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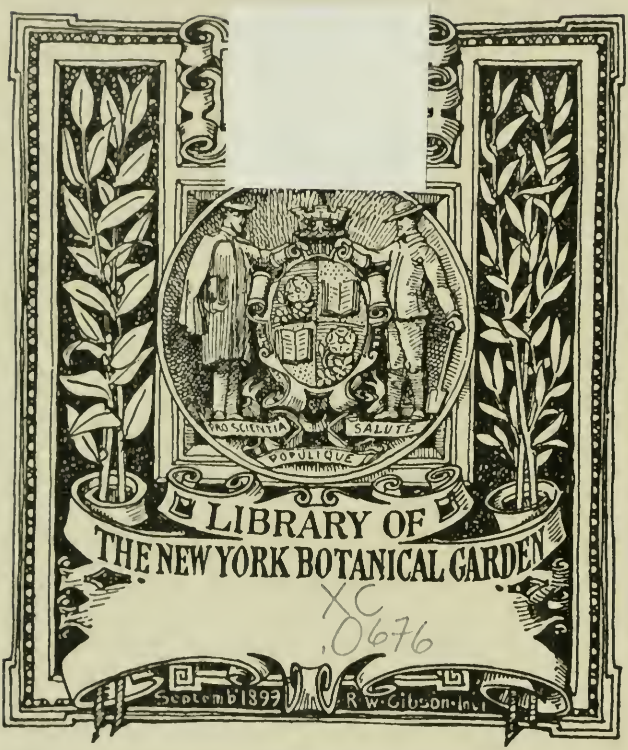

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# THE NEW YORK BOTANICAL GARDEN

VOLUME X

1921-1923

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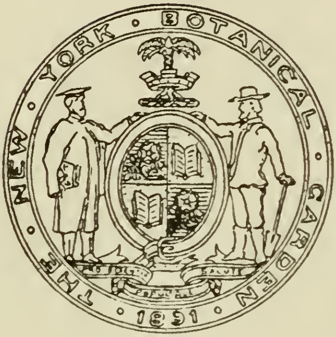

VOLUME X

(Nos. 226-250)

WITH 16 PLATES AND 31 FIGURES

1921–1923

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# SOME PLANTS FROM TROPICAL SEA GARDENS

By MARSHALL AVERY HOWE

NEW YORK
1921

Reprinted, without change of paging, from NATURAL HISTORY, 20: 560-568. F 1921. ["November-December, 1920."]

# Some Plants from Tropical Sea Gardens

By

MARSHALL AVERY HOWE

Curator of the Museums and Herbarium of the New York Botanical Garden

[*Reprinted from* NATURAL HISTORY, VOL. XX, NO. 5, pp. 560–568, 1920]

THE MERMAID'S WINEGLASS, *Acetabulum crenulatum,* an exquisite green seaweed. photographed (natural size) soon after being taken from the waters of Biscayne Bay at Miami, Florida. This dainty plant is of occasional occurrence in shallow bays of Bermuda, southern Florida, and the West Indian islands. In Biscayne Bay it sometimes covers areas of considerable size to the exclusion of nearly all other kinds of marine vegetation. The elegant, radiately chambered cups are bright green when living, but they have a delicate coating of lime and they usually become chalky white soon after being gathered

# Some Plants from Tropical Sea Gardens

By MARSHALL AVERY HOWE

Curator of the Museums and Herbarium of the New York Botanical Garden

A VISITOR from the north is often disappointed by his first sight of a tropical strand, which commonly shows little or no conspicuous vegetation between the tide lines. Particularly is this true if he is familiar with the rocky coasts of northern New England, where a large share of the richly abundant marine plant life is exposed freely to view with every ebbing tide. Probably the usual poverty of the strictly littoral marine flora in the tropics is due chiefly to the scorching effects of the tropical sunshine, although there are, of course, here as elsewhere, numerous more or less wide areas where a bottom of loose shifting sand, allowing no stable foothold or anchorage, precludes the development of any conspicuous vegetation.

But there are also extensive rocky shores, submerged reefs, and bottoms strewn with old corals or calcareous pebbles, where light, heat, aëration, and suitable anchorage combine to furnish ideal conditions for the development of marine gardens. If the observer can wade into such a place at low tide, especially on a calm morning before the daily trade wind arises to ruffle the surface of the water, the sight is one that is long to be remembered. Or perhaps he can row over it on one of the calm days such as occasionally occur in late spring or in summer, or can view it even in less placid weather from a glass-bottomed boat at some winter resort.

In addition to the graceful, often brilliantly colored or iridescent algæ—the plants proper—there are commonly also in such a garden stately corals and sea fans, which are colonial animals. These animals, because they are attached and have no more power of locomotion than a tree, are ordinarily looked upon as plants by the uninitiated. In fact, the "sea gardens" that are exhibited through glass-bottomed boats to patrons of southern winter resorts are sometimes almost exclusively "zoölogical gardens." Besides the colonial animals firmly attached to the home spot there are often also gaily colored tropical fish swimming in and out among the other organisms and giving a touch of active life to these submarine beauty spots.

Although the adjective "tropical" is used in our title and elsewhere in this discussion, the wealth of the marine vegetation in the subtropics of our North American coasts and adjacent islands is probably even greater than that of the tropics, strictly speaking. In respect to number and variety of species of "seaweeds" or algæ the richest areas in the northern half of the western hemisphere—at least the richest visited by the writer—would appear to be Bermuda, the Florida Keys, and the coast of California. It is possible, however, that Guadeloupe,[1] wholly within the tropics, deserves to be considered in this connection. Parts of the Bahamas, of Cuba, Jamaica, and Porto Rico, and of the Caribbean coasts of Panama are well supplied with marine algæ, but, taken as a whole, they do not give the collector the impression of wealth that he obtains from prowling about in the waters of the Florida Keys and Bermuda.

The "Sargasso Sea," in any such magnitude and character as was described by some of the early navigators and as was represented on some of the maps made only fifty years ago, seems to be more or less of a myth. Yet, floating mats[2] of *Sargassum*, several feet or, rarely, several rods in width are frequently met with, as one steams southward from New York or Halifax, or cruises about among the West Indian islands. Floating *Sargassum* is found particularly in the path of the Gulf Stream, which sometimes brings it far to the north, occasionally casting it ashore after

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[1] The algal flora of this island has been intensively studied by French scientists and the list of marine species and varieties attributed to it reaches the imposing total of 811, a number considerably greater than that thus far attributed in any published paper to any of the three other regions. The determinations on which the Guadeloupe list is based are not altogether critical, however, and the sum total is swollen by the inclusion of numerous varietal or form names.

[2] These mats consist chiefly of two species, *Sargassum natans* and *S. fluitans*, which are certainly known only in a free floating condition.

1921

THE MERMAN'S SHAVING BRUSH, *Penicillus capitatus*, from Bermuda. (About one half natural size)

a storm on Long Island, Martha's Vineyard, and Nantucket. As is well known, it is accompanied by a characteristic fauna of bryozoa, crustaceans, small mollusks, and the like, and fishes which go along with it to feed on the small animals that it carries. Species of *Sargassum* are difficult to limit and define, but it is safe to say that a dozen or more occur in the West Indian region. Most of these are surf plants, growing firmly attached to rocks and reefs in exposed places. They are found near the low-water mark, and, with their cousins of the genus *Turbinaria*, they take the place, in the south, of the northern rockweeds of the genera *Fucus* and *Ascophyllum*, both taxonomically and ecologically, although never so conspicuous and massive as the latter often are.

The genus *Sargassum*, like all the other algæ, belongs to the large group of plants known in the books as "thallophytes"—a group in which the plant body, according to the bookmakers, is not differentiated into root, stem, and leaf; yet it is very difficult, if not impossible, to frame a definition of a leaf which may not apply to the leaflike structures shown by the species of *Sargassum*. In other words, a *Sargassum* is a "leafless" plant that appears to have leaves.

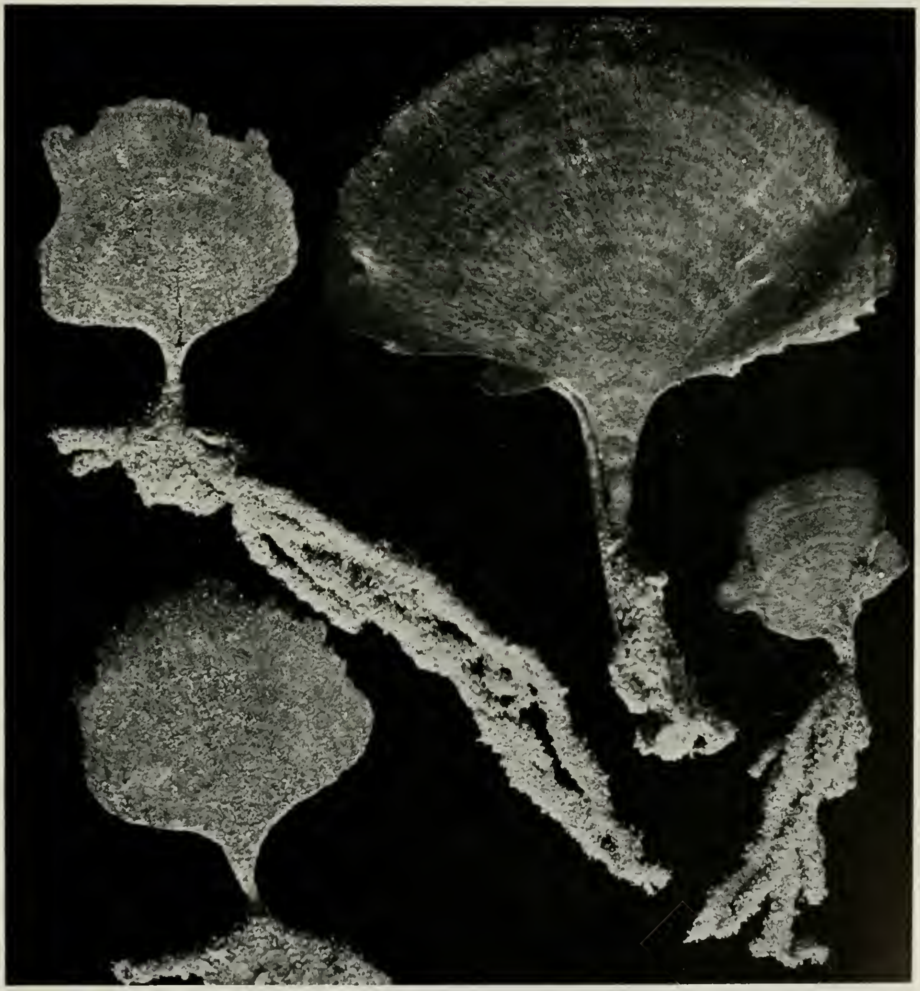
The larger algæ are divided into three great groups, which are often spoken of in an untechnical way as the "greens," the "browns," and the "reds," these names being abbreviated translations of the technical group names, which have been based upon the prevalent colors shown by representatives of these groups. The "browns" include the largest kinds of seaweeds, such as the kelps and rockweeds of the North Atlantic and the giant kelps of our Pacific coast, individuals of which often reach a length of more than one hundred feet and the extensive beds of which are now being used as a source of potash for the American farmer and gardener. In the American tropics, the more conspicuous members of the brown group include, besides *Sargassum* and *Turbinaria*, already mentioned, representatives of several other genera.

It is perhaps in the large group of algæ known colloquially as the "greens" that one finds the most interesting and curious as well as the most beautiful of the tropical sea plants. In these, the leaf-green or chlorophyll, characteristic of plants in general, is found essentially free from admixture with other pigments. In many of them, however, the plant body is more or less coated or permeated with lime, so that it is often whitish, at least in the older parts, or speedily becomes so after being taken from the water and exposed to the light.

Of the group of calcified green algæ the four species of *Penicillus*, indigenous to the sea bottoms of Bermuda, southern Florida, and the West Indies, are among the most curious. In these, as is suggested by the Latin name, the plant body takes the form of a brush, its component filaments being closely interwoven to make a cylindric or flattened stalk and then, at the top, set free and forking, each enclosed in a porous sheath of lime, they constitute the head or bristles of the brush. One sort, perhaps the commonest, is sometimes known as the merman's shaving brush, or is occasionally referred to by the less particular and meticulous as the mermaid's shaving brush.

A relative of the plant just described and one that grows in similar situations is the mermaid's fan. There are several species of this generic group (*Udotea*), in all of which the delicate root hairs penetrate the calcareous sand and attach to themselves small particles of this sand, thus making anchorage hawsers in a bottom that is not altogether stable. The rootlike part, in the attached algæ, is supposed to serve simply as a holdfast. These sea plants often affix themselves to smooth hard rock, or sometimes to pieces of iron or glass, from which they can evidently draw little or nothing in the way of nourishment. Their food is apparently derived directly from the surrounding water and air and is taken in directly by the general surface of the plant. In the case of these Udoteas and their relatives, however, with their highly developed systems of sand-burrowing rhizoids, it may be suspected that these rhizoids play a part in the gathering of food as well as in anchoring the plant. What are commonly called "sea fans" by frequenters of the sea are organisms of a very different nature from those here described under the name of mermaid's fan. They are larger and are colonial animals related to the corals.

Another interesting and attractive member of the group of lime-coated green algæ is the sea fir (*Rhipocephalus phœnix*), the center of whose distribution appears to be the Bahama Banks. This plant is usually from two to six inches high and when growing on the sea bottom is very suggestive of the little German Christmas trees that were



THE MERMAID'S FAN, *Udotea conglutina*, from Bimini Harbor, Bahama Islands. (Natural size)

A CALCIFIED AND SEGMENTED GREEN SEAWEED, *Halimeda simulans,* from Porto Rico. (About four fifths natural size)

once sold in this country for holiday decorations. It is dark green when living but is soon bleached to a chalky white after being killed and exposed to the light. In general structure, it is somewhat intermediate between the brushes and the fans, being brushlike in general habit but having numerous small overlapping fans for branches.

The writer once enjoyed the privilege of being becalmed for two days on the Bahama Banks in a small sloop. On these banks are hundreds of square miles where the water is mostly from one to twenty feet deep. The bottom here is chiefly of more or less compacted oölitic sand, consisting of clean white nearly spherical granules that suggest fish roe both in form and size. Such a bottom rarely becomes muddy to any appreciable extent and the waters above it are wonderfully clear, so much so that when a breathless calm makes the surface of mirror-like smoothness one can see the vegetation and animal life of the sea bottom in twelve or twenty feet of water almost as distinctly as if the water were only two feet deep. On wide areas of the Bahama Banks the merman's shaving brushes, the mermaid's fans, the sea firs, and their relatives are the dominant features of the marine flora, sometimes forming a continuous carpet on the floor of the sea.

Prominent among the relatives of the Udoteas are eight or ten kinds of *Halimeda,* in all of which the calcified plant body is regularly jointed or segmented. In most of the species of this genus the lime is abundant and the system of joints gives a certain degree of flexibility to a plant that would otherwise be quite rigid and stonelike. One of the species, at least, sometimes occurs in great masses, and the quantities of lime left by its decay are, in places, important factors in reef building and land forming. The fact that it is a more rapid grower than the corals seems to give it a certain advantage over them in the matter of secreting and depositing lime, even though the proportion of lime in its make-up is not so great.

Perhaps the most dainty and exquisite of the green algæ is the mermaid's wineglass, *Acetabulum crenulatum,* which grows in shallow bays and protected places, ranging as far north as Bermuda and southern Florida. It is rarely found in any great quantity, yet occurs in considerable abundance on old shells and pebbles, mostly in ten or fifteen feet of water or less, in the bays lying between the keys and mainland of southern Florida. The actual height of the plants is usually from two to four inches. The elegant cup-shaped disk which surmounts the graceful stalk is largely reproductive in function, each of its radial chambers containing at maturity, in the present species, from 200 to 500 subglobose, firm-walled spores, scarcely visible to the unaided eye, each of which produces on germination a number of smaller motile cells which are sexual in nature. At least three other species of this genus occur in the West Indian region.

Among the larger green seaweeds of the warmer parts of the earth are some that are not calcified and of these the species of *Caulerpa*—a dozen or more of them in Bermuda, southern Florida, and the West Indies—deserve especial mention. These present themselves in a great variety of graceful and attractive forms, some of them suggesting delicate feathers, others looking like clusters of green grapes, the inflorescence of grasses, the twigs of cypress trees, or sprays of running pine. They are found in tide pools, on the roots of the red mangrove in lagoons, and creeping on the sea bottom down to a depth of a hundred feet or more. Individual plants of some of the kinds get to be four or five feet long. A curious thing about them is that, although they are plants of considerable size, no one has yet certainly detected in them any spores or other special reproductive organs. They seem to maintain themselves by simply continuing to grow at one end while dying off at the other, or to propagate their kind by accidentally detached fragments. It nevertheless seems probable that they produce some sort of minute reproductive cells which have thus far escaped observation and detailed description. Doubtless much remains to be learned about the life history of the Caulerpas and many of their relatives by some one so situated that he can watch the living plants continuously throughout the year, with a compound microscope and needed accessories at hand.

A species of *Valonia,* taking the form of a

A GREEN SEAWEED, *Caulerpa racemosa*, that suggests bunches of grapes, photographed (not in place) at the mouth of the Guánica Harbor, Porto Rico. (About one half natural size) balloon or an irregularly oval sac, ranging in size from the dimensions of a robin's egg to those of a hen's egg, and filled with a fluid protoplasm, is often found washed up on beaches in the West Indian region and is, in Bermuda at least, often referred to as "sea bottles." Dark green and iridescent in life, it becomes clear and translucent after being killed and exposed to the light for a time and may be as attractive then as when living. Children sometimes pick it up on the beaches and by skilfully exerted pressure playfully squirt the liquid contents into each other's faces. These little "bottles" grow in shallow water mixed in with seaweeds of the soft mossy kinds or under shelving rocks near the low-water line. Another kind of *Valonia*, consisting of somewhat smaller ovoid or bottle-shaped segments that branch and cohere in large masses, is often beautifully iridescent and very attractive when seen growing in the water.

It is in the large group of marine plants known nontechnically as the red algæ that we find the greatest variety in the tropics, although as individuals the "reds" are rarely so numerous or so conspicuous as are many of the "browns" and "greens." Many of the most interesting and beautiful of the "reds" are so small that their wondrous symmetry and beauty are revealed only to the user of a hand lens or a compound microscope. Several are so delicate or have such a soft gelatinous texture that when floated out on paper and dried under pressure they adhere so closely to the paper and have so little substance that they are sometimes taken for paintings by those who do not stop to realize that no human hand could trace lines of such delicacy and symmetry as these "flowers of the sea" often possess. One of the coarser red seaweeds of the tropics, *Bryothamnium triquetrum*, looks a little more like some land plants. The main axes have three rows of short toothed or fringed branchlets, giving these axes a three-angled or three-winged effect. The individual plants form dense clumps one or two feet in thickness, but they sometimes grow associated in large numbers, forming extensive beds.

The red algæ, like the greens and the browns, contain chlorophyll, the green color substance common to plants in general, but they have also another pigment that modifies or obscures the green, so that the plants appear to be of some shade of red, pink, or purple, or sometimes almost black. The red pigment is soluble in fresh water, and the green is not, so that red seaweeds washed up on the beach and exposed to rain often become green or show zones or spots of green in the more exposed parts. On the other hand, the green is soluble in alcohol while the red is not, so that the two pigments may be easily separated. The red algæ that are really and strikingly red are, with few exceptions, inhabitants of deeper water than the greens and the browns and are usually collected by dredging—or by being found washed ashore, particularly after a storm.

Several kinds of red algæ as well as of "browns" are extensively used by the Chinese and Japanese as articles of food.[1] The agar-agar of commerce, derived from red algæ, is a food in the Orient, but is known in America best as a nutrient medium for laboratory cultures of bacteria and fungi. Another product of red seaweeds, known as "funori," is manufactured by the Japanese to the amount of two or three million pounds a year and is used by them for sizing for cloth, for which purpose it seems to have certain advantages over starch. Most of these marine algæ from which the Japanese derive products that sell for several millions of dollars a year have close relatives in American waters, but apart from the recent development of the kelp potash industry in California and the use of seaweeds as a fertilizer for the land by farmers living in the vicinity of the sea, the inhabitants of the United States have thus far made little practical use of the plant life of the ocean.

On the coast of Massachusetts the Irish moss or carrageen (*Chondrus crispus*) used for making sea-moss jellies or puddings, is collected to the value of a few thousand dollars a year, and the "dulse" (*Rhodymenia palmata*), which is eaten raw as a sort of salad or relish, is gathered in still smaller quantities and offered for sale

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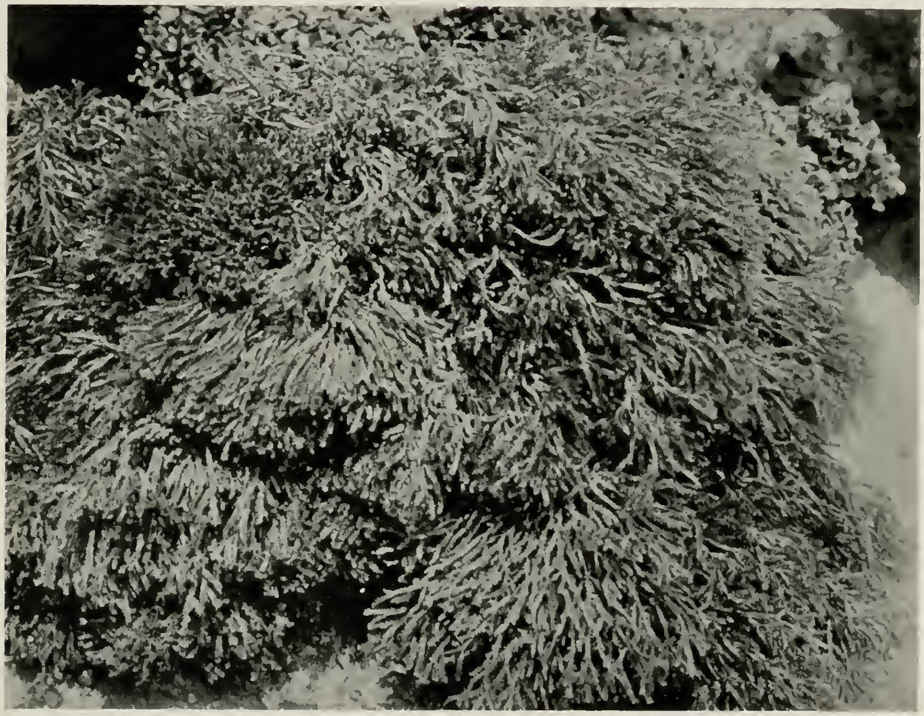
[1] See paper, by the writer, on "Some Economic Uses and Possibilities of the Seaweeds." *Journal of the New York Botanical Garden,* XVIII, 1917, pp. 1–15.

in the water-front markets of New York and Boston. But with the increase of the population of our country, and with the certain advance of science and its applications, it is probable that the future will witness a widely extended utilization of the plant resources of the sea.

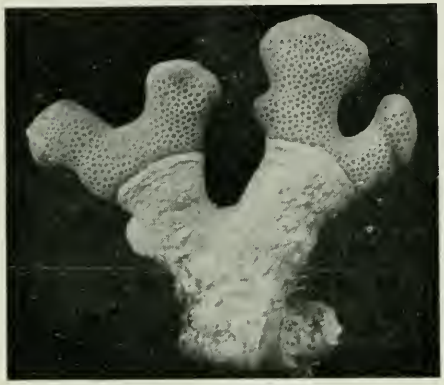
In at least three of the natural families of the red algæ the plant body takes up lime from the sea water and becomes more or less hard and stonelike. In one of these families in particular (the Corallinaceæ, so called on account of a superficial resemblance to the corals) the plant, except for the inconspicuous reproductive cells and almost equally inconspicuous apical or superficial layers of new tissue, is almost as hard as any limestone rock. It has become apparent in recent years that in many parts of the world these lime-secreting sea plants are and have been an important factor in the building of reefs, a line of activity that in the past has been attributed almost exclusively to the coral animals, even though, as would now appear, these coral animals are often of secondary importance. But the coral-like seaweeds are always plants, however coral-like they may look. In microscopic structure and modes of reproduction they are just as truly plants as are any of the seaweeds of the soft mossy kinds. Yet it is not at all surprising that those who have not studied such things sometimes confuse these hard stonelike plants with the corals and that even the naturalists of a hundred years ago often did likewise.



A LARGE RED SEAWEED, *Bryothamnium triquetrum*, of the American tropics and subtropics, photographed (not in place) at the mouth of Guánica Harbor, Porto Rico. (About one third natural size.) At Key West, Florida, this species forms large mats on the floor of the ocean, mostly at a depth of from twenty to fifty feet

The lime-secreting plant often forms a crust that gradually creeps over, covers, and smothers coral animals. Plant crusts of these kinds are usually small and thin and are probably of not much importance in building reefs. But there are many different kinds of these hard lime-secreting plants and some of them occur in large masses and form extensive reefs. Certain species are of a delicate pink color, so that one may easily imagine what an attractive

ONE OF THE STONY, LIME-SECRETING CORAL-LIKE SEA PLANTS, *Goniolithon strictum*, from Key West, Florida. (About one half natural size)



AN ENCRUSTING SEAWEED, *Goniolithon solubile*, growing on a living coral, from Porto Rico. (About two thirds natural size.) The lime-secreting plant is conquering the lime-secreting colonial animal, gradually covering and smothering the coral polyps

display a reef must make when exposed, or even when visible through calm water.

There are coralline algæ which grow attached to the shells of members of the clam or mussel family. The intimate attachment is probably unwelcome to the clam, although the overshadowing presence of the shrubby stonelike alga may render the clam a service by covering and protecting it from some of its enemies. The algæ in general are not very particular as to their points of attachment, although something substantial and firm in the way of a substratum seems usually to be preferred.

Living corals are found only in the warmer seas; coral-like plants occur not only in the tropics, but also in temperate and frigid waters. Explorers in the Arctic regions have reported great beds of them on the floor of the ocean, mostly in water that is from 60 to 120 feet deep.

A few years ago the Royal Society of London sent a party of naturalists to the South Pacific to study the mode of origin of the so-called coral islands. The island of Funafuti of the Ellice Islands group was chosen for special study because it was believed to be "a true coral island." By means of a drill, borings were made to a depth of a little more than 1100 feet, the cores brought up were carefully studied, and the various groups of animals and plants that had contributed to the upbuilding of this island were ranked in order of their relative importance. The first rank was given to red algæ of the coralline family; the second to lime-secreting green algæ of the genus *Halimeda;* third rank was awarded to the group of microscopic animals known as Foraminifera; and fourth rank to the corals. So Funafuti seems to be "a true coral island" which, strictly speaking, is not a coral island at all!

American geologists are finding evidence that certain limestones, now high and dry, in various parts of the United States and the West Indies, are made up chiefly of the remains of lime-fixing plants that flourished when those parts of the earth's crust were under the surface of the sea. So these hard limy sea plants, living and dying century after century and rising "on stepping-stones of their dead selves," are not only making land today, but their ancestors and relatives did the same thing thousands of years ago.[1] And no small part of the pleasure and satisfaction of exploring the sea gardens of the tropics comes from observing bits of evidence as to how this great work is still being accomplished.

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[1] For a further discussion of this subject, see a paper by the writer on "The Building of Coral Reefs." *Science*, XXXV, No. 909, May 31, 1912, pp. 837–42.

CONTRIBUTIONS FROM THE NEW YORK BOTANICAL
GARDEN No. 227

# SCROPHULARIACEAE OF COLOMBIA—I.

BY

FRANCIS W. PENNELL

NEW YORK
1920

Reprinted, without change of paging, from PROCEEDINGS OF THE ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA, 1920

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# SCROPHULARIACEAE OF COLOMBIA—I.

BY FRANCIS W. PENNELL.

For a period of eight months, during 1917 and 1918, the writer was engaged in scientific work in Colombia. No attempt will now be made to tell the story of his adventures there, nor to give more than the briefest summary of his impressions of Tropical or Andine vegetation. A short narrative of my explorations and a comparative sketch of the plant-life seen has already been presented in the *Journal of The New York Botanical Garden* for June, 1918. I will simply say that my travels took me from the northern seacoast to the Andes east of Neiva in 3° north latitude, from the prairies and lowland forest of the Orinoco drainage, from the Magdalena and Sinu valleys, upward through every zone of vegetation to the summits of each of the three ranges of the Andes The greatest diversity of life was seen, and the collections of plants, brought from nearly all points visited, include much that is new to science.

From July 6 to August 16, 1917, it was my privilege to work with Dr. Henry H Rusby, of the College of Pharmacy, New York City—a companionship which to a botanical novice in a strange land was invaluable. All specimens made on and before August 16, while numbered consecutively with those made by myself alone later, are to be cited as Rusby & Pennell. . . .

Detailed maps of Colombia are difficult to obtain, and many of our collecting-stations were at small towns, or single houses. Consequently, although in the lists of specimens given I am stating the Department in which each point is located, it seems important to give a full list of the localities from which our plants have come. Arranging these in the order of our itinerary, and grouping them according to broad natural areas of topography, should enable anyone to place approximately any station. For each point the Department is stated. The names of houses are placed in quotation marks.

Northern Seacoast:
    July 6, 1917. Cartagena, Bolívar.

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Along Rio Magdalena:
July 8, 1917. Barranquilla, Bolívar
" 10, " Calamar, "
" 11, " El Banco, Magdalena
" 12, " Gamarra and Carpentiera, Magdalena
" 14, " Puerto Berrio, Antioquia
" 15, " Buenavista, Caldas.

Plain of Tolima:
July 16, 1917. Mariquita and San Lorenzo, Tolima.

Plain of Upper Magdalena:
July 19, 1917. Girardot, Cundinamarca
" 21, " Espinal to Cuamo, Tolima
" 22, " Cuamo to Rio Saldaña, Tolima
" 22, " Rio Saldaña to Natagaima, Huila
" 24, " Quebrada de Angeles, "
" 25, " Quebrada de Angeles to Rio Cabrera, Huila
" 26, " Rio Cabrera to Villavieja, "
" 27, " Villavieja to Neiva, "
" 30, " Neiva, Huila.

Cordillera Orientál:
July 30 to August 8, 1917. Excursion from Neiva over the crest of the Cordillera to "Balsillas", and return.

Along Upper Magdalena:
August 8–9, 1917. Neiva, Huila
" 12, " Natagaima, Huila
" 13, " Boca Saldaña, Huila.

Railroad from Girardot to Bogotá:
August 14, 1917. Portillo, Anapoima, San Joaquin, Hospicio, La Esperanza, Cachipay, Zipacon and Anolaima, Cundinamarca.

Upper western slopes of Cordillera Orientál:
August 16, 1917. Bogotá. Cundinamarca.

Eastern slopes of Cordillera Orientál:
August 22, 1917. Chipaque, Cundinamarca
" 23, " Caquezá, "
" 24, " Caquezá to Rio Sananie, Cundinamarca
" 24, " Quetame to "Susumuco," "
" 25–26, 1917. "Susumuco," "

Plain of Meta:
August 26 to September 2, 1917. Villavicencio, Meta.

Eastern slopes of Cordillera Orientál:
September 4, 1917. Villavicencio to "Buenavista," Meta
" 4, " "Buenavista" to "Pipirál," Cundinamarca
" 5, " "Pipirál" to "Susumuco," "
" 5, " "Guayabetál," "
" 6, " "Guayabetál" to "Monte Redondo," Cundinamarca
" 7, " "Monte Redondo" to Quetame, "
" 7–8, " Caquezá, "
" 8, " Ubagué, "

Summit of Cordillera Orientál:
September 8, 1917. Paramo de Cruz Verde, Cundinamarca.

Upper western slopes of Cordillera Orientál:
September 12, 1917. Bogotá and Mt. Guadalupe, Cundinamarca
" 13, " Bogotá (Rio San Francisco), "
" 15, " Tequendama, "
" 17, " Bogotá (Monserrate), "
" 18, 23, " Bogotá (Chapinero), "

Summit of Cordillera Orientál:
September 20, 1917. Paramo de Cruz Verde, Cundinamarca.

Upper western slopes of Cordillera Orientál:

September 20, 26, 1917. Bogotá (Rio San Cristobal), Cundinamarca
" 22, 24, " " (Rio del Arzobispo), "
" 24, 25, " " (Las Cruces), "
" 26, " " (Cerro de Focha), "
Summit of Cordillera Orientál:
September 27, 1917. Paramo de Choachi, Cundinamarca.
Upper western slopes of Cordillera Orientál:
September 30, 1917. Bogotá (San Cristobal), Cundinamarca
October 4–8, " " "
" 6, " " (Chapinero), "
" 6, " Rio Teusaca, "
" 12, " Bogotá (Rio San Cristobal) "
" 13–15, " Sibaté to El Peñon, "
" 20–24, " Zipaquirá to Mt. Chuscal, "
" 23, " Nemacón, "
" 28, " Tequendama, "
" 29, " Sibaté to El Peñon, "
Summit of Cordillera Orientál:
November 14, 1917. Paramo de Cruz Verde, Cundinamarca.
Lower western slopes of Cordillera Orientál:
November 28–30, 1917. Fusagasugá, Cundinamarca
December 1–4, " Pandi and Icononzo, Cundinamarca.
Plain of Upper Magdalena:
December 4–5, 1917. Melgar and Girardot, Cundinamarca.
Eastern slopes of Cordillera Centrál:
December 11, 1917. Libano, Tolima
" 15–17, " "Rosalito," between Murillo and Paramo de Ruiz, Tolima
" 16–17, " Paramo de Ruiz, Tolima
" 17–18, " Murillo, "
" 18–29, " Libano ("La Trinidad" and "La Virginia"), Tolima
" 29–30, " "El Convenio," Tolima.
Plain of Tolima:
December 30, 1917. San Lorenzo, Tolima
January 6, 1918. Guayabal and San Felipe, Tolima
" 3, 7, " Honda and Mariquita, "
Along Rio Magdalena:
January 9–10, 1918. Brazuela de Perales, Antioquia
" 11–13, " Puerto Berrio and Malena, Antioquia
" 14, " Vuelta de Acuña, "
" 14, " Opposite Boca Carare, "
" 15, " Cañabetál, Bolívar.
" 15, " Boca de Rosario, Puerto Nuevo and Boca Sogomosa, Santander
" 16, " El Banco, Magdalena
" 18–19, " Magangué, Bolívar.
Plain of Bolivar:
January 24, 1918. Buenavista, Bolívar
" 25, " Sincé and Corozál, Bolívar
" 26, " Sincelejo, "
" 27, " Chinu and Sahagun, "
" 28, " Cienaga de Oro and Ceretė, Bolívar
" 30, " Monteria. "
Along Rio Sinu:
February 3, 1918. "Medellin," Bolívar
" 4, " "Los Hurtados," Bolívar
" 5, " Morales, "
" 6, " Barro Blanco, "
" 8, " Tierra Alta and Boca Tai, Bolívar

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| “ 10–11, “ | “Angostura” and Frasquillo, | “ |
| “ 13–14, “ | Boca Verde. | “ |
| Upper slopes of Cordillera Occidentál: | | |
| February 23, 1918. | Paramo de Chaquiro, Bolívar | |
| “ 25, “ | Cascada Chorron. | “ |
| Along Rio Antizales: | | |
| February 25–26, 1918. | Antizales, Bolívar. | |
| Along Rio Esmeralda: | | |
| February 26, 1918. | Boca Antizales, Bolívar | |
| “ 27, “ | “Las Dantas” to “Puerto Canoa,” Bolívar | |
| “ 28, “ | “Puerto Canoa” to “Salvajin.” | “ |
| Along Rio Sinu: | | |
| March 1, 1918. | Boca Esmeralda, Bolívar | |
| “ 4, “ | Boca Verde, | “ |
| “ 5–6, “ | Frasquillo and “Angustura,” Bolívar | |
| “ 7–10, “ | Boca Tai and Tierra Alta, | “ |
| “ 11, “ | Morrocoquiel, | “ |
| “ 12, “ | “Los Hurtados,” | “ |
| “ 21, “ | Montería, | “ |
| “ 23, “ | Vilches, | “ |
| “ 25, “ | “El Pueblo,” below Lorica. | “ |
| Northern Seacoast: | | |
| March 26 27, 1918. | Cartagena and Turbaco, Bolívar | |
| April 1, “ | Santa Marta, Magdalena. | |

Of chief interest has been the comparison of the vegetation of different altitudinal life-zones, and these upon the slopes of the three divergent Cordilleras of the Andes. The central axis of the Andes, entering Colombia from the South, soon divides into three ranges, all of which, rising from the midst of a broad low Tropical plain, reach high elevations. Also in the northeast is the wholly isolated Sierra Nevada de Santa Marta. Upon each mountain system, one ascends from Tropical lowland, forest or prairie (“Sabana”), through Subtropical forest, through Temperate forest or “Sabana,” to the “Paramo,” as the treeless chill slopes above timber-line are called. Temperature and moisture cause the floras of the different zones to differ, and similarly the isolation of the different mountain systems accounts for a divergence in the floras of the same zone on each chain.

Dr. Frank M. Chapman, in his “Distribution of Bird Life in Colombia,” has given us a masterly presentation of this problem, and I adopt his system of life zones and his terminology of each. As stated in his summary on page 85 of volume 36 of the *Bulletin of The American Museum of Natural History*, these are:

Tropical Zone—sea-level to 4,500–6,000 ft. (1350–1800 meters).
Subtropical Zone—4,500–6,000 ft. to 9,000–9,500 ft. (2,700–2,850 meters).
Temperate Zone—9,000–9,500 ft. to 11,000–13,000 ft. (3,300–3,900 meters).
Paramo Zone—11,000–13,000 ft. to snow-line, 15,000 ft. (4,500 meters).

My observations have led me to occasional slight modifications of his limits, as in placing the lower limit of the Paramo above Bogotá at only 3100 meters. Here local conditions explain such a change. But in general outline, and in nearly all details, his scheme may be adopted for plants as for animals. Plants seem more subject to geographical differentiation than animals, so that in certain genera the same zone on different Cordilleras has related, but never the same, species. A fuller discussion of this subject will be given in the concluding paper of this series—now I wish but to make the summary of distribution accompanying each species of this study intelligible.

The vegetation of a land so diverse as Colombia is immensely rich; consequently upon a short expedition it has been impossible to follow out in comparative study any wide number of families. A few groups well selected, and so far as possible all their species considered, will give data for geographical botany nearly as precise as would the comparing of many families. I have studied the Scrophulariaceae, keeping a record of each species, and making a careful floral description of each. For the Temperate and Paramo zones, and for the Tropical prairies, this family furnishes an excellent index to floral areas. My collections were mainly in these regions, and of herbaceous plants, so that from a phytogeographical viewpoint, the selection of this family has been justified. It is my hope to follow this study with that of some allied group requiring forest environments, probably of the Gesneriaceae.

The present paper gives the results of a study of only about one-half the Scrophulariaceae of Colombia—those which we may call the Antirrhinoid genera. These fall into several tribes, each predominant or restricted to a special life-zone. The Gratioleae are mainly Tropical, while wholly so are the Russelieae and Angelonieae. The Mimuleae, Hemimerideae and Fagelieae, the last with many conspicuous species, predominate in the Temperate Zone of the mountain-slopes. The genus *Bartsia*, of the Rhinanthoid Scrophulariaceae and so yet to be studied, is best developed in the Paramo Zone.

Necessarily the chief basis of this study has been my own collections. I have however revised all the collections from Colombia which I know to be in the United States. These are surprisingly meagre, and from widely scattered localities. The chief are those made by H. H. Smith in the Sierra Nevada de Santa Marta in 1899–1901; by I. F. Holton near Bogotá and in Vallé in 1852–1856;

and—more imperfect—certain series of specimens made in southern Colombia by F. C. Lehmann and at widespread stations over the country by José Triana. To the custodians of the herbaria which have loaned me specimens, the United States National Museum, Gray Herbarium, and Field Museum of Natural History, as well as to my colleagues at The New York Botanical Garden, I am under obligation.

Also, I would mention my indebtedness to that group of Colombian workers whom I had the privilege of meeting in 1917, the growth of whose museum at Bogotá has been phenomenal. Especially would I thank Brothers Aristé-Joseph and Ydinael, Hermanos Cristianos of the Universidad de La Salle. A further word of appreciation must be given to Sr. Santiago Cortés of Bogotá, who, working long alone, has been able to give to the world only the first volume of his "Flora de Colombia."

The following study is primarily systematic, and keys are given throughout. New species and those seen by the writer are carefully described. Synonomy for Colombia is cited fully, otherwise only those names are included which are of first descriptions of Colombian species. The original statement of distribution, or of type-specimen is quoted, and the effort is made to firmly establish the nomenclature used. But it must be said that, as most of the types are in Europe and inaccessible to me, and as Colombia's flora is as yet very partially known, we cannot be certain of the identity of some of these. But I believe that, with very few exceptions, the names now used will be permanent.

For each species a statement of environment and distribution is given, the latter made as definite as our knowledge permits, and analysed accordingly to life-zone and Cordillera. Lastly is given a list of specimens seen, these grouped under the Departments which at present (1920) are in force. State-outlines in Colombia have been so shifting that these limits have not always been easily ascertainable. The herbaria in which specimens may be consulted are indicated by the symbols:

A—The Academy of Natural Sciences of Philadelphia.
C—Field Museum of Natural History, Chicago, Ill.
H—Gray Herbarium of Harvard University, Cambridge, Mass.
U—United States National Museum, Washington, D. C.
Y—New York Botanical Garden, Bronx Park, New York City.

My own collections may all be consulted at The New York Botanical Garden. Duplicates are being distributed to many herbaria.

At the conclusion of the systematic portion of this study there is planned a synopsis of the geographic distribution of the Scrophulariaceae of Colombia, and also a series of brief sketches of those collectors in Colombia to whom reference will have been made in the text.

### Key to Antirrhinoid Scrophulariaceae of Colombia.[1]

Corolla with the posterior lobes external in the bud. (ANTIRRHINOIDEAE.)

- Capsule septicidal, or loculicidal by a simple median split, the septum breaking from the capsule-wall or rupturing. Corolla not spurred. Leaves opposite or whorled in threes (except in *Capraria*).
  - Corolla, even if saccate anteriorly, without a horn-like process at the base of the anterior lobes. Capsule septicidal, or loculicidal. Seeds, if reticulate, with lines not raised or wing-like.
    - Stigma two-lipped.
      - Capsule septicidal, or secondarily also somewhat loculicidal, splitting to base; placentae simple. Sepals distinct or nearly so (except in *Vandellia* and *Torenia*). Leaves, or rarely only the capsule, somewhat glandular-punctate. Inflorescence simply racemose (if several pedicels are in one axil, then no common peduncle is evident). Corolla yellow, blue or white. I. GRATIOLEAE.
      - Capsule loculicidal (only tardily septicidal if at all), or indehiscent; placentae branched and widely spreading. Sepals united over one-half length. Leaves and capsule not glandular-punctate. Inflorescence racemose, or of axillary cymes a single one of which is terminal to the primary peduncle. Corolla yellow, two-ridged and pubescent within on the anterior side. II. MIMULEAE.
    - Stigma capitate.
      - Corolla conspicuously zygomorphic, the tube scarcely developed and the anterior lobes much exceeding the posterior ones. Capsule without placental hairs, and dehiscing only distally. Seeds ridged, not reticulate. Leaves opposite, or the upper alternate.
        - Stamens four; anther-sacs with membranous walls. Corolla orange, flattened, its lobes all evident, the tube split to base between the posterior lobes. Sepals five, less than one-half the length of the capsule.

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[1] The warning must be given that the keys to tribes and genera are prepared for Colombian species, and contrasts may not hold for extra-limital genera and species.

Capsule scarcely dehiscing loculicidally. Seeds blackish. Inflorescence simply racemose. Stem quadrangular. III. HEMIMERIDEAE.

Stamens two; anther-sacs with firm walls. Corolla yellow, its lips concave-saccate or the posterior much reduced, the individual lobes scarcely or not evident, the tube not split to base between the posterior lobes. Sepals four, at least one-half the length of the capsule. Capsule dehiscing loculicidally as well as septicidally. Seeds brown. Inflorescence cymose, two pedicels of each cyme being terminal to the primary peduncle. Stem terete or nearly so. IV. FAGELIEAE.

Corolla red, nearly regular, tubular, the short lobes nearly equal. Capsule filled with slender hairs between which are the scattered seeds, dehiscing to base septicidally. Seeds reticulate, not ridged. Leaves whorled in threes, and the stem with six angles. Inflorescence of axillary cymes, two pedicels of each being terminal to the primary peduncle. V. RUSSELIEAE.

Corolla violet-blue, saccate anteriorly and with a fine horn-like process at the base of the anterior lobes. Capsule loculicidal, the septum only tardily if at all splitting sagittally. Seeds reticulate, the reticular lines raised into wing-like processes. Inflorescence simply racemose. VI. ANGELONIEAE.

Capsule loculicidal, the septum and adjacent capsule-wall persisting, the remaining wall splitting irregularly. Corolla blue, with a spur at the base of the anterior petal. Leaves alternate. VII. ANTIRRHINEAE.

Corolla with the antero-lateral or anterior lobes external in the bud. (RHINANTHOIDEAE.[2])

I. GRATIOLEAE.

Leaves alternate, serrate. Stamens five. Corolla essentially regular, the five lobes equally distinct. 1. *Capraria.*

Leaves opposite or whorled in threes. Stamens four, three or two (the posterior one lost). Corolla more or less zygomorphic, the two posterior lobes united over one-half their length.

Leaves entire to serrate-dentate. Capsule globose to lanceolate in outline. Seeds not regularly cylindric nor spirally ridged, disposed in more than one row within each valve of the capsule.

Corolla with the ridges to the antero-lateral sinuses, if developed, low and not projecting beyond those points (so anterior filaments simple). Style not with a semi-persistent callose base. Septum rupturing, so that the

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[2] To be considered in a second paper.

placental mass eventually stands free. Pedicels frequently bibracteolate. Stem, if quadrangular, with the angles not conspicuously ridged or winged.

Anther-sacs proximate, no connective arms developed. Seeds reticulate. Leaves sessile or nearly so.

Pedicels bibracteolate. Sepals five.

Pedicels bibracteolate at base (remote from the calyx). Corolla yellow, pubescent within at base of posterior lobes. Sepals unequal, and leaves serrate. Plant repent-ascending.
2. *Mecardonia.*

Pedicels bibracteolate at apex (just beneath calyx). Corolla violet-blue or white.

Filaments four, all with anthers. Bractlets 1 mm. or less long, much shorter than the sepals.

Sepals unequal, the outer much larger than the narrow innermost. Corolla pubescent within at base of posterior lobes, or glabrous, violet-blue or white. Capsule globose-ovoid to oblong. Leaves serrate to entire, and stems, erect or ascending.
3. *Caconapea*[3]

Sepals uniform. Corolla pubescent within at base of the anterior lobes. Capsule depressed-globose. Leaves serrate and stem repent-ascending. 4. *Conobea.*

Filaments two, the anterior rudimentary or wanting. Bractlets 5–10 mm. long, equaling or exceeding the nearly uniform sepals. Corolla pubescent at base of the posterior lobes, white or pinkish-tinged. Leaves serrate and stem ascending or erect. 5. *Gratiola.*

Pedicels not bracteolate. Sepals four or five. Corolla blue or white.

Corolla glabrous within. Sepals unequal, the innermost narrowest. Leaves palmately veined, entire or slightly undulate. Pedicels tending to deflex in fruit. Plants repent.

Outermost sepal cordate, much exceeding the linear-attenuate innermost ones; five sepals always present. Capsule oblong or ovoid-oblong, acute, brown, much shorter than the sepals. Styles united to apex. Corolla blue or white. 6. *Monocardia.*

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[3] *Bramia monnieri* (L.) Pennell, a repent herb, with broadly rounded entire leaves, corolla with distinct posterior lobes, and outer sepal scarcely longer than the innermost, is widespread in Tropical America, and must surely occur on moist semi-brackish sands along the Colombian coast. See, Proc. Acad. Nat. Sci., Phila. 1919: 243, 1920.

Outermost sepal ovate-oblong, scarcely longer than the lanceolate innermost, one of which may be lost. Capsule nearly globose, obtuse, pale-brown, little shorter than the sepals. Styles distinct near apex. Corolla white.

Corolla 4 mm. long, appearing four-lobed because the three petals forming the anterior lip are all evident. Stamens four. Sepals five or four. 7. *Macuillamia.*

Corolla 2 mm. long, appearing three-lobed because the anterior petal is lost, leaving the anterior lip two-lobed. Stamens three (only one of the antero-lateral pair developed). Sepals four. 8. *Hydranthelium.*

Corolla white, densely hirsute within over bases of all lobes. Sepals four, uniform. Leaves pinnately veined, serrate-dentate. Pedicels permanently ascending-spreading. Plant erect. 9. *Scoparia.*

Anther-sacs separated on short arms of the connective. Seeds longitudinally striate, the striae frequently tuberculate. Corolla blue or white. Plants erect.

Pedicels bibracteolate, 1 mm. long or less. Corolla blue, pubescent within on the anterior side. Capsule acuminate. Seeds tuberculate-striate. Leaves cordate-clasping at base. Tall herb. 10. *Stemodia.*

Pedicels not bracteolate. Corolla pubescent within on the posterior side, or glabrous. Seeds minutely roughened-tuberculate or smooth. Leaves narrowed at base.

Leaves sessile or nearly so, in whorls of three. Corolla 9–13 mm. long, glabrous within, blue. Capsule acuminate. Seeds minutely roughened-tuberculate. Style semi-persistent. Tall herb. 11. *Unanuea.*

Leaves evidently petioled, opposite. Corolla 4–8 mm. long, pubescent within on the posterior side, blue or white. Capsule acutish. Seeds smooth, with rounded ridges. Style soon deciduous. Low herbs. 12. *Lendneria.*

Corolla violet-blue or white, with two raised ridges (each formed by the adherence of a filament) to the antero-lateral sinuses, and which frequently project as knob-like processes beyond those points (the free portion of the filament appearing as a lateral outgrowth of the adherent portion). Style with a semi-persistent, frequently enlarged and callose base. Septum persistent, with the attached placentae. Pedicels never bracteolate. Stem quadrangular, the angles ridged or slightly winged.

Sepals united over one-third length. Filaments all with anthers. Seeds not with transverse lines. Leaves petioled, serrate-dentate. Angles of stem slightly winged.

Pedicels 1–2 mm. long. Sepals united nearly one-half their length, much shorter than the capsule. Corolla straight, the tube strongly horizontally flattened, the posterior lip purple-brown, elsewhere corolla white throughout, pubescent within on ridges to antero-lateral sinuses; the free portions of the anterior filaments appearing as upcurved from the apices of these ridges. Capsule accuminate, finely pubescent to glabrous. Seeds tuberculate. Leaves oval, rounded, narrowed at base. Plant repent, pubescent.
13. *Vandellia.*

Pedicels 10–25 mm. long. Sepals united over three-fourths length, equaling or slightly longer than the capsule. Corolla decurved, the tube scarcely or not flattened horizontally, blue or white, glabrous within on the ridges to antero-lateral sinuses; the free portions of the anterior filaments appearing as outgrowths proximad to the apices of these ridges which therefore terminate as short knobs. Capsule mucronate or acute, glabrous. Seeds shallowly pitted. Leaves ovate or lanceolate-ovate, acute, truncate-cuneate at base. Plants repent to erect, glabrous. 14. *Torenia.*

Sepals distinct or nearly so. Antero-lateral filaments without anthers. Seeds with fine transverse lines. Leaves sessile, mostly clasping, slightly crenate or entire. Angles of stem ridged, not winged. Corolla blue. Plant diffused-ascending, glabrous.
15. *Ilysanthes.*

Leaves pinnatifid. Capsule linear-attenuate in outline. Seeds regularly cylindric, spirally ridged, disposed in one row within each valve of the capsule. Corolla purple-blue. Plant low, branched, erect. 16. *Schistophragma.*

II. MIMULEAE.

Capsule oblong, dehiscing loculicidally, its walls dry, membranous, brownish. Calyx-tube longer than and enclosing the capsule, its ribs slightly winged, its lobes decidedly unequal, the posterior longest. Corolla 10–15 mm. long, yellow, with many red-brown spots within throat on the anterior side. Leaves broadly ovate, shortly petioled, 1–4 cm. long. Inflorescence of axillary simple pedicels. Stem obscurely angled, not winged. Plant low, repent-ascending. 17. *Mimulus.*

Capsule globose, indehiscent, its walls fleshy, white. Calyx-tube shorter than the capsule, its ribs not winged, its lobes slightly unequal, the posterior longest. Corolla 15–18 mm. long, yellow throughout. Leaves lanceolate, cordate-clasping at base, 15–20 cm. long. Inflorescence of axillary several-branched cymes, borne upon conspicuous peduncles. Stem with angles narrowly winged. Plant tall, erect, widely branched from base. 18. *Leucocarpus.*

III. HEMIMERIDEAE. 19. *Alonsoa.*

IV. FAGELIEAE. 20. *Fagelia.*

V. RUSSELIEAE. 21. *Russelia.*

VI. ANGELONIEAE. 22. *Angelonia.*

VII. ANTIRRHINEAE. 23. *Linaria.*

### 1 CAPRARIA Linné.

*Capraria* L., Sp. Pl. 628. 1753.

Type species, *Capraria biflora* L.

**1. Capraria biflora** L.

*Capraria biflora* L., l. c. 628. 1753. "Habitat in Curassao." Specimens from Curaçao seen in herbarium New York Botanical Garden.

*Capraria lanceolata* Vahl, Ecl. Am. 2: 47. 1798. "Habitat ad St. Martham. von Rohr." Not *C. lanceolata* L. f., Suppl. 284. 1781. Von Rohr's plant was the pubescent form prevalent in Colombia, but appears to have represented an abnormal state in which the pedicels are short and arise from an abbreviated branch.

*Capraria semiserrata* Willd., Sp. Pl. 3: 324. 1800. New name for *C. lanceolata* Vahl.

*Capraria semiserrata berterii* A. DC.; Benth. in DC. Prod. 10: 429. 1846. "Ad Stam. Martham (Bert.! in h. DC.)." An entire-leaved state.

A widespread species of lowland Tropical America, growing mostly on and near the seashore, but extending inland on river-banks, plains and waste land. Very variable, but with most states found in the same region or even in the same colony. Varies in size of leaves, in form of leaves from linear-lanceolate to nearly ovate, and in serration from entire to sharply serrate-dentate; varies in the length of the pedicels; varies in length of and attenuation of the sepals, in size of corolla from 8 to 10 mm. long, and somewhat pubescent or glabrous within anteriorly, and in capsules from oblong to ovoid, and from round and emarginate to acutish. Most conspicuously does the plant vary in pubescence, from glabrous throughout, through states with the stem pubescent and the pedicels glabrous or the pedicels sparsely pubescent—pubescent either with short or long hairs—to forms densely hirsute on stems, pedicels, sepals and the midribs and margins of the leaves. The last state (forma *hirta*[4] Loes. in Bull. Herb. Boiss. ser. II, 3: 284. 1903. "Habitat in Guatemala, in dept. Chiquimula in ruderalibus ad S. Juan Ermita: Sel[er] n. 3314." Isotype seen in herbarium New York Botanical Garden) prevails in Colombia.

River-banks, flats and sandy waysides, at altitudes below 200 meters, Tropical zone; the typical form near the Caribbean shore (doubtless also along the Pacific shore), forma *hirta* Loes. (indicated in lists by asterisk) along the lower river-courses and across the Sabana of Bolívar.

Antioquia. *Brazuela de Perales, on Rio Magdalena (river-flat, alt. 150 m.), Pennell 3704; *Vuelta de Acuña, on Rio Magdalena (sandy loam, alt. 125–130 m.), Pennell 3789.

Bolívar. *Calamar (along Rio Magdalena, alt. 15–25 m.), Rusby & Pennell 20; Cartagena, I. F. Holton 582 (H, Y), (roadside, alt. 5–10 m.), Rusby & Pennell 3 (somewhat pubescent with short hairs). *Sincé (edge of thicket, alt. 120–170 m.), Pennell 4039; *Turbaco (thin loam over white rock, alt. 150–200 m.), Pennell 4761; *Vilches, on Rio Sinu (orchard, alt. 20–50 m.), Pennell 4711.

Magdalena. *Bonda (open damp place, alt. 45 m.), H. H. Smith 1331 (C, H, U, Y). Don Jaco (near the coast), H. H. Smith 551 (C, H, U, Y). Playa Brava (open plain near the coast), H. H. Smith 2823 (Y). Santa Marta (railroad bank, alt. 0–10 m.), Pennell 4771. Around Rio Frio (between the Cienaga de Santa Marta and the foothills, alt. 0–100 m.), H. Pittier 1611 (U).

### 2 MECARDONIA Ruiz and Pavon.

*Mecardonia* R. & P. [Fl. Peruv. et Chil. Prod. 95. 1794, generic diagnosis]; Syst. Veg. Fl. Peruv. et Chil. 164. 1798.

Type species, *M. ovata* Ruiz & Pavon,[5] of Peru.

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[4] This state has been described also as *Capraria lanceolata* Vahl, and C. *semiserrata* Willd. (above), as *C. hirsuta* H. B. K., Nov. Gen. et Sp. 2: 355. 1818, from Mexico, and as *C. biflora β pilosa* Griseb., Fl. Brit. W. I., 427, 1861, from the Bahamas. The first name should be used if this be accounted a distinct species, the last if a variety, and *hirta* if a form.

[5] *Mecardonia ovata* Ruiz & Pavon, Syst. Veg. Fl. Peruv. et Chil. 164. 1798. "Habitat in Peruviae plateis ad Chinchao et Cuchero vicos." Description appears to be certainly that of *M. procumbens* (Mill.) Small, a wide-spread plant to be expected in Peru. The only discrepancy is in describing the calyx as heptaphyllous, although it is stated that the two small outer leaves are deciduous. Possibly the bractlets at the base of the pedicel were noted approximating the flower in very young buds, or more probably an error of vision was made, and because later it could not be checked the imagined bractlets were considered to be deciduous.

**1. Mecardonia procumbens** (Mill.) Small.

*Erinus procumbens* Mill., Gard. Dict. ed. VIII. n. 6. 1768. "Houst. MSS."
*Herpestis caprarioides* H. B. K., Nov. Gen. et Sp. 2: 368. 1818. "Crescit locis arenosis, siccis Regni Novo-Granatensis in ripa fluminis Magdalenae juxta El Peñon [Humboldt & Bonpland]."
*Monniera procumbens* (Mill.) Kuntze, Rev. Gen. 463. 1891.
*Mecardonia procumbens* (Mill.) Small, Fl. S. E. Un. St. 1065. 1338. 1903.
*Bacopa procumbens* (Mill.) Greenm. in Field Col. Mus., Bot. Ser. 2: 261. 1907.
*Herpestis procumbens* (Mill.) Urb., Symb. Bot. 4: 558. 1911.

Moist open soil, along streams in loam or sand, at altitudes below 1200 meters. Tropical zone, doubtless throughout lowland Colombia, largely as a weed. Also in the Sabana of Bogotá, at an altitude of 2600 meters, probably introduced. Widespread throughout Tropical America.

Antioquia. Opposite Boca Carare (forest along R. Magdalena, alt. 125 m.), Pennell 3829.

Bolívar. Boca Verde on Rio Sinu (field along river, alt. 100–200 m.), Pennell 4568; Cañabetal (sand along river, alt. 90–100 m.), Pennell 3874; Sincelejo (thicket, alt. 150–200 m.), Pennell 4068.

Caldas. Buena Vista (moist open sand, alt. 170–180 m.), Rusby & Pennell 63.

Cundinamarca. Bogotá (desiccated soil in meadow, alt. 2600 m.), Pennell 1909 [small-leaved form which has been described as *Herpestis chamaedryoides* H. B. K.]; Icononzo (loam slope, alt. 900–1000 m.), Pennell 2777.

Huila. Natagaima (soil frequently overflowed by river, alt. 400–450 m.), Rusby & Pennell 1182; Quebrada de Angeles above Natagaima (gravel, alt. 450–600 m.), Rusby & Pennell 286.

