5	Travelers Rest, Greenville Co., S.C.	*R. McVaugh* 8645
	5	Athens, Clarke Co., Ga.	*A. Cronquist* 5273
glabra Nutt.	8	Talihina, Le Flore Co., Okla.	*G. T. Robbins* 2352
	8	Hugo, Choctaw Co., Okla.	*Constance and Lundell* 3255
	8	Kosse, Falls Co., Tex.	*Constance and Cory* 3246
	8	San Felipe, Austin Co., Tex.	*Constance and Lundell* 3212

TABLE 1—*Continued*

Name	n or 2n number	Locality	Collector
bipinnatifida Michx.	9	Sitten's Gulf, Dade Co., Ga.	*W. H. Duncan* 2431
	9	Bloomington, Monroe Co., Ind.	*C. B. Heiser, Jr.* 2065
Purshii Buckl.	9	Morgantown, Monongalia Co., W.Va.	*E. L. Core*
fimbriata Michx.	9	"Indian Gap," Swain Co., N.C.	*Camp and Stupka*
Section Gymnobythus			
viscida (Benth.) Torr.			
var. *albiflora* (Nutt.) A. Gray	11	Davy Brown Camp, Santa Barbara Co., Calif.	*Mathias and Lewis*
	11	Santa Barbara, Santa Barbara Co., Calif.	*C. F. Smith* 908
Section Euphacelia			
thermalis Greene	11	Porcupine Valley, Modoc Co., Calif.	*McMillan and Nobs* 1533
vallis-mortae Voss	11	Daylight Pass, Inyo Co., Calif.	*M. L. Bowerman* 4231
platyloba A. Gray	11	Tollhouse, Fresno Co., Calif.	*E. Carter* 103
Palmeri Torr.	11	Wolf Hole, Mohave Co., Ariz.	*Parker, McClintock, and Robbins* 6297
	11	Tuweep, Mohave Co., Ariz.	*Parker, McClintock, and Robbins* 6254
neomexicana Thurb.			
var. *alba* (Rydb.) F. Macbr.	11	Bordenville, Park Co., Colo.	*A. N. Carter* 393
	11	Russell, Costilla Co., Colo.	*Parker and McClintock* 7002
scariosa Brandg.	11	San Ignacio, Baja Calif., Mexico.	*Carter, Alexander, and Kellogg* 1973
	11	Arroyo del Salto, Baja Calif., Mexico	*A. Carter* 2592
robusta (F. Macbr.) Johnst.	11	Big Bend Park, Brewster Co., Tex.	*C. C. Albers* 46,213
integrifolia Torr.	11	Roman Nose Park, Blaine Co., Okla.	*G. J. Goodman* 4068
	11	Carlsbad highway, El Paso Co., Tex.	*R. McVaugh* 8137
	11	Malone Mts., Hudspeth Co., Tex.	*U. T. Waterfall* 6661
coerulea Greene	11	Columbus, Luna Co., N.M.	*R. McVaugh* 8118
magellanica-californica-heterophylla complex			
californica Cham.			
var. *patula* (Brand) Jepson (TOPOTYPE)	11	Stonewall Mine, San Diego Co., Calif.	*A. Carter* 1792

Piersoniae L. Williams	11	Grand Teton Park, Teton Co., Wyo.	*Parker and McClintock* 6954
	11	Teton Pass, Teton Co., Wyo.	*Constance* 3260
urticacea Greene	11	Jacob's Lake, Coconino Co., Ariz.	*Parker, McClintock, and Robbins* 6212
Greenei J. T. Howell	10	Scott Mt., Siskiyou Co., Calif.	*Constance and Mason* 3200
Dalesiana J. T. Howell	8	Scott Mt., Trinity Co., Calif.	*Constance and Shan* 3070
Section Eutoca			
ixodes Kell.	11	San Martin Is., Baja Calif., Mexico	*R. Moran* 3043
hirtuosa A. Gray (TOPOTYPE)	11	San Telmo, Baja Calif., Mexico	*Constance* 3114
suaveolens Greene	12	Eagle Rock, Santa Cruz Co., Calif.	*Constance and Macbride* 3308
Douglasii (Benth.) Torr.	11	Manzana Creek, Santa Barbara Co., Calif.	*C. F. Smith* 1981
	11	Coalinga, Fresno Co., Calif.	*Constance* 2804
Section Euglypta (Microgenetes)			
gymnoclada Torr.	13	Sparks, Washoe Co., Nev.	*Constance* 3292
	13	Reese River, Lander Co., Nev.	*Constance* 3296
glandulifera Piper	13	Narrows, Harney Co., Ore.	*Constance* 3301
bicolor Torr.	13	Bodie, Mono Co., Calif.	*Wiggins and Rollins* 577
	13	Reno–Pyramid Lake, Washoe Co., Nev.	*E. H. Naumann*
	13	Sparks, Washoe Co., Nev.	*Constance* 3293
	13	Winnemucca, Humboldt Co., Nev.	*Constance* 3298
Leibergii Brand	13	Horse Ridge, Deschutes Co., Ore.	*Constance* 3303
calthifolia Brand	11	Death Valley, Inyo Co., Calif.	*M. L. Bowerman* 4239
Miltitzia			
lutea (H. & A.) A. DC.	12	State line, Owyhee Co., Ida.	*Maguire and Holmgren* 26,386
glandulifera (Torr.) Heller	12	Sparks, Washoe Co., Nev.	*Constance* 3291
parviflora (A. Gray) Brand	12	Juniper Lake, Harney Co., Ore.	*Constance* 3300
glaberrima (Torr.) Brand	13	Reese River, Lander Co., Nev.	*Constance* 3297
Emmenanthe rosea (Brand) Const., comb. nov.[a]	18	Arroyo del Puerto, Stanislaus Co., Calif.	*Constance et al.* 3286
Wigandia macrophylla C. & S.	19	Jacala-Chapulhuacán, Hidalgo, Mexico	*Moore and Wood* 3650
sp.	38	Pedregal, D.F., Mexico	*Moore and Wood* 3683
Lemmonia californica A. Gray	7	Upper Lockwood Valley, Ventura Co., Calif.	*C. F. Smith* 2000
	7	Bartlett Mt., Lake Co., Calif.	*M. S. Baker* 10,977

TABLE 1—*Concluded*

Name	n or 2n number	Locality	Collector
Eriodictyon			
angustifolium Nutt.	14	Chloride, Mohave Co., Ariz.	*Gould and Darrow* 4283
capitatum Eastw.	14	Pine Canyon, Santa Barbara Co., Calif.	*H. L. Mason* 13,208
Nama			
Section Conanthus			
aretioides H. & A.	7	Reno–Pyramid Lake, Washoe Co., Nev.	*E. H. Naumann*
	7	Steamboat Springs, Washoe Co., Nev.	*Constance* 3290
parviflorum (Greenm.) Const., comb. nov.[b]	7	Carson Sink, Churchill Co., Nev.	*Constance* 3294
	7	Winnemucca, Humboldt Co., Nev.	*Constance* 3299
	14	Horse Ridge, Deschutes Co., Ore.	*Constance* 3302
Section Eunama			
demissum A. Gray	7	Black Mts., Inyo Co., Calif.	*M. L. Bowerman* 4230
	7	Big Sandy River, Yavapai Co., Ariz.	*Gould and Darrow* 4237
var. *linearis* C. L. Hitchc.	7	Miller's Landing, Baja Calif., Mexico	*Constance* 3128
Coulteri A. Gray	7	La Paz–Los Planes, Baja Calif., Mexico	*A. Carter* 2627
	7	Magdalena Plain, Baja Calif., Mexico	*Constance* 3159
sandwiciense A. Gray	7	Waimanalo Beach, Oahu, Hawaiian Islands	*W. H. Wagner, Jr.*, 5448
jamaicense L.	14	San Diego, Duval Co., Tex.	*Constance* 3224
	14	Laredo, Webb Co., Tex.	*Constance and Lundell* 3239
undulatum H.B.K.	7	Ixmiquilpán, Hidalgo, Mexico	*Moore and Wood* 3739
hispidum A. Gray	7	Falfurrias, Brooks Co., Tex.	*Constance and Lundell* 3230
	7	Rio Grande City, Starr Co., Tex.	*Constance and Lundell* 3237
sericeum Willd.	7	Zimapán, Hidalgo, Mexico	*H. E. Moore, Jr.* 1743
Section Zonolacus			
stenocarpum A. Gray	7	La Purísima, Baja Calif., Mexico	*Constance* 3144
	7	Palm Grove, Cameron Co., Tex.	*Constance and Lundell* 3235
Hesperochiron californicus (Benth.) S. Wats.	8	Bear Valley, Nevada Co., Calif.	*Constance and McMinn* 3043
Romanzoffia sitchensis Bong.	11	Crawford Bay, B.C., Canada	*H. Murray*

[a] Emmenanthe rosea (Brand) Const., comb. nov. (*Emmenanthe penduliflora* var. *rosea* Brand in Engler, Pflanzenreich 4[251]: 134. 1913.)
[b] Nama parviflorum (Greenm.) Const., comb. nov. (*Conanthus parviflorus* Greenm. Erythea 7: 117. 1899: *Nama densum* var. *parviflorum* C. L. Hitchc. Amer. Journ. Bot. 20: 420. 1933.)

FIGURE A

Chromosomes of Eucrypta, Hydrophyllum, Nemophila, and Phacelia. × 1150.

1. *Eucrypta micrantha*, I M; *M. L. Bowerman* 4228.
2. *Hydrophyllum virginianum*, I A; *Constance* 3258.
3. *Nemophila phacelioides*, I M; *Constance and Lundell* 3213.
4. *Nemophila maculata*, I M; *H. L. Mason.*
5. *Phacelia glabra*, I M; *Constance and Cory* 3246.
6. *Phacelia bipinnatifida*, I M; *C. B. Heiser, Jr.* 2065.
7. *Phacelia fimbriata*, I A; *Camp and Stupka.*
8. *Phacelia viscida* var. *albiflora*, I M; *C. F. Smith* 908.
9. *Phacelia thermalis*, I M; *McMillan and Nobs* 1533.
10. *Phacelia vallis-mortae*, II M; *M. L. Bowerman* 4231.
11. *Phacelia platyloba*, I M; *E. Carter* 103.

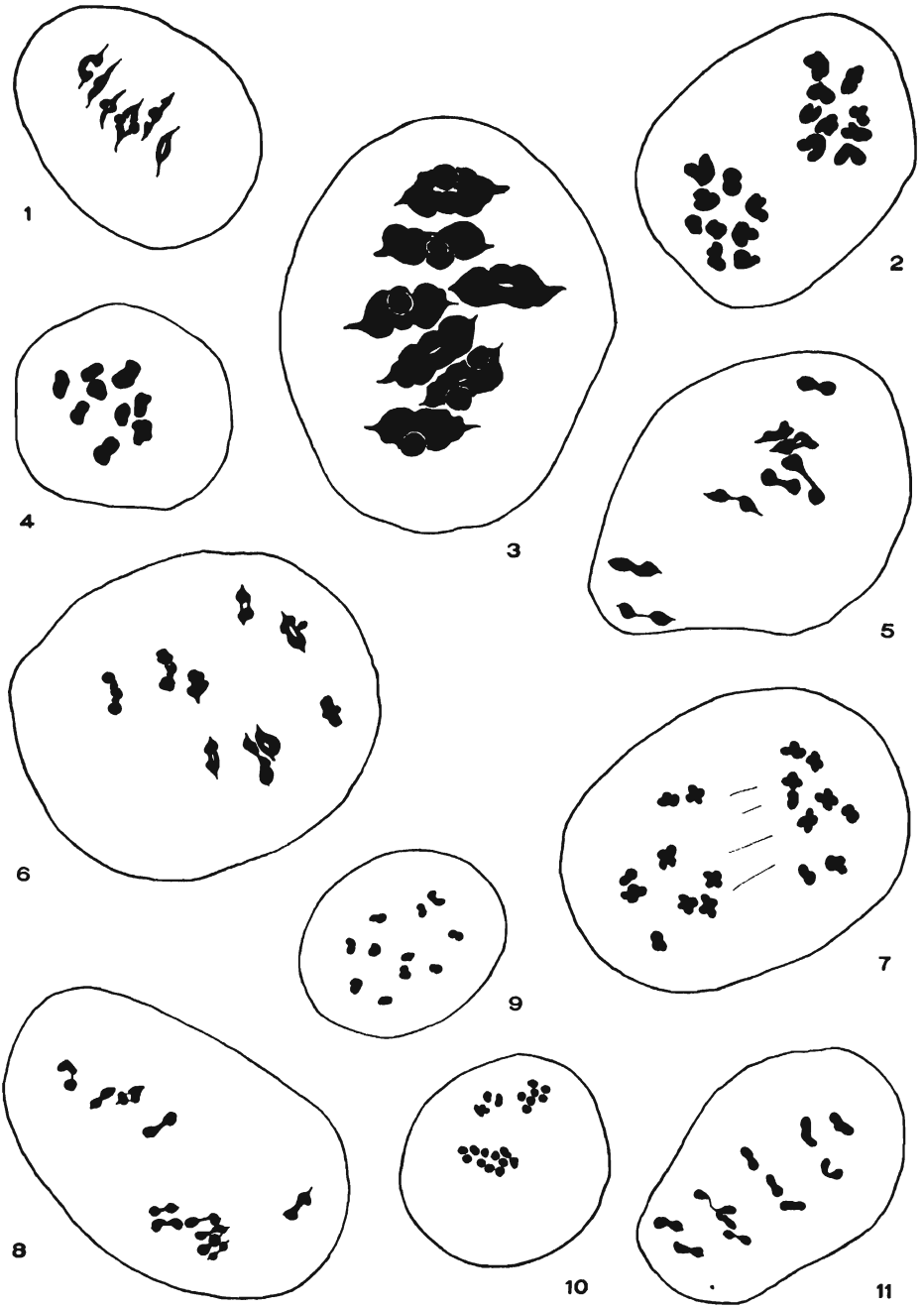


Figure A

FIGURE B

Chromosomes of Phacelia. × 1150.

12. *P. strictiflora* var. *strictiflora*, I M; *Constance and Lundell* 3243.
13. *P. strictiflora* var. *Lundelliana*, I M; *Constance and Cory* 3249.
14. *P. strictiflora* var. *Robbinsii*, II M; *G. T. Robbins* 3063.
15. *P. strictiflora* var. *connexa*, I M; *Constance* 3251.
16. *P. patuliflora* var. *patuliflora*, I M; *Constance and Lundell* 3231.
17. *P. patuliflora* var. *teucriifolia*, I M; *Constance and Cory* 3248.
18. *P. laxa*, I M; *Constance and Lundell* 3214.
19. *P. hirsuta*, I M; *Constance and Cory* 3245.
20. *P. gilioides*, I M; *H. H. Iltis* 4084.
21. *P. maculata*, I M; *R. McVaugh* 8645.

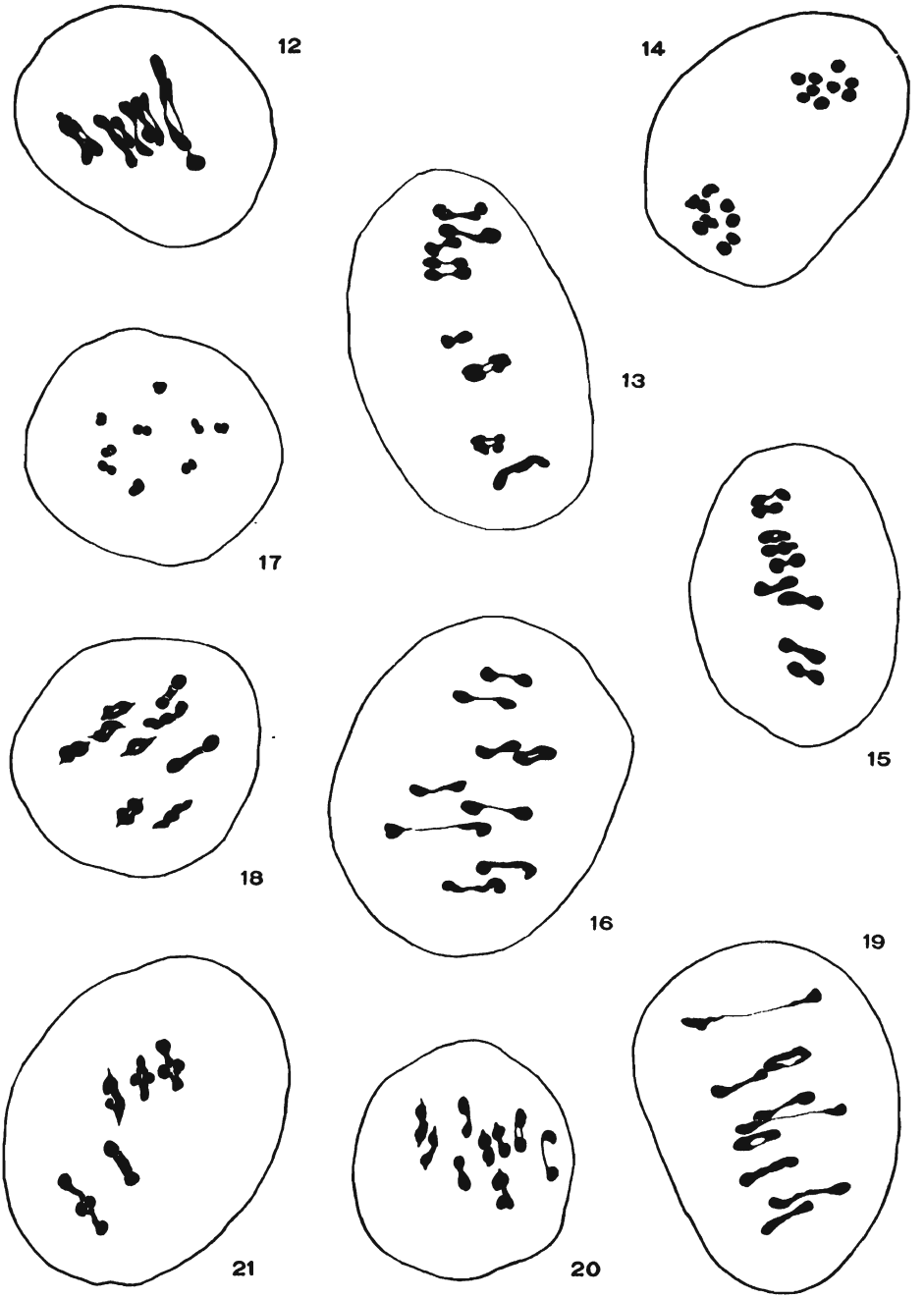


Figure B

FIGURE C

Chromosomes of Phacelia. × 1150.

22. *P. Palmeri*, II T; *Parker, McClintock, and Robbins* 6297.
23. *P. neomexicana* var. *alba*, I M; *A. N. Carter* 393.
24. *P. scariosa*, I M; *Carter, Alexander, and Kellogg* 1973.
25. *P. robusta*, II M; *C. C. Albers* 46,213.
26. *P. integrifolia*, I M; *R. McVaugh* 8137.
27. *P. californica* var. *patula*, I M; *A. Carter* 1792.
28. *P. Piersoniae*, Diak.; *Constance* 3260.
29. *P. urticacea*, II M; *Parker, McClintock, and Robbins* 6212.