Magdalena. Masinga (damp clearings, alt. 90–750 m.), H. H. Smith 1326 (Y), Agua Dulce, H. H. Smith 1326 (Y).

Meta. Villavicencio (moist meadow along Rio Guatiquia, (alt. 500 m.), Pennell 1556.

Tolima. Honda (moist sandy field, alt. 250–300 m.), Pennell 3620; Libano (field on "La Trinidad," alt. 900–1200 m.), Pennell 3368.

Valle. La Paila, I. F. Holton 579 (Y).

### 3. CACONAPEA Chamisso.

*Caconapea* Cham. in Linnaea 8: 28. 1833.

Type species *C. gratioloides* Cham., of Brazil.

Pedicels 5–10 mm. long, one to an axil. Corolla 5–7 mm. long, pubescent or puberulent within over base of posterior lobes; lobes violet, throat yellow within, especially on the anterior side and lined with violet, the posterior lobes united nearly to apex.

Corolla 7 mm. long, pubescent within. Anthers all uniform. Sepals strongly dissimilar, the outer ovate, all puberulent. Capsule septicidal, with thick protuberant placentae, in dehiscence portions of the septum remain adhering to the walls. Seeds conspicuously reticulate. Leaves lanceolate-elliptic, crenate-serrate. Stem sharply quadrangular, 1–3 dm. tall. 1. *C. auriculata.*

Corolla 5 mm. long, puberulent within. Anthers of posterior filaments larger. Sepals slightly dissimilar, the outer lanceolate, all somewhat pubescent. Capsule loculicidal, with thin placentae, placed along median line of the septum which ultimately breaks free from the lateral walls. Seeds finely reticulate. Leaves linear, entire. Stem obscurely quadrangular, .3–.5 dm. tall. 2. *C. debilis.*

Pedicels less than 2 mm. long, usually several to an axil. Corolla 2–3 mm. long, glabrous within; lobes white or violet, throat white and without lines. Placentae thin, attached to median line of septum. Seeds finely reticulate.

Leaves tapering to the narrow base. Stem pilose with spreading white hairs. 3. *C. axillaris.*

Leaves rounded-clasping at base. Stem appressed-pubescent or glandular-dotted.

Corolla deciduous, white throughout, its posterior lobes united nearly to apex. Exterior sepals rounded, all glabrous or obscurely puberulent. Stem whitish with appressed reflexed hairs. 4. *C. appressa.*

Corolla persistent, lobes violet-blue, its posterior lobes united only three-fifths length. All sepals acute, each with a tuft of white hairs at apex. Stem yellowish with sessile glands. 5. *C. conferta.*

1. **Caconapea auriculata** (Rob.) Pennell, comb. nov.

*Herpestis auriculata* Rob. in Proc. Am. Acad. 26: 172. 1891. "Wet places near Guadalajara [Mexico]; November, 1889 [C. G. Pringle] (n. 2937)." Later collections of Pringle from near Guadalajara, 4623 and 6148, seen in herbarium of Columbia University at The New York Botanical Garden.

*Bacopa auriculata* (Rob.) Greenm. in Field Col. Mus., Bot. Ser. 2: 262. 1897.

Stem 1–3 dm. tall, sharply four-angled, glabrous to slightly puberulent above. Leaves 1–1.7 cm. long, .5–.8 cm. wide, oblong-lanceolate, crenate, often dentate at and near base, obtuse, rounded-clasping at base; glabrous or glabrate. Pedicels solitary, 5–10 mm. long, puberulent. Bractlets linear-subulate, less than 1 mm. long. Sepals obscurely puberulent: outermost 4 mm. long, ovate, obtuse to acute, obscurely veined; two median slightly shorter and more narrowly ovate; two innermost 3 mm. long, linear-attenuate, somewhat hyaline. Corolla 7 mm. long; posterior lobes united nearly to apex; pubescent within tube, especially on anterior side, pubescent in horizontal line over bases of posterior lobes; within tube yellow, extending to base of anterior lobes, distally and over lobes violet-blue, with longitudinal fine deep-violet lines. Filaments glabrous, the postero-lateral pair slightly shorter, its anthers equalling those of the antero lateral pair; posterior filament represented by a tiny knob. Style glabrous, at apex bifid and bearing two plate like stigmas. Capsule 2.5–3 mm. long, globose-ovoid, glabrous, dehiscing septicidally, the lateral portions of the septum adhering to the capsule wall. Placentae protruding into the cells, not coalescent. Seeds .4 mm. long, crescentic-cylindric, truncate at the apex, brown, with evident longitudinal lines and cross-reticulations.

Wet open soil, sandy or loam, at altitudes of 500 to 800 meters, Tropical zone, llanos of upper Magdalena valley. Doubtless in the Sabina of Bolívar and elsewhere in northern Colombia. Ranges northward to Mexico.

Cundinamarca. Melgar (moist open clayey loam, alt. 500–600 m.), Pennell 2885.

Huila. Neiva (seepy place in plain, alt. 550–600 m.), Rusby & Pennell 1067.

Tolima. San Lorenzo (open springy loam, w. of, alt. 600–800 m.), Pennell 3531.

**2. Caconapea debilis** Pennell, sp. nov.

Stems ascending, repent and matted below, becoming erect and .3–.5 dm. tall, obscurely four-angled, finely pubescent with reflexed appressed white hairs. Leaves .4–.6 cm. long, .07–.1 cm. wide, linear, obtuse, clasping (but not dilated) at base, nerveless beneath; finely pubescent on the midrib beneath or glabrous throughout. Pedicels solitary, 5–7 mm. long, finely pubescent with reflexed hairs. Bractlets linear-subulate, less than .5 mm. long. Sepals: outermost 3.5 mm. long, linear-lanceolate obtuse; two median slightly shorter but nearly similar, these three green, glabrous or nearly so, except for a frequent terminal tuft of short hairs; the two innermost 3 mm. long, lanceolate-linear, acuminate, with broad scarious margins and ciliate with minute white hairs. Corolla 5 mm. long; posterior lobes united nearly to apex; externally minutely pubescent, within slightly pubescent over bases of the posterior lobes, elsewhere glabrous; within tube pale, yellowish on anterior side, lined with violet, distally over lobes violet. Filaments glabrous, the postero-lateral pair shorter, its anthers more than twice larger than those of the antero-lateral pair. Style glabrous, with two plate-like stigmas. Capsule 2 mm. long, oblongpyriform, rounded and retuse at apex, glabrous, dehiscing loculicidally. Placentae thin, linear, flattened against the persistent septum. Seeds about .2 mm. long, oval, slightly crescentic, yellowish-brown, obscurely ridged to somewhat reticulate at maturity.

Type, shallow pool in llano, east of Villavicencio, Meta, altitude about 450 meters, collected in flower and fruit September 2, 1917, F. W. Pennell 1623 in herbarium New York Botanical Garden.

Nearest to *Herpestis reptans* Benth. of Brazil, which is described as having leaves .2–.3 cm. wide, linear-lanceolate, prominently nerved beneath, all sepals obtuse and seeds yellow.

Shallow pools in llano, at an altitude of 450 meters, Tropical zone in Meta.

3. **Caconapea axillaris** (Benth.) Pennell, comb. nov.

*Herpestis axillaris* Benth. in DC. Prod. 10: 396. 1846. "Ad aquas stagnantes in campis Deluvia Sanctae Marthae (Purdie!) . . . (v. in herb. Hook.)."
*Monniera axillaris* (Benth.) Kuntze, Rev. Gen. 463. 1891.

Tropical zone, in Magdalena. No specimens seen.

4. **Caconapea appressa** Pennell, sp. nov.

Stem .7–1.5 dm. tall, obscurely four-angled, below glabrous, above pubescent with reflexed white hairs. Leaves 1–2 cm. long, .3–.4 cm. wide, lanceolate-linear, entire, tapering from the rounded-clasping base, glabrous, glandular-dotted. Pedicels 1–5 in an axil, 1–2 mm. long, pubescent with reflexed hairs. Bractlets filiform-subulate, less than 1 mm. long. Sepals glabrous, densely glandular-punctate: outermost 3 mm. long, ovate; the next nearly as wide, the median one-sided, narrower, these three obtuse, somewhat reticulate, glabrous; the two innermost narrowly lanceolate, attenuate, costate, with the margins hyaline and ciliolate. Corolla 2–2.5 mm. long; posterior lobes united nearly to apex; glabrous throughout; white throughout. Filaments glabrous, the postero-lateral pair slightly shorter and its anthers slightly smaller. Style glabrous, bearing two approximate stigmas. Capsule 2 mm. long, narrowly cylindric oblong, glabrous, dehiscing septicidally and loculicidally, none of the septum adhering to the capsule wall. Placentae narrow, thin, a little raised line median to the persistent broad septum. Seeds .5 mm. long, cylindric, tapering to each end, brown, with longitudinal ridges and fine cross lines.

Type, moist depression in llano east of Villavicencio, Meta, altitude about 450 meters, collected in flower and fruit, August 28 and September 2, 1917, F. W. Pennell 1460, in herbarium New York Botanical Garden.

Moist soil, in llanos, at an altitude of 450 meters, Tropical zone, in Meta.

5. **Caconapea conferta** Pennell, sp. nov.

Stem .5–1.8 dm. tall, obscurely four-angled, below glabrous, above puberulent with sessile yellowish glands. Leaves 1–2 cm. long, .2–.4 cm. wide, narrowly lanceolate, tapering from the rounded-clasping base, entire, densely glandular-dotted. Pedicels 1–5 in an axil, less than 1 mm. long, puberulent with sessile glandular dots. Bractlets filiform-subulate, less than 1 mm. long. Sepals densely glandular-puberulent, each tipped with a tuft of white hairs: outermost 3 mm. long, narrowly ovate; two median narrower and one-sided, these three acuminate; two innermost 2.5 mm. long, lanceolate-attenuate, somewhat hyaline-margined and more ciliolate. Corolla 3 mm. long; posterior lobes united $\frac{3}{5}$ length; glabrous throughout; its tube white, lobes violet-blue, darker distally within. Filaments glabrous, bluish, the postero-lateral pair slightly shorter; anthers all of about the same size, light-yellow. Style glabrous bearing two stigmas. Capsule 2 mm. long, ellipsoid-oblong, glabrous, dehiscing septicidally and loculicidally, none of the septum adhering to the capsule-wall. Placentae narrow, thin, median to the persistent broad septum. Seeds .3 mm. long, cylindric, slightly irregularly curved, rounded, brown, with fine longitudinal ridges.

Type, moist depression, in llano east of Villavicencio, Meta, altitude about 450 meters, collected in flower and fruit August 28 and September 2, 1917, F. W. Pennell 1435; in herbarium New York Botanical Garden.

Moist soil in llanos, at an altitude of 450 meters, Tropical zone, in Meta.

### 4. CONOBEA Aublet.

*Conobea* Aubl., Hist. Pl. Guiane Fr. 2: 639. pl. 258. 1775.

Type species, *C. aquatica* Aubl., of Guiana.

1. **Conobea scoparioides** (C. & S.) Benth.

*Sphaerotheca scoparioides* Cham. & Schlechtd. in Linnaea 2: 606. 1827.
"E Brasilia aequinoctiali misit Sellow."
*Conobea scoparioides* (C. & S.) Benth. in DC. Prod. 10: 391. 1846.

Tropical zone, collected only in Choco, but doubtless widespread in northern and eastern Colombia. Widespread through eastern lowland South America.

Choco. Novisa, J. Triana (H, Y).

### 5. GRATIOLA Linné.

*Gratiola* L., Sp. Pl. 17. 1753.

Type species, *G. officinalis* L., of Europe.

1. **Gratiola bogotensis** Cortés, sp. nov.

Spreading extensively by rootstocks. Aerial stems erect or decumbent at base, succulent, slightly puberulent, 1–4 dm. tall. Leaves oblong-lanceolate, 1.5–2.5 cm. long, .3–.8 cm. wide, clasping by a rounded base, distally dentate and glandular-punctate, finely puberulent to glabrate. Pedicels 1–2 mm. long. Bractlets similar to and equaling or slightly exceeding the lanceolate calyx-lobes, 5–10 mm. long. Corolla 12–14 mm. long, its tube four-angled, yellowish, with fine brown lines, its lobes spreading, white, somewhat pinkish-tinged or at times the corolla strongly pink. Antero-lateral filaments evident, each capped by two small rudimentary anthers. Capsule ovoid, 5 mm. long. Seeds .5 mm. long, obovoid, conspicuously alveolate-reticulate.

Type, wet grassy place, base of mountain above Chapinero, near Bogotá, Cundinamarca, altitude 2700–2800 meters, collected in flower and fruit September 23, 1917, Pennell 2108 in Herb. New York Botanical Garden. This was collected in company with Sr. Santiago Cortés, who designated it by the name here given.

A near ally or possibly geographical variety, of *Gratiola peruviana* L., Sp. Pl. 17. 1753, based upon Feuillée's description and drawing of a plant found in the mountains of Chile, at 26° S. L. Feuillée's plant is well-matched by a specimen collected by Otto Kuntze in February, 1892, at Ervilla, Chile, and which has the stem less fleshy, the leaves broader and the pedicels slightly longer than does our plant.

Wet grassy places, springheads and ditches. at altitudes of 2600 to 3200 meters, Temperate zone, ascending, in dwarf form, to Paramo, Cordillera Orientál, and Cordillera Centrál, southward at least into Ecuador.

Cundinamarca. Bogotá (ditch in meadow, alt. 2600 m.), Pennell 1908, (wet grassy place near Chapinero, alt. 2700–2800 m.) Pennell 2108, (southwest of Las Cruces, open spring-head, alt.

2600–2700 m.) Pennell 2158; Sibaté (wet loam, alt. 2700–2800 m.), Pennell 2451; Ubaqué (wet ditch, edge of paramo, alt. 3000–3200 m.), Pennell 1902, Zipaquirá (Mt. Aquila, edge of pool, just below paramo, alt. 3100 m.), Pennell 2532.

Nariño. Tuquerres (alt. 3000 m.), Triana (H, Y).

Tolima. Murillo (pool, alt. 2600–2800 m.), Pennell 3155.

### 6. **MONOCARDIA**[6] Pennell, gen. nov.

Stems much branched, terete, repent, the apices ascending. Leaves sessile, slightly clasping, oblong to orbicular, entire, palmately-veined from base, obscurely glandular-dotted and not odorous. Pedicels axillary, 6–20 mm. long, pubescent, not bracteolate. Calyx of 5 very dissimilar sepals; outermost (posterior) heart-shaped; two antero-laterals smaller, obliquely, or but one-half cordate- or truncate-ovate, three outer prominently reticulate; two postero-laterals (innermost) linear-attenuate, only ⅔ length of outermost and usually slightly longer than the capsule. Corolla 3–7 mm. long, the widely-spreading lobes longer than the tube, the two posterior lobes united nearly throughout; glabrous throughout, blue or white. Stamens four, glabrous, didynamous (the posterior filaments shorter and usually anthers smaller); anthers uniform, the narrow sacs closely connivent, each opening its entire length. Style glabrous, little exceeding the sepals. Stigmas distinct, flat. Capsule 2–4 mm. long, much shorter than calyx, oblong or ovoid-oblong, acute, brown, septicidal and loculicidal; the septum with adherent thin placentae, persisting plate-like. Seeds .2–.3 mm. long, oblong, blackish-brown, ridged and with cross-reticulations.

Type species, *M. violacea* Pennell.

*Hydrotrida* Small, in general aspect like this genus, differs in possessing a circle of bristles surrounding the ovary, pubescence within over the bases of the corolla-lobes, two bracteoles below the calyx, and more conspicuous glands which exhale a strong aromatic odor.

Pedicels and sepals with spreading hairs. Stems and leaves beneath pubescent. Corolla blue.
  Corolla 6–7 mm. long. Calyx 5–7 mm. long. Leaves 1.2–1.8 cm. long, and nearly as wide. Stems densely hirsute, 2–3 dm. long. 1. *M. violacea.*
  Corolla 4–5 mm. long. Calyx 4–6 mm. long. Leaves .7–1.8 cm. long, ovate-oblong. Stems pubescent, less than 1.5 dm. long.

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[6] Name from μόνος, one, and καρδία, heart, in allusion to the single large cordate sepal.

Leaves 1.2–1.8 cm. long, the younger pubescent along midrib beneath. Sepals 5–6 mm. long. 2. *M. lilacina.*
Leaves .7–.9 cm. long, the younger pubescent over the entire surface beneath. Sepals 4–5 mm. long. 3. *M. humilis.*
Plant glabrous throughout. Corolla white, 3–3.5 mm. long. 4. *M. albida.*

**1. Monocardia violacea** Pennell, sp. nov.

Stems fleshy, 2–3 dm. long or longer, densely hirsute with yellowish hairs. Leaves ovate- or oval-orbicular, 1.2–1.8 cm. long, 1–1.4 cm. wide, obtuse, pubescent beneath along midrib proximally, distally glabrous and obscurely reticulate. Pedicels 10–20 mm. long, hirsute with spreading hairs. Sepals all ciliate: the three outer 5–7 mm. long, the innermost pubescent on the midrib. Corolla 6–7 mm. long; tube yellow, distally purplish, the lobes violet. Filaments violet-bluish; anthers white. Capsule 3–4 mm. long, narrowly oblong. Seeds .3 mm. long, brown.

Type, wet loam, along trail in forest, near Villavicencio, Meta, altitude 450 meters, collected in flower and fruit August 28, 1917, F. W. Pennell 1480; in Herb. New York Botanical Garden. Only specimen seen.

Wet loam in forest at an altitude of 450 meters. Tropical zone, in Meta, and in Panama. Doubtless wide-spread in northern South America.

**2. Monocardia lilacina** Pennell, sp. nov.

Stems slightly fleshy, .5–1.5 dm. long, pubescent with spreading hairs. Leaves ovate-oblong, 1.2–1.8 cm. long, .8–1.1 cm. wide; obtuse, pubescent beneath along midrib proximally. Pedicels 8–12 mm. long, pubescent with spreading hairs. Sepals all ciliate: the three outer 5–6 mm. long, two innermost pubescent on the midrib, shorter. Corolla 4–5 mm. long, violet within throat, the lobes pale-blue. Filaments of anterior stamens pale-blue, of posterior violet; anthers pale-blue. Capsule 2.5–3 mm. long, ovoid-oblong. Seeds .2–.25 mm. long, blackish.

Type, wet loam, along trail in forest, near Villavicencio, Meta, alt. 450 meters, collected in flower and fruit August 28, 1917. F. W. Pennell 1476; in Herb. New York Botanical Garden.

Wet loam in forest, at altitudes of 450 to 500 meters, Tropical zone, in Meta.

Meta. Villavicencio (wet trail in forest, alt. 500 m.), Pennell 1378, (alt. 450 m.), Pennell 1476, (wet place near Rio Guatiquia, alt. 500 m.), Pennell 1547.

3. **Monocardia humilis** Pennell, sp. nov.

Stems not fleshy, .2–1 dm. long, pubescent with spreading hairs. Leaves ovate-oblong, .7–.9 cm. long, .3–.8 cm. wide, obtuse, at least when young hirsute over entire under surface, not evidently reticulate. Pedicels 6–9 mm. long, pubescent with spreading hairs. Sepals all ciliate: the three outer 4–5 mm. long, pubescent over entire outer surface. Corolla 4–5 mm. long, violet within throat, the lobes pale-blue. Filaments of anterior stamens pale-blue, of posterior violet; anthers pale-blue. Capsule 2–3 mm. long, ovoid-oblong. Seeds .2–.25 mm. long, blackish.

Type, sandy soil, seepy place in plain east of Neiva, Huila, alt. 550–600 meters, collected in flower and fruit August 8, 1917, Rusby & Pennell 1065; in Herb. New York Botanical Garden.

Wet open soil, sandy or loam, at altitudes below 800 meters, Tropical zone, llanos of upper Magdalena valley, and in Panama. Doubtless in the Sabana of Bolívar.

Huila. Neiva (sandy seepy place in plain east of N., alt. 550–600 m.), Rusby & Pennell 1065.

Tolima. San Lorenzo (swale west of S. L., alt. 600–800 m.), Pennell 3544.

4. **Monocardia albida** Pennell, sp. nov.

Stems not fleshy, .3–1.5 dm. long, glabrous. Leaves ovate-oblong, .7–1.5 cm. long, .3–1 cm. wide, obtuse, glabrous. Pedicels 7–14 mm. long, glabrous. Sepals glabrous: the three outer 4–5 mm. long. Corolla 3–3.5 mm. long, dull white throughout. Filaments and anthers white. Capsule 2–3 mm. long, narrowly elliptic-oblong. Seeds .2–.3 mm. long, blackish.

Type, wet loam, trail in forest, Villavicencio, Meta, alt. 450 meters, collected in flower and fruit August 28, 1919, F. W. Pennell 1477; in Herb. New York Botanical Garden.

Wet loam in forest at altitudes of 450 to 500 meters, Tropical zone, in Meta.

Meta. Villavicencio (wet trail in forest, alt. 450 m.), Pennell 1477, (moist meadow near Rio Guatiquia, alt. 500 m.), Pennell 1555 (plant much smaller than 1477).

### 7. MACUILLAMIA Rafinesque.

*Macuillamia* Raf. [Neogenyton 2.1825, generic description only.] Autik. Bot. 44, 1840.

Type species, *Monniera rotundifolia* Mich., of Illinois.

1. **Macuillamia limosa** Pennell, sp. nov.

Extensively repent. Stem slightly succulent, finely pubescent rather densely so distally. Leaves 1.2–1.7 cm. long, 8–10 mm. wide obovate-elliptic, entire, narrowed at base, rounded at apex, with 7 or 9 longitudinal veins. Pedicels slender, 10–15 mm. long, finely pubescent, in flower ascending, soon reflexing below the leaf-like bracts. Sepals 2.5–3 mm. long, obtuse, somewhat pubescent; two outer ovate-oblong; two median lanceolate-oblong; the innermost one narrower or wanting. Corolla 4 mm. long, the lobes spreading, slightly longer than the tube, the two posterior united to apex; glabrous throughout, white. Filaments white. Anthers purplish. Styles distinct near apex; stigmas semi-capitate. Capsule 2–2.5 mm. long, nearly globose, obtuse. Seeds .6 mm. long, cylindric-oblong, reticulate, brown.

Type, open pool in clayey loam, Melgar, Cundinamarca, altitude 400–500 meters, collected in flower and fruit December 4–5, 1917, F. W. Pennell 2927; in Herb. New York Botanical Garden.

Open pools and ditches, in shallow still water, at altitudes below 500 meters, Tropical zone, in the Magdalena and Cauca valleys, and doubtless through northern Colombia. Ranges northward to Mexico.

Antioquia. Puerto Berrio (shallow water, alt. 125–135 m.), Rusby & Pennell 32.

Cundinamarca. Melgar (pool in clayey loam, alt. 400–500 m.), Pennell 2927.

Tolima. Espinal to Cuamo (ditch, loam, alt. 350–400 m.), Rusby & Pennell 179.

Valle. La Paila, I. F. Holton 581 (H, Y).

### 8. HYDRANTHELIUM Humboldt, Bonpland and Kunth.

*Hydranthelium* H. B. K., Nov. Gen. et Sp. 7: 202. pl. 646. 1825.

Type species, *H. callitrichoides* H. B. K., of Venezuela.

1. **Hydranthelium braunii** Ernst.

*Hydranthelium braunii* Ernst, in Vargasia 1: 189. 1870.

"Hallé el 19 de Setiembre de 1869 en uno de los pozos de la sabana delante el camposanto de la Merced [Caracas]," Venezuela.

Open wet soil, at an altitude of 30 meters, Tropical zone, in Magdalena; doubtless eastward near the Caribbean coast through Venezuela.

Magdalena. El Libano plantation, (Santa Marta region, open land on border of swamp and flooded during heavy rains, alt. 30 m.),

H. H. Smith 2544 (C, H, U, Y). (Plants small, largest .8 dm. long, and in flower only, youngest leaves slightly undulate-lobed.)

### 9. SCOPARIA Linné.

*Scoparia* L., Sp. Pl. 116. 1753.

Type species, *S. dulcis* L.

1. **Scoparia dulcis** L.

*Scoparia dulcis* L., l. c. 116. 1753. "Habitat in Jamaica, Curassao"; ex L., Hort. Cliff. 320. 1737. "Crescit in Curassao & Jamaica." No specimens from Curaçao seen but the plant here considered unquestionably occurs there.
*Capraria dulcis* (L.) Kuntze, Rev. Gen. 459. 1891.

Open soil, loam or sand, river-banks, fields, along trails and in towns, at altitudes below 1500 meters, Tropical zone, doubtless throughout lowland Colombia. Ranges throughout Tropical America, a weed of South American origin.

Antioquia. Vuelta de Acuña on Rio Magdalena (sandy loam shore, alt. 125–130 m.), Pennell 3790.

Bolívar. Boca Verde on Rio Sinu (cacaotale, alt. 90–120 m.), Pennell 4233; Buenavista, east of Sincé (open grassy place), Pennell 3991; Calamar (along Rio Magdalena, alt. 15–25 m.), Rusby & Pennell 17; Vilches on Rio Sinu (loam, alt. 20–50 m.), Pennell 4713.

Cundinamarca. Girardot (field, alt. 350–400 m.), Rusby & Pennell 113; Pandi (open slope, alt. 900–1100 m.), Pennell 2816.

Huila. Cordillera Oriental, east of Neiva (open foot-hill, alt. 700–1500 m.), Rusby & Pennell 460.

Magdalena. Bonda (alt. 45 m., common weed in open places below 900 m.), H. H. Smith 1330 (C, H, U, Y).

Meta. Villavicencio (streets, alt. 525 m.), Pennell 1372, (roadside, alt. 500 m.), Pennell 1572.

Tolima. Libano (field, alt. 700–900 m.), Pennell 3426.

Valle. La Paila, I. F. Holton 587 (Y).

### 10. STEMODIA Linné.

Type species, *S. maritima* L., of Jamaica.

*Stemodia* L., Syst. Nat. ed. X, 1118. 1759.

1. **Stemodia durantifolia** (L.) Sw.

*Capraria durantifolia* L., Syst. Nat. ed. X. 1116. 1759. ". . . Sloan. Jam. t. 174." Ex Sloane, Jam. 196. pl. 124. f. 2: "Grows in the sandy savannas [of Jamaica]."
*Stemodia durantifolia* (L.) Sw., Obs. Bot. 240. 1791.
*Stemodacra durantifolia* (L.) Kuntze, Rev. Gen. 466. 1891.

Occurs in two color-forms, blue, and lavender or "pale-pink."

River-flats and moist, or frequently desiccated, ditches, in open land, at altitudes below 500 meters, Tropical zone, near the Caribbean Coast, along the Rio Magdalena, and on the Sabana of Bolívar. Ranges from Mexico to Brazil and in the West Indies.

Antioquia. Brazuela de Perales (river flat along Rio Magdalena, alt. 150 m.), Pennell 3698 [corolla blue].

Bolívar. Cartagena (moist arroyo, 12 km. s. e. of C., alt. 50–100 m.), Pennell 4729 [corolla blue], (open ditch, 14 km. s. e. of C., alt. 50–100 m.), Pennell 4730 [corolla lavender]; Sincé (desiccated pool in prairie, alt. 120–170 m.), Pennell 4047 [corolla lavender].

Huila. Quebrada de Angeles, above Natagaima (alt. 450–500 m.), Rusby & Pennell 263 [corolla blue].

Magdalena. Carpentiera (along Rio Magdalena, alt. 50–60 m.), Rusby & Pennell 28; Mamatoca (open boggy ground, 5 m. s. of M., alt. 30 m.), H. H. Smith 1360 (C, H, U, Y) [corolla pale pink].

### 11. **UNANUEA** (Ruiz and Pavon.) gen. nov.

*Unanuea* R. & P., (Ic. Fl. Per. Ined.),

Erect, much-branhed shrubby herbs or low shrubs, at least 8–10 dm. tall. Stems 4-angled. Leaves mostly whorled in threes, lanceolate to ovate, acute to acuminate, serrate to dentate, shortly petioled. Pedicels axillary, slender, as long as or longer than the calyces, not bracteolate. Sepals five, uniform, linear to lanceolate, entire. Corolla 9–13 mm. long, tubular-campanulate with spreading lobes, the posterior united three-fourths length; externally puberulent, within glabrous, purple-blue. Stamens four, didynamous (the posterior filaments shorter), glabrous, anthers-sacs elliptic, each stalked on a short arm of the connective. Style glabrous. Stigmas distinct, flattened. Capsule brown, ovate in outline, acuminate, dehiscent septicidally (even through septum) and slightly also loculicidally; placentae adherent to septum, roughened by funicles. Seeds oblong, minutely roughened-tubercular.

Differs from *Stemodia* L., which has corolla-lobes not widely spreading, pubescent or glabrous within on the anterior side, two bracteoles on the pedicel beneath the calyx, and the leaves sessile and clasping; from *Lendneria* Minod, which are herbs low and spreading, with smaller corollas densely pubescent within over the bases of the posterior lobes and with evidently petioled leaves. Both *Stemodia* and *Lendneria* are genera of the Tropical life-zone, while *Unanuea* is of the Subtropical and Temperate zones.

Type species, *Stemodia suffruticosa* H. B. K., of Ecuador.

1. **Unanuea dentata** (Minod) Pennell, comb. nov.

*Stemodia suffruticosa* H. B. K., f. *dentata* Minod in Bull. Soc. Bot. Genéve ser. II. 10: 201. 1918. "In Andibus Ecuadorensibus (R. Spruce, n. 5066!)." Isotype seen in Gray Herbarium of Harvard University.

At an attitude of 2600 meters, Temperate zone, southern Cordillera Centrál southward into Ecuador.

Cauca. Mozoco, Moras Valley, Tierra Adentro (alt. 2600 m.), H. Pittier 1326 (U). ["A shrub, 1 m. high; fl. deep purple."]

### 12. LENDNERIA Minod.

*Lendneria* Minod, in Bull. Soc. Bot. Genéve, ser. II. 10: 240. 1918.

Type species, *Capraria humilis* Soland.

Pedicels 1–2 mm. long. Corolla 4 mm. long, its lobes blue, the posterior united two-thirds length. Hairs within corolla over base of posterior lobes not knobbed. Anther-sacs circular, slightly separated on very short connective-arms. Capsule globose, 2 mm. long, much shorter than the sepals. Seeds pale yellowish, nearly cylindric. 1. *L. humilis.*

Pedicels longer, mostly 7–20 mm. long. Corolla 8 mm. long, its lobes white, the posterior united nearly to apex. Hairs within corolla over base of posterior lobes knobbed. Anther-sacs oblong, distinctly separated on stout connective-arms. Capsule in outline oblong-ovate, 4–5 mm. long, about equaling the sepals. Seeds brown-black, nearly oblong. 2. *L. angulata.*

1. **Lendneria humilis** (Soland.) Minod.

*Capraria humilis* [Soland. in] Ait., Hort. Kew. 2: 354. 1789. "Nat. of the East Indies. John Gerard Koenig, M.D. Introd. 1781, by Sir Joseph Banks, Bart." Identified by Bentham in DC. Prod. 10: 383. 1846, as species here considered, his determination with an "!" Our plant has been occasionally reported as an introduction into the Old World Tropics.

*Stemodia parviflora* Ait., Hort. Kew., ed. II. 4: 52. 1812. "Nat. of South America. Cult. 1759 by Mr. Ph. Miller." Miller's plant was derived from Houston who collected at Cartagena in Colombia as well as in Mexico and the West Indies. The original introduction of Houston, published as *Erinus verticillatus* Mill., Gard. Dict. n. 5. 1768, differs so essentially from the account of Aiton's plant, especially in denoting a plant with glabrous stems and leaves, as to lead to the supposition that the latter was described from specimens of a different origin.

*Stemodia arenaria* H. B. K., Nov. Gen. et Sp. 2: 357. pl. 175. 1818. "Crescit in ripa inundata fluminis Magdalenae prope Banco et El Peñon inter Mompox et Morales."

*Lendneria humilis* (Solander) Minod in Bull. Soc. Bot. Genéve, ser. II. 10: 240. 1918.

Corolla-tube yellowish, lobes blue-violet, tube and lobes, especially on the posterior side, with deep violet lines. Seen also (Pennell 4709) with corolla very pale, a distinct color-form.

Moist soil, river-banks and waste-land, frequently a weed near habitations, at altitudes below 200 meters, Tropical zone, along the

Rio Sinu in Bolívar, the Rio Cauca in Valle, and the Rio Don Diego in Magdalena; doubtless wide-spread elsewhere. Ranges from Mexico to Argentina and in the West Indies.

Bolívar. Boca Verde, on Rio Sinu (gravelly river-bank, alt. 90–120 m.), Pennell 4197, (field along river, alt. 100–200 m.), Pennell 4567; Frasquillo, on Rio Sinu (grove along river in village, alt. 90–120 m.), Pennell 4610; Vilches, on Rio Sinu (shaded yard, alt. 20–50 m.), Pennell 4708 [corolla blue], 4709 [corolla pale-blue], 4710 [corolla intermediate in color between 4708 and 4709].

Magdalena. Open sandy ground by the Rio Don Diego, near the sea, H. H. Smith 2730 (Y).

Valle. La Paila, I. F. Holton 580 (H, Y).

2. **Lendneria angulata** (Oersted) Pennell, comb. nov.

*Stemodia angulata* Oersted in Kjoeb. Vidensk. Meddel. 1853: 22. 1853. "I Naerheden af Cartago i Costa-Rica."

Certainly distinct from *Stemodia jorullensis* H. B. K., Nov. Gen. et Sp. 2: 358. 1818, which is described as 1–1½ feet tall and with leaves in threes, incised or doubly serrate.

Moist soil in shade, river-banks and waste land, at altitudes below 600 meters, Tropical zone, along the Rio Sinu in Bolívar, and in Magdalena; doubtless wide-spread in northern Colombia. Ranges northward to Guatemala.

Bolívar. Frasquillo, on Rio Sinu (shady soil along river, alt. 70–100 m.), Pennell 4192.

Magdalena. Minca (damp door-yard, in crevices of bricks, alt. 600 m.), H. H. Smith 1328 (C, H, U, Y).

### 13. VANDELLIA Browne.

*Vandellia* Browne; L., Mant. Pl. 1: 12, 89. 1767.

Type species, *V. diffusa* L.

1. **Vandellia diffusa** L.

*Vandellia diffusa* L., Mant. Pl. 1: 89. 1767. "Habitat in Insula S. Thomae. D. D. Browne." Description inaccurate in describing the calyx as quadripartite (but with upper lobe subbifid), its lobes equal, the lower lip of corolla as bilobed, and the capsules as one-celled, but is nevertheless certified by Bentham, DC. Prod. 10: 416. 1846 as being the plant here considered.

*Lindernia diffusa* (L.) Wettst. in Nat. Pflanzenfam. $4^{3b}$: 79. 1891.
*Pyxidaria diffusa* (L.) Kuntze, Rev. Gen.: 464. 1891.

Moist open soil, along trails and in towns, at altitudes below 1500 meters, Tropical zone; widely distributed through tropical America, in situations to suggest its having been naturalized. Apparently introduced from the Ethiopian Region of the Old World Tropics.

Cundinamarca. Icononzo (along trail in forest, alt. 1400–1800 m.), Pennell 2871.

Magdalena. River Don Diego (open sandy wet ground near sea, alt. 0–10 m.), H. H. Smith 2729 (H, Y).

Meta. Villavicencio (moist depression in llano, e. of, alt. 450 m.), Pennell 1466; (streets of town, alt. 525 m.), Pennell 1575, (gravel along Rio Guatiquia, alt. 500 m.), Pennell 1590.

Tolima. Mariquita (prairie, depression, alt. 250–300 m.), Pennell 3639.

### 14. TORENIA Linné.

*Torenia* L., Sp. Pl. 619. 1753.

Type species, *T. asiatica* L., of India.

Bracts leaf-like, the upper smaller; inflorescence an elongate raceme. Pedicels 20–25 mm. long. Sepals 4–5 mm. long. Corolla 5–7 mm. long, its posterior lobes united $\frac{2}{3}$–$\frac{4}{5}$ length and equaling the anterior; anterior lobes widely horizontally spreading; within glabrous, blue on posterior lobes and distally on anterior lobes, these yellowish-white proximally with an arch of deep-violet at the base of the anterior lobes. Capsule 3–4 mm. long, obtuse and mucronate. Leaves ovate, 1–1.5 cm. long. Plant repent-ascending. 1. *T. crustacea.*

Bracts minute, subulate; inflorescence congested at the nodes. Pedicels 10–15 mm. long. Sepals 9–11 mm. long. Corolla 8–9 mm. long, its posterior lobes united nearly to apex and shorter than the anterior lobes; antero-lateral lobes placed sagitally, the anterior lobe horizontal and longest; within pubescent over bases of anterior lobes, white or on anterior side somewhat blue-violet. Capsule 8–10 mm. long, acute. Leaves lanceolate-ovate, 1.2–2.5 cm. long. Plant ascending-erect.

Corolla on anterior lobe blue-violet, and on antero-laterals with blue-violet streaks. Leaves dentate. 2. *T. thouarsii.*

Corolla white throughout. Leaves crenate-serrate. 2a. *T. thouarsii nivea.*

**1. Torenia crustacea** (L.) Cham. & Schlecht.

*Capraria crustacea* L., Mant. 87. 1767. "Habitat in Amboina; China." Amboina plant, described by Rumphius, Herb. Amb. 5: 461. pl. 170 f. 3, verified by Dr. E. D. Merrill, Interp. Rumph. Herb. Amb. 468, as the plant here considered.

*Torenia crustacea* (L.) C. & S. in Linnaea 2: 570. 1827.

*Vandellia crustacea* (L.) Benth., Scroph. Ind. 35. 1835.

*Lindernia crustacea* (L.) F. Muell., Census 97. 1882.

*Pyxidaria crustacea* (L.) Kuntze, Rev. Gen. 2: 464. 1891.

Moist open soil, along trails and in towns, at altitudes of 500 to 600 meters, Tropical zone; introduced from Oriental Region of Old World Tropics.

Cundinamarca. Melgar (moist loam, open slope, along trail, alt. 500–600 m.), Pennell 2878, 2879 [form smaller throughout].

Meta. Villavicencio (streets and yards, alt. 525 m.), Pennell 1527.

2. **Torenia thouarsii** (Cham. & Schlecht.) Kuntze.

> *Nortenia thouarsii* Cham. & Schlecht. in Linnaea 3: 18. 1828. "In Brasiliae provincia Rio Janeiro in uliginosis post Botafoginam . . . legit Beyrich, in insulis Madagascaria et Mauritii Depetit Thouars. . . . Willd. Hb. n. 11,547 (planta madagascariensis a Thouarsii comm.)."
> *Torenia nortenia* Steud., Nom., ed. II. 2: 692. 1841.
> *Torenia thouarsii* (Cham. & Schlecht.) Kuntze, Rev. Gen. 468. 1891.

This has usually been known as *Torenia parviflora* Ham.

Moist banks, in edge of forest, at an altitude of 500 meters, Tropical zone; wide-spread through lowland tropical South America, growing as if a native plant. However, as this American plant appears to be indistinguishable from the plant of the Old World, and the remaining species of the genus are all Palaetropic it appears nearly certain that our plant is an introduction. From the Ethiopian and Oriental regions of the Old World Tropics.

Meta. Villavicencio (moist shaded bank near Rio Guatiquia, alt. 500 m.), Pennell 1528, (moist meadow and swamp in forest, near Rio Guatiquia, alt. 500 m.), Pennell 1560.

2a. **Torenia thouarsii nivea** Pennell, var. nov.

Leaves smaller, 1.2–1.5 cm. long, crenate-serrate, rather than dentate. Corolla white throughout. Probably a color-form identical with plants of the Old World Tropics and introduced therefrom.

Type, wet sand along Rio Guatiquia, altitude 500 meters, collected in flower and fruit August 30, 1917, F. W. Pennell 1531; in herbarium New York Botanical Garden.

### 15. ILYSANTHES Rafinesque.

*Ilysanthes* Raf., Ann. Nat. 13. 1820.

Type species, *I. riparia* Raf., of the Ohio.

1. **Ilysanthes inaequalis** (Walt.) Pennell.

> *Gratiola inaequalis* Walt., Fl. Carol. 61. 1788. [South Carolina.]
> *Ilysanthes inaequalis* (Walt.) Pennell in Torreya 19: 149. 1919.

Wet soil near streams, at an altitude little above sea-level, Tropical zone, in Magdalena. Probably wide-spread, and also in the

Subtropical and Temperate zones. Through lowland South America south to Paraguay; ranges northward into Temperate North America.

Magdalena. Rio Buritaca (observed only in a swampy place, bank of R. B., close to the sea—50 m. e. of Santa Marta), H. H. Smith 1329 (C, H, U, Y).

### 16. SCHISTOPHRAGMA Bentham.

*Schistophragma* Benth. in DC. Prod. 10: 392. 1846

Type species, *S. pusilla* Benth.

1. **Schistophragma pusilla** Benth.

*Schistophragma pusilla* Benth. in DC. Prod. 10: 392. 1846. "In Mexico pr. Tehuantepec (Alaman!) . . . (v. s. comm. a. cl. DC.)." Description from a dwarf plant, which explains the variety following.
*Schistophragma pusilla major* Benth., l. c. 392. 1846. "In campis aridis pr. Sta Martha (Purdie!) . . . (v. in herb. Hook.)."
*Conobea pusilla* (Benth.) B. & H., Gen. 2: 951. 1876.

Open dry, stony soil, at altitudes below 300 meters, Tropical zone, in Magdalena, and doubtless spread across northern Colombia. Ranges northward to Mexico.

Magdalena. Bonda (alt. 60 m.), H. H. Smith 1970 (C, H, U, Y).

["Rare on open, stony and dry ground, hillsides or banks below 1000 f."]

### 17. MIMULUS Linné.

*Mimulus* L., Sp. Pl. 634. 1753.

Type species, *M. ringens* L., of Virginia.

1. **Mimulus glabratus** H. B. K.

*Mimulus glabratus* H. B. K., Nov. Gen. et Sp. 2: 370. 1818. "Crescit prope Moran Mexicanorum, alt. 1330 hex. [= 2527 m.]. Varies, even in same colony, with leaves obviously petioled or nearly sessile, and with all parts of the plant, including the flower, relatively large or relatively small. The latter state is doubtless the basis of *M. andicola* H. B. K. from Ecuador.

Corolla lemon-yellow, within throat on anterior side golden and spotted with many red-brown spots.

Along streams, springheads, swales and brooks, at altitudes of 2300 to 3200 meters, Temperate zone, ascending as a dwarfed plant to Paramo, and descending rarely into the Subtropical zone, both slopes of Cordillera Oriental, in Cundinamarca. Doubtless throughout this and the other Cordilleras. Ranges through the Andes southward to Bolivia and with many breaks, through the mountains of Central America and Mexico, northward to Colorado and the plains of North Dakota.

Cundinamarca. Bogotá (ditch in field near Rio San Cristobal, alt. 2800 m.), Pennell 2194, 2279, (wet open spring-head, alt. 2700–2800 m.), Pennell 2296; Chipaque (wet roadside, alt. 2300–2400 m.), Pennell 1326; Sibaté (wet roadside, alt. 2620 m.), Pennell 2387; Zipaquirá (springhead in meadow, alt. 2650 m.), Pennell 2533; Mt. Chuscal, west of Zipaquirá (swale on paramo, alt. 3100–3200 m.), Pennell 2600; Guasca (alt. 2700 m.), Triana.

### 18. LEUCOCARPUS D. Don.

*Leucocarpus* D. Don in Sweet, Brit. Flow. Gard. II. pl. 124. 1831.

Type species, *Conobea alata* Graham, of Mexico.

1. **Leucocarpus perfoliatus** (H. B. K.) Benth.

*Mimulus perfoliatus* H. B. K., Nov. Gen. et Sp. 2: 371. 1818. "Crescit in Regno Novo-Granatensi. . . . A Mutisio cum Bonplandio communicatus." Described as with leaves connate, but this appearance has misled subsequent workers, including Bentham in his characterization of *Leucocarpus*. The plant actually has opposite cordate-clasping leaves.

*Leucocarpus perfoliatus* (H. B. K.) Benth. in DC. Prod. 10: 335. 1846.

This species has usually been called *L. alatus* (Graham) D. Don, based upon *Conobea alata* Graham (1830) of Mexico, a plant more carefully described and under an appropriate name. The character of length of calyx-lobes, used by Bentham, is of no significance, the lobes varying in the same specimens and usually seeming relatively longer when in the bud.

Corolla yellow throughout, with two pubescent ridges within throat anteriorly. Plant shrubby below, from a perennial root sending up a clump of many long densely floriferous stems. Fruit fleshy, chalky-white.

Along stream banks in forest, at altitudes of 1350 to 2000 meters, probably from all slopes of the Cordilleras, and also on the Sierra Nevada de Santa Marta. Subtropical zone. Ranges from Mexico to Bolivia. The seeds are doubtless carried by birds.

Huila. Cordillera Orientál, east of Neiva (along rocky stream in forest, alt. 1500–2000 m.), Rusby & Pennell 600.

Magdalena. Las Nubes (damp clearing near stream, alt. 1350 m.), H. H. Smith 1405 (C, H, U, Y).

Tolima (?). "Forets de Quindio" (2200 m.), J. Triana (U).

Valle. Jicaramata, "circum flumen Toluam", I. F. Holton 578.

### 19. ALONSOA Ruiz and Pavon.

*Alonsoa* R. & P., Syst. Veg. Fl. Peruv. et Chil. 150. 1798.

Type species, *A. caulialata* R. & P., of Peru.

Leaves coarsely serrate or dentate, the largest 5–6 cm. long. Corolla 10 mm. long. Filaments thick. Anthers infundibuliform-

explanate. Capsule 9–10 mm. long, narrowly ovoid, conspicuously attenuate. Seeds black, the furrows nearly as wide as the intervening ridges. Stem above, pedicels and calyces usually glabrous, rarely somewhat glandular-pubescent.
1. *A. meridionalis.*

Leaves uniformly serrate, the largest 8–9 cm. long. Corolla 5–6 mm. long. Filaments thin. Anthers widely and flatly explanate. Capsule 6 mm. long, pyramidal, shortly attenuate. Seeds dark-brown, the furrows much narrower than the intervening ridges. Stem above, pedicels and calyces glandular-pubescent, densely pubescent at the bases of the petioles.
2. *A. serrata.*

**1. Alonsoa meridionalis** (L. f.) Kuntze.

*Scrophularia meridionalis* L. f., Suppl. 280. 1781. "Habitat in Nova Granada. D. Mutis." Type probably from Bogotá.

*Hemimeris mutisii* H. B. K., Nov. Gen. et Sp. 2: 376. 1817. "Crescit prope Santa Fe de Bogota [Humboldt & Bonpland]."

*Alonsoa mutisii* (H. B. K.) G. Don, Gen. Syst. 4: 513. 1838.

*Alonsoa meridionalis* (L. f.) Kuntze, Rev. Gen. 2: 457. 1891. The plant of Venezuela noted by Kuntze, and described as so variable in color, is *A. parviflora* (H. B. K.) G. Don.

Corolla uniformly dull-orange. Filaments dull-yellow. Anthers yellow.

Waysides and grassy slopes, around the margins of the Sabana of Bogotá, on the western slope of the Cordillera Oriental; at altitudes of 2600 to 2900 meters. Temperate zone.

Cundinamarca. Zipaquirá, Pennell 2564 (Y); Bogotá, Holton (Y), Pennell 1309 (Y), Pennell 2099 (Y), Pennell 2332 (Y); (Plateau de Bogotá), J. Triana (Y); El Peñon, s. w. of Sibaté, Pennell 2410 (Y), [pedicels unusually glandular-pubescent].

**2. Alonsoa serrata** Pennell, sp. nov.

Stem 6 dm. tall, four-angled, angles slightly winged, stem glabrous below, glandular-pubescent above. Leaves opposite, 8–9 cm. long, the blades ovate, uniformly serrate, slightly paler beneath, glabrous, on petioles less than one-half length of blade. Racemes indefinite, terminal on the stem and branches; bracts sessile, the lowermost ovate and somewhat serrate, nearly 2 cm. long, the upper lanceolate, smaller. Pedicels spreading, 10–11 mm. long, glandular-pubescent. Sepals oblong-lanceolate, acute, glandular-pubescent, 3–4 mm. long. Corolla 5–6 mm. long. Filaments slender. Anthers widely explanate. Style 2–2.5 mm. long. Stigma capitate. Capsule 6 mm. long pyramidal, slightly attenuate to an obtuse apex, glabrous. Seeds .8–.9 mm. long, cylindric, dark-brown, with about 8 rounded longitudinal ridges separated by deep narrow furrows; the whole surface finely alveolate-reticulate.

Type, Santa Marta Mountains, collected in flower and fruit about April, 1899, H. H. Smith 1497; in Herb. New York Botanical Garden. The note for 1497 is stated by Smith to have been lost, but he tells us that the plant is "probably from Valparaiso, 4500 ft. [ = 1350 m.]" altitude. I suspect that this plant came from much higher than this.

Rusby has compared this with Purdie's plant from Santa Marta and has written on our sheet "Purdie's plants are more hairy than this," an excellent confirmation of Purdie's specimens cited in DC. Prod. 10. 250: being this same species.

Magdalena. Valparaiso, Santa Marta Mts., H. H. Smith 1497 (C, H, U, Y).

### 20. FAGELIA Schwencke.

*Fagelia* Schwencke, [in Verh. Bataafsh. Genootsch. Rotterdam 1: 474. pl. 13. 1774, generic diagnosis only]; J. F. Gmel., Syst. Nat. 40. 1791.
*Calceolaria* L., in Kongl. Vetensk. Acad. Handl. 31: 288, 1770, not *Calceolaria* Fabr., Enum. Meth. Pl. Host. Med. Helmstad. ed. II. 37. 1763.

Type species, *F. flavicans* J. F. Gmel., probably from Ecuador.

Anther-sacs proximate on the simple filament, both alike and fertile. Anterior lip of corolla ( = sac) not over twice width of posterior lip ( = hood). Leaves entire to coarsely serrate-dentate, the blades at times triangular. [CHEILONCOS Kranzl.]
  Capsule ovate or broader, no longer than broad, thick-walled, shorter than or but slightly exceeding the sepals. Corolla 8–25 mm. long, with the posterior lip broadly truncate to notched. Filaments stout, not or but little longer than the oblong anthers. Inflorescence corymb-like, both secondary branches developed, and at least some of the lateral flowers without bracts.
    Shrubs. Glutinous above, on stems, pedicels, sepals and leaves. Leaf-blades lanceolate, entire to slightly serrate, shortly petiolate. Corolla appearing broader than long because the sac is pressed tightly against hood; orifices to lips broad and rounded, so sac is shallow.
      Calyx 4–6 mm. long. Leaves glaucous beneath. Plant less glutinous. Branches of the inflorescence once branched, so that flowers occur in fours. 1. *F. microbefaria.*
      Calyx 2–3 mm. long. Leaves slightly paler beneath. Plants very glutinous. Branches of the inflorescence irregularly twice branched, so that flowers occur usually in clusters of more than four. 2. *F. fruticosa.*
    Herbaceous throughout. Not glutinous, but often with stalked glands. Leaf-blades lanceolate to broadly triangular, serrate to doubly dentate. Corolla evidently elongated sagittally, with sac usually not pressed against hood and so

with its orifice evident; orifice to hood narrow, or truncate; to sac truncate, with sac deep.

Calyx 4–5 mm. long, shorter than or about equaling the capsule. Leaves sessile. Stem densely glandular-pubescent.

Leaves narrowed at base, elliptic-lanceolate, dentate, on both surfaces densely ferruginous-pubescent with dark-jointed hairs. Stem below densely, above sparsely pubescent. Inflorescence of a few wide-spreading branches. Corolla 8–10 mm. long. Anthers about 1.5 mm. long. 3. *F. lehmanniana.*

Leaves rounded-clasping at base, lanceolate, crenate-serrate (with spinulose serrations), above glabrate, beneath paler and finely pubescent. Stem below apparently glabrate, above pubescent with short gland-tipped hairs. Corolla about 12–15 mm. long. Anthers about 2.5 mm. long. 4. *F. crenata.*

Calyx 7–12 mm. long, longer than the capsule. Leaves petioled, petiole at times broadly winged.

Anther-sacs stiffly divaricate (so anthers straight), opening throughout or from distal apices. Capsule with gland-tipped hairs. Corolla slightly pubescent within at base. Style 1.5–4 mm. long. Wing of petiole less than one-third width of blade or wanting.

Leaves 3–5 mm. long, the petioles wingless.

Stem pubescent throughout with glandless hairs. Calyx-lobes obtuse to acute. Corolla 15–20 mm. long. Style 1.5 mm. long. Leaves 3–4 cm. long, obtuse to acutish, simply or somewhat doubly crenate-serrate, beneath pale and densely pubescent. Secondary branches of the inflorescence not or scarcely branched.

5. *F. saxatilis.*

Stem pubescent distally with gland-tipped hairs. Calyx-lobes acuminate. Corolla about 10 mm. long. Style 3 mm. long. Leaves 4–5 cm. long, acuminate, irregularly somewhat doubly serrate with acute teeth, beneath lighter green and somewhat pubescent. Secondary branches of the inflorescence repeatedly branched.

6. *F. bogotensis.*

Leaves 11–17 cm. long, the petioles winged proximally or throughout, the wing connate with that of opposite leaf.

Petioles broadly winged proximally, distally very narrowly margined; leaf-blades broader than long, irregularly shallowly crenate-dentate. Corolla with posterior lobes not united to apex, so leaving a deep narrow orifice into hood. Anther-sacs broadly contiguous. 7. *F. trilobata.*

Petioles nearly uniformly winged throughout; leaf-blades longer than broad, sharply doubly serrate-dentate. Corolla with posterior lobes united nearly or quite to apex, so leaving slight if any median orifice into hood. Anther-sacs narrowly contiguous.

Corolla 8–10 mm. long; hood with slight median orifice. Anthers 2 mm. long, the sacs opening throughout. Style 1.5–1.8 mm. long. Capsule 3–4 mm. long. Winged petiole usually 12–18 mm. wide, and somewhat dentate. Plant pubescent above with some gland-tipped hairs. 8. *F. alata*.

Corolla 13–15 mm. long; hood truncate, without apical median orifice. Anthers 3.5 mm. long, the sacs opening from distal apex but not throughout. Style 4 mm. long. Capsule 5–6 mm. long. Winged petiole 8–13 mm. wide, entire. Plant pubescent throughout with glandless hairs. 9. *F. nevadensis*.

Anther-sacs curved (so anther horseshoe-shaped), opening from proximal apices partially or throughout. Capsule pubescent with glandless hairs. Corolla glabrous within at base. Style 5 mm. long. Wing of petiole more than one-third width of blade.

Leaves sharply dentate, above glabrate, beneath paler and finely pubescent. Stem glabrate below, somewhat hirsute above. Calyx 8–10 mm. long. 10. *F. tolimensis*.

Leaves obtusely dentate, above pubescent, beneath softly pubescent to tomentose. Stem hispid below, hirsute-pubescent above. Calyx 9–11 mm. long. 11. *F. perfoliata*.

Capsule narrowly pyramidal, longer than broad, thin-walled, nearly twice as long as the sepals. Corolla 5–6 mm. long, nearly globose, with posterior lip attenuate to a shallowly notched apex. Filaments slender, several times longer than the hemispheric anthers. Inflorescence appearing as if with flowers axillary, normally one secondary branch developing repeatedly through an indefinite number of nodes. 12. *F. ovata*.

Anther-sacs separated on two arms of the connective (filament wanting or very short), dissimilar, the anterior tending to become sterile. Anterior lip two to four times the width of the posterior. Leaves pinnately lobed. [APOSECOS Benth.]

Anterior anther-sac fertile, brown or yellowish. Style .6–.8 mm. long. Calyx 3–5 mm. long. Pedicels and stems above pubescent with gland-tipped hairs.

Leaves 2–4 cm. long, the blades with one or two partial pairs of segments, the sinuses of which are narrow and reach only one-half to two-thirds the distance to the midrib. Calyx 3–4 mm. long. 13. *F. micrantha.*

Leaves 2–10 cm. long, the blades with usually three pairs of segments, the proximal sinuses of which are usually broad and reach nearly to the midrib. Calyx 4–5 mm. long. 14. *F. radiculoides.*

Anterior anther-sac sterile, yellow or orange-yellow. Style 1–2 mm. long. Calyx 5–9 mm. long.

Anterior anther-sac light-yellow. Corolla 5–7 mm. long. Leaf-blades with shallow crenately-toothed lobes. Distally finely pubescent with glandless hairs. 15. *F. crenatiloba.*

Anterior anther-sac orange-yellow. Corolla 7–21 mm. long. Leaf-blades with deep sharply serrate lobes.

Stems above and pedicels pubescent with few-celled gland-tipped hairs. Blades of lowermost leaves with shallow lobes. Base of petioles very narrowly connate. Calyx-lobes slightly serrate, obviously ciliate with gland-tipped hairs. Style 1–1.3 mm. long. Capsule pubescent with short gland-tipped hairs. 16. *F. chelidonioides.*

Stems above and pedicels hirsute with many-celled dark-jointed hairs. Blades of all leaves pinnatisect nearly to the midrib. Base of petioles obviously connate. Calyx-lobes decidedly serrate, hirsute on the back and margin. Style 1.8–2 mm. long. Capsule pubescent with glandless (or in *pinnatisecta* with interspersed gland-tipped) hairs.

Corolla 15–21 mm. long. Calyx-lobes ovate, acute. Capsule 6 mm. long. Leaves 5–8 cm. long, 3–5 cm. wide. 17. *F. scalaris.*

Corolla 8–10 mm. long. Calyx-lobes lanceolate or narrowly ovate, acuminate. Capsule 4 mm. long. Leaves 3–5.5 cm. long, 2–3 cm. wide. 18. *F. pinnatisecta.*

1. **Fagelia microbefaria** (Kränzl.) Pennell, comb. nov.

*Calceolaria microbefaria* Kranzl, in Ann. k. k. Naturh. Hofm. Wien 22: 193. 1907. "Kolumbien, Ostkordilleren, Provinz Pamplona, zwischen Urban und Las Vetas in 3300 m ü. d. M. (Linden Nr. 730!)."

Stem 1–2 meters tall, much branched, woody, with grayish-brown bark, the twigs reddish- or yellowish-brown, glutinous and finely pubescent. Leaves 6–8 cm. long, the blades lanceolate, acuminate, serrate to entire, at times slightly revolute, 12–17 mm. wide; each narrowed to a petiole 5–10 mm. long; blades above green, pubescent on the midrib or pulverulent or quite glabrous, beneath glaucous, sparsely puberulent to glabrous, reticulate; somewhat glutinous on upper surface. Corymb bractless, the secondary branches slightly if at all branched, so that the inflorescence simulates a stalked four-flowered umbel. Peduncle and pedicels somewhat glutinous and pubescent with brown hairs. Calyx 4–6 mm. long, the lobes triangular-ovate, obtusish to acute, entire, puberulent, glutinous. Corolla: posterior lip 6–7 mm. long, 7–9 mm. wide, with broad rounded orifice; anterior lip 12–13 mm. long, 8–10 mm. wide, with rounded orifice opening into two-thirds or more of its length; sac pressed against hood so that corolla appears broader than long; externally finely puberulent, within glandular-pubescent proximally, especially about bases of filaments. Filaments stout, less than 1 mm. long. Anther 2.5 mm. long, brown, the walls thin, the sacs contiguous, opening throughout and eventually through the thin connective. Style 3 mm. long. Capsule 5 mm. long, broadly ovate, acute, puberulent. Seeds .4–.5 mm, long, oblong, obtuse, ridged, red brown.

Thickets, along streams and at edge of forest, also in thicket-islands in Paramo, at altitudes of 2800 to 3300 meters; Temperate zone of western slope of Cordillera Orientál, from Santander to Cundinamarca.

Cundinamarca. Rio Frio, west of Zipaquirá (along stream-banks), Pennell 2570, 2605; Mt. Chuscal, west of Zipaquirá (thicket-island in paramo), Pennell 2584; Sibaté (bushy hillsides southwest of), Pennell 2389.

2. **Fagelia fruticosa** Pennell, sp. nov.