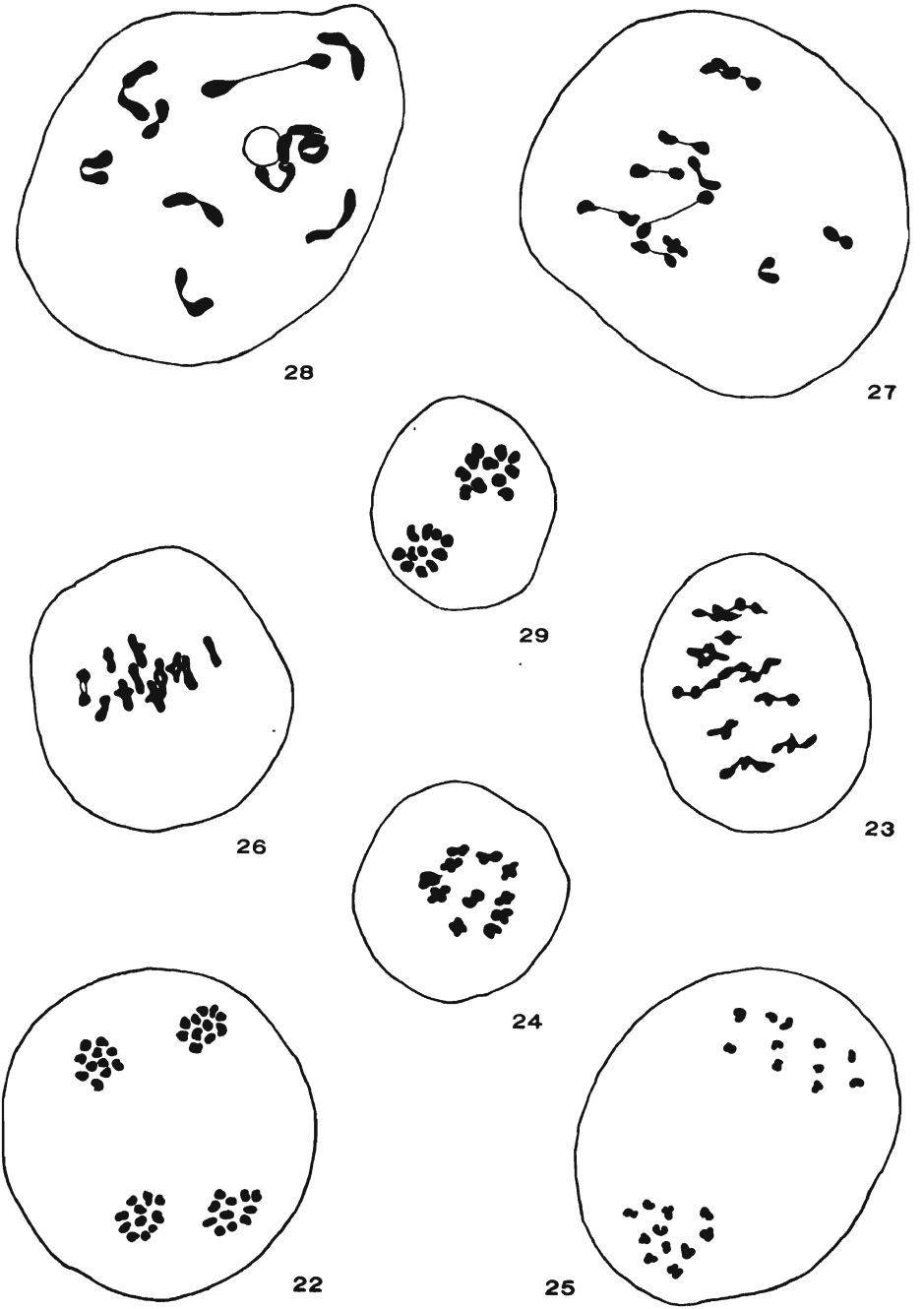


Figure C

FIGURE D

Chromosomes of Phacelia and Miltitzia. × 1150.

30. *Phacelia Greenei*, I M; *Constance and Mason* 3200.
31. *Phacelia Dalesiana*, II M; *Constance and Shan* 3070.
32. *Phacelia ixodes*, II M; *R. Moran* 3043.
33. *Phacelia hirtuosa*, II M; *Constance* 3114.
34. *Phacelia suaveolens*, I M; *Constance and Macbride* 3308.
35. *Phacelia Douglasii*, II M; *C. F. Smith* 1981.
36. *Phacelia gymnoclada*, Diak., *Constance* 3292.
37. *Phacelia glandulifera*, II M; *Constance* 3301.
38. *Phacelia bicolor*, II M; *Wiggins and Rollins* 577.
39. *Phacelia Leibergii*, II A; *Constance* 3303.
40. *Phacelia calthifolia*, I M; *M. L. Bowerman* 4239.
41. *Miltitzia lutea*, I M; *Maguire and Holmgren* 26,386.
42. *Miltitzia glaberrima*, I A; *Constance* 3297.

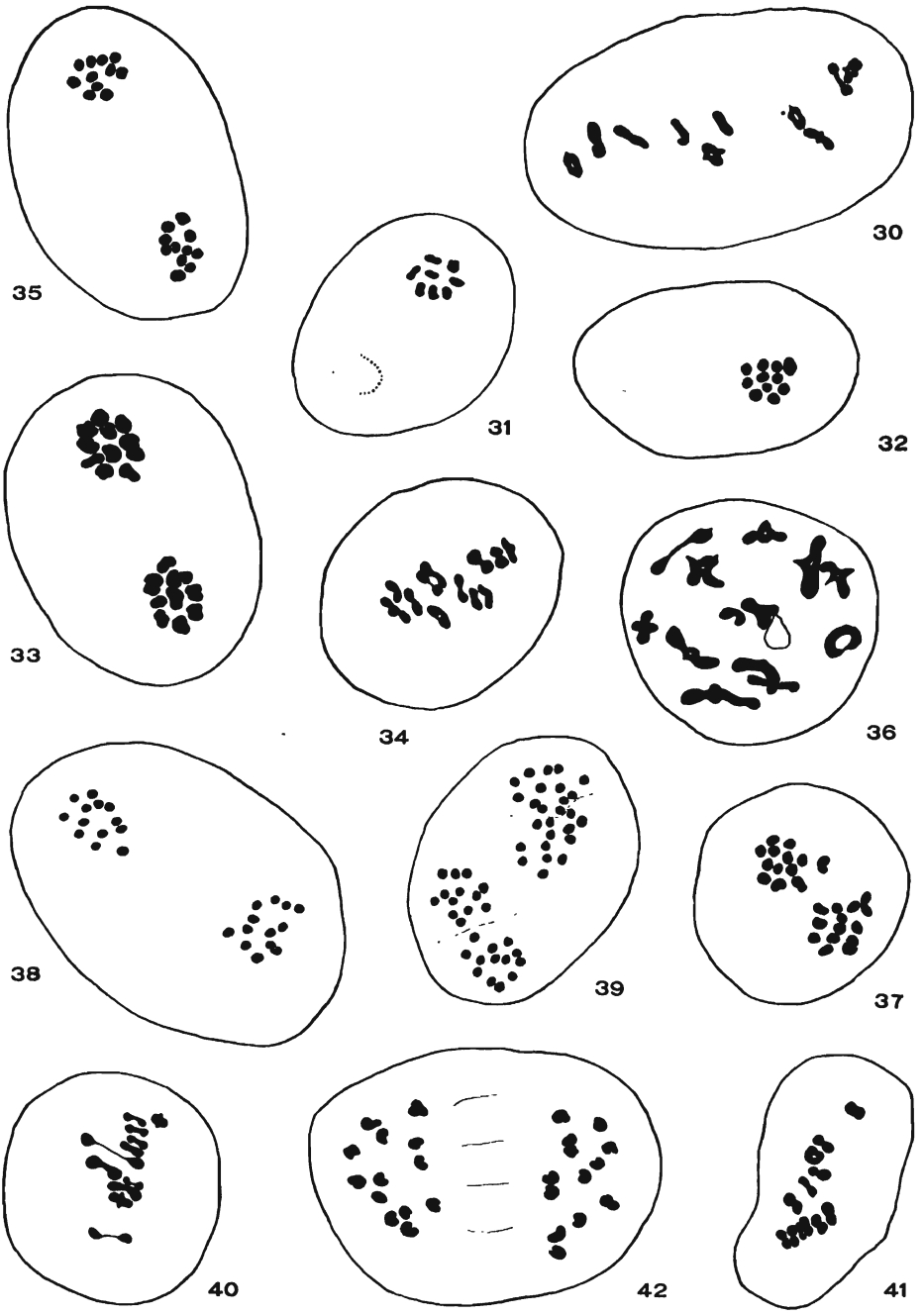


Figure D

FIGURE E

Chromosomes of Emmenanthe, Wigandia, Lemmonia, Eriodictyon, Nama, Hesperochiron, and Romanzoffia. × 1150.

43. *Emmenanthe rosea*, I M; *Constance, Holm, Rodriguez, Wagner, and Wood* 3286.
44. *Wigandia macrophylla*, Diak.; *Moore and Wood* 3650.
45. *Wigandia* sp., I M (34II and 2IV); *Moore and Wood* 3683.
46. *Lemmonia californica*, I M; *C. F. Smith* 2000.
47. *Eriodictyon angustifolium*, Diak.; *Gould and Darrow* 4283.
48. *Eriodictyon capitatum*, I M; *H. L. Mason* 13,208.
49. *Nama aretioides*, II M; *Constance* 3290.
50. *Nama parviflorum*, I A; *Constance* 3299.
51. *Nama demissum* var. *linearis*, II M; *Constance* 3128.
52. *Nama Coulteri*, I M; *Constance* 3159
53. *Nama sandwiciense*, Pollen grain division; *W. H. Wagner, Jr.* 5448.
54. *Nama jamaicense*, I M; *Constance* 3224.
55. *Nama undulatum*, II M; *Moore and Wood* 3739.
56. *Nama sericeum*, I M; *H. E. Moore., Jr.* 1743.
57. *Nama stenocarpum*, I M; *Constance* 3144.
58. *Hesperochiron californicus*, I M; *Constance and McMinn* 3043.
59. *Romanzoffia sitchensis*, I M; *H. Murray.*

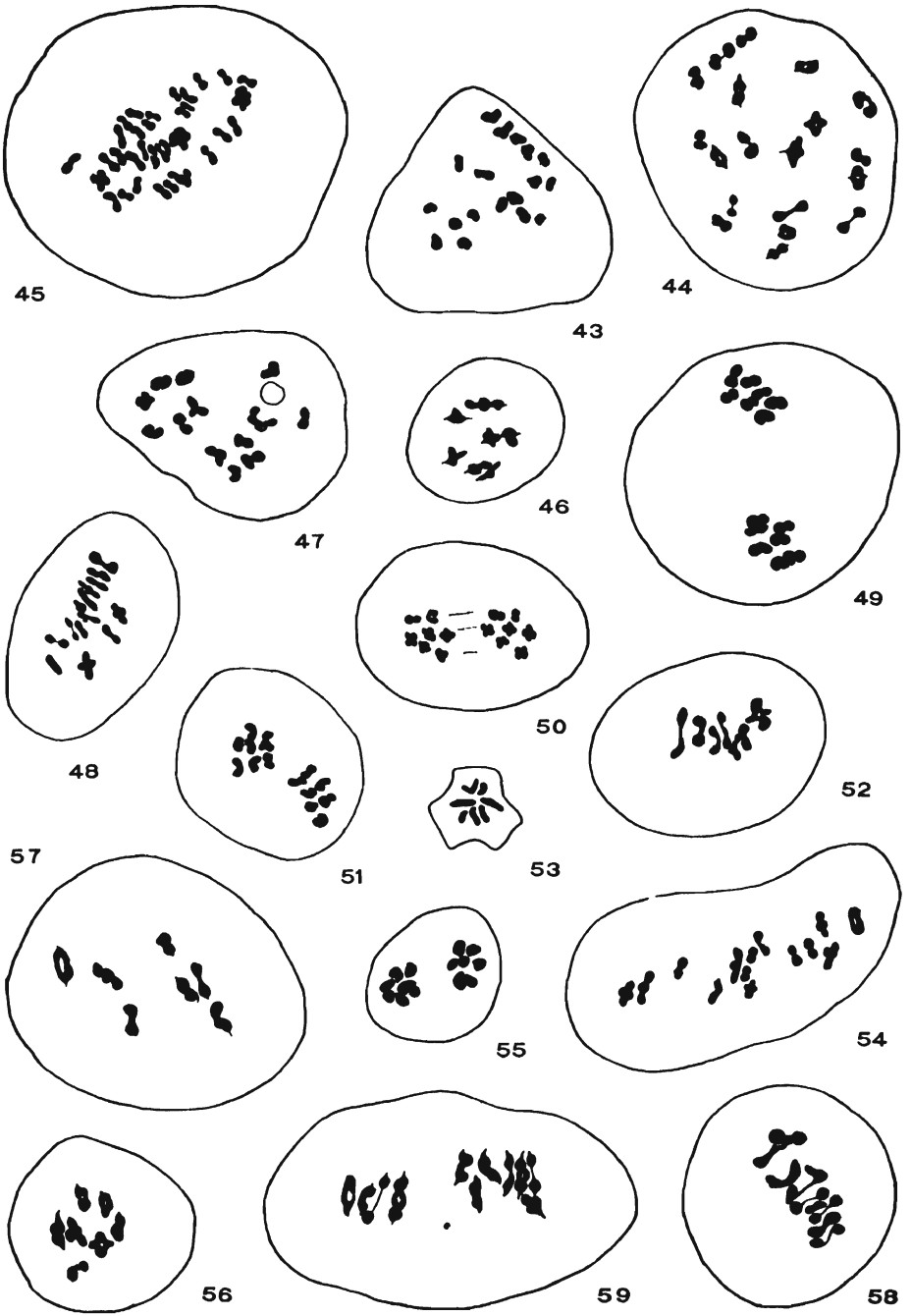


Figure E

SUPPLEMENTARY NOTES ON CREPIS IV: NEW AND NOTEWORTHY SPECIES

BY

ERNEST B. BABCOCK

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SUPPLEMENTARY NOTES ON CREPIS IV: NEW AND NOTEWORTHY SPECIES

BY
ERNEST B. BABCOCK

SINCE PUBLICATION of the monograph on *Crepis* (Babcock, 1947*a*, *b*) additional material has come to my attention, calling for the description of several new species and providing valuable information on the distribution and variability of other species. Three supplementary notes (1949*a*, *b*, 1950) have already been published. This paper deals with specimens collected on two recent botanical expeditions and some miscellaneous collections. The herbaria cited, with their generally recognized abbreviations, are as follows: Herbarium Botanischer Garten und Museum, Dahlem (B); Musei Nationalis Hungarici, Budapest (BP); private herbarium of Peter H. Davis of the Royal Botanic Garden, Edinburgh (Davis); Herbarium Ministeri Iranici Agriculturae (Iran); Herbarium Facultatis Agronomicae, Keredj or Karadj, Iran (KAR); Naturhistoriska Riksmuseet, Stockholm (S); Botanisches Institut der Universität, Sofia, Bulgaria (SO); University of California, Berkeley (UC); Naturhistorische Museum, Botanische Abteilung, Wien, Austria (W).

SPECIMENS COLLECTED BY K. H. AND F. RECHINGER

Crepis asadbarensis Bornm. (Fedde, Repert. Spec. Nov. Reg. Veg. 41: 317. 1937). One collection, no. 6445 (UC, W), in 1948, provides the first material of this little-known species to become available to me and makes possible the following description, which will be a sufficient aid in identification.

Perennial (?), 4 dm. high, with erect rigid stem; narrowly lanceolate cauline leaves, cymose-corymbiform inflorescence, and few medium or large heads on short stout peduncles; stem and leaves yellowish green, canescent-tomentulose, gland-pubescent with very fine short hairs; heads with more than 50 florets, the ligules and style branches yellow; involucre *ca.* 13 mm. long; outer involucral bracts *ca.* 10, linear, acuminate, unequal, the longest ½–¾ as long as the inner ones, dark green, glabrous; inner bracts *ca.* 13, lanceolate, acuminate, dorsally canescent-tomentose and with a few short dark glandless setae, ventrally sparsely appressed-pubescent with white shining hairs; corolla *ca.* 18 mm. long, the tube *ca.* 5 mm. long, pubescent with short and long 2-celled acicular trichomes, the ligule 2 mm. wide, pubescent dorsally; anther tube *ca.* 5 mm. long, appendages 0.5 mm. long, filaments short; style branches 3 mm. long, 0.15 mm. wide; mature achenes (according to Bornmüller) 8–9 mm. long, yellowish brown, gradually attenuate into a short beak, finely ribbed; pappus *ca.* 9 mm. long, 2-seriate, the setae white, rather fine, soft. Synonyms: *C. djimilensis* Bornm., Bull. Herb. Boiss., 2d ser., 7:494. 1907 (non C. Koch); "*C. rigida*" Boiss., Fl. Or. 3:834. 1875.

Northern Iran: Elburs Mountains, 2,300–3,200 m. The following localities are mentioned by Bornmüller: Gateschar, Asadbar, Totschal, Assem-Warak, Hessarband. Rechinger's station is Prov. Mazanderan: distr. Nur, between Kamarband and Naftab peak, calcareous rocks, 3,200 m.

This species belongs in section 10 (Berinia) and is closest to *C. pannonica,* from which it is very distinct in habit and leaf shape, in the acuminate bracts of the involucre and the inner bracts with ventral pubescence, and especially in the longer, strongly attenuate or somewhat beaked achenes. This species is known only from the region of the Elburs Mountains, whereas *C. pannonica* is a widespread species.

C. elbrusensis Boiss. One collection, no. 6438, in 1948 (UC, W), from Mazanderan Prov.: Nur distr., between Kamarband and Naftab peak, 3,200 m., is only the fourth collection of this species known to me, and the first in recent years. Fortunately, mature achenes were available and plants cultivated in our greenhouse have reproduced the distinctive features of this hitherto little-known species. *Chromosome number,* $2n = 10$. This number was anticipated as the most probable one for the five species of section 16 (Lagoseris) because of the intermediate phylogenetic position of this section, which stands between section 22 (Pterotheca) and the more primitive species of section 10 (cf. Babcock, 1947*a*, pp. 69, 71). *C. sancta,* the only species in section 22, also has 5 pairs of chromosomes.

C. foetida L. subsp. *vulgaris* (Bisch.) Babc. One specimen, no. 5585 (UC), is minor variant 48 = f. *fallax* (Boiss.) Babc., collected in Prov. Mazanderan: Talar River valley, Sorkhabad, *ca.* 1,400 m., in 1948. This station extends the known range of this subspecies eastward from northern Syria to the Caspian Sea, thus making its southern limit nearly continuous eastwardly with that of subsp. *rhoeadifolia.*

C. foetida L. subsp. *vulgaris* (Bisch.) Babc. m.v. 57. One specimen, no. 5631, in 1948 (UC), resembles m.v. 14 in habit, being only 7 cm. high, with a long root, thickened at the caudex, and numerous *short* stems which are 2–3-branched, the branches pedunculate. Involucres shortly gland-pubescent as in subsp. *vulgaris,* but the outer bracts as long as in subsp. *rhoeadifolia* and the style branches dark green. This combination of characters indicates hybridity between the two subspecies. But the habit of the plant is reproduced in pot-grown plants in the greenhouse, which shows this to be an ecotype adapted to a maritime environment. This plant was identified by Rechinger as var. *maritima* Boiss., which is a synonym of f. *radicata* (S. et S.) Babc. (cf. m.v. 14, in Babcock, 1947*b*, p. 692).

C. frigida (Boiss.) Babc. One collection, no. 6052 (UC, W), Gorgan (Djordjan), east of Asterabad, northern slope of Mt. Shahvar, above Hadjilang, opposite Ortaessaidan, 3,000–3,200 m., July 26–27, 1948. The seven small specimens which I have seen correspond closely with typical material from central and southern Turkey, the only notable variations being: absence of yellow hairs or setules on lower face of leaves (but this variation has already been observed in some of Kotschy's plants from Mt. Koschan, Bulgar Dagh,

Cilicia); achenes about 6 instead of 5 mm. long; pappus 5–6 mm. long instead of 4 mm.; receptacular paleae shorter instead of longer than the achenes and hence difficult to demonstrate in immature heads. None of these variations is of sufficient importance to require the recognition of a new subspecies. Therefore, this new station is an important extension of the geographical range of this species, northeastern Iran being about 1,800 kilometers to the east of the easternmost stations known in Turkey. The fact that these specimens resemble typical material so closely makes the following observations on the chromosomes of seedlings grown from them especially valuable. *Chromosome number,* $2n = 10$. The chromosomes appear to be distinct in size and shape from those of *C. elbrusensis*. A report on the chromosomes of these two species, the first representatives of section 16 (Lagoseris) to be studied cytologically, will be published elsewhere.

C. heterotricha DC. subsp. *lobata* Babc. One collection (UC, W), no. 6473, in 1948, from Prov. Mazanderan: distr. Kudjur, Mt. Ulodj, calcareous substrate, 3,200–3,400 m. As far as I know, this is only the second collection of this distinctive subspecies since the original one of Bornmüller in the Elburs Mountains. Another and probably older collection is mentioned below (p. 386). The Kudjur district includes a range of mountains just south of and parallel with the Elburs Mountains. Rechinger's material resembles the type closely, and the nearly mature achenes are 5.5 mm. long, narrowly columnar, and many-ribbed.