Stem 1–2 meters tall, much branched, woody, with grayish bark, the twigs reddish and glutinous-puberulent or slightly pubescent. Leaves 5–6 cm. long, the blades lanceolate, acuminate, slightly serrulate to entire, at times slightly revolute, 12–13 mm. wide; each narrowed to a petiole 4–7 mm. long; blades above dark-green and puberulent, beneath paler and reticulate, on both surfaces strongly glutinous. Corymb bractless, the secondary branches soon branching so as to simulate an umbel. Peduncle and pedicels glutinous and somewhat pubescent with brown hairs. Calyx 2–3 mm. long, the lobes broadly ovate, acute, entire, puberulent, glutinous. Corolla: posterior lip 6–7 mm. long, 7–8 mm. wide, with broad rounded orifice; the anterior lip 12–13 mm. long, 8–9 mm. wide, with rounded orifice opening into two-thirds or more of its length; sac pressed against hood so that corolla appears broader than long; externally finely puberulent, within pubescent proximally, especially near the filaments. Filaments stout, less than 1 mm. long. Anthers nearly 2 mm. long, brown, the walls thin, the sacs contiguous, opening throughout and through connective. Style 3 mm. long. Capsule 5 mm. long, broadly pyramidal, acute, glandular-puberulent. Seeds.

Plant more glutinous and drying blacker than *Fagelia microbefaria.*

Type, forest at margin of Paramo de Ruiz, Tolima, altitude 3200–3500 meters, collected in flower December 16, 1917, F. W. Pennell 2998; in Herb. New York Botanical Garden.

Shrub belt about and below paramo, Temperate zone, eastern slope of the Cordillera Centrál, in Tolima.

3. **Fagelia lehmanniana** (Kränzl.) Pennell, comb. nov.

*Calceolaria lehmanniana* Kränzl. in Fedde, Rep. Nov. Spec. 1: 100. 1905. "Columbien: Dpto. Cauca; an feuchten Orten an den oberen Gehängen des Vulcan de Sotará und auf dem Paramo de Barbillas in 3000 bis 3300 m ü. d. M. (F. C. Lehmann, no. 6134!)"; not *C. lehmannii* (Hieron) Hieron. in Engl. Bot. Jahrb. 20. Beibl. 49: 57. 1894.

At altitudes of 2800 to 3300 meters, Temperate Zone, southern Cordillera Centrál, from Cauca to Pasto.

Pasto. Puruquai, J. Triana in 1851–7 (Y).

4. **Fagelia crenata** (Lam.) Kuntze.

*Calceolaria crenata* Lam., Encyc. Meth., Bot. 1: 556. 1785. "Trouvée au Pérou par M. Joseph de Jussieu (v. s. in herb. Juss.)." Jussieu collected mainly in Ecuador.
*Fagelia crenata* (Lam.) Kuntze, Rev. Gen. 495. 1891.

At an altitude of 3000 meters, Temperate Zone, southern Cordillera Centrál, from Pasto to Ecuador.

Cauca. Valle de Quintero above Pitaio, R. Palo basin, Central Cordillera, H. Pittier 1425 (U).

Pasto. "Tuquerres et Puruquai," J. Triana in 1851–7. "Judabolsa."

5. **Fagelia saxatilis** (H. B. K.) Kuntze.

*Calceolaria saxatilis* H. B. K., Nov. Gen. et Sp. 2: 382. 1817. "Crescit locis saxosis montis Chimborazo in summa planitie Sisgun, alt. 1750 hex. [ = 3325 meters] . . . [Humboldt & Bonpland]."
*Fagelia saxatilis* (H. B. K.) Kuntze, Rev. Gen. 460. 1891.

Stem about 1 meter tall, much branched, herbaceous, green or reddish, pubescent with white hairs, densely so above. Leaves 3–4 cm. long, the blades ovate, cordate or truncate at base, obtuse, each narrowed to a petiole 5–10 mm. long; blades above green, finely pubescent, beneath pale and densely pubescent, with some sessile glands; petiole white-lanate. Corymb bracted at base, its secondary branches usually quite simple. Pedicels lanose with glandless white hairs. Calyx 8–14 mm. long, the lobes ovate, obtuse to acute, obscurely lobed, lanose-pubescent. Corolla: the posterior lip 3–4 mm. long the two lobes united nearly to apex (so strongly hooded with shallow median orifice); anterior lip 20–25 mm. long, 10–12 mm. wide, with orifice opening about one-third of its length; sac upcurving toward hood, the orifice opening externally; externally glandular-pruinose, within slightly pubescent at base on anterior side. Filaments 2 mm. long. Anthers 2 mm. long, brown, the walls thick, the sacs broadly contiguous, opening throughout and through the thin connective. Style 1.5 mm. long. Capsule 5–6 mm. long, broadly globose-pyramidal, obtuse, thick-walled, puberulent with gland-tipped hairs. Seeds .5 mm. long, oblong, distally acute, finely ridged, brown.

Thickets, along streams and at edge of forest, at altitudes of 2700 to 3300 meters; Temperate zone of eastern slope of Cordillera Centrál, from Tolima to Ecuador. Collected also above Bogotá, where probably an escape.

Tolima. "Rosalito," near Paramo de Ruiz (along stream in meadow), Pennell 2990. Also recorded by Kränzlin from Paramo de Ruiz, Purdie.

Cundinamarca. Guadalupe, above Bogotá, Bro. Ariste-Joseph A230 (U).

### 6. **Fagelia bogotensis** Pennell, sp. nov.

Stem probably about 1 meter tall, branched, herbaceous, pubescent with white hairs, distally these gland-tipped. Leaves 4–5 cm. long, the blades triangular ovate, cordate, acuminate, irregularly dentate with acute lobes 3–4 cm. long, 2.5–3 cm. wide; each on a wingless petiole 10–20 mm. long; blades above green, pubescent, beneath lighter green and moderately pubescent, without sessile glands; petiole pubescent, some hairs gland-tipped. Corymb leafy-bracted at base, its secondary branches becoming much branched. Peduncles and pedicels hirsute with gland-tipped hairs. Calyx 10–12 mm. long, the lobes ovate, acuminate, entire, hirsute-pubescent. Corolla: the posterior lip 4 mm. long, the two lobes united nearly to apex (so strongly hooded, with shallow median orifice); anterior lip about 10 mm. long, with orifice opening less than ½ of length; sac upcurving toward hood, the orifice opening externally; externally glandular-pruinose, within somewhat pubescent at base. Filaments 1.5 mm. long. Anthers 2.5 mm. long, brown, the walls thick, the sacs broadly contiguous, opening from proximal end, eventually to the distal apex. Style 3 mm. long. Capsule 6–8 mm. long, urceolate-pyramidal, acute, thick-walled, pubescent with short gland-tipped hairs. Seeds .3 mm. long, oblong, mucronately acute at each end, ridged, brown

Type, Bogotá, Cundinamarca, alt. 2600 meters, collected in 1851–1857 by J. Triana; in Herb. Columbia University at The New York Botanical Garden.

At an altitude of slightly over 2600 meters, Temperate zone of western slope of Cordillera Oriental, in Cundinamarca.

7. **Fagelia trilobata** (Hemsl.) Rusby.

> *Calceolaria trilobata* Hemsl., Biol. Centr. Am., Bot. 2: 439. 1881–2. "Guatemala, Volcan de Fuego, 7000 to 10,000 feet (Godman & Salvin, 239). Colombia. Hb. Kew. The description was mainly drawn up from Hotton's [= Holton's] Colombian specimen, n. 575." Species an aggregate, and to be typified by I. F. Holton 575. An isotype of this, in Herb. Columbia University at The New York Botanical Garden is labeled "Rio Arzobispo, in montibus juxta Bogotam, legit . . . 23 Oct. 1852." A redescription, from this specimen, is given below.
>
> *Fagelia trilobata* (Hemsl.) Rusby in Mem. Torr. Bot. Club 6: 93. 1896. As to synonomy only.

Stem probably about 1 meter tall, branched, herbaceous, pubescent with white hairs, distally these gland-tipped. Leaves 15–17 cm. long, the blades triangular, slightly three-lobed, cordate, tapering to an acute tip, irregularly crenate-dentate, with callous-tipped lobules, 9–10 cm. long, 11–12 cm. wide, each on a petiole 6–7 cm. long its wing distally very narrow, proximally expanding to 3–4 cm. wide and connate with that of opposing leaf; above green, pubescent, beneath pale-green and slightly pubescent, more so on the veins, narrow-winged portion of petiole pubescent, some hairs with glandular tips. Corymb leafy-bracted at base, its secondary branches much branched. Peduncles and pedicels hirsute with gland-tipped hairs. Calyx 12 mm. long, the lobes ovate, acuminate, obscurely lobate, hirsute-pubescent. Corolla: the posterior lip 5–6 mm. long, the two lobes not united to apex, so not hooded, with deep, narrow median orifice; anterior lip 10–12 mm. long, with orifice opening much less than one-half of length; sac upcurving toward hood; externally glandular-pruinose, within somewhat pubescent at base. Filaments 2 mm. long, widening distally. Anthers 3.5 mm. long, brown or yellowish, the walls thick; the sacs broadly contiguous, opening throughout, the septum between very thin, and ultimately (?) breaking. Style 4 mm. long. Capsule glandular-puberulent, not seen mature.

Thickets along stream, at an altitude between 2600 and 3000 meters, Temperate zone of western slope of Cordillera Oriental, in Cundinamarca.

8. **Fagelia alata** Pennell, sp. nov.

Stem about 1 meter tall, little branched herbaceous, pubescent with white hairs, distally lanose and with short-stalked glands. Leaves 11–17 cm. long, the blades triangular-ovate, cordate, acuminate, coarsely doubly dentate (dentate with the lobules triangular and dentate), 7–10 cm. long, 6–8 cm. wide; each on a petiole 4–7 cm. long, this broadly winged throughout (in middle 10–18 mm. wide), entire to crenate-dentate, proximally slightly expanding and connate with that of opposing leaf; above green, beneath pale green, on both surfaces slightly pubescent, more so on younger growth. Corymb bractless, its secondary branches repeatedly branched. Peduncles and pedicels pubescent with longer white glandless, and with shorter gland-tipped hairs. Calyx 8–9 mm. long, the lobes lanceolate, acuminate, slightly serrate-dentate or some entire, glandular-puberulent. Corolla: the posterior lip 2–3 mm. long, 5 mm. wide, arched, the two lobes united very nearly to apex (so hooded with slight median aperture); anterior lip 8–9 mm. long, 7 mm. wide, with orifice opening much less than ½ length (not strongly upcurving toward hood); externally minutely glandular-puberulent, within minutely pubescent at base on anterior side, lemon-yellow margin of sac very finely purple-spotted. Filaments .5–.7 mm. long, narrowing distally. Anthers 2 mm. long, yellowish, the walls thick; the sacs narrowly contiguous, opening throughout, the septum between thin and ultimately breaking. Style 1.5–1.8 mm. long. Capsule 3–4 mm. long, urceolate-pyramidal, emarginate, pubescent with short gland-tipped hairs. Seeds .2–.3 mm. long, oblong, distally obtuse, ridged, black-brown.

Type, moist bank in forest, loam soil, western slope of Cordillera Oriental, east of Neiva, Huila, altitude 1800–2300 meters, collected in flower and fruit August 1–8, 1917, Rusby & Pennell 579, in Herb. New York Botanical Garden.

Moist banks in forest at an altitude between 1800 and 2300 meters, Subtropical zone of the western slope of Cordillera Oriental, in Huila.

9. **Fagelia nevadensis** Pennell, sp. nov.

Stem erect, nearly 1 meter tall, branched, pubescent, lanose distally, with long glandless white dark-jointed hairs. Leaves 16 cm. long, the blades ovate, cordate, acuminate, doubly and sharply dentate, (dentate with lobules irregularly and sharply dentate), 10 cm. long, 8–9 cm. wide, each on a petiole 6 cm. long, uniformly winged throughout (in middle 8–13 mm. wide), entire, proximally slightly expanding and connate with that of opposing leaf; above green, beneath slightly paler, slightly pubescent on both surfaces. Corymb leafy-bracted at base, its secondary branches long, each dividing above a long peduncular portion into six to eight pedicels. Peduncles and pedicels hirsute with glandless white hairs and with short-stalked glands. Calyx 11–12 mm. long, the lobes ovate, acuminate, entire, pubescent. Corolla: the posterior lip about 5 mm. long, 6 mm. wide, arched, the two lobes united to apex (so hooded, truncate without apical aperture); anterior lip 13–14 mm. long, 12–14 mm. wide, with orifice opening much less than one-half length of sac (sac strongly upcurving toward hood); externally glabrous, within pubescent at base on anterior side. Filaments .8 mm. long. Anther straight, 3.5 mm. long, grayish, its walls firm; sacs contiguous, permanently separated by a firm septum, each opening by a slit from the distal apex which does not reach the proximal end. Style 4 mm. long. Capsule 5–7 mm. long, pyramidal, somewhat obtuse, puberulent, with short-stalked glands. Seeds .2–.3 mm. long, irregularly oblong, ridged and transverse-lined, dark-brown.

Type, damp hillside, clearing at Las Nubes, slopes of Sierra Nevada de Santa Marta, Magdalena, collected in flower and fruit December 15, 1898–1901, Herbert H. Smith 1404, in herbarium New York Botanical Garden; isotypes in Gray Herbarium, United States National Museum, and Field Museum of Natural History. Said to be from "4500 feet" [= 1350 meters], such a low elevation for a plant of this genus as to force the suspicion that datum is erroneous. The specimen is more probably from some slope much higher, surely over 2000 meters altitude.

10. **Fagelia tolimensis** Pennell, sp. nov.

Stem lax, ascending, 1 to 2 meters long, branched, reddish, herbaceous, glabrate below, above slightly hirsute with dark-jointed hairs. Leaves 8–10 cm. long; the blades triangular-lanceolate, cordate or truncate, acuminate, irregularly and somewhat doubly dentate (dentate with lobules shallowly triangular and irregularly acutely toothed), 6–7 cm. long, 2.5–3.5 cm. wide; each on a petiole 2–3 cm. long, broadly winged throughout (in middle 12–15 mm. wide), irregularly shallowly crenately dentate, proximally expanding and connate with that of opposing leaf; above dark-green, minutely pubescent, becoming glabrate, beneath pale-green, permanently pubescent, especially on the veins. Corymb leafy-bracted at base, its secondary branches soon much branched (pedicels long and slender) Peduncles and pedicels hirsute with dark-jointed hairs, these of various lengths. Calyx 8–10 mm. long, the lobes ovate, acuminate, entire, pubescent. Corolla: the posterior lip 3–4 mm. long, 5 mm. wide, arched, the two lobes united to apex (so hooded, without median aperture); anterior lip 12–14 mm. long. 10 mm. wide, with orifice opening about one-half length (sac strongly upcurving toward hood), externally slightly pubescent to glabrate, within glabrous throughout. Filaments 1.2 mm. long. Anthers horseshoe-shaped, brown; each sac 2 mm. long, contiguous, splitting its entire length, septum between sacs thin, but apparently not rupturing. Style 5 mm. long, proximally pubescent. Capsule pubescent with white glandless hairs; not seen mature.

Type, moist mossy loam, margin of forest, "Rosalito" (east of Paramo de Ruiz), Tolima, altitude 2800–3100 meters, collected in flower December 15–17, 1917, F. W. Pennell 2979; in Herb. New York Botanical Garden.

Nearest to *Fagelia purpurascens* (Sodiro) Pennell, comb. nov., of Ecuador, but appears distinct in having leaves more sharply cut, stem less pubescent, pedicels more slender and sepals shorter.

Moist soil, edge of forest, at an altitude between 2800 and 3100 meters, Temperate zone of eastern slope of Cordillera Centrál, in Tolima.

11. **Fagelia perfoliata** (L. f.) Kuntze.

*Calceolaria perfoliata* L. f., Suppl. 86. 1781. "Habitat in Nova Granada. Mutis." Type probably from Bogotá.
*Fagelia perfoliata* (L. f.) Kuntze, Rev. Gen. 460. 1891.

Stems lax, ascending, 1–2 meters long, somewhat branched, reddish-brown, pubescent throughout, above densely so, with hairs not or slightly dark-jointed. Leaves 8–13 cm. long, the blades triangular-lanceolate to ovate, cordate to truncate, acuminate, irregularly and somewhat doubly dentate (dentate with lobules shallowly triangular and shallowly dentate), 5–8 cm. long, 3.5–5.5 cm. wide; each on a petiole 3–5 cm. long, broadly winged throughout (in middle 15–20 mm. wide), slightly crenate-dentate to entire, proximally expanding and connate with that of opposing leaf; above green, beneath whitish-green, pubescent on both surfaces, densely canescent beneath. Corymb leafy-bracted at base, its secondary branches soon much branched (pedicels long and slender). Peduncles and pedicels villous, with spreading dark-jointed hairs, these mostly long. Calyx 9–11 mm. long, the lobes ovate, acuminate, entire, pubescent. Corolla: the posterior lip 4–5 mm. long, 5–6 mm. wide, arched, the two lobes united to apex (so hooded without median aperture); anterior lip 13–14 mm. long, 7–8 mm. wide, with orifice opening about one-half length (sac strongly upcurving toward hood), externally slightly pubescent to glabrate, within glabrous throughout. Filaments about 1 mm. long. Anthers horseshoe shaped, brown, each sac 1.8 mm. long, contiguous, splitting from proximal end its entire length, septum between sacs thin and rupturing. Style 5 mm. long, proximally pubescent. Capsule 5 mm. long, urceolate-pyramidal, acutish, pubescent with white glandless hairs. Seeds .5 mm. long, lanceolate, distally acuminate, ridged, and transverse-lined, brown.

Moist bushy slopes, along streams in shrub-zone, at altitudes of 2700 to 3000 meters, Temperate zone of western slope of Cordillera Orientál, in Cundinamarca.

Cundinamarca. Rio San Cristobal, near Bogotá (bushy mountain-slope, alt. 2800–3000 m.), Pennell 2380; Chipaque (moist roadbank above, alt. 2800–2900 m.), Pennell 1317; Sibaté (bushy slopes near, alt. 2700–3000 m.), Pennell 2485; Bogotá (alt. 2700 m.), J. Triana (U, Y).

12. **Fagelia ovata** (Smith) Kuntz.

*Calceolaria ovata* Smith, Ic. Ined. 1:3 pl. 3. 1789. "Ex Peru semina setulit Dombey."
*Fagelia ovata* (Smith) Kuntz, Rev. Gen. 460. 1891.

Stem erect or ascending, 1–4 dm. tall, branched, pubescent with white gland-tipped hairs. Leaves 2.5–3.5 cm. long, the blades ovate, narrowed to nearly truncate at base, acute, obscurely simply serrate with shallow teeth, 2.3–3 cm. long, 1–1.5 cm. wide, each on a petiole .2–.5 cm. long, not winged, lanose with gland-tipped hairs; green, beneath slightly paler, pubescent on both surfaces. Inflorescence apparently axillary; actually at each node two pedicels occur, at right angles to which are two leaves from the axil of one of which usually develops the branch which indefinitely repeats this manner of branching. Pedicels pubescent with gland-tipped hairs. Calyx 3 mm. long, the lobes ovate, acutish, entire, pubescent. Corolla: the posterior lip 3–4 mm. long, 4–5 mm. wide, arched, the two lobes united throughout, distally attenuate to a slightly notched apex (so hooded); anterior lip 5 mm. long, 5 mm. wide, widest at base, with orifice opening much less than one-half length of sac

(sac, upcurved toward hood, its anterior surface incurved forming a broad pouch into which anthers shed pollen and into which the stigma grows, apparently ensuring self-pollination); externally glabrous, within with a few hairs about base. Filaments 1.5 mm. long. Anthers .6 mm. long elliptic or hemispheric, yellow, the walls thin; sacs contiguous by a broad contact, opening throughout. Style 1.2 mm. long. Capsule 5–6 mm. long, narrowly pyramidal, obtusish, thin-walled sparsely puberulent with short-stalked glands. Seeds .1–.2 mm. long, oval, obtuse, ridged and transverse-lined, brown.

Type, moist roadside below Chipaque, Cundinamarca, altitude 1800–2200 m., collected in flower August 23, 1917, F. W. Pennell 1327; in Herb. New York Botanical Garden.

Moist shaded banks, at altitudes of 1300 to 2200 meters, Subtropical zone of eastern slope of Cordillera Oriental, in Cundinamarca.

Cundinamarca. Chipaque (moist roadside below, alt. 1800–2200 m.), Pennell 1327; Quetame to Monte Redondo (moist cliff, along stream in woodland, alt. 1300 m.), Pennell 1352, (moist bank, alt. 1400–1500 m.), Pennell 1854.

13. **Fagelia micrantha** Pennell, sp. nov.

Stem spreading and laxly ascending, 2–3 dm. long branched, sparsely pubescent below with short few-celled gland-tipped hairs. Leaves 2–4 cm. long, the blades acute or obtusish at apex, irregularly pinnately lobed with 1–2 pairs of segments, the incisions usually reaching $\frac{1}{2}$ to $\frac{2}{3}$ the distance to the midrib, the lobules and main portion of the blade irregularly dentate, 1.5–3 cm. long, 1.5–2.5 cm. wide; each on a petiole .5–1 cm. long, slightly winged, proximally clasping stem and slightly connate with that of opposing leaf; above deep-green, with sparse scattered pubescence soon becoming glabrous, beneath pale-green and nearly glabrous. Corymb leafy-bracted at base (the two primary flowers developed), the secondary branches scarcely or not longer than the primary pedicels, usually once dividing, and bracted with reduced leaves. Peduncles and pedicels pubescent with short gland-tipped hairs. Calyx 3–4 mm. long, the lobes oblong-ovate, obtuse, slightly serrate, pubescent proximally. Corolla: the posterior lip about 2 mm long and 2 mm. wide, arched, the two lobes united and slightly hooded, free toward apex (leaving a narrow arched aperture into hood); anterior lip 5–6 mm. long, 4–5 mm. wide, with narrow base, hooded almost entire length (sac strongly upcurving against hood): externally glabrous or minutely puberulent at base, within glabrous. Filaments none. Anther with two sacs separated on two arms of the connective, both sacs fertile; opening throughout, the anterior projecting into orifice, smaller; posterior arm (with sac) 1.5 mm. long, anterior arm (with sac) 1 mm. long. Style 6–.8 mm. long. Capsule glabrous, not seen mature.

Type, along streamlet, edge of forest, "Rosalito" (between Murillo and Paramo de Ruiz), Tolima, altitude 2800–3100 meters, collected in flower December 17, 1917, F. W. Pennell 3145; in Herb. New York Botanical Garden. Growing with 3119, *F. crenatiloba.*

Along streamlets, edge of forest, at an altitude between 2800 and 3100 meters, Temperate zone of eastern slope of Cordillera Central, in Tolima.

**14. Fagelia radiculoides** Pennell, sp. nov.

Stem spreading and laxly ascending, 1–15 dm. long, branched, glabrate, above pubescent with spreading gland-tipped hairs. Leaves 2–10 cm. long, the blades acute to acuminate at apex, pinnately lobed with usually three pairs of lanceolate segments, the incisions extending nearly to the midrib, the lobules and terminal segment irregularly serrate-dentate, 1.5–6 cm. long, 1.5–6.5 cm. wide; each on a petiole .5–4 cm. long, narrowly winged, proximally slightly expanding and connate with that of opposing leaf; above deep-green, with scattered hairs or glabrous, beneath glaucous, glabrous or pubescent on the midrib. Corymb leafy-bracted at base (the two primary flowers developed), the secondary branches long and repeatedly dividing, bracted throughout. Peduncles and pedicels pubescent with gland-tipped hairs. Calyx 4–5 mm. long, the lobes ovate, acute to obtusish, obscurely slightly serrate, pubescent proximally and on margin with gland-tipped hairs. Corolla: the posterior lip 1.5–2 mm. long, 2 mm. wide, arched, the two lobes united and slightly hooded, free toward apex (leaving a narrow arched aperture into hood); anterior lip 6–7 mm. long, 4–5 mm. wide, narrowed at base, hooded almost entire length (sac strongly upcurving against hood); externally and internally glabrous. Filaments none. Anther with two sacs separated on two arms of the connective, both sacs fertile, opening throughout, of about equal size, each arm (with sac) about 1 mm. long. Style .7–.8 mm. long. Capsule 3–4 mm. long, broadly globose-pyramidal, rounded and slightly notched, somewhat pubescent with gland-tipped hairs.

Seeds .5–.6 mm. long, oblong, obtuse, ridged (with rounded ridges) dark-brown.

Type, moist rocky cañon, Rio San Francisco, above Bogotá, Cundinamarca, altitude 2700–2800 meters, collected in flower and fruit September 13, 1917, F. W. Pennell 1942; in Herb. New York Botanical Garden.

Moist or wet soil, springheads, swales and cliffs, partially shaded or open, at altitudes of 2600 to 3200 meters, occasionally descending to 1500 meters, Temperate zone, ascending to Paramo, where dwarfed, and to Subtropical zone, where more rank; on both slopes of the Cordillera Orientál, in Cundinamarca.

Cundinamarca. Zipaquirá (springhead in meadow, alt. 2650 m.), Pennell 2534; Mt. Chuscal, west of Zipaquirá, (swale on paramo, alt. 3100–3200 m.), [only 1–2 dm. tall; leaves in some plants more pubescent], Pennell 2602; Bogotá (moist rocky cañon on Rio San Francisco above, alt. 2700–2800 m.), Pennell 1942, (moist bank, base of mount, alt. 2700–2800 m.), Pennell 2293; Sibaté (wet road-bank, alt. 2600–2800 m.), Pennell 2386; Ubagué (moist loam in shrub-zone above, alt. 2700–3000 m.), Pennell 1898; Monte Redondo to Quetame (wet bank, alt. 1400–1500 m.) [plant especially rank], Pennell 1855.

### 15. **Fagelia crenatiloba** Pennell, sp. nov.

Stem ascending, 3–6 dm. long, little branched, glabrous or nearly so, above pubescent with white several-celled glandless hairs. Leaves 5–7 cm. long, the blades obtuse or acutish at apex, pinnately lobed with 2–3 pairs of segments, the incisions rarely extending over $\frac{1}{2}$–$\frac{2}{3}$ the distance to the midrib, the lobules and main portion of blade crenately dentate, 3.5–5 cm. long, 3–4 cm. wide; each on a petiole 1.5–2 cm. long, slightly margined, glabrous or nearly so, proximally somewhat expanding and connate with that of opposing leaf; above green and with scattered pubescence, beneath pale-green and the midrib and principal veins pubescent. Corymb leafy-bracted at base (the two primary flowers developed), its secondary branches longer, once or twice dividing and bracted throughout with reduced leaves. Peduncles and pedicels finely pubescent with several-celled glandless hairs. Calyx 5–6 mm. long, the lobes ovate, obtuse or acutish, slightly serrate, slightly pubescent, especially proximally. Corolla: the posterior lip 1–2 mm. long, 2–2.5 mm. wide, arched, the two lobes united and slightly hooded, free toward apex (leaving a narrow or triangular slit-like aperture into hood);

anterior lip 5–7 mm. long, 4–5 mm. wide, narrowed at base, hooded almost entire length (sac strongly upcurving against hood); externally glabrous or finely puberulent proximally, within glabrous. Filament none or very short. Anther with the two sacs separated on two arms of the connective, each (including sac) about 1.5 mm. long; posterior sac .6–.7 mm. long, whitish, opening throughout, fertile, concealed within hood; anterior sac shorter, projecting into orifice, partially or wholly sterile. Style 1 mm. long. Capsule nearly globose, finely pubescent with glandless hairs; not seen mature.

Type, along streamlet, edge of forest, "Rosalito," (between Murillo and Paramo de Ruiz), Tolima, altitude 2800–3100 meters, collected in flower December 17, 1917, F. W. Pennell 3119; in Herb. New York Botanical Garden.

Along streamlets, edge of forest, at an altitude between 2800 and 3100 meters, Temperate zone of eastern slope of Cordillera Centrál, in Tolima.

16. **Fagelia chelidonioides** (H. B. K.) Kuntze.

*Calceolaria chelidonioides* H. B. K., Nov. Gen. et Sp., 2: 378. 1818. "Crescit in radicibus montis Javirac prope Quito, alt. 1500 hex. [= ca. 2850 m.] [Humboldt & Bonpland]."

*Fagelia chelidonioides* (H. B. K.) Kuntze, Rev. Gen. 2: 459. 1891.

*Fagelia diversifolia* Pennell, in Addisonia 4: 73, pl. 153. "Type . . . collected on a moist bank at Chipaque, Department of Cundinamarca, Colombia, at an altitude of about 8700 feet, August 23, 1917, my number 1320, and is preserved in the hebarium of the New York Botanical Garden." Specimens seen later appear to unite this with the plant from Ecuador.

Stem erect or ascending, 3–9 dm. tall, little branched, sparsely pubescent, more so about nodes, with few-celled gland-tipped hairs. Leaves 4–15 cm. long, the blades acute to acuminate at apex, the lower ovate and shallowly pinnately lobed, irregularly serrate-dentate, the upper pinnately lobed nearly to the midrib with two or three pairs of oval or ovate, irregularly doubly serrate-dentate segments, (the odd terminal segment largest), 3–10 cm. long, 2.5–7.5 cm. wide, each on a petiole 1–5 cm. long, slightly margined, glandular-pubescent, proximally slightly expanding and clasping the stem, usually slightly connate with that of opposing leaf; green above, pale green beneath, with scattered pubescence on both surfaces. Corymb leafy-bracted at base (the two primary flowers developed), its secondary branches elongated, several times dividing and bracted throughout with reduced leaves. Peduncles and pedicels finely pubescent with few-celled gland-tipped hairs. Calyx 7–8 mm. long, the lobes ovate, acuminate, slightly serrate (the few serratures not callous-tipped), slightly pubescent on the back, and conspicuously ciliate with gland tipped hairs. Corolla: the posterior lip about 3 mm. long, 3–4 mm. wide, arched, the two lobes united and hooded, but not to apex (leaving a narrow slit like aperture into hood), anterior lip 10–15 mm. long, 11–13 mm. wide, narrowed at base, hooded almost entire length (sac strongly upcurving against hood); externally glabrous or puberulent on posterior lip, within pubescent about base and within posterior lip. Filament none. Anther with the two sacs separated on two arms of the connective, each about 1.5–1.8 mm. long; posterior sac 1.2 mm. long, yellowish, opening throughout, fertile, concealed within hood; anterior sac short, orange-yellow, sterile, projecting into the orifice, the club-like dark connective arm serving as a lever against which entering insect pushes, thus forcing the fertile sac out through the slit like aperture of the hood and against back of insect. Style 1.1–1.3 mm. long. Capsule 8 mm. long, globose-pyramidal, obtuse, pubescent with short gland-tipped hairs. Seeds .6–.7 mm. long, oblong, obtuse, ridged (with high rounded ridges), brown.

Moist soil, roadside ditches and banks, frequently cultivated and possibly introduced from Ecuador, at altitudes of 2000 to 2700 meters, Subtropical zone of eastern slope of Cordillera Oriental, in Cundinamarca; also obviously from cultivation at Bogotá and at "Balsillas", east of Neiva in Huila; also from the Subtropical zone of the Cordillera Occidental, in Valle. In Ecuador.

Cundinamarca. Chipaque (moist bank, alt. 2600–2700 m.), Pennell 1320; Ubagué (moist soil, alt. 2000–2500 m.), Pennell 1877; [Zipaquirá (moist ditch on hill—alt. 2900 m.), evidently escaped from garden, Pennell 2567].

[Huila. "Balsillas," on Rio Balsillas (cult. in garden, alt. 2000–2100 m.), Rusby & Pennell 692.]

Cauca. Cuestá de Tocotá, road from Buenaventura to Cali, western Cordillera; alt. 1500–1900 m., H. Pittier 698 (U).

### 17. **Fagelia scalaris** Pennell, sp. nov.

Stem erect or ascending, about 1 meter tall, little branched, pubescent to hirsute above with many-celled dark-jointed not or scarcely gland-tipped hairs. Leaves 5–8 cm. long; the blades acuminate at apex, pinnatisect (cut nearly to midrib) with 2 or 3 pairs of lanceolate-ovate, irregularly serrate-dentate segments (the odd terminal segment largest), 4–6 cm. long, 3–5 cm. wide; each on a petiole 1–2 cm. long, very narrowly winged, hirsute, proximally slightly expanding and connate with that of opposing leaf; green, beneath paler, with scattered pubescence on both surfaces Corymb leafy-bracted at base (the primary flowers sometimes not developed), its secondary branches (one or both developed) long, once or twice dividing and bracted throughout with reduced leaves. Peduncles and pedicels hirsute with yellowish-white dark-jointed hairs. Calyx 6 mm. long, the lobes ovate, acute, serrate (with shallow callous-tipped serratures), densely hirsute. Corolla: the posterior lip 2–3 mm. long, 4 mm. wide, arched, the two lobes united and hooded, but not to apex (leaving a slit-like aperture into hood), anterior lip 15–21 mm. long, 14–18 mm. wide, narrowed at base, with narrow orifice, hooded almost entire length (sac strongly upcurving against hood); externally pubescent with short hairs on posterior lip, with longer hairs on base of anterior lip, within pubescent at base. Filaments very short or not developed. Anthers straight, 4 mm. long, the two sacs separated on two arms of the connective; posterior sac 1.5 mm. long, yellowish, opening throughout, fertile, concealed within hood; anterior sac short, orange-yellow, sterile, projecting into the orifice, the club-like dark connective-arm serving as a lever against which entering insect pushes, thus forcing the fertile sac out through the slit-like aperture of the hood and against back of insect. Style 2 mm. long. Capsule 6 mm. long, globose pyramidal, obtuse, pubescent with glandless hairs. Seeds .6–.7 mm. long, oblong, obtuse, ridge-angled, brown.

Type, swale, "Balsillas," on Rio Balsillas, altitude 2000–2100 meters, collected in flower and fruit August 3, 1917, Rusby & Pennell 710; in Herb. New York Botanical Garden.

Swales, at an altitude of 2000 to 2100 meters, Subtropical zone of eastern slope of Cordillera Oriental, in Huila.

**18. Fagelia pinnatisecta** Pennell, sp. nov.

Stem ascending, 2–6 dm. tall, little branched, pubescent above with many-celled dark-jointed not or scarcely gland-tipped hairs. Leaves 3–5.5 cm. long; the blades acuminate at apex, pinnatisect (cut nearly to midrib) with three pairs of lanceolate, irregularly serrate-dentate segments, (the odd terminal segment largest) 2–3.5 cm. long, 2–3 cm. wide; each on a petiole 1–2 cm. long, narrowly winged, somewhat hirsute, proximally slightly expanding and connate with that of opposing leaf; green and pubescent above, beneath pale, and hirsute pubescent on the main veins, sparsely so over surface. Corymb leafy-bracted at base (the primary flowers not developed), its secondary branches long, once or twice dividing and leafy-bracted throughout with reduced leaves. Peduncles and pedicels hirsute with yellowish-white dark-jointed hairs. Calyx 7–9 mm. long, the lobes lanceolate or narrowly ovate, acuminate, serrate (with not or scarcely callous-tipped serratures), hirsute, especially proximally. Corolla: the posterior lip 2–3 mm. long, 2–3 mm. wide, arched, the two lobes united and hooded, but not to apex (leaving a narrow aperture into hood); anterior lip 8–10 mm. long, 6–7 mm. wide, narrowed at base, hooded over $\frac{2}{3}$ length (sac strongly upcurving against hood); externally and within slightly pubescent about base. Filaments very short or none. Anther with the two sacs separated on two arms of the connective, each about 1.6–1.8 mm. long; posterior sac 1.2 mm. long, yellowish, opening throughout, fertile, concealed within hood; anterior sac short, orange-yellow, sterile, projecting into the orifice, the club-like dark connective-arm serving as a lever as in *F. scalaris*. Style nearly 2 mm. long. Capsule 4 mm. long, broad-globose, rounded, pubescent with glandless and some gland-tipped hairs. Seeds .6–.7 mm. long, oblong, obtusish, ridge-angled, brown.

Type, swale, "Balsillas," on Rio Balsillas, altitude 2000–2100 meters, collected in flower and fruit August 3, 1917, Rusby & Pennell 721, in Herb. New York Botanical Garden. From the same swale as 710, *F. scalaris*.

Swales, at an altitude of 2000 to 2100 meters, Subtropical zone of eastern slope of Cordillera Oriental, in Huila.

### 21. RUSSELIA Jacquin.

*Russelia* Jacq., Enum. Pl. Carib. 25. 1760.

Type species, *R. sarmentosa* Jacq., of Cuba.

**1. Russelia colombiana** Pennell, sp. nov.

Herb, or shrubby below, diffuse, reaching 5 feet long. Stem 6-angled below, sharply 4-angled above, glabrous or with sparse pubescence. Leaves in threes, the upper opposite, ovate, 5 cm. long, 3 cm. wide, truncate at base, strongly acuminate, sharply serrate-dentate with ascending teeth (bracts lance-ovate, coarsely toothed), glabrous nearly from the first, green, with brown wax dots on upper surface. Inflorescence much elongated, of axillary cymes. Cymes hirtellous, 5–15-flowered. Calyx 4 mm. long, with brown wax dots, its lobes narrowly ovate with caudate pubescent tips nearly equaling the length of the body, slightly pubescent. Corolla red, 10–11 mm. long, its lobes 1.5 mm. long, the posterior united $\frac{1}{2}$–$\frac{2}{3}$ their length; externally glabrous, within on anterior side pubescent with yellow hairs. Stamens and pistil glabrous throughout. Capsule brown, globose-ovoid, 4.5–5 mm. long, with a slender beak 1–1.5 mm. long.

Related to *R. sarmentosa* Jacq. of Cuba, which differs in the stem being 4-angled, its leaves smaller, with rounded teeth and obtuse at apex, its sepals with shorter caudate tips, its corollas slightly larger, 12–14 mm. long, and its capsules smaller, excluding the beak, only 4 mm. long.

Type, in mountain forest, on the Agua Dulce road, between Santa Marta and the Sierra Nevada, altitude 450 meters [ = 1500 feet], collected in flower and fruit November 22, 1898, Herbert H. Smith 1361; in Herb. New York Botanical Garden; isotypes in United States National Herbarium, Gray Herbarium and Field Museum of Natural History.

Forest, at an altitude of 450 meters, Tropical zone on lower slopes of Sierra Nevada de Santa Marta in Magdalena.

### 22. ANGELONIA Humboldt and Bonpland.

*Angelonia* Humb. & Bonpl., Pl. Aequin 2: 92. 1809.

Type species, *A. salicariaefolia* H. & B.

1. **Angelonia salicariaefolia** Humb. & Bonpl.

*A. salicariaefolia* Humb. & Bonpl., Pl. Aequin. 2: 92. pl. 108. 1809. "Habitat in America meridionali ad Caracas." . . . "Croit sur les collines arides de gneiss, qui avoisinent la ville de Caracas, a une hauteur de cinq ou six cents toises [ca. 1000–1200 m.] ou-dessus du niveau de l'ocean." Specimen from Caracas, Otto Kuntze 1407, seen in Herb. New York Botanical Garden.

Gravelly slopes, rather moist, along the lower western slopes of the Cordillera Orientál, and the similar eastern slopes of the Cordillera Centrál, doubtless continuously encircling the upper Magdalena Valley; in the Cauca valley; extending eastward along the northern lower slopes of the Venezuelan Andes; at altitudes of 450–1400 meters. Tropical zone.[4]

Cundinamarca. Anapoima, J. Triana (Y); Fusagasugá, I. F. Holton 577 (Y); Fusagasugá to Pandi, Pennell 2714 (Y); Icononzo, Pennell 2761 (Y).

Tolima. San Lorenzo, (first foothill of Cordillera Central, west of), Pennell 3517 (Y).

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[4] *Angelonia angustifolia* Benth.

Specimens collected from plants cultivated at "Medellin," on the bank of the Rio Sinu, Bolívar, Pennell 4141 (Y) appear to be this commonly cultivated species of Mexico. The two plants are readily distinguished:

Herbage densely glandular-pubescent. Leaves lanceolate., clasping at base. 1. *A. salicariaefolia.*

Herbage glabrous or sparsely glandular-pubescent. Leaves linear-lanceolate, narrowed at base. 2. *A. angustifolia.*

Huila. Neiva (open slope of first foothill of Cordillera Oriental, east of), Rusby & Pennell 1082 (Y); Quebrada de Angeles, above Natagaima, Rusby & Pennell 284 (Y).

Valle. Cali, H. Pittier 632 (V).

### 23. LINARIA Miller.

*Linaria* Mill., Gard. Dict. ed. IV. 1754.

Type species, *Antirrhinum linaria* L., Sp. Pl. 616. 1753, of Europe.

**1. Linaria texana** Scheele.

*Linaria texana* Scheele in Linnaea 21: 761. 1848. "Zwischen Houston und Austin [Texas] haufig: Römer." Type not seen nor verified, but description evidently of plant here characterized.

Meadow-land, on the Sabana of Bogotá, at an altitude of 2600 to 2650 meters, certainly introduced. Widespread through western temperate North America, and collected extensively in Andine and Temperate South America, probably always as a weed.

Cundinamarca. Sibaté (meadow on sabana, alt. ), Pennell 2469; Hacienda de Tequendama, I. F. Holton (Y).

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# A GRAFT-CHIMERA IN THE APPLE

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# A GRAFT-CHIMERA IN THE APPLE

## Evidence That the Two Distinct Types of Fruits on the Same Tree Are Not Due to Bud Sporting or Top-Grafting

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THE accompanying plate illustrates two distinct sorts of fruits borne on an apple tree that has evidently never been top-grafted. The fruit shown at the right is typical of the King variety; the other is nearly identical with the fruits of the Rockbury Russet. The two types of fruit are quite distinct in respect to size, color, character of skin, flavor, and texture, and the leaves of the branches bearing them are noticeably different especially as to size.

The tree which bears these two kinds of foliage and fruits stands in the vicinity of Geneva, N. Y., in an orchard owned by Mr. T. D. Whitney. Mr. Whitney helped plant the tree in 1862, has resided on the place ever since, and has for many years observed the dual nature of the tree.[1]

At the present time the tree is large and well developed and is about 30 feet in height and in spread. Most branches bear the Russet fruits. About 20 of the smaller branches bear King fruits and these branches are well scattered, being found among the tip branches of all of the large main divisions of the trunk.

### EVIDENCE OF THIS AS A CHIMERA

The occurrence of two more or less distinct kinds of fruit on the same tree may be due to any one of three causes, as follows: (1) vegetative variation or bud sporting, (2) the usual consequence of top-grafting, or (3) an unusual and somewhat indirect result of grafting, which gives a plant in which the two kinds of cells belonging to stock and scion become associated together in the same branches, giving what is now known as a chimera.

Dr. U. P. Hedrick, of the Geneva Experiment Station, is convinced that bud sporting has not occurred in the tree in question. He does not consider it probable that these two types of fruit which differ so widely in several characters can be so closely related as to be parent stock and bud sport.

Mr. Whitney is positive that the tree was never top-grafted. His continuous association with the orchard from the time of its planting to date, his wide knowledge of apples, and his definite recollection of this particular tree make this point seem certain. The scattering branches which bear King fruits have not grown from King scions that were grafted to branches of a Russet tree.

### CHIMERAL FRUITS FOUND

Very definite evidence that the King branches are not simple top-grafts is also seen in the chimeral fruits which are sometimes found. Such fruits have a segment that is King while the rest are Russet. These show that the two cells of the King and Russet varieties are associated together in single twigs, leaves and fruits. Such a combination has thus far not been produced as a direct result of grafting but chimeras of this class or rank very frequently occur in bud sports, they have now been produced experimentally, and they have also arisen incidentally as indirect products of grafting, giving what has frequently been called "mixed plants."

Several cases of "mixed plants" have long been known to horticulturists and for many years these plants aroused much discussion as to their origin and nature. One of these is the Bizzaria or-

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[1] The writer recently had the pleasure of visiting this interesting tree together with Dr. U. P. Hedrick, Mr. O. M. Taylor, and Mr. W. O. Gloyer, of the staff of the New York Experiment Station, all of whom shared in the observations recorded here.

TWO VARIETIES OF FRUITS ON THE SAME TREE

An interesting case of a graft-chimera in the apple is shown in these two distinct sorts of fruits produced by the same tree. The fruit at the right is of the King variety, and the one at the left is a Russet. The tree bearing these fruits has two different kinds of foliage well scattered throughout the branches. The fruits differ distinctly in size, color, flavor and texture. Enlarged about one-fourth. (Fig. 28.)

ange which appeared in Florence, Italy about 1644. On some of its branches oranges are produced, on others citrons develop, and on other branches the fruits are part orange and part citron as shown on page 522 of Vol. 5 of this Journal (December, 1914). Another plant known as *Cytisus Adami* originated in 1825 as a branch of a plant grown from a graft between *Cytisus purpureus* and *Laburnum vulgare.* Some branches of this plant are pure *Cytisus purpureus*, others are pure *Laburnum vulgare*, others are various mixtures of the two, and others bear leaves that are intermediate in character. Several types of plants are known which appear to be mixtures of the two species *Crataegus monogyna* and *Mespilus germanica.* All of these have been propagated vegetatively and have been objects of more than usual interest. How these plants originated has been a matter of no little discussion and speculation among botanists and horticulturists.

### GRAFTING TO PRODUCE CHIMERAS

The experimental production of chimeras in rather recent years has shown very clearly how such plants can arise incidentally through the practice of grafting. By a simple but ingenious arise incidentally through practice of grafting. By a simple but ingenious method of experimentation Dr. Winkler, now Director of the Botanical Garden at Hamburg, produced such plants under observation and control. He used the tomato and nightshade, two distinct and well-known species with marked differences in leaves, flowers and fruit. He made grafts, and when the scions were well established he decapitated the branches by cutting through the points of contact between scion and stock, thus exposing on the cut surface the two kinds of tissue and the lines of contact between them. On this surface a callus formed from which buds arose. If a bud arose entirely from the part that was nightshade the branch was nightshade only; if from tomato tissue the branch was pure tomato. If, however, a branch arose over the line of juncture it was composed partly of tomato and partly of nightshade tissue.

### TWO KINDS OF CELLS IN SAME BRANCH

Such branches were called "chimeras." The simpler of these show vertical lines of differentiation; one sector bears the leaves, flowers, and fruits of the tomato while the rest of the branch bears those of the nightshade. Such branches and the plants grown from them by vegetative propagation are called "sectoral chimeras." In such an association of two kinds of cells, each sort retains its own character and the leaves, flowers, and fruits of the two sectors are readily to be identified.

Occasionally, however, branches arose which produced leaves, flowers and fruits that were intermediate or mixed in character. One of these (named *Solanum tubingense*) bears simple leaves like the nightshade but the leaves are more or less lobed and are hairy as the tomato. Another (*Solanum proteus*) resembles the tomato more than the nightshade; the stems and leaves are hairy but the fruits are smaller than those of the tomato. Several types of intermediates were produced and for a time it was believed that these were true graft-hybrids resulting from the actual fusion of certain vegetative cells of the tomato and the nightshade in the region of contact in the graft. Later, however, a study of the internal and minute structure of the cells in these plants revealed that the two kinds of cells characteristic of the tomato and the nightshade are both present, and that one kind exists as one or more continuous layers covering the other kind. It was found that *Solanum tubingense* has one outside or periclinal layer of tomato cells covering a core of nightshade tissue and that *S. proteus* has two such periclinal layers. Other types of the intermediates have one or more outermost layers of nightshade cells covering tissue of the tomato. The plants were thus found to be periclinal chimeras. A photo of four of these intermediates or periclinal chimeras is shown in *The Journal of Heredity*, Vol. 5, No. 12, and an excellent discussion of how such chimeras are produced is there given.

Similar study of *Cytisus Adami* and the *Crataegus-Mespilus* so-called graft-hybrids showed that they are also periclinal chimeras with one or more cell-layers of one species covering a body of cells of the other species.

### INTERACTION OF DIFFERENT KINDS OF CELLS

The rather intimate association of the cells of two different species in the same stem, leaf, flower, and fruit is especially interesting in view of the mutual interactions, mechanical and physiological, that may occur. The evidence indicates that the two kinds of cells remain independent in respect to their own hereditary characteristics, but in the periclinal chimera they interact producing organs that are intermediate in character. Slight differences in the arrangement of the same two kinds of cells also produces vegetative and floral structures and fruits that are quite different in appearance.

While the investigations indicate that the supposed graft-hybrids are in nature only periclinal chimeras, the production of true graft-hybrid through a fusion of vegetative cells is still to be considered possible. In fact Dr. Winkler has presented evidence that this is the case in one adventitious branch that arose from a decapitated graft between the tomato and the nightshade.

The production of sectoral and periclinal chimeras by experimental means readily shows how such branches can arise incidentally on plants grafted by the ordinary methods. New and adventitious buds may arise from the region of union between stock and scion, especially if the upper part of the scion dies. If such a bud arises over the line of contact it may develop as a chimera. Dr. Winkler's studies show that sectoral associations develop more frequently than do the periclinal.

### CHIMERAS THROUGH BUD SPORTING

It should be noted that intra-varietal sectoral and periclinal chimeras frequently arise through bud sporting. Such partial bud sports have been described frequently in the pages of this journal, especially for such conspicuous cases as the loss of green color which is carried on into various new branches.

Some of the albomarginate types of variegated plants (of *Pelargonium* for example) are clearly periclinal associations of green and white cells all of which belong to the particular variety. In the original sport, most probably, a single cell lost the ability to produce the green pigment and this cell was so placed in the growing point that its multiplication by division gave one or more layers of white cells. Once established the relative position of the white and the green cells was maintained rather uniformly in the subsequent development of branches.

It is also to be noted that, in many sorts of variegated plants, though the pattern strongly simulates a chimeral arrangement, it is really due to physiological conditions affecting development of color in the leaf as a whole. In these the colored and colorless areas often cut across cell layers or histogens. Much remains to be learned regarding the development of such local areas of infectious chlorosis, as well as the development of various patterns of anthocyanin coloration in flowers and foliage.

### PROBABLE ORIGIN OF THIS CHIMERA

Mr. Whitney's tree bearing Russet and King fruits is evidently a chimera that has grown from a bud that arose on the line of contact between scion and stock, and is hence to be considered as a graft-chimera. Presumably a scion of King was grafted to the root of a seedling of the Russet in the method of ordinary nursery practice. At any rate the tree is clearly an inter-varietal chimera: some branches are composed of sectors of tissue of two varieties; lateral branches arising from the sector of King are pure for King; those arising from the part that is Russet are pure for that variety, and those that happen to arise from the line of contact continue to be sectoral chimeras. It is possible that in some of the branches the two kinds of tissue are in periclinal relationship and that some fruits possess a skin of one variety and a core or body of the other. Rather careful examination of a large number of fruits by one competent to judge the flavor would be necessary to determine this point.

CONTRIBUTIONS FROM THE NEW YORK
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# A BOTANICAL EXCURSION TO THE BIG CYPRESS

By JOHN K. SMALL

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# A Botanical Excursion to the Big Cypress

By

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Head Curator of the Museums and Herbariums of the New York Botanical Garden

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# A Botanical Excursion to the Big Cypress

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THE most extensive physiographic trinity or the largest prairie-marsh-swamp region, and at the same time the least known area in the eastern United States, is in southern Florida. The "Big Cypress," or the Big Cypress Swamp, lies south of the Caloosahatchee River between the Everglades and the Gulf of Mexico. The greater part of our population is ignorant even of this geographic designation. To the few who have seen it printed on maps the name signifies nothing, or conveys but a vague idea. Only a score or two of surveyors, hunters, and prospectors, out of the hundred million inhabitants of the United States, have any definite knowledge of its physical geography.

The second week of May, 1917, we were on the very edge of the Big Cypress when we navigated Lake Hicpochee during a cruise to Lake Okeechobee. The day we returned from that cruise, which was described in former papers,[1] an opportunity to explore some of the mysteries of the Big Cypress unexpectedly presented itself. Mr. W. Stanley Hanson, a bird inspector with the United States Biological Survey, and a naturalist well acquainted with the Big Cypress, had come to Miami across country from Fort Myers, whence he was about to retrace his course. The opportunity to accompany him on a trip through largely unknown territory was a temptation too great to be resisted. Consequently, we prepared a Ford for a week's run, and the next day set out for Fort Myers. Miami and Fort Myers are about 120 miles distant from each other, in a direct line, but the intervening area could have been conveniently, or at least expeditiously, traveled only in an aëroplane. The shortest course possible for us followed a curve more than 250 miles in length.

In order to bring us to our most distant objective which lay across the Everglades only about sixty miles from Miami, we had to make a detour around the Everglades and Lake Okeechobee at their head. The facilities for making an examination of the country and a collection of specimens of its vegetation were generously furnished by Mr. Charles Deering, of Miami.

The first stage of our course lay along the eastern coast of Florida between Miami and Fort Pierce. Miami, Fort Pierce, and Fort Myers are about equidistant one from the other, or, straight lines connecting the three places would form an equilateral triangle. The territory included in the triangle, made up mostly of everglades, prairies, cypress swamp, and pineland, together with Lake Okeechobee situated near one side of the triangle, was essentially uninhabited, except for the scattered settlements in the Caloosahatchee River region. Between Miami and Fort Pierce pinelands and sand dunes (scrub[2]) predominate; between Fort Pierce and Fort Myers are pinelands and prairies; while between Fort Myers and Miami lie prairies, cypress swamps, and the Everglades.

Mr. Hanson preceded us to West Palm Beach, where we overtook him. It was late in the evening when we reached Stuart, where we had to spend the night because of a high wind which made the ferryman hesitate to carry us across the Saint Lucie River. An early start the next morning brought us to Fort Pierce in time for breakfast. Thence we started on the second leg of the triangle, proceeding in a southwesterly direction.

Between Miami and Fort Pierce our course took us through not fewer than forty towns.[3] After leaving Fort Pierce only four settlements were encountered, two established settlements and two embryonic colonies.

After Fort Pierce disappeared from view we sped westward through pinelands and across the Halpatiokee Swamp, where countless turtles and snakes basked in the sun about the water pools that lined the road.

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[1] *Journal of the New York Botanical Garden*, Vol. XIX, 1918, pp. 279–90. THE AMERICAN MUSEUM JOURNAL, Vol. XVIII, 1918, pp. 684–700

[2] These are quiescent inland dunes of snow-white sand.

[3] These lie outside of the triangle of uninhabited territory referred to in a previous paragraph.

A TRANQUIL JUNGLE STREAM ON THE INDIAN PRAIRIE

Fisheating Creek, or, in less commonplace parlance, "Thlathtopopkahatchee," is still little known, because it runs through nearly uninhabited country. It rises as a drain for a greatly elongated (twenty-five mile) slough which lies near or forms the western boundary of the southern extension of the lake region of Florida. The creek is almost equal in length to the slough it drains. It meanders through pine woods and through prairies, ultimately reaching Lake Okeechobee. Its banks are often hammock clad. Live oaks, sweet bays, and red maples predominate on the shores, and in some places conifers—pine or cypress—or cabbage trees replace the hammock. Occasionally long stretches of water are completely concealed by floating carpets of water hyacinth, and others, clear of all aquatic plants, sharply mirror the bordering vegetation

After crossing the swamp another stretch of sandy pine woods was traversed with difficulty, as the combined power of the engine and the pushing ability of the occupants of the car were necessary to get through the twelve miles of loose sand. Finally the Onoshohatchee River and the first habitation in about forty miles came into view. We soon reached Okeechobee City—then a settlement of several scores of houses. In the fall of 1913 when we went up the Onoshohatchee River from Lake Okeechobee this place had been indicated on the map and staked out by the surveyors, but had not yet been colonized.

At this point we again left civilization behind. From Okeechobee City to Fisheating Creek the country was devoid even of roads, and we took to an old trail dating back perhaps to a period before the Seminole wars. By degrees Okeechobee City disappeared as we hurried around the curves, not to say coils, in the trail, and after passing some miles of pinelands we suddenly came into the bottoms or prairies of the Kissimmee River. These bottom lands are like immense lawns, perfectly level, carpeted with a turf of various grasses, and often extending as far as the eye can see. There were thousands of semiwild cattle grazing on the broad green prairies.

All had gone well thus far, but at the Kissimmee River a series of apparently predestinated troubles began. The trails on either side of the river were connected by a ferry which consisted of a flatboat large enough to hold a car, and a small motor boat of barely sufficient capacity to drag the flatboat around the bends and over the sand bars in the river. In order to cross the river, which there is less than a hundred feet wide, it was necessary to go about a half mile down stream because of the erosion of the banks. Once in the stream the current of the river—say, three miles an hour—carried the ferryboat along at a greater speed than the motor boat could maintain. Time and again the ferryboat would bump into the river banks, first on one side, then on the other, and would, in turn, bump against the stern of the little motor boat and knock off the rudder. Even after the ferryboat drifted out of sight, we who were left behind for the second trip could hear the ferryman nailing the rudder on his disabled boat.

We lost several hours of valuable daylight while waiting for the ferryman to replace dead batteries with live ones. As the short twilight deepened we ran up a slight incline through a strip of pine woods, making all haste compatible with the innumerable curves in the trail and the proximity of pine stumps, and found ourselves on the great Indian Prairie. This comprises a large part of an immense region lying west of Lake Okeechobee, north of the Caloosahatchee River, and east of Peace River. The prairie is high and dry all the year round and is uninterrupted, except by a single stream, Fisheating Creek, one of the larger feeders of Okeechobee. Up to a short time ago it was practically uninhabited, except by wandering Indians. At the present time a half dozen or more "—ports," "—dales," "—monts," "—burgs," and even "—Cities" have been put on the map, and a railroad bisects the region,—so, farewell to its natural features.

In order to save time, we decided to cross the prairie that night, and we certainly had a weird ride. The trail at times was distinct, but at other times almost blind. Although the prairie was a dead level, the optical illusion created in the darkness was that of running down hill and jumping off the earth. We had some obstructions to progress in the form of forks in the trail which would, we knew, either come together farther on or diverge indefinitely and thus lead to some other part of the state. At each fork, the four in our party would hold a council, and in each instance consult the stars. The stars always put us on the right trail, and toward midnight, after passing several half-discerned Indian camps, we saw a few faint lights of human habitation appear, and finally we reached the recently established colony of Palmdale on Fisheating Creek, or, in Seminole, "Thlathtopopkahatchee."

We did not hesitate to disturb the peaceful slumbers of the inhabitants, who were as glad to see us as we were to see them, which fact they showed in a substantial manner by arising from their slumbers and preparing a midnight meal. After a few hours' rest we made an early start for Labelle, which is an old settlement situated at about the head of natural navigation on the Caloosahatchee River.

The Indian Prairie extends nearly or quite to the Caloosahatchee. Unfortunately, a road had been laid out to connect Palmdale with Labelle. It is well we decided to stop at Palmdale until daylight, for although we could travel the almost trackless prairie in the dark with ease, we could barely traverse this new road in broad daylight. The deep sand had become very loose, and it took more than the engine to get the cars over a good many miles of the road.

Just south of Palmdale we crossed Fish-eating Creek, which is an exceedingly picturesque stream meandering through the almost uninhabited prairie, between banks either exposed to the sun, or clothed with shrubs and bright-colored asters or hammocks of oaks, ash, and maple, which in some places give way to groves of palmettos that often lean far over the water's edge. After leaving the hammocks which border the creek we drove out on the prairie again, and few trees came into view for a distance of about eighteen miles, until the hammocks bordering the Caloosahatchee appeared.

Perhaps the most interesting creature on these prairies was the burrowing owl. This bird had honeycombed the prairie in many places with its burrows. These tunnels, often six to eight feet long, are about a foot beneath the surface of the sand. At one end is an opening approximately six inches in diameter, while at the other end is a nest. The old owls were so tame that one could almost pick them up, and often they would sit perfectly quiet while the automobiles passed them at a distance of not more than two feet.[1]

On this same prairie many interesting plants were observed and collected. Milkweeds were represented by species of *Asclepias* and *Asclepiodora,* while more conspicuous was the purple water willow (*Dianthera crassifolia).* Low milkworts *(Polygalæ)* with white and yellow flowers were prominent in the landscape, and clumps of the native beardtongue (*Pentstemon multiflorus*) towered above all the other herbaceous plants. There a white-flowered heliotrope replaced the common yellow-flowered heliotrope of the region lying east of the Okeechobee basin and the Everglades.