C. multicaulis Lebeb. subsp. *genuina* (Rgl.) Babc. Two specimens, nos. 6051, 6104, in 1948 (UC), from Prov. Gorgan (Djordjan), east of Asterabad in the eastern extremity of the Elburs Mountains, Mt. Shahvar, near Hadjilang, 2,400–2,800 m., extend the known distribution of this subspecies westward from Kashmir almost to the Caspian Sea, an air-line distance of about 1,800 kilometers. Thus the distributional area of subsp. *genuina* probably includes the northern part of the area of subsp. *congesta*.

C. parviflora Desf. Two specimens, no. 3847a (UC, W), from Prov. Kerman: Djamal Bariz Mountains, and no. 5535 (UC, W), from Prov. Gorgan (Djordjan), near Bander Gaz, both collected in 1948, extend the known range of this species eastward to southeastern and northeastern Iran.

C. sancta (L.) Babc. subsp. *obovata* (Boiss. et Noë) Babc. One specimen, no. 3779, in 1948 (UC), from Prov. Kerman: Djamal Bariz Mountains, between Bam and Djiroft, Deh Bakri, *ca.* 2,100 m., is a new and distinct minor variant of this subspecies. Leaves and lower stems densely hirsute with white, glandless hairs up to 3 mm. long; leaves narrowly oblanceolate, subpinnatifid; stems numerous, *ca.* 20 cm. high, 4–8-headed; heads, flowers, and fruits typical.

SPECIMENS COLLECTED BY PETER H. DAVIS

Crepis foetida L. subsp. *rhoeadifolia,* m.v. 58. Two specimens, no. 15192 (Davis), collected in Anatolia: Prov. Isparta, distr. Sutculer (Isauria/Pisidia), Cimenova, western side of Sarp dagh, stony slopes, edge of fallow fields, 1,500 m., July 28, 1949, possess characters of both this subspecies and

subspecies *vulgaris*. They resemble the latter in size of involucre and shape of the outer or marginal achenes; but in size and habit the plant is more like the former subspecies as it occurs in this region, and the strongly setaceous indumentum is typical of subsp. *rhoeadifolia*. Further, in one of the two plants the length of the outer involucral bracts is typical of this subspecies. The receptacle is ciliate but not paleaceous. Therefore, while the plants may have come from a segregating population resulting from hybridization between the two subspecies, the most practical disposition of these specimens is to classify them under subsp. *rhoeadifolia* as a new minor variation.

C. foetida L. subsp. *commutata* (Spr.) Babc. One collection, no. 16082 (Davis), from Anatolia: Prov. Konya; distr. Beyschir (Isauria), foot of Dedegöl dagh, near Kurucuova, dry fields, 1,200–1,300 m., August 4, 1949. In its marked reduction, caused by drought, this form resembles the depauperate plant known as f. *coa* (DC.) Babc. (cf. m.v. 54, in Babcock, 1947*b*, p. 701).

C. frigida (Boiss.) Babc. One collection, no. 16552 (Davis, UC), from Anatolia: Prov. Adana; distr. Kɛraisah (Cilicia), Bulgar dagh, between Meydan yayla and Sari tepe yayla, mobile limestone scree, September 2, 1949. Based on these plants and the specimens of Rechinger, cited above (p. 385), it is possible to present below a more accurate description of this species than the one given in my monograph.

Perennial, with small rosettes and scapiform stems, 0.3–0.8 dm. high, borne on long slender shoots arising from a subterranean stem; caudex slender, woody, leafy at crown; caudical leaves rosulate, up to 8 cm. long, 1.5 cm. wide, petiolate, oblanceolate to spatulate, obtuse or acute, denticulate to lyrately pinnatifid with 3–4 pairs of small oblong lateral lobes, densely canescent-tomentose on upper face, sometimes densely pubescent, notably on lower face, with yellow hairs or setules; stems pedunculate, slender, terete, tomentulose, more or less gland-pubescent; heads erect, medium, about 30-flowered; involucre cylindric-campanulate, 9–12 mm. long, 3–5 mm. wide at middle in fruit, canescent-tomentose; outer bracts 7–9, unequal, longest ⅓–⅔ as long as the inner, lanceolate, acute; inner bracts 12–16, lanceolate, acuminate, dorsally pubescent with glandular or glandless setules, ventrally glabrous, scarious-margined, rounded-carinate dorsally and obscurely spongy-thickened at base in fruit; receptacle flat, paleaceous with setiform paleae longer than the achenes, not exceeding the pappus; corolla about 12 mm. long; ligule 1.5 mm. wide; teeth 0.25 mm. long; corolla tube *ca.* 4 mm. long, pubescent with coarse straight several-celled trichomes 0.7 mm. long; anther tube 3 × 1 mm. when opened out; appendages 0.5 mm. long, narrow, obtuse; filaments 0.3 mm. longer; style branches yellow, *ca.* 1 mm. long, narrow, obtuse at apex; achenes light brown, 5–6.5 mm. long, uniform, columnar or curved, subterete, slightly attenuate upward, with small pale pappus disk, narrowed at the lightly calloused base, 15-ribbed, ribs close, rounded, smooth; pappus white, 4–5, 6 mm. long, 3-seriate, rather fine, soft, deciduous in clumps. Flowering July–August; flowers yellow. Chromosomes, $2n = 10$.

C. pinnatifida (Willd.) Froel. One collection, two plants, no. 16542 (Davis), from Cilicia: Prov. Adana; distr. Kavaisah, Bulgar dagh at Meydan yayla above Pozanti, growing through *Onobrychis cornuta,* 2,400 m., September 1, 1949. This is a noteworthy collection, since most of the few specimens now available in European herbaria were collected about a century ago.

SPECIMENS FROM OTHER COLLECTIONS

Crepis alpina L. One specimen, *Behboudi 146* (Iran), collected in Prov. Kermanshah: Sarpol-e Zabab, April 25, 1948, definitely confirms the statement in my monograph (1947*b*, p. 679) that this species occurs in northwestern Persia. In fact, Kermanshah is in midwestern Iran.

C. bithynica Boiss. Synonym: *C. Fodorii* Pénzes, Ann. Mus. Nationalis Hungarici, Pars Botanica, 31: 116–117; pl. 2, fig. 3; text fig. 7. 1937–1938. The type of *C. Fodorii* (BP) was collected in Bulgaria on Mt. Pirin in Banderica valley at 1,900–2,000 m. altitude in July, 1935; and other specimens collected at 1,800 m. altitude were sent to the writer by Dr. Pénzes. Earlier collections of this species from Mt. Pirin, by Stefanoff in 1929 and Georgieff in 1932, are cited in my monograph (1947*b*, p. 499). As is emphasized by Pénzes, these specimens from Mt. Pirin have taller scapes than Boissier's type. It should be noted also that the outer involucral bracts are more nearly equal and a little shorter in the Mt. Pirin plants. But these differences seem hardly sufficient for the recognition of distinct species or even of subspecies, since this amount of variability is not unusual in other species of *Crepis.* Furthermore, only a few specimens have been collected in both regions; and, therefore, the range of variation in this species is still unknown.

As was stated in the monograph (*loc. cit.*), the type material and other plants from the type region correspond closely with specimens from the Balkan Peninsula, in such minute details as size and shape of corolla, anther tube and anther appendages, and even the amount and arrangement of the glandular cells at the apex of the corolla teeth. On the other hand, the differentiating characters mentioned by Pénzes, the longer scapes and less pubescence on the leaves in *C. Fodorii,* are such as may be expected to occur among plants in any region according to local differences in environment.

One further detail requires comment. Concerning the number of ribs or costae on the achenes, questions may arise because of the differences reported in my description of *C. bithynica* (*loc. cit.*) and the original description of *C. Fodorii.* In my monograph the achenes are described as "15-striate," whereas in Pénzes' description they are said to be "10-subcostate." It now appears that subcostate or *narrowly ribbed* is a better descriptive term for the achenes of this species than striate; but the *number* of ribs is usually, if not always, more than ten. There were no achenes in the material of *C. Fodorii* sent to me by Dr. Pénzes, but the specimens of *C. bithynica* collected at two localities on Mt. Pirin by Stefanoff and Georgieff have achenes with 13–15 ribs. Furthermore, among some fragments from the type of Boissier, I find achenes also with 13–15 narrow ribs.

C. demavendi Bornm. One specimen, *Gauba 1484* (KAR), from Iran: Prov. Teheran; Elburs Mountains, Mt. Demavend, above Pelur, 2,800 m., is almost certainly this species, although it has no mature heads; it is at the lower limit of size for this species; and the leaves are pubescent on both sides with fine white glandular and glandless hairs. The leaves of typical plants were described by me as glabrous. Nevertheless, upon close examination of the isotype now in the Herbarium of the University of California, I find a few white glandless hairs on the lower face of some leaves. At the same time, the indumentum of the peduncles and involucres of Gauba's plant is identical with that of the type, and the flowers are similar, except for their smaller size. As far as I know, this is only the second time that *C. demavendi* has been collected.

C. divaricata (Lowe) F. Schultz. Three specimens (UC) collected in Porto Moniz, Madeira, at a place called "Tabugal," in 1948, were sent to me through the courtesy of the Director of the Museum in Funchal and the kindness of Mrs. H. P. Olmo. This collection derives special importance from the fact that heretofore the existence of this species on the Island of Madeira elsewhere than at the type locality has not been reported. In 1930 I found a few plants growing at the type locality, which is at the extreme *eastern* end of the island. This new collection from the extreme *western* end of the island shows that this species has not yet become extinct on the main island (cf. Babcock, 1947*b*, p. 816). It also throws new light on the problem of the extreme variability of *C. vesicaria* subsp. *andryaloides*, also of Madeira. I have pointed out (*ibid.*, p. 856) that some of this variability may have resulted from earlier hybridization with *C. divaricata*, but that *C. vesicaria* subsp. *andryaloides* appeared to have been completely isolated from that species. The discovery of this population of *C. divaricata* greatly increases the probability that such natural crossing took place, for two reasons. In the first place, Porto Moniz is only 12 miles (about 18 kilometers) from the Ribeiro do Inferno, where I collected *C. vesicaria andryaloides* in 1930. It is not unlikely, therefore, that the two species are even now in contact. In the second place, the existence of *C. divaricata* at both ends of the island indicates that this species was formerly widespread there. That it has had an even wider distribution is proved by its two variants from the adjacent Deserta Islands.

Minor variant 1 of *C. divaricata* was first collected on "Flat Dez'a," which undoubtedly is Deserta Grande, by Lowe, in 1850. Among the specimens recently sent to me I find one from Deserta Grande which was collected by de Costa in April, 1938, and which is certainly this same form. Hence, this species probably still exists on another island of the Madeira Archipelago. It would be very interesting to compare living specimens of the typical and variant forms and to test the fertility of hybrids between them.

The idea that the remarkable aggregation of forms which I assembled under *C. vesicaria* subsp. *andryaloides* is the result of repeated crossing and backcrossing between *C. vesicaria* subsp. *taraxacifolia* and *C. divaricata* seems by far the most probable explanation, now that *C. divaricata* is known to exist in

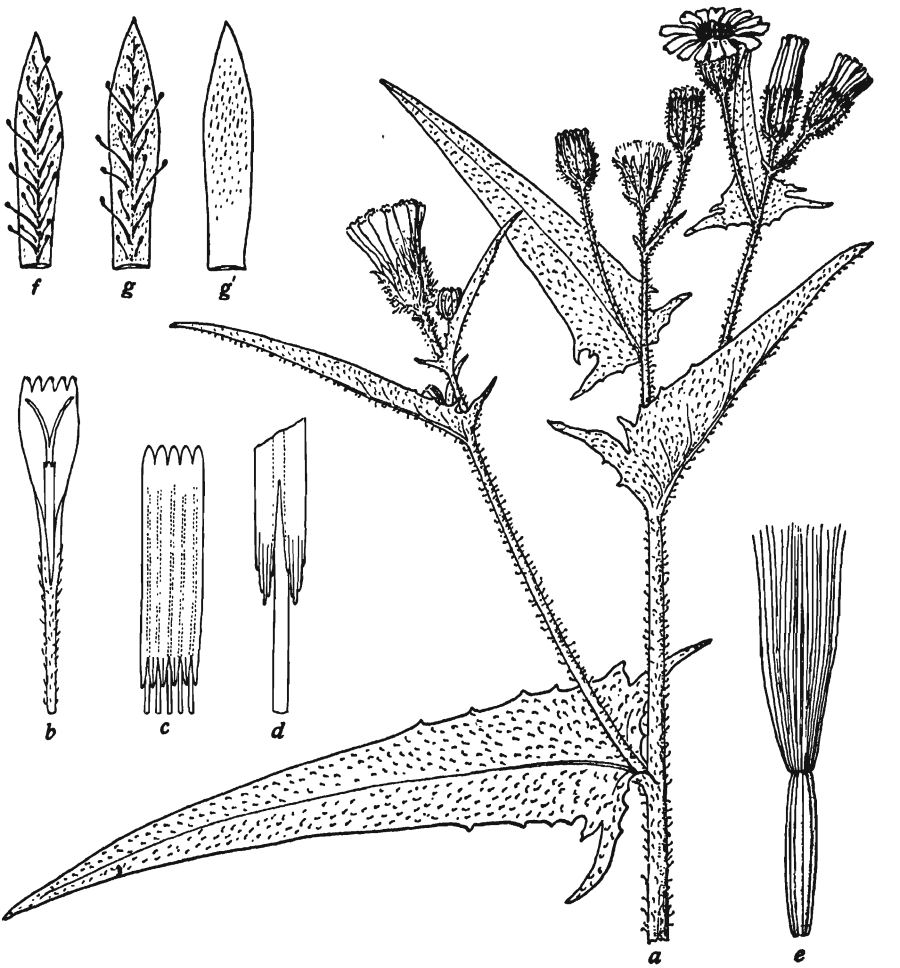


Fig. 1. *Crepis foliosa* sp. nov. *a*, upper part of the type specimen, × 1; *b*, floret lacking ovary, × 4; *c*, anther tube, split and opened out, × 8; *d*, detail of appendages, × 32; *e*, immature achene, × 8; *f*, inner involucral bract, from outer series, × 4; *g*, *g'*, an innermost inner bract, outer and inner faces, × 4. (Drawings by the author; inking by Miss Anna Hamilton.)

western Madeira and hence may have been still more widespread in the island in recent times.

C. foetida L. subsp. *vulgaris* (Bisch.) Babc. One specimen, *Pravitz 859* (S), collected in Iran: Prov. Gilan; Enseli (shore of Caspian Sea), provides further evidence of the eastward extension of range of this subspecies. Gilan lies just west of Mazanderan Province.

Crepis foliosa sp. nov. Herba annua, 2.3 dm. alta, pubescens pilis tenuis glandulosis; folia caudicalia ephemeres; folia caulina 5–9 cm. longa 2 cm. lata, infera oblanceolata petiolata, supra lanceolata sessiles auriculares, auriculis longis acuminatis; caulis erectus fistulosus sulcatus remote et recte ramosus, ramis 6–8 cm. longis arcuatis foliosis bi- vel tricepitibus; pedunculi

4–12 cm. longi tomentulosi; capitula erecta parva multiflora; involucrum campanulatum, 7–8 mm. longum, 4 mm. latum tomentulosum et dense pubescens, pilis fuscis glandulosis, squamis exterioribus 6–7 circa ⅓ interiorum aequantibus subulatis, squamis interioribus 13–14 lanceolatis acutis ventre pubescentibus; corolla 11 mm. longa, ligulâ 1 mm. lata, dentibus 0.2–0.5 mm. longis, tubo 3 mm. longo pubescente; antherae 3.5–4 mm. longae, appendicibus 0.5 mm. longis lanceolatis acutis, filamentis 0.4 mm. longioribus; rami styli 2 mm. longi 0.1 mm. lati viridi; achaenia (immatura) 2.75 longa 0.5 mm. lata paululum attenuata 10-costata tenue spiculata; pappus albus 4 mm. longus 1-seriatus tenuus mollis.

Annual, 2.3 dm. high, pubescent throughout with fine short pale gland-hairs; caudical leaves few, ephemeral (only remnants remaining on this specimen), oblanceolate or spatulate, long-petiolate; lowest cauline leaves (1–5 cm. from base) *ca.* 7 cm. long, oblanceolate, shortly petiolate and auriculate, middle cauline leaves *ca.* 9 cm. long, 2 cm. wide near the base, lanceolate, acuminate, irregularly dentate and denticulate, sessile, amplexicaul, auriculate, the auricles about as long as the width of the blade, narrow, acuminate, upper cauline leaves similar to the middle ones, mostly *ca.* 5 cm. long; stem erect, terete, fistulose, sulcate, tomentulous, remotely and regularly branched beginning near the base, branches 6–8 cm. long, arcuate, terminating in 2 or 3 heads on short peduncles subtended by leaves similar to the upper cauline leaves; aggregate inflorescence racemiform; peduncles 4–12 mm. long, tomentulous; heads erect, small, many-flowered; involucre campanulate, 7–8 mm. long, 4 mm. wide at base, tomentulous, densely pubescent with longer and shorter pale brown gland-hairs; outer involucral bracts 6 or 7, subulate, ⅓ as long as the inner ones, acuminate, becoming lax; inner bracts 13 or 14, lanceolate, acute or acuminate, appressed-pubescent on inner face; corolla 11 mm. long; ligule 2 mm. wide, teeth 0.2–0.5 mm. long; corolla tube 3 mm. long, pubescent with short (up to 0.15 mm.) 1- or 2-celled aciculate trichomes; anther tube 3.5–4 mm. long, 1 mm. wide when opened out, appendages 0.5 mm. long, lanceolate, acute, filaments 0.4 mm. longer; style branches 2 mm. long, 0.1 mm. wide, green; achenes (not fully mature) light brown, 2.75 mm. long, 0.5 mm. wide, moderately attenuate to both ends, with slightly expanded pappus disk and finely calloused hollow base, 10-ribbed, the ribs rather prominent, rounded, finely spiculate; pappus white, 4 mm. long, 1-seriate, the setae equally fine, soft, united at base. Flowering July–August, flowers yellow. See plate 46 and figure 1.

Known only from the type specimen in Herb. Mus. Palat. Vindob. (W), Th. Teploukhoff, Plantae Uralenses, no. 37, Utka, prope Pratsoufinsk (?), July 24, 1892, flowers and immature achenes. Utka River is a tributary of the Volga and is the boundary between the Tatar Republic and Mordwin Province to the south. It flows through the Volga flax lands.

This station is within the geographic area of *C. tectorum,* but the plant shows more resemblance to *C. nicaeënsis* in its involucres, flowers, and, especially, its achenes. At the same time, it is very distinct from both of those

TABLE 1

SYNOPTICAL COMPARISON OF CREPIS FOLIOSA WITH C. TECTORUM AND C. NICAEËNSIS

Crepis tectorum	*Crepis foliosa*	*Crepis nicaeënsis*
Upper cauline leaves linear or filamentous, with no or very small auricles	Upper cauline leaves lanceolate, with conspicuous auricles	Upper cauline leaves linear or bractlike, with no or very small auricles
Stem usually branched above the middle, lower branches longer, aggregate inflorescence corymbiform	Stem remotely branched from base upward, branches equally short, forming a racemiform panicle	Stem branched near the top or from the middle, aggregate inflorescence corymbiform
Indumentum: stem tomentulous and sometimes finely pubescent; leaves glabrous, tomentulous or puberulent	Indumentum: stem tomentulous and glandular pubescent with fine short pale hairs; leaves with similar gland-hairs	Indumentum: stem densely hispidulous below; basal leaves hispidulous with short yellow glandless hairs
Outer involucral bracts about 12	Outer involucral bracts 6 or 7	Outer involucral bracts 7–9
Inner involucral bracts pubescent on inner face	Inner involucral bracts pubescent on inner face	Inner involucral bracts usually glabrous on inner face
Corolla 13 mm. long, ligule 2.5 mm. wide, anther appendages oblong, obtuse	Corolla 11 mm. long, ligule 2 mm. wide, anther appendages lanceolate, acute	Corolla 11 mm. long, ligule 1.6 mm. wide, anther appendages lanceolate, acute
Achenes 3–4 mm. long, dark purplish brown, strongly attenuate to the apex	Achenes (not fully mature) 2.75 mm. long, light brown, moderately attenuate to both ends	Achenes about 3 mm. long, golden brown, moderately attenuate to both ends
Pappus 4–5 mm. long, 1-seriate	Pappus 4 mm. long, 1-seriate	Pappus 4–5 mm. long, 2-seriate

species in its large upper cauline leaves with conspicuous auricles, its racemiform branching habit, and its indumentum (see table 1). Therefore, *C. foliosa* is classified in section 24 (Phytodesia), between *C. nicaeënsis* and *C. capillaris*. Since the pollen grains are 3-pored and about 30 μ in diameter, this is a diploid plant and the diploid chromosome number is probably 8, possibly 6.