After contending with the sand for several hours we reached the Caloosahatchee River and came to the town of Labelle, where we did not delay, but went directly up the Caloosahatchee several miles to Fort Thompson. There we found a number of magnificent live oaks around the old barracks which date from the period of the Seminole wars. After making a number of photographs in that region we returned to Labelle and at once started down the south bank of the Caloosahatchee River for Fort Myers.

We now left the prairies behind and entered the flatwoods, where the arboreous vegetation is made up almost entirely of pine trees. Peninsular Florida, especially the southern part, lacks what is ordinarily understood as altitudes, in fact, most of it is decidedly flat. It might well be called a large sand bar. Notwithstanding this disadvantage, it reveals an astonishing number of surprises in the matter of diversity. The Big Cypress is one of the larger surprises. Its area is about half that of the

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[1] Out of curiosity we decided to dig into one of the burrows. Starting at the opening, we began by lifting the sand out very carefully. Of a sudden we were startled by the rattle of a rattlesnake. After proceeding a few inches farther we heard two rattlesnakes; before going much farther into the burrow a third rattlesnake began to rattle. The digging became more exciting as we worked farther in and as the snakes rattled more loudly. When we neared the end of the burrow we cautioned one another to be careful not to get our hands too close to the snakes.

This seemed to be an excellent opportunity to get good photographs of living rattlesnakes. Consequently the camera was set up and everything prepared for the opening of the end of the burrow. As there was no woody growth on the prairie the question of getting sticks with which to fight the snakes arose. After considerable search several surveyor's stakes were found, and with these we prepared nooses for capturing the serpents alive. With extreme caution we approached the end of the burrow; the snakes began to rattle more viciously. Finally the sand was removed from the top of the end of the burrow, and to our surprise we found four young owls, three large and one small, but—no snakes!

It was the three larger owls that were making the noise of a rattlesnake, and imitating it so well that all of us who had had personal experience with rattlesnakes were deceived. We decided that this experience proved that the stories we used to hear of owls, prairie dogs, and rattlesnakes living peacefully together in the same burrow were fantastic. Of course, a rattlesnake might enter an owl's burrow, either to seek shelter or food; but it is a difficult matter for any one well acquainted with the habits of rattlesnakes to believe that a husky rattler would be considerate and restrain his appetite, with such a tempting morsel as a young owl or young prairie dog lying about in his den. (For further notes on this subject see: *The American Naturalist,* Vol. XLI, pp. 725–726; Vol. XLIII, pp. 754–55; *Birds of the World,* pp. 536–37.) After photographing owls instead of rattlesnakes, we replaced them in their nest and rebuilt their burrow, as well as we could, by making a roof of brush over which we replaced the sand.

Palms and pine trees are often a favorite refuge for wild turkey and deer. A flock of turkeys took refuge in this particular grove just as we suddenly rounded a sharp curve in the trail. In the Big Cypress there may be prairies so extensive that woody vegetation can be seen merely as a dark line along the distant horizon, or again we may see at one time associations of palms and pines, pure pine woods, solid broad-leaved hammocks, cypress heads, and combinations of cypress head and hammock

Everglades, and although it abuts directly on the western side of them, it has but little in common with them. Instead of being a vast prairie-marsh like the Everglades, the Big Cypress exhibits a variety of conditions and plant associations. There are pinelands, prairie, sloughs, cypress heads, hardwood hammocks, palmetto hammocks, and lakes.

Early in the afternoon we were prepared to strike into the wilderness. After leaving Fort Myers, roads disappeared and we took to mere trails through the pine woods in a southeasterly direction. As we proceeded, strange plants and strange birds began to appear. White terrestrial orchids (*Gymnadeniopsis nivea*) and single-flowered spider lilies (*Hymenocallis humilis*) dotted the dry prairies, while uliginous creepers with various colored flowers formed encircling mats about all the shallow ponds. Ponds and pools were the favorite feeding places for the wood ibis, the white ibis, cranes, and herons. The hammocks hid many flocks of wild turkeys in their depths.

For some distance outside of Fort Myers we traveled through unbroken pine woods. As we went on, the pine trees became more scattered and areas of prairie came into view. Farther on, the prairie began to increase and the pines appeared only here and there as isolated colonies. A little farther on cypress trees appeared, and we were really in the Big Cypress. Here, too, the cabbage palm was much in evidence, and in some places it formed hammocks of almost pure growth. As we proceeded, the prairies grew larger and the cypress grew less, until there was open prairie in all directions almost as far as the eye could see. Then the hammocks clothing the Okaloacoochee Slough appeared in the distance as a mere line on the horizon. It is said that the Seminole word "Okaloacoochee" signifies "boggy-slough." Consequently the usually associated word "slough" is really superfluous.

As we approached the slough we observed immense flocks of ibis collecting at their rookery for the night. The confused sounds they made as they flew over the tops of the tall trees could be heard for a distance of a mile. The sight of the great flocks of ibis and the racket of their croaks or squawks as they collected in their rookery we shall long remember.

We drove into a small hammock within half a mile of the slough and prepared to camp there for the night. Many interesting plants were collected on the prairies near the slough before darkness drove us back to camp. Indian plantains (*Mesadenia)*, foxgloves *(Agalinis)*, and heliotropes (*Heliotropium*) grew nearly everywhere. Fully as interesting as the native plants was the climbing black-eyed Susan (*Thunbergia alata*), which we found extensively naturalized on the prairie near the Okaloacoochee. The plants now growing there may be the descendants of specimens introduced and cultivated in gardens the Seminoles maintained there fully a century ago.

The following morning we broke camp about daybreak and proceeded to cross the slough. We parked our cars in its midst on the very spot where, it is said, more than sixty years ago Lieutenant Harsuff's company of engineers had their sanguinary clash with Chief Billy Bowlegs—after they had destroyed the old chief's garden just to "see old Billy cut up."

The larger trees of this hammock consist of the bald cypress or river cypress (*Taxodium distichum*). It was a favorite spot for the Indians to obtain logs for making their dugout canoes. In the rainy season there is commonly about six feet of water in the slough. After the rainy season the water table is naturally lowered by seepage. The waters, evidently, find their way directly into the Everglade basin, and directly or indirectly into the Gulf of Mexico. In the dry season most of the slough can be traversed on foot. It was the custom of the Indians to go to the slough in the dry season, cut down the trees they selected for making the canoes, and then wait for the wet season and high water to float the logs out toward the western coast.

We went down the slough afoot just as the thousands of birds in the rookery were awakening. The birds mostly represented several species of ibis, and were present by the hundreds and thousands on the large cypress trees. In fact, they were so crowded on some of the giant cypresses that they were continually falling off for want of sufficient room to stand. As a consequence of not having been much disturbed by man, they were so tame that one could walk

In the Okaloacoochee Slough dead trees as well as living serve as part of the ibis rookery, for the birds are so numerous that any available space is used. Their nests are rude cradles of sticks in the trees or on ledges of rock. During the day the birds leave the rookery, traveling in more or less definite groups or companies. This photograph was taken in the morning, after the greater number of the birds had departed

A NATURAL AMBUSCADE

From such beautiful coverts—perhaps from this very spot—commands of the United States Army fought the Indians during the Seminole wars. A riotous growth of shrubs whose stems are intertwined with woody vines form an almost impenetrable thicket extending back to a wood of river cypress in the lower part of the slough. The hammock floor is a mass of ferns and small herbs; Boston and sword ferns in particular are prevalent. There are at least fifty other kinds of ferns—many of them epiphytic—which display the greatest possible variety in structure and contour toward them, set up a camera, and photograph them at short range.

There was water in the lower parts of the slough, but none was visible, for the surface was completely covered with a soft carpet of various small aquatics. These were distributed in patches of beautiful shades of green. In the higher parts of the slough ferns and flowering plants grew in about equal profusion and remarkable luxuriance. The growth reminded me of that in the hammocks of the eastern shore of Lake Okeechobee.[1] The large, straplike leaves of the spider lily and the paddle-like leaves of the golden club or bog torches (*Orontium*) were very conspicuous. The leaves of the golden club here at its most southern known station were fully three feet long, while the fruiting spadices lying around on the ground were thrice the size of any that I have ever observed at the north. The lizard's-tail (*Saururus*) was also there in great abundance.

Thus these typically northern plants, the lizard's-tail and golden club, are there intimately associated with such typically southern plants as the water hyacinth and the water lettuce. Other southern elements represented are the Boston fern (*Nephrolepis exaltata*) and the wild coffee (*Psychotria undata*).

After making a collection of all the plants observed and photographing the more interesting views, we returned to our cars, crossed the slough, and set out over the prairie in the direction of Rocky Lake, which lies in an uncharted spot in the Big Cypress between the Okaloacoochee Slough and the Everglades. As we proceeded, palmetto hammocks, hardwood hammocks, and cypress heads became more numerous on the prairie. At last we came to the hammock surrounding Rocky Lake, which is known to the Seminoles as Okee-hy-yot-lochee, a word said to mean "wide-open-water," where we camped for lunch, and made collections of the plants. This lake is contained in a rock basin several acres in extent. It is said that it is fully seventy-five feet deep, and abounds in fish and alligators. Of course, it would be somewhat of an exaggeration to say that one could walk across the lake on the alligators' backs; but they were more numerous than I have ever seen them elsewhere.

After lunch we set out for the ruins of an Indian mission[2] which some years before had been established near the site of the one-time Fort Shackleford, and then abandoned. After leaving Rocky Lake the trail wound in and out between hammocks and cypress heads until finally more open prairie was reached.

When we arrived at the Seminole mission we were now not more than four miles from the western edge of the Everglades. A unique specimen of the cabbage tree was observed—a five-fingered object, with ~~five~~ branches of about equal length arising from the trunk, just above the surface of the ground and all in one plane. Probably nowhere is this duplicated. Many interesting plants were found in the vicinity, especially several loosestrifes (*Lythrum*), and a false indigo (*Amorpha*) which is apparently different from any known species.

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[1] See *Journal of the New York Botanical Garden*, Vol. XV, pp. 69–79; Vol. XIX, pp. 279–290. The AMERICAN MUSEUM JOURNAL, Vol. XVIII, pp. 684–700.

[2] The old Seminole mission thirty-five miles beyond Immokalee was established about 1910–11 through the instrumentality of William Crane Gray, then Bishop of southern Florida, for the Protestant Episcopal Church, the work being undertaken by Dr. William J. Godden, of Greenwich, England, who happened then to be touring the United States. Dr. Godden, a man of high connections and attainments, soon won the love of both red and white men. Originally, he started a small hospital and social center for the Seminoles at a point about seventy miles back from Fort Myers, near the historic site of old Fort Shackleford. He called this first settlement Glade Cross—because of its proximity to the Everglades and the large white cross he mounted against a cabbage palm. But when a couple of red patients died in the hospital no more Seminoles could be induced to come near the place. The mission was thereupon transferred to the lonely outpost called Boat Landing, on the edge of the Everglades, at that time the head of all the canoe trails of the region. It was not long, though, before the partial drainage of the Everglades dried the canoe trails, and Boat Landing ceased to be a port of call, or any port at all. So the doctor once more moved his mission, this time to about the center of the present Seminole Reservation, five or six miles from his former locations, right in the heart of the Big Cypress, where he hoped to establish an experimental farm. He put up a number of buildings—a store, a dispensary, various shelters. He employed the Seminoles to dig a couple of miles of drainage ditches about the place. He himself worked far harder than anyone else—without pay, mostly alone, always devoted, perfectly kind—while his people in England urged him to return to them. He died at the mission, suddenly, presumably of heart failure, in 1914. And now Glade Cross is jungle again; only a few broken canoes mark the site of Boat Landing; and the last site of all, still called "Godden's Mission," is merely a weedy, haunted ruin. The doctor's body was buried at Immokalee, a Seminole word which signifies "My Home."—Perley Poore Sheehan.

YOUNG OWLS AT THE FAR END OF A BURROW IN THE SAND

We sometimes find in the sand of the prairie a hole about six inches in diameter—the entrance to the home of the burrowing owls. Such holes occur in "towns" of from three to twelve or more; some parts of the prairie are so honeycombed with burrows that we marvel how they and the nests in them are preserved from destruction during heavy rains. The nest is built about six or eight feet from the opening of the burrow and commonly is only six or eight inches beneath the surface. The parent owls are rather tame and may be approached within a few feet, but the young birds are vicious in appearance, voice, and manner—at least when disturbed. How could anyone

A FLOATING MEADOW OF FLOWERS

The water hyacinth (which completely covers the water in this tributary of the Caloosahatchee) always improves the landscape, and usually is not the impediment to navigation that it has the reputation of being. Moreover, the more or less extensive areas of bright blue flowers set above the deep green leaves are unique in our flora. Live oaks, laurel oaks, and water hickories line the banks of this stream, and the long growths of Florida moss reach from the spreading limbs of the trees to the water

A GIANT TREE OF THE FLORIDA "BIG CYPRESS"

The brilliant green of the river cypress, which largely forests the sloughs, is intensified by contrast with the waving grayish white streamers of Florida moss and the gay pink and white plumage of the nesting ibis. In the widespreading limbs of the giant trees hundreds of the birds roost and when they rise in their powerful flight the sun burnishes their outstretched wings with a metallic sheen that adds a further touch of the picturesque to the landscape. The birds covered the top of this tree when it was photographed, outlining it against the sky, but their colors on the light background failed to impress the photographic plate

NATURE GIVES THEM A FORMAL ARRANGEMENT

Relatively slender and narrow-branched trunks are characteristic of the pond cypress so that it is not adapted to support rookeries. It harbors great quantities of air plants and, although it does not bear a copious growth of Florida moss, several other species of *Tillandsia* cling to its branches,—often through the accumulation of generations the plants form masses out of all proportion to the size of the tree. Pond cypresses are usually evenly spaced as if following an architectural plan, whether they are distant from one another, as here shown, or set so closely together that passage between their trunks is difficult

Wild orange trees, some with sour fruits, others with sweet, occur in the hammocks of the Big Cypress. Of course, some of these are the remnants of trees planted by the Seminoles; but others may be derived from ancestors planted there by the aborigines of that region or by the Spanish adventurers themselves.

The cypress of the region outside of the large sloughs was the pond cypress (*Taxodium ascendens*). The prairies were showy flower gardens. Several species of *Polygala*, several of *Sabbatia*, three or four kinds of terrestrial orchids, and a number of other conspicuous plants, both monocotyledons and dicotyledons, often covered acres in extent. A yellow-flowered bladderwort grew copiously in extensive patches in the dry white sand! Many rare and little-known plants were collected for future study.

Rocky Lake proved to be the lunch station. While in a temporary camp near the shore the writer rescued two animals from living graves. On two different occasions, while going to the lake for a drink of water, he was startled by agonizing cries. In the first instance, a large water moccasin had caught a mocking bird and was attempting to swallow it. In the second instance, another moccasin had caught a frog which he was trying to slip down his throat. In each case the victim went free and, it is to be hoped, survived.

After recrossing the Okaloacoochee Slough, instead of retracing our former course we turned more to the westward and headed for the colony of Immokalee. After passing through stretches of forest and prairie we came in view of the scattered houses of the settlement. This colony, situated about thirty miles in a direct line from Fort Myers, comprises a general store and a few dwelling houses. We reached Fort Myers shortly after sunset, and early the following morning started up the Caloosahatchee River by the same course we had taken several days before. Numerous stops were made along the way for collecting plants and taking photographs. Palmdale, where we took the trail over the great Indian Prairie, was reached early in the afternoon. The herbaceous vegetation and magnificent palmetto hammocks not visible in the dark gave an entirely different impression of the prairie region. Some of the same genera of plants were common to both the Indian Prairie and the Big Cypress but the species were usually different. The Caloosahatchee River is evidently a natural boundary between different floral regions. The most striking feature in the vegetation of this prairie, however, is the cabbage tree. This palm grows in small clumps and also forms hammocks from one to many acres in extent, surpassing in luxuriance any growth of it I had seen previously.

After the usual bumping of banks and sand bars the ferry landed us on the opposite shore of the Kissimmee River whence we at once set out over a trail which seemed to have endless windings, but which finally brought us to Okeechobee City. From there, after a night's rest, we journeyed to Fort Pierce, collecting as we found favorable places in the pine woods and in the swamps, and next day we started on the final stage of our return trip to Miami. The city was reached without further incident, except the passing survey of a large hammock on a high sand dune along Saint Lucie Sound or Lower Indian River, which has already been partly described[1] and which has been designated for thorough exploration.

This preliminary survey deeply impressed upon us the wonderful natural history of that little-known region. Our time was limited and the region was large, but some day, before drainage and other depredations of civilization, not to mention vandalism, have removed the bloom from that still unspoiled garden, we hope to make another and longer visit to the land of the Big Cypress.

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[1] *Journal of the New York Botanical Garden*, Vol. XIX, pp. 76–77.

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# "VERONICA" IN NORTH AND SOUTH AMERICA

By FRANCIS W. PENNELL

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# "VERONICA" IN NORTH AND SOUTH AMERICA.

Francis W. Pennell

This study is the outgrowth of several attempts to revise our knowledge of the species of "Veronica" growing in different portions of the Western Hemisphere. Whether in our own "Local Flora," in the Rocky Mountain or the Southeastern States, or in Colombia and Ecuador, certain wide-ranging species were encountered, and the effort to verify the nomenclature in many instances took the reviewer into problems of the identity of Old World allies. On these accounts it has seemed best to consider in one study the plants of this group in both North and South America, and also to include known naturalized species.

Of all the tribes of the Scrophulariaceae mentioned by von Wettstein in his great revision of the family in "Die Natürlichen Pflanzenfamilien," that of the Digitaleae, to which *Veronica* is assigned, probably has least coherence. The plants at least should agree in having the antero-lateral lobes of the corolla external in aestivation and in not being parasites. I know of no offenders against the latter criterion. But, because they possess not only posterior corolla-lobes external but also form characteristic glands on the fruit or in the leaves, I have recently transferred the two lowland Tropical genera *Capraria* and *Scoparia* to the essentially Tropical tribe Gratioleae. This restricts the Digitaleae to a more likely distribution through the Temperate or Arctic zones and the cooler zones of Tropical mountains. I can not further analyze the tribe here, except to say that *Digitalis* itself, through possessing styles distinct at apex and a

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leaves occur in the perennial species, while the extreme stages of capsule-lobing and flattening, of few and large seeds, and of alternate leaves are in the relatively few annual sorts. Also, as is the general habit in allied genera, the original *Veronicellas* were surely erect herbs.

In *Euveronica* the stem continues indefinitely as a vegetative axis, its leaves opposite throughout, while the inflorescence is localized in specialized axillary racemes. This is the inflorescence of *Hebe,* but the diversity of capsule-structure tells us that such localization must have originated independently in these two groups. Elsewhere in this tribe I know it only in the Chinese *Botryopleuron* Hemsley, which seems to be separated by little else from *Calorhabdos* Bentham. The flowers in the racemes of *Euveronica* are alternate as they are in all inflorescences of *Veronicella.* This accords with the view that these racemes are reduced branches, and not formed by the forking of originally simple pedicels. No stages suggesting the latter alternative are known to exist, and the fact that remote axillary flowers occur in *Veronicella* only in some profoundly modified annual species makes such a derivation very improbable. The species of *Euveronica* are all perennial, and such an erect-growing species as *V. latifolia,* which has a scarcely notched capsule, shows a close approximation in habit to the most primitive group of *Veronicella,* including species such as *V. maritima* and *V. mexicana.*

A few words need be said concerning age and distribution of various species. Contrary to expectation and certain widely advanced theories, it is not those species whose structures proclaim them as most ancient which are necessarily most widely dispersed. Structurally none of our species can make better claim to antiquity than *Veronica mexicana,* yet this species occurs only in a limited area in the mountains of northern Mexico. Obviously it has no close kindred in our flora, and so must, I believe, be considered a relict. Again, *V. Copelandii,* our only other species definitely retaining the posterior sepal, is known from but a few mountains in California. On the other hand, the group of *Veronica alpina* and *V. Wormskjoldii* has a wide range through Temperate North America and Eurasia, although it has become divided geographically into several well-marked species. But it is the obviously non-primitive species which have prospered most and have become or are becoming very widespread. These possess peculiar skill in taking advantage of natural, or recently of man-made, methods of dispersal. Of species naturally distributed, *Veronica serpyllifolia humifusa* and *V. Anagallis-aquatica* have become nearly cosmopolitan within their respective climates and environments, while carried by human agency and today aggressive weeds in our land are *Veronica serpyllifolia, V. peregrina* and its variety *xalapensis, V. arvensis, V. persica,* and *V. officinalis.* To this list, otherwise of Palaearctic origin, America has contributed *Veronica peregrina,* thus showing that the New World may develop sufficiently aggressive plants.

I must thank the curators of the United States National Museum, New York Botanical Garden and Philadelphia Academy of Natural Sciences who have placed their rich collections at my disposal. Also I have seen specimens of certain species from the Gray Herbarium. Probably nearly 4000 sheets have been examined in the present study. It has been with hesitation but I trust to the clearing of the problems involved, that I have ventured so freely into Eurasian botany.

### KEY TO GENERA AND SUBGENERA.

- Capsule dehiscing loculicidally, its walls and septum thin. Herbs, the stem dying with the leaves.
  - Corolla white or pinkish, its lobes much shorter than the tube. Capsule acute, longer than wide, not flattened, dehiscing by short apical slits. Seeds slightly reticulate. Plant 10–20 dm. tall, with leaves in whorls of four or five. Main stem terminating in an inflorescence... I. VERONICASTRUM
  - Corolla blue or white, its lobes nearly as long as or usually longer than the tube. Capsule acutish to deeply notched, as broad as or broader than long, more or less flattened contrary to the septum, dehiscing by longer slits which extend at times even to the base. Seeds not reticulate. Plants lower, with leaves, at least the lowermost, opposite, or very rarely in whorls of three or four..................... II. VERONICA
    - Main stem terminating in an inflorescence, its flowers remote and axillary or densely crowded, in all cases the upper bract-leaves alternate.............................. Subgenus 1. *Veronicella*
    - Main stem never terminating in an inflorescence, the leaves opposite throughout and the flowers all in axillary racemes............ Subgenus 2. *Euveronica*
- Capsule dehiscing septicidally, the thick septum splitting and each carpel opening distally by a median slit through the septal wall. Leaves opposite throughout, and flowers all in axillary racemes. Shrubs or small trees, the coriaceous leaves in falling leaving conspicuous scars...... III. HEBE

### I. **VERONICASTRUM** [Heister] Fabr.

*Veronicastrum* [Heister] Fabr., Enum. Meth. Pl. Hort. Helmstad. 111. 1759. (Checked only in second edition, 205. 1763.) Type species, *Veronica virginica* L.

1. **Veronicastrum virginicum** (L.) Farwell.

*Veronica virginica* L., Sp. Pl. 9. 1753. "Habitat in Virginia." Plant grown in the Clifford Garden in Holland, and carefully described by Linné, Hort. Cliff. 7. 1737. No pubescence on leaf mentioned.

*Veronicastrum album* Moench, Meth. Pl. Hort. Marburg. 437. 1794. " . . . . . *Veronica virginica* Linn." Grown in the Marburg Garden, Germany.

*Calistachya alba* Raf. in Med. Repos. New York. II. **5**: 352. 1808. Based on *Veronica virginica* L. Type species of *Calistachya* Raf., not *Callistachys* Vent., 1804.

*Veronica quinquefolia* Stokes, Bot. Mat. Med. **1**: 28. 1812. "In a garden . . . . . *V. virginica* L." Evidently name chosen as more appropriate than "virginica." Two varieties, or actually forms, *alba* and *incarnata*, are listed.

*Leptandra virginica* (L.) Nutt., Gen. N. Am. Pl. **1**: 7. 1818. Type species of *Leptandra* Nutt.

*Eustachya alba* Raf., Cat. Ky. 14. 1824. Based upon *Veronica virginica* L. *Eustachya* Raf. in Am. Mo. Mag. **4**: 190. 1819, was a new name for *Calistachya* Raf. Name antedated by *Eustachys* Desv., 1810.

*Leptandra virginica purpurea* Eaton, Man. Bot. ed. V. 275. 1829. " ——— " Described as with "flowers purple." Credited to Pursh, who however assigned his color variety no name. According to Pursh, Fl. Am. Sept. 10. 1814: "On the mountains of Virginia I observed a . . . . variety with purple flowers."

*Leptandra purpurea* Raf., Med. Fl. **2**: 20. 1830. "Confined to the savannas of the South and the West [of the United States]." Carefully described; a purplish-flowered, single-spiked plant with sessile leaves in whorls of three. Three varieties, or actually forms, named.

*Leptandra alba* Raf., l. c. 21. 1830. "The most common species, being found all over the United States." Described with white flowers and semi-petiolate leaves in whorls of usually five. Several varieties, or actually forms, named.

*Leptandra villosa* Raf., l. c. 21. 1830. "Mr. Schriveinitz [Schweinitz] has found it in North Carolina." Careful description of the form with leaf-blades pubescent beneath. This may be considered a forma **villosa** (Raf.) Pennell, comb. nov.

*Eustachya oppositifolia* Raf., New Fl. Am. **2**: 21. 1837. "Mts. Apalaches of Virginia." Apparently an opposite-leaved *virginica*, a form which I have never seen.

*Calistachya virginica lanceolata* Farwell in Mich. Acad. Sci. Rep. **17**: 176. 1915. "Farwell No. 1165, July 18, 1891, from Ypsilanti [Michigan]." A narrow-leaved form.
*Veronicastrum virginicum* (L.) Farwell, Drugg. Circ. **61**: 231. 1917.

Meadows and open woods, from Vermont, southern Ontario and Minnesota to Georgia and eastern Texas. Southward forma *villosa* is more prevalent.

Variable, but certainly one species. Varying in number of leaves in whorl (five, four, rarely three, or in *oppositifolia* even two), in leaf-form from lanceolate to nearly ovate, pubescent or nearly or quite glabrous below (forma *villosa* with whole under surface velvety), in inflorescence being of one or several racemes, and in color of corolla and filaments, varying from white through pinkish to lighter shades of violet-purple.

### II. **VERONICA** L., Subgenus 1. VERONICELLA (Fabr.)

*Veronicella* [Heister] Fabr., Enum. Meth. Pl. Hort. Helmstad. ed. II. 205. 1765. Type species, *Veronica hederaefolia* L., of Europe.

A. Perennials, from subterranean stems (rootstocks). Only the upper leaf-axils flower-bearing, so that inflorescence is formed of definite racemes.

B. Capsules only slightly flattened, even the lowermost on pedicels shorter than the capsule-length: inflorescence appearing a spike. Style two or three times the length of the capsule. Leaf-blades lanceolate. Plants 4–10 dm. tall.

Petals broadly oblong. Leaves opposite or in threes, rarely in fours, 3–15 cm. long, the blades acute to acuminate, dentate-serrate to sharply and somewhat doubly serrate. Plant 4–10 dm. tall........................1. *V. maritima.*

Petals oblong-lanceolate. Leaves always opposite, 3–6 cm. long, the blades acutish, crenate or crenately serrate. Plant 2–4 dm. tall.........2. *V. spicata.*

B′. Capsules strongly flattened, the lowermost on pedicels nearly or quite as long as the capsule-length; inflorescence obviously a raceme. Style slightly, if at all, longer than the capsule.

C. Capsule as long as or longer than wide, less deeply or not notched. Corolla violet-blue, rarely nearly white, glabrous within. Leaf-blades obtuse, acutish to acuminate. Stems erect, nearly or quite from the base.

Calyx 5-parted, the posterior lobe over half the length of the others. Leaf-blades lanceolate, acuminate, irregularly dentate. Plants 5–6 dm. tall......................3. *V. mexicana.*

Calyx 4-parted, or with a rudiment of the fifth lobe. Leaf-blades ovate to oblanceolate, obtuse to acutish, entire to serrate. Plants less than 3 dm. tall.

Style longer than the capsule. Filaments equaling or exceeding the corolla. Calyx-lobes unequal, the anterior longer. Leaf-blades entire.

  Leaf-blades oblong-elliptic, hirsute-pubescent, acute. Sepals five, the posterior much the smallest, the others slightly unequal. Capsule scarcely notched. Corolla 5 mm. long......4. *V. Copelandii*

  Leaf-blades elliptic-oval, glabrous or glabrate, obtuse to acutish. Sepals four, decidedly unequal. Capsule strongly notched. Corolla 5–7 mm. long........5. *V. Cusickii.*

Style shorter than or nearly as long as the capsule. Filaments shorter than the corolla. Calyx-lobes of uniform length. Leaf-blades, at least the lower, crenate to serrate.

  Capsule rounded or acutish, not notched. Style nearly as long as the capsule. Sepals canescent, not ciliate, nearly equaling the capsule. Corolla twice as long as the sepals. Stem-leaves elliptic-oblanceolate. Plant 1 dm. tall or less, the inflorescence minutely pubescent..............................6. *V. fruticans.*

  Capsule slightly notched. Style less than half the length of the capsule. Sepals conspicuously ciliate, one-half to two-thirds the length of the capsule. Corolla less than twice as long as the sepals. Stem-leaves elliptic to ovate. Plants mostly 1–3 dm. tall, the inflorescence hirsute-pubescent.

    Capsule glabrous. Sepals glabrous on back, ciliate on margins with non-glandular hairs. Plant usually 1–2 dm. tall..............................7. *V. alpina.*

    Capsule pubescent. Sepals usually pilose on back as well as margins.

      Leaf-blades serrate, the largest nearly cordate at base. Capsule and sepals with hairs which have attenuate non-glandular tips, the sepals less pilose or glabrous on back. Plant usually 1–1.5 dm. tall, with pedicels becoming 8–11 mm. long........................8. *V. Stelleri.*

      Leaf-blades crenate-serrate to nearly entire, rounded at base. Capsule and sepals with hairs which have rounded glandular tips, the sepals densely pilose on back. Plant usually 1.5–3 dm. tall, with pedicels 2–5(–10) mm. long.

        Corolla mostly 6–7 mm. long. Pedicels mostly 5–10 mm. long. Leaf-blades mostly ovate, frequently serrate....9a. *V. Wormskjoldii nutans.*

Corolla mostly 4–6 mm. long. Pedicels mostly 2–5 mm. long. Leaf-blades mostly oblong-ovate, rarely evidently serrate. .9. *V. Wormskjoldii.*

C′. Capsule obviously wider than long, notched one-fourth length. Corolla white or bluish, with deep-blue lines on the posterior side, the tube pubescent within. Style nearly as long as the capsule. Leaf-blades ovate-oblong or oval, obtuse, obscurely crenate. Stems extensively repent, ascending at apex.

Stem throughout and pedicels minutely pubescent with upcurved hairs. Corolla about 2 mm. long, white or whitish, with blue lines on posterior side. Capsule mostly 3–4 mm. wide........................10. *V. serpyllifolia*

Stem distally and pedicels finely pubescent with longer mostly spreading hairs. Larger throughout, the corolla mostly about 3 mm. long, pale-bluish with deeper blue lines on posterior side. Capsule mostly 4–5 mm. wide........................10a. *V. serpyllifolia humifusa.*

A′. Annuals, fibrous-rooted, but without subterranean stems. Most leaf-axils flower-bearing, so that inflorescence appears to be of "axillary" flowers.

B. Pedicels shorter than the lanceolate to linear sepals. Capsule strongly flattened. Seeds many, less than 1 mm. long, flat, smooth or nearly so. Plants erect.

Leaf-blades, excepting the lowermost, sessile, those of the lower stem-leaves oblanceolate, nearly entire to dentate. Corolla whitish throughout. Capsule greenish, notched, the minute style hidden between the capsule-lobes. Plant glabrous or with minute usually gland-tipped hairs.

Plant glabrous..............................11. *V. peregrina.*

Plant pubescent with short gland-tipped hairs, which are usually present even on the capsule........................11a. *V. peregrina xalapensis.*

Leaf-blades petioled, or the upper nearly sessile, those of the lower stem-leaves ovate, crenate-serrate. Corolla deep violet-blue. Capsule yellowish-brown, pubescent with slightly gland-tipped hairs, strongly flattened, notched nearly or about one-third length, the longer style reaching about to the capsule-lobes. Plant pubescent with white glandless or obscurely gland-tipped hairs..................12. *V. arvensis.*

B′. Pedicels longer than the ovate sepals. Capsule relatively turgid. Seeds few, 1.3–3 mm. long, convex-arched, roughened. Plants repent.

Leaf-blades ovate, serrate to dentate. Sepals shortly ciliate. Capsule slightly flattened, deeply notched, pubescent. Seeds 1.3–1.5 mm. long, brown.

Capsule-lobes united at least two-thirds their length. Leaf-blades dentate, truncate or cordate at base. Stem finely pubescent with glandless hairs.

Petals not exceeding the ovate sepals. Capsule-lobes rounded, the most distal point of each about midway between the style and the lateral margin. Style shorter than the capsule.

Leaf-blades oblong-ovate, crenate-serrate. Capsule 4–5 mm. wide, with a narrow notch about one-third depth of capsule; the stout style (less than 1 mm. long) about equaling the capsule-lobes.................................13. *V. agrestis.*

Leaf-blades ovate, dentate with rounded teeth. Capsule 4 mm. wide, less deeply and narrowly notched; the slender style (1–1.5 mm. long) surpassing the capsule-lobes...................14. *V. polita.*

Petals much exceeding the narrowly ovate sepals. Capsule-lobes acutish in profile, the most distal point of each near the lateral margin. Style as long as the capsule.................................15. *V. persica.*

Capsule-lobes united only at base. Leaf-blades serrate, narrowed at base. Stem pubescent with gland-tipped hairs...............16. *V. biloba.*

Leaf-blades broadly and shallowly cordate, 3–5-lobed, the lobes rounded and entire. Sepals broadly ovate, conspicuously ciliate. Capsule turgid, scarcely notched at apex, glabrous. Seeds 2.5–3 mm. long, blackish. .17. *V. hederaefolia.*

### 1. VERONICA MARITIMA L.

*Veronica maritima* L., Sp. Pl. 10. 1753. "Habitat in maritimis Europae macris apricis." According to Linné, Fl. Lapp. 5. 1737: "Ad fines Alpium Lapponicarum iuxta mare septentrionale saepius conspicitur, in toto itinere nullibi coposior visa est, quam in maritimis Tornoensibus." Type carefully described by Sir. J. E. Smith, and specimen from Tornea, collected by C. P. Laestadius, seen in Herb. New York Botanical Garden. This is a form with long-acuminate, sharply serrate leaves.

*Veronica longifolia* L., l. c. 10. 1753. "Habitat in Tataria, Austria, Svecia." Diagnosis quoted from Linné, Hort. Ups. 7. 1748, where this plant is more fully described and is cited: "Habitat in Tataria." Sir J. E. Smith, in Rees Cyclop. **37**: Art. Veronica, no. 10, 1819, discussing the specimens in the Linnean Herbarium, carefully contrasts these two Linnean species. *V. longifolia* he distinguishes by its leaves less deeply and doubly serrate, on shorter petioles, and calyx shorter (not longer) than the tube of the corolla, its lobes broad, ovate and nearly equal (not unequal and narrow). All which contrasts certain plants; however each character varies, and it seems difficult or impossible to distinguish these as species.

Roadsides and waste land, from the Magdalen Islands and Prince Edward Island to Quebec, Connecticut and central New York. Introduced from northern Eurasia.

What is here termed *Veronica maritima* presents remarkable variability, and whether it constitutes one polymorphic species, one species with varieties, or a group of closely related species, must be decided by field-study in the lands in which it is native. Until Old World students arrive at a much more definite consensus of opinion, there seems to be slight profit in our attempting further analysis and identification of the large number of named variants of this group. But to show the range of variation seen in American material I present this doubtless artificial outline of forms:

Corolla (of at least largest flowers) 5.5–7 mm. long. Filaments much exceeding the corolla. Leaves opposite or in threes, 6–15 cm. long, long-acuminate, sharply serrate.
Leaf-blades beneath pubescent over most of surface. The most prevalent form northward, Magdalen Islands and Nova Scotia to Massachusetts and northern New York.......... *Forma A*
Leaf-blades beneath glabrous or slightly pubescent on veins. In Nova Scotia and Massachusetts. Evidently a mere variant of Forma A.......................................... *Forma B*
Corolla 4–5.5 mm. long.
Leaf-blades beneath pubescent over entire surface and usually also above. Filaments nearly twice as long as the corolla.
Leaves in threes or fours, 8–10 cm. long, the blades linear-lanceolate, long-acuminate, sharply serrate. Buckfield and Cliff Island, Maine. Probably the typical *V. maritima* L. As in Forma A, but smaller-flowered........... *Forma C*
Leaves opposite, 3–5 cm. long, the blades oblong-lanceolate, acute, dentate-serrate. In Quebec, Massachusetts, and central New York.................................. *Forma D*
Leaf-blades beneath glabrous, or slightly pubescent on the veins, lanceolate, or oblong-lanceolate.
Leaves opposite, or very rarely in threes, 3–10 cm. long, the blades acuminate or acute, dentate-serrate or somewhat sharply serrate. Filaments usually only slightly longer than the corolla. The most prevalent form southward, and possibly a distinct species. On Prince Edward Island; from Maine to Vermont and Connecticut; in Martinique........................................ *Forma E*
Leaves opposite, 5–8 cm. long, the blades obtuse or acutish, crenate-serrate. Filaments much exceeding the corolla. An anomalous form, perhaps a hybrid containing some *Veronica spicata* ancestry. Elmira, New York.......... *Forma F*

Perhaps even the little-understood *Veronica spuria* L. is to be included in this aggregate species. If so, as this name has precedence of position, according to the American Code[1] it must be adopted. *Veronica spuria* L., Sp. Pl. 10. 1753 ("Habitat in Europa australiore,

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[1] Priority of position within a work, or as in this case on a single page, affords an unfortunate rule to follow, because it does not indicate any time-precedence in the author's mind. Perhaps a better principle would be to select, among 'species' actually seen by the author, that earliest known by him. In the case above, Linné knew *Veronica spuria* and *longifolia* from 1748, but *V. maritima* from 1737.

Sibiria"), is really adopted from Linné's Hortus Upsalensis, where the plant is more fully described, contrasted with *V. maritima,* and stated to be from Sibiria. A plant with stems and under surface of leaves glabrous, the latter with acute (not acuminate) serratures, from Siberia, would appear to be the same as certain specimens seen in Herb. New York Botanical Garden from Altai and Manchuria. These all have very short petioles, a feature especially stressed by Sir J. E. Smith in his re-description of the Linnean plant, and so appear to be in contrast with any form seen of *V. maritima* L. It will be noticed that this interpretation of *Veronica spuria* L., is not that of Ledebour, Fl. Ross. **3**: 231. 1846, and others, who hold the name for a plant with leaves narrowed at base.

2. VERONICA SPICATA L.

*Veronica spicata* L., Sp. Pl. 10. 1753. "Habitat in Europae borealis campis." A specimen was in the Linnean Herbarium in 1753, and the plant is included in Flora Suecica from Sweden. Several specimens from Sweden seen in Herb. New York Botanical Garden.

Roadside, Stockholm, northern New York. Introduced from northern Eurasia.

3. **Veronica mexicana** S. Wats.

*Veronica mexicana* S. Wats. in Proc. Am. Acad. **23**: 281. 1888. "On cool damp bluffs of streams in the Sierra Madre, Chihuahua, C. G. Pringle (n. 1349), Sept., 1887." Isotype[2] seen in Herb. Columbia University at New York Botanical Garden.

Mountain slopes, at altitudes of 1950 to 2400 meters; Sierra Madre of southern Chihuahua and Durango.

4. **Veronica Copelandii** Eastw.

*Veronica Copelandii* Eastw. in Bot. Gaz. **41**: 288. *f. 2.* 1906. "Collected on Mount Eddy [California] at an elevation of 2500$^{m}$ by Dr. Edwin Bingham Copeland, August 18, 1903, distribution of C. E. Baker, 1903, no. 3931." Isotype, collected on Mount Eddy, Siskiyou County, and distributed by C. F. Baker, seen in Herb. New York Botanical Garden.

Alpine slopes, known only from the mountains of Siskiyou, and perhaps adjoining counties in northern California.

5. **Veronica Cusickii** A. Gray

*Veronica Cusickii* A. Gray, Syn. Fl. N. Am. **2**$^{1}$: 288. 1878. "Alpine region of the Blue Mountains, W. Oregon. W. C. Cusick."

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[2] The word "Isotype" is used to designate a specimen of the original collection, other than the type itself. See Torreya **19**: 13. 1919.

*Veronica Allenii* Greenm. in Bot. Gaz. **25**: 263. 1898. "Collected by O. D. Allen along Paradise river on Mt. Rainier [Washington], altitude 1700$^{m}$, August 20, 1897, no. 95a." Isotype seen in Herb. New York Botanical Garden. Differs, as stated by Greenman, "in its smaller flowers, the white corolla, and less exserted stamens and style." As stated by Macbride and Payson, "typical *V. Cusickii* is common on Mt. Rainier," so that it seems probable that *Allenii* is better considered as an albino form, forma **Allenii** (Greenm.) Pennell, comb. nov. However the single collection known differs from *V. Cusickii* by the following contrast: corolla 3–4 mm. long, white (not 5–6 mm. long, blue), and sepals less unequal. The plant should be re-collected and studied.

*Veronica Cusickii Allenii* (Greenm.) Macbr. & Pays. in Contrib. Gray Herb. II. **49**: 67. 1917. I should not consider an albino state, occurring with its species, as of rank higher than forma.

Mountain slopes, Cascade and Olympic mountains of Washington. eastward to Coeur d'Alene Mountains of northern Idaho and Blue Mountains of northeastern Oregon.

6. **Veronica fruticans** Jacq.

*Veronica fruticans* Jacq., Enum. Stirp. Vind. 2,200. 1762. "Crescit copiose in herbidis saxosisque montium Schneeberg, Schneealbl, Gans. &c. [Austria]." Description of calyx as covered with a very light pubescence, of the corolla as larger than *V. alpina* (by which name *V. pumila* Allioni is intended) and more blue, indicate that this name belongs to the plant now discussed rather than to *V. fruticulosa* L. The Greenland plant has been known by the later name *Veronica saxatilis* Scop.

East Greenland (Lange), and on Disco Island, West Greenland. Through the mountains of western Eurasia, Scandinavia, Scottish Highlands and Alps.

Veronica fruticulosa L., Sp. Pl. ed. II. 15. 1762. ("Habitat in Alpibus Austriae, Helvetiae, Pyrenaeis".) From Linné's brief description, the description and plate of Haller cited (Stirp. Helv. **1**: 532. *pl. 9.* 1742), the south European range assigned, and the identification by Sir. J. E. Smith (in Rees Cyclop. **37**: Art. Veronica, no. 20) who had Linné's specimen before him, this name must be held for the pink-flowered, larger, slightly glandular-pubescent, longer- and at times dentate-leaved plant of the Alps and Pyrenees. Linné's description of the calyx as glabrous is apparently inaccurate, as this is somewhat glandular-pubescent. Scopoli, in his Flora Carniolae, ed. II. **1**: 11 and 19. 1772, well contrasts *Veronica fruticulosa* and *V. fruticans,* although describing both as new species from Carniola.

The former, his *V. frutescens,* is a plant of lower and subalpine stations, while the latter, his *V. saxatilis,* is truly alpine. For contrasting illustrations see Reichenbach, Ic. Fl. Germ. et Helv. **20:** *pl. 1717.* 1862.

7. **Veronica alpina** L.

*Veronica alpina* L., Sp. Pl. 11. 1753. "Habitat in alpibus Europae." Based primarily upon the plant described in Linné, Fl. Suec. 5. no. 13. 1745, where the locality is stated: "Habitat in Alpibus Lapponicis monte Wallewari." This in turn is based upon Linné, Fl. Lapp. 7. no. 7. *pl. 9. f. 4.* 1737, where Linné's own Lapland plant is well described and illustrated. Obviously the name must be given to the species of northern Europe now considered, Linné using the term "alps" as applicable to any high mountain.

*Veronica alpina corymbosa* Hornem., Fl. Dan. fasc. **33:** 3. *pl. 1921.* 1829. "Auf der Insel Disco in Groenland. Gefunden von Capitain-Lieutenant Holbϕll." Figured as with an abbreviated, but obviously young raceme. Specimen from Disco Island seen in Herb. New York Botanical Garden.

Open slopes, East Greenland. Also in Scandinavia, and the Highlands of Scotland.

Under this name have long been included two species which may be distinguished as follows:

| | |
|---|---|
| Capsule glabrous. Sepals glabrous on back, ciliate on margins, apparently but little shorter than the corolla. Plant usually 1–2 dm. tall, usually little branched at base ................ | *V. alpina* |
| Capsule pubescent with glandless hairs. Sepals pilose on back as well as margins, much shorter than the corolla. Plant usually .5–1 dm. tall, usually much branched at base ....... | *V. pumila* |

Veronica pumila Allioni, Fl. Pedem. **1:** 75. *pl. 22. f. 5.* 1785 ("In saxosis summae alpis Albergian dictae"), is stated by Allioni to differ from "Veronica alpina" of the Italian Alps, in its leaves 'not crenate, but dentate, rugose and more acute.' Individual variants of the South European "alpina" answer this characterization, and Bertolini, in his Flora Italica **1:** 89. 1833, assures us that he has obtained specimens proving this to be but a state. Frequently the leaves of variants are dentate and more acute.

This is the species known as "Veronica alpina" through southern Europe, the Pyrenees, Cevennes, and Alps, and as var. *lasiocarpa* in northern Europe, Scandinavia, and the Highlands of Scotland. Wahlenberg, in his Fl. Carpat. Princip. 5. 1814, called this *Veronica alpina australis,* and the true "alpina" *V. alpina lapponica.*

8. **Veronica Stelleri** Willd.

*Veronica Stelleri* Willd.; Link, Jahrb. $1^3$: 40. 1820. "In Herbar. [Willdenow bei Berlin] aus Kamtschatka von Pallas gesandt." According to Chamisso and Schlechtendahl, in Linnaea **2**: 557. 1827: "*Veronica Stelleri* Pallas in Herb. Willd. n. 192. . . . . quam e Camtschatca et e Curilis Pallas habuit, in Unalaschka insula Aleutorum legimus frequentem." By them very fully described, and contrasted with their *V. alpina unalaschkensis*. Specimen from "Mts. of Unalaska, 2000 ft.," collected by A. Kellogg no. 295, seen in United States National Herbarium.

On the Aleutian and Pribiloff Islands, Alaska.

9. **Veronica Wormskjoldii** Roem. & Schult.

*Veronica Wormskjoldii* R. & S., Syst. **1**: 101. 1817. "*V. villosa* Wormskjold . . . . In Grönlandia." Evidently the species now considered.

*Veronica alpina unalaschkensis* C. & S. in Linnaea **2**: 556. 1827. "Legimus [Chamisso et Eschscholtz] in montosis insulae Unalaschka Aleutorum." Collections from Unalaska made by C. F. Baker 4988, W. L. Jepson 86, 135, C. H. Merriam in 1891, and C. V. Piper 4527, seen.

*Veronica alpina Wormskjoldii* (R. & S.) Hook. in Bot. Mag. **57**: *pl. 2975.* 1830.

*Veronica mollis* Raf., New Fl. Am. **4**: 38. 1838. "From Origon, seen alive in gardens." Apparently this species is intended, but the flowers are described as "pale blue" and "large."

*Veronica alpina villosa* (Wormskj.) Lange, Consp. Fl. Groenl. 261. 1887. "(*V. villosa* Wormskj. mscr.) . . . . V. Gr. [West Greenland]: Avangnardlek 62° 25′ (Holst.)."

Moist, grassy ledges and meadows, West Greenland, northern Labrador, Gaspé County, Quebec, Hudson Bay, and Alaska, southward, in the east on Mt. Katahdin, Maine,[3] and the White Mountains, New Hampshire, in the west through the Rocky Mountains to northern New Mexico, the San Francisco Mountains of Arizona and the Ruby Mountains of Nevada, and through the Cascade Mountains and Sierra Nevada to California.

There appears to be a tendency for plants of the Pacific ranges from Alaska to California to have styles slightly longer, usually ¼ to ⅓ the length of the capsule, rather than ⅙ to ¼. Northward is the following more pronounced variant.

9a. **Veronica Wormskjoldii nutans** (Bong.) Pennell, comb. nov.

*Veronica nutans* Bong. in Mém. Acad. Petersb. **2**: 157. 1833. "Dr. Mertens a . . . cueillies a l'île de Sitcha." An old specimen in Herb. Columbia University labeled simply "Veronica nutans Bong. Sitcha," may be an isotype.

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[3] Reported by Fernald, in RHODORA **3**: 176. 1901 (as *V. alpina* L.).

Along the Alaskan coast from Sitka to Kodiak Island, while northward and on the mountains inland typical *Wormskjoldii* occurs.

10. Veronica serpyllifolia L.

*Veronica serpyllifolia* L., Sp. Pl. 12. 1753. "Habitat in Europa & America septentrionali ad vias, agros." Specimen in the Linnean Herbarium, and plant cited in the Flora Suecica as occurring "in pascuis sterilioribus riguis frequens," are evidently of the species now considered.

Meadows, barrens and open woodland, from Newfoundland and Ontario to Minnesota, South Carolina and Missouri, mostly common; British Columbia; Costa Rica; Jamaica; Venezuela. Introduced from western Eurasia, or perhaps also native, in which case our plant, which is not montane, would appear to have been independently derived from the wide-spread mountain variety, *humifusa.*

10a. **Veronica serpyllifolia humifusa** (Dickson) Vahl.

*Veronica humifusa* Dickson in Trans. Linn. Soc. **2**: 288. 1794. "I found [it] upon very high mountains, and under wet shady rocks [Scotland. James Dickson in 1789]." Description not intended to apply to the variety now considered, but to a depressed form of it. Also is inaccurate (as stated by me in Torreya **19**: 166. 1919) in calling for a plant with leaves often in threes and fours, a condition which I have not observed within this species. However this must be a form of *serpyllifolia,* and this name has long been current in British floras for denoting an alpine more pubescent depressed variety of that species. Surely the depressed habit must prove ecologic, but, as understood long ago by Sir J. E. Smith (Fl. Brit. **1**: 19. 1800), there is a hirtous *V. serpyllifolia* in the upland, "in montosis." Four specimens in Herb. Columbia University, collected along streams in the Clava Mountains, Forfarshire, Scotland, show well this variety. The stems are but 5 cm. long, ascending or even erect at apex, and above are pubescent with spreading hairs. That the plants are but dwarves of this wide-spread variety is confirmed by their obviously large corollas. The plants are so dwarfed that, due to the crowding of the pairs, the leaves might seem whorled.[4] American plants from high altitudes become likewise dwarf and spreading.

*Veronica neglecta* F. W. Schmidt, Fl. Boem. **1**: 12. 1794. Description not seen, but in Roemer & Schultes, Syst. Veg. **1**: 102. 1817, we are informed that *neglecta* is "hirsuta, pilis brevibus confertis," while Koch, Syn. Fl. Germ. et Helv. 529. 1837, terms it a "forma maior, fol. ovatis." This combined description surely indicates our plant.

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[4] Prof. Fernald has suggested that Dickson intended to describe his plant as bearing three or four pairs of leaves.

*Veronica serpyllifolia humifusa* (Dickson) Vahl, Enum. Pl. **1**: 65. 1805.

*Veronica ruderalis* Vahl, l. c. 66. 1805. "Habitat in ruderatis versuris et humidis locis frigidis Peruviae." Re-naming, with a rearranged description, of the plant called by Ruiz and Pavon (Fl. Peruv. et Chil. **1**: 6. 1798) "Veronica serpillifolia" and obtained by them "in ruderatis, versuris et humidis locis frigidis Pillao [Peru]." Description distinctive of the variety now considered.

*Veronica serpyllifolia neomexicana* Cockerell in Am. Nat. **40**: 872. 1906. "I found it at the top of the Las Vegas Range in New Mexico, at 11,000 feet, June 28, 1902." Isotype seen in Herb. New York Botanical Garden.

*Veronica funesta* Macbr. & Pays. in Contrib. Gray Herb. II. **49**: 68. 1917. "Oregon: Swan Lake Valley, June 21, 1896, Elmer I. Applegate, no. 424 (Type, Gray Herb.)." Type, collected "along mountain streams," seen in Gray Herbarium. The filaments are obviously shorter than in *V. Cusickii* A. Gray, and the (immature) capsule is wider than long.

Alpine meadows, reaching sea-level northward, from Labrador to Alaska, south, eastward to northern Maine and Vermont, westward through all high ranges of Canada and the United States, at scattered stations in Mexico[5] (Popocatepetl and Ixtaccihuatl), and through the Andes from Colombia to Bolivia. Through the mountains of Eurasia, from Scandinavia, Scotland and the Pyrenees to the Himalayas. Very wide-ranging, and certainly the parent of the species, *V. serpyllifolia.*

In Eurasian botany this pubescent larger-flowered plant of mountains has repeatedly been distinguished from *Veronica serpyllifolia,* specifically, varietally, or as but a mountain-form of that species. Among names proposed for it are: *Veronica serpyllifolia pubescens* Spenner, Fl. Frib. 351. 1826, from Germany; *V. serpyllifolia borealis* Laestad. in Nov. Act. Soc. Ups. **11**: 211. 1839, from Sweden; *V. serpyllifolia major* Baumg., Enum. Stirp. Transsilv. **1**: 20. 1816, from Transsilvania; *V. serpyllifolia major* Schur., Enum. Pl. Transsilv. 500. 1866, also from Transsilvania (name apparently independently chosen; plant well-described); and *V. serpyllifolia alpina* Hook., Brit. Fl. 4. 1830, from Scotland. *Veronica fontana* Willd.; Link, Jahrb. **1**$^3$: 41. 1820, is a name which has been used in Alaskan botany.

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[5] To be expected on all high cordilleras of Mexico and Central America.

11. **Veronica peregrina** L.

*Veronica peregrina* L., Sp. Pl. 14. 1753. "Habitat in Europae hortis, arvisque." Diagnosis quoted from Linné, Fl. Suec. 6. no. 15. 1745, where we are told that the plant "habitat in cultis & terra nuda Upsaliae, rarissima apud nos hodie plana, olim forte copiosior evasura." A plant of 'cultivated fields and bare earth,' known from a single locality in Sweden, and there 'formerly abundant but now very rare,' would seem to have been an adventive. That this was Linné's opinion is shown by the specific name chosen, meaning "foreign."

*Veronica caroliniana* Walt., Fl. Carol. 61. 1788. Type doubtless from lower South Carolina. The radical leaves are described as subincised, cauline subserrate. Evidently this is a pronounced phase of the 'romana' type, discussed below, and it is well-interpreted by such a specimen as House 3179 from Clemson College, South Carolina.

*Veronica carnulosa* Lam., Ency. Meth., Illust. **1**: 47. 1791. "Ex Europa & America septentr. in arvis."

Moist soil, river-banks, gardens and cultivated fields, usually appearing as a weed; wide-spread through eastern North America from New Brunswick to Iowa, Florida and Texas; also seen from British Columbia, Alaska, New Mexico, Oregon, Bermuda and Jamaica. Westward passes into the yet more widely ranging variety *xalapensis*.

In the Species Plantarum, 1753, Linné twice described this species, once from plants known living to him, as *Veronica peregrina*, and once from a specimen from southern Europe in his herbarium as *V. romana*. *V. peregrina* was supposed to possess leaves lanceolate-linear and very entire, while *V. romana* had these oblong and subdentate. The leaves of this species vary from one state to the other, and on each individual the larger leaves tend to the "romana" type. As *romana* has priority of position on page 14 of the Species Plantarum, and its diagnosis is descriptive of a specimen in the Linnean Herbarium, a claim might be made that this name should be used for our plant. However the citations in the synonomy of *V. romana* all pertain to another species, later separated by Linné as *Veronica acinifolia* (Sp. Pl. ed. II. 19. 1762), and the specific name "romana" was adopted from "Veronica minima, clinopodii minoris, folio glabro, romana. Bocc. mus. 2. p. 29. t. 102." As the Linnean diagnosis would also include Boccone's plant, which was clearly illustrated in the latter's Museo di Piante Rare della . . . Italia . . . 19. *pl. 102.* 1697, I think we should hold *romana* for this species, placing *acinifolia* in its synonomy.

11a. **Veronica peregrina xalapensis** (H.B.K.) Pennell

*Veronica xalapensis* H.B.K., Nov. Gen. et Sp. **2**: 389. 1818. "Crescit in Regno Mexicano prope Xalapa (alt. 630 hex.) in nemoribus Liquidambaris Styracifluae [Humboldt & Bonpland]."

*Veronica chillensis* H. B. K., l. c. 390. 1818. "Crescit in cultis Regni Quitensis prope Chillo, alt. 1340 hex. [Humboldt & Bonpland]." Described as differing from *V. xalapensis* in having stem repent, leaves wider (oblong-spatulate instead of oblong), and calyx-lobes narrower (lanceolate instead of oblong), at length reflexed. All these are points of normal variation in this variety, excepting that the plant is never truly repent. In the full description the word "repentes" is followed by the truer statement "adscendentes."

*Veronica peregrina xalapensis* (H.B.K.) Pennell in Torreya **19**: 167. 1919.

Environment as in *Veronica peregrina,* with which over an extensive area transitional forms occur; wide-spread and usually common through western North and South America from Alaska and Yukon to Chile and Argentina, in the Tropical portions of its range found only on the upper Cordilleras; eastward, in the United States frequent nearly to the Mississippi River, and sporadically eastward, probably as an introduction, to New England; also, probably also introduced, in Brazil.

12. VERONICA ARVENSIS L.

*Veronica arvensis* L., Sp. Pl. 13. 1753. "Habitat in Europae arvis, cultis." Diagnosis quoted from Linné, Fl. Suec. 6. no. 16. 1745, where we are told that the plant occurs in Sweden "in agris ruderatis cultis frequens." Our American introduced plant agrees well with the description of this.

Gardens and fields, or in dry woods, on cliffs and talus slopes, mostly common from Newfoundland to Iowa, Georgia and Oklahoma; southern Alaska to Oregon; Bermuda; Jamaica; Argentina. Introduced from Eurasia.[6]

13. VERONICA AGRESTIS L.

*Veronica agrestis* L., Sp. Pl. 13. 1753. "Habitat in Europae cultis, arvis." Diagnosis quoted from Linné, Fl. Suec. 6. no. 17. 1745, where the plant is said to occur in Sweden "in agris, areis,

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[6] This species frequently grows in such "native" environments that the question of its being indigenous to the Northeast has been raised. But its weed-like character, ensuring its early introduction, and the fact that its American range is not so great as would be expected of such a species if native, leads me to think it introduced. See also Fernald in RHODORA **2**: 137. 1900. In the case of this and *Veronica officinalis* L., below, the burden of proof is on those who would claim them indigenous to both hemispheres.

cultis." According to the statement of Fries, Novit. Fl. Suec. 65. 1819, the Linnean *agrestis* is identical with his own *V. versicolor,* being the only one of Fries' segregates common or previously known in Sweden. Two specimens from Sweden seen in Herb. New York Botanical Garden, one collected at Scania by N. H. Nilsson in 1881.

Roadsides and rocky places, Newfoundland to Quebec and New Brunswick; on ballast at New York City and Philadelphia; Bermuda. Introduced from central and northern Europe.

14. VERONICA POLITA Fries

*Veronica polita* Fries, Novit. Fl. Suec. 63. 1819. "Ubique in arvis Scaniae [Sweden]." In the second edition of the Novitiae we are told that this is the only known station in Sweden. Well described, and in the second edition contrasted with the *V. agrestis* L. (*V. versicolor* Fries), both of which species of Fries were soon after illustrated in Reichenbach's Kupfersammlung kritischer Gewächse, plates 246 and 277 respectively. I am unable to maintain Fries' contrast as to pubescence and the veining of the sepals. For further discussion of this name and of the uncertain identity of the older *Veronica didyma* Tenore, Prod. Fl. Nap. 6. 1811, of Italy, see Ernst Lehmann in Bull. Herb. Boiss. II. **8**: 237–244. 1908. Tenore's mention of leaves profoundly crenate suggests *polita*, which is the species of this group commonest in southern Italy.

*Veronica crenulata* Sesse & Mociño, Fl. Mex. 5. 1892. "Habitat in montibus Sancti Eremi PP. Carmelitarum [Mexico. Mociño & Sesse]." Description appears to be of the species now considered, which is well-established in Mexico. Not *V. crenulata* Hoffm., 1803.

Ballast, roadsides and gardens, occasional from New York to Ohio, Florida and Texas; central Mexico; Argentina. Introduced from central and southern Eurasia.

15. VERONICA PERSICA Poir.

*Veronica persica* Poir., Encyc. Meth., Bot. **8**: 542. 1808. "Croît dans la Perse. On la cultive au Jardin des Plantes de Paris (V. v.)." Apparently this is our species, but description differs from prevalent forms in stating the leaves to be very obtuse and ordinarily slightly longer than the pedicels and the corolla to be shorter than calyx. However these states are easily reconcilable to certain stages or forms, and our species is a plant well-known from Persia. Lehmann doubtfully identifies *persica* as this species, but Lacaita (in Jour. Bot. **56**: 55. 1918), after examination of Poiret's type, declares these identical.

*Veronica precox* Raf., Atl. Jour. 79. 1832. "Grown in the [Bartram's Botanic] Garden [near Philadelphia] from seeds received from a place unknown." Not *V. praecox* All., 1789.

*Veronica diffusa* Raf., New Fl. Am. **4**: 38. 1838. "Native of ——————, naturalized on the Schuylkill near Philadelphia." Re-naming of *V. precox* Raf.

*Veronica rotundifolia* Sesse & Mociño, Fl. Mex. 5. 1892. "Habitat in Eremo P. P. Carmelitarum [Mexico, Mociño & Sesse]." Description apparently of the species now considered, although it may be that I have transposed the application of this name and *V. crenulata* S. & M. Not *V. rotundifolia* Ruiz & Pavon, 1798.

Fields and roadsides, occasional, or westward locally common, through Temperate North America, from Newfoundland and southern Alaska, south to Georgia, Texas and California; Mexico; Jamaica; Colombia; Chile. Introduced from southern Eurasia.

Our plant has also been known as *Veronica Tournefortii* C. C. Gmel., *V. Buxbaumii* Tenore, and *V. byzantina* (Smith) B.S.P. The two last are subsequent names, dating as species from 1811 and 1888 respectively. The original description of *V. Tournefortii* C. C. Gmel., Fl. Bad. **1**: 39. 1805, was composite, based upon a plant escaped from the botanic garden to fields near Carlsruhe, Baden, and upon a specimen brought by Tournefort from the Levant, which had recently been described as *V. filiformis* Smith (in Trans. Linn. Soc. **1**: 195. 1791.). The former element was probably our species, but the name *Tournefortii* should be applied to Tournefort's plant, and this is the basis of *V. filiformis*, a distinct though related species. Moreover the name was antedated by *Veronica Tournefortii* F. W. Schmidt, Fl. Boem. 7. 1793. (Description not seen, but the publication of this name verified by Lacaita in his discussion of this whole problem in Jour. Bot. **55**: 271–276. 1917.)

16. Veronica biloba L.

*Veronica biloba* L., Mant. 172. 1771. "Habitat inter Cappadociae segetes. D. Schreber."

Collected at Yonkers, New York, by E. P. Bicknell; also at Logan, Utah, by C. P. Smith, 1604 and 2167, and by him commented upon (under the name of *V. campylopoda* Boiss.) and illustrated in comparison with *V. persica* Poir., in Muhlenbergia **6**: 61. 1910.

*Veronica campylopoda* Boiss., Diagn. Pl. Nov. **4**: 80. 1844, distinguished from *V. biloba* as having its leaves and sepals narrower, the former hardly denticulate to entire above, its pedicels recurved, its seeds strongly rugulose and its style longer, half the length of the capsule, seems not to be definitely separable by any of these characters. Sir J. D. Hooker, Fl. Brit. India **4**: 295. 1884, assures us that the plant lacks distinctness—"I cannot distinguish it as a variety even"— and in confirmation of his statement that "the seeds vary much in depth of pitting," it may be mentioned that Reichenbach's plate cited by Boissier as illustrative of true *biloba* shows seeds deeply rugulose. Our plants seem quite intermediate, with the leaf-breadth and leaf-serration of *biloba*, but with the pedicels tending slightly to recurve and with the seeds and style as described for *campylopoda*. They match well a specimen of Boissier's collected at Roscheya, Syria, May, 1846, and named by him *Veronica campylopoda*.

17. Veronica hederaefolia L.

*Veronica hederaefolia* L., Sp. Pl. 13. 1753. "Habitat in Europae ruderatis." Diagnosis quoted from Linné, Fl. Suec. 7. no. 18. 1745, where the plant is said to occur "in Scania [Sweden] campestri in ruderatis ad urbes & pagos." Specimen from Sweden, from herbarium of Per Larson, seen in Herb. Columbia University.

(?) *Veronica reniformis* Raf. in Med. Repos. New York **5**: 360. 1808. "In New Jersey [C. S. Rafinesque in 1803–4]." I am unable to be certain of the identity of this from the short description: "stem procumbent, branched ['branded'], leaves sessile, reniform, hairy, entire, flowers axillar, solitary." It is possibly *V. hederaefolia* L., in which case the petioles must have been so short as to be unnoticed, or *V. arvensis* L., with unusually obscure serration of leaf, or else some introduced species not since reported from America.

Orchards and roadsides, occasional from New York to North Carolina. Introduced from Europe.

(*To be continued.*)

# "VERONICA" IN NORTH AND SOUTH AMERICA

FRANCIS W. PENNELL

(*Continued from p. 22.*)

## II. **VERONICA** L., Subgenus 2. EUVERONICA Pennell

*Veronica* L., Sp. Pl. 9. 1753. Type species, *V. officinalis* L.,[7] of Europe.

A. Capsule pubescent. Stems, pedicels, leaves and sepals pubescent. Leaf-blades oval or ovate, crenate-serrate to dentate. Plants of dry soil.

Leaf-blades dentate, cordate or truncate at base. Sepals 3.5–5 mm. long, linear-lanceolate, exceeding the capsule. Capsule with hairs not glandular nor dark-jointed. Plant ascending or erect.

Sepals unequal, the longest 4–5 mm. long. Capsule slightly notched. Style 4–5 mm. long, longer than the capsule. Leaf-blades sessile or nearly so. Racemes over 10-flowered, the pedicels more than 1 mm. long.

Corolla 7–8 mm. long, violet-blue, the largest lobes ovate. Anterior sepals much exceeding the posterior. Capsule longer than wide. Racemes 30–60-flowered, the pedicels scarcely exceeding their bracts. Leaf-blades coarsely dentate. Stem erect, 4–8 dm. tall.............................18. *V. latifolia.*

Corolla 5–6 mm. long, paler violet-blue, the largest lobes nearly orbicular. Anterior sepals slightly exceeding the posterior. Capsule wider than long. Racemes 10–20-flowered, the pedicels much exceeding their bracts. Leaf-blades crenately dentate. Stem ascending, 1–3 dm. tall....19. *V. Chamaedrys.*

Sepals equal or nearly so, 3.5–4 mm. long. Capsule deeply notched, wider than long. Style

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[7] Selected, among the several species common to both Linné and Tournefort, which answer Linné's generic characterization in Genera Plantarum, ed. V. 10. 1754, and are native to Linné's country Sweden, because of its officinal nature. This species had a long historic right to the name "Veronica."

.5 mm. long, much shorter than the capsule. Leaf-blades shortly petioled. Racemes 5–10-flowered, the pedicels less than 1 mm. long.................................20. *V. javanica.*

Leaf-blades oval, crenate-serrate, narrowed to a petiolar base. Sepals 2–3 mm. long, oblong-lanceolate, shorter than the capsule. Capsule as wide or wider than long, notched, with hairs dark-jointed and some of them glandular. Style 2.5–3.5 mm. long, shorter than the capsule. Plants repent, ascending at apex.

Corolla 8–9 mm. long, violet-blue. Capsule 5 mm. long, as wide as long, its lobes rounded, the most distal point of each midway between the style and the lateral margin. Racemes 3–5-flowered, the pedicels longer than the capsule. Leaf-blades about 2 cm. long, crenate-serrate with very low teeth, hirsute above, glabrous beneath, conspicuously ciliate. Stem less than .5 dm. long............21. *V. grandiflora.*

Corolla 3–4 mm. long, pale-lavender, with lavender blue lines on the posterior side. Capsule 3–4 mm. long, wider than long, its lobes with the most distal point of each near the lateral margin. Racemes 20–30-flowered, the pedicels shorter than the sepals or capsules. Leaf-blades 2–5 cm. long, crenate-serrate with prominent teeth, pubescent on both surfaces but not obviously ciliate. Stem extensively repent, 2 dm. long or longer................22. *V. officinalis.*

A′. Capsule glabrous or with a few minute gland-tipped hairs. Stems, pedicels, leaves and sepals glabrous, or very rarely pubescent. Leaf-blades oblong-ovate to linear, finely serrate to entire. Aquatics.

B. Capsule not conspicuously wider than long, and scarcely or not two-lobed. Sepals nearly or quite equaling the capsule, slightly unequal, the anterior longer. Leaf-blades oblong-ovate to lanceolate, obtuse to acuminate, serrate to crenate-serrate. Stem glabrous or pubescent with minute gland-tipped hairs. Racemes usually of more than 10 flowers, the relatively stout pedicels ascending-spreading.

Leaf-blades all petioled, prevailingly ovate-oblong, acutish to obtuse. Racemes usually 10–25-flowered, the pedicels 5–13 mm. long. Plants mainly emersed, glabrous throughout. Capsule slightly wider than long, notched.

Leaf-blades oblong-oval, widest at or above the middle, narrowed at base, mostly broadly rounded at apex. Style 1.5–2 mm. long, obviously shorter than the capsule. Plant extensively repent, ascending at apex....23. *V. Beccabunga.*

Leaf-blades lanceolate to ovate, widest at or near the base, mostly acute or acutish at apex. Style 2–3 mm. long, scarcely shorter than the capsule. Plant repent only at base, soon ascending-erect..............24. *V. americana.*

Leaf-blades, at least the upper on the flowering-stems, sessile and clasping, obtuse to acuminate. Racemes 15–60-flowered, the pedicels 3–8 mm. long. Plants of deeper water, usually mostly submersed.

Capsule 2.5–4 mm. long. Style 1.3–2 mm. long. Cauline leaf-blades acute to acuminate.

Sepals acute to acuminate. Capsule scarcely wider than long, not or slightly notched. Leaf-blades serrate with close teeth (four or more to 1 cm.). Racemes usually 30–60-flowered, with pedicels 4–8 mm. long.

Stem distally, rachis and pedicels glabrous. Capsule globose-ovoid, acutish or rounded, not or scarcely emarginate. Style 1.5–2 mm. long. Leaf-blades oblong-ovate, mostly broadest about the middle, the lower usually obviously narrowed at base or petioled.

Sepals acuminate, 4–5 mm. long. Capsule 3–4 mm. long. Pedicels 5–8 mm. long................25. *V. Anagallis-aquatica.*

Sepals acute, 2.5–4 mm. long. Capsule 2.5–3 mm. long. Pedicels 3–5 mm. long...........25a. *V. Anagallis-aquatica Brittonii.*

Stem distally, rachis and pedicels finely pubescent with minute gland-tipped hairs. Capsule nearly globose, slightly emarginate. Style 1.3–1.5 mm. long. Leaf-blades lanceolate, mostly broadest near the base, all obviously clasping..............................26. *V. glandifera.*

Sepals obtuse to acutish. Capsule obviously wider than long, evidently notched. Leaf-blades crenate-serrate with remote teeth (two to three to 1 cm.), lanceolate, all clasping. Racemes usually 15–30-flowered, the pedicels 3–6 mm. long.

Stem distally, rachis and pedicels glabrous. Style 1.4–1.6 mm. long...............27. *V. catenata.*

Stem distally, rachis and pedicels finely pubescent with minute gland-tipped hairs. Style 1.5–1.8 mm. long 27a. *V. catenata glandulosa.*

Capsule 2 mm. long, globose, not or scarcely notched. Style .7–1 mm. long. Cauline leaf-blades oblong-lanceolate, obtuse or obtusish. Stem distally, rachis and pedicels usually pubescent with minute gland-tipped hairs...........................28. *V. undulata.*

B′. Capsule much wider than long, strongly two-lobed. Sepals shorter than the capsule, equal. Leaf-blades linear or lanceolate, remotely setaceous-toothed or entire. Stem glabrous or pubescent with glandless hairs. Racemes 5–20-flowered, the filiform pedicels reflexing in fruit..........29. *V. scutellata.*

18. Veronica latifolia L.

*Veronica latifolia* L., Sp. Pl. 13. 1753. "Habitat in Helvetia, Bithynia." The identity of this species has been much disputed, on one side being such statements as Bentham in DC., Prod. **10**: 469. 1846, who considers it to be a broad-leaved form of *V. Teucrium* L., on the other Kerner in Oesterr. Bot. Zeitschr. **23**: 367–369. 1875, who makes a strong plea for its identification as *V. urticaefolia* Jacq., Fl. Austr. **1**: 37. *pl. 59.* 1773. Certainly some of the synonyms cited by Linné appear to be *V. urticaefolia,* a species very readily distinguished by its slender stem, thin smooth leaves which are sharply serrate and long-acuminate, and its shorter racemes, on the slender pedicels of which are borne the short sepals and small pinkish corollas. Linné's description, in the use of the words "foliis rugosis dentatis," certainly does not describe *urticaefolia,* and moreover one can scarcely believe that he would have omitted characterization of the leaf-acumination. Sir J. E. Smith, in Rees Cyclop. **37**: Art. Veronica, no. 58, describes the Linnean specimen and emphatically asserts its kinship to *V. Teucrium* L., not to *urticaefolia* Jacq. In the absence of citation to other specimens studied by Linné, the specimen of the Linnean Herbarium should stand as type. Sir J. E. Smith carefully contrasts this with *V. Teucrium* L., but study of the varying leaf-form of the latter confirms Bentham's view as to their identity.

*Veronica Teucrium* L., Sp. Pl. ed. II. 16. 1762. "Habitat in Germania." Linné possessed no specimen of this in his herbarium, which readily explains his describing as new a narrower-leaved form of this species than his own *V. latifolia.* The specific name is derived from "Teucrii IV tertia species Clus. hist. 1 p. 349." L'Ecluse, Rar. Pl. Hist. 349. 1601, figures and briefly describes a plant, which is an ovate-leaved form of the species, and says that it grows "in herbosis collium jugis [Pannoniae . . . . Austriae Moraviae . . . . & Bohemiae]." Linné's description of his plant as with leaves "ovatis rugosis dentatis" shows the similarity of this to his own *latifolia.*

Roadsides, pastures and waste land, New Hampshire to Ontario, New Jersey and Ohio; introduced from Europe.

19. Veronica Chamaedrys L.

*Veronica Chamaedrys* L., Sp. Pl. 13. 1753. "Habitat in Europae pratis." The diagnosis is essentially taken from Linné, Fl. Suec. 5, no. 12. 1745, where the plant is stated to occur in Sweden "in pratis ubique." Evidently this is the species now considered. Several specimens from Sweden seen, one collected by Dr. W. A. Murrill at Upsala, July, 1902, being probably a topotype.

Roadsides and meadows, occasional from Prince Edward Island to Ontario, New Jersey and Ohio. Introduced from Europe.

20. VERONICA JAVANICA Blume.

*Veronica javanica* Blume, Bijdr. Fl. Nederl. Ind. 742. 1826. "Crescit in cacumine Sederato et ad cataractas fluvii Tjikundul montis Gede [Java]." The brief original description, especially in the phrase "spicis axillaribus," would seem to denote the plant here considered. I have followed Sir J. D. Hooker, Fl. Brit. Ind. **4**: 296. 1884, in adopting this name, as the only named specimen which I have for comparison, Griffith 3921 from East Himalaya distributed by Kew Gardens as "Veronica Maddenii Edg.," is evidently this species. There is also a previously unnamed specimen, in Herb. New York Botanical Garden, from the Liu Kiu Islands.

Petropolis, Brazil, collected by J. Ball in 1882. Introduced from the Oriental Region.

21. **Veronica grandiflora** J. Gaertn.

*Veronica grandiflora* J. Gaertn. in Novi Comm. Acad. Petrop. **14**: 531. *pl. 18, f. 1.* 1770. "Kamtschatkam pro patria sua . . . . in pratis alpinis . . . ., referente Stellero, copiose nascitur." A full description, and a carefully drawn illustration, make the application of this name unmistakable, although the capsule is described as smooth (the word "laevis" however, not the word "glaber"). Apparently this was accidentally renamed by the younger Linné (Suppl. 83. 1781), who says of it: "*Veronica kamtchatica* Gaertner Act. petropol. Habitat in Kamtschatka." Specimens, L. Stejneger 106, etc., seen from Bering Island, along the coast of Kamchatka.

Western Aleutian Islands (Kiska and Attu Islands). Also in Kamchatka.

Similar to, but much larger than, *Veronica aphylla* L., Sp. Pl. 11. 1753, of the Alps of Europe; differs by having its stems frequently 1 dm. long, its peduncles longer, its leaves 2.5–4 cm. long (not 1–2 cm. long), obovate and more acute, its corollas 8–9 mm. long (not 5 mm. long), and its style 8–9 mm. long, exserted, probably as long as the capsule (not 4 mm. long and only one-half to two-thirds length of capsule).

22. VERONICA OFFICINALIS L.

*Veronica officinalis* L., Sp. Pl. 11. 1753. "Habitat in Europae sylvestribus sterilibus." Refers to Linné, Mat. Med. 4, no. 11. 1749; then to Linné, Fl. Suec. 4, no. 8. 1745, where the plant is said to occur in Sweden "frequens in sylvis praesertim exustis," and its medical uses are mentioned. The Linnean specimens are more fully described by Sir. J. E. Smith in Rees Cyclop. **37**: Art. Veronica. no. 53. 1819. Specimen in Herb. New York Botanical Garden, collected at Upsala, Sweden, July, 1902, by Dr. W. A. Murrill, is probably a topotype.

Fields, barrens and open woods, mostly common; from Newfoundland and Michigan to North Carolina and Tennessee. Apparently introduced from Eurasia, although usually in seemingly native habitats.

23. Veronica Beccabunga L.

*Veronica Beccabunga* L., Sp. Pl. 12. 1753. "Habitat in Europa ad rivulos." Diagnosis quoted from Linné, Fl. Suec. 5. no. 11. 1745, where it is stated that in Sweden the plant "habitat in fossis, rivulis, scaturiginibus passim," and that it is the "Beccabungae Herba Conserva, Aqua" of the Pharmacopoeas.

Running brooks, ditches and wet fields, well established in Quebec, also at Rochester, New York and Perth Amboy, New Jersey. Introduced from Eurasia, where this species is as wide-spread as on this continent is the following near relative.

24. **Veronica americana** Schwein.

*Veronica Beccabunga americana* Raf., Med. Fl. **2**: 109. *pl. 94.* 1830. "Grows from Canada to Virginia and Kentucky, near waters, brooks, &c." Well described, and contrast given with *V. Beccabunga* as understood by Rafinesque. Apparently this plant was independently redescribed under this name by Torrey in Fl. New York **2**: 41. 1843, whose type I have seen in Herb. Columbia University.

*Veronica americana* Schwein.; Benth. in DC. Prod. **10**: 468. 1846. "*Veronica americana* (Schweinitz! mss.) . . . . . In America boreali a Canada et Carolina usque ad flum. Oregon et in ins, Sitcha . . . . . . (v. s.)" Specimen seen in Herb. Academy of Natural Sciences of Philadelphia, labeled "Bethl." [= Bethlehem, Pennsylvania], collected by Schweinitz, may be an isotype. Well contrasted with *V. Beccabunga* L., instancing leaf-form and more erect habit.

*Veronica americana hirsuta* Coleman, Cat. Fl. Pl. S. Michigan 27, 1874. "Southern peninsula of Michigan." Described as "plant quite large, 24 to 30 inches high, very hirsute." I have never seen a pubescent form of this species, and Coleman's specimen, if extant, should be studied.

*Veronica americana crassula* Rydb. in Mem. New York Bot. Gard. **1**: 353. 1900. "In bogs, at an altitude of 2000–2500 m. Montana: Little Belt Pass, 1896, Flodman, 778 (type)." Type seen in Herb. New York Botanical Garden. This represents the dwarfed alpine state of the species, which may better be considered a forma.

*Veronica oxylobula* Greene, Pittonia **5**: 113. 1903. "Type specimens from Golden City, Colorado, collected by myself in 1871." Supposed to be distinguished by "its entire or subentire foliage and the longer and almost acute capsules," features of variability within this species.

*Veronica crenatifolia* Greene, l. c. 114. 1903. "The type . . . is Baker, Earle and Tracy's n. 33, from along the Mancos River in southern Colorado, 22 June, 1898." Isotypes seen in Herb. New York Botanical Garden and U. S. National Herbarium. Apparently supposed to be distinguished by its smaller size and crenate leaves, variations frequent in *V. americana.*

Swamps, springs and woodland rills, from Newfoundland, Ontario and Alaska, south, eastward to South Carolina and Tennessee, westward to Chihuahua, California, and the Valley of Mexico; also on the Commander Islands on the western side of Bering Sea. Generally common over this wide area.

*Veronica americana* appears to be only inconstantly distinguishable from *V. Beccabunga* by its leaf-form and more erect habit. The leaf is mostly narrower, widest near the truncately rounded or subcordate base, narrowing to the acute or obtuse apex, and borne on frequently shorter pedicels. The capsule-shape is the same, nearly globose, flattened and emarginate at apex, the corolla, sepals and pedicels are of about the same length as in that species, but the last are usually more slender. The styles are longer and usually more slender in *americana.* The leaves vary from serrate through crenate to nearly or quite entire.

25. **Veronica Anagallis-aquatica** L.

*Veronica Anagallis-aquatica* L., Sp. Pl. 12. 1753. "Habitat in Europa ad fossas." Description quoted from Linné, Fl. Suec. 5, no. 10. 1745, where the plant is stated to occur in Sweden "in fossis ad vias & paludes Uplandiae, Scaniae &c." Described with leaves serrate, and with citations to Tournefort and Bauhin who both term the leaves oblong. The Swedish plant is well described by Nyman, Utkast Sv. Vaxt. Naturh. Sver. Fanerog. 164. 1867, who tells us that its leaves are lanceolate or oval-lanceolate, pointed, and its capsules are rounded, very shallowly notched. All which indicates the present broad-leaved plant with scarcely or not notched capsules, not another plant of northwestern Europe which has elongate acuminate leaves, and capsules decidedly notched, as broad as or broader than long. Our plant has the lower leaves and those of autumnal shoots narrowed or petioled at the base, a condition mentioned in such exact descriptions as Hayek, Fl. Steiermark **2**: 168. 1912; also the short round form of these autumnal leaves is mentioned in Villars, Hist. Pl. Dauphine **2**: 14. 1787.

*Veronica lepida* Phil. in Anal. Univ. Chile **91**: 110. 1895. "Habitat ad Vicum Cartajena (haud procul a Valparaiso [Chile]), Februario, 1895 lecta." Described because the petioled lower leaves were noticed.

*Veronica micromera* Wooton & Standley in Contrib. U. S. Nat. Herb. **16**: 174. 1913. "Type in the U. S. National Herbarium, no. 686250, collected along ditches about Shiprock, on the Navajo Reservation [New Mexico], July 25, 1911, by Paul C. Standley (no. 7283). Altitude 1,425 meters." Type seen in U. S. National Herbarium. A dwarf form, with small leaves which are more obviously narrowed at base.

Slow-flowing streams, wide-spread through North and South America; specimens seen from Michigan, Utah, New Mexico, Arizona, Argentina and Chile. Also of wide occurrence in Eurasia; specimens seen from Germany, Switzerland, Italy, Albania, Algeria and Syria. Of this critical species-group this is the most widely dispersed and probably the original element.

25a. **Veronica Anagallis-aquatica Brittonii** (Porter) Pennell, comb. nov.

*Veronica Anagallis latifolia* Britton in Bull. Torr. Bot. Club **12**: 49. 1885. "In the latter part of September, 1883, . . . . . near Mahwah, Bergen Co., New Jersey, I noticed [it] in a small stream . . . ." Type seen in Herb. Columbia University. Not *V. Anagallis latifolia* Schultz, Prod. Fl. Stargard. Suppl. 3. 1819 (which is *V. Anagallis-aquatica* L.).

*Veronica Brittonii* Porter; Pennell in Torreya **19**: 168. 1919. "Type, base of Marble Hill, above Phillipsburg, New Jersey, collected in flower and fruit June 24, 1892, T. C. Porter; in herbarium Columbia University at the New York Botanical Garden."

Slow-flowing streams, western Connecticut to northern Pennsylvania. For list of localities see Torroya **19**: 170. 1919.

Perhaps not worthy of even varietal distinction.

26. **Veronica glandifera** Pennell

*Veronica perfoliata* Raf., New Fl. Am. **4**: 37. 1838. "Florida." Description almost certainly of the plant now considered, which however is not authentically known from so far south. The clasping opposite leaves of *V. glandifera*, till closely seen, appear connate. Not *V. perfoliata* R. Br., 1810.

*Veronica glandifera* Pennell in Torreya **19**: 170. 1919. "Type, vicinity of Suffolk, Nansemond County, Virginia, collected in flower and fruit, May 27, 1893, N. L. Britton and J. K. Small; in herbarium Columbia University at the New York Botanical Garden."

Slow-flowing streams, in limestone, Virginia and Ohio to North Carolina and Tennessee. Perhaps intergrades with *V. catenata glandulosa.*

The petioled leaves of late-summer shoots are well shown on specimens of Bruce Fink 262 from Oxford, Ohio, collected August 8, 1908.

While in pubescence this species parallels Palaearctic derivatives of *Veronica Anagallis-aquatica* L., I am unable to place our plant of eastern North America as of the same species as any of these. Such species are: *V. anagalloides* Guss., Pl. Rar. Sic. 5. *pl. 3.* 1829, which has a capsule decidedly longer than wide, and not or scarcely emarginate; *V. oxycarpa* Boiss., Diagn. I. **7**: 44. 1846, with acute capsule and leaves narrowed at base; and *V. salina* Schur, Enum. Pl. Transsilv. 492. 1866, very similar to *V. anagalloides.*

27. **Veronica catenata** Pennell, sp. nov.

Flowering stem 1–3 dm. long, glabrous throughout. Leaves lanceolate, acute or acutish, crenate to nearly entire, 3–5 cm. long, 1 cm. wide, all clasping, when submersed elongating and reaching 12 cm. long and 2 cm. wide. Racemes axillary to the upper leaves, 6–12 cm. long, 15–25-flowered. Bracts narrowly lanceolate, 4–5 mm. long. Pedicels 3–5 mm. long, glabrous. Sepals 3–3.5 mm. long, lance-ovate, obtusish. Corolla-lobes pale-blue. Style 1.2–1.7 mm. long. Capsule 3 mm. long, 3.5 mm. wide, broad-globose, decidedly emarginate. Seeds 0.5 mm. long, yellow-brown.

Type, Hot Springs, South Dakota, collected in flower and fruit June 16, 1892, P. A. Rydberg 926, in Herb. New York Botanical Garden. Named from the chain-like aspect of the long racemes of short-pedicelled flowers.

Slow-flowing. streams, plains, from North Dakota and Saskatchewan to Kansas and New Mexico, southward west to Nevada and southern California.

27a. **Veronica catenata glandulosa** (Farwell) Pennell, comb. nov.

*Veronica Anagallis-aquatica glandulosa* Farwell in Rep. Mich. Acad. Sci. **19**: 249. 1917. "Zoo Park, near Royal Oak [Michigan], [Farwell] No. 4323, July 13, 1916." Not *V. Anagallis-aquatica glandulosa* Schur, Enum. Pl. Transsilv. 492. 1866. Description inadequate, but apparently of the plant now considered. As this is a small plant and moreover is the only glandular-pubescent "Anagallis-aquatica" known from Michigan, I apply the name to this.

Slow-flowing streams, western New York to Minnesota, South Dakota, Kentucky and Oklahoma; also in western Massachusetts and in southeastern and southern Pennsylvania. Probably intergrades with *V. glandifera,* and for the latter, in Torreya **19**: 170, I have mistaken plants of our New York "Local Flora."

28. VERONICA UNDULATA Wall.

*Veronica undulata* Wall.; Roxb., Fl. Ind. **1**: 147. 1820. "Discovered in the Turraye [India] by Mr. W. Jack." Specimen in Herb. Columbia University, labeled "Nepal Wallich," may be an isotype.

Ballast, Portland, Oregon, and Mobile, Alabama. Introduced from southeastern Asia, where it occurs from northern India through southern China, and in Japan.

Occasionally nearly or quite glabrous, but then readily distinguished by the small size of the capsule and style.

29. **Veronica scutellata** L.

*Veronica scutellata* L., Sp. Pl. 12. 1753. "Habitat in Europae inundatis." Diagnosis quoted from Linné, Fl. Suec. 4. no. 9. 1745, where the plant is said to grow in Sweden "in locis per hyemem inundatis frequens." Evidently the plant now considered.

*Veronica uliginosa* Raf. in Am. Mo. Mag. **2**: 175. 1818. "Veronica scutellata Pursh . . . . Fl. Am. Sept. **1**: 11." In his Fl. Am. Sept. 11. 1814, Pursh states of "Veronica scutellata" that "the American plant has longer leaves than any of the European specimens I have seen," a condition not verified by the material at hand to-day though Pursh's statement evidently misled Rafinesque into assuming for it specific distinctness.

*Veronica connata* Raf., Med. Fl. **2**: 110. 1830. "In west Kentucky." Very briefly characterized and leaves said to be "connate;" surely they were merely cordate-clasping and opposite.

Meadows and swales, Newfoundland and Yukon to Virginia, Indiana, Wyoming, and California.

Occasionally occurs in a form more or less pubescent throughout, forma **villosa** (Schumacher) Pennell [*Veronica scutellata villosa* Schumacher, Enum. Pl. Saell. **1**: 7. 1801; also *V. scutellata pilosa* Vahl, Enum. Pl. **1**: 70. 1805; *V. scutellata pubescens* Koch, Syn. Fl. Germ. et Helv. 524. 1837.]. This occurs sporadically occasional throughout the range of the species.

## III. **HEBE** Commerson

*Hebe* Comerson; [Juss., Gen. Pl. 105. 1789, generic diagnosis only;] J. F. Gmelin, Syst. Nat. **2**: 27. 1791. Type species, *Hebe magellanica* J. F. Gmel.

Leaves lanceolate, acuminate to a small blunt tip, entire, not revolute, 6–7 cm. long. Racemes 5–13 cm. long, many-flowered. Sepals acuminate, 2–3 mm. long. Corolla with the oblong lobes shorter than or but little longer than the narrow tube. Stamens and style longer than the corolla and conspicuously exserted, the latter slender, 5–6 mm. long. Capsule oval in outline, relatively thin-walled. Stem minutely pubescent when young, especially between and proximad to bases of leaves, becoming glabrate; bark slightly wrinkled in drying.

Racemes 13 cm. long; rachis, pedicels and lanceolate sepals finely pubescent. Corolla 5 mm. long, its lobes slightly shorter than the tube. Leaves attenuate-acuminate. Internodes on flowering shoots about 3 cm. long.................................... 1. *H. salicifolia*

Racemes 5–7 cm. long; rachis, pedicels and lance-ovate sepals puberulent. Corolla not seen. Leaves narrowing to a blunt tip. Internodes on flowering shoots less than 1 cm. long............................. 2. *H. blanda*

Leaves elliptic-oval, apiculate, the margin revolute, callose, and at times obscurely crenate, 2–3 cm. long. Racemes 2 cm. long, few-flowered. Sepals acute to obtuse, 4 mm. long. Corolla 8 mm. long, the broadly ovate lobes much longer than the broad tube. Stamens not longer than the corolla, the stout style 4 mm. long. Capsule elliptic-oval in outline, thick-walled. Stem densely and persistently pubescent with pale hairs on side between and proximad to bases of leaves, below leaf-bases reddish, glabrous and shining; bark much wrinkled in drying... 3. *H. elliptica*

1. **Hebe salicifolia** (Forst.) Pennell, comb. nov.

*Veronica salicifolia* Forst., Fl. Ins. Austr. Prod. 3. 1786. "[Noua Zeelandia, G. Forster]." Several specimens from New Zealand seen, and one collected by A. H. Cockayne 8041, and labeled "*Veronica salicifolia* Forst. Typical South Island form," shows precisely the slender finely pubescent pedicels, small flowers, and acuminate, almost attenuate leaves of our plant. Type species of genus *Panoxis* Raf., Med. Fl. **2**: 109. 1830.

*Veronica Fonkii* Phil. in Linnaea **29**: 110. 1857–8. "En las playas y barrancas de Chonos,' in litore et valleculis, legit . . . Dr. Fr. Fonk." Specimen in Herb. Columbia University, labeled "*Veronica Fonki* Ph. Chonos, legit Philippi, com. am Treviranus 1864," is doubtless an isotype. This seems to be the same as the plant of New Zealand.

Chonos, Chile. Also in South Island, New Zealand.

2. **Hebe blanda** (Cheesem.) Pennell, comb. nov.

*Veronica amabilis blanda* Cheesem., Man. New Zealand Fl. 506. 1906. "Port Chalmers [Otago, South Island, New Zealand] Petrie! . . . . . ." Specimen in Herb. New York Botanical Garden, collected at Anita Bay, Otago (where it forms "a considerable part of the 'coastal Scrub'") appears to be exactly our plant, and to agree with Cheeseman's variety.

Southern Patagonia. Also in South Island, New Zealand.

3. **Hebe elliptica** (Forst.) Pennell, comb. nov.

*Veronica elliptica* Forst., Fl. Ins. Austr. Prod. 3. 1786. "[Noua Zeelandia, G. Forster]," Several specimens from New Zealand seen, two from Port Otway and Tuesday Bay respectively, agreeing exactly with our plant. Also a specimen from the Auckland Islands, Wilkes Expedition, is quite the same.

*Veronica decussata* [Soland. in] Ait., Hort. Kew. **1**: 20, 1789. "Nat. of Falkland Islands. Introd. 1776, by John Fothergill." Described as with bracteoles on pedicels, an appearance probably caused by the terminal bractlets of the raceme appearing, while the bud of the rachis is suppressed.

*Hebe magellanica* J. F. Gmel., Syst. Nat. **2**: 27. 1791. Based upon *Hebe* Juss., Gen. Pl. 105. 1789, where the name is attributed to Commerson and the plant said to be from Magellan. Evidently collected by Commerson at the Straits of Magellan in 1767–8.

*Veronica Simpsonii* Phil. in Anal. Univ. Chile **1873**: 26. 1873. "Enrique Simpson trajo de las orillas del rio Aysen, en Patagonia." The careful description of the branch, leaves, fruiting inflorescence, capsules and seeds appears to denote the species now considered.

Southern Patagonia and Falkland Islands. Also in the Auckland Islands and South Island of New Zealand.

### NOMINA EXCLUDENDA.

*Veronica caroliniana* Poir., Encyc. Meth., Bot. **8**: 520. 1808. "Communiquée par M. Bosc, qui l'a recueillie dans la Caroline." This is *Cynoctonum Mitreola* (L.) Britton, of the Loganiaceae. Not *V. caroliniana* Walt., 1788.

*Veronica cinerea* Raf., New Fl. Am. **4**: 39. 1838. "From Origon." Description of plant as "cinereous villose, leaves alternate . . . . flowers spicate very dense sessile . . . . stamens very long" appears to denote some species of *Synthyris*.

*Veronica fluminensis* Vell., Fl. Flum. 11. 1825; Icones **1**: *pl. 25.* 1827. "Abunde provenit locis umbrosis ad vias maritimas Regii Praedii Sanctae Crucis [Brazil]." Description and illustration show a plant of the Acanthaceae.

*Veronica litoralis* Vell., Fl. Flum. 10. 1825; Icones **1**: *pl. 24.* 1827. "Silvis maritimis Regii Praedii Sanctae Crucis [Brazil] prope litus, ad loca arenosa habitat." Description and illustration show a plant of the Acanthaceae.

*Veronica marilandica* L., Sp. Pl. 14. 1753. "Habitat in Virginia." According to B. D. Jackson (in Proc. Linn. Soc. **14**. Suppl.: 150. 1912), Linné transferred his specimen bearing this name to *Polypremum procumbens* L. Both his description and that in Gronovius' Fl. Virg. 4. 1739, indicate this plant of the Loganiaceae. I cannot locate the reference which is erroneously cited as: "*Veronica marilondica* Murr. Comm. Gotting. **11**: t. 3. 1782."

*Veronica missurica* Raf. in Am. Monthly Mag. **3**: 175. 1818. New name for *Veronica reniformis* Pursh, which was a species of *Synthyris*. See below.

*Veronica Purshii* G. Don, Gen. Hist. Dichl. Pl. **4**: 573. 1838. "Native on the banks of the Missouri. *V. reniformis* Pursh . . ., but not of Rafin." A species of *Synthyris*. See below.

*Veronica reniformis* Pursh, Fl. Am. Sept. **1**: 10. 1814. "Collected by Messrs. Lewis and Clark in boggy soil, on the banks of the Missouri . . . . v. s. in Herb. Lewis." Type was apparently a plant collected on Hungry Creek, in what is now Montana, June 26, 1806, and an isotype of this in the Herbarium of the Academy of Natural Sciences of Philadelphia was determined by Robinson and Greenman [in Proc. Acad. Nat. Sci. Phila. **1898**: 39. 1898] as *Synthyris reniformis major* Hook. Pursh's description is inaccurate, but I think must certainly apply to this collection which is the species, *S. major* (Hook.) Heller.

*Veronica rotundifolia* Ruiz & Pavon, Fl. Peruv. et Chil. **1**: 6. 1798. "Habitat copiose in Peruviae uliginosis ad Pillao vicum." This is a species of *Sibthorpia.*

*Veronica sparsiflora* Raf., Atl. Jour. 79. 1832. Described from a plant in the Bartram Botanical Garden, Philadelphia, Pa., which was said to have been "native of Arkansas or Texas, received from Prof. Nuttall." I know of no American species at all fitting this description: "stem erect, simple round solid, leaves opposite sessile cuneate oblong entire obtuse. Raceme terminal lax very long, flowers scattered, bracts linear oblong obtuse, pedicels filiform. Capsules bilobed subcompressed. Annual . . . . . Stem 1 or 2 feet high. Flowers vernal purpurescent handsome. Corolla rotate, segments of the calix unequal oblong, obtuse . . . . ." Is it a foreign species, or not a *Veronica?*

NEW YORK BOTANICAL GARDEN.

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BOTANICAL GARDEN—No. 231

# TYPES OF FLOWERS AND INTERSEXES IN GRAPES WITH REFERENCE TO FRUIT DEVELOPMENT

By A. B. STOUT

NEW YORK
1921

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# New York Agricultural Experiment Station.

GENEVA, N. Y.

# TYPES OF FLOWERS AND INTERSEXES IN GRAPES WITH REFERENCE TO FRUIT DEVELOPMENT

A. B. STOUT

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*Connected with Grape Culture Investigations.

†Members of the faculty of the New York State College of Agriculture affiliated with this Station.

TECHNICAL BULLETIN NO. 82

# TYPES OF FLOWERS AND INTERSEXES IN GRAPES WITH REFERENCE TO FRUIT DEVELOPMENT*

A. B. STOUT †

## INTRODUCTION

The types of flowers in grapes have long aroused interest among both the growers and the breeders of grapes who are concerned not only with the quality and the productiveness of seeded varieties, but with the development of the seedless or partially seedless varieties. Breeders of grapes are also finding it desirable, if not necessary, to determine as fully as possible how the development of the desirable distribution of the sexes in the flowers may be regulated, controlled, or influenced by breeding and by selection of parentage.

It is well recognized that the production of fruit in any variety and in any seedling plant depends, first of all, on the development of stamens and pistils and their power to function as sex organs in fertilization and in fruit and seed formation. This is well illustrated by the flower types of the best varieties of grapes now in general cultivation.

Self-fruitful varieties like the Delaware, Niagara, Winchell, and Concord have flowers in which both stamens and pistil are well developed and highly functional *inter se*. The stamens are *erect* or *upright* (Figs. 13–21) and their anthers contain pollen much of which is viable and capable of functioning in fertilization. Both kinds of sex organs are present and functional *inter se* in the same flower. The plants are *perfect hermaphrodites*. They set fruit to self-pollination.

Other varieties like Brighton, Lindley, Barry, and Massasoit have flowers whose stamens are recurved and more or less aborted and the pollen which they contain is much shrivelled and defective, and is entirely or almost entirely incapable of functioning in fertili-

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* This is the first report of work done in cooperation with the New York Botanical Garden.

† Director of the Laboratories, New York Botanical Garden.

zation (Figs. 32–39). Such varieties are slightly or even not at all fruitful if left to themselves for self-pollination. The pistils, however, are well formed and are capable of forming fruits containing seeds if properly cross-pollinated with good pollen. Since the stamens are more or less impotent these plants are called *imperfect hermaphrodites.* Such varieties have been called " self-sterile " and the pollen has been spoken of as " impotent " or " lacking in affinity " with pistils. There is, however, very general agreement among those who have investigated the condition of the pollen (Beach 1902, Booth 1902, Dorsey 1914, and Detjen 1917)[1] that the sterility is due to the *poor condition of the pollen* which is thus *unable to function at all.*

The so-called " self-sterility " in these varieties of grapes is, therefore, very different from the " self-sterility " of certain varieties of plums, apples, pears, and cherries, in which the flowers are perfect but the viable pollen is capable of functioning only in certain cross-fertilizations with other varieties or other individuals. In the grape the sterility, it appears, is due solely to imperfect development of stamens and pollen. In the plum the pollen is physiologically incompatible with the female elements of the same plant, of plants of the same clonal variety, and also of certain other plants of diverse origin. In progenies grown from the seed of plants having this type of sterility (Stout 1918, 1920) all degrees of self- and cross-compatibilities and incompatibilities are often in evidence.

Studies made of grapes indicate that the imperfections in the stamens very generally, but not always, involve a recurving of filaments which gives a very different flower from that of the perfect hermaphrodite with its erect stamens.

Among all wild species of American grapes and in seedlings of cultivated sorts another type of flower, the purely *staminate,* has long been recognized. In this the pistil is much aborted and entirely functionless or is even lacking, but the stamens are well developed and yield much viable pollen. A plant with such flowers is highly fertile as a male parent in cross-pollination but is itself fruitless. It appears that wild species of American grapes consist only of *staminate* plants and *imperfect hermaphrodites* except perhaps for rather rare cases when individuals are found bearing some or even all perfect flowers.

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[1] See Literature Cited, p. 15.

Still another type of flower is seen in the grapes that produce seedless or nearly seedless fruits. Here the pistils are capable of developing into fruits but the ovules, if present, do not develop into seeds. According to Müller-Thurgau (1898), the fruits of the seedless raisins develop under the stimulus of pollen-tube growth. Pollination causes development of fruit but does not result in seed formation. Such varieties as Sultana and Sultanina, therefore, are fully seedless when grown under ample opportunity for both self- and cross-pollination. This seems clearly to indicate that in the fully seedless varieties no ovules capable of developing to full maturity are present. Nothing definite seems to be known regarding the exact origin of these seedless varieties and no seedless grape has yet become of commercial value in the eastern United States. The types of flowers which they possess have, however, been observed among seedlings and are to be considered in judging the value of the various flower types appearing in seedlings.

It seems certain that the flowers borne by the greater number of seedlings obtained in breeding grapes can be classed broadly as (1) staminate, (2) perfect hermaphrodite, and (3) imperfect hermaphrodite. No purely female types are known. For describing the general heredity of sex in grapes, such a grouping is useful (Hedrick and Anthony 1915, Detjen 1917). It has, however, been recognized that a sharp distinction between these types does not exist. As Booth (1902) remarks " the whole path is marked by transitional forms; thus there are no distinct classes of self-sterile and self-fertile grapes, but all gradations exist from one extreme to the other." *It is in the study and selection of these intergrading intersexual forms that the possibility of finding types with the degree or kind of femaleness which exists in the seedless types seems most promising.*

In continuing the studies of the inheritance of sex in grapes in progress at the New York Agricultural Experiment Station, and especially with reference to the production of the flower types that give seedless fruits, it has seemed advisable to describe in more detail the variations in the development of the flowers. A general survey has revealed at least one new type of flower here designated as having crinkled stamens, a wide range of variations in the length of stamens among flowers classed as perfect hermaphrodites, and various intermediates between the typically upright and the reflexed one chews the pulp. The fruits produced in 1920 ranged from 7 to 18 thirty-seconds of an inch in diameter. They are of good size for seedless sorts, but smaller than the fruits of the Concord, and as shown in Plate III the bunches are well filled.

A typical flower from one of these plants is shown in Fig. 6. The stamens are unusually long, the anthers are well developed, and at least 95 per cent of the pollen germinated in each of two tests on the three strengths of sugar-agar media used.

These plants bearing seedless grapes are strongly male, but their seedlessness is, it seems to me, due to what we may properly call a weak grade of femaleness.

Figure 7 shows a flower of a plant bearing near-seedless or partially seedless fruits. The stamens are erect and well developed tho only of medium length. In tests for germination about 50 per cent of the pollen produced tubes. As is the case in Fig. 6, pistils of good size are present and from the appearance of the flower alone the plant would be considered as a perfect hermaphrodite. However, of the fruits examined, 27 were entirely seedless and ranged from 9 to 13 thirty-seconds of an inch in diameter; 8 fruits contained one soft seed each and ranged from 12 to 16 thirty-seconds of an inch in diameter; 52 fruits contained one well-developed seed each and were from 12 to 18 thirty-seconds of an inch in diameter; while only 5 fruits contained as many as two seeds each and these were 14, 15, 16, 17, and 18 thirty-seconds of an inch in diameter, respectively. The fruits are hence low in number of seeds, many are seedless, and none of the 1920 crop had more than two seeds. The fruits were of good quality and the bunches were uniformly well filled. (See Plate IV.)

This plant is a seedling from Triumph crossed with Delaware both of which are seeded grapes. A sister seedling bore fruits ranging from 15 to 19 thirty-seconds of an inch in diameter but none were seedless, altho no fruit contained more than two seeds.

A seedling derived from the cross Triumph x Dutchess has produced fruits ranging from 10 to 20 thirty-seconds of an inch in diameter. Many of the smaller fruits are seedless and of those examined none had more than two seeds.

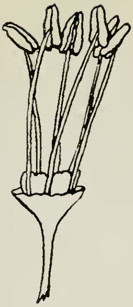
All of these plants bearing seedless or near-seedless fruits have flowers with erect stamens with filaments of medium or long lengths and pistils of medium size. Descriptive records of the Station for

# EXPLANATION OF PLATES

The flowers here illustrated are shown about four times their natural size. The original drawings for these were made to the same scale but there were some differences in the reduction for the various plates. Fig. 10 is enlarged about 110 times and Figs. 25, 37, and 39 about 350 times. The photos of Plates III and IV were taken natural size and are here reproduced as taken.

## PLATE I

All figures are of staminate types of fruitless plants. Rudiments of pistils are present in Figs. 3, 4, and 5, but there is no stigmatic surface in Fig. 3. All are from seedlings: Fig. 1 of a plant of unknown parentage, Fig. 2 of America selfed, Fig. 3 of the cross *Vitis Berlandieri* x *V. riparia*, Fig. 4 of the cross Solonis x Riparia No. 616, and Fig. 5 of Croton selfed.



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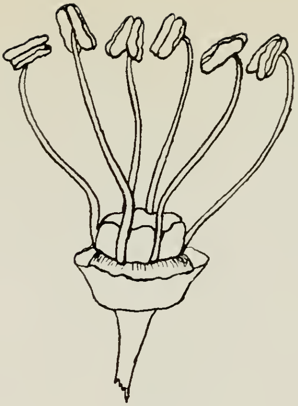

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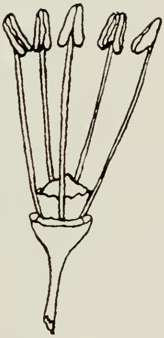

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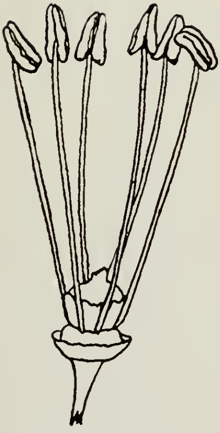

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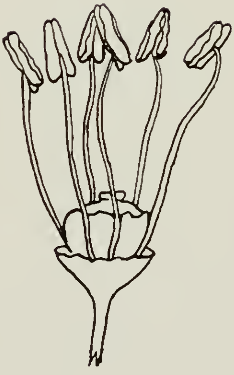

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Plate I

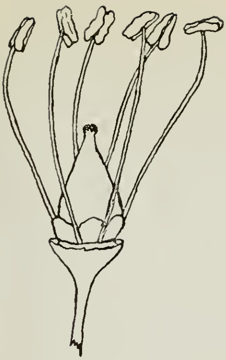
## PLATE II

Fig. 6. Typical flower of plant producing seedless fruits, a seedling of Concord Seedless.

Fig. 7. Flower of near-seedless plant, a seedling of Triumph x Delaware.

Figs. 8 and 9. Two flowers one with and one without pistil, borne in same cluster on a seedling of Solonis x Riparia. Fig. 10. Shows few potent and viable pollen among many shriveled grains from these flowers (x 110).

Figs. 11 and 12. Two flowers, both highly staminate, one with rudimentary pistil, other with pistil functional in fruit and seed production. From a seedling of Dutchess x Seibel No. 2.



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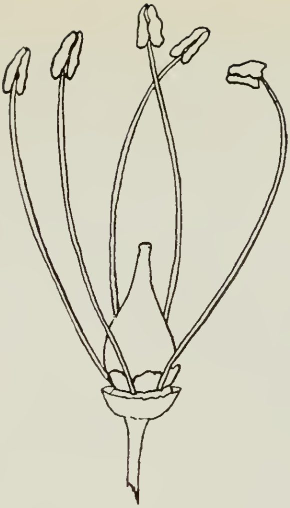

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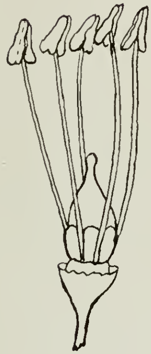

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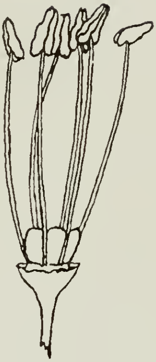

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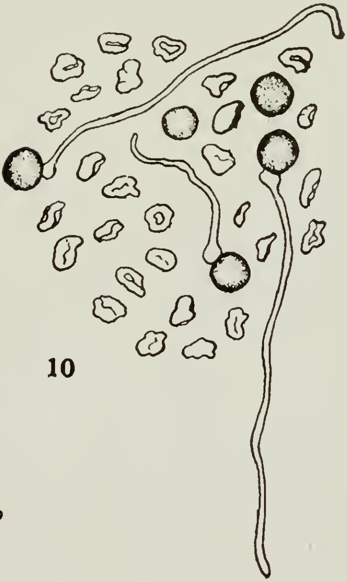

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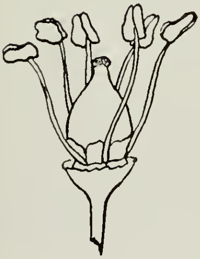

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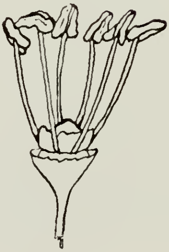

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Plate II

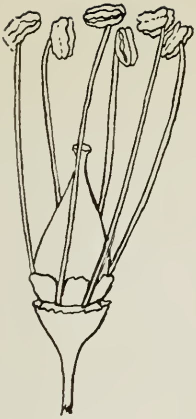
Plate III.—Cluster of Seedless Fruits borne by Seedling of the Concord Seedless. Flower of this Plant shown in Fig. 6

Plate IV.— Cluster of Fruits, Many Seedless and none with more than two Seeds, borne by a Seedling of Triumph x Delaware. Flower shown in Fig. 7.

## PLATE V

All perfect hermaphrodites with erect stamens. Highly functional both as males and females.

Fig. 13 of Wilder; Fig. 14 of Cottage; Fig. 15 of Worden; Fig. 16 of Concord; Fig. 17 of Seedling of Hexamer (selfed); Fig. 18 of Muscat Hamburg; Fig. 19 of Blauer Portugieser; Fig. 20 of Kensington; and Fig. 21 of seedling of Lindley x Niagara.



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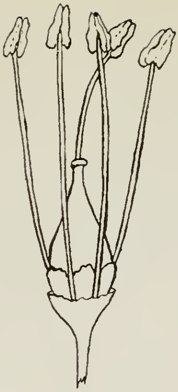

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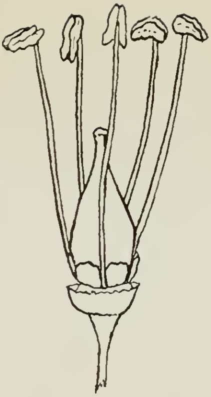

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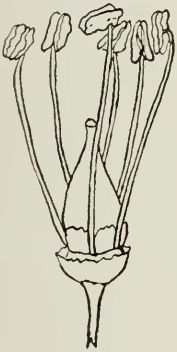

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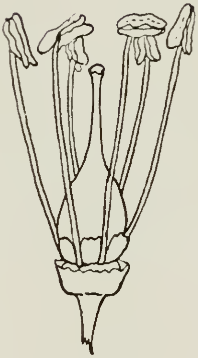

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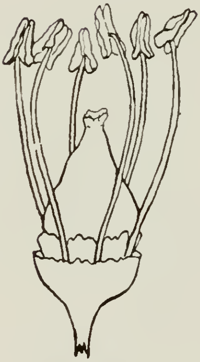

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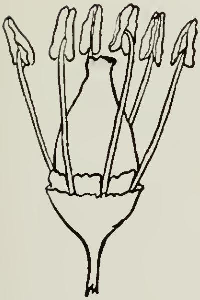

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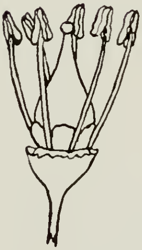

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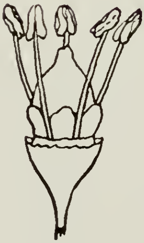

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Plate V

## PLATE VI

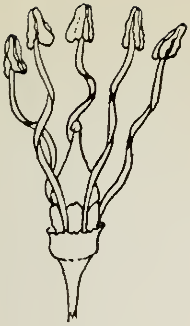
Figs. 22 and 23 are flowers with crinkled stamens; Fig. 24 is a stamen 20 times natural size; and Fig. 25 the shrivelled pollen magnified about 350 times. For ancestry of the plants bearing these see page 11.

Fig. 26. Flower with crinkled stamens from a second generation seedling of Salem x Worden.

Fig. 27. Flower with spreading stamens from seedling of Janesville selfed.

Fig. 28. Flower with strongly spreading stamens from seedling of Janesville selfed.

Fig. 29. Showing slightly recurving stamens of seedling of Clinton x Diana.



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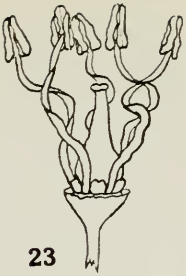

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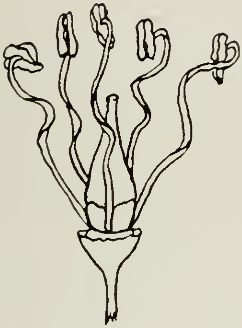

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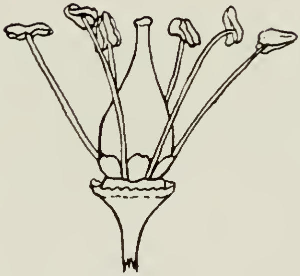

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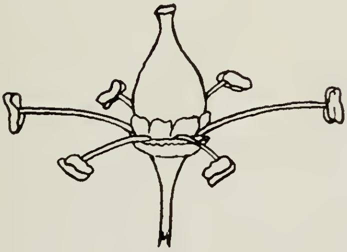

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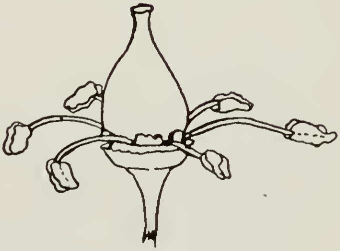

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Plate VI

## PLATE VII

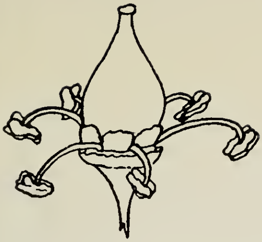
Fig. 30. Recurving or semi-reflexed stamens of seedling of Janesville selfed.

Fig. 31 flower just before, and Fig. 32 flower just after calyx is shed showing short stamens that become reflexed. (From Barry.)

Fig. 33. Flower of seedling of Noah selfed.

Fig. 34 flower of Aminia, Fig. 35 of Brighton, Fig. 36 of Massasoit, and Fig. 38 of Merrimac, all with strongly reflexed stamens.

Fig. 37 pollen of Massasoit, and Fig. 39 of Merrimac enlarged 350 times.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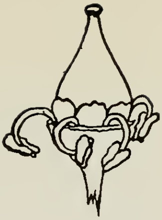
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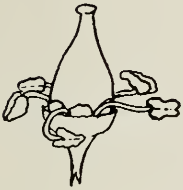
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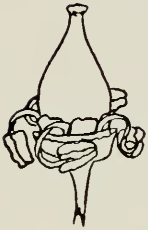
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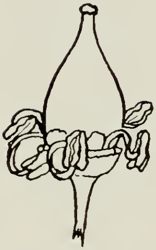
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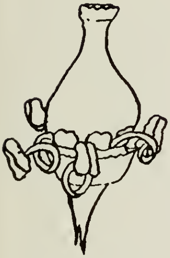
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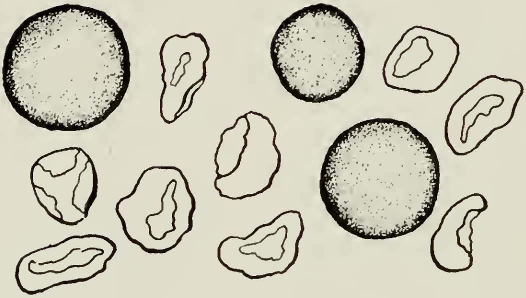
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38

39

Plate VII

flowers of such sorts as Hubbard Seedless and the Sultanina (the Thompson Seedless, a raisin grape widely cultivated on the Pacific Coast) indicate that these also have flowers of this general type. In respect to *maleness* the sex of these plants is highly developed, but their seedlessness shows that *femaleness* is weak and but partially developed. In the case of plants that produce seedless and seeded fruits in the same cluster there is indication that femaleness is irregular in its development and may appear in various grades among flowers of a single cluster altho such a mixing may not be apparent in the general appearance of the flowers, and not especially conspicuous in the general appearance of the clusters of fruit. (See Plate IV.)

Noll (1902) has called fruits which are produced without pollination *parthenocarpic.* The available evidence indicates that this is a relatively rare phenomenon. Such types should probably be classed quite differently than those in which pollination is required for any setting of fruit. They may perhaps be regarded as more strongly female or at least as strongly fruitful. There may be some question as to whether parthenocarpy is a phenomenon of vegetative or of reproductive vigor. However, the numerous grades of seedlessness which are found show, it seems to me, that when pollination is required seedlessness is to be regarded as a stage in the series of intersexes.

### PLANTS WITH TWO OR MORE FLOWER TYPES INTERMIXED

In some plants it is plainly evident from an examination of the flowers that such extreme types as the purely staminate and what resembles the perfect hermaphrodite are intermingled in the same cluster. The latter may, however, give no fruit, seedless fruits, seeded fruits, or various mixtures of these. Figures 8 with 9 and 11 with 12, show this condition.