This only known station for the species is about 1,700 kilometers from the nearest known stations for other species in section 24. It would be of interest to learn of the distributional area of *C. foliosa* and to observe the plant under cultivation. In the light of the evidence now available on the processes of speciation in *Crepis*, it is very probable that *C. foliosa* is more closely related to the species of section 24 than to *C. tectorum*, *C. Bungei*, and *C. ircutensis*.

C. frigida (Boiss.) Babc. Two sheets of specimens (B) collected by Ellenberg in Turkey: Ala-Dag, no. 325 at 3,100 m. altitude, on August 23, 1938, and no. 393 at 3,150 m. altitude, on August 24, 1938, were loaned to me by Dr. Johannes Mattfeld and have been identified as this species. The locality here designated as Ala-Dag is presumably in the eastern Cilician Taurus, which is within the known area of distribution of this species.

C. Gaubae Bornm. (Fedde, Repert. 41: 318, pl. 128. 1937). One collection, *Gauba 1501* (KAR), Iran: Prov. Kazvin; Keredj, "beim Heurigen." Although there are only two small specimens, which lack caudical and lower cauline leaves, the original description and accompanying plate make identification absolutely certain. Nevertheless, there are important omissions in the original description, and, in order to make identification easier in the future, the following description is given.

Annual or monocarpic, 2–3 dm. high, pale yellowish green; stem reddish near base, nearly glabrous, slender, erect, branched from near the base or from the middle, or simple and 1-headed; branches elongated, pedunculate, somewhat thickened near the head; caudical and lower cauline leaves narrowly lanceolate, acute, gradually attenuate to the base, remotely runcinate-dentate or subentire or, rarely, subpinnatifid, the terminal lobe elongated; middle cauline leaves sessile, acutely auriculate or subhastate, narrowly lanceolate, acuminate; heads erect, medium or small, *ca.* 50-flowered; involucre urceolate at maturity, 10–15 mm. high, 6–15 mm. wide, yellowish green; outer involucral bracts *ca.* 10, nearly equal, *ca.* ½ as long as the inner ones, nearly glabrous or sparsely setulose, becoming scarious and lax; inner bracts lanceolate, acuminate, densely setulose *and pubescent* with pale-yellow glandless setules *and short fine gland-hairs intermixed,* becoming strongly carinate, *enclosing the marginal achenes;* corolla *ca.* 12 mm. long, the tube 4–5 mm. long, pubescent with short acicular hairs, ligule *ca.* 1 mm. wide, pubescent toward the base; anther tube 2 mm. long, appendages 0.4 mm. long, filaments slightly longer than the appendages; style branches 1.5 mm. long, 0.1 mm. wide, yellow; *achenes biform;* marginal achenes stramineous, 5–6 mm. long, shortly beaked, laterally compressed, 0.7 mm. wide dorsoventrally, densely spiculate, dorsally striate, with narrow basal scar; inner achenes tawny, 9–12 mm. long, 0.5 mm. wide, constricted at the narrow calloused base, attenuate into a slender beak 4–6 mm. long, terete or somewhat compressed, *ca.* 20-ribbed, ribs fine, rounded, somewhat unequal, spiculate; pappus white, *ca.* 6 mm. long, 2-seriate, the setae fine, stiff but pliable, persistent. Flowers yellow, the ligules intensely purple on outer face.

The date of this collection is not given. Presumably it was made in 1935 or 1936 when the specimens cited in the original description (also from Keredj) were taken. Some of the mature achenes were sown in our greenhouse, but they failed to germinate. Hence, it is impossible to report on the number of chromosomes in this species; but undoubtedly the haploid number is either 5 or 4.

This species is probably closest to *C. Kotschyana* Boiss. and *C. Thomsonii*

Babc., from both of which it is very distinct in the much larger outer involucral bracts, larger corolla, longer style branches, and differently shaped marginal achenes (in *C. Gaubae* the marginal achenes are abruptly constricted into a beak about ⅓ as long as the whole achene).

C. heterotricha DC. subsp. *lobata* Babc. One specimen, *Gabriel 243* (W), collected in Persia: "Kuh Lahlezar" (?), is almost certainly this subspecies, although mature achenes are lacking. There is no date, and the locality is dubious, but evidently this is not the type locality.

C. macedonica Kitan. (Bull. Inst. Bot. Sofia 1: 372–376. 1950). One collection (SO, UC), B. Kitanoff, August 8, 1948, from Mt. Deshat on the boundaries of Yugoslavia, Macedonia, and Albania, in gravel at the foot of the north peak, Deli-seniza, 2,130 m., brings before us this interesting new species. But, unfortunately, the part of the collection which was sent to me appears to be a mixture of two distinct new species. The material before me consists of two plants (with flowers and nearly mature achenes) which correspond closely with figures 1 and 2, page 374, in Kitanoff's publication cited above, together with a fragment from a different plant, a flower stem bearing three heads, one in anthesis, the others younger, and one lower cauline leaf.

My attention was first caught by the very different shape of this leaf on the fragment (fig. 2, *a'*) and that of the lower cauline leaves of typical plants (fig. 2, *a*). This observation led to comparison of the floral characters, and a thorough examination revealed even more striking differences (see table 2).

TABLE 2

COMPARISON OF TYPICAL CREPIS MACEDONICA WITH ATYPICAL FRAGMENT

	C. macedonica	Atypical fragment
Corolla	14–15 mm. long	18–23 mm. long
Ligule teeth	equal, 0.5 mm.	unequal, 0.5–1.5 mm.
Corolla tube	3.5 mm., nearly glabrous	5 mm., sparsely pubescent
Anther tube	5 mm. long	5.5–6 mm. long
Anther appendages	0.5 mm., truncate	0.7 mm., acuminate
Style branches	2.5 mm. long	4 mm. long

Although the involucres are closely similar in the two species, the inner bracts of the atypical fragment are slightly longer and broader (fig. 2, *e'*).

The original description by Kitanoff, in Latin, is based for the most part on the type or isotypes. But the following sentences are beyond question descriptive of florets taken from the atypical fragment (or plant—I do not know how much more material of this second species exists in the Sofia Herbarium): "Flosculi 18–23 mm. longi, ligulis 3 mm. latis, denticulis ca. 1 mm. longis, apice crassiculis et rubellis. Flosculi tubus 4–5 mm. longus sparse albopilosus." There are also certain inaccuracies in the original description. For example, the underground part of the plant is mistaken for a rhizome, although it is obviously a woody taproot. This error, in turn, led to the mistake of classifying the species in section 4 (Brachypodes), whereas it obviously belongs in section 10 (Berinia), subsection E (Divaricatae), and is much

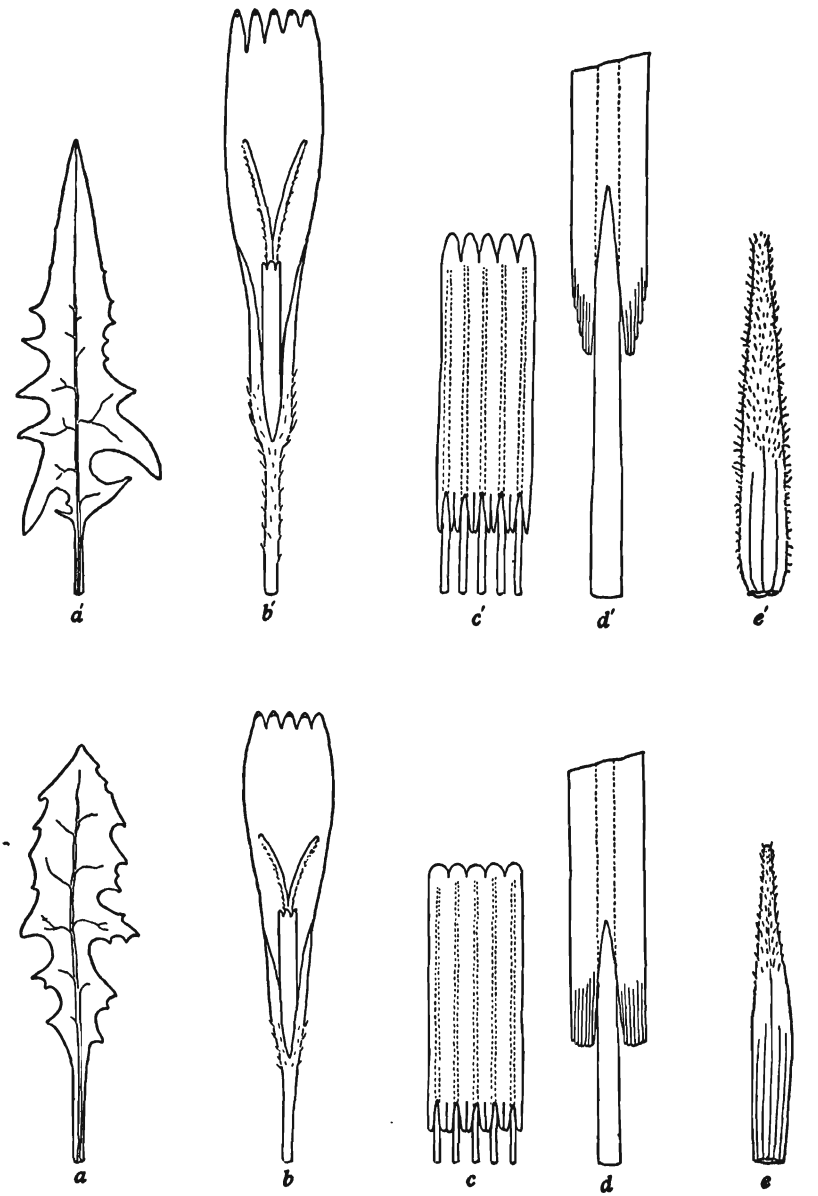


Fig. 2. *a–e, Crepis macedonica* Kitan.; *a'–e'*, atypical fragment; *a, a'*, lower cauline leaves, × 1; *b, b'*, florets lacking ovary, × 4; *c, c'*, anther tubes, split and opened out, × 8; *d, d'*, details of appendages, × 32; *e, e'*, inner involucral bracts, inner face, × 4. (Drawings by the author; inking by Miss Anna Hamilton.)

closer to *C. albanica* than to *C. terglouensis*, with which it is compared by Kitanoff. It therefore becomes necessary to publish a new description of this species, based on the two specimens before me.

C. macedonica Kitan. (sec. 10, E, near *C. albanica* [Jav.]. Cf. Babcock, 1947*b*, p. 468). Perennial, 7–10 cm. high; taproot vertical, slender, woody; caudex short, 5–8 mm. wide, covered with scarious bases of old leaves, sparsely brown-woolly; caudical leaves numerous, 4–9 cm. long, 0.8–2 cm. wide, oblanceolate, acute, irregularly runcinate-pinnatifid to lyrately pinnate, with large acutely dentate terminal lobe and acute rapidly reduced lateral lobes, the petiole narrow, much broadened at base, longer or shorter than the blade, reddish purple and like the blade canescent-tomentulose or floccose; cauline leaves 2, the lower one similar to the caudical leaves, the upper bractlike; stems 1–3, furcate or rarely simple, the branches divaricate, arcuate, pedunculate, aggregate inflorescence corymbiform; heads medium, *ca.* 50-flowered; involucre broadly campanulate, 10–12 mm. long, 5–7 mm. wide at base, like the peduncle canescent-tomentose; outer involucral bracts 10–14, subulate-acuminate, dark green and glabrate toward the apex, unequal, the longest ¾–⅚ as long as the inner bracts; inner bracts 16–20, lanceolate, acuminate, shortly ciliate at the apex, appressed-pubescent on upper half of inner face; receptacle convex, alveolate, the fimbrillae shortly ciliate; corolla 14–15 mm. long; ligule 2.5–3 mm. wide, the teeth equal, 0.5 mm. long; corolla tube 3.5 mm. long, glabrous except near the base of the ligule which is sparsely pubescent with very short (up to 0.2 mm.) acicular trichomes; anther tube 5×1.5 mm. when slit and opened out; appendages 0.5 mm. long, oblong, truncate; filaments extend 0.5 mm. beyond appendages; style branches 2.5 mm. long, 0.15 mm. wide, yellow; pollen grains abundant, regular in size, average diameter *ca.* 33 μ; achenes (nearly mature) stramineous, 5.5–6 mm. long, 0.7 mm. wide, columnar, somewhat attenuate at the apex, with slightly expanded pappus disk, narrowed at the pale-calloused hollow base, *ca.* 15-ribbed, the ribs unequal, rounded, glabrous; pappus white, 7–8 mm. long, 2-seriate, the setae unequal in length and width, the coarsest *ca.* 50 μ wide at base, persistent, coming away in clumps. Flowering July–August, flowers yellow.

Known only from the type locality.

Stained preparations of pollen from unopened florets (stained with dilute cotton blue after washing in alcohol) showed the abundant grains to be echinolophate, as would be expected, 3-pored and nearly uniform in size, averaging about 33 μ in diameter. It is probable that the haploid chromosome number is either 5 or 4. This species stands closest to *C. albanica* (Jav.) Babc.

Publication of a description of the other new species, represented in our material by the atypical fragment mentioned above, must wait until more material is available. The following data may be of some use to the future author of this new species:

Stem 9 cm. high, 2-furcate, branches divaricate, pedunculate, leaf sparsely canescent-tomentose, *ca.* 6 cm. long, 2 cm. wide, the petiole 1 cm. long, broader

at the base, the blade lanceolate, acuminate, irregularly pinnate, lower lobes oblong, acute, the others triangular, the apical part (2 cm. long) entire, strongly acuminate; peduncles slightly thickened near the head and canescent-tomentose like the involucre; involucres broadly campanulate, 11–13 mm. long, 6–7 mm. wide at base; outer involucral bracts 10–12, dark green and glabrate near the apex, lanceolate, acuminate, unequal, the longest ¾ as long as the inner bracts; inner bracts 18–20, lanceolate, acuminate, strongly ciliate on the margin and at apex, appressed-pubescent on upper half of inner face; corolla 18–23 mm. long; ligule 3 mm. wide; ligule teeth unequal, 0.5–1.5 mm. long; corolla tube 5 mm. long, sparsely pubescent with short (up to 0.3 mm.) acicular trichomes; anther tube 5.5–6 × 1.5 mm. when slit and opened out; appendages 0.7 mm. long, acuminate; filaments extending beyond appendages 1 mm.; style branches 4 mm. long, 0.2 mm. wide, yellow; pollen grains from unopened florets uniform, 3-pored, *ca.* 33 μ in diameter; achenes (juvenile) columnar, slightly constricted at apex and base, striate; pappus white, 8 mm. long, 2-seriate, the setae unequal in length and width, the coarsest *ca.* 50 μ wide at base, persistent, coming away in clumps. Flowering July–August, flowers yellow.

C. Marschallii (C. A. Mey.) F. Schultz. One specimen, collected by *Gauba* in 1935 (KAR) at Babal, Prov. Mazanderan, Iran, is unquestionably this species and it extends the known geographic distribution of *C. Marschallii* eastward to the south end of the Caspian Sea.

C. quercifolia Bornm. et Gauba (? see description, Fedde, Repert. 41:319. 1937). One specimen, *Behboudi 169* (Iran), collected in May, 1948, in Iran: Prov. Kermanshah; Zarab-e Gilan, is probably this species, which has been known hitherto only from the type (*Gauba 905*) in Herb. Bornm. (now at Berlin?). But, if it is this species, the specimen now before me is a reduced variant, which differs from the original description in certain respects, most notably: *peduncles* short, canescent-tomentulose and sparsely setulose with purplish eglandular setules; *involucral bracts* dark green, the outer ones linear, inner ones 9 mm. long, lanceolate, acuminate, setulose with yellowish eglandular setules; corolla 11 mm. long; anther tube *ca.* 3 mm. long; pappus 4 mm. long. Unfortunately, the original description gives no data on the flowers, and the specimen in hand has no mature achenes. However, from the original description, there is no doubt that *C. quercifolia* is very distinct from *C. Marschallii* (to which it is obviously related), and the specimen reported here seems to show more resemblance to *C. quercifolia* than to *C. Marschallii* in its leaves and indumentum. Another (fragmentary) specimen in the same herbarium, *Gauba 2693,* collected in Iran: Prov. Shiraz, in 1936, is an even more reduced plant and lacks mature heads, but it resembles the foregoing in habit, leaves, involucre, and indumentum.

C. sancta (L.) Babc. subsp. *nemausensis* (Gouan) Thell., a minor variant with outer involucral bracts small, as in subsp. *bifida.* One specimen, *Mirdamadi 1506* (KAR), collected in Prov. Azerbaijan: Meshkambar, near Tabriz, establishes the spread of this subspecies as far east as the Caspian

Sea. The *bifida*-like involucre is another indication that the two subspecies are intercrossing where they come in contact (cf. Babcock, 1947*b*, pp. 731, 733).

C. sancta (L.) Babc. subsp. *nemausensis* (Gouan) Thell. m.v. 5. One specimen, *Haradjian 3937* (W, Herbarii Delessertiani editae), collected in northern Syria: between Hassan Beyli and [place name illegible], 450–760 m., appears to be a distinct form of this subspecies, possibly an ecotype. The luxuriant, leafy rosette is 1.5 dm. in diameter, but the few-headed stems are only 5–6 cm. high. The indumentum is typical throughout, but the awns of the paleae are black, and the anther tubes are black at the apex. There are no mature heads.

C. Sibthorpiana Boiss. et Heldr. One collection, *Davis 18160* (UC), consisting of several plants in flower but without fruits, is unquestionably this very rare species. The type collection of Heldreich was made in 1846 on Mt. Stravapodia in Sphakia of western Crete, presumably in the Madaras or White Mountains. The second locality to be reported is Mt. Psiloriti of central Crete. The new station, where it was collected by Davis in 1950, is also in the White Mountains of western Crete, namely, Lepha Ore: Svowricht (?), above Katsiveli, rocky slopes, 2,200 m. Thus far, I have been unable to obtain living material of this species.

C. willemetioides Boiss. Two specimens (B) collected by *Dr. E. Gauba* in northern Persia, Elburs, "Pole Zangule," no. 1589 at an altitude of 2,300 m., and no. 1590 at an altitude of 2,400 m., were loaned to me by Dr. Johannes Mattfeld of the Berlin Botanic Garden and have been identified as this species. The name Elburs presumably refers to the Elburs Mountains. But, in addition to "Elbursgebirge," Stielers Handatlas designates as "Elburs" a small region adjacent to Talysch, which is south of Baku in Azerbaijan. If this is the region where these specimens were collected, the new locality greatly extends westward the known geographic distribution of *C. willemetioides*. Otherwise, the area of distribution reaches from Transcaspian Province and the northeastern Persian frontier westward into Mazanderan Province at the south end of the Caspian Sea.

THE NUMBER OF SPECIES IN THE GENUS

To the 196 species of *Crepis* recognized as valid in the monograph, the following should be added, making the total number now known to me 204.

C. asadbarensis Bornm. Fedde, Repert. Spec. Nov. Reg. Veg. 41: 317. 1937.

C. dobrogica Babc. Trav. Bot. déd. à René Maire (Mém. hors-série Soc. d'Hist. Nat. Afr. Nord. II: 10. 1949).

C. flexiscapa Rech.f. Denkschr. Akad. Wiss. Wien, Math.-Nat. Klasse, 105 (2): 164. 1943 (cf. Babcock, 1947*b*, p. 719).

C. foliosa Babc. Described above, p. 389.

C. Gaubae Bornm. Fedde, Repert. Spec. Nov. Reg. Veg. 41: 318.

C. macedonica Kitan. Bull. Inst. Bot. Sofia 1: 372. 1950.

C. Nemetzii Rech.f. Fedde, Repert. Spec. Nov. Reg. Veg. Beih. 98: 56. 1938 (cf. Babcock, 1949*a*).

C. quercifolia Bornm. Fedde, Repert. Spec. Nov. Reg. Veg. 41: 319. 1937.

The distribution of these eight newly recognized species is also worthy of comment. As might be expected, in view of the evolutionary history of the genus, they are mostly from the eastern Mediterranean region, including Iran.