The plant bearing the flowers shown in Figs. 8 and 9 produced no fruit in 1920 which suggests that the pistils that are formed are functionless. The erect stamens are of good size and the anthers dehisce normally but only about 5 per cent of the pollen germinated. The grains that did not germinate were with few exceptions shriveled and aborted (Fig. 10).

The plant bearing the flowers shown in Figs. 11 and 12 produced a " light " crop in 1920, the clusters were decidedly " loose," the berries irregular in size, and some of them were nearly seedless. Such crops are characteristic of many seedlings and also of some of the commercial varieties. A mingling of flowers in which there are various grades of development in the pistils is at least one of the causes of such incomplete fruiting. Purely staminate flowers and flowers with functionless pistils are fruitless, and other grades are seedless, near seedless, or strongly seeded. Irregular fruiting from year to year may, in some cases, be due in a large degree to variation in the proportions of the various types of flowers present.

### PERFECT HERMAPHRODITES WITH UPRIGHT STAMENS

Marked differences in length of filaments, size of anthers, and size and shape of pistils are to be seen among flowers of this general class. The flowers illustrated in Figs. 13 to 20 are from well-known varieties. All of these sorts are highly productive of fruits that contain seeds. Altho the number of seeds characteristic of the variety may differ somewhat, all are strongly female and the fruitfulness depends on fertilization and on the development of seeds. As shown in the figures, the stamens of a variety may be so short that they scarcely reach above the stigma (Kensington, Fig. 20) and in another variety they may be at least twice that length (Cottage, Fig. 14). All grades between the extremes of length are to be seen among the varieties and the seedlings usually classed together as having upright stamens. In all the well-known cultivated varieties of this class, European as well as American, so far as tested by the writer, the pollen is remarkably viable with at least 75 per cent of all grains germinating in tests. In many seedlings, however, the pollen is mostly shrivelled and not viable in the germination tests, and the presence and general vigor of erect stamens is not a sure indication that the stamens are functional.

### IMPERFECT HERMAPHRODITE WITH ERECT CRINKLED STAMENS

In these the stamens are ascending but the filaments are variously twisted or crinkled in irregular and incomplete spirals. (See Figs. 22 to 26.) The anthers appear on general examination, to be perfectly formed and to dehisce normally (Fig. 24). Repeated tests for germination of the pollen were made for several plants bearing these flowers but no germination was obtained. So far as observed all pollen grains are irregularly shrivelled (Fig. 25).

The crinkled-stamen type of flower was found in each one of 34 sister plants, but the length of filaments and the degree of crinkling differed somewhat as is shown by comparing Figs. 22 and 23. In 1920 all but 2 of the 34 plants produced seeded fruit and of these 7 bore a " full " crop, 9 a " medium " crop, 9 a " light " crop, and 7 a " very light " crop. With the exception of two plants, these seedlings were able to function as females in fruit and seed production.

The ancestry of this series of 34 plants is well known for three generations. First, Winchell was crossed with Diamond (both classed as hermaphrodites with upright stamens), and Station Seedling No. 123 with upright stamens was obtained. This seedling was used as a pollen parent on Worden, also with upright stamens, and three seedlings, all with upright stamens, Nos. 931, 933, and 934, were obtained. The 34 plants derived from selfing seedling No. 933 were all of the type with crinkled stamens. Of the progeny obtained by selfing the sister plants, 931 and 934, 24 have bloomed and have only the normal erect stamens of the perfect hermaphrodite. As to length, the stamens of 1 were short, of 20 medium, and of 3 long.

It appears that the plants with this crinkled type of stamen are not able to function as males. Functionally their sex is quite like that of the imperfect hermaphrodites with reflexed stamens. One might consider that in these there is a combination of the " reflexed " character of filament with the " upright." The appearance of this type of flower in all of 34 sister plants after three generations of parentage with normal upright stamens suggests the phenomenon of the so-called mass mutation.

Another plant was found bearing flowers with crinkled but less erect stamens (Fig. 26). In this case the filaments may be considered as tending to be recurved. This plant is a seedling derived from selfing Station Seedling No. 4574 (having normal upright stamens), which was an offspring of Salem (reflexed) crossed with Worden (upright). In this case the reflexed character was present in one grandparent.

Whether the crinkled character of stamen is to be considered as due to a recombination of hereditary units, as an intermediate between reflexed and upright, or as a mutation, it is a new type of flower to be recognized in classifying the flowers of grapes.

### FLOWER TYPES WITH SPREADING OR SEMI-REFLEXED STAMENS

Frequently among the seedlings there are plants with flowers whose stamens have nearly straight or slightly recurved filaments which at the time of complete anthesis stand at a decided angle from the axis of the pistil. In general these may be considered as intermediate between erect and recurved. Flowers of this sort from four plants are shown in Figs. 27 to 30. In these the anthers are well formed and dehisce quite normally, but the pollen was of irregular sizes, more or less shrivelled, and not viable in germination tests. These plants are able, therefore, to function only as females.

### FLOWER TYPES WITH RECURVED STAMENS

The general character of this sort of flower is shown in Figs. 31 to 38, all but one of which are from well-known varieties long recognized as fully or very decidedly self-fruitless. The stamens may be strongly but simply recurved as seen in the flower of Barry (Fig. 32), extremely recurved and curled as in Massasoit (Fig. 36), or of various gradations between such conditions. The filaments are sometimes very slender. The anthers are in various grades of development; and in Barry (Figs. 31 and 32) thay are small in size, many appear to contain no pollen, and some do not dehisce. In other varieties the anthers are uniformly larger and dehisce well and a part of the pollen appears to be normal (Fig. 37).

The writer made extensive tests for germination of pollen both in varieties and in seedlings having reflexed stamens. In many cases all of the grains were irregularly shrivelled and devoid of granular contents. In other cases some of the grains became spherical on the sugar-agar media and appeared to have granular contents (Fig. 37), but in no case did any pollen from recurved stamens germinate. It should be noted, however, that seeds have evidently been obtained at the Geneva Station from selfing and crossing several of these varieties. Possibly a few of the grains are capable of germinating on pistils but incapable of germinating on media that give excellent germination of the pollen from staminate types and from hermaphrodites with normal upright stamens.

## DISCUSSION AND CONCLUSION

A summary of the variations in the flowers of cultivated varieties of grapes and of seedlings from them shows that there are many grades in the relative development of pistils and stamens.

Complete loss of femaleness is seen in only a few cases, but various grades of rudimentary pistils are present that are incapable of yielding fruits of any kind. This evidence suggests that it is a weak grade of femaleness which is responsible for the development of seedless fruits. In near-seedless sorts. femaleness is of still another grade but below that of high seed production.

A complete morphological loss of stamens has not been found. The least male plants are perhaps among those with recurved stamens, small sterile anthers, and only aborted pollen. Such plants are able to function as females only. Plants with erect crinkled stamens and some plants with normal upright filaments are likewise unable to function as males because of impotent pollen. In the extremes there is complete loss of one or the other sex, at least functionally. Between these extremes there are various grades of relative development and functioning ability of pistils and stamens. In the perfect hermaphrodites both of these organs are highly developed and functional, and it is these types that include all of the most important and productive of the seeded grapes.

It appears that, in individual plants, the stamens are more uniform than the pistils; at least they appear to be rather uniform in respect to length of filaments and general character of anthers. The intermixing of flowers of several types in the same cluster seems to involve especially variations in the condition of the pistils. The most obvious of these are mixtures of staminate flowers and of perfect flowers that are capable of development into fruits with seeds. The type of pistil that produces seedless fruits may also be present.

Variations in the character of pistils in flowers from year to year have been observed. (See especially Detjen, 1917 for plant named "Hope.") There is some evidence that the fruit production of the self-fruitless varieties can be influenced by girdling and bending (Beach, 1902), but whether such treatment changes the character of the stamens by rendering them more potent as the results would perhaps suggest is not determined.

The variations in the morphological development of stamens and pistils and in their ability to function as sex organs are to be described as phenomena of intersexualism. The abortion of pollen in reflexed, in crinkled, and in other stamens is seen in flowers that are highly pistillate and functional as females. Conversely extreme loss of femaleness is seen in staminate types in which maleness is highly developed. In these extremes the loss of sex is one-sided. Such one-sided impotence is characteristic of intersexualism as distinct from the sterility of hybridity which tends to affect both sexes in the individual quite the same.

Cases of sterility in grapes due to hybridity are reported by Detjen (1919) in $F_1$ hybrids between *Vitis vinifera* (*Malaga*) and *V. rotundifolia* in which flowers of the external form of the perfect hermaphrodites are mostly or entirely sterile and impotent in both stamens and pistils. Such sterility appears to be largely absent in hybrids between *V. vinifera* and the more northern species of native American grapes. Many varieties known to have originated thus have perfect flowers with both sets of sex organs highly functional. A systematic study of known hybrids between *V. vinifera* and native species from which such a variety as Concord originated is needed to determine to what extent, if at all, sterility from hybridity is present along with intersexualism.

The results of the breeding work already obtained at the Station indicate clearly that the use of seedless and near-seedless plants as male parents in crosses with varieties that are strongly female (perfect and imperfect hermaphrodites) gives progeny that are strongly female and seed producing. The $F_1$ offspring of many crosses of standard seeded varieties with Hubbard Seedless have all been strongly pistillate, yielding seeded fruit. Weak femaleness (seen in seedless fruits) is in this case dominated or swamped by the strong femaleness of the seed parent. However, the seeded character of $F_1$ individuals is no index of the variation in intersexes that may appear in later generations in which the segregation of at least some plants bearing seedless fruits may be expected. The use of other seedless sorts in such crosses may, however, give different results.

The most effective course in breeding for the development of seedless sorts is suggested by the conditions of intersexualism. Most individuals and varieties producing seedless or near-seedless fruits are strongly staminate. The former can be used as male parents on the latter, which do produce a few viable seeds. Plants strongly male and seedless can be crossed with plants strongly male but weakly female and near-seedless and, also, the self-fertilized progeny of the latter may be obtained. In this way families weak in femaleness may undoubtedly be obtained in which a considerable number of individuals will produce seedless fruits.

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# NOTES ON ROSACEAE–XIII

PER AXEL RYDBERG

NEW YORK
1921

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# Notes on Rosaceae—XIII

PER AXEL RYDBERG

## ROSES OF THE COLUMBIA REGION

In this region I here include the states of Oregon and Washington, together with British Columbia and northern Idaho. Most important are the roses of the Cascade Mountains. In the northern part many of the species of the Rocky Mountains have invaded the region, not only on the western slopes of the Rockies but also in the Cascades; in the Siskiyou Mountains of southwestern Oregon there are also found some Californian species; and in eastern Oregon some of those belonging to the Great Basin are found. Since my revision in the North American Flora we have received in exchange a collection from British Columbia, from the Geological Survey of Canada; and Professor J. K. Henry of the University at Vancouver has sent in another collection for determination. Also, I have seen collections from southeastern Oregon made by Miss Eastwood and Dr. Rehder for the Arnold Arboretum.

### Key to the groups of species

Styles much exserted, about equaling the stamens; stipules adnate; sepals reflexed, deciduous; styles united; stem climbing, with curved prickles. I. SYNSTYLAE.

Styles not exserted, or only slightly so; stigmas forming a head closing the mouth of the hypanthium.

  Pistils numerous; styles as well as the upper part of the hypanthium persistent.

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[The Bulletin for May (48: 141–158. *pl. 3*) was issued May 25, 1921.]

| | |
|---|---|
| Stem climbing, with scattered prickles, rarely with intermixed bristles; sepals more or less lobed; foliage glandular-punctate, sweet-scented. | II. CANINAE. |
| Stem not climbing, at least the young shoots bristly; prickles infra-stipular or lacking; sepals entire or the outer sometimes with one or two lobes; foliage not very sweet-scented. | III. CINNAMOMEAE. |
| Pistils few; styles deciduous with the upper part of the hypanthium, which falls off like a ring. | IV. GYMNOCARPAE. |

## I. SYNSTYLAE

| | |
|---|---|
| Stipules pectinately lobed and glandular-ciliate; corymb many-flowered. | 1. *R. multiflora.* |
| Stipules merely serrate; corymb one- to few-flowered. | 2. *R. arvensis.* |

### 1. ROSA MULTIFLORA Thunb.

See my notes in the preceding paper of this series.* The species has been reported as a ballast plant at one station in Washington.

### 2. ROSA ARVENSIS Huds.

The following specimens were sent to me by J. C. Nelson, principal of the high school at Salem, Oregon, for determination. In the accompanying letter Mr. Nelson wrote among other things: "He [the collector] reports this form as common in the vicinity of Vancouver [Washington], apparently fully spontaneous. The flowers were always single, and the petals of a wonderful shade of pearly white." The specimens apparently belong to the so-called Ayrshire Rose, which is by some regarded as a form of *R. arvensis*, by others as a hybrid of the same. The leaflets are larger and more pointed and the sepals more inclined to be lobed than in the wild English form of that species.

WASHINGTON: Vancouver, *R. V. Bradshaw 1053.*

## II. CANINAE

| | |
|---|---|
| Leaflets suborbicular or broadly oval, mostly rounded at the apex; hypanthium in fruit obovoid or broadly ellipsoid, abruptly contracted at the apex; sepals tardily deciduous or persistent. | 3. *R. rubiginosa.* |
| Leaflets ovate or oval, acute or short-acuminate; hypanthium in fruit narrowly ellipsoid, tapering at both ends; sepals early deciduous; styles glabrous or nearly so. | 4. *R. micrantha.* |

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* Bull. Torrey Club 47: 47. 1920.

### 3. ROSA RUBIGINOSA L.

The European sweet brier, often cultivated, has established itself at several places in Oregon and Washington. It is very variable and the naturalized specimens show also much variation. One of these many forms, which is rather more glandular than usual, was mistaken for a native species and published by Dr. E. L. Greene as new, under the name *R. Walpoleana*. The author placed it in the GYMNOCARPAE, a group to which it has no relation.

### 4. ROSA MICRANTHA Borrer

See Bull. Torrey Club 47: 49. 1920. This species also is naturalized in Oregon and Washington.

## III. CINNAMOMIAE

- Infra-stipular prickles not present; branches unarmed or bristly, not prickly.
  - Stem densely bristly even in age; flowers solitary.
    - Hypanthium decidedly pear-shaped or ellipsoid, acute at the base, with a distinct neck at the top.
      - Sepals rarely more than 1 cm. long; bark yellowish green. 5. *R. collaris.*
      - Sepals 2–3 cm. long; bark brown.
        - Leaflets obovate, sparingly hairy beneath. 6. *R. Butleri.*
        - Leaflets elliptic, densely pubescent beneath. 7. *R. acicularis.*
    - Hypanthium subglobose, almost without a neck. 8. *R. Bourgeauiana.*
  - Stem unarmed or when young covered with more or less deciduous bristles; flowers corymbose.
    - Fruit ellipsoid; leaflets serrate. 32. *R. Pringlei.*
    - Fruit subglobose; leaflets crenate. 9. *R. anacantha.*
- Infra-stipular prickles present.
  - Flowers mostly solitary; petals usually 2.5 cm. long or more (except in No. 11); hypanthium in fruit 12–20 mm. thick.
    - Prickles straight or nearly so.
      - Hypanthium densely prickly. 10. *R. MacDougalii.*
      - Hypanthium not prickly or rarely slightly so.
        - Leaflets more or less double-toothed, more or less glandular-granuliferous beneath; stipules and rachis glandular.
          - Pedicels and calyx densely bristly but hypanthium glabrous; leaflets oval, rarely 2 cm. long; prickles weak; petals 15 mm. long. 11. *R. yainacensis.*
          - Pedicels and calyx not bristly, sometimes slightly glandular-hispid.

Leaves very thin, pale and slightly glandular-puberulent, but not muriculate beneath. 12. *R. Nutkana.*

Leaves thicker, dark green on both sides, conspicuously glandular-muricate beneath. 13. *R. muriculata.*

Leaflets simple-toothed, puberulent beneath, but not glandular-granuliferous or -muricate; rachis rarely glandular. 14. *R. Spaldingii.*

Prickles more or less curved.

Prickles very large, flat, pubescent; twigs densely glandular and pubescent. 15. *R. Durandii.*

Prickles slender, glabrous, not conspicuously flattened; twigs not conspicuously glandular, mostly glabrous.

Sepals not glandular-hispid; leaflets 2–4 cm. long, not conspicuously glandular double-toothed. 16. *R. columbiana.*

Sepals conspicuously glandular-hispid; leaflets 1–2 cm. long, conspicuously glandular double-toothed. 17. *R. myriadenia.*

Flowers mostly corymbose, if solitary the petals 2 cm. long or less; fruit rarely more than 1 cm. in diameter.

Prickles more or less curved.

Leaflets softly villous beneath; prickles stout, flattened; hypanthium with a neck. 18. *R. californica.*

Leaflets very finely puberulent and somewhat glandular-pruinose beneath; prickles not flattened; hypanthium without a distinct neck.

Leaflets with simple teeth, not copiously glandular-pruinose beneath. 19. *R. puberulenta.*

Leaflets with double gland-tipped teeth, conspicuously glandular-puberulent beneath. 20. *R. delitescens.*

Prickles straight or nearly so.

Hypanthium normally neither prickly or bristly.

Hypanthium globose; neck usually obsolete.

Sepals lanceolate, with long, caudate-attenuate or sometimes foliaceous tips, more than 1 cm. long.

Stipules, petiole, and rachis copiously glandular; leaflets double-toothed, with gland-tipped teeth, densely glandular-pruinose or muriculate beneath.

Leaflets orbicular or rounded oval. 13. *R. muriculata.*

Leaflets oblong to oval. 22. *R. Fendleri.*

Stipules, petiole, and rachis not glandular or the stipules slightly glandular-dentate.

Leaflets glabrous or nearly so.

Leaflets broadly oval, 3–5 cm. long. 21. *R. rivalis.*

Leaflets obovate or elliptic, rarely 3 cm. long. 23. *R. Woodsii.*

Leaflets more or less pubescent beneath.

Leaflets villous or pilose beneath, rounded or broadly oval. 25. *R. myriantha.*

Leaflets finely puberulent beneath.

Leaves obovate, more or less pale or glaucous beneath; prickles comparatively long, spreading. 24. *R. Macounii.*

Leaflets elliptic or oval, equally green on both sides; plant with few short ascending prickles.

Sepals decidedly glandular; leaflets thin and soft. 26. *R. pisocarpa.*

Sepals not glandular, or slightly so on the margins; leaflets rather thick. 27. *R. ultramontana.*

Sepals ovate, less than 1 cm. long, not conspicuously caudate; leaflets simple-toothed; puberulent beneath. 28. *R. Covillei.*

Hypanthium elongate with a distinct neck; leaves finely puberulent beneath.

Leaflets light green, coarsely toothed; hypanthium in fruit pyriform. 31. *R. pyrifera.*

Leaflets dark green above, finely toothed; hypanthium in fruit ellipsoid.

Plant unarmed or nearly so; fruit 1 mm. broad. 32. *R. Pringlei.*

Plant with slender prickles; fruit 6–8 mm. broad. 33. *R. Eastwoodiae.*

Hypanthium densely bristly or prickly; leaflets orbicular in outline.

Leaflets subsessile. 29. *R. spithamea.*

Leaflets with petiolules, 1–4 mm. long. 30. *R. adenocarpa.*

### 5. Rosa collaris Rydberg

The following specimens are doubtfully referred to this species: Washington: Fort Colville, 1880, *S. Watson 123.*

### 6. ROSA BUTLERI Rydberg

This species belongs to the Rocky Mountain region and was originally described from northwestern Montana. The following specimens from British Columbia are referred here:

BRITISH COLUMBIA: Camloops, May 24, 1912, *A. Thorpe.*

### 7. ROSA ACICULARIS Lindl.

See Bull. Torrey Club. **47**: 56. 1920. This is a common species throughout the northern Rockies and the Cascade Mountains.

### 8. ROSA BOURGEAUIANA Crépin

See notes in Bull. Torrey Club **47**: 57. 1920. In the Columbia region, this species has been found only north of the Canadian boundary.

BRITISH COLUMBIA: Okanogan Landing, Golden, *Pense;* Skeena River, *J. K. Henry.*

### 9. ROSA ANACANTHA Greene

This species is related to the eastern *R. blanda,* but differs in the crenate instead of serrate leaflets and the smaller fruit. It is known only from the type locality, in salt marshes near Tacoma, Washington.

### 10. ROSA MACDOUGALII Holz.

This is regarded by many as a form of *R. Nutkana.* It differs not only in the hispid fruit but also in the fact that the teeth of the leaflets are seldom double as they are in *R. Nutkana* and the leaflets are rarely glandular-granuliferous. Neither could it be referred as a form of *R. Spaldingii,* for in the latter the leaflets are pubescent beneath. The following specimens belong here:

IDAHO: Landing-Cuprum road 1901, *Cusick 2533, 2352;* Farmington Landing, 1892, *Sandberg, MacDougal & Heller 572, Heller 3256.*

OREGON: Rye River Valley, *Leiberg 4410.*

WASHINGTON: Pullman, 1896, *Elmer 72, 74.*

### 11. ROSA YAINACENSIS Greene

Until lately this species was known only from the type locality. The habit, long prickles, and large fruit suggest *R. Nutkana,* but it is unique in the group on account of its densely glandular-bristly pedicels. It evidently is a good species unless of hybrid origin. It might have been produced by *R. Nutkana* and *R. gymnocarpa.*

OREGON: Yainax Indian Reservation, *Mrs. Austin.*

CALIFORNIA: Crescent City, Del Norte County, 1912, *Eastwood 2270.*

### 12. ROSA NUTKANA Presl

Although an easily distinguished species (except from the two next following species), it has been mistaken for *R. fraxinifolia* (i.e. *R. blanda*) and *R. Woodsii.* It has also been named *R. caryocarpa* Dougl. and *R. Lyalliana* Crépin; but these names have not been published, except in synonymy.

### 13. ROSA MURICULATA Greene

This is closely related to *R. Nutkana* and is perhaps not distinct. It differs in the thicker and smaller leaves, densely glandular-muricate beneath, and in the often corymbose inflorescence. As it is more common on the Vancouver Island than the preceding species, there may be a possibility that it is the original *R. Nutkana* Presl. In such a case the plant known as that species would be without a published name.

### 14. ROSA SPALDINGII Crépin

This has been confused with *R. Nutkana* but differs in the simple-toothed leaflets, which are decidedly pubescent but scarcely at all glandular-granuliferous beneath. Dr. Watson merged it in *R. Nutkana*, and this fact probably influenced Crépin to withdraw his species. The plant had been recognized before: Borrer in Hooker's Flora included it in *R. cinnamomea*, which it approaches more than any other American species does, differing principally in the longer and straight prickles; Nuttall recognized it as a species, *R. megacarpa*, but this name was published only as a synonym in Torrey & Gray's Flora; in the meantime Rafinesque had published it as *R. macrocarpa* Nutt. It is common through the northern Rockies as well as the Cascades.

### 15. ROSA DURANDII Crépin

This was based on *E. Hall 146*, which was referred to *Rosa kamtschatica* by Dr. Gray. Dr. Watson in his monograph reduced it to a synonym of *R. Nutkana*. Crépin, probably influenced by Watson's treatment, later retracted his species. In my opinion *R. Durandii* is perfectly distinct from *R. Nutkana*. The leaves are thicker, more hairy than in that species, and rarely double-toothed; the prickles are not like those of *R. Nutkana*, but curved, short, strongly flattened and pubescent. As long as only Hall's specimens were known, the specimens might have been regarded as freaks, but specimens almost exactly like these have since been collected.

OREGON: *E. Hall 146;* Brownville, 1895, *Canby;* near Springfield, *Coville & Applegate 1076.*

BRITISH COLUMBIA. Queen Charlotte's Island, *Dawson 8144* (?).

IDAHO: Lower Priest River, *Leiberg 2883*. This specimen is very peculiar, nearly unarmed, but with the pubescence of the leaves and twigs of *R. Durandii.*

### 16. ROSA COLUMBIANA Rydberg

This also is related to *R. Nutkana* but differs in the strongly curved prickles. It is a rather local plant, the following specimens belonging here:

IDAHO: Little Potlatch River, 1892, *Sandberg, MacDougal & Heller 381;* Kooteney County, *Sandberg.*

OREGON: Forest Grove, 1893 and 1894, *Lloyd.*

### 17. ROSA MYRIADENIA Greene

This species has the habit, toothing, and glandular pubescence of *R. muriculata*, but the leaflets are smaller and the prickles are decidedly curved; these characters would place it in the key next to *R. columbiana*. From this it differs in the smaller and more pubescent leaves. It is known only from the type locality, Huckleberry Mountains, Jackson County, Oregon.

### 18. ROSA CALIFORNICA Cham. & Schlecht.

This Californian species has been collected in the extreme southern part of Oregon.

### 19. ROSA PUBERULENTA Rydberg

This species belongs to the Great Basin and is related to *R. arizonica* and *R. neomexicana*. The following specimens are referred here, though somewhat doubtfully:

WASHINGTON: Wilson Creek, *Sandberg & Leiberg;* Rattlesnake Mountains, *Cotton 469.*

OREGON: Antelope Creek, *Applegate 2399;* Cold Spring, *Coville & Applegate 1122;* Wallowa, *Samson & Pearson 78.*

### 20. ROSA DELITESCENS Greene

This is related to *R. californica* but characterized by the double-serrate leaflets, glandular-pruinose beneath and with gland-tipped teeth, and by the subglobose fruit. It is known only from the type locality in the Siskiyou Mountains, Oregon.

### 21. ROSA RIVALIS Eastwood

This species belongs to the Californian flora (see notes, Bull. Torrey Club 44: 74. 1917) but the following specimen has been collected in Oregon:

OREGON: Cold Spring, Crook County, 1898, *Coville & Applegate 131.*

### 22. ROSA FENDLERI Crépin

### 23. ROSA WOODSII Lindl.

### 24. ROSA MACOUNII Greene

These three species belong to the Rocky Mountain region but extend west into the Cascade Mountains. They will be treated in a subsequent paper.

### 25. ROSA MYRIANTHA Carr.

This is primarily a Californian rose (see notes, Bull. Torrey Club 44: 75, 76. 1917), but the following specimens belong here:

OREGON: Barlow Gate, *Lloyd;* lower Albina, Portland, *Sheldon 10659;* Wimmer, *Hammond 119,* in part.

### 26. ROSA PISOCARPA A. Gray

### 27. ROSA ULTRAMONTANA (S. Wats.) Heller

These two species have been treated previously, under the Roses of California and Nevada (see Bull. Torrey Club 44: 77, 78. 1917). Though the former has its best development in the

Columbia region, especially west of the Cascades and the latter in the northern part of the Great Basin, which includes eastern Oregon, both extend north into British Columbia.

### 28. ROSA COVILLEI Greene

This species and *R. Bolanderi* are characterized among the cinnamon roses by the short ovate, short-acuminate sepals. *R. Covillei* is known only from the type locality, near Naylor, Klamath County, Oregon.

### 29. ROSA SPITHAMAEA S. Wats.

This species of northern California has been collected at one locality in the Columbia region:—

OREGON: Wimmer, *Hammond 120*.

### 30. ROSA ADENOCARPA Greene

Notwithstanding Dr. Greene's remark, "despite all its peculiar characteristics, a genuine member of this gymnocarpa group," I am compelled to exclude it. The upper part of the hypanthium and calyx show no sign of being deciduous, the sepals are not those short ones of the *R. gymnocarpa* allies, and the hypanthium is bristly. These characters and the dwarf herbaceous stems indicate that the plant is related to *R. spithamaea*, where I have placed it. It is known only from the type locality, Mt. Grayback, southwestern Oregon.

### 31. ROSA PYRIFERA Rydberg

This species is related on one hand to *R. Macounii* and on the other to *R. ultramontana* and *R. pisicarpa*, but differs from them all in the pear-shaped hypanthium, which has a more distinct neck. It is common in the northern Rockies, but the following specimens are from the Columbia region:—

WASHINGTON: Clarks Spring, *Kraeger 47*.

OREGON: Powder River Mountains, 1896, *Piper;* Horse Creek Canyon, *Sheldon 8138;* Thompson Creek, *Brown 86;* Ashland, *Walpole 375;* Tygh Valley, *Walpole 336;* Cow Creek, *Coville 1162;* Blue Mountains, *Cusick 1697*.

### 32. ROSA PRINGLEI Rydberg

See notes, Bull. Torrey Club 44: 79. 1917. The following specimens are from the region:

OREGON: Wallowa River, 1897, *Sheldon 8687* (?).

WASHINGTON: Klickitat County, 1885, *Suksdorf.*

BRITISH COLUMBIA: Armstrong Pass, 1912, *E. Wilson;* Elgin, *Miss Edstrom.*

### 33. ROSA EASTWOODIAE Rydberg

This is related to *R. Pringlei* but the plant has smaller leaves, smaller flowers and fruit, and is usually prickly. The fruit is only 6–8 mm. in diameter. To this belong:—

CALIFORNIA: Sisson, Siskiyou County, 1912, *Eastwood 2100*, mainly.

OREGON: Waldo, Josephine County, 1912, *Eastwood 2168.*

## IV. GYMNOCARPAE

Leaves glabrous beneath.
  Flowers mostly 2–4 together, leafy-bracted; upper stipules broadly dilated; leaflets with broadly ovate teeth, indistinctly reticulate beneath; fruit 6–8 mm. broad. 37. *R. dasypoda.*
  Flowers usually solitary, not leafy-bracted; stipules narrow; leaflets with lanceolate or ovate lanceolate teeth; fruit 6 mm. in diameter or less.
    Leaves not very thin, pale and indistinctly reticulate beneath; sepals 1–1.5 cm. long. 35. *R. leucopsis.*
    Leaves very thin, scarcely paler on the lower surface, which is distinctly reticulate with semi-pellucid veinlets; sepals less than 1 cm. long.
      Leaflets 5–7, usually more than 1.5 cm. long; teeth ovate-lanceolate in outline; terminal leaflet usually rounded at the base. 34. *R. gymnocarpa.*
      Leaflets 7–9, usually less than 1.5 cm. long, the terminal one usually acute or cuneate at base; teeth lanceolate in outline. 36. *R. prionota.*
Leaves pubescent beneath. 38. *R. Bridgesii.*

### 34. ROSA GYMNOCAPRA Nutt.

This species is one of the most common roses in the Columbia region (see my notes, Bull. Torrey Club 44: 82. 1917). As stated there Dr. Greene described twelve species belonging to the group and some of these will be discussed here.

*Rosa glaucodermis* Greene. Dr. Greene pays especial attention to the ashy gray bark and the petioluled leaflets, characters which I think are not distinctive. In the typical *R. gymnocarpa* the bark is often light in color on old stems, and many specimens from the range of the typical *R. gymnocarpa* have more or less petioluled leaflets, such as *Jones 1088* and *R. S. Williams 876* from Montana, *Sheldon 8521* from Oregon, and *Allen 72* from Washington. I therefore regard this as a synonym of *R. gymnocarpa.*

*Rosa abietorum* Greene, I take as an unusually bristly *R. gymnocarpa.* I have been unable to find any constant character.

*Rosa amplifolia* Greene. I have not been able to distinguish this from *R. gymnocarpa.* Dr. Greene's remarks, "the leaves are so very large and have so much the color, texture and pattern of *R. acicularis*, that but for the small solitary flowers this would have passed readily with many for that species," are at least confusing. *R. acicularis* has rather thick, elliptic leaflets, decidedly pubescent beneath. Dr. Greene must have had an erroneous idea of *R. acicularis.*

### 35. ROSA LEUCOPSIS Greene

This is so close to *R. gymnocarpa* that I hesitated to admit it as a species. In *R. gymnocarpa* and *R. prionota* the leaflets are very thin and reticulate with semi-pellucid veins. In *R. leucopsis* the leaves are not so thin and the veins are faint and not at all pellucid. Otherwise the three plants are very similar. The species was described from fruiting material; the plant becomes paler in age.

*Rosa Helleri* Greene is evidently the same plant in flowers and shows only slight variation from the type of *R. leucopsis.* The Idaho specimens are mostly like those of the type of *R. Helleri*, but two numbers of Sandberg, MacDougal & Heller are almost identical with the type of *R. leucopsis.*

### 36. ROSA PRIONOTA Greene

This has been discussed before (see Bull. Torrey Club **44**: 32. 1917).

*Rosa piscatoria* Greene I regard as an unusually strong and bristly plant of *R. prionota.*

*Rosa apiculata* Greene was so named on account of the form of the fruit, "which is elongated, fully twice as long as broad, ending in a narrow necklike apiculation." The type sheet bears eight fruits. Of these only four are twice as long as broad, three are ellipsoid, but not as long, and one is nearly globose, slightly pear-shaped; four of them (three of the longer and one of the short-ellipsoid ones) have a conspicuous neck; one of the short-ellipsoid ones has no neck and the other three a short one. Miss Cooley's specimens from Vancouver Island, which from the locality should belong to this species and which agree with it in all respects except the fruit, has three fruits. One of these is elongated-ellipsoid, one somewhat pear-shaped and one subglobose; all with obsolete neck. They cannot be distinguished from *R. prionota.*

To *R. prionota* belongs the following specimens from the Columbia region:

Washington: Whiddley Island, *Saunders* (type of *R. apiculata*).

British Columbia: Nanaino, *Miss Cooley.*

### 36. Rosa dasypoda Greene

See notes, Bull. Torrey Club 44: 83. 1918. To this species belong the following specimens:

Oregon: Wallowa County, *Sheldon 8815* and several other numbers; Siskiyou Mountains, *Applegate 2251;* without locality, *E. Hall 143;* Toledo Canyon, *Rusby;* Wimmer, *Hammond 117.*

Washington: Chehalis County, *Heller 3897.*

British Columbia: Chilliwack Valley, *Macoun 79841, 24748;* between Kettle and Columbia River, *Macoun 64008, 64007;* Esquimalt, *Macoun 79840.*

### 37. Rosa Bridgesii Crépin

See Bull. Torrey Club 44: 83. 1917. To this species belong the following:—

Oregon: between Union Creek and Whiskey Creek, *Applegate 2622;* Huckleberry Mountains, *Coville 1434.*

## HYBRIDS

The following hybrids have been recorded from this region:—

### Rosa acicularis × Fendleri

British Columbia: Golden, *J. K. Henry.*

### Rosa acicularis × muriculata

British Columbia: Narramantha, Lake Okanogan, *J. K. Henry.*

### Rosa Bourgeauiana × muricata

British Columbia: Hazelton, Skeena River 1915, *J. K. Henry.*

### Rosa gymnocarpa × Nutkana

British Columbia: Crescent 1915, *J. K. Henry.*

### Rosa Nutkana × pisocarpa

British Columbia: Savannas, 1892, *F. E. Lloyd.*

### Rosa pisocarpa × Spaldingii

Eastern Oregon: 1900, *Cusick 2418.*

### Rosa gymnocarpa × pisocarpa

Oregon: Siskiyou Mountains, 1904, *Rehder.*

### Rosa gymnocarpa × muriculata

British Columbia: Cameron Lake, Vancouver Island, 1912, *J. K. Henry.*

### Rosa gymnocarpa × Woodsii

British Columbia: Skeena River 1915, *J. K. Henry.*

New York Botanical Garden

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# A REARRANGEMENT OF THE BOLIVIAN SPECIES OF CENTROPOGON AND SIPHOCAMPYLUS

H. A. GLEASON

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# A rearrangement of the Bolivian species of Centropogon and Siphocampylus

H. A. Gleason

Of forty species enumerated in the following article, six have been known to science for from fifty to ninety years, while thirty-four bear names not over thirty years old. Modern investigation of the two genera begins with Zahlbruckner, who in 1891* described three new species from the collections of Mandon. In 1892 Britton published in his enumeration† of the South American plants collected by Rusby a list of fifteen species and two varieties of these genera, of which eight species and both varieties were described as new. This was followed in 1896 by Rusby's paper‡ on the Bolivian collections of Miguel Bang, in which four species were mentioned, including three described as new. Zahlbruckner in 1897§ monographed the Lobeliaceae of Bolivia and recognized nine species of *Centropogon*, of which two were published as new, and twenty species and three varieties of *Siphocampylus*, of which eight species and the three varieties were regarded as new, making a total of thirty-four. Rusby listed|| several species of both genera and described one as new in 1907, and in 1912 described**

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* Ann. K. K. Naturhist. Hofmus. Wien 6: 432–444. 1891.

† Bull. Torrey Club 19: 371–374. 1892.

‡ Mem. Torrey Club 6: 72–74. 1896.

§ Bull. Torrey Club 24: 371–385. 1897.

|| Bull. N. Y. Bot. Gard. 4: 400–404. 1907.

** Bull. N. Y. Bot. Gard. 8: 121–123. 1912.

[The Bulletin for June (48: 159–188) was issued August 1, 1921.]

three new species of *Siphocampylus* and one of *Centropogon* from the collections of Williams. Lauterbach published* a single variety in 1910, and in 1913 Zahlbruckner added three species† from the collections of Herzog.

Not all of these various species and varieties still stand just as they were published, but it is worthy of note that the studies in which they appeared were so exhaustive of the material at hand and subsequent collections have been so scanty that the present paper adds but one new species, although a second, recognized by Zahlbruckner and given a manuscript name by him, is here published. It is nevertheless fair to assume that more extended collection in Bolivia will bring to light probably a score or more new species.

Zahlbruckner's work was based largely on the same material as that used by Britton and Rusby, with additional specimens from certain European herbaria. The types of Britton's and of Rusby's species, and either the types or isotypes of most of Zahlbruckner's species, are in the collections at the New York Botanical Garden.

The four cited articles by Britton and Rusby include mere enumerations of the species with detached descriptions of their new species and varieties. Zahlbruckner gives in his monograph somewhat more detailed descriptions of the new species and frequent notes on the supposed affiliation of the others, and prefaces each genus with a key to the species included. His keys, however, are in general based on minor characters. While obviously related species are in most cases keyed out together, the characters used in distinguishing them are not of fundamental importance, give little idea of the relationship of the species, and can not be successfully used for the species of other South American countries.

*Centropogon* and *Siphocampylus* present the usual lobeliaceous structure. The leaves are almost always alternate, usually ample in size, and with a wide variation in shape, texture, and pubescence. The inflorescence is in a strict sense a terminal raceme, which by shortening of the internodes and suppression of the bracteal leaves becomes a terminal corymbose or subumbellate cluster, or by

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* Buchtien, Contr. Flora Bolivia 1: 187. 1910.

† Med. Rijks Herb. 19: 49–53. 1913.

elongation of the internodes and better development of the subtending leaves is reduced to a series of solitary axillary flowers. The hypanthium, varying from depressed hemispheric to cylindric, bears five sepals, ranging from a size approximating the length of the corolla-tube to almost suppressed. The large corolla is usually brightly colored, with five equal or unequal, long or short, spreading, erect, or depressed lobes. The filaments usually surpass the corolla, and the anther-tube is frequently hirsute; in almost all species the two anterior anthers bear an appendage or tuft of hairs at the apex. The foliage is in some cases glabrous, but in most species is pubescent to tomentose with simple, branched or stellate hairs.

The distinctions between *Centropogon* and *Siphocampylus* are difficult and in herbarium material frequently obscure or lacking; as a result, sheets of what is obviously one species have been classified by Zahlbruckner himself in both genera. In *Centropogon* the fruit is a dry or leathery indehiscent berry. This flattens out in pressing and is thin enough to show the impression of the small seeds within. In *Siphocampylus* the fruit is a stiff, firm-walled capsule, but in many or even most herbarium sheets available mature fruit is not at hand. In the former genus, also, the summit of the ovary is described as truncate, that is, as almost completely adnate to the hypanthium, while in the latter it is stated to be conical, with a free distal portion, and adnate to the hypanthium only at its base. This condition does obtain in the ripened fruit, but can not always be demonstrated in flower. Between the baccate and the capsular species there is extensive parallelism; so extensive that a doubt may legitimately arise whether the characters of the fruit are really of generic value.

Because of this parallelism, the species of the two genera have not been kept separate in this paper but have been keyed out side by side, using the shape of the corolla as the primary distinction between groups. Three such groups have been distinguished, of which one includes only species of *Centropogon* (in the usual sense), the second only species of *Siphocampylus*, and the third species of both genera. To obviate the necessity of descriptions, the analytical key has been made more detailed than necessary for the mere separation of the species.

In both genera, the species show unusually clear lines of demarcation, and are separated by characters of the hypanthium, corolla, anther-tube, inflorescence, foliage, and pubescence. But since these characters show little correlated variation, the delimitation of species-groups and the determination of intrageneric relations become a matter of some difficulty, which is increased rather than lessened by extending the study to other South American countries.

Both genera find their center of distribution with the greatest number of species in the Andean region of northwestern South America from Colombia to Bolivia. Other South American and all North American forms are to be referred to this center for their geographical origin.

## CONSPECTUS OF THE SPECIES

I. Corolla relatively short and broad, but large, the tube equaling or little exceeding the lobes, thick and firm in texture, white, yellowish, ochroleucous, or dull purple; corolla-lobes all depressed, the upper somewhat exceeding the lower; sepals ample, equaling or longer than the hypanthium; flowers solitary, on long axillary peduncles.

*A*. Hypanthium turbinate, broader than high when pressed, prominently ribbed anther-tube glabrous, or pubescent only on the connectives; corollas white or cinereous, the lobes equaling or exceeding the tube in length; fruit capsular, so far as known.

1. Anther-tube glabrous, except the terminal brush.

*a*. Sepals triangular-subulate, 4 mm. long, much shorter than the hypanthium.

1. SIPHOCAMPYLUS TUNARENSIS A. Zahlb. Bull. Torrey Club **24**: 376. 1897.

The specimen in the herbarium of the New York Botanical Garden is fragmentary and does not permit the verification of Zahlbruckner's detailed description, but is sufficient to demonstrate its close relation to the following three species. Fruit has not been seen.

*b*. Sepals linear, equaling or exceeding the hypanthium in length.

2. SIPHOCAMPYLUS RUSBYANUS Britton, Bull. Torrey Club **19**: 372. 1892.

Sepals 10 mm. long by 2 mm. wide; leaf-blades ovate-elliptic, 5–9 cm. long, acute or obtuse, rugose above, reticulate beneath, abruptly narrowed into a petiole 10–15 mm. long.

3. SIPHOCAMPYLUS VATKEANUS A. Zahlb. Bull. Torrey Club **24**: 377. 1897.

Sepals little exceeding the hypanthium; leaf-blades oblong-lanceolate, 6–10 cm. long, 2–3 cm. wide, acuminate, tomentose on the reticulate veins beneath, obtuse or rounded at base, on petioles 1–2 cm. long.

2. Anther-tube white-woolly.

4. SIPHOCAMPYLUS RADIATUS Rusby, Mem. Torrey Club **6**: 73. 1896.

Sepals 20–25 mm. long, 3–4 mm. wide, somewhat dilated below; leaf-blades lanceolate, 15–25 cm. long, acuminate, flat above, not conspicuously reticulate, gradually narrowed below to an indefinite petiole or sessile base.

4*a*. SIPHOCAMPYLUS RADIATUS MINOR A. Zahlb. Bull. Torrey Club **24**: 376. 1897.

Plant smaller in all its parts; pedicels surpassing the leaves.

*B*. Hypanthium short-cylindric, higher than broad when pressed, or depressed-hemispheric; corolla-lobes usually shorter than the tube; anther-tube densely woolly; fruit baccate, so far as known.

1. Sepals linear or narrowly lanceolate, four to ten times as long as broad, longer than the short-cylindric hypanthium, equaling or exceeding the corolla-tube, with rounded sinuses nearly or quite as broad as the sepals; leaf-blades large, elliptic, 15–25 cm. long.

5. CENTROPOGON INCANUS (Britton) A. Zahlb. Bull. Torrey Club **24**: 374. 1897.

*Siphocampylus incanus* Britton, Bull. Torrey Club **19**: 373. 1892.

Petals and sepals densely floccose with yellowish gray hairs; filaments little exserted, the anther-tube barely surpassing the corolla; leaf-blades 5–10 cm. long, abruptly acuminate, floccose below and somewhat so above.

6. CENTROPOGON BRITTONIANUS A. Zahlb. Bull. Torrey Club **24**: 373. 1897.

*Siphocampylus giganteus latifolius* Britton, Bull. Torrey Club **19**: 373. 1892.

Petals and sepals thinly pubescent; filaments long (2 cm. or more)-exserted; leaf-blades 4–7 cm. broad, gradually acuminate, thinly tomentose on the veins beneath, puberulent above.

In both genera, the species show unusually clear lines of demarcation, and are separated by characters of the hypanthium, corolla, anther-tube, inflorescence, foliage, and pubescence. But since these characters show little correlated variation, the delimitation of species-groups and the determination of intrageneric relations become a matter of some difficulty, which is increased rather than lessened by extending the study to other South American countries.

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6*a*. CENTROPOGON BRITTONIANUS BREVIDENTATUS Zahlb. & Rechinger, Med. Rijks Herb. **19**: 51. 1913.

The authors state that the variety differs from the species in sepals only 10–12 mm. long and in much narrower and longer corolla-lobes.

2. Sepals broadly ovate to oblong, less than four times as long as wide, mostly shorter than the corolla-tube and not much exceeding the hypanthium, with narrow acute sinuses; hypanthium depressed-hemispheric or somewhat urceolate.

*a*. Sepals broadly ovate-triangular, herbaceous.

7. **Siphocampylus tunicatus** A. Zahlb. in herb.

Hypanthium and foliage nearly glabrous; leaf-blades broadly elliptic to obovate, 20–25 cm. long, 7–13 cm. wide, thin, abruptly acuminate; additional characters as in the key.

TYPE collected April, 1892, in Bolivia, at an altitude of 3000 m., by Otto Kuntze, and deposited in the herbarium of the New York Botanical Garden. A second sheet from the same collector comes from Santa Rosa, Bolivia, and is possibly a part of the same collection. The fruit is unknown but the floral characters show unmistakably the close relation of the species to the two following, *Centropogon Mandonis* and *C. gloriosus*, and it is quite probable that it will eventually be transferred to the genus *Centropogon*.

*b*. Sepals oblong or oblong-ovate, thick and firm, serrulate.

8. CENTROPOGON MANDONIS A. Zahlb. Ann. K. K. Naturhist. Hofmus. Wien **6**: 438. 1891.

Corolla-tube about twice as long as the erect, narrowly oblong sepals; filaments much surpassing the corolla; anther-tube hirsute with tawny hairs; leaves acute.

9. CENTROPOGON GLORIOSUS (Britton) A. Zahlb. Bull. Torrey Club 24: 373. 1897.

*Siphocampylus gloriosus* Britton, Bull. Torrey Club **19**: 373. 1892.

Corolla-tube one third to one half longer than the oblong-ovate, frequently spreading or reflexed sepals; filaments about equaling the corolla; anther-tube hirsute with purple hairs; leaves long-acuminate.

II. Corolla tubular, slender, straight or somewhat curved, usually constricted above its base, little if any wider at the throat than at the base; corolla-lobes linear or linear-deltoid and regularly tapering from base to apex, all erect or slightly spreading, the lateral and ventral fissures usually progressively deeper than the dorsal; filaments equaling or barely exceeding the dorsal petals; the two ventral anthers with a terminal brush of separate hairs; fruit capsular, so far as known.

*A*. Hypanthium well developed and the ovary consequently mainly inferior.

1. Flowers in leafy corymbs, leafy racemes, or solitary in the axils of normal foliage leaves.

*a*. Anther-tube glabrous, except for the terminal brush, or with a few scattered hairs only.

*i*. Flowers axillary, subtended by normal foliage leaves.

* Sepals linear, exceeding the hypanthium; leaves much longer than wide.

† Peduncles well developed, equaling or surpassing the flowers, which exceed the subtending leaves.

‡ Leaves in whorls of three.

10. SIPHOCAMPYLUS ORBIGNIANUS A. DC.; DeCandolle, Prodr. 7: 405. 1839.

*Siphocampylus volubilis* Britton, Bull. Torrey Club **19**: 372. 1892.

Leaf-blades ovate to ovate-oblong, sharply and irregularly dentate; sepals filiform, much exceeding the hypanthium; corolla scarlet.

The wealth of herbarium material indicates that this is the commonest Bolivian species of the two genera. It is distinguished at once by its verticillate leaves.

‡‡ Leaves alternate, oblong or elliptic to linear.

§ Corolla yellow or yellowish; leaf-blades linear to narrowly lanceolate, subentire, undulate, or with minute spinulose teeth.

11. SIPHOCAMPYLUS KUNTZEANUS A. Zahlb. Bull. Torrey Club **24**: 378. 1897.

Anther-tube surpassing the corolla; leaves neatly linear, crowded, conduplicate.

12. SIPHOCAMPYLUS AUREUS Rusby, Mem. Torrey Club **6**: 72. 1896.

*Siphocampylus aureus latior* A. Zahlb. Bull. Torrey Club **24**: 378. 1897.

Anther-tube not exserted; leaves linear-lanceolate, membranous, flat.

§§ Corolla red.

|| Leaf-blades narrowly oblong-linear, narrowed below to an indefinite petiole, thick, remotely denticulate.

13. SIPHOCAMPYLUS WILLIAMSII Rusby, Bull. N. Y. Bot. Gard. **8**: 122. 1912.

|| || Leaf-blades lanceolate to ovate-lanceolate, petioled, membranous, sharply and irregularly spinulose, 8–12 cm. long.

14. SIPHOCAMPYLUS BOLIVIENSIS A. Zahlb. Ann. K. K. Naturhist. Hofmus. Wien **6**: 443. 1891.

Sepals equaling or barely exceeding the subglobose hypanthium; stems stout; leaves firm, brownish and scabrously pubescent beneath.

15. SIPHOCAMPYLUS DUBIUS A. Zahlb. Bull. Torrey Club **24**: 385. 1897.

Sepals longer than the depressed-hemispheric hypanthium; stems slender; leaves thin, green and puberulent on the veins beneath.

†† Peduncles short, equaling or shorter than the flowers, which do not surpass the subtending leaves; hypanthium turbinate; sepals linear, reflexed; leaf-blades oblong, short-petioled; stems climbing.

16. SIPHOCAMPYLUS MEMBRANACEUS Britton, Bull. Torrey Club **19**: 372. 1892.

Leaves thin, membranous, sharply spinulose-dentate, veiny; peduncles equaling the corolla.

17. SIPHOCAMPYLUS OBLONGIFOLIUS Rusby, Mem. Torrey Club **6**: 73. 1896.

Leaves firm, minutely and remotely spinulose; peduncles shorter than the corolla.

** Sepals narrowly triangular, shorter than the hypanthium.

18. SIPHOCAMPYLUS CORREOIDES A. Zahlb. Bull. Torrey Club **24**: 382. 1897.

Foliage and flowers tomentulose; leaf-blades broadly ovate, undulate and spinulose-denticulate, 15–25 mm. long.

*ii.* Flowers in terminal corymbs or much abbreviated racemes; hypanthium turbinate or somewhat urceolate; sepals about equaling the hypanthium, distant, with rounded sinuses; leaf-blades sharply and saliently serrate, of an ovate type, firm, dull-green.

19. SIPHOCAMPYLUS CORYMBIFERUS Pohl. Plant. Brasil. **2**: 112. *pl. 175.* 1831.

*Lobelia corymbifera* Presl, Prodr. Monogr. Lobel. 37. 1836.

*Siphocampylus gracilis glabris* Britton, Bull. Torrey Club **19**: 374. 1892.

Leaves glabrous.

20. SIPHOCAMPYLUS GRACILIS Britton, Bull. Torrey Club **19**: 374. 1892.

*Siphocamplyus corymbiferus gracilis* A. Zahlb. Bull. Torrey Club **24**: 384. 1897.

Leaves softly pubescent.

iii. Flowers in crowded leafy racemes.

21. SIPHOCAMPYLOS TUPAEFORMIS A. Zahlb. Ann. K. K. Naturhist. Hofmus. Wien **6**: 440. 1891.

Hypanthium hemispheric or somewhat urceolate, ribless or faintly nerved; flowers 40–45 mm. long, approximately equaling the ascending, straight or gently curved pedicels; leaves softly pubescent beneath.

*b.* Anther-tube conspicuously woolly in five strongly marked lines; leaf-blades lanceolate or broader, rounded at base; sepals much longer than the hypanthium, which is strongly ribbed at maturity.

* Leaf-blades long-acuminate, ovate-lanceolate to lance-oblong, sharply and irregularly spinulose-denticulate.

22. SIPHOCAMPYLUS ARGUTUS A. Zahlb. Bull. Torrey Club **24**: 383. 1897.

Leaf-blades thin, glabrous beneath, not prominently reticulate; petioles straight or curved.

23. SIPHOCAMPYLUS BILABIATUS A. Zahlb. Bull. Torrey Club **24**: 382. 1897.

*Siphocampylus bilabiatus glabratus* Lauterbach; Buchtien, Contr. Flora Bolivia **1**: 187. 1910.

Leaf-blades firm, pubescent beneath, prominently reticulate; petioles sigmoid.

** Leaf-blades ovate-oblong, 5–8 cm. long, broadly rounded or subcordate at base, obtuse or rounded at apex, minutely and remotely denticulate.

24. SIPHOCAMPYLUS SUBCORDATUS Rusby, Bull. N. Y. Bot. Gard. **8**: 121. 1912.

2. Flowers in terminal, leafless, bracted racemes; pedicels flexuous in anthesis, 1 cm long or less; hypanthium turbinate, strongly ribbed or subangulate, somewhat constricted at the throat, equaling or exceeding the relatively short sepals; calyx-sinuses broad.

*a.* Hypanthium glabrous; leaf-blades falcate, conduplicate.

25. SIPHOCAMPYLUS ANGUSTIFLORUS Schlecht.; Lechler, Pl. Lechler. Peruv. *2649*.

Specimens of this species have not been seen: the distinction between it and the following are taken from Zahlbruckner.

*b.* Hypanthium pubescent; leaf-blades flat.

26. SIPHOCAMPYLUS FLAGELLIFORMIS A. Zahlb. Bull. Torrey Club **24**: 380. 1897.

*Siphocampylus angustiflorus* Britton, Bull. Torrey Club **19**: 372. 1892; not *S. angustiflorus* Schlecht.

Leaf-blades lanceolate or narrowly elliptic-ovate, acuminate, 40–60 mm. long, 15–22 mm. wide, sharply serrulate, glabrous and conspicuously veiny beneath.

27. **Siphocampylus altiscandens** sp. nov.

Stems puberulent, climbing 40 feet high on trees; leaves rather crowded, the blades flat, firm in texture, ovate-oblong, acute or subacuminate, entire or remotely and minutely serrulate, almost glabrous above, minutely puberulent beneath, the larger ones 60–75 mm. long by 25–35 mm. wide; inflorescence secund, the pedicels 10 mm. long or less; flowers deflexed; hypanthium thinly pubescent, turbinate or obconic, 4 mm. high; sepals triangular, 1 mm. long, with recurved tips; corolla rose-color, 30–35 mm. long, its lobes linear, erect or spreading; filaments about equaling the petals; anthers glabrous below, all more or less hirsute at the tip.

TYPE, *Bang 2553*, collected at Uchimachi, Corvico, Bolivia, July 20, 1894, and deposited in the herbarium of Columbia University. His field notes state that it grows in damp forests and that only two plants were seen, from which forty specimens were collected. It is sharply distinguished from the preceding species by its leaf characters.

*B.* Hypanthium very small in proportion to the flower and the ovary mainly free; corolla scarlet, 6–7 cm. long; leaf-blades of a lanceolate or ovate type; sepals usually serrulate; stems climbing: anther-tube glabrous.

1. Sepals linear to linear-oblong, prominently reflexed; leaves sharply acuminate.

28. SIPHOCAMPYLUS ELEGANS Planch. Flore des Serres **6**: 19. 1850.

Leaf-blades thick and firm, elongate-lanceolate, rounded or truncate at base.

*Siphocampylus elegans boliviensis* A. Zahlb. Bull. Torrey Club **24**: 381. 1897.

The single specimen examined, *Mandon 498*, does not agree perfectly with Planchon's figure and may prove specifically distinct.

29. SIPHOCAMPYLUS REFLEXUS Rusby, Bull N. Y. Bot. Gard. 4: 403. 1907.

*Siphocampylus elegans cordatus* A. Zahlb. Bull. Torrey Club 24: 381. 1897.

Leaf-blades thin, ovate-lanceolate, with a long narrow acumination, distinctly cordate at base.

2. Sepals ovate-oblong, erect or somewhat spreading; leaves acute to subacuminate.

30. SIPHOCAMPYLUS ANDINUS Britton, Bull. Torrey Club 19: 373. 1892.

III. Corolla tubular, stout, conspicuously ventrally curved, little or not at all constricted at base, distinctly ampliate toward the throat, corolla-lobes with broad bases, more or less oblique, and curved or directed anteriorly, the two upper usually distinctly larger and broader than the three lower, the lower fissures little if any deeper than the dorsal; fruit baccate, so far as known.

*A.* Ventral anthers terminating in a tuft of loose hairs, dorsal anthers sparsely pilose; hypanthium distinctly urceolate; foliage and flowers strongly tomentulose; petals all about equal, broadly and obliquely triangular, acute; filaments long-exserted; leaves petioled, the blades oblong-lanceolate, acute.

31. CENTROPOGON UNDUAVENSIS (Britton) A. Zahlb. Bull. Torrey Club 24: 374. 1897.

*Siphocampylus unduavensis* Britton, Bull Torrey Club 19: 373. 1892.

*B.* Ventral anthers terminating in a stiff scale composed of united hairs; hypanthium hemispheric to campanulate; foliage and flowers not tomentulose; at least the much smaller lower petals terminating in linear or subulate strongly curved appendages.

1. Sepals linear to triangular, with broad flat sinuses; leaf-blades narrowly to broadly oblong or obovate.

* Leaf-blades broadly oblong, almost entire.

32. CENTROPOGON YUNGASENSIS Britton, Bull. Torrey Club 19: 371. 1892.

Leaves firm, glabrous; sepals triangular, distinctly shorter than the hypanthium.

** Leaf-blades narrowly oblong denticulate or crenate.

33. **Centropogon aggregatus** (Rusby) comb. nov.

*Siphocampylus aggregatus* Rusby, Bull. N. Y. Bot. Gard. 8: 122. 1912.

Filaments tomentose toward the summit; anther-tube pubescent in lines; sepals equaling the hypanthium or a little shorter; leaves crenate.

34. CENTROPOGON SURINAMENSIS (L.) Presl, Prodr. Monogr. Lobel. 48. 1836.

*Lobelia surinamensis* L. Sp. Pl. ed. 2, 1320. 1763.

Filaments glabrous or with scattered hairs; anther-tube sparsely hirsute or glabrous; sepals serrate, distinctly exceeding the hypanthium: leaves denticulate.

2. Sepals linear-triangular to ovate, with narrow acute sinuses; leaf-blades oblong-lanceolate to lanceolate, usually sharply denticulate; flowers in terminal corymbose clusters.

* Sepals narrowly linear-triangular, entire, much longer than the hypanthium.

35. CENTROPOGON AMPLIFOLIUS Vatke, Linnaea **38**: 716. 1874.

** Sepals triangular-ovate to broadly ovate.

36. CENTROPOGON BANGII A. Zahlb. Bull. Torrey Club **24**: 372. 1897.

Sepals triangular-ovate, entire, shorter than the hypanthium.

37. CENTROPOGON ROSEUS Rusby, Bull. N. Y. Bot. Gard. **8**: 123. 1912.

Sepals broadly ovate, foliaceous, denticulate.

IV. Species of uncertain position, specimens of which have not been seen.

38. CENTROPOGON MAGNIFICUS Zahlb. & Rechinger, Med. Rijks Herb. **19**: 50. 1913.

Evidently a member of the first group of this conspectus; compared by the authors with *C. Mandonis* Zahlb., from which it differs in its fewer flowers on longer pedicels, straight-edged sepals, denser pubescence on the corolla, obviously lignified twigs, and stiffer rough leaves.

39. CENTROPOGON HERZOGI Zahlb. & Rechinger, Med. Rijks Herb. **19**: 49. 1913.

Evidently a member of the second section of this conspectus, as indicated by the description of the corolla; flowers axillary, hypanthium globose or subglobose, sepals short, acute, broadly triangular, anther-tube glabrous, except the terminal tuft.