Balkan Peninsula: *C. dobrogica, C. Nemetzii, C. macedonica.*

Crete: *C. flexiscapa.*

Iran: *C. asadbarensis, C. Gaubae, C. quercifolia.*

Russia: *C. foliosa.*

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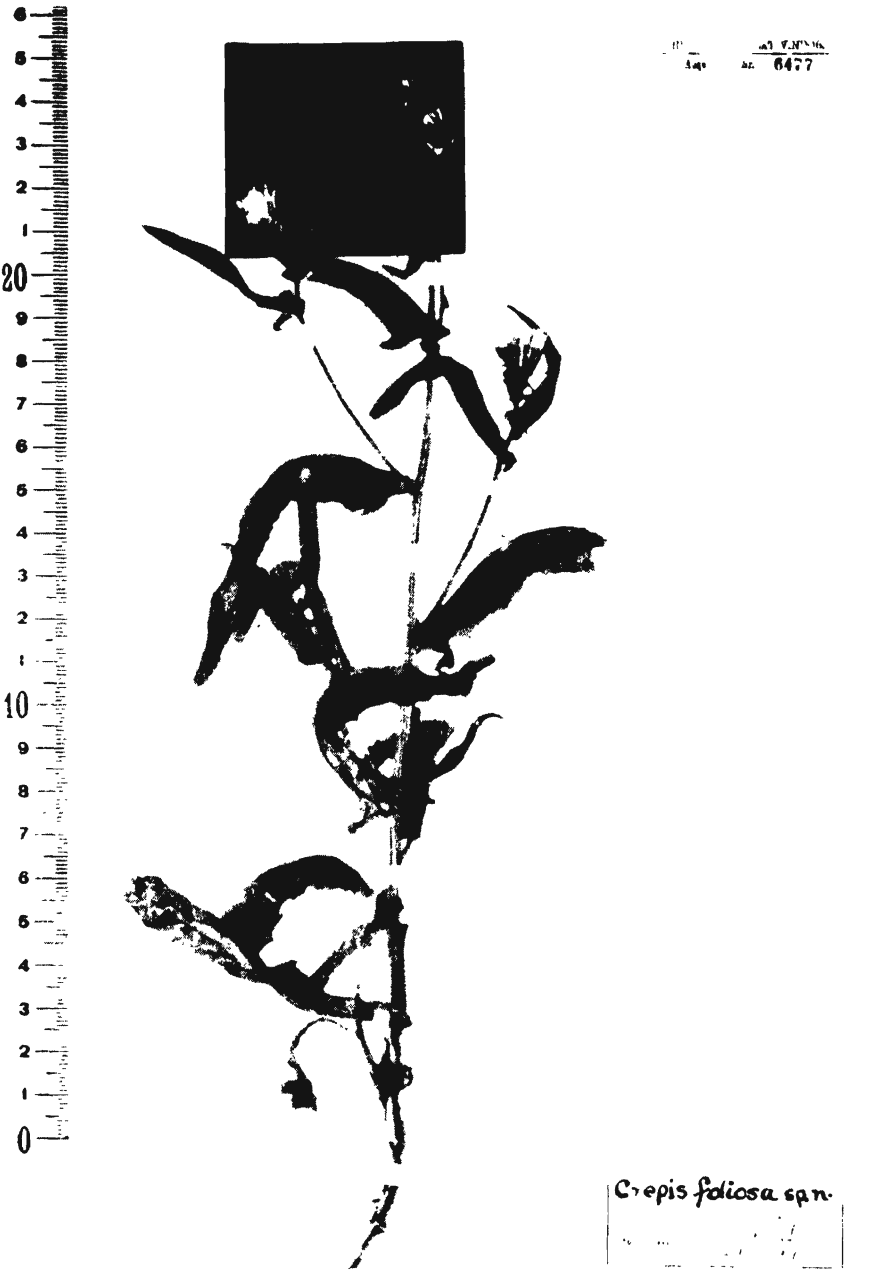
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Crepis foliosa sp. nov. Typus et specimen unicum. (Photograph by V. Duran.)

A REVISION OF THE ANDEAN GENUS NIPHOGETON (UMBELLIFERAE)

BY

MILDRED E. MATHIAS and LINCOLN CONSTANCE

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IN ENDEAVORING to provide accurate determinations for collections of Umbelliferae secured within recent years in northern South America, principally by Wendel H. Camp, José Cuatrecasas, Julian A. Steyermark, and the wartime Colombian Cinchona Mission, the writers came independently to the conclusion that the plants treated here were overdue for taxonomic study. The first species of this group was described under the genus *Ligusticum*, the second under *Petroselinum*, and the next three under *Apium*. DeCandolle (1830) created the section *Oreosciadium* in *Apium* for the three last-mentioned species and placed with them the unrelated *A. Commersonii* DC., *A. fractophyllum* Hornem., and *A. australe* Thouars. Schlechtendal erected the genus *Niphogeton*[1] in 1856 for one of the component species, and the following year Weddell elevated DeCandolle's section *Oreosciadium* to generic rank, including within it three species, five varieties, and three subvarieties. Wolff (1908) described the monotypic genus *Urbanosciadium* in this same complex.

Subsequent authors recognized the present group of species as constituting the distinct genus *Oreosciadium* (Bentham, Koso-Poliansky) or as either a subgenus (Drude) or a section (Wolff) of *Apium*. In the last revision of *Oreosciadium*, as a section of *Apium*, Wolff (1927) recognized three subsections (*Simplicifolia*, *Pinnatifolia*, *Ranunculifolia*) and a total of nine species, five varieties, and one subvariety. In 1930 Macbride resurrected *Niphogeton* Schlecht., clearly saw its essential identity with *Oreosciadium* Wedd., and transferred to the former a number of Peruvian species. Up to the present time, however, some species have remained under each of the four generic designations: *Apium*, *Niphogeton*, *Oreosciadium*, and *Urbanosciadium*. One of the objectives of the present study is to bring these species into a generic grouping more appropriate to their apparently intimate relationship.

There has been general agreement that these plants fall among the Apioid or Ligusticoid Umbelliferae. Bentham (1867) referred to them as "Genus ab Apio carpophoro, a *Caro* petalis, ab utroque habitu differt." Koso-Poliansky (1916) placed the genus in his Ligusticoideae-Gymnomestomeae-Careae-Carinae. Wolff (1908), however, compared *Urbanosciadium* with *Oreomyrrhis* Endl. When compared with the genera treated in the North American Flora (Mathias & Constance 1944–1945), *Niphogeton* seems most reminiscent of the Ligusticoid genus *Podistera* S. Wats., but it is by no means congeneric with it.

As to the generic distinctness of the group, Weddell (1857) remarked: "Ce groupe est, comme on le voit, un démembrement du genre *Apium* du *Prodromus*; et les plantes qui le composent me semblent se distinguer très nettement du genre auquel elles ont été rapportées: 1° par le forme du fruit: 2° par leur columelle con-

[1] Greek: νιφο-, γειτων, snow neighbor, a common-gender word here interpreted as feminine, following the usage of Macbride.

stamment bifide; 3° par leur pétales non apiculés; 4° par la présence d'un involucre et d'un involucelle. Plus voisines des *Petroselinum*, elles s'en distinguent néanmoins aussi facilement par leurs pétales, qui ne sont ni acuminés ni infléchis à l'extrémité, et par leur étamines incluses. Les Oreosciadium diffèrent enfin des plantes de l'un et de l'autre des groupes qui j'ai nommés par leur distribution géographique, limitée a le chaîne des Andes, où quelques-unes s'élèvent jusqu'au niveau des neiges perpétuelles." And, according to Macbride (1930), "Although Wolff . . . follows DeCandolle in regarding this group as only a section of *Apium*, I think it is more properly treated, as by Bentham and Hooker and by Weddell, as a distinct genus. In general it is quite different, both in habit and habitat, and it always has involucral bracts. It is true that one section of *Apium* as defined by Wolff (sect. *Helosciadium*) is provided with bracts, but the species constituting it are aquatic or lowland weeds with the aspect of *Apium*, an aspect so totally different from that of the high andean plants considered here that to associate the latter in the same genus is not only inconvenient but seems unreasonable. Besides, the section *Helosciadium* of *Apium* may be as closely related, from a genetic standpoint, to *Sium* (with which it has often been allied) as to *Apium*, and might conveniently be kept distinct from both. At any rate, the species comprising *Niphogeton* constitute a group too aberrant for inclusion in *Apium*, regardless of the disposition made of *Helosciadium*."

We agree with Macbride that the species referred here to *Niphogeton* are generically distinct from *Apium* proper by the combination of their perennial habit, involucrate umbels, petals without an inflexed apex, biparted carpophore, and their geographical and ecological restriction to the páramos of the Andes. Their removal from *Apium* will free that genus of a strongly discordant element, and their disposition in a separate genus will serve to focus attention upon the morphological trends expressed by this group of species.

As in the case of many other plants with aromatic herbage, the species of *Niphogeton* apparently have been prized by the natives as medicinal herbs. Most of the data on such usage are documented by fragmentary notes by various collectors, which have been transcribed on herbarium labels. Thus, *N. ternata* is referred to by Triana as "Apio de monte"; Kalbreyer calls it "Culantrigo (Medicinal pl.)." The epithet, "Apio del páramo," is applied to *N. angustisecta* by Kalbreyer, Uribe, and St. John. Purdie says of this species, "A concoction of this is used in fevers"; Kalbreyer adds that it is "used much internell for stomach complaints," and St. John refers to it as "Medicine for stomach ache." Uribe relates that the species is "Usado por curar los dientes y endurecer los encias." Finally, Purdie notes of *N. pusilla*, "Same considered medicinal."

Our work has been greatly facilitated by the opportunity to see the material of the genus deposited in the following herbaria, to whose curators we are deeply indebted: Chicago Museum of Natural History (F); Institut de Botanique Systematique de l'Université, Conservatoire Botanique, Ville de Genéve (G); Gray Herbarium, Harvard University (GH); Royal Botanic Gardens, Kew (K); Instituto de Biología, Universidad Nacional de México (MEXU); New York Botanical Garden (NY); Laboratoire de Phanerogamie du Museum National d'Histoire Naturelle, Paris (P); Naturshistoriska Riksmuseet, Stockholm (S); University of

California, Berkeley (UC); University of California, Los Angeles (LA); United States National Museum, Smithsonian Institution (US); United States National Arboretum, Plant Industry Station, Beltsville, Maryland (USNA); Naturhistorisches Museum, Vienna (W). Efforts to obtain materials from several South American herbaria proved uniformly unsuccessful. In addition to specimens, we have been greatly aided by the availability for study of the photographs taken in European herbaria by Mr. J. Francis Macbride (cited as [F]) and by Mr. Ellsworth P. Killip (cited as [K]). Although we have seen most of the actual type specimens, our concept of some entities hinges critically on these photographs.

Niphogeton Schlecht.

Apium § *Oreosciadium* DC. Prodr. 4: 101. 1830; H. Wolff in Engler, Pflanzenreich 90 (4[228]): 46–52. 1927.

Niphogeton Schlecht. Linnaea 28: 481. 1856; F. Macbride, Field Mus. Publ. Bot. 8: 125–126. 1930; Candollea 5: 395. 1934, 6: 16. 1934.

Oreosciadium Wedd. Chlor. Andin. 2: 203. 1857; Benth. & Hook. Gen. Pl. 1[3]: 889. 1867; K.-Pol. Bull. Soc. Mosc. II. 29: 196. 1916.

Apium subgen. *Oreosciadium* Drude in E. & P. Pfl. 3[8]: 185. 1898.

Urbanosciadium H. Wolff, Bot. Jahrb. 40: 302. 1908.

Low, cespitose and bushy to slender and scrambling caulescent to subacaulescent or acaulescent perennial herbs, usually branching at or near the sometimes woody base, the branches erect or ascending, the herbage green to glaucous, glabrous to puberulent, scaberulous, or hirsutulous, the foliage usually subcoriaceous; basal leaves densely rosulate to loosely clustered, linear-oblong or lanceolate to orbicular or obovate, simple, ternate, pinnate, or pinnately decompound; petioles stout or slender, sheathing at least toward the base; leaves rather remote on vigorously growing shoots, the petioles usually wholly sheathing and often conspicuously inflated in the upper cauline leaves; inflorescence terminal and lateral, rarely terminal only, often corymbose, with usually one to several lateral peduncles arising in the axils of the cauline leaves, the peduncles slender to stout; involucre of 2–15 (?) linear-filiform to obovate, entire, lobed, or pinnatifid bracts usually exceeding the rays; rays (1–)3–20, angled, spreading, spreading-ascending, or ascending, subequal to unequal (abortive in *N. Sprucei*); involucel of 1–7 linear to obovate, entire to pinnatifid bractlets, usually exceeding the pedicels; pedicels 1–10, angled, spreading or spreading-ascending, subequal to unequal; calyx teeth obsolete; petals (where known) oblong to ovate, obtuse or acute but without a narrowed, inflexed apex, white or with a colored midvein; stamens included or exserted; stylopodium depressed- to low-conic, the styles short, spreading or erect; carpophore stout, divided to the base, the halves divergent at the apex; fruit oblong to ovoid, compressed laterally, the ribs prominent, acute or obtuse to corky-winged; vittae solitary in the intervals, 2 on the commissure, sometimes a smaller vitta in the apex of each rib; seed often channeled under the vittae, the face plane or concave.

Type species.—*Ligusticum ternatum* Willd. ex R. & S. (*Niphogeton ternata* (Willd.) Math. & Const.).

Distribution.—Andean páramos, at altitudes of 6,700–15,000 feet, Venezuela and Colombia to Peru and Bolivia.

KEY TO THE SPECIES AND VARIETIES

A. Leaves ternate, pinnate, or pinnately compound.
  B. Plants woody at the base; leaves ternate, the leaflets entire to deeply 3- to 5-parted.
    C. Foliage green, not glaucescent; fruit tapering toward the apex, the pericarp dull.
      D. At least some leaflets 3- to 5-toothed or -parted, 5–30 mm. broad.
        E. Plants 8–20 dm. tall; fruit 3.5–4 mm. long, 2.5 mm. broad, the ribs obtuse, prominently corky-winged, much broader than the intervals; region of Bogotá, Colombia ..... 1b. *N. ternata* var. *orientalis*
        EE. Plants 2–7.5 dm. tall; fruit 3 mm. long, 1.5–2 mm. broad, the ribs acute, unwinged, much narrower than the intervals; Venezuela to Ecuador ..... 1a. *N. ternata* var. *ternata*
      DD. Leaflets all entire, 1.5–5 mm. broad ..... 2. *N. angustisecta*
    CC. Foliage glaucescent; fruit subtruncate, scarcely tapering, the pericarp shining.
      F. Leaflets entire or shallowly tridentate; bracts and bractlets glabrate; vittae rather small; northern to central Colombia ..... 3. *N. Josei*
      FF. Leaflets deeply 3- to 5-lobed; bracts and bractlets ciliolulate (obscurely so in Ecuadorean material); vittae large; central Colombia to Ecuador ..... 4. *N. glaucescens*

BB. Plants herbaceous throughout; leaves pinnate to pinnately decompound.
G. Plants caulescent; leaves pinnately decompound; rays well developed.
H. Plants low, bushy, 0.5–3.5 dm. tall; peduncles up to 1 dm. long, little exceeding the foliage; involucre exceeding the rays, the rays 0.3–2.5 cm. long.
I. Plants glabrate or hirsutulous; leaf sheaths and bracts not prominently scarious and inflated; involucre shorter than the fruit; stylopodium low-conic, the styles 0.2- 0.5 mm. long; fruit ribs not corky-thickened.
J. Foliage glabrous to minutely scaberulous or puberulent, not hirsutulous; rays and pedicels puberulent to glabrate
5a. *N. dissecta* var. *dissecta*
JJ. Foliage hirsutulous at least on the sheaths of the outer leaves; rays and pedicels hirsutulous.....5b. *N. dissecta* var. *ciliata*
II. Plants densely scaberulous; leaf sheaths and bracts prominently scarious and inflated; involucre exceeding the fruit; stylopodium depressed-conic, the styles 0.5–1 mm. long; fruit ribs corky-thickened.....6. *N. scabra*
HH. Plants slender, 3–10 dm. tall; peduncles 1–3 dm. long, greatly exceeding the foliage; involucre much shorter than the rays, the rays 1–6.5 cm. long.
K. Plants glabrous, the peduncles glabrous beneath the umbel; rays spreading-ascending; fruit 3–4 mm. long, 2–2.5 mm. broad.....8. *N. magna*
KK. Plants scaberulous, the peduncles densely scaberulous beneath the umbel; rays rather strictly ascending; fruit 5 mm. long, 2.5–3 mm. broad
9. *N. stricta*
GG. Plants acaulescent; leaves pinnate; rays abortive.....7. *N. Sprucei*
AA. Leaves simple, entire to deeply trilobed.
L. Plants distinctly caulescent, 1–3 dm. tall, with several to many cauline leaves; leaf blades 1.2–7 cm. long; inflorescence terminal and lateral.
M. Basal leaves oblong to ovate, obscurely tridentate to deeply trilobed; bracts and bractlets linear or filiform, entire.
N. Basal leaves densely rosulate, ovate, 15–20 mm. broad, deeply trilobed; bracts and bractlets minutely ciliolulate; styles 0.5 mm. long, spreading
10. *N. Killipiana*
NN. Basal leaves rather remote, oblong, 4–7 mm. broad, obscurely tridentate; bracts and bractlets glabrous; styles very minute, erect or ascending
11. *N. lingula*
MM. Basal leaves spatulate with numerous crenations distally; bracts and bractlets prominent, spatulate, lobed.....12. *N. Kalbreyeri*
LL. Plants subacaulescent, 1 dm. or less tall, with 1 or 2 bractlike cauline leaves; leaf blades 1 cm. or less long; inflorescence strictly terminal.....13. *N. pusilla*

1. **Niphogeton ternata** (Willd. ex R. & S.) Math. & Const., comb. nov.

Scrambling perennial herb 2–20 dm. tall, woody at the base, glabrous except for the puberulent inflorescence, or puberulent throughout, the foliage dark green, subcoriaceous; leaves ovate to orbicular, 1.5–4.5 dm. long, 1–5 cm. broad, ternate, the leaflets short-petiolulate to sessile, oblanceolate to obovate, 0.5–3 mm. broad, entire or shallowly 3- to 5-toothed to deeply 3- to 5-parted and the divisions 3- to 7-toothed or -lobed, acute, mucronate; petioles slender, 2–9 cm. long, the lower half in the basal leaves forming an oblong sheath, the upper petioles wholly sheathing; inflorescence terminal and lateral, 1–3 lateral peduncles arising in the axils of the uppermost leaves, 1–7 cm. long; involucre of 5–7 bracts 5–20 mm. long, linear to linear-oblanceolate, entire or occasionally 2- or 3-fid at the apex, usually exceeding the rays; rays 4–10, 4–20 mm. long, spreading or spreading-ascending, unequal; involucel of 5–7 bractlets like the bracts, 5–10 mm. long, usually exceeding the pedicels; pedicels 3–7, 2–12 mm. long, unequal, spreading-ascending; petals oval, obtuse, white; stylopodium low-conic, the styles 0.3 mm. long, spreading; fruit ovoid, 3–4 mm. long,

1.5–2 mm. broad, the ribs prominent, acute, and much narrower than the intervals or prominently corky-winged, obtuse, and much broader than the intervals; vittae large, sometimes a smaller vitta solitary in the apex of each rib; seed face shallowly concave.

1a. **Niphogeton ternata** var. **ternata**

Ligusticum ternatum Willd. ex Schlecht.; R. & S. Syst. Veg. 6: 555. 1820.
Apium montanum Kunth in H.B.K. Nov. Gen. & Sp. 5: 17. 1821.
Apium ranunculifolium Kunth in H.B.K. Nov. Gen. & Sp. 5: 18, *pl. 421.* 1821.
Oreosciadium montanum α Wedd. Chlor. Andin. 2: 204. 1857.
Oreosciadium montanum β ranunculifolium Wedd. Chlor. Andin. 2: 205. 1857.
"*Apium montanum* subsp. *ranunculifolium* H.B.K." fide Drude in E. & P. Pfl. 3[8]: 185. 1898.
Apium ternatum Thell. Mém. Soc. Neuchat. Sc. Nat. 5: 393. 1913, not Pallas ex Steud. 1840, nor Schlecht. ex R. & S 1820, nor Siebold 1830.
Apium ternatum var. *ranunculifolium* Thell. Mém. Soc. Neuchat. Sc. Nat. 5: 394. 1913.
Laserpitium ternatum Willd. ex Thell. Mém. Soc. Neuchat. Sc. Nat. 5: 394. 1913, as synon.
Apium ternatum var. *genuinum* H. Wolff in Engler, Pflanzenreich 90 (4[228]): 51. 1927.

Plants 2–7.5 dm. tall; leaves ovate to orbicular, 1.5–4.5 cm. long, 1–3.5 cm. broad, the leaflets entire or shallowly 3- to 5-toothed to deeply 3- to 5-parted, and the divisions 3- to 5-toothed or -lobed; peduncles 1–7 cm. long; fruit 3 mm. long, the ribs prominent, acute, unwinged, much narrower than the intervals.

Type locality.—"In America meridionali," *Humboldt & Bonpland.*

Distribution.—Páramos at 9,000–13,000 feet altitude, Andes of Venezuela, Colombia, and Ecuador.

Specimens examined.—VENEZUELA. Táchira: Páramo de Tamá, *F. Cardona 290* (F, UC, US). COLOMBIA. Bolívar: below Páramo de Chaquiro, Cordillera Occidental, *F. W. Pennell 4308* (F, GH, NY-part, US). Norte de Santander: Boqueron, Ocona–Pamplona, *W. Kalbreyer 1996* (K). Santander: Páramo del Almorzadero, Cordillera Oriental, *Cuatrecasas & Garcia-Barriga 9975* (F, US). Caldas: Cerro Tatama, Cordillera Occidental, *F. W. Pennell 10,568* (US). Cundinamarca: Guadalupe, Bogotá, *O. Haught 5632* (US); Páramo de Choachi, near Bogotá, *F. W. Pennell 2234* (NY, US-fragment); Río Arroz, Páramo de Sumapaz, *F. R. Fosberg 20,821* (USNA). Meta: Río Arroz, above confluence of Quebrada Pedregal, *F. R. Fosberg 20,920* (UC, USNA). Huila: Santa Leticia, región de Moscopán, *Garcia-Barriga & Hawkes 12,894* (US). Valle del Cauca: Los Farallones, páramo en el cerro la Torre, Cordillera Occidental, *J. Cuatrecasas 17,833* (Fac. Agron. El Valle). Cauca: Páramo de Buena Vista, Huila group, Central Cordillera, *H. Pittier 1119* (US); Cabeceras del Río Palo, Alto de los Casitas, Cordillera Central, *J. Cuatrecasas 18,977* (GH, UC); Llano de Paletará, Cordillera Central, *F. W. Pennell 6924* (GH, US, but not NY); Páramo del Puracé al sur del Volcán, San Francisco, Cordillera Central, *J. Cuatrecasas 14,605* (LA, UC); Cordillera Central, Puracé in páramo, *K. von Sneidern 1857* (GH, NY, S), *2477* (S); 5 km. E of Puracé, *E. L. Core 213* (UC, USNA); páramo N of Volcán Puracé, near Laguna San Rafael, *F. R. Fosberg 22,347* (UC, USNA); Carretara a La Plata, de Puracé al Alto de San Rafael, *Garcia-Barriga & Hawkes 12,837* (LA, US); Silvia, Páramo de las Delicias, *S. Yepes-Agredo 102* (F); Valley of Río Cocuy, W slopes of Páramo de Puracé, Central Cordillera, *Killip & Lehmann 38,529* (LA, US); Almaguer, *Humboldt & Bonpland 2061* (Photo [F 18,263] of Berlin specimen: F, GH, UC, US; photo [K 378] of Paris specimen: F, NY, S, US-type collection of *A. montanum*), *2061* (Photo [F 18,262] of Berlin specimen: F, GH, UC, US; photo [K 379] of Paris specimen: F, US-type collection of *A. ranunculifolium*). Cauca-Nariño: Almaguer et Pasto, *J. J. Triana 2755* (G, K, MEXU, P). Nariño: Páramo de Delicias, *F. C. Lehmann* (F, K); Azufral near Tuquerres, *E. André 3258* (K). Putumayo: Lado sur la Laguna de la Cocha, Páramo de Santa Lucia (nacimiento del Río Alisales), *J. Cuatrecasas 11,867-A* (US). ECUADOR. Imbabura: slopes near shore of Laguna de San Marcos, N of Cayambe Peak, *I. L. Wiggins 10,515* (UC). Pichincha: Antisana, *W. Jameson 843* (K, US); Páramo of Cayambe, *F. Hall* (K). Tungurahua: Cordillera de Llanganates, near Las Torres, *E. Asplund 9819* (S). Azuay: the eastern Cordillera 4–6 km. N of Sevilla de Oro, *W. H. Camp E-4757* (LA, NY, UC).

Kunth, Weddell, Drude, Thellung, and Wolff have all attempted to recognize at least two entities (of various taxonomic grade) here on the basis of the degree of division of the leaflets. Typically, the leaflets of *Apium montanum* were supposed to be entire or very shallowly trilobed, and those of *A. ranunculifolium* more deeply lobed, incised, or parted. This actually appears to be a highly variable character of degree, and material available to us from Colombia completely breaks down the supposed distinction. Such a population as that represented by *Pittier 1119,* for instance, could well have provided the types of both *A. montanum* and *A. ranunculifolium,* and it should be noted that Humboldt and Bonpland's two collections were both made at Almaguer, also in Cauca. We have been unable to find any other character or structure correlated with this variation in foliar dissection.

1b. **Niphogeton ternata** var. **orientalis** Math. & Const., var. nov.

Planta 8–20 dm. alta gracilis foliis orbiculatis 2.5–4.5 cm. longis 3–5 cm. latis foliolis 3-5-lobatis segmentis ultimis 3- 7-dentatis lobatisve pedunculis 2.5–5.5 cm. longis fructu 3.5–4.5 mm. longo 2.5–3 mm. lato costis obtusis prominenter suberoso-alatis valleculis valde latioribus.

Plants 8–20 dm. tall, slender; leaves orbicular, 2.5–4.5 cm. long, 3–5 cm. broad, the leaflets deeply 3- to 5-parted, and the divisions 3- to 7-toothed or -lobed; peduncles 2.5–5.5 long; fruit 3.5–4.5 mm. long, 2.5–3 mm. broad, the ribs prominently corky-winged, obtuse, much broader than the intervals.

Type locality.—COLOMBIA. Cundinamarca: La Preña, Bogotá, November, 1844, *J. Goudot* (P-type; K).

Distribution.—Páramos of the Cordillera Oriental, 7,500–10,000 feet altitude, Andes of Cundinamarca, Colombia.

Specimens examined.—COLOMBIA. "Colombia," *J. C. Mutis 4043* (US). Cundinamarca: Andes de Bogotá, Bogotá, *J. J. Triana 2736* (G, K, MEXU, NY, P; US-photo of NY specimen); Bogotá, *I. F. Holton 643* (K, NY; US-photo of NY specimen), *E. André 1298* (K), 1844, *J. Goudot* (P-type; K), *Mrs. Tracey 249* (K); mountains E of Bogotá, *T. A. Sprague 202* (K); Usaquén near Bogotá, *J. Bequaert 30* (GH, US); Cerros de Monserrate a Chapinero, cerca a Bogotá, camino de "El Granizo" a "San Luis," *H. Garcia-Barriga 11,924* (UC, US); Monserrate, camino a Chipaque, *H. Garcia-Barriga 11,953* (UC, US); Cerro de Monserrate, Bogotá, *N. C. Fassett 25,865* (USNA); above Chipaque, just below Páramo de la Cruz Verde, *F. R. Fosberg 20,241* (USNA); Macizo de Bogotá, Quebrada de Chicó, *J. Cuatrecasas 5070* (UC, US); Guadalupe, Bogotá, *O. Haught 5047* (US); Monserrate, near Bogotá, Cordillera Oriental, *Killip, Garcia-Barriga & Gutierrez 38,009* (LA, US); Mt. Serrate, prés Sta. Fe de Bogotá, 1861, *J. de Parseval-Grandmaison* (GH); Páramos de Une, *M. T. Dawe 370* (K, US); Tocansipa, Bogotá, *J. Linden 1295* (K, P).

Early in our study we noted that some of the plants of this species had corky-winged fruit remarkably different from that ascribed to *Apium ternatum.* Moreover, these plants all had the "ranunculifolium" type of foliage, and we hoped we had discovered two correlates that might justify the traditional separation of the plants of this group into two distinct taxa. Further investigation revealed, however, that many plants with unwinged fruits had foliage apparently identical with that of plants bearing winged mericarps. In addition, winged fruits were not found on any plants from Cauca, the source of the type of *A. ranunculifolium,* which appears to have the fruit typical of *Niphogeton ternata* var. *ternata.* The only truly distinctive correlation we have been able to discover is a geographical one, the winged-fruited plants apparently being confined to the Cordillera Oriental of

Cundinamarca, where *N. ternata* var. *ternata* (judging from available mature specimens) is only sparsely represented. This fruit character is not, of course, an absolute one, since plants here referred to *N. ternata* var. *ternata* show some variability in the shape, prominence, and thickening of the fruit ribs.

2. **Niphogeton angustisecta** (H. Wolff) Math. & Const., comb. nov.

Oreosciadium montanum α s. v. Wedd. Chlor. Andin. 2: 204. 1857.

Apium ternatum var. *genuinum* subvar. *angustisectum* H. Wolff in Engler, Pflanzenreich 90 (4[238]): 51. 1927.

Scrambling perennial herb 1–5 dm. tall, woody at the base, glabrous or puberulent above, the foliage green and subcoriaceous; leaves triangular, 1–4 cm. long, 2–6 cm. broad, ternate, the leaflets subsessile, spreading, linear to lanceolate, 1–4 cm. long, 1.5–5 mm. broad, entire, acute, mucronate, the margins chartaceous; petioles slender, 1.5–5 cm. long, the lower half in the basal leaves forming an oblong sheath, the upper petioles wholly sheathing; inflorescence terminal and lateral, 1 or 2 lateral peduncles arising in the axils of the uppermost leaves, 1.5–5 cm. long; involucre of 3–5 bracts 5–30 mm. long, linear to linear-oblanceolate, entire or occasionally 2- or 3-fid at the apex, usually about equaling the rays; rays 5–9, 5–25 mm. long, spreading or spreading-ascending, unequal; involucel of 3–6 bractlets like the bracts, 2–6 mm. long, usually exceeding the pedicels; pedicels 3–8, 2–10 mm. long, spreading-ascending, unequal; petals oval, acute, white; stylopodium low-conic, the styles 0.2–0.5 mm. long, spreading; fruit ovoid, 2.5–3 mm. long, 2 mm. broad, the ribs prominent, acute, about equaling the intervals; vittae large; seed face shallowly concave.

Type locality.—"Colombia, Dept. Santander, auf Bergwiesen bis 3000 m. ü. M." [Boqueron, Ocano to Pamplona, Norte de Santander], *W. Kalbreyer 1192.*

Distribution.—Páramos at 8,000–11,500 feet altitude, Andes of Venezuela and northern Colombia.

Specimens examined.—VENEZUELA. Mérida: Páramo de Pozo Negro between San José and Beguilla, *J. A. Steyermark 56,280* (F, LA, UC). COLOMBIA. Bolívar: below Páramo de Chaquiro, Cordillera Occidental, *F. W. Pennell 4308* (NY-part). Norte de Santander: Boqueron, Ocano to Pamplona, *W. Kalbreyer 1192* (K-type collection); Pamplona, *M. de Garganta 862* (F, LA); Páramo de Cachira, 1845, *W. Purdie* (K). Santander: Páramo de Mogotocoro, near Vetas, Cordillera Oriental, *Killip & Smith 17,600* (GH, US); Motocoro, 2 km. S of Vetas, Río Surata, *H. St. John 20,745* (UC, USNA); Páramo de las Puentes above La Baja, Cordillera Oriental, *Killip & Smith 18,217* (GH, US). Boyacá: Socha, *L. Uribe Uribe 1618* (US).

Although Wĕddell remarked of *Oreosciadium montanum*, "Des formes intermédiares nombreuses relient parfaitement entre elles les diverses varietés que j'ai signalées," and included within that species not only *N. angustisecta* but also *N. glaucescens*, we believe the two latter to be abundantly distinct on the basis of the material we have examined. The distinctive narrow and entire leaflets of *N. angustisecta*, combined with the localization of these plants in northern Colombia and adjacent Venezuela, appear to justify according them full specific status.

3. **Niphogeton Josei** Math. & Const., sp. nov. (fig. 1)

Herba caespitosa vel porrecta simul basi suffruticosa glabra vel sparsim puberula 1–3.5 dm. alta foliis glaucescentibus basilaribus confertis ovatis vel triangularibus 0.5–2 cm. longis 0.6–2.5 cm. latis ternatis foliolis sessilibus adscendentibus oblongis vel oblanceolatis 2–4 mm. latis integris vel apice breviter tridentatis obtusis vel acutis submucronatis marginibus chartaceis petiolis gracilibus 0.5–3 cm. longis basi anguste vaginatis pedunculis 1–5.5 cm. longis involucri bracteis 3–5 linearibus integris glabris plerumque radios superantibus 4–8 mm. longis radiis 4–7 patenti-adscendentibus subaequalibus puberulentis vel glabratis 2–8 mm. longis involucelli bracteolis glabris 3–5 bracteis similibus 2–7 mm. longis plerumque pedicellos superantibus pedicellis 2–5

patenti-adscentibus subaequalibus puberulentis vel glabratis 2–4 mm. longis petalis ovalis obtusis albis stylopodio breviter conoideo stylis patentibus 0.5 mm. longis fructu ovoideo 2–3 mm. longo 1.5–2 mm. lato costis prominentibus acutis vittae diametro medio inter maximum minimumque seminium faciebus parum concavis.



Fig. 1. *Niphogeton Josei* Math. & Const. A. Habit, × ½; B. Carpophore, × 10; C. Petals, × 7; D. Fruit, × 8; E. Fruit cross section, × 18.

Cespitose or scrambling perennial herb 1–3.5 dm. tall, woody at the base, glabrous or sparsely puberulent throughout, the foliage glaucescent; leaves densely clustered toward the base, ovate to triangular, 0.5–2 cm. long, 0.6–2.5 cm. broad, ternate, the leaflets sessile, spreading, oblong to oblanceolate, 2–4 mm. broad, entire or shallowly tridentate at the apex, obtuse or abruptly acute, submucronate, the margins chartaceous; petioles slender, 0.5–3 cm. long, the lower half in the basal leaves forming an oblong or lanceolate sheath, the uppermost petioles often wholly sheathing; inflorescence terminal only, or terminal and lateral, with a single lateral peduncle in the axil of the uppermost leaf, 1–5.5 cm. long; involucre of 3–5 bracts 4–8 mm. long, linear, entire, glabrous, usually exceeding the rays; rays 4–7, 2–8 mm. long, spreading-ascending, subequal, puberulent or glabrate; involucel of 3–5 bractlets like the bracts, 2–7 mm. long, glabrous, usually

exceeding the pedicels; pedicels 2–5, 2–4 mm. long, spreading-ascending, subequal, puberulent or glabrate; petals broadly oval, obtuse, white; stylopodium low-conic, the styles 0.5 mm. long, spreading; fruit ovoid, 2–3 mm. long, 1.5–2 mm. broad, the ribs prominent, acute, about equaling the intervals; vittae of intermediate size; seed face shallowly concave.

Type locality.—Colombia, Boyacá: Nevada del Cocuy, Cordillera Oriental, Las Lagunillas, Tabloncito, altitude 3,930 m., field and woods, September 13, 1938, *J. Cuatrecasas 1579* (US #1,773,053).

Distribution.—Páramos at 9,000–12,000 feet altitude in the Cordillera Oriental, Andes of northern Colombia.

Specimens examined.—COLOMBIA. Santander-Boyacá: Páramo de Birolin, 35 km. S of Charalá, 20 km. NW of Duitama, *F. R. Fosberg 21,907* (UC, USNA). Boyacá: Nevada del Cocuy, Las Lagunillas, Tabloncito, *J. Cuatrecasas 1579* (US-type); SE slope of Cordillera de Consuelo, headwaters of Río Guina, 20 km. NE of Belen, *F. R. Fosberg 21,716* (UC, USNA). Cundinamarca: Andes de Bogotá, Bogotá, 1851–57, *J. J. Triana* (K); Macizo de Bogotá, Páramo de Usaquén, *J. Cuatrecasas 9427* (F, UC, US).

This species is undoubtedly close to *N. glaucescens*, but its narrower and entire or shallowly toothed leaflets, nearly glabrate herbage, smaller vittae, and slightly more northern range appear to make it a tenable species. It is a pleasure to name it for Dr. José Cuatrecasas in recognition of his great and continuing contribution to our knowledge of the botany of Colombia.

4. **Niphogeton glaucescens** (Kunth) F. Macbr. Field Mus. Publ. Bot. 8: 126. 1930.

Apium glaucescens Kunth in H.B.K. Nov. Gen. & Sp. 5: 18. 1821.
Oreosciadium montanum β ranunculifolium s. v. *glaucescens* Wedd. Chlor. Andin. 2: 205. 1857.
Oreosciadium glaucescens Hieron. Bot. Jahrb. 20: Beibl. 49: 72. 1895.

Cespitose or scrambling perennial herb 1–4 dm. tall, woody at the base, hirtellous to glabrate throughout, the foliage glaucescent, subcoriaceous; leaves densely clustered toward the base, orbicular, 1–2 cm. long, 1–3 cm. broad, ternate, the leaflets sessile, spreading, obcuneate to obovate, 3–12 mm. broad, deeply 3- to 5-lobed, obtuse or acute, mucronate; petioles slender, 0.5–1.5 cm. long, the lower half in the basal leaves forming an oblong sheath, upper petioles wholly sheathing; inflorescence terminal and lateral, with 1 or 2 lateral peduncles arising in the axils of the uppermost leaves, 1–3.5 cm. long; involucre of about 5 bracts 5–12 mm. long, linear to oblanceolate, entire or occasionally deeply 3- to 5-lobed, ciliolulate, usually about equaling the rays; rays 5–9, 3–10 mm. long, spreading or spreading-ascending, unequal; involucel of 3–5 bractlets like the bracts, 3–10 mm. long, ciliolulate, usually exceeding the pedicels; pedicels 2–6, 2–5 mm. long, spreading-ascending, unequal; petals broadly oval, obtuse, white; stylopodium low-conic, the styles 0.2–0.4 mm. long, spreading; fruit ovoid, 2–3 mm. long, 1–1.5 mm. broad, the ribs prominent, acute, narrower than the intervals; vittae large; seed face shallowly concave.

Type locality.—"Crescit locis subfrigidis Regni Novae Granatae, in Paramo de Almaguer, alt. 1500 hex.," *Humboldt & Bonpland 2062.*

Distribution.—Páramos at 8,500–11,000 feet altitude, Andes of central Colombia to northern Ecuador.

Specimens examined.—COLOMBIA. Cundinamarca: Páramo de Guasca, *H. Garcia-Barriga 11,628* (UC), *W. H. Hodge 6475* (GH, UC); Páramo de Guasca, 8 km. E of Guasca, *F. R. Fosberg 21,691* (UC, USNA); Páramo de Cruz Verde, near Bogotá, *F. W. Pennell 2069* (GH, US); Cruz Verde, 14 km. SSE of Bogotá, *Grant & Fosberg 9242* (UC, USNA); 2–4 km. N of Páramo de la Cruz Verde, 15 km. S of Bogotá, *F. R. Fosberg 20,212* (USNA); Macizo de Bogotá, Alto de las Cruces-Guadalupe, *J. Cuatrecasas 5535* (F, US); Bogotá, *C. Sandeman 5932* (K); Guadalupe, Bogotá, *O. Haught 5637* (US); upland E of Sesquilé, *O. Haught 5928* (US); Páramo de Guerrero, *F. C. Lehmann* (K); Páramo de Zipaquirá entre Zipaquirá y Pacho, Cordillera Oriental, *J. Cuatrecasas 9553* (LA, UC, US); Páramo de Sumapaz, Alto San Juan, 18 km. E of Cabrera, *F. R. Fosberg 20,719* (USNA); Páramo de Sumapaz, Río Arroz, *F. R. Fosberg 20,811* (UC,

USNA); Páramo de Sumapaz, Laguna Larga, 23 km. E of San Bernardo, *F. R. Fosberg 20,655* (USNA); Quebrada San Francisco, back of Bogotá, *F. R. Fosberg 22,058* (UC, USNA); hills W of Laguna de Guatavita, 9 km. NNW of Guatavita, 6 km. S of Sesquilé, *F. R. Fosberg 21,350* (USNA). Tolima: Páramo de Ruiz, *W. Purdie* (K). Cauca: Carretara de Popayán a Totoró, Alto de Angosi, *Garcia-Barriga & Hawkes 12,733* (Inst. Cienc. Bogotá); Páramo de Pitayo, *T. Hartweg 1034* (K); Volcán de Sotara, *F. C. Lehmann 6211* (F, K, US); Paletará, *F. C. Lehmann 3499* (F, K, US); "Llano de Paletará," Cordillera Central, *F. W. Pennell 6924* (NY; but not GH, US); Almaguer, *Humboldt & Bonpland 2062* (Photo [K 380] of Paris specimen: F, NY, S, US-type collection of *A. glaucescens*). ECUADOR. Carchi: "Am río Tun (Cordill v. Tulcan), Nord-Ecuador," *F. C. Lehmann 662* (K, US); Páramo del Azufral, E of Angel, *Y. Mexia 7509* (F, GH, NY, S, UC, US, W).