40. CENTROPOGON CARDINALIS Zahlb. & Rechinger, Med. Rijks, Herb. **19**: 51. 1913.

Evidently a member of the third group of this conspectus, possibly related to *C. Bangii* Zahlb.; inflorescence a short terminal raceme, hypanthium globose, sepals short, triangular, entire, anther-tube glabrous, except the terminal appendage, leaves obovate-elliptic.

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# STERILITY AND FERTILITY IN HEMEROCALLIS

By A. B. STOUT

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# STERILITY AND FERTILITY IN SPECIES OF HEMEROCALLIS

For a number of years problems of fertility and sterility in numerous species of plants that freely and naturally propagate by vegetative means have been under investigation by the writer. In these studies several species of *Hemerocallis* have received considerable attention, and a brief preliminary report of the results obtained with them has been given (Journal N. Y. Bot. Garden **20**: 104–105, May, 1919). Certain aspects of the research await the blooming of seedlings that are now being grown and the testing of wild plants of several species which it is hoped can be obtained from their native home in the orient. But the results already obtained, and in part published, supplement and to some degree extend the observations recorded in a recent number of the Torreya (**21**: 12–13, Jan. and Feb. 1921) and for this reason may be briefly summarized for the readers of this journal.

It is to be noted that the double-flowered form of *Hemerocallis fulva* reported in Torreya (**18**: 242) and referred to later (Torreya **21**: 13) is undoubtedly an old and well known sort. A double-flowered variety of this species is reported by Thunberg in his Flora Japonica published in 1784 and there identified as the double-flowered plant which Kaempfer (Amoen. Exot. 1712) thought was an *Iris*. At the present time two double-flowered varieties are recognized (Bailey, Cyclopaedia of Horticulture) as belonging to *H. fulva*. One of these, var. *Kwanso*, is illustrated in color in Gartenflora in 1866 (plate 500) and there said to have been introduced into Europe by von Siebold. This is evidently the double-flowered form most widely found in cultivation in Europe and America. The other variety (*flora plena*) is illustrated in color in Flora des Serres

(1869–1870) and there called *H. disticha* var. *flora plena* (*disticha* is now considered as a synonym of *fulva*). The colored plate shows this to be quite different from var. *Kwanso* in appearance. The writer has never seen this variety. A double-flowered variety has also long been known in the species *H. Dumortierii.*

A thorough search of the literature indicates that no one has ever reported fruit on the single-flowered type of *H. fulva.* This orange-colored day lily is widely distributed over Europe and America. Its complete failure to produce fruit and seeds has often been noted. Only one variety of it (var. *maculata*) appears to have been involved (probably as a pollen parent) in the production of hybrids.

In the writer's experiments with this species many intra-specific pollinations have been made between plants obtained from such widely different sources as Wisconsin, Michigan, New York, Vermont and England with complete failure in every case. The ovaries of flowers thus pollinated do not start to enlarge, and about 72 hours after the flowers open the entire flower falls leaving only spurs as shown at *a* in Fig. 4.

But the pollen of this species used in controlled crossing on *H. flava* has given pods (Fig. 2) with seeds and the hybrids resulting are now being grown. The reciprocal cross between these two species failed to yield mature pods. Pollen of *H. fulva* on *H. minor* has given seed but no germination was secured.

Pollen of *H. Thunbergii* and of *H. aurantiaca* has been used on many flowers of *H. fulva.* Usually the pods begin to form and seeds start to develop with some of them, but as a rule the pods fall when about one third mature (*b* in Fig. 4). In a few instances, however, mature pods with ripe seeds (Fig. 5) have been secured, but no germination has yet been obtained in such seeds. The reciprocals of these crosses likewise produce seed rarely. From the results of crossing *H. fulva* with *H. flava*, *H. aurantiaca* and *H. Thunbergii* it appears that its pollen and ovules are potent and are able to function in certain relations, but that the compatibility in these combinations is of a weak grade.

The literature gives conflicting reports regarding seed production in *H. flava.* Some investigators have reported plants of it to be self-fertile, others have reported the plants they have studied to be self-sterile. Both self-compatible and self-incompatible plants have been found among plants of this species grown in the New York Botanical Garden. Such conditions are often seen in a species in which self-incompatibility is present, especially if the species is propagated by seed (*Cichorium Intybus, Nicotiana Forgetiana, Eschscholtzia californica, Brassica pekinensis, Brassica chinensis,* and others). The most highly self-compatible plants produce pods in abundance, but in them are many shrivelled ovules in which fertilization may not have occurred and seeds in various stages of embryo abortion together with seeds that are fully matured and viable (Fig. 3). This condition is also specially characteristic of plants that are not fully self-compatible.

A third species, *H. Thunbergii,* has in the author's experience proved to be only feebly self-compatible. Very many carefully made self-pollinations fail (see 6, 7 and 8), but many pods do mature and these contain some seeds which will germinate. All the plants of this species which are growing in the New York Botanical Garden have behaved quite the same, but these may have all descended from a single parent through vegetative propagation. A wide range of self-compatibility may be exhibited by the seedlings which are to be tested as soon as they bloom.

The type of sterility in these species is, undoubtedly, that of physiological incompatibility operating between the organs concerned in sexual reproduction. The readiness with which these species propagate from pieces of the roots and by rhizomes has practically eliminated the use of seeds in commercial propagation. Such a method tends to perpetuate the grade of self-compatibility of the original plant which was used. It is possible that the plants of the single-flowered type of *fulva* now growing in America and Europe may have all come by vegetative propagation from a single plant which happened to be fully self-incompatible. According to Clusius (*Plàntarum Historia,* p. 137) this species was commonly in cultivation in middle Europe as early as 1601. Since then its cultivation has been extended over large areas of Europe and America, and in many sections it has escaped from cultivation and is spreading widely, purely by vegetative means of propagation.

It can be predicted with confidence that a search in the region where *H. fulva* is native and wild will reveal plants that are producing seed or at least strains that will prove compatible with the self-incompatible strain now found in the United States. Focke showed that such a condition as this existed in *Lilium bulbiferum.* After failing for years to get seed by selfing and crossing plants of this species obtained from various parts of Germany, he obtained wild plants from the native habitat in Tyrol and these he found compatible with strains that previously failed to produce seed.

It has very generally been held that the seed sterility of such plants as *Hemerocallis fulva, Lilium bulbiferum, Lilium tigrinum,* etc., is "correlative." That is, the vegetative organs of propagation are conceived to divert and utilize the available food so that the embryos in seeds are virtually starved to death during stages in development, or perhaps organs are so poorly nourished that they do not function previous to fertilization. But evidence is increasing to the effect that seed production in these plants is relative and depends on whether fertilizations are compatible, quite as is the case in numerous species of plants that are naturally propagated only by seeds. The experimental proof of this is sometimes difficult to obtain in the plants that are propagated vegetatively.

When self-compatible and self-incompatible plants are found and the latter prove to be highly seed-producing in certain crosses, as is the case with *Hemerocallis flava,* the evidence of incompatibilities is clear. The American strain of *Hemerocallis fulva* has sex organs that do function to some extent in certain inter-specific crosses and will, undoubtedly, produce abundant seed when it can be tested with stocks from a dif-

EXPLANATION OF PLATE

1. Pod of a plant of *H. flava;* the result of self-pollination showing that the plant is self-compatible.

2. Pod on same plant as 1; the result of controlled cross-pollination with pollen of *H. fulva.*

3. Seeds from such a pod as shown in 1 and 2; some ovules become mere rudiments of seeds and evidently are not fertilized; some embryos die during the development of seeds; some seeds develop fully and are viable.

4. Flowering branch of *H. fulva* near close of period of bloom. (*a*) Spur left when flowers fall. (*b*) Pod 10 days old, from cross with pollen of *H. Thunbergii,* but becoming wrinkled and about to fall. Occasionally such pods contain one or two partly developed seeds.

5. Mature pod of *H. fulva* from cross-pollination with *H. Thunbergii.* Such pods are rare. As far as known to the writer this is the first time the fruit of this species has been illustrated.

6, 7 and 8. All from a single plant of *H. Thunbergii.* All flowers carefully self-pollinated. Some pods (*a*) maturing and yielding a few viable seeds; some pods (*b*) becoming much shrivelled; no good pods on branch shown at 8. Results characteristic of feebly self-compatible plants of this species.

ferent seed source. But to obtain these, plants from widely different geographical sections or even wild plants from the native habitat may need to be secured.

A. B. STOUT.

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# PHYTOGEOGRAPHICAL NOTES ON THE ROCKY MOUNTAIN REGION

## X. GRASSLANDS AND OTHER OPEN FORMATIONS OF THE MONTANE ZONE OF THE SOUTHERN ROCKIES

P. A. RYDBERG

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# Phytogeographical notes on the Rocky Mountain region
## X. Grasslands and other open formations of the Montane Zone of the Southern Rockies

Per Axel Rydberg

In a previous article* I have discussed the wooded formations of the Montane Zone. In this article the remaining formations are taken up. In these, the plants of the plains and foothills make up a larger proportion of the vegetation than in the wooded formations. The river valleys, meadows, and hog backs have a flora much more like that of similar habitats in the foothill region and even on the plains. The transcontinental elements and those from the prairie region are much more numerous.

The formations have been arranged so that the hydrophytic are first taken up and then the mesophytic, the most xerophytic being left until the last. The species followed by a dagger, "†", are confined to the Southern Rockies.

## A. AQUATIC FORMATIONS

Lakes are not very common in the Montane Zone of the Southern Rockies. In the higher parts they are mostly glacial, fed by the snow fields, and contain little vegetation. The brooks are swift and rarely form lakes or ponds in the higher regions. Most of the lakes are found in the lower river valleys and "Parks"

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* Bull. Torrey Club 47: 441–454. 1920.

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of Colorado, and here we find most of the aquatic vegetation. The majority of the phaneorgamic plants are found also in the plains and prairie regions. To these belong a score of species of *Potamogeton* which here are omitted. Besides these the following species are found:

### 1. Transcontinental and eastern

*Sparganium angustifolium*
*Sparganium minimum*
*Triglochin palustris*
*Triglochin maritima*
*Alisma brevipes*
*Sagittaria latifolia*
*Phragmites Phragmites*
*Catabrosa aquatica*
*Panicularia grandis*
*Panicularia borealis*
*Panicularia septentrionalis*
*Eleocharis palustris*
*Scirpus validus*
*Lemna trisulca*
*Lemna gibba*
*Lemna minor*
*Persicaria coccinea*
*Batrachium trichophyllum*
*Batrachium flaccidum*
*Batrachium Drouetii*
*Ranunculus Purshii*
*Sisymbrium Nasturtium-aquaticum*
*Callitriche palustris*
*Callitriche autumnalis*
*Hippuris vulgaris*
*Sium cicutifolium*
*Menyanthes trifoliata*
*Veronica americana*
*Utricularia vulgaris*
*Utricularia minor*

### 2. Western

*Crunocallis Chamissonis*
*Nymphaea polysepala*

### 3. Endemic

*Panicularia pauciflora*
*Agrostis depressa*†
*Cardamine cordifolia*†
*Cardamine infausta*†
*Ranunculus intertextus*†

## B. SEDGE BOGS

The sedge bogs are found where the drainage is poor or in low places around lakes, ponds, and streams. In most cases the most numerous plants are species of *Carex*, but many grasses also are intermixed, and in some places they are predominant. Of these *Alopecurus aristulatus* and *Agrostis alba* are the most frequent and, in the lower part of the zone, species of *Calamagrostis*. The composition of the bog vegetation consists of the following plants:—

### 1. Continental and eastern

*Deschampsia coespitosa*
*Phalaris arundinacea*
*Calamagrostis elongata*
*Calamagrostis canadensis*
*Calamagrostis hyperborea*
*Beckmannia erucaeformis*
*Panicularia nervata*
*Alopecurus aristulatus*
*Eriophorum angustifolium*
*Eriophorum gracile*
*Carex gynocrates*
*Carex diandra*
*Carex disperma*
*Carex canescens*
*Carex brunnescens*
*Carex leptalea*
*Carex aurea*
*Carex paupercula*
*Carex Buxbaumii*
*Carex aquatilis*
*Carex lanuginosa*
*Carex viridula*
*Carex rostrata*
*Carex retrorsa*
*Rumex occidentalis*
*Rumex mexicanus*
*Ranunculus sceleratus*
*Cardamine pennsylvanica*
*Parnassia parviflora*
*Argentina Anserina*
*Geum rivale*
*Viola palustris*
*Veronica Wormskjoldii*
*Elephantella groenlandica*
*Gnaphalium uliginosum*
*Senecio pauciflorus*
*Lycopodium annotinum*
*Equisetum arvense*
*Equisetum pratense*
*Equisetum variegatum*

### 2. Western

*Poa interior*
*Agrostis humilis*
*Agrostis grandis*
*Agrostis asperifolia*
*Agrostis idahoensis*
*Muhlenbergia comata*
*Carex simulata*
*Carex athrostachya*
*Carex tenuirostris*
*Carex Raynoldsii*
*Carex Kelloggii*
*Juncus Mertensianus*
*Iris missouriensis*
*Limnorchis viridiflora*
*Limnorchis borealis*
*Rumex hymenosepalus*
*Alsine strictiflora*
*Alsine obtusa*
*Alsine calycantha*
*Ranunculus alismaefolius*
*Ranunculus Eschscholtzii*
*Argentina argentea*
*Vicia oregana*
*Vicia sparsiflora*
*Epilobium brevistylum*
*Epilobium occidentale*
*Dodecatheon pauciflorum*
*Castilleja exilis*
*Mimulus Lewisii*
*Galium subtriflorum*
*Aster occidentalis*
*Aster Burkei*
*Erigeron salsuginosus*
*Gnaphalium sulphurescens*
*Arnica longifolia*

### 3. Endemic

*Alopecurus occidentalis*
*Graphephorum Shearii*†
*Panicularia pauciflora*
*Agrostis Rossae*
*Agrostis melaleuca*
*Agrostis Bakeri*†
*Carex pseudoscirpoidea*
*Carex ebenea*†
*Juncus truncatus*
*Juncus Hallii*
*Sisyrinchium alpestre*†
*Rumex praecox*†
*Rumex subalpinus*†
*Rumex densiflorus*†
*Ranunculus inamoenus*
*Ranunculus acriforme*
*Ranunculus micropetalus*†
*Caltha rotundifolia*†
*Aconitum porrectum*†
*Aconitum columbianum*
*Clementsia rhodantha*
*Vicia dissitifolia*†
*Epilobium ovatifolium*†
*Epilobium americanum*
*Epilobium stramineum*
*Epilobium Drummondii*
*Epilobium wyomingense*
*Angelica pinnata*
*Primula incana*
*Dodecatheon philoscia*†
*Dodecatheon radicatum*†
*Anthopogon thermalis*
*Swertia scopulina*
*Myosotis alpestris*
*Castilleja sulphurea*
*Castilleja wyomingensis*
*Orthocarpus purpureo-albus*
*Erigeron minor*
*Erigeron lonchophyllus*
*Arnica rhizomata*
*Arnica foliosa*
*Senecio cymbalarioides*
*Senecio nephrophyllus*
*Senecio crassulus*
*Senecio semiamplexicaulis*
*Senecio rapifolius*
*Senecio dispar*
*Senecio perplexans*

## C. SPRINGY PLACES

The springs and the wet places in their vicinity usually have a flora of their own. This consists of hydrophytes, growing either in the water itself or on the muddy shores. As a rule the plants are small in size.

### 1. Eastern and transcontinental

*Eleocharis acicularis*
*Lemna trisulca*
*Lemna minor*
*Lemna gibba*
*Sisymbrium Nasturtium-aquaticum*
*Parnassia parviflora*
*Tillaeastrum aquaticum*
*Callitriche palustris*
*Callitriche autumnalis*
*Epilobium adenocaulon*
*Myosotis alpestris*

### 2. WESTERN

*Muhlenbergia filiformis*
*Juncus Mertensianus*
*Crunocallis Chamissonis*
*Parnassia fimbriata*
*Micranthes arguta*
*Androsace filiformis*
*Mimulus Langsdorfii*

### 3. ENDEMIC

*Agrostis depressa*†
*Cardamine cordifolia*
*Cardamine infausta*†
*Radicula alpina*
*Micranthes rhomboidea*
*Micranthes arnoglossa*
*Oxypolis Fendleri*†
*Primula incana*
*Pleurogyne fontana*
*Mimulus puberulus*

## D. SANDY RIVER BANKS

The flora of the sandy river banks and sand-flats along the water courses is very meager. Besides some of the species which are enumerated below, under the heading "Sand-draws," there are found the following which require more moisture:—

*Eleocharis acicularis*
*Scirpus pauciflorus*
*Muhlenbergia Wolfii*†
*Sagina saginoides*
*Alsinopsis macrantha*†
*Myosurus aristulatus*
*Ranunculus reptans*
*Halerpestes Cymbalaria*
*Radicula alpina*
*Subularia aquatica**
*Tillaeastrum aquaticum**
*Gilia calcarea*†
*Androsace filiformis*
*Androsace diffusa*†
*Androsace subulifera*†
*Mimulus moschatus*
*Mimulus puberulus*
*Limosella aquatica**
*Erigeron minor*

## E. ALLUVIAL RIVER BANKS

The formations on the alluvial river banks and river flats are of three kinds. Along the smaller brooks, especially in the upper portion of the zone, they resemble much those of the Subalpine Zone, the most important plants being species of *Mertensia*, *Epilobium* and *Juncoides*. In the lower part of the zone *Urtica gracilis* and various composites constitute the greater part of the vegetation. At middle altitudes species of *Delphinium* and *Aconitum* often take their places. Very few of the plants are transcontinental or eastern.

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* Growing mostly in shallow water with sandy bottom.

### 1. TRANSCONTINENTAL

*Juncoides parviflorum*
*Juncoides intermedium*
*Juncoides spicatum*
*Urtica gracilis*
*Epilobium adenocaulon*
*Veronica Wormskjoldii*
*Artemisia biennis*

### 2. WESTERN

*Amaranthus Powellii*
*Delphinium multiflorum*
*Epilobium occidentale*
*Rudbeckia occidentalis*
*Senecio triangularis*

### 3. ENDEMIC

*Delphinium occidentale*
*Delphinium reticulatum*
*Delphinium robustum*†
*Delphinium elongatum*†
*Delphinium ramosum*†
*Delphinium cucullatum*†
*Aconitum insigne*
*Aconitum lutescens*
*Aconitum Bakeri*†
*Epilobium Palmeri*†
*Epilobium rubescens*†
*Epilobium stramineum*†
*Mertensia ciliata*
*Mertensia Leonardi*†
*Mertensia brevistyla*†
*Scrophularia occidentalis*
*Rudbeckia ampla*
*Rudbeckia montana*†
*Helianthella quinquenervis*
*Cirsium Parryi*†
*Cirsium scopulorum*†
*Cirsium Centaureae*†
*Cirsium Eatonii*
*Cirsium coloradense*†
*Cirsium oreophilum*†
*Cirsium foliosum*
*Cirsium griseum*†

## F. MEADOWS

By meadows I mean here the more moist meadows of the richer bottom lands. There are also grasslands which bear hay-making grasses in the dryer portions of the valleys, which I have included in the Dry Valley Formation. The grasses of the wet meadows consist mostly of species of the tribes Agrostideae and Festuceae. Those of the latter are mostly of the tribe Hordeae and are found on the plains also. The list of grasses is given in an earlier article* and is here omitted.

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* Bull. Torrey Club **43**: 635–636. 1915.

### 1. Eastern and transcontinental

*Carex stenophylla*
*Carex lanuginosa*
*Carex interior*
*Juncus Vaseyi*
*Juncus bufonius*
*Polygonum ramosissimum*
*Capnodes aureum*
*Arabis ovata*
*Draba nemorosa*
*Vicia trifida*
*Viola nephrophylla*
*Viola septentrionalis*
*Viola pedatifida*
*Artemisia biennis*

### 2. Western

*Juncus longistylis*
*Juncus confusus*
*Juncodes comosum*
*Anticlea elegans*
*Polygonum sawatchense*
*Polygonum Watsonii*
*Potentilla Bakeri*
*Potentilla Nuttallii*
*Potentilla diversifolia*
*Drymocallis glandulosa*
*Lupinus argenteus*
*Astragalus striatus*
*Astragalus goniatus*
*Viola venosa*
*Viola vallicola*
*Oenothera Hookeri*
*Lavauxia flava*
*Collomia linearis*
*Orthocarpus luteus*
*Antennaria corymbosa*
*Arnica Rydbergii*
*Arnica fulgens*
*Agoseris laciniata*

### 3. Endemic

*Juncus Jonesii*
*Carex pseudoscirpoidea*
*Veratrum tenuipetalum*†
*Calochortus Gunnisoni*
*Calochortus Nuttallii*
*Calochortus acuminatus*
*Polygonum Engelmannii*
*Claytonia rosea*
*Thalictrum venulosum*
*Thalictrum megacarpum*
*Arabis rhodantha*
*Potentilla filipes*
*Potentilla juncunda*
*Potentilla pulcherrima*
*Potentilla plattensis*
*Potentilla propinqua*
*Potentilla Nelsoniana*
*Fragaria pauciflora*
*Drymocallis convallaria*
*Trifolium Rydbergii*
*Trifolium Kingii*†
*Astragalus sulphurescens*
*Aragallus albiflorus*
*Lathyrus brachycalyx*†
*Viola bellidifolia*
*Primula incana*
*Anthopogon thermalis*
*Castilleja brunnescens*†
*Plantago Tweedyi*
*Campanula Parryi*
*Erigeron consobrinus*†
*Gnaphalium exilifolium*†

### 1. Eastern and transcontinental

*Calamagrostis purpurascens*
*Poa crocata*
*Festuca rubra*
*Carex concinna*
*Carex Halleri*
*Ibidium strictum*
*Draba nemorosa*

### 2. Western

*Carex Rossii*
*Ibidium porrifolium*
*Allium Geyeri*
*Eriogonum ovalifolium*
*Polygonum sawatchense*
*Eurotia lanata*
*Cerastium strictum*
*Draba nitida*
*Sieversia grisea*
*Sieversia ciliata*
*Collomia linearis*
*Phacelia sericea*
*Lappula floribunda*
*Campanula petiolata*
*Aster apricus*
*Macronema suffruticosum*
*Antennaria pulcherrima*
*Antennaria anaphaloides*
*Balsamorrhiza sagittata*
*Wyethia amplexicaulis*
*Arnica Parryi*
*Arnica mollis*

### 3. Endemic

*Muhlenbergia* (3 species)†
*Poa* (8 species)†
*Festuca ingrata*
*Festuca saximontana*
*Festuca* (3 other species)†
*Allium Brandegei*
*Allium recurvatum*
*Erythronium parviflorum*†
*Erythronium utahense*
*Cerastium* (4 species)
*Draba* (3 species)
*Lesquerella curvipes*†
*Lithophragma australis*†
*Potentilla* (5 species)
*Pachylophus macroglottis*
*Pachylophus hirsutus*
*Amarella scopulorum*
*Dasystephana affinis*
*Dasystephana Forwoodii*
*Tessaranthium* (5 species)†
*Phlox Kelseyi*
*Mertensia* (7 species)†
— *Valeriana* (4 species)†
*Solidago* (3 species)
*Aster andinus*
*Erigeron viscidus*†
*Townsendia strigosa*†
*Helianthella uniflora*
*Tetraneuris leptoclada*
*Tetraneuris lanigera*
*Senecio Fendleri*

## K. HOG-BACKS AND DRY RIDGES

The flora of the hog backs in the Montane Zone, especially in its upper part, resembles that of the Subalpine Zone; in the lower regions there are many of the species of the dry plains added. Besides these there are a few restricted to the Montane Zone; nearly all of these are endemics. The flora consist of the following:

### 1. Eastern or transcontinental

*Juniperus sibirica*
*Carex praticola*
*Carex stenophylla*
*Calamagrostis purpurascens*
*Bouteloua gracilis*
*Koeleria gracilis*
*Poa crocata*

### 2. Western

*Lewisia rediviva*
*Oreobroma pygmaea*
*Oreobroma nevadensis*
*Draba lutea*
*Sedum stenosepalum*
*Petrophytum caespitosum*
*Leptodactylon purgens*

### 3. Endemic

*Lesquerella alpina*
*Eriogonum* (6 species)†
*Physaria vitulifera*
*Physaria acutifolia*
*Trifolium nanum*
*Trifolium dasyphyllum*†
*Kentrophyta aculeata*
*Kentrophyta Wolfii*†
*Aragallus minor*
*Phlox depressa*
*Phlox Kelseyi*
*Chrysopsis pumila*
*Townsendia strigosa*†
*Townsendia montana*†
*Erigeron ursinus*
*Antennaria rosulata*†
*Tetraneuris lanigera*†
*Tetraneuris brevifolia*
*Senecio Purshianus*
*Senecio Fendleri*†
*Senecio werneriaefolius*†

## SAND HILLS AND SAND-HILL DRAWS

While the best developed sand and sand-hill draws are found in the region of the Great Plains east of the Rockies, and in the desert plains of the Great Basin west of the same; they are found also in the Submontane and Montane Zones. In the latter the sand-draws are found mostly in the bottoms of the canyons and the sandhills in the so-called "Parks" of Colorado and in some of the broader river valleys. Most of the species characteristic of both are also found on the Great Plains and are such as have migrated along the rivers to higher altitudes. The following species are components of the flora. None of these are transcontinental or common to the Rockies and the Canadian Zone. A few are common to the Rocky Mountains and the Sierra Nevada Region, but most of them are endemics, either of the Great Plains or the Great Basin, or both.

*Eriocoma hymenoides*
*Muhlenbergia pungens*
*Stipa speciosa*
*Oryzopsis Webberi*
*Sitanion elymoides*
*Arenaria confusa*
*Arenaria polycaulos*
*Peritoma serrulatum*
*Epilobium paniculatum*
*Gayophytum intermedium*
*Gayophytum ramosissimum*
*Gayophytum racemosum*
*Nuttallia multiflora*
*Nuttallia densa*
*Nuttallia speciosa*
*Cryptantha Torreyana*
*Lithospermum multiflorum*
*Helianthus petiolaris*

## M. ROCK SLIDES

The rock slide flora of the upper Montane Zone resembles that of the Subalpine, which has already been described.* In lower altitudes the following species appear, all of which are endemic to the Southern Rockies except *Viola biflora*, which is found also in Europe.

*Elymus ambiguus*†
*Aquilegia saximonana*†
*Aragallus Hallii*†
*Limnobotrya montigena*†
*Viola biflora*†
*Pseudopteryxia anisata*†
*Pseudopteryxia aletifolia*†
*Polemonium confertum*†
*Polemonium mellitum*†
*Polemonium Brandegei*†
*Pentstemon stenosepalus*†
*Senecio Fendleri*†
*Senecio amplectens*†
*Senecio canovirens*†

New York Botanical Garden.

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* Bull. Torrey Club 44: 453. 1917.

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# STUDIES OF WEST INDIAN PLANTS—X

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# Studies of West Indian plants—X

Nathaniel Lord Britton

## 60. UNDESCRIBED SPECIES FROM TRINIDAD

### **Eleocharis savannarum** sp. nov.

Rootstocks very slender, elongated; culms filiform, weak, smooth, 6–15 cm. long, the upper sheath membranous, its mouth oblique; spikelet ovoid, 3–4 mm. long; scales oblong or ovate-oblong, about 2 mm. long, obtuse, nearly white with a greenish midvein; achene trigonous, obovoid, about 0.5 mm. long, truncate; tubercle low, nearly flat, apiculate; bristles none.

Moist hole on the O'Meara Savanna, Trinidad (*Britton 2491*).

### **Eleocharis oropuchensis** sp. nov.

Roots fibrous, finely filiform; culms finely filiform, densely tufted, weak, 5 cm. long or less, the upper sheath membranous, oblique at the summit. Spikelets terminating culms, and sessile at the base of the plant; compressed, 2–3 mm. long, ovate, about 6-flowered; their scales ovate-oblong, pale or brown with pale margins and keel, subdistichous, blunt, 1.5 mm. long; style 3-cleft; achene trigonous, smooth, pale, about 0.5 mm. long, about as long as the 3 or 4 bristles; tubercle conic, one fourth as long as the achene.

In mud in sunny, grassy situations, Trinidad; type from Oropuche Lagoon (*Britton, Hazen and Freeman 1155*, March 29, 1920).

I am indebted to Mr. N. E. Brown for comparing this little plant with West Indian and South American species in the Kew Herbarium, where he was unable to match it. He remarks upon its unusual character of having both terminal and basal spikelets, and compares it with *Chaetocyperus Jamesoni* Steud. from Guayaquil, Ecuador (*Jameson 369*), pointing out important differences, however.

### **Rynchospora aripoensis** sp. nov.

Perennial by short horizontal rootstocks; culms filiform, tufted, smooth, erect, 2–4 dm. high, longer than the filiform leaves. Spikelets few, 2 mm. long, ovoid, acute, 1-fruited, sessile in 1 or 2 small clusters subtended by a filiform bract 1–3 cm. long; scales ovate, brown, acute; bristles none; achene obovate-elliptic, 1 mm. long, smooth, light brown; tubercle compressed-conic, acute, one third to one half as long as the achene.

Grassy plain, Aripo Savanna, Trinidad (*Britton 2934*). Perhaps most nearly related to *R. Chapmani* M. A. Curtis of the eastern United States.

### **Bromelia aurea** sp. nov.

Leaves numerous, rigid, linear, long-attenuate, 6–8 dm. long, about 3 cm. wide, armed with distant curved prickles 4–5 mm. long. Scape rather slender, shorter than the basal leaves, bearing several prickle-armed small leaves; inflorescence brownish-floccose, about 3 dm. long; bracts lanceolate, membranous, acuminate, 2–4 cm. long; bractlets ovate, membranous, strongly nerved, mucronate, about 1 cm. long; flowers 2 to several together, the clusters 2–3 cm. apart; sepals similar to the bractlets, about 1 cm. long; petals linear, bright yellow, about 3 cm. long and 2 mm. wide.

Wooded hillside, near western end of Monos Island, Trinidad (*Britton, Britton and Brown 2736*). In flower April 4, 1921. Related to *B. chrysantha* Jacq. of Venezuela.

### **Aechmea porteoides** sp. nov.

Leaves firm in texture, linear with a somewhat broadened base, about 8 dm. long, 4–7 cm. wide, sharply acute, the margins armed with very numerous, approximate, nearly black, slightly curved spinules 4 mm. long or less; inflorescence paniculate, as long as the leaves or longer, its ultimate branches spreading, about 6 cm. long, stellate-pubescent, slender, few-flowered; bracteoles subulate-acicular, 4–6 mm. long; flowers blue, about 20 mm. long; sepals striate, about 1 cm. long, with a terminal spinule 2–3 mm. long; ovary about 1 cm. long, oblong.

On the ground in mountain forests, Trinidad. Type from Mount Tocuche (*Britton, Hazen and Mendelson 1342*). In flower April 5, 1920. Related to *A. Fendleri* of Venezuela.

### **Tillandsia viscidula** sp. nov.

Basal leaves tufted, linear, 2.5–3.5 dm. long, flat, gradually narrowed upward, abruptly contracted at the apex and short-acuminate, the base expanded and dark-blotched. Stem 3–5 dm. high, erect, bearing leaves similar to the basal ones, but smaller, the upper ones 7 cm. long or less; panicle 3–5 dm. long, few- to several-branched, viscid; flowers yellow, distant, sessile, about 2 cm. long, at first appressed, later spreading, about as long as the bracts.

On trees, Trinidad. Type from Moruga (*Britton and Broadway 2430*). Related to *T. aloifolia* Hook.

### **Alpinia silvicola** sp. nov.

Rootstocks rather stout, scaly. Sterile stem 2–3 m. high; leafy; leaves oblong, thin, glabrous, closely many-veined, 3–5 dm. long, 6–10 cm. wide, the apex acuminate, the base narrowed, the petioles 1–2.5 cm. long, the sheaths striate; lower leaves reduced to thin sheathing scales. Fertile stems about 3 dm. high, pubescent above, with a few, narrow scales 3–4 cm. long; spike dense, several- to many-flowered, 7–10 cm. long; bracts 1-flowered, shorter than the flowers; calyx about 1.5 mm. long, pubescent, its lobes broad; corolla yellow, about 2 cm. long; fruit oblong, about 3 cm. long, its juice blue-black.

Forests of the northern mountain range, Trinidad. Type from Mount Tocuche (*Britton, Hazen and Mendelson 1301*).

### **Calathea trinitensis** sp. nov.

Leaves erect, oblong to oblong-lanceolate, glabrous, the blade up to 1 m. long and 3 dm. wide, rather shorter than the slender petiole, rather abruptly narrowed at the base, the apex abruptly tipped, the midvein prominent, the innumerable lateral veins close together. Scape glabrous, about 7 dm. high; spike dense, about 2 dm. long; bracts oblique, many-veined, 3–4 cm. long, their spreading tips acute; flowers yellow, about 3 cm. long, the segments linear, parallel-veined, acute.

Forest, heights of Aripo, Trinidad (*Britton and Freeman 2360*). In flower March 16, 1921.

### **Ficus ierensis** sp. nov.

A tree up to 10 m. high or higher, glabrous. Leaves broadly elliptic or elliptic-orbicular, subcoriaceous, pinnately 5- to 9-veined on each side of the rather prominent midvein, rounded at the apex, cordate at the base, 10–20 cm. long, the stout petiole one fourth to one third as long as the blade; fruiting peduncles slender, about 1 cm. long; fruit globose, 12–18 mm. in diameter; bracts 2 or 3, broad, rounded, nearly as long as the fruit; ostiolum sunken, about 2 mm. in diameter.

Hillsides in relatively dry districts, Trinidad. Type from North Post Road (*Britton, Hazen and Mendelson 774*). Similar to *F. crassinervia* of Hispaniola, to which species it has been referred, and also related to *F. Urbaniana* Warburg, of the Lesser Antilles.

### **Ficus arimensis** sp. nov.

Twigs stout. Leaf-blades firm in texture, obovate, about 2 dm. long and twice as long as wide, distantly pinnately veined, the base subcuneate, the apex rounded and short-cuspidate; fruit subglobose, sessile, about 8 mm. in diameter (immature).

Arima, Trinidad (*J. Dannouse*). Collected in 1905.

### **Ficus Mendelsonii** sp. nov.

A tree up to 16 m. high. Leaves elliptic to obovate-elliptic, the blade thin, smooth, 10–15 cm. long, about twice as long as wide, distantly pinnately veined, triple-veined just above the base, the base rounded or obtuse, the apex abruptly short-acuminate; petioles slender, 2–6 cm. long; peduncles slender, 1–2 cm. long; fruit globose, pale, 10–15 mm. in diameter, the ostiolum deeply concave; basal bracts 2, triangular-ovate, about 2 mm. long.

Forests in moist or wet districts, Trinidad. Type from the northern hills between North Post and Maqueripe (*Britton, Hazen and Mendelson 879*).

### **Phoradendron chaguaramasanum** Trelease sp. nov.

Scarcely forked, the moderate branches with basal cataphyls only, androgynous?. Internodes short (2 × 10–30 mm.), at first papillately roughened, quadrangular and somewhat 4-winged, little flattened. Cataphyls a single pair, nearly basal, deeply notched. Leaves spatulate-oblong, obtuse to subtruncate, scarcely 1 × 2.5 cm., cuneately subpetioled for 5 mm., fleshy, drying yellow, 1- or obscurely 3-nerved from the base. Spikes solitary, very short (about 5 mm.), with 2 or 3 very short characteristically 4-flowered joints; peduncle about 1 mm. long; scales ciliolate. Immature fruit subglobose, scarcely 2 mm. in diameter, reddish, verrucose; sepals yellow, erect, not meeting.

Chaguaramas, Trinidad (*Britton 2718*, the type, April 4, 1921).

### **Phoradendron caerulescens** Trelease sp. nov.

Pseudodichotomous, the moderate branches with basal cataphyls only, androgynous?. Internodes short (2–3 × 10–20 mm.), smooth, glossy, quadrate, the upper ancipitally dilated to a width of 4 mm. below the nodes. Cataphyls a single pair, basal, glossy brown, tubular-bifid. Leaves round-elliptical, submucronately acuminate, 1.5 × 2–2.5 cm., cuneately subpetioled for about 5 mm., cartilaginous-margined, about 5-nerved, at first delicately blue-glaucous. Spikes solitary, short (scarcely 15 mm.) with 3 or 4 short 4-flowered joints; peduncle 1 mm. long; scales slightly ciliolate. Fruit (immature) small, globose, deeply immersed, verrucose: sepals inflexed.

Chacachacare Island, Trinidad (*Britton and Hazen 1726*, April 13, 1920), the type; also from the same locality, on *Capparis* (*Britton, Freeman and Watts 2701, 2708*, 1921).

Of the *Emarginatae*, but with inflexed sepals, and in this, as well as in its flattened twigs, related to *P. Ottonis* Eichler of Venezuela.

### **Seguiera ierensis** sp. nov.

A climber with slender twigs and branches, the prickles 2–25 mm. long. Leaves oblong or oblong-lanceolate, 6–16 cm. long, acute or acuminate at the apex, narrowed or obtuse at the base, or the upper ones smaller and obtuse, the petioles 2–7 mm. long; panicles many-flowered, 5–9 cm. long, puberulent; pedicels 2–3 mm. long; perianth-segments unequal, elliptic to obovate, 3–3.6 mm. long, rounded, concave; stamens about 20 with filiform filaments and linear anthers.

McBean Estate, Carapachaima, Trinidad, April 30, 1918 (type). Forest, Ortoire River, Guayaguayare Road (*Britton, Freeman and Nowell 2527*, barren).

### **Seguiera cordata** sp. nov.

Twigs slender; prickles stiff, nearly straight, about 8 mm. long. Leaves broadly ovate, subcoriaceous, glabrous, 14 cm. long or less, cordate or subcordate at the base, acute at the apex, or small ones obtuse at both ends, the venation prominent beneath, impressed above, the stout petioles 6–8 mm. long; panicles many-flowered, about 6 cm. long; bractlets ovate, 1 mm. long, about as long as the pedicels or a little shorter; sepals 1–1.5 mm. long.

Lobajos near Erin, Trinidad (*Trinidad Herbarium 9122, W. E. Broadway*, May 14, 1920).

### **Chrysobalanus savannarum** sp. nov.

An irregularly branching shrub 0.5–4 m. high, the glabrous twigs slender. Leaves obovate to elliptic-obovate, 1.5–3.5 cm. long, strongly reticulate-veined above, faintly veined beneath, obtuse or acutish at the apex, narrowed at the base, the petioles 1.5–2 mm. long; flowers few, in small axillary clusters not longer than the leaves, or these terminating short leafy twigs; pedicels short, puberulent; calyx silky-pubescent, its lobes short, broad, obtuse; petals cuneate-spatulate, rounded at the apex, 3–3.5 mm. long; drupe oblong or narrowly oblong-obovoid, obtuse, about 8 mm. long and 4 mm. in diameter.

Grassy plain, Aripo Savanna, Trinidad (*Britton, Hazen and Freeman 2005*, April 21, 1920).

### **Acacia quadricostata** sp. nov.

A woody vine, up to 8 m. long, the old stems 4-ribbed or 4-flanged, about 8 cm. thick near the base, the twigs 4-angled, armed with recurved prickles about 3 mm. long. Leaves 2-pinnate, 6–17 cm. long; stipules wanting; petiole slender, bearing a sessile, circular gland; rachis glabrous, sometimes bearing a few minute prickles; rachilla very slender, angular; leaflets 35 pairs or fewer, sessile, linear-lanceolate, acutish, 6–8 mm. long, about 1 mm. wide, truncately inequilateral at the base, the midvein somewhat eccentric, the lateral veins few, glabrous, except for a characteristic line of yellowish hairs on the underside of the midvein near the base; legume linear-oblong, flat, densely puberulent, 5–9 cm. long, nearly 2 cm. wide, narrowed at the base with a short stipe, acute and short-tipped; seeds orbicular, dark brown, about 7 mm. in diameter.

Hillside, Chacachacare Island, Trinidad (*Britton, Freeman and Watts 2685*), in fruit April 3, 1921. The prickles are persistent upon the old stems and branches.

### **Erythrina pallida** Britton and Rose sp. nov.

A small tree, 4 meters high; young growth puberulent; second year growth glabrate with shining gray bark; spines at base of leaves stout, reflexed, 6–8 mm. long; leaves large; rachis 2 cm. long or more, glabrous; leaflets 3, broadly ovate, sometimes obliquely so, acuminate, 12–15 cm. long, green above, very pale beneath, glabrous on both sides at least when mature; inflorescence subsessile, paniculate, 1–2 dm. long; pedicels stout, about 1 cm. long; calyx 1.5 cm. long, nearly truncate, except a small protuberance on the lower side; corolla salmon-colored, narrow, 7 cm. long; fruit with a long slender stipe 3 cm. long; tipped with a rigid persistent style, 2 cm. long, moniliform, 8–10-seeded; seed 8 mm. long, 6 mm. broad.

Hillsides and roadsides, Trinidad. Type from roadside near Carenage (*Britton 2656*), April 4, 1921. Commonly planted as a fence tree in Trinidad.

### **Elaphrium trinitensis** Rose sp. nov.

A gnarled tree, 5 meters high, fragrant; branches glabrous, often short and spur-like, with brownish bark; leaves simple, borne at the end of stubby branches, the petiole not winged, 12 mm. long or less, the blade broadly ovate, 2.5 cm. long or less, entire, glabrous; flowers solitary or in small panicles sometimes only 3- or 4-flowered; pedicels 3 to 5 mm. long, glabrous; fruit 3-angled, glabrous, 8 to 10 mm. long; nutlet white, 3-angled.

Western end of Monos Island, Trinidad (*Britton, Britton and Brown 2739*), April 4, 1921.

### **Phyllanthus graminicola** sp. nov.

Annual, with fibrous roots, glabrous; stem slender, erect, becoming much branched, 1–3 dm. high, the branches almost filiform. Leaves oblong-elliptic, thin, faintly pinnately veined, 4–10 mm. long, the apex obtuse, the base more or less narrowed, the petiole about 1 mm. long; stipules minute; flowers nearly sessile; calyx of the pistillate flowers deeply 6-parted, the linear segments at length about 1 mm. long; fruit depressed, 1.5 mm. in diameter; seeds about 0.6 mm. long.

Moist grassy situations at low elevations, Trinidad. Type from grassy roadside, Carenage (*Britton and Hazen 12*). In fruit February 25, 1920. Related to *P. carolinensis* Walt. of the eastern United States, which has larger fruit and seeds and broader pistillate calyx-segments.

### **Clusia tocuchensis** sp. nov.

A tree about 18 m. high, the twigs rather stout. Leaves borne at the ends of the twigs, obovate, coriaceous, glabrous, about 10 cm. long, 4–5 cm. wide, rounded at the apex, cuneate at the base, rather finely pinnately veined, the short stout petiole only about 5 mm. long; fruit globose, 10–15 mm. in diameter; carpels about 7; styles stout, 3–4 mm. long; stigmas flat, obliquely oblong, the center depressed.

Forest, Mount Tocuche, Trinidad (*Britton, Hazen and Mendelson 1247*). In fruit April 3–5, 1920.

### **Terminalia nyssaefolia** sp. nov.

A tree up to 20 m. high, the slender twigs glabrous. Leaves chartaceous, obovate, 7–12 cm. long, 4–6 cm. wide, entire, abruptly short-acuminate at the apex, cuneate at the base, strongly reticulate-veined, glabrous and bright green above, pale green, dull and strigose-pubescent on the veins beneath, the strigose and ciliate petioles 5–10 mm. long; fruit compressed, 2-winged, broader than long, 2–3.5 cm. broad, 1.5–2.5 cm. long, notched at the apex, at base abruptly contracted into a stalk about 2 mm. long, the thin striate wings about one half as wide as the seed-bearing part.

Coastal woods, Manzanilla, Trinidad (*Britton 2177*). In fruit (fruit fallen) March 9, 1921.

### **Combretum trinitense** sp. nov.

Vine-like, woody, the stems up to 6 m. long, the branches long and slender, the twigs glandular. Leaves elliptic or elliptic-lanceolate, chartaceous, 8–12 cm. long, 5 cm. wide or less, the midvein prominent beneath, impressed above, the lateral veins about 7 on each side of the midvein, slender, curved upwardly, the upper surface glabrous, reticulate-veined, the under surface impressed-glandular, the glandular petioles 6–7 mm. long; fruiting racemes 6–10 cm. long; fruit oblong, 10–15 mm. long, the four thin wings glandular, the pedicels about 2 mm. long.

Hillside thicket, Chacachacare Island, Trinidad (*Britton, Freeman and Watts 2699*). In fruit April 3, 1921.

### **Myrcia arimensis** sp. nov.

A small tree, the slender young twigs rather densely strigose. Leaves elliptic to elliptic-ovate, chartaceous, 4–6 cm. long, reticulate-veined, punctate, dark green and shining above, pale green beneath, the apex acute, the base narrowed, the strigose or glabrate petioles 3–5 mm. long; panicles several- to many-flowered, 5–7 cm. long, their slender branches spreading; flowers nearly or quite sessile; calyx-lobes rounded; immature fruit globose, about 5 mm. in diameter.

Arima, Trinidad (*J. Dannouse*, Feb. 10, 1905).

### **Eugenia Baileyi** sp. nov.

A tree up to 12 m. high or higher, the twigs terete, rather slender. Leaves coriaceous, glabrous, broadly elliptic, 12–16 cm. long, 9–12 cm. wide, rounded at the apex, obtuse at the base, strongly pinnately veined, abundantly punctate, the stout petioles 1–1.5 cm. long; fruit lateral, oblong or ovoid-oblong, about 2 cm. long and 1 cm. thick, pale, puberulent, nearly sessile.

Forest, Morne Bleu, Trinidad (*Britton, Freeman and Bailey 2246*). In fruit March 13, 1921.

### **Hydrocotyle Hazenii** Rose sp. nov.

A delicate creeping plant, rooting at the nodes; petioles slender, 2 to 5 cm. long, pubescent and more pronounced just below the blade; blade nearly orbicular, 2.5 cm. in diameter or less, glabrous and paler beneath, somewhat hairy or glabrate above, the sinus usually narrow, the margins doubly crenate, the crenations low and broad; peduncle slender, hairy above, longer than the petiole; flowers in a small compact umbel; pedicels 1 to 2 mm. long.

Among wet rocks, Maracas Waterfall, Trinidad (*Britton, Hazen and Mendelson 1660*, April 10, 1920).

### **Psammisia recurvata** sp. nov.

Stems branched, about 5 m. long. Leaves coriaceous, glabrous, elliptic-ovate, 10–20 cm. long, 7–10 cm. wide, pinnately 7-veined from near the base, with numerous curved transverse veinlets, the venation impressed above, prominent beneath, the apex acute, the base narrowed, the stout petiole 1–2 cm. long; flowers several in short axillary racemes; bractlets ovate, acute, about 2 mm. long; pedicels stout, recurved, glabrous, 2–3 cm. long; ovary subglobose, glabrous; calyx subcampanulate, persistent, about 6 mm. long in fruit, its lobes rounded, apiculate, their margins thickened; corolla-tube about 4 cm. long, red, the short limb white; fruit globose, about 1 cm. in diameter, many-seeded.

Forest bank, near summit of Mount Tocuche, Trinidad (*Britton, Hazen and Mendelson 1294*).

Specimens of this plant were mixed by Grisebach with those of another and the complex described by him (Fl. Br. W. I. 143) as *Thibaudia latifolia* Griseb., subsequently referred by Bentham and Hooker to *Vaccinium*; it would appear that the name *latifolia* should go with this other species, which, however, is not a good *Vaccinium*.

### **Sophoclesia trinitensis** sp. nov.

Pendent from forest trees; stem slender, sparingly branched, short-villous when young, 1–4 m. long. Leaves subcoriaceous, glabrous or nearly so, ovate or some of them ovate-lanceolate, 1.5–3.5 cm. long, from about one half to two thirds as wide as long, triplinerved with a pair of delicate veins at the base, this venation rather distinct beneath, obscure above, the apex bluntly pointed, the base rounded or subtruncate, the villous petiole about 2 mm. long; peduncles filiform, glabrous, somewhat shorter than the leaves; ovary globose, glabrous or with a few hairs; corolla white, glabrous, about 5 mm. long; fruit blue or mauve, glabrous, about 5 mm. in diameter.

Forests, in wet districts, Trinidad. Type from Mount Tocuche (*Britton, Hazen and Mendelson 1316*). In flower and fruit April 3, 1920.

*Sophoclesia major* (Griseb.) Benth. & Hook., also of Trinidad, differs in its ovate-orbicular rounded, subcordate leaves and densely pilose ovary.

### **Cavendishia Urichiana** sp. nov.

A much-branched, woody vine, up to 6 m. long, glabrous throughout, the branches slender. Leaves oblong-lanceolate to oblong-elliptic, somewhat fleshy, dark green above, bright green beneath, chartaceous in drying, triple-nerved, 10–15 cm. long, 3–5 cm. wide, the nerves rather prominent beneath, slightly impressed above, the apex acuminate, the base narrowed, the petiole 8–10 mm. long, rather stout; flowers fascicled on the twigs or in the leaf-axils, bracteolate, the bractlets ovate, acute, 2–3 mm. long; pedicels slender, 8–20 mm. long; calyx-limb with 5 short acute teeth, expanded above the ovary; corolla-tube subcylindric, about 2 cm. long, scarlet, the limb 4 mm. long, white, with 5 ovate-lanceolate teeth; stamens shorter than the corolla; style slender, exserted; immature fruit subglobose, crowned by the calyx-limb.

Climbing on forest trees, Heights of Aripo, Trinidad (*Britton and Freeman 2364*, March 16, 1921). Specimens were brought from the same place a few days earlier by Mr. F. W. Urich, Entomologist of the Trinidad Department of Agriculture, and he guided us to it. The plant from which the type specimens were taken is wonderfully elegant when in bloom, displaying long wands of the scarlet, white-tipped flowers, and is locally called "clove-plant."

### **Diospyros ierensis** sp. nov.

A tree, 12 m. high or higher, the twigs and leaves glabrous. Leaves chartaceous, oblong to elliptic, 10–15 cm. long, 7 cm. wide or less, bluntly short-acuminate at the apex, narrowed or obtuse at the base, reticulate-veined, the venation prominent beneath, the stout petiole 10–14 mm. long; fruiting calyx 2–2.5 cm. broad, nearly flat, wrinkled, 4-lobed, the lobes broad and short; fruit subglobose, about 4 cm. in diameter (not quite mature); seeds about 8.

Forest near the summit of Mount Tocuche, Trinidad (*Britton, Hazen and Mendelson 1243*). In fruit April 5, 1920.

Specimens collected by J. Dannouse at Guanapo, Trinidad, showing imperfect flowers about 1 cm. wide (*Trinidad Herb. 6415*) are probably referable to this species.

### **Chrysophyllum** (?) **minutiflorum** sp. nov.

A tree about 15 m. high, the young leaf-buds puberulent, otherwise glabrous. Leaves thin-chartaceous, oblong-lanceolate, 13 cm. long or less, 2.5–5 cm. wide, long-acuminate at the apex, narrowed at the base, delicately pinnately and reticulate-veined, the rather slender petioles 10–15 mm. long; flowers green, several to many in sessile axillary fascicles; bractlets minute; pedicels very slender, thickened upward, 5–8 mm. long; calyx about 1.5 mm. long, its 3 or 4 lobes rounded; corolla-segments 3 or 4, minute; stamens 3 or 4.

Forest, Arima, Trinidad (*Britton, Britton and Brown 2403*). In young flower March 18, 1921.

The flowers are too young to enable the generic status of this tree to be certainly determined. Mr. N. E. Brown has identified specimens as the same as Crueger's *no. 247* in the Kew Herbarium, from Trinidad, which is a leafy branch and a detached fruit. The leaves are also the same as those of Trinidad Herbarium *no. 1454*, also leafy shoots with the remains of a fruit which was, apparently, about 2 cm. long, attached, and with some flowers even younger than those of our *2403*.

### **Evolvulus bocasanus** sp. nov.

Perennial, shrubby, branched, 3–4 dm. high, the branches nearly erect or ascending, strigose. Leaves lanceolate to oblong, 2–5 cm. long, 5–15 mm. wide, strigose on both sides, acute or obtuse at apex, obtuse at base, pinnately few-veined, the veins nearly parallel, the petiole 1–2 mm. long; peduncles filiform, axillary, 3 cm. long or less, 1–few-flowered; bracts lanceolate, acuminate, 2–3 mm. long; pedicels 2–10 mm. long; calyx strigose, 3–4 mm. long, 5-lobed to about the middle, the lobes lanceolate, acute; corolla rotate, bright blue, 8–15 mm. broad.

Hillsides, Bocas Islands, Trinidad; type from Chacachacare (*Britton, Freeman and Watts 2674*). In flower April 3, 1921. This is the species recorded from Trinidad by Grisebach as *Evolvulus alsinoides* L., at least in part.

### **Solanum ierense** sp. nov.

A shrub about 2 m. high, the slender unarmed branches divergent, glabrous, the young twigs stellate-pubescent. Leaves thin, ovate or elliptic-ovate, 5 cm. long or less, delicately pinnately few-veined, sparingly stellate-pubescent above, densely stellate-pubescent beneath, the apex acute or obtuse, the base obtuse or narrowed, the slender petioles 4–10 mm. long; flowers solitary or geminate (rarely 3) in the axils on nearly filiform pubescent peduncles 2.5 cm. long or less; calyx stellate-pubescent, 5–7-cleft, the lobes linear-lanceolate, acuminate; corolla white, 5–6-cleft, its lobes linear-lanceolate, acuminate, 10 mm. long; stamens 5 or 6, all alike, the anthers somewhat attenuate, 8 mm. long, the filaments 1–2 mm. long; immature berry globose, about 7 mm. in diameter.

Hillside, Chacachacare, Trinidad (*Britton, Freeman and Watts 2706*). In flower and young fruit April 3, 1921.

### **Solanum Hazenii** sp. nov.

A tree up to about 5 m. high with a woody trunk about 1.5 dm. in diameter. Leaves broadly elliptic, rather thin and flaccid, 10–20 cm. long, 8–15 cm. wide, strongly pinnately veined on the under side, the apex short-acuminate, the base obtuse, the upper surface finely stellate when young, glabrous when old, the under surface persistently stellate-tomentulose, the stout, stellate-tomentulose petioles 3 or 4 cm. long; inflorescence stalked, about equalling the leaves, many-flowered, tomentulose; pedicels short; flower-buds subglobose, rounded, tomentulose; calyx tomentulose, deeply lobed, 5 mm. long, the lobes obtuse; corolla white, 20 mm. broad, 5-lobed to below the middle, the lobes broadly ovate, acute; stamens all alike, the anthers 3 mm. long, about twice as long as the filaments; berry globose, black, about 8 mm. in diameter.

Hillsides, northwestern parts of Trinidad mainland and on the adjacent Bocas Islands. Type from Saddle Road (*Britton and Hazen 156*).

### **Solanum capillipes** sp. nov

A shrub, about 2 m. high, the slender young branches pilose, the older branches glabrous. Leaves oblong-elliptic to elliptic-lanceolate, membranous, all alike, pinnately veined, glabrous, somewhat darker green above than beneath, 10–15 cm. long, 3–6 cm. wide, acuminate, the slightly inequilateral base narrowed, the petioles about 1 cm. long; racemes lateral, few-flowered, glabrous; peduncles very slender, 2.5 cm. long or less; pedicels filiform, spreading, 1–3 cm. long; calyx obconic, about 5 mm. long; corolla white, deeply lobed, 5–6 mm. broad; stamens all alike, the oblong anthers obtuse, 1.5 mm. long, nearly sessile; fruit globose, 6–7 mm. in diameter.

Forests in wet districts, southern Trinidad. Type from forest, Ortoire River, Guayaguayare Road (*Britton, Freeman & Nowell 2521*).

### **Codonanthe** (?) **triplinervia** sp. nov.

A somewhat fleshy, epiphytic woody vine, 1–2 m. long, the young twigs sparingly pubescent. Leaves ovate or ovate-lanceolate, 8 cm. long or less, 2–3.5 cm. wide, glabrous, rather thin, triplinerved, the apex acuminate, the base narrowed or obtuse, the slender, sparingly pubescent petioles 6–12 mm. long; flowers solitary or 2–4 together at the nodes; bractlets linear, pubescent, acute, 6 mm. long or less; pedicels slender, pubescent, about as long as the bractlets; calyx 10–12 mm. long, sparingly pubescent below, deeply cleft, its segments linear-oblong, acute; corolla 3–3.5 cm. long, white, the throat yellow within, its tube slightly bent just above the gibbous base, about 1 cm. long, the subcampanulate throat about 1.5 cm. long, the somewhat spreading limb with rounded, translucent lobes.

On forest trees, Trinidad; type from Ortoire River, Guayaguayare Road (*Britton, Freeman and Nowell 2543*). In flower March 25, 1921.

### **Sabicea trinitensis** Standl. sp. nov.

Vine, the stems about 2 m. long, pubescent with dense short ascending rufescent hairs; stipules 5–6 mm. long, rounded-ovate, obtuse or subacute, finely ciliolate but otherwise glabrous; petioles 8–14 mm. long, densely hirtellous with ascending hairs; leaf-blades elliptic or oblong-elliptic, 9–10.5 cm. long, 4.5–6 cm. wide, acute or subacute, abruptly contracted at base, hispidulous above along the costa, elsewhere scaberulous, appressed-pilose beneath along the veins, glabrate elsewhere; flowers few, sessile in the leaf-axils, subtended by two green bracts similar to the stipules; hypanthium about 3 mm. long; glabrous or with a few appressed white hairs; calyx-lobes linear, 2–3 mm. long, green, plane, obscurely ciliolate; corolla appressed-hirsute, the tube 6–7 mm. long, the lobes lanceolate, acuminate, 3 mm. long.

Type in the U. S. National Herbarium, No. 1,059,334, collected in a thicket of the O'Meara Savanna, Trinidad, March 22, 1921 (*Britton 2489*).

The proposed species is most nearly related to *S. hirsuta adpressa* Wernham, which has been reported from Trinidad. It differs essentially, however, in the short narrow calyx-lobes and in the short scant pubescence of the upper leaf-surface.

## 61. UNDESCRIBED SPECIES FROM JAMAICA

### **Pilea Maxoni** sp. nov.

Stem trailing, freely rooting at the nodes, 3–6 dm. long or longer, rather densely pubescent, the pubescent branches erect, 6–12 cm. high or higher. Stipules ovate-orbicular, rounded, submembranous, 3–6 mm. long, sometimes broader than long; leaf-pairs nearly equal; leaves ovate, regularly crenate, 1–3 cm. long, acute, acuminate, or some of the smaller ones obtuse at the apex, obliquely obtuse or rounded at the base, 3-nerved from above the base, sparingly pubescent and reticulate-veined beneath, the upper surface nearly veinless, with long, flat scattered hairs and some short ones, the linear glochides largely marginal only; petioles slender, pubescent, as long as the blades or shorter; pistillate inflorescence paniculate, slender-peduncled, about 6 cm. long, the staminate shorter; sepals lanceolate or oblong-lanceolate.

Rocky woods in the Cockpit Country, Jamaica. Type, *Maxon & Killip 1555*, from near Mocho, above Catadupa, April 3, 1920; previously collected near Troy, June 28, 1904 (*Maxon 2834*), our specimen of this number barren.

### **Zanthoxylum Harrisii** P. Wilson sp. nov.

An unarmed tree 15–18 m. high, with grayish-brown branches. Leaves equally pinnate, 2–3.5 dm. long, the petioles and rachis terete, glabrous or nearly so; leaflets 8–12, alternate or sometimes opposite, short-petioluled, elliptic-lanceolate to elliptic, 7–15 cm. long, 4–5 cm. broad, coriaceous, acuminate at the apex, inequilateral at the base, entire, lustrous above, the midvein impressed, paler beneath, the midvein prominent; inflorescence terminal or lateral in the axils of the upper leaves, the branches densely puberulent; staminate flowers: calyx lobes 5, triangular-ovate; petals 5, lanceolate, 3 mm. long, 1.5 mm. broad, stamens 5, exserted.