Weddell regarded this as a variant of *Oreosciadium montanum* (*N. ternata*), but we do not believe it to be even very closely related to that complex. The Ecuadorean specimens and some of those from Cauca and Tolima are glabrate, as in the type collection, but there seems to be no correlated variable, so we regard the species as a rather compact entity.

5. **Niphogeton dissecta** (Benth.) F. Macbr. Field Mus. Publ. Bot. 8: 126. 1930.

Bushy to slender perennial herb 0.5–3.5 dm. tall, usually prolifically branched, glabrous or less commonly somewhat minutely scaberulous and puberulent, or hirsutulous, the foliage bright green or grayish green or bluish green; leaves loosely clustered to subrosulate at the base, oblong to ovate, 1.5–8 cm. long, 1–7 cm. broad, 1- or 2-pinnate, the leaflets cuneate to obovate, 3–12 mm. long, 1.5–5 mm. broad, deeply lobed or pinnatifid, the ultimate divisions linear, 1–6 mm. long, 1–1.5 mm. broad, apiculate to long-mucronate; petioles slender, 2–15 cm. long, the lower ¼ to ½ in the basal leaves forming an oblong sheath, the uppermost petioles wholly and often rather prominently sheathing; inflorescence terminal and lateral, corymbose, with 1–6 lateral peduncles arising in the axils of the cauline leaves, 0.5–10 cm. long; involucre of 3–7 bracts 4–35 mm. long, linear to spatulate or obovate, deeply lobed to pinnatifid, rarely some entire, exceeding the rays; rays 5–12, 3–30 mm. long, spreading or spreading-ascending, unequal; involucel of 3–5 bractlets like the bracts, 1–10 mm. long, linear to spatulate, rarely obovate, entire to lobed or pinnatifid, exceeding the pedicels; pedicels 2–10, 2–15 mm. long, spreading or spreading-ascending, unequal; petals ovate-lanceolate, acute, white or with a green midvein; stylopodium low-conic, the styles 0.2–0.5 mm. long, spreading; fruit oblong to ovoid, 2–4 mm. long, 1.5–2.5 mm. broad, the ribs prominent, acute, narrower than to about equaling the intervals; vittae large, sometimes a smaller vitta in the apex of each rib; seed channeled under the vittae, the face shallowly concave.

5a. **Niphogeton dissecta** var. **dissecta**

Petroselinum dissectum Benth. Pl. Hartweg. 188. 1845.
Niphogeton andicola Schlecht. Linnaea 28: 481. 1856.
Oreosciadium dissectum α Wedd. Chlor. Andin. 2: 204. 1857.
Oreosciadium dissectum β *asperum* Wedd. Chlor. Andin. 2: 204. 1857.
Apium dissectum Drude in E. & P. Pfl. 3[8]: 185. 1898.
Apium Weberbaueri H. Wolff, Repert. Nov. Sp. 17: 175. 1921.
"*Apium dissectum* var. α *typicum* Wedd." fide H. Wolff in Engler, Pflanzenreich 90 (4[228]): 49. 1927.
"*Apium dissectum* var. β *asperum* Wedd." fide H. Wolff in Engler, Pflanzenreich 90 (4[228]): 49. 1927.
Niphogeton dissecta var. *aspera* F. Macbr. Field Mus. Publ. Bot. 8: 125. 1930.
Niphogeton Weberbaueri F. Macbr. Field Mus. Publ. Bot. 8: 126. 1930.
Niphogeton Jahnii Rose ex Pittier, Man. Pl. Usual Venez. 233, 439. 1926, nom. nud.

Plants glabrous to somewhat scaberulous or puberulent, the foliage bright green; leaves loosely clustered to subrosulate, oblong to ovate, 1.5–8 cm. long, 1–7 cm. broad, the leaflets 3–12 mm. long, 1.5–8 mm. broad, the ultimate divisions linear, 1–1.5 mm. broad, apiculate to mucronate; peduncles 1–10 cm. long; involucre of 3–7 bracts 4–35 mm. long; involucel bractlets entire to lobed or pinnatifid; pedicels 2–10, 2–15 mm. long; fruit oblong to ovoid, 2–4 mm. long.

Type locality.—"In monte Guagua-Pichincha, altit. 14,500 ped.," Ecuador, *T. Hartweg 1037.*

Distribution.—Páramos at 7,000–13,000 feet altitude, Andes of Venezuela, Colombia, Ecuador, Peru, and Bolivia.

Specimens examined.—VENEZUELA. Lara: between Buenos Aires and Páramo de Rosas, *J. A. Steyermark 55,487* (F, UC). Mérida: Páramo del Molino, *A. Jahn 935* (GH, US-basis of *N. Jahnii*). COLOMBIA. Magdalena: High mountains of the Nevada de Santa Marta, 1844, *W. Purdie* (K-part). Caldas: along streamlets, Páramo del Quindío, Cordillera Central, *Pennell & Hazen 9882* (GH, S, US) Tolima: Pic Tolima, Azufral grande, *J. Goudot* (G, K, P); Páramo de Ruiz, 1845, *W. Purdie* (K). ECUADOR. "Cerrode el Barbara, S. Ecuador," *E. André 4494* (F, GH, K, NY). Pichincha: on Guagua, Pichincha, *T. Hartweg 1037* (K-type; P, W; F-fragment; photo [F 17,187] of Berlin specimen: F, GH, UC, US-type collection of *P. dissectum*); Guamani Pass E of Pifo, Cordillera Oriental, *J. A. Ewan 16,428* (UC, USNA); vicinity of Quito, Rucu Pichincha, *E. Asplund 3574* (S); Pichincha, *W. Jameson 120* (K-part, LA, W), *298* (G, GH, P), *105* (K), *106* (photo [US 31]: F, S, US), *Anthony & Tate 190* (US), *C. Firmin 613* (US), *A. Sodiro 614* (G), 1855, *J. P. Couthouy* (GH), *E. André 3877* (F, NY); Pichan, *I. Holmgren 548* (G, S, US); Páramo de Cayambe, *F. Hall* (K). Tungurahua: Mount Carihuayrazo, *E. Asplund 3460* (S). Azuay: Páramo de Tinajillas, 30–50 km. S of Cuenca, *W. H. Camp E-2247* (LA, NY, UC); "Oriente Border," Páramo del Castillo, E of El Pan, *W. H. Camp E-1627* (NY, UC); in páramo along Pan-American Highway 42 km. S of Cuenca, *I. L. Wiggins 10,777* (UC). Loja: Horta-Naque, *R. Espinosa 978* (UC). Santiago-Zamora: trail between Pailas and El Pan, *J. A. Steyermark 54,337* (F, LA). PERU. Junin: Prov. Tarma, auf Hochgebirgssteppen, W. Huacapistana, *A. Weberbauer 2258* (Photo [F 17,188] of Berlin specimen: F, GH, UC, US-type of *A. Weberbaueri*). Cuzco: "Agapata limites niv. aetern. summ. Cordill.," *W. Lechler 1976* (G, K, P, S, W; photo [F 3474] of Berlin specimen: F, GH, UC, US-type of *N. andicola*); near glaciers of the Auzangate, Prov. Quispicanchi, *A. Weberbauer 7768* (F, G, S, US); Valle del Paucartambo, hacienda Lauramarca, *F. L. Herrera 2323* (F). BOLIVIA. La Paz: viciniis Sorata, inter Pampa de Chiliata et montem Illampu, prope Puerto del Inca, *G. Mandon 589* (F, GH, K, NY, S, W); Alaska Mine, Cordillera Real, *G. H. H. Tate 63* (NY); Unduavi, *H. H. Rusby 1767* (F, NY, US), *O. Buchtien 2430* (NY, US), *9007* (NY).

This species, which Wolff termed a "species collectiva," has the broadest range of any member of the genus, is perhaps the best-represented in herbaria, and is certainly the most variable. Rose indicated three "new species" in this complex by herbarium annotations, and we have been tempted from time to time to lop off one or another of the extreme phases as named entities. A careful analysis of all these, however, has revealed a paucity of critical characters likely to withstand the impact of additional material. The variations are primarily in the size and growth form of the plants, the size, shape, and dissection of the leaves, the amount of roughness or puberulence of the herbage, and the number and size of various structures. Ecuadorean specimens fit the original description in being essentially glabrous, but much material, both to the south (where it culminates in the following variety) and to the north, shows some roughness or puberulence unaccompanied by any concomitant variation. The type of *N. andicola*—a name whose application has been somewhat confused—appears to have been derived from such a population, as does the basis of Weddell's variety *asperum*. Nothing in the original description of *Apium Weberbaueri* appears to be sufficiently distinctive to keep this proposed segregate aloof from *N. dissecta* as here circumscribed.

5b. **Niphogeton dissecta** var. **ciliata** (Wedd.) F. Macbr. Candollea 6 : 16. 1934.

Oreosciadium dissectum γ ciliatum Wedd. Chlor. Andin. 2: 204. 1857.

"*Apium dissectum* var. γ *ciliatum* Wedd." fide H. Wolff in Engler, Pflanzenreich 90 (4[236]) : 49. 1927.

Niphogeton ciliatum Rose ex Pittier, Man. Pl. Usual Venez. 233, 439. 1926, nom. nud.

Plants more or less hirsutulous throughout, the foliage grayish- or bluish-green; leaves densely rosulate, oblong, 1.5–8 cm. long, 1–4 cm. broad, the leaflets 3–8 mm. long, 1.5–5 mm. broad, the ultimate divisions linear to linear-oblong, 1–3 mm. broad, those of the outer leaves obtuse or acute, densely hirsutulous, those of the inner leaves long-mucronate, hirsutulous-ciliolulate to glabrate; peduncles rather stout, 0.5–9 cm. long, hirsutulous; involucre of 5–7 bracts 5–30 mm. long, hirsutulous; rays 8–12, 3–25 mm. long, hirsutulous; involucel bractlets usually lobed or pinnatifid, hirsutulous; pedicels 3–10, 2–8 mm. long, hirsutulous; fruit ovoid, 2–3 mm. long.

Type locality.—"Venezuela: Sierra Nevada de Mérida, h. 3550 m.," *J. J. Linden 414.*

Distribution.—Páramos at an altitude of 6,700–16,000 feet, Andes of Venezuela, Colombia, and Ecuador.

Specimens examined.—VENEZUELA. Trujillo: Páramo de la Cristalina, *A. Jahn 49* (US). Mérida: Sierra Nevada de Mérida, Andes de Truxillo et de Mérida, *J. J. Linden 414* (P-type; G, K, W; photo [F 28,334] of Geneva specimen: F, GH, UC), *Funck & Schlim 1190* (G, P; photo [F 28,334] of Geneva specimen: F, GH, UC), *E. P. de Bellard 213* (US); Páramo de Campanerio, *J. Hamburg-Tracy 100* (K), *167* (K); Alto de Mucuchíes, La Tapa, cabeceras del Mifafi, entre Barro Negro y Torondoy, *W. Gehriger 105* (F, G, NY, US); El Aquila above Páramo de Mucuchíes, *J. A. Steyermark 57,044* (F, LA); Páramo de Timotes, *A. Jahn 582* (US). COLOMBIA. Nariño: Páramo of Cerro San Francisco above Cordoba, *J. A. Ewan 16,251* (UC, USNA). ECUADOR. Tungurahua: Cordillera de Llanganates near Las Torres, *E. Asplund 9905* (S).

Their grayish- or bluish-green foliage and the more or less hirsutulous condition of the herbage of the plants gathered together here seems to warrant according them varietal status. There unquestionably are transitions to puberulent forms of typical *N. dissecta*, and further field observation will be necessary to test the validity of this segregation. The variation in the distribution of pubescence in the plants examined is astonishing, the inner and cauline leaves appearing often to be completely glabrate. The Colombian and Ecuadorean collections cited are remarkable for the large size of all their parts and for the remoteness of their stations from all the other collections. It appears advisable, however, to assign them here until more material is available from Colombia and Ecuador.

6. **Niphogeton scabra** (H. Wolff) F. Macbr. Candollea 5 : 395. 1934.

Ligusticum peucedanoides Presl γ *longifolium* Presl ex DC. Prodr. 4: 159. 1830.

Oreosciadium scabrum H. Wolff, Bot. Jahrb. 40: 305. 1908.

Apium scabrum H. Wolff, Repert. Nov. Sp. 17: 175. 1921; Engler, Pflanzenreich 90 (4[236]) : 49, *f. 3.* 1927.

"*Apium peucedanoides* Reiche var. β *longifolium* Presl" fide H. Wolff in Engler, Pflanzenreich 90 (4[236]) : 35. 1927.

Low, bushy perennial herb 0.5–2.5 dm. tall, branching prolifically, the branches stout, conspicuously scaberulous throughout, the foliage light green; leaves densely rosulate at the base, oblong-oval, 2.5–6 cm. long, 2–4 cm. broad, 1- or 2-pinnate, the leaflets cuneate to obovate, 5–15 mm. long, 2–8 mm. broad, apiculate, strongly scaberulous on the margins and veins; petioles 3–10 cm. long, the lower half to the entire petiole in the basal leaves with an inflated, scarious, scaberulous sheath, the upper petioles broadly inflated and wholly sheathing; inflorescence terminal and lateral, densely corymbose, with 1 or 2 lateral peduncles arising in the axils of the

cauline leaves, the peduncles quite stout, 1.5–10 cm. long; involucre of about 5 bracts 15–30 mm. long, spatulate to obovate, with a prominently inflated scarious sheath and a pinnatifid blade, exceeding the umbellets, prominently scaberulous; rays 8–12, 5–25 mm. long, spreading or spreading-ascending, unequal; involucel of about 5 bractlets like the bracts, 5–15 mm. long, entire or lobed, conspicuously scaberulous, exceeding the umbellets; pedicels 3–7, 1–5 mm. long, spreading or spreading-ascending, unequal; petals oval, acute, white with a green midvein; stylopodium depressed-conic, the styles 0.5–1 mm. long, spreading; fruit ovoid, 3–4 mm. long, 2–2.5 mm. broad, with a thin, loose, shining pericarp, the ribs very prominent and somewhat corky-thickened, about equaling the intervals; vittae moderately large; seed face shallowly concave.

Type locality.—"Peru: ad viam ferream inter oppida Lima et Oroya ad hacienda Arapa prope Yauli, ad rupes, in 4400 m altitudine," *A. Weberbauer 350.*

Distribution.—Páramos at 12,500–15,000 feet altitude, Andes of Peru.

Specimens examined.—"Chile," *T. Haenke 76* (photo [F 31,806] of Vienna specimen: F, GH, UC, US; photo of Geneva specimen: UC-basis of *Apium peucedanoides* var. *longifolium* Presl); without locality, *J. Pavon 62* (G). PERU. Junin: Morococha, near Mt. Puipui, *V. Grant 7586* (LA, UC); Huaron, *Macbride & Featherstone 1127* (F, US); "Ad viam ferream inter oppida Lima et Oroya ad hacienda prope Yauli, ad rupes," *A. Weberbauer 350* (photo [F 17,189] of Berlin specimen: F, GH, UC, US-type). Lima: "Oberhalb der Stadt Lima," *A. Weberbauer 5178* (G); Casapalca, *Macbride & Featherstone 838* (F, S, US, W). Cuzco: Valle del Paucartambo, hacienda Acapana, *F. L. Herrera 215?* (F, S).

The identification of the Haenke collection with this species is now largely a matter of historical interest, but it does delete one more obscure name from the list of those which must be accounted for in any general treatment of Andean Umbelliferae. The other Haenke collection associated with this in the description of *Ligusticum peucedanoides* has been properly referred to *Apium* by Reiche and by Wolff, where it constitutes the name-bringing synonym.

The low, bushy habit, the crowded inflorescence, the roughness of the herbage, the stout stems and peduncles, and the conspicuously scarious and inflated sheaths and bracts combine to make this a markedly distinct species. The fruit is also strikingly dissimilar to that of *N. dissecta*, although the two species have been confused in the past.

7. **Niphogeton Sprucei** (H. Wolff) Math. & Const., comb. nov.

Apium Sprucei H. Wolff, Repert. Nov. Sp. 17: 176. 1921.

Acaulescent, cespitose perennial herb 0.3–1 dm. tall, glabrous throughout, the foliage glaucescent, subcoriaceous; leaves densely clustered at the base, oblong, 1–3 cm. long, 6–10 mm. broad, pinnate, the leaflets sessile, spreading, crowded, broadly ovate, 2–5 mm. long, deeply ternately or palmately 3- to 5-parted, obtuse, callous-tipped; petioles slender, 1–2 cm. long, narrowly sheathing toward the base; inflorescence terminal, of 1–3 scapose peduncles 3–8 cm. long; involucre of 10–15 (?) bracts 4–5 mm. long, linear-oblong, entire (the Jameson collection with 1 bract ca. 10 mm. long, spatulate, palmately lobed distally), exceeding the rays and about equaling the pedicels; rays 1–several, up to 5 mm. long or abortive, spreading, unequal; involucel of a few bractlets like the bracts, mostly shorter than the pedicels; pedicels 3–5, 3–7 mm. long, ascending, unequal; petals oval, obtuse, white with a colored midvein; stylopodium low-conic, the styles 0.2–0.3 mm. long, spreading; fruit ovoid, 2–3 mm. long, 1.5–2 mm. broad, the ribs prominent, acute, narrower than the intervals; vittae large; seed face plane to shallowly concave.

Type locality.—"Ecuador, Andes Quitenses in pastibus alpinis mts. Titaicum," *R. Spruce 5797.*

Distribution.—Known only from the high Andes near Quito, Ecuador.

Specimens examined.—ECUADOR. Mt. Titaicum, *Spruce 5797* (W-type, but not K; photo [F 31,810] of Vienna specimen: F, GH, UC, US); "Quito, Andes," *Jameson 54* (K).

It should be explained immediately that the only material of this species we have been able to locate is that cited above, which bears a total of three umbels. For this reason it has not been practicable to dissect them, and the nature of the involucre, rays, involucel, and pedicels must remain somewhat problematical until more material is extant. Wolff's description of the plant as having a simple umbel at first suggested to us that he had erroneously referred a species of *Oreomyrrhis* here; also, the Kew collections under the type number are all of *Oreomyrrhis*. However, it is abundantly clear from the two specimens cited that the petals, fruit, carpophore, and other features are all clearly indicative of *Niphogeton,* whereas the acaulescent habit, unique leaves, and abortive rays make it very sharply distinct from all other species of the genus.

The type specimen shows that the uppermost group of 3–5 pedicels, at least, is joined into a very short ray at their base, and there is at least one well-defined ray in the Jameson collection; it is less easy to see whether the same situation prevails for the other pedicels. Unless these particular umbels are abnormal, this fact would seem to indicate that we have to deal here with an abortively rayed compound umbel rather than with a simple umbel.

8. **Niphogeton magna** F. Macbr. Field Mus. Publ. Bot. 8: 126. 1930.

Stout perennial herb 4–6 dm. tall, glabrous, the foliage bluish green; leaves loosely clustered at the base, oblong-oval, 10–20 cm. long, 6–8 cm. broad, pinnately decompound, the ultimate divisions linear, acute, 2–6 mm. long, 1 mm. or less broad, the petioles slender, 10–20 cm. long, the lower ⅓ to ¼ in the basal leaves forming a linear-oblong, scarious-winged sheath, the upper petioles wholly sheathing; inflorescence terminal and lateral, with 1 or 2 lateral peduncles arising in the axils of the cauline leaves, 10–30 cm. long; involucre of apparently few bracts ca. 1 cm. long, sublinear, entire or pinnate, shorter than the rays; rays 8–20, 2.5–5 cm. long, spreading-ascending, unequal; involucel of a few bractlets like the bracts, ca. 4 mm. long, entire, exceeding the pedicels; pedicels 5–10, 2–4 mm. long, spreading-ascending, unequal; petals and stamens not seen; stylopodium depressed-conic, the styles ca. 1 mm. long, spreading; fruit ovoid, 3–4 mm. long, 2–2.5 mm. broad, the ribs corky-thickened, obtuse, much broader than the intervals; vittae rather large; seed face shallowly concave.

Type locality.—"Peru: At base of limestone cliff, La Oroya," May 27–June 7, 1922, *Macbride & Featherstone 968.*

Distribution.—Known only from the type collection, made at about 12,000 feet altitude.

Specimen examined.—PERU. Junin: La Oroya, *Macbride & Featherstone 968* (F-type; G, US).

This very distinct species appears to connect *N. dissecta* and *N. scabra* with the following species, with which it agrees in size and other characters. It is satisfying to be able to dispose of the monotypic *Urbanosciadium.*

9. **Niphogeton stricta** (H. Wolff) Math. & Const., comb. nov.

Urbanosciadium strictum H. Wolff, Bot. Jahrb. 40: 302. 1908.

Slender perennial herb 3–10 dm. tall, more or less scaberulous throughout, the foliage bright green above, paler beneath; leaves loosely clustered at the base, ovate-lanceolate, 5-8 cm. long, 4–7 cm. broad, pinnately decompound, the ultimate divisions lanceolate, acute, 1–3 mm. long, 3 mm. or less broad, the petioles slender, 4–25 cm. long, the lower ½ to ⅓ in the basal leaves forming a broadly oblong, scarious-winged sheath, the upper petioles wholly sheathing; inflorescence terminal and lateral, with 1 or 2 lateral peduncles arising in the axils of the cauline leaves, 6–20 cm. long, densely scaberulous beneath the umbel; involucre of 2 bracts 10–30 mm. long,

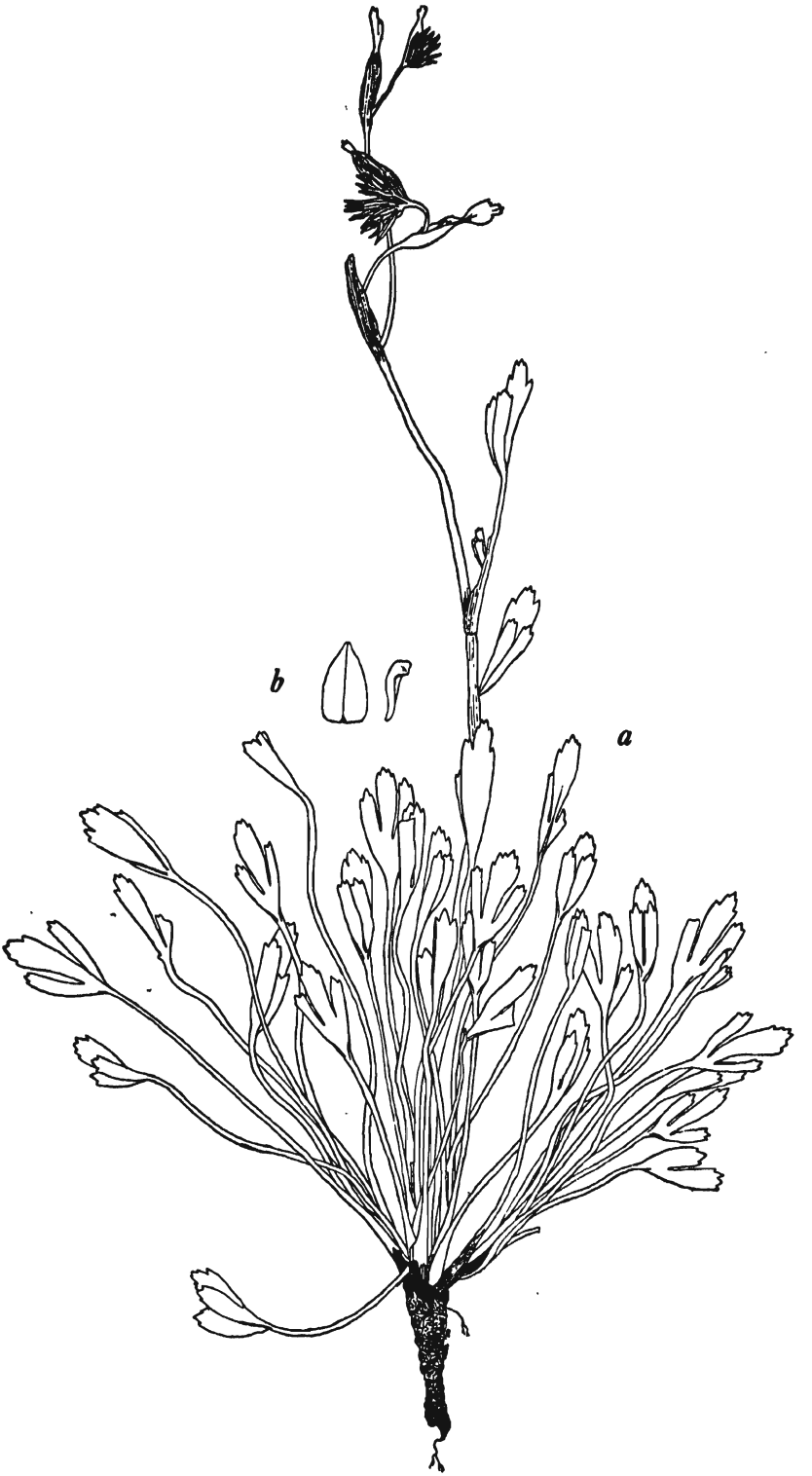


Fig. 2. *Niphogeton Killipiana* Math. & Const. A. Habit, × ½; B. Petals, × 12½.

ovate-lanceolate, foliaceous, caducous, the blade bipinnate, much shorter than the rays; rays 7–13, 1–6.5 cm. long, rather strictly ascending, unequal; involucel of 3–6 linear-lanceolate, entire bractlets 3–5 mm. long, scaberulous, exceeding the pedicels, caducous; pedicels 5–10, 2–7 mm. long, spreading-ascending, unequal; petals oval, obtuse, white with a purplish midvein; stamens exserted; stylopodium low-conic, the styles ca. 1 mm. long, spreading; fruit ovoid, about 5 mm. long, 2.5–3 mm. broad, the ribs prominent, acute, somewhat corky, broader than the intervals; vittae large; seed channeled under the vittae, the face shallowly concave.

Type locality.—"Peru: Ancachs: inter Samanco et Caraz infra haciendam Cajabamba, in formatione aperta vel dense herbis—imprimis graminibus—et fruticibus composita, in 3,000–3,500 m. altitudinis," *A. Weberbauer 3153.*

Distribution.—Páramos at 9,000–12,000 feet altitude, Andes of northern Peru.

Specimens examined.—Peru. Ancachs: inter Samanco et Caraz infra haciendam Cajabamba, *A. Weberbauer 3471* (photo [F 3,471] of Berlin specimen: F, GH, UC, US-type). Lima: Río Blanco, *Macbride & Featherstone 641* (F); near Antaicocha, Cerro Colorado, E of Canta, *F. W. Pennell 14,649* (F); Infiernillo, Huarochiri, *E. Asplund 11,509* (S).

It is strange that Wolff should have attempted to relate this strikingly distinct species to *Oreomyrrhis,* a genus characterized by an acaulescent habit, hirsute herbage, simple umbels, a polyphyllous and somewhat connate involucre, inflexed petal apices, a conical stylopodium, and usually linear-oblong fruits. Wolff's *Urbanosciadium* is unlike *Oreomyrrhis* in all these respects and, indeed, agrees with the opposed conditions as represented in the majority of the species of *Niphogeton.* Until the discovery of *N. magna,* it may have been unthinkable to look within *Niphogeton* for plants of such stature and habit, but these two species give the appearance of being rather closely related.

10. **Niphogeton Killipiana** Math. & Const., sp. nov. (fig. 2)

Herba hirtella vel puberula caespitosa circa 3 dm. alta foliis viridibus eis basilaribus rosulatis ovatis 2–4 mm. longis 1.5–2 cm. latis fere usque ad basim trilobatis lobis integris vel crenato-dentatis vel iterum lobatis lobo medio eis lateralibus longiore petiolis gracilibus 5–10 cm. longis basi anguste vaginatis pedunculis circa 2 cm. longis involucri bracteis circa 5 circa 1 cm. longis linearibus acutis ciliolatis radios superantibus radiis (immaturis) circa 5 patentibus vel patenti-adscendentibus subaequalibus puberulentis 2–3 mm. longis involucelli bracteolis circa 5 bracteis similibus ciliolatis pedicellos superantibus 5–8 mm. longis pedicellis (immaturis) circa 5 puberulentis patenti-adscendentibus 1–3 mm. longis petalis oblongo-ovatis obtusis albis stylopodio breviter conoideo stylis patentibus circa 0.5 mm. longis fructu (valde immaturo) ovoideo circa 1 mm. longo 0.8 mm. lato costis prominentibus acutis vittis nobis ignotis.

Cespitose perennial herb about 3 dm. tall, somewhat hirtellous and puberulent throughout, the foliage light green; basal leaves densely rosulate at the base, ovate, 2–4 cm. long, 1.5–2 cm. broad, deeply trilobed nearly to the base, the central lobe longer than the laterals, the lobes entire to shallowly crenate-dentate or lobed; petioles slender, 5–10 cm. long, the lower ⅓ to ¼ in the basal leaves forming a linear-oblong, scarious-winged sheath, the upper cauline leaves wholly sheathing; inflorescence terminal and lateral, with one or more peduncles arising in the axils of the uppermost leaves, about 2 cm. long; involucre of about 5 bracts ca. 1 cm. long, linear, entire, acute, ciliolulate, exceeding the rays; immature rays about 5, 2–3 mm. long, spreading or spreading-ascending, subequal, puberulent; involucel of about 5 bractlets like the bracts, 5–8 mm. long, ciliolulate, exceeding the pedicels; immature pedicels about 5, 1–3 mm. long, puberulent; petals oblong-oval, obtuse, white; stylopodium low-conic, the styles about 0.5 mm. long, spreading; very immature fruit ovoid, ca. 1 mm. long, 0.8 mm. broad, the ribs prominent, acute; vittae not seen.

Type locality: Colombia, Antioquia: Cerro de la Vieja, 2,900 m. alt., 26 December 1938. *Bro. Daniel 1681* (US #1,743,931).

Distribution: Known only from the type collection.

We fully recognize that a policy of describing new species on the basis of a single sheet is generally indefensible, and that to launch a "new" member of the Umbelliferae without having access to any mature fruit is especially inadvisable. In this case, however, the foliage of the plant in question is so remarkable that its description is indispensable to any reconstruction of foliar trends within the genus. The peculiar simple but deeply trilobed leaves appear to connect the following simple-leaved species with the group of ternate-leaved members previously discussed. We should, therefore, like to call attention to the existence of this entity in the hope of inspiring field collectors to hunt for additional and better material.

In dedicating this species to our good friend Mr. Ellsworth P. Killip we wish to call attention to the great services he has performed in gathering together an excellent collection of South American material at the National Museum, and to the skillful and generous assistance he has always cheerfully rendered to specialists concerned with various groups of plants. His suggestions of affinity on herbarium sheets and his judicious selection of materials for study and comparison have been a large factor in promoting our studies.

11. **Niphogeton lingula** (Wedd.) Math. & Const., comb. nov.

Oreosciadium lingula Wedd. Chlor. Andin. 2: 205, *pl. 69, B.* 1857.
Apium lingula Drude in E. & P. Pfl. 3[8]: 185. 1898.

Slender perennial herb 1.5–2 dm. tall, woody at the base, obscurely puberulent above or glabrate throughout, the foliage subcoriaceous; leaves rather remote throughout, oblong, 1.2–2.7 cm. long, 4–7 mm. broad, simple, obscurely tridentate at the apex, the teeth apiculate; petioles slender, 2.5–4 cm. long, the lower half in the basal leaves forming a linear-oblong sheath, the upper petioles wholly sheathing; inflorescence terminal and lateral, with 1–5 lateral peduncles arising in the axils of the uppermost leaves, 1–3.5 cm. long; involucre of about 5 bracts 3–12 mm. long, linear-filiform, entire, shorter than to about equaling the rays; rays 4–8, 3–8 mm. long, spreading or spreading-ascending, subequal; involucel of 4 or 5 bractlets like the bracts, 3–6 mm. long, about equaling the pedicels; pedicels 2–5, 2–4 mm. long, wing-margined, spreading-ascending, subequal; petals oval, obtuse, white; stylopodium depressed-conic, the styles ca. .05 mm. long, erect or ascending; fruit about 2 mm. long, 1.5 mm. broad, the ribs low, filiform, much narrower than the intervals; vittae rather large; seed face plane.

Type locality.—"Pic de Tolima," Colombia, *J. Goudot.*

Distribution.—Páramos at 9,500–13,000 feet altitude, Andes of central Colombia.

Specimens examined.—COLOMBIA. Cundinamarca: Páramo de Sumapaz, Alto San Juan, 18 km. E of Cabrera, *F. R. Fosberg 20,792* (USNA). Tolima: Pic de Tolima, *J. Goudot* (P-type; K, W; photo [K 385] of Paris specimen: F, US; photo [F 31,808] of Vienna specimen: F, GH, UC, US-type collection). Caldas: Páramo del Quindío, *Pennell & Hazen 9875* (GH, NY, US).

The distinctness of this species and the excellence of the illustration that accompanies its original publication have prevented any serious confusion of it with any other.

12. **Niphogeton Kalbreyeri** (H. Wolff) Math. & Const., comb. nov.

Apium Kalbreyeri H. Wolff, Repert. Nov. Sp. 17: 175. 1921.

Cespitose perennial herb 1–3 dm. tall, somewhat hirtellous and puberulent throughout, the foliage deep green above, paler beneath, subcoriaceous; basal leaves densely rosulate, oblong- to obovate-spatulate, 3–7 cm. long, 0.8–2.5 cm. broad, simple, obliquely crenate distally with numerous crenations, the margins entire below, obscurely ciliolulate, narrowed below the middle

into a broad, flat, many-nerved petiole 2–11 cm. long, narrowly sheathing at the base; cauline leaves triangular to ovate, truncate or sessile-clasping above, crenate to incised-crenate; inflorescence terminal and lateral, with 1 to many lateral peduncles arising in the axils of the upper leaves, 1–6 cm. long; involucre of about 5 bracts 5–12 mm. long, linear- to obovate-spatulate, shallowly 3- to 5-lobed at the apex, ciliolulate, shorter than the rays; rays 3–15, 3–17 mm. long, spreading or spreading-ascending, puberulent, subequal; involucel of 3–5 bractlets like the bracts, 4–6 mm. long, ciliolulate, about equaling the pedicels; pedicels 5–10, 3–6 mm. long, spreading-ascending, angled, puberulent, subequal; petals oval, obtuse or acute, white; stylopodium low-conic, the styles 0.2 mm. long, spreading; fruit ovoid, 2.5–3 mm. long, 2 mm. broad, the ribs prominent, acute, broader than the intervals; vittae large, sometimes a smaller vitta in the apex of each rib; seed channeled beneath the vittae, the face nearly plane.

Type locality.—"Colombien: Santander" [Ocano to Pamplona, Norte de Santander], *W. Kalbreyer 1197*.

Distribution.—Páramos at 9,500–12,500 feet altitude, Andes of southwestern Venezuela and northeastern Colombia.

Specimens examined.—VENEZUELA. Táchira: Páramo Tamá, *F. Cardona 294* (US); limestone outcrops, Páramo de Tamá, *J. A. Steyermark 57,366* (F, LA, UC; photo of Chicago specimen: GH, LA, UC). COLOMBIA. Norte de Santander: Páramo de Cachira, 1845, *W. Purdie* (K); Páramo de Romeral, *Killip & Smith 18,693* (US); Páramo por arriba del Piñuelal, SE of Pamplona, *M. de Garganta 1046* (LA, UC); Ocana to Pamplona, *W. Kalbreyer 1197* (K-isotype).

The remarkable foliage, involucre, and involucels of this species set it apart as, without question, one of the most distinct and striking members of the genus.

13. **Niphogeton pusilla** (Wedd.) Math. & Const., comb. nov.

Oreosciadium lingula s. v. *pusilla* Wedd. Chlor. Andin. 2: 205. 1857.

Cespitose, subacaulescent perennial herb 3.5–10 cm. tall, the stems purplish, somewhat hirtellous and puberulent throughout, the foliage subcoriaceous; basal leaves densely rosulate, oblong to oval, 6–10 mm. long, 1.5–4 mm. broad, simple, obscurely tridentate at the apex, the margins somewhat inrolled and densely ciliolulate, the petioles slender, 6–15 mm. long, the margins approximate, strongly ciliolulate, sheathing only at the very base; cauline leaves 1 or 2, bractlike, entire, sessile-clasping; inflorescence terminal only, the peduncles 0.5–3.5 cm. long, puberulent; involucre of 4 or 5 linear bracts 3–10 mm. long, entire, apiculate, about equaling the rays; rays 4–6, 1–6 mm. long, spreading or spreading-ascending, puberulent, subequal; involucel of 1–3 linear bractlets like the bracts, 1–5 mm. long, exceeding the pedicels; pedicels 1–3, 2 mm. or less long, spreading-ascending, angled, puberulent, subequal; petals oval, obtuse, white with a purplish midvein; stylopodium low-conic, the styles about 0.2 mm. long, spreading; fruit ovoid, 2.5 mm. long, 2 mm. broad, the ribs prominent, acute, broader than the intervals; vittae rather small; seed face shallowly concave.

Type locality.—"San Urban, dans la province de Pamplona," Colombia, *Funck & Schlim, 1641*.

Distribution.—Páramos at 9,500–13,000 feet altitude, Andes of northeastern Colombia in the Cordillera Oriental.

Specimens examined.—COLOMBIA. Norte de Santander: Páramo de Colorado, Victoria Real, 1845, *W. Purdie* (K). Norte de Santander-Santander: Páramo de Santurbán, *H. St. John 20,769* (UC, USNA). Santander: "San Urban dans la province de Pamplona," *Funck & Schlim 1641* (P-type; photo [K 385] of Paris specimen: F, US); Páramo de Santurbán, near Vetas, *Killip & Smith 17,508* (GH, US); Páramo de Santurbán, *Araque & Barkley 18S704* (US). † Cundinamarca: "St. Fe de Bogotá," *W. Purdie* (GH); "Páramos, Andes N. Granada," *W. Purdie* (GH).

Weddell's "subvariety" was long lost to view, and Wolff (1927) remarked that he had seen no material referable to it. The Paris specimen of *Oreosciadium lingula* (and Killip's photograph of it), however, reveals five plants of the Goudot collection of typical *N. lingula* on the right-hand side of the sheet and a single specimen

by Funck and Schlim at the lower left. This latter is unmistakably conspecific with the plants we have grouped under *N. pusilla*. These tiny subacaulescent plants are so dissimilar in appearance from such species as *N. dissecta, N. magna,* and *N. stricta* that it is difficult to believe that they can belong to the same genus, but they agree even with these species in all essential generic characters. The Purdie collections listed above as questionably from Cundinamarca are more likely both fragments of the collection by the same man in Norte de Santander, the only one of his collections of this species represented at Kew.

SPECIES EXCLUDED

Apium andinum (Rusby) H. Wolff in Engler, Pflanzenreich 90 (4^{228}): 52. 1927 (not *A. andinum* Phil. 1894) = Apium leptophyllum (Pers.) F. v. Muell.

Oreosciadium acaule (Torr.) A. Gray, Proc. Amer. Acad. 7: 343. 1868 = Aletes acaulis (Torr.) Coult. & Rose

Oreosciadium andinum Rusby, Bull. N. Y. Bot. Gard. 4: 366. 1907 = Apium leptophyllum (Pers.) F. v. Muell.

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