St. George's, Portland, Jamaica, March 30, 1918 (*Harris 12878*).

### **Salvia clarendonensis** sp. nov.

A spreading shrub with weak stems and branches 2–3 m. long, the twigs, petioles and inflorescence puberulent. Leaves slender-petioled, membranous, oblong-lanceolate, serrulate, glabrous above, puberulent beneath, acuminate at the apex, narrowed or obtuse at the base, 5–15 cm. long; racemes slender, 7–10 cm. long; bracts linear-lanceolate, the lower ones sometimes 1 cm. long; pedicels very short; calyx about 5 mm. long, its ovate cuspidate teeth shorter than the tube; corolla rose-purple, 1–1.2 cm. long.

Peckham woods, Upper Clarendon, Jamaica (*Harris 12787*).

### **Gesneria jamaicensis** sp. nov.

A glabrous shrub, up to 3.3 m. high, the young twigs and leaves resiniferous, the branches terete. Leaves oblong to elliptic, subcoriaceous, 7–12 cm. long, 2.5–5 cm. wide, acute or acuminate at the apex, closely serrate except near the entire, acute or acutish base, pinnately veined, the rather stout petioles 5–10 mm. long; peduncles axillary, slender, 1-flowered, about as long as the leaves; calyx-tube obconic or turbinate, 6–8 mm. long; calyx-lobes linear-lanceolate, bluntish, 8–10 mm. long, 1 mm. wide; corolla crimson or rose-pink, its tube subcylindric, 8–10 mm. long, its spreading lobes orbicular, strongly veined, erose, about 4 mm. broad; stamens included; filaments distinct, about 8 mm. long; anthers nodding; staminodium a little shorter than the filaments; style glabrous, 2-lobed; capsule broadly turbinate, about 8 mm. long.

Ipswich, St. Elizabeth, Jamaica (*Harris 12509*, type); Mulgrave, St. Elizabeth, Jamaica (*Harris 12374*).

Nearest related to *G. Harrisii* Urban, which has a sulphur-yellow corolla with oval lobes, the calyx-lobes filiform, the leaves crenate-dentate.

## 62. UNDESCRIBED SPECIES FROM CUBA

### **Scleria motemboensis** sp. nov.

Annual with fibrous roots; culms solitary or few together, slender, erect, villous, about 3 dm. high. Leaves narrowly linear, villous, 1–1.5 mm. wide; inflorescence glomerate-spicate; glomerules of 2 or 3 sessile spikelets; bracts linear, long-ciliate, 3–4 mm. long; achene white, shining, 1.5 mm. in diameter, apiculate, faintly longitudinally striate, with 4 pores at each side of the subtrigonous base.

Small lagoon, Sabana de Motembo, Santa Clara, Cuba (*Léon and Loustalot 9405*). Nearest to *S. Lindleyana* Clarke of South America.

**Ouratea savannarum** Britton & Wilson sp. nov.

A glabrous shrub 5 m. high, the slender twigs grayish-brown, often somewhat flexuose. Leaves coriaceous, elliptic-lanceolate to elliptic-ovate, 4–8 cm. long, 2–3.8 cm. broad, acuminate at the apex, rounded at the base, faintly pinnately nerved, the margin spinose-serrate; petioles short, stout, 3–4 mm. long; inflorescence terminal, 6–11 cm. long; pedicels slender, 1–1.5 cm. long; buds ovoid; sepals oblong-lanceolate to oblong-elliptic, 7–7.5 mm. long, 3.2–3.5 mm. broad, obtuse at the apex; petals obovate, 9 mm. long, 7 mm. broad, crenulate; anthers oblong-lanceolate or oblong, 2.5 mm. long, subsessile; style 6–7 mm. long; fruit unknown.

Sabana de San Marcos, Santa Clara, Cuba (*Léon 9205*).

**Banara Brittonii** Roig sp. nov.

A slender shrub about 4 m. high, the young twigs densely pubescent. Leaves oblong to oblong-lanceolate or ovate-lanceolate, 4–7 cm. long, 1.5–3 cm. wide, acute at the apex, more or less inequilateral and rounded at the base, glabrous and shining above, reticulate-veined and densely pubescent beneath with short, whitish, mostly appressed hairs, the margin revolute, serrulate; petioles 5–8 mm. long, slender, with one or two orbicular glands at the summit; inflorescence terminal, inclined or pendulous, 5–7 cm. long, the branches puberulent, pedicels slender, 3–5 mm. long; sepals oblong-elliptic to oblong-ovate, 2.5 mm. long, obtuse at the apex, the margin ciliate; petals oval to suborbicular, about as long as the sepals, yellow; stamens indefinite; anthers rounded; style 1.5 mm. long; fruit globose (immature?), 4 mm. in diameter, becoming black in drying.

Rocky limestone soil, Cayo Mono, inside the swamp near San Pedro, Isle of Pines (*M. Cremata*, May 17, 1920).

**Psidium Loustalotii** Britton & Wilson sp. nov.

A small shrub, with short, grayish, often spine-like twigs. Leaves elliptic to oval, 2–4 mm. long, 1.5–3 mm. broad, rounded at both ends, dark green and more or less minutely hispidulous above, paler and strigillose beneath, coriaceous, the short petiole 0.5 mm. long or less; pedicels axillary, solitary, 2 mm. long; young fruit ellipsoid, 5 mm. long, 4 mm. in diameter, black.

Sabana de Motembo, Santa Clara, Cuba (*Léon & Loustalot 9394*).

**Jacquinia Roigii** P. Wilson sp. nov.

Shrub or tree?; twigs and branches glabrous. Leaves obovate, 4–8 cm. long, 1.4–2.7 cm. broad, strongly spine-tipped at the apex, cuneate at the base, 3-nerved, in whorls of 4 or more with distinct internodes between the whorls; pedicels 3.5 cm. long; sepals long-ciliate; fruit ellipsoid, 1.7 cm. long, 1.1 cm. broad.

Cañete, Oriente, Cuba (*J. T. Roig 69*).

### **Tabebuia saxicola** sp. nov.

A much-branched shrub, about 3 m. high, the short, stiff twigs white-lepidote. Leaves simple, entire, oblong or oblong-lanceolate, 2–4 cm. long, 5–11 mm. wide, acute at the apex, narrowed at the base, the upper surface pale green, loosely lepidote and with very obscure venation, the under-surface reticulate-veined and densely white-lepidote, the petioles 1–3 mm. long; flowers solitary or 2 together at the ends of short twigs; peduncles 1 cm. long or less; calyx narrowly campanulate, lepidote, persistent, about 7 mm. long, irregularly toothed; corolla 2–2.5 cm. long; capsule 4–5 cm. long, about 8 mm. thick.

Rocky top of highest mogote near Sagua la Grande, Santa Clara, Cuba (*Léon and Loustalot 9477*). In both flower and fruit August 12, 1920.

## 63. A NEW TOURNEFORTIA

### **Tournefortia barbadensis** N. E. Brown

Stem probably scrambling, with the young parts minutely adpressed-puberulous. Leaves very spreading; petiole about 3 lines long; blade 1½–2¾ in. long and 6–10 lines broad, lanceolate, gradually tapering from about the middle to an acute apex, subacute or slightly rounded at the base, glabrous above, thinly and microscopically puberulous beneath. Cymes lateral below the ends of the branches, 2–3½ in. in diameter, on peduncles 3–5 lines long, lax, with the primary and sometimes the secondary forkings subhorizontally diverging, then branching in a zigzag manner, minutely adpressed-puberulous; branches about 3 lines apart and ⅓ in. long, very slender, variously curved, with the small slender flowers about 1 line apart. Pedicels ¼–½ line long. Calyx very small, about ½ line long, lobed almost to the base; lobes subulate or deltoid-subulate. Corolla minutely puberulous outside, with a rather slender tube about 1¼ line long, swollen at the upper part, and filiform lobes 1 line long. Ovary and style glabrous.

Barbados: Middle School, Christ Church, *Bovell & Freeman 404*, and without precise locality, *Lane 428* (in Herb. Kew), type

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# CYCLIC MANIFESTATION OF STERILITY IN BRASSICA PEKINENSIS AND B. CHINENSIS

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# CYCLIC MANIFESTATION OF STERILITY IN BRASSICA PEKINENSIS AND B. CHINENSIS

A. B. STOUT

(WITH SEVEN FIGURES)

The transition from asexual or vegetative growth to the condition of flower and fruit production in hermaphrodite plants is to be recognized as a most fundamental aspect of sexuality. Furthermore, the inter-relations that exist between vegetative and reproductive vigor and the influence of the former on the latter are reflected and exhibited in certain phenomena of sterility.

It is now certain that vegetative vigor and the internal interrelations incident to it may limit reproductive vigor and sexuality. The limitation from these causes may take place in two ways: (1) they may interfere with or influence the morphological development of flowers or other reproductive organs, and (2) they may affect the functioning powers of organs that are fully formed. If these influences are marked, one or more types of sterility may appear.

Only recently observations have indicated that, at least in some cases, the compatibilities and the fertility of the sex organs may vary rather definitely within the cycle of vegetative and reproductive development characteristic of the particular species. A phenomenon of this sort is reported by EAST and PARK (4), who found that in the few plants which are self-compatible in certain species and hybrids of *Nicotiana*, the self-compatibility develops only at the end of the flowering period. Cases of cross-compatibility appearing only at the end of the period of bloom are reported also. A very decided case of the development of self-compatibility only at the close of the period of bloom was observed by the writer, in a plant of *Lythrum Salicaria*, and reported at the annual meeting of the Botanical Society of America for 1917. These observations suggested that new evidence on the old problem of the relation between vegetative vigor and reproductive vigor, as expressed in the formation of flowers and the functioning of the parts in seed formation, may be obtained by experimental means from a study of the fluctuations in fertility that are to be seen in those feebly self-compatible individuals which are to be found in species in which general sexual incompatibilities are strongly developed.

A subsequent report of a more detailed study on this problem (STOUT 11), however, showed that in *Verbascum phoeniceum*, *Eschscholtzia californica*, and *Cichorium Intybus* the various grades of self-compatibility operate very uniformly throughout the entire period of bloom, and that there are in the feebly self-compatible plants of these species no specially marked tendencies to self-compatibility at any definite phase of the blooming period. It was also found that in *Nicotiana Forgetiana* Hyb. Hort. and in *Lythrum Salicaria* end-bloom self-compatibility develops as an infrequent individual variation rather than as a phenomenon characteristic of the self-compatible plants. In these species there is no cyclic production of fruits and seeds which would indicate a general relation between vegetative vigor and the development of self-compatibility.

Such a cyclic occurrence of self-compatibility was found, however, and reported for *Brassica pekinensis*, and it was noted that the highest degree of self-compatibility attained by any given plant appeared very uniformly during the period of mid-bloom. Further studies with this species have since been made which show this to be the rule for all those individuals that are self-compatible in any degree. Similar behavior has also been found in cultures of *Brassica chinensis* and in hybrids between this species and *B. pekinensis*. So far as known to the writer, this is the most uniform and definite case of a general and definite periodicity in the modification of sexual compatibilities within a blooming period. In these species, also, flower abortion appears in the transition of vegetative to reproductive vigor, exhibiting an influence of vegetative vigor on the morphological development of flowers.

## Material and methods

Several strains of the "head" sorts of *Brassica pekinensis*, commonly known as Chinese cabbage or Pe-tsai, and one strain of the loose-leaved or headless sort (the Nanking variety) were grown from seeds furnished by the Office of Foreign Seed and Plant Introduction of the United States Department of Agriculture. The seeds of the strain of *B. chinensis* which have been grown were obtained from China by a Chinese student at Columbia University for the gardener in charge of the greenhouses belonging to the University, and the writer obtained seeds from the first lot of plants there grown. From controlled cross-pollinations between plants of the two species, seeds were obtained and plants of an $F_1$ hybrid progeny were grown.

The greater number of plants have been grown in pots in a greenhouse and brought into bloom during the winter and spring before they could suffer from the heat of summer. When thus grown, plants of the head varieties of *B. pekinensis* form a rather loose headlike rosette, much smaller and less compact than when grown under field culture, after which they shoot up into flower. Plants of the Nanking variety of *B. pekinensis* and plants of *B. chinensis* do not form a head even under the best of field culture; a very loose rosette of leaves develops, and this grades up into the leaves of the flowering stem. Pot grown plants of these species closely resembled field grown plants except that they were smaller.

A few plants of all strains have been grown to full maturity in the garden, both as spring and autumn crops. Such plants were larger than the pot grown plants and more flowers were produced, but their behavior in respect to fertility and sterility was identical with that of plants grown in the greenhouse. Special effort was taken to make controlled self-pollinations throughout the entire period of blooming.[1] Numerous plants have bloomed alone or in isolation from other species of *Brassica*, both in the greenhouses and in the field, and hand pollinations were made from one to four days apart as long as the plants bloomed. The plants not grown in isolation were "bagged." Flowering branches were inclosed in glassine paper bags on or within a day or two following the opening of the first flowers; the plants were visited at least twice a week (at first

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[1] During the winter season of 1919–1920 the writer was greatly aided by the voluntary assistance of Mrs. MORTIMER J. FOX. Miss HESTER M. RUSK has assisted in the research and made many of the pollinations of the plants grown in 1920–1921. Through this efficient assistance and cooperation the many pollinations necessary to the research were accomplished.

many were visited daily), and pollen from fully dehiscent stamens in liberal amounts was placed on pistils of all freshly opened flowers. After the cyclic modification of self-compatibility was recognized, frequent cross-pollinations were made to test the functional power of pistils and stamens during the periods of self-incompatibility preceding and following the period of mid-bloom. The potency of the pollen has been studied by germination tests, and a cytological study of the phenomena of pollen tube growth and fertilization is under way.

## Sterility in Brassica pekinensis and B. chinensis

Three distinct and quite different types of sterility are in evidence during the period of bloom in both these species.

I. One type is to be classed in general with impotence (Stout 12), but here two very distinct types of impotence may be observed. These may be described as (1) flower abortion of the first flowers, and (2) arrested development of the last flowers that start to form.

II. In some plants of both species, axial proliferations develop from the pistils of many flowers, and the pistils of such flowers are functionless in respect to fruit production.

III. Among the flowers that open fully and are capable of functioning in certain relations, various grades of incompatibilities are in evidence, and self-compatibility whenever present is most strong during the period of mid-bloom.

### I. Impotence

(1) Flower abortion.—Frequently in *Brassica pekinensis* the first flowers on the main stalk and often also the first flowers on laterals are completely aborted. The flower buds remain small and do not open, but soon become dead and black. A rather characteristic case of flower abortion is shown in fig. 1, which is of a pot grown plant of *B. pekinensis* blooming in February. Nearly forty of the first flowers of the main branch aborted, after which the flowers were completely formed, normal in appearance, and fully capable of functioning in certain fertilizations. The uppermost lateral branch coming into bloom later than the main axis had only five flowers that aborted, and the next lower lateral had no aborted

flowers. On such plants the lateral branches which come into bloom at the time when the main branch is producing normal flowers as a rule have normal flowers from the first (figs. 1–3). This coordination between flowers opening simultaneously on different branches as to kind of development is very marked. At first view, this abortion of flowers appears to resemble the blasting of flowers which frequently occurs in all sorts of plants as the direct effect of unfavorable environmental influences, but here the phenomenon is due primarily to internal conditions. As grown in the various cultures, the plants came into bloom at various times, some were producing mid-bloom and potent flowers, while other plants by them and just coming into bloom showed flower abortion. The abortion, therefore, is essentially self-induced.

FIG. 1.—Typical case of flower abortion in plant of *Brassica pekinensis;* about forty of first flowers on main axis aborted; there are five such flowers on uppermost lateral and none on second lateral, showing correlation in morphological character according to time of blooming.

Flower abortion of the first flowers is the rule among plants of the varieties of *B. pekinensis* which form leafy heads and which are grown in the field under conditions which favor the development of heads. In such plants, if left to bloom, the flowering branches are at first inclosed within the head. At the time when the flowering branches first come to the light, they are somewhat blanched and tender, and the first flowers are already aborted. This condition of itself suggests that, in this case, temperature and light conditions are important factors which are concerned in the abortion of the first flowers.

FIG. 2.—Chart showing distribution according to dates of flower abortion, self-incompatibility, self-compatibility, and arrested development on main branch and on uppermost lateral with all its laterals; relative sizes of pods indicated; number of seeds per pod given for all but main branch.

Flower abortion, however, is quite pronounced in many plants of *B. pekinensis* grown in pots and in which the head is scarcely developed. In the Nanking variety in which the leaves form only a loose rosette, about one-third of the plants grown have had some

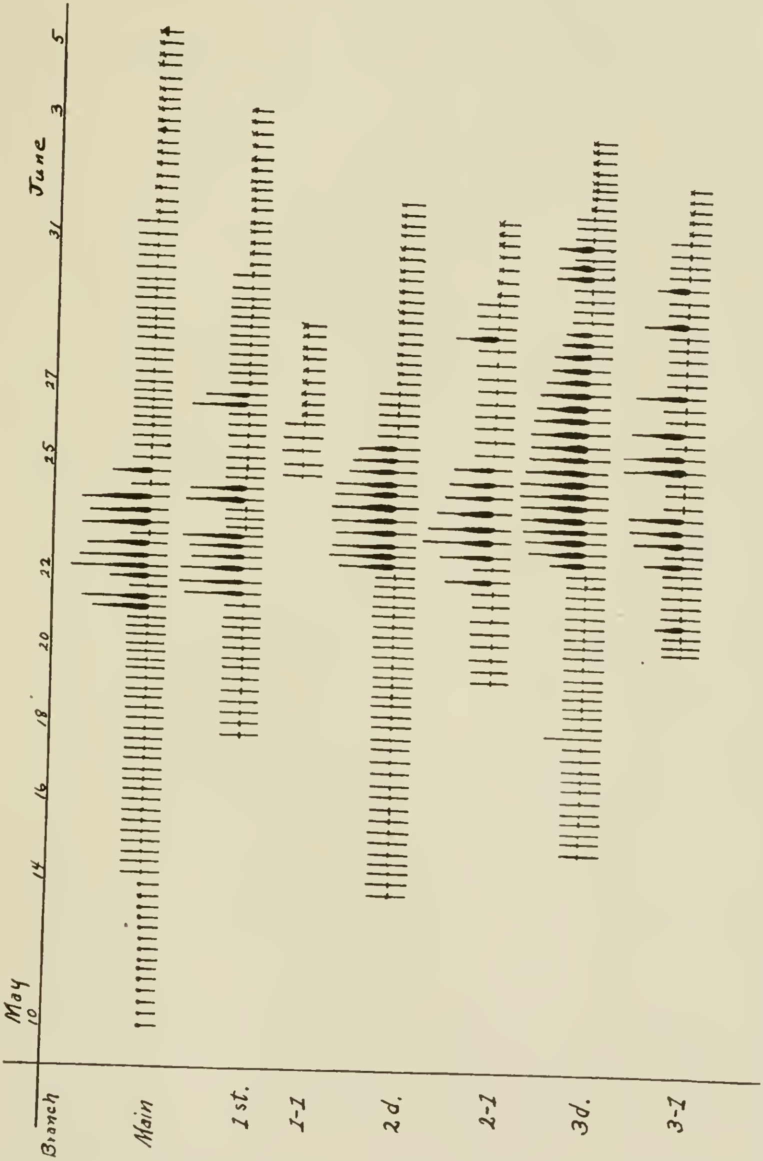

FIG. 3.—Chart for all flowering branches of plant; flower abortion, self-incompatibility, and self-compatibility all cyclic, and each closely coordinated in the various branches according to date of bloom.

aborted flowers, but usually only a few of the first flowers abort. Flower abortion also appears in many plants of *B. chinensis* which have very loose rosettes of leaves.

In these species flower abortion occurs as a transitional stage between a period of vigorous vegetative vigor and a period of flower formation and seed production. The plants which exhibit abortion are not able to pass at once into complete reproductive activity in producing potent flowers. The amount of abortion is greatest in the varieties of *B. pekinensis* in which vegetative vigor is most marked and in which excessive vegetative growth can readily be induced by good cultural conditions and which have been selected and bred for this feature. Flower abortion occurs in numerous plants of these sorts that are grown in pots, as it does in many plants of the loose-leaved kinds, but it apparently tends to be less marked in these.

Flower abortion is here undoubtedly correlated with the degree of vegetative vigor. It is not merely due to a stifling of flowers from simple direct injury because of inclosure within a head, however, but to a constitutional feature of which the formation of a leafy head or rosette is an extreme expression. In this sense the abortion of flowers is self-induced and to some degree hereditary. Usually the transition from aborted flowers to apparently normal flowers is sudden and complete (fig. 1). Sometimes, however, the first flowers to appear after the aborted ones, or the first flowers when there are no aborted ones, are poorly developed, are plainly immature and undersized, and especially in *B. chinensis* there may be premature opening.

(2) ARRESTED DEVELOPMENT OF LAST FLOWERS.—At least some of the last flowers which begin to form remain immature and functionless. In the first of such flowers the corollas wither quickly and may become dry and papery without falling. Then the flowers become smaller in size and more incomplete in development until at last they are mere stubs of tissue. Usually from six to ten flowers in these various stages of arrested development may be counted at the tip of each branch. On short, lower, lateral branches and on secondary or later laterals all of the flowers may fail to develop fully. This condition is shown in the illustrations. The distribution of flowers that fail to develop is indicated in figs. 2 and 3.

This type of sterility, of course, is very common in all sorts of flowering plants, and is clearly associated with old age and death of the entire plants or of the individual flowering branches. In these species of *Brassica* it is unusually conspicuous, and begins to develop when growth has ceased and parts of the plant, especially the basal leaves, are dying or even dead and falling from the plant. Flowers that have aborted or developed poorly at the beginning of the period of bloom, and those in which development is arrested, are all functionless. Their failure to produce fruit is entirely independent of any sort of fertilization. It is clearly due to impotence.

## II. PROLIFERATION

In a few plants of several strains of both *Brassica chinensis* and *B. pekinensis*, noticeable axial proliferations develop. The axis anlage inclosed within the carpels of the pistil grows and branches until it bursts open the pistil. The pedicel of the flower enlarges; the proliferated branch may become several inches long and bear as many as twenty-five flowers, many of which are able to function in seed production. Proliferation may be regarded as the sterilization of a pistil by vegetative growth of the tissue beneath and within it. In the end it is the expression of a tendency to vegetative vigor which culminates in the production of many more pistils and stamens.

Although proliferation is often irregular in its distribution, it is most frequent during the earlier portion of the period of bloom. Frequently it is most highly developed in the first flowers of plants which show little or no flower abortion, but it often does appear later. The last flowers of those which open normally as a rule are free from proliferations. This abnormality is certainly to be regarded as an expression of excess vegetative vigor, as a result of which the axis about which flower parts are grouped resumes active vegetative growth. The stamens in many of the flowers whose axes proliferate seem to be normal, but the pistils are not productive of fruit.

Another type of excessive vegetative vigor is seen in the development of green leaves at the base of each flower, giving a leafy inflorescence. This has only been observed in a few plants, and its possible relation to the production of flowers and to their impotence has not been determined.

## III. Physiological incompatibility

During the phase when the flowers are completely developed, many flowers are produced that are capable of producing pods and seeds. In general the plants produce such flowers in abundance, in succession for a period of about twenty days, and with continuous and rather rapid elongation of branches (cf. fig. 1 with 4 and 6). A free and indiscriminate functioning of the organs in seed production, however, is decidedly limited by incompatibilities in fertilization.

Self-incompatible plants.—Plants may be completely self-incompatible throughout, as was the case for the plant shown in fig. 4. The first six flowers on the main branch aborted, but the very first flowers on the three uppermost laterals were normal. A few flowers at the ends of the branches failed to develop. In all, about seventy flowers on the main branch, forty on each of the first and second laterals, and fifty on the third lateral were capable of functioning. Three lower branches, which bore together about one hundred normal flowers and were like the third lateral in general appearance, were not included in the photograph. This plant grew in isolation in a greenhouse, and self-pollinations were made by hand at least three times a week throughout the period of bloom. At least two hundred flowers were carefully self-pollinated, but not a pod resulted. The pods which were formed on this plant were all from compatible cross-pollinations. Six fine large pods near the base of the main stem were all from flowers that opened rather early; the two first flowers on the first lateral yielded fine pods to a cross; and large pods containing viable seeds were obtained by crossing some of the very last flowers to open normally on the main stem and on the first and second laterals. The stamens were apparently normal throughout the time when flowers opened normally; pollen from many stamens examined at different times was found to be plump and normal in appearance, and the use of pollen in certain crosses covering the entire period of normal bloom resulted in seeds. Such tests have been made repeatedly on numerous plants with results as noted, which show that the failure to set seed to self-pollination is due to a sexual incompatibility between reproductive elements that are capable of functioning in certain other relations.

FIG. 4.—Plant of *B. pekinensis,* completely self-incompatible but producing good pods containing viable seeds to compatible crosses at any time while flowers are fully developed.

FIG. 5.—Feebly self-compatible plant of *B. chinensis;* first two flowers and last to open normally on main axis highly fertile in compatible cross.

A total of 1371 plants of these two species of *Brassica* and hybrids between them have been tested at the time this is written, and of these 653 were found to be completely self-incompatible. Plants were thus classed when no pods developed to selfing at any time throughout the entire period of bloom. There were, however, several grades to be seen in respect to the length of time the pistils remained attached to the plant. In the plant shown in fig. 4, with few exceptions, the pistils of flowers selfed fell soon after the petals had fallen. In other plants, and especially plants of *B. chinensis*, nearly all the pistils of selfed flowers remained attached only during the period of mid-bloom.

Self-compatible plants.—A total of 718 plants of the various cultures grown were self-compatible in some degree. For the purpose of a general classification the self-compatibility was judged as *feeble*, *medium*, and *strong*, but there were many grades within each class with no sharp distinctions between them. The weakest grade includes the cases in which, most typically, a few small pods containing only aborted seeds developed. In some cases pods of good size were formed, as is shown in fig. 5, but the seeds were all

Fig. 6.—Plant of *B. pekinensis*, highly self-compatible during period of mid-bloom; no flower abortion; first flowers to bloom on laterals were self-compatible, showing correlation with main branch in physiological character according to time of bloom.

shriveled and not viable. Such plants were classed as feebly self-compatible. Plants whose self-compatibility was classed as medium produced some viable seeds. The number of pods, the number of shriveled seeds, and to some extent the number of viable seeds varied greatly among plants thus grouped. The plants classed as strongly self-compatible produced numerous pods, and the total number of viable seeds was high. In these also the number of pods, their size, and the numbers of viable and of shriveled seeds varied greatly. The various grades of self-compatibility were seen among sister plants that were as nearly identical as is possible in regard to vegetative vigor, number of branches and flowers produced, and as to calendar dates for period of blooming.

It was readily recognized that the self-compatibility of such plants was most strong during the period of mid-bloom, and that previous to and following this period there was complete self-incompatibility. A highly self-compatible plant grown in isolation and carefully self-pollinated from day to day appeared at the end of the fruiting period, as shown in figs. 6 and 7. Repeated tests by crossings showed that in these, as in the case of the self-incompatible

FIG. 7.—Plant of *B. chinensis;* no flower abortion; plant highly self-compatible; showing cycle of self-compatibility with climax at time of mid-bloom.

plants, the flowers that opened normally during the time of self-incompatibility were functional in compatible crosses. The results of a test of this sort are shown in fig. 5. The cyclic development of self-compatibility with its coordination among the various branches of an individual according to time of bloom is shown in figs. 2 and 3.

There is evidence from other species (SIRKS 10) that various grades of cross-compatibility may exist between the individuals of the same race or species, that the group relations may be variable in different cultures of the same species or race (EAST and PARK 4), and that in general cross-incompatibilities appear with much the same irregularity in heredity and in expression as do self-incompatibilities.

The writer's studies with these plants have been chiefly concerned with self-compatibility. In the species of *Brassica* studied the cross-relations have not been studied sufficiently to state with certainty whether the grades of cross-incompatibility undergo cyclic changes like those of self-incompatibility, but perhaps it may be assumed that certain of the weaker grades of cross-incompatibility do thus operate.

### Heredity of mid-bloom self-compatibility in pedigreed lines of descent

In the first or "parent" series grown of both *Brassica pekinensis* and *B. chinensis*, of a total of 253 plants there were 21 plants that produced viable seeds to self-pollination during the period of mid-bloom. From such seeds pedigreed progenies were grown through two generations, to test the inheritance of self-compatibility and to determine the result of repeated selection for this character. A summary of the records for the various series and families grown to date is presented in table I. In these records the first series of plants grown are given arbitrary numbers. The number of a series with that of the self-compatible plant used as a seed parent is employed in designating the series of succeeding generations. Thus the line of descent and the relationship of the various series of sister plants are fully indicated.

In one series of the selfed $F_1$ generation of *B. pekinensis* (series 1–2) comprising 88 plants, 24 were strongly self-compatible. In

## TABLE I

RECORDS OF SELF-COMPATIBILITY FOR FAMILIES OF *Brassica pekinensis*, OF *B. chinensis*, AND OF HYBRIDS BETWEEN THESE SPECIES

| ANCESTRY, GENERATION, AND SELF-COMPATIBILITY OF PARENT | RECORD FOR PROGENY | | | | |
|---|---|---|---|---|---|
| | Total number of plants | Number self-incompatible | Self-compatible | | |
| | | | Feeble | Medium | Strong |
| Brassica pekinensis | | | | | |
| P series 1, seeds of S.P.I. no. 44892 | 9 | 7 | 0 | 1 | 1 |
| P series 2, seeds of S.P.I. no. 44935 | 10 | 6 | 2 | 1 | 1 |
| P series 3, seeds of S.P.I. no. 44291 | 20 | 19 | 0 | 1 | 0 |
| P series 4, seeds of S.P.I. no. 44312 | 12 | 9 | 1 | 0 | 2 |
| P series 5, seeds of S.P.I. no. 44292 | 8 | 8 | 0 | 0 | 0 |
| P series 34, seeds of S.P.I. no. 38783 | 114 | 67 | 45 | 2 | 0 |
| P series 15, seeds of S.P.I. no. 45187 | 61 | 55 | 5 | 1 | 0 |
| $F_1$ series 1–2, parent strongly self-compatible | 88 | 25 | 19 | 20 | 24 |
| $F_1$ series 2–1, parent strongly self-compatible | 7 | 7 | 0 | 0 | 0 |
| $F_1$ series 3–1, parent medium self-compatible | 80 | 43 | 27 | 7 | 3 |
| $F_2$ series 1–2–9, parent strongly self-compatible | 36 | 5 | 19 | 9 | 3 |
| $F_2$ series 1–2–18, parent strongly self-compatible | 133 | 14 | 99 | 18 | 2 |
| $F_2$ series 1–2–29, parent strongly self-compatible | 46 | 24 | 21 | 1 | 0 |
| $F_2$ series 1–2–38, parent strongly self-compatible | 60 | 1 | 43 | 15 | 1 |
| $F_2$ series 3–1–1, parent strongly self-compatible | 19 | 15 | 2 | 2 | 0 |
| $F_2$ series 3–1–9, parent strongly self-compatible | 16 | 10 | 6 | 0 | 0 |
| $F_2$ series 3–1–32, parent strongly self-compatible | 18 | 12 | 6 | 0 | 0 |
| Brassica chinensis | | | | | |
| P series 8 | 19 | 4 | 4 | 8 | 3 |
| $F_1$ series 8–1, parent strongly self-compatible | 111 | 42 | 56 | 12 | 1 |
| $F_1$ series 8–5, parent medium self-compatible | 48 | 43 | 3 | 2 | 0 |
| $F_1$ series 8–6, parent strongly self-compatible | 57 | 28 | 26 | 2 | 1 |
| $F_1$ series 8–15, parent strongly self-compatible | 122 | 40 | 74 | 7 | 1 |
| $F_2$ series 8–1–13, parent strongly self-compatible | 13 | 7 | 5 | 1 | 0 |
| $F_2$ series 8–5–32, parent medium self-compatible | 18 | 7 | 10 | 1 | 0 |
| $F_2$ series 8–5–39, parent medium self-compatible | 9 | 7 | 1 | 1 | 0 |
| $F_2$ series 8–15–5, parent strongly self-compatible | 48 | 30 | 16 | 2 | 0 |
| $F_2$ series 8–1, no. 39×8–1 no. 32 (medium×medium) | 30 | 23 | 7 | 0 | 0 |
| $F_2$ series 8–5, no. 39×8–5 no. 41 (medium×self-sterile) | 32 | 15 | 17 | 0 | 0 |
| $F_2$ series 8–5, no. 30×8–5 no. 17 (both self-sterile) | 16 | 15 | 1 | 0 | 0 |
| $F_2$ series 8–5, no. 27×8–5 no. 32 (self-sterile×medium) | 8 | 7 | 0 | 1 | 0 |
| Brassica chinensis×B. pekinensis | | | | | |
| $F_1$ 8–5, no. 23×2 no. 3 (both self-incompatible) | 19 | 19 | 0 | 0 | 0 |
| $F_1$ 8–5, no. 19×3 no. 16 (both self-incompatible) | 34 | 27 | 5 | 2 | 0 |
| $F_1$ 8–5, no. 18×3–1 no. 63 (medium×self-sterile) | 50 | 12 | 14 | 19 | 5 |

the next generation of this family, the progeny of four strongly self-compatible plants, 275 plants were grown. Of these only 44 were completely self-incompatible. There were, however, only 6 plants as highly self-compatible as the immediate seed parents. The majority of the plants (182 in number) were feebly self-compatible and did not produce any viable seeds to selfing. This family, however, was somewhat more highly self-compatible than was the family derived from plant no. 1 of series 3, in the second generation of which only 2 plants out of 53 produced viable seeds to selfing.

Selection for the highest grades of self-compatibility in *B. chinensis* was also carried through the second generation. In the $F_1$ generation, 26 out of 338 plants produced viable seeds to selfing. In the $F_2$, 5 out of 88 plants produced such seeds. The proportion of self-compatible plants was low and remained about the same, not being appreciably increased or decreased in the second generation. No plants classed as highly self-compatible were found in the $F_2$, but this may have been due to the proportionally smaller number of plants grown in this generation.

Four series comprising 86 plants were grown from seeds obtained by crossing certain plants of the $F_1$. Of these, 25 were feebly self-compatible and one plant produced viable seeds. The $F_1$ hybrids between the two species exhibited the three types of sterility characteristic of the parent species. There was no indication of a general impotence of both sex organs (pistils and stamens) such as often results from hybridity. During the time when flowers opened normally, branches left to open pollination produced pods and viable seeds, and about 100 plants of this generation grown in the field and left to open cross-pollination produced pods in abundance.

As to mid-bloom self-compatibility, the $F_1$ hybrids were like the pure bred parents. Relatively few were highly self-compatible. In one series, derived from crossing a plant of a medium grade self-compatibility and one completely self-incompatible, of 50 plants, 12 were fully self-incompatible, 14 were feebly self-compatible, 19 were self-compatible of medium grade, and 5 were highly self-compatible. Two series were grown from parents that were self-incompatible. In one of these all of the 19 progeny were self-incompatible; in the other series of 34 plants 27 were fully self-incompatible, 5 were feebly self-compatible, and 2 were self-compatible of medium grade during the period of mid-bloom.

SUMMARY.—The results obtained in these various pedigreed cultures show that self-compatibility is a character which is not directly hereditary. Self-compatibility occurs sporadically in a few members of these prevailing self-incompatible species. This character does not breed true. Selection for self-compatibility does not immediately lead to the establishment of self-compatible races. Neither is self-compatibility nor self-incompatibility dominant in crosses. There is some indication, however, that certain races may be secured in which the mode of distribution in respect to self-compatibility is higher than in others.

## Discussion and conclusion

The strains of *Brassica pekinensis* and *B. chinensis* studied were previously selected and bred for excessive leafy growth rather than for fruit and seed production, yet they are reproduced exclusively by seeds. The vegetative vigor is not in the least utilized in the development of parts which may propagate the plants vegetatively. In their habit of growth and bloom, the stage of sexual reproduction in these plants quickly follows a period of remarkably vigorous vegetative development, hence these species are favorable material in which to study the correlative relations of the asexual or the vegetative phase to the sexual or reproductive (by seeds) phase in the complete life cycle.

The two types of sterility, impotence (including flower abortion and arrested development), and proliferation, or the destruction of a pistil by vegetative growth, as they occur in *B. pekinensis* and *B. chinensis*, are both phenomena associated with the formation of floral organs. The other type of sterility, physiological incompatibility or relative sterility which is present, is concerned with the physiological inter-relations of the sex organs in the various processes of fertilization.

These three types of sterility develop and operate in these two species and in their hybrids in intimate correlation with the cyclic alternation of vegetative and reproductive vigor. Flower abortion occurs normally as a transitional stage between the formation of green leaves and the production of functional sporophylls. Those plants which exhibit flower abortion are not able to pass directly from producing green leaves or leaves with branches at the nodes to the production of flowers, and flower abortion occurs as a transitional stage. The abortion of flowers appears in the phase where vegetative vigor is waning, but before reproductive vigor is fully in evidence. There is also a marked agreement among the various branches of a plant as to the grade of development reached at any one date of blooming (figs. 1–3), which indicates a definite relation between the condition causing flower abortion (and also normal flower formation) and a condition of the plant as a whole. These phenomena, therefore, have many aspects characteristic of physiological correlation.

The arrested development of flowers at the ends of branches after a period of vigorous blooming of the plant is obviously due to an extreme waning of vigor and the approaching death of the plant as a whole, and of course is a phenomenon prevalent in all sorts of plants. Axial proliferation from the pistils is to be considered as a resumption of vegetative growth after the differentiation of the pistils has been accomplished.

Turning to the functional relations of the sex organs in these two species of *Brassica*, at least to the compatibility in self-fertilization, it is seen that they also exhibit a periodicity on their occurrence which forms a very definite cycle. A total of 718 plants that were self-compatible to some degree have now been observed in these two species and in hybrids between them. With the exception of a few individuals in which pods developed irregularly, the maximum of self-compatibility was reached during the mid-bloom of the plant (figs. 2, 3, 5–7). Previous to and following this period, the self-compatibility grades into complete self-incompatibility or into a much weaker grade of self-compatibility. Furthermore, the climax of self-compatibility is remarkably coordinated among the different branches according to the time of blooming quite as is the earlier development of flower abortion.

The remarkably uniform development of self-compatibility during the time of mid-bloom in *Brassica chinensis*, *B. pekinensis*, and hybrids between them, is convincing evidence that the functions of fertilization are here operating in a cycle of intensities. The period of mid-bloom may be considered as the time when conditions are most favorable for fertilization. The cross-fertilizations which are highly effective both previous to and following the maximum for self-compatibility are hence to be considered as indicating a different and possibly a stronger grade of sexual relation. It seems conclusive that, judged by the functional relations in fertilization, the physiological properties of the sex organs in these plants vary in a rather definite cycle.

It is clear that self-compatibility as contrasted with certain grades of cross-compatibility in these species of *Brassica* is limited to a specific period following the transition from vegetative to reproductive activity and limited by the waning senility of the plant as a whole. Self-compatibility appears coincidently with the climax of the reproductive activity.

Sexual reproduction itself is generally characterized as a phenomenon of maturity (COULTER 3). The differentiations of sex as indicated by anatomical features and by the physiological compatibilities are perhaps to be considered as a smaller cycle operating within the larger alternation of vegetative and reproductive phases and subject to the same biogenetic regulation.

In the flowering plants especially, there is great diversity among species in the relative development of their vegetative and reproductive habits and in the inter-relations between these two phases. Perhaps the most universal of the biogenetic conditions incident to the transition from the vegetative to the reproductive phase is that change in nutrition which leads to the accumulation of carbon compounds. This is an internal condition that arises in the plant as a whole in the course of maturity, in contrast with relative excess of nitrogenous material that is characteristic of the vegetative stage. The decided influence of nutritive relations in regulating development and in influencing fruitfulness has recently been discussed by KRAUS and KRAYBILL (7), who have emphasized the fact that a well-balanced development, especially in regard to fruitfulness of fruit-bearing plants, is associated with a proper balance between nitrogen and carbohydrate metabolism.

It is not to be considered, however, that a single simple change in nutrition is the sole biogenetic factor regulating the appearance of maturity and its attending morphogenesis of flowers. In flowering plants, such as the species of *Brassica* whose sterilities are reported in this paper, there is progressive differentiation of parts in reference to metabolic activities which is most obvious in respect to the manufacture, distribution, and consumption of food. It has been shown that there are also special stimulating and inhibiting influences which in a decided manner regulate and correlate development. That these influences may be substantive and special (but metabolic) and different from food materials was postulated by SACHS (8) in one of the latest of his papers; that some influences are stimulative and correlative in the sense of nervelike impulses or even electrical stimuli have repeatedly been shown in studies of the nature of transmission and excitation in phenomena of dominance and control in correlative growth and development (CHILD 1).

It is to be noted that the complete life cycle of flowering plants involves two periods of vegetative vigor and maturity; one for the sporophyte and one for the gametophyte. The former culminates in the production of spores and the latter in the production of gametes. The generations are antithetic. In its length of life, vigor of vegetative growth, and reproductive power (number of gametes), the gametophytic phase has become relatively weak and highly specialized. In the sporophyte great vegetative vigor is correlated with great reproductive vigor in the production of spores (which are, however, in themselves asexual) and in the nurture of the gametophyte and the embryo. Sex differentiation in the great group of flowering plants has been pushed back during the progress of evolution into the sporophytic stage of the entire cycle, and here sexuality now culminates in seed formation in which the nutrition of the embryo is a most important factor. Sexual reproduction in these higher plants has become more and more inter-related with the vegetative phase of the sporophyte and subject to its internal and biogenetic regulation.

The decided influence of such regulation is seen in the fact that in the great group of hermaphrodite plants, the whole trend of the morphological and physiological differentiations constituting sexuality is initiated in the morphogenesis of flowers. The cells of pistils and stamens are not only alike in their preformed genetic composition, but they are identical in this particular with the cells that entered into the preceding vegetative structures. CORRENS (2) has noted that the regeneration from sister cells of the egg and sperm (the archegonial and antheridial cells) in certain monoecious mosses shows that, at least in hermaphrodites and monoecious plants, maleness and femaleness are carried equally by both male and female gametes. The male gametophytes and their most highly specialized male cells are male only because of a temporary suppression of femaleness. Likewise the femaleness of egg cells is a temporary and one-sided expression of cells carrying both sex potencies. The various expressions of maleness and femaleness even in the sex generation, at least in hermaphrodite plants, according to CORRENS, are "phenotypic" or biogenetic expressions independent of any qualitative differentiation in the component units of the germ plasm. The expressions of the so-called factors for sex or the so-called inhibitors of one or the other sex are hence independent of corresponding differentiations in germ plasm which may have arisen during sporogenesis. The expression of sex, therefore, is on the same basis as are the somatic differentiations that arise among the various parts of the individual. It hence becomes a most fundamental biological problem to consider and to determine as far as possible what conditions determine these differences in the level of the so-called "physiological gradient."

Maturity, with its transition from the vegetative to the reproductive phase, whether giving homologous or antithetic alternation or a continuation of either, occurs in cycle after cycle with remarkable uniformity. This emphasizes the phylogenetic or hereditary aspect of particular phases of the development. One may assume a "gene" or a "factor" for maturity, and assume that it is gradually awakened from a dormant condition to the exercise of its influence at a particular time and in a particular group of cells. One may further assume that the loss of such a gene would throw a line of progeny into a condition of perpetual immaturity, so that flowers or other reproductive organs could never be formed. The evidence is decidedly against such a view. The loss of maturity, as seen especially in the complete failure of flower formation, has very universally been shown to be due to the indirect influence of such external factors as light, heat, and nutrition on the metabolism and attending correlations in the organism (see numerous papers by MÖBIUS, VÖCHTING, KLEBS, SACHS, and GOEBEL, and recent papers by GARNER and ALLARD 5 and 6, and by SETCHELL 9).

That species or strains showing flower abortion and physiological incompatibility are different genetically from others that do not show such sterilities is obvious. That these types of sterility are more completely hereditary in some species than in others is clear. That these characteristics are not definitely and directly represented as such in the germ plasm by hereditary units is very evident from the results of genetical studies. Self-compatibility and self-incompatibility especially are not found to be alternative conditions in tests by crossing or in line breeding; the heredity is decidedly irregular and sporadic even when compatibilities are not cyclic in their appearance as they are in *Brassica chinensis* and *B. pekinensis*.

The various types of sterility seen in these species of *Brassica* decidedly indicate a mutually limiting relationship between vegetative and reproductive vigor. Their irregular inheritance, their appearance at definite periods in the cycle of development of the plant as a whole, and especially the cyclic manifestation of self-compatibility, indicate that the morphological and physiological differentiations of sex are regulated and determined by those internal and biogenetic processes which in general determine the cycle of growth, development, and maturity in the life of the individual.

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# STUDIES OF WEST INDIAN PLANTS—XI

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# Studies of West Indian plants---XI

Nathaniel Lord Britton

## 64. UNDESCRIBED SPECIES FROM CUBA

### **Juniperus saxicola** Britton & Wilson, sp. nov.

A densely branched small tree, 3–8 m. high. Leaves all subulate-acicular, subimbricate, somewhat spreading, 4–7 mm. long, about 1 mm. broad at the base, lustrous; fruit blue, broadly ellipsoid or subglobose, 5 mm. long, 3–4 mm. in diameter.

On rocks, crest of Sierra Maestra, Oriente (*Léon 10798*, type); also collected on Farallones de Regino, Estribo Turquino (*Léon 11024*).

### **Myrica cacuminis** Britton & Wilson, sp. nov.

A shrub, 3–4 m. high, much branched, the slender twigs densely pilose. Leaves elliptic to suborbicular, 7–18 mm. long, short-petioled, sharply few-toothed or entire, coriaceous, pinnately few-veined, pubescent on both sides, the apex rounded, the base rounded or obtuse; flowers and fruit not seen.

Pico Turquino, Oriente (*Léon 10973*, type; *Bucher 19*).

### **Pilea ovalifolia** Britton & Wilson, sp. nov.

Stems creeping, rather stout, rooting at the nodes. Leaves chartaceous, elliptic, obtuse or rounded at the apex, rather coarsely crenate, pinnately 3-nerved, glabrous, those of each pair often unequal in size; larger leaves up to 5.5 cm. long, 3.4 cm. wide, with petioles 1.5–3 cm. long; smaller leaves 2.5–4 cm. long, 1.5–2.6 cm. wide, the petioles 1–2 cm. long; upper leaf-surface densely covered with minute linear raphides, the lower surface papillose; pistillate inflorescence longer than the leaves, peduncled, its branches spreading; achenes ovate, about 0.9 mm. long.

Sierra Maestra, Oriente (*Léon 10767*).

### **Pilea membranacea** Britton & Wilson, sp. nov.

Stem slender, puberulent. Leaves membranous, lanceolate to ovate, acuminate, coarsely toothed, 3-nerved, glabrous, those of each pair unequal in size; larger leaves up to 5 cm. long, 1.8 cm. wide, with slender petioles 0.7–1 cm. long; smaller leaves 1–2 cm. long, 0.6–1 cm. wide, the petioles 2–4 mm. long; upper leaf-surfaces covered with minute white linear raphids, those of

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the lower surface rather inconspicuous; pistillate inflorescence slender, longer than the leaves; achenes elliptic, 1 mm. long.

Sierra Maestra, Oriente (*Léon 10815*).

**Pilea micromeriaefolia** Britton & Wilson, sp. nov.

Stems elongate, woody, procumbent, the branches erect or ascending, 4-angled, scaly encrusted. Leaves in whorls of 3's or 4's, lanceolate, 0.8–1 cm. long, about 2 mm. wide, acute at the apex, obtuse at the base, glabrous, the petioles 1 mm. long or less; upper leaf-surfaces covered with linear raphides, those on the lower surface coarser; inflorescence not seen.

Brecha de Regino, Estribo Turquino, Oriente (*Léon 11008*).

**Pilea yarensis** Britton & Wilson, sp. nov.

An erect monoecious herb, 2–3.5 dm. high. Leaves membranous, broadly elliptic, acuminate at the apex, acute at the base, crenate-dentate, 3-nerved, glabrous above, often slightly pubescent on the midvein beneath, those of each pair unequal in size; larger leaves up to 15 cm. long, 6 cm. wide, with slender petioles sometimes 3.5 cm. long; smaller leaves up to 11 cm. long, 5 cm. wide, with petioles 1–2 cm. long; upper leaf-surface papillose, densely covered with linear raphides, those of the lower surface often indistinct; staminate inflorescence equalling or longer than the leaves, the peduncles sometimes 1 dm. long, the branches spreading, the perianth about 1.5 mm. long; pistillate inflorescence equalling or shorter than the leaves; achenes elliptic, 0.8 mm. long.

Bank of the Yara River, Sierra Maestra, Oriente (*Léon 10736*).

**Pilea ermitensis** Britton, sp. nov.

Stems slender, densely covered with linear raphides. Leaves oblong, oblong-lanceolate or elliptic, membranous, acute, entire, 3-nerved, glabrous, those of each pair unequal in size; larger leaves up to 3 cm. long, 6–7 mm. wide, with petioles 3 mm. long; smaller leaves 1–1.7 cm. long, 4–5 mm. wide, the petioles short; raphides of the upper leaf-surface minute, linear-filiform, those of the lower surface scattered, more conspicuous and stouter; inflorescence often shorter than the petioles, the flowers borne in globose heads 1.5–2 mm. in diameter; achenes elliptic-ovate, about 0.5 mm. long.

La Ermita, Oriente (*Hioram 4921*).

**Pilea crenata** Britton & Wilson, sp. nov.

Stem creeping, often rooting at the nodes, the branches erect or ascending, pilose. Leaves chartaceous, oval to suborbicular, rounded at the apex, rounded or acute at the base, crenulate, 3-nerved, glabrous above, pilose on the nerves beneath, those of each pair often unequal in size; larger leaves up to 3 cm. long, 2.5 cm. wide, with slender petioles 1.5–2 cm. long; smaller leaves 1–2 cm. long, 1–2 cm. wide, the petioles 0.7–1 cm. long; upper and lower leaf-surfaces densely covered with linear raphides; pistillate inflorescence as long as or shorter than the leaves: achenes about 0.6 mm. long.

Sierra Maestra, Oriente (*Léon 10766*, type; *Léon, Clement and Roca 9872*).

**Coccolobis monticola** Britton, sp. nov.

Branches slender, glabrous; young twigs pubescent. Ocreae cylindric, 1 cm. long or less; leaves coriaceous, light green, 3–6 cm. long, reticulate-veined on both sides, shining above, dull and black-dotted beneath, the apex acute, the base obliquely obtuse, the petioles about 2 mm. long; racemes very slender, glabrous, densely many-flowered; ocreolae subtruncate, about 0.5 mm. long; pedicels glabrous, about 1 mm. long; calyx about 1 mm. long.

Sierra Maestra, Oriente (*Léon 10713*).

**Coccolobis saxicola** Britton, sp. nov.

A shrub about 3 m. high, glabrous throughout, the twigs short, stout, more or less tortuous. Ocreae subtruncate, 4–6 mm. long; leaves coriaceous, elliptic to obovate, 9 cm. long or less, the veins somewhat impressed above, prominent beneath, reticulate-veined on both sides, the apex abruptly short-acuminate, the base narrowed or obtuse, the petioles 5–15 mm. long; fruiting racemes slender, solitary, 6–9 cm. long; pedicels numerous, about 1.5 mm. long; ocreolae truncate, less than 1 mm. long, subpapillose, the sepals ovate.

On rocky crest in woods, Loma del Gato, Cobre Range of Sierra Maestra, Oriente (*Léon, Clement and Roca 10167*).

**Talauma** (?) **orbiculata** Britton & Wilson, sp. nov.

Tree 6–8 m. tall, with glabrous branches. Leaves orbicular, 8–12 cm. in diameter, rounded or subtruncate at the apex, rounded or truncate at the base, glabrous and prominently reticulate-veined on both sides, the midrib flat above, prominent beneath, the petioles rather slender, 3–6 cm. long, flat or shallowly grooved above, glabrous; sepals broadly elliptic, 2.6 cm. long, 2–2.3 cm. broad; petals thick, oblong or elliptic, about 2 cm. long, 0.8–1 cm. wide; carpels tomentulose.

Loma de Quintin, Nagua, Oriente (*Léon 10955*).

**Persea anomala** Britton & Wilson, sp. nov.

A shrub or tree, sometimes 10 m. tall, with appressed-pubescent twigs. Leaves lanceolate to ovate or elliptic, 4–10 cm. long or less, 1.8–5.5 cm. broad, rounded, obtuse, or acutish at the apex, rounded or somewhat acutish at the base, glabrous and reticulate-veined on both sides, the petioles slender, 1–1.8 cm. long; branches of the inflorescence pubescent with appressed hairs; calyx pubescent, greenish, its lobes unequal, the outer broadly ovate, about 1 mm. long, 0.7 mm. broad, the inner elliptic or broadly ovate, 1.7–2 mm. long, 1.5–1.7 mm. broad; berry subglobose, 11 mm. long, black.

Sierra Maestra, Oriente (*Léon 10707*, type; *10975; 10976; 10079; 11057*).

**Persea similis** Britton & Wilson, sp. nov.

Twigs appressed-pubescent. Leaves elliptic, 4–7 cm. long, acute or short-acuminate at the apex, acute at the base, dark green and glabrous above, the midvein impressed, paler beneath and pubescent with short appressed hairs, the lateral veins rather indistinct on both sides; petioles 3–4 mm. long; inflorescence pubescent with appressed brownish hairs; calyx-lobes elliptic to oval, 1.8 mm. long, about 1 mm. broad, appressed-pubescent.

Sierra Maestra, Oriente (*Léon 11058*).

**Nectandra reticularis** Britton & Wilson, sp. nov.

A shrub with pubescent twigs. Leaves elliptic-lanceolate, 3.5–6.8 cm. long, 1–2.3 cm. broad, acute to acuminate at the apex, acute at the base, glabrous, dark green, shining and reticulate-veined above, paler and reticulate-veined beneath; petioles 7 mm. long or less; inflorescence long-peduncled, the peduncle puberulent; flowers short-pedicelled; calyx white, its lobes elliptic, 1.5 mm. long, about 1 mm. broad, puberulent; drupe ellipsoid, about 1.1 cm. long, 6 mm. in diameter.

Sierra Maestra, Oriente (*Léon 10746*, type; *10958*).

**Rubus turquinensis** Rydberg, sp. nov.

Stem terete, 1–2 m. high, densely fuscous, villous-tomentose and with numerous stalked glands, armed with somewhat compressed curved pubescent prickles 4–8 mm. long; leaves of the branches 3-foliolate, those of the main stem not seen; petiole and ribs of the leaflets villous-tomentose, glandular, and slightly prickly; petiolule of the terminal leaflet 7–15 mm. long, those of the lateral leaflets 1–4 mm. long; leaflets lanceolate, long-acuminate, mostly rounded at the base, finely and closely serrate, 3–10 cm. long, dark-green, sparingly pubescent and somewhat glandular-granuliferous above, paler and somewhat fuscous and densely short-villous, almost subvelutinous, beneath; racemes 3–6 cm. long, 5–10-flowered; peduncles and pedicels densely pubescent and glandular, slightly prickly; sepals lanceolate, acuminate, 5–6 mm. long, glandular and pubescent without, grayish-tomentose within; berry about 1 cm. long and 7–9 mm. thick; drupelets many, glabrous.

Type collected on the top of Pico Turquino, Oriente, Cuba, July 23, 1922, *Léon 10755* (New York Botanical Garden); also at an altitude of 1600 m. on the same mountain, *10756*.

*R. turquinensis* is a member of the *Adenotrichi*, differing from *R. costaricanus* and *R. adenotrichos* in the narrower lanceolate long-acuminate, instead of broadly ovate, abruptly acuminate leaflets; from *R. Vera-Crucis* in the more dense pubescence and the texture of the leaves. It is more closely related to *R. irasuensis* and *R. miser*. In habit, leaf-form, and pubescence it resembles the former, but the inflorescence is mostly simple, the sepals narrower, and the drupelets perfectly glabrous; neither have any 5-foliolate leaves been seen. From *R. miser* it differs in the shorter sepals and the thicker leaflets, with shorter petioles, more numerous and more prominent lateral veins, and much closer serrations.

### **Polygala scabridula** Blake, sp. nov.

Virgate leafy shrub 2–3 m. high, the branches erect, hispidulous. Petioles hispidulous, 2 mm. long; leaf blades obovate, 1.3–1.8 cm. long, 9–12 mm. wide, broadly rounded at apex, rounded or cuneate-rounded at base, coriaceous, scabrid-hispidulous above with persistent ascending hairs, similarly pubescent beneath; racemes axillary, the axis few-flowered, about 1 mm. long, the peduncle obsolescent; pedicels glabrous, 1.2 mm. long; flowers immature; sepals deltoid-ovate, ciliolate, obtuse, 1.1 mm. long; wings similar, 1.4 mm. long and wide; keel ciliate, otherwise subglabrous, 2.5 mm. long; capsule subquadrate, rather broadly margined, slightly wider at the apex, ciliolate, otherwise glabrous, 6 mm. long, 8.5 mm. wide, lobed for about 1/3 its length; seed ellipsoid, sparsely pubescent, 4 mm. long; aril orange, 1.8 mm. deep, with repand lateral margin, the dorsal lobe 1 mm. long.

Sabana de Motembo, Santa Clara, August 9–10, 1920 (*Léon and Loustalot 9333*).

This species is related to *Polygala portoricensis* (Britton) Blake, of Porto Rico, which has larger emarginulate leaves, and a smaller, less deeply lobed capsule.

**Polygala rhynchosperma** Blake, sp. nov.

Slender erect annual, 14–25 cm. high, simple or few-branched above, evenly but not densely puberulous with short, thickish, incurved or subappressed eglandular hairs. Leaves alternate except for 1 or 2 basal whorls, rather crowded, short-petioled, the blades linear, 6–14 mm. long, 0.5–1.3 mm. wide, acute, cuspidulate, 1-nerved, sparsely puberulous like the stem, erect; peduncles 5–15 mm. long; racemes slender, cylindric, gradually narrowed to an obtuse apex, loose below, 2–9 cm. long, the axis becoming 10.5 cm. long and more, puberulous like the stem; bracts oval or obovate, caducous, 1.5 mm. long, puberulous at base, with rather short abrupt caudate purplish tips; pedicels glabrous, 1 mm. long, clavellate; sepals pinkish white with greenish center, glabrous, the upper oval-ovate, obtuse, 1.5 mm. long, the 2 lower oblong, obtuse, 1.2–1.5 mm. long, sometimes obscurely 1-denticulate on each side near apex; wings pinkish (when dried), obovate, 3 mm. long, 1.5 mm. wide, rounded or obtuse, scarcely clawed, 3-nerved; upper petals slightly shorter than keel, the free portion obliquely ovate, obtuse, 3-nerved; keel 3–3.2 mm. long, slightly surpassing the wings, the crest on each side of a deeply trifid lamella and a 2- or 3-fid or 2-parted lobe with linear segments; capsule pendulous at maturity, slightly surpassing the wings, elliptic-oblong, emarginate, 3.3 mm. long, 1.5 mm. wide; seeds subcylindric, 2.2 mm. long, densely short-pilose, distinctly rostrate at base (beak conic, 0.4 mm. long); aril fastened to upper half of beak, 0.7 mm. long, the 2 lobes rhombic, acute or obtuse, appressed; stigma with short blunt retrorse lower lobe and substipitate penicillate upper lobe.

Sabana del Cerro, near Zarzal, Oriente, July, 1922 (*Léon 10990;* type No. 1,049,981, U. S. National Herbarium).

Among North American species *Polygala rhynchosperma* is nearest *P. paniculata* L., which is densely stipitate-glandular and has shorter wings and an erostrate seed. The Venezuelan *P. Funkii* Chod., known to me only from Chodat's description and figures, is evidently closely related, having similar bracts, seed, and stigma. It is described as glabrous, with acute lance-elliptic sepals, acute wings, and a crest composed on each side of an acute triangular entire lamina and an undivided linear lobe.

**Polygala ambigens** Blake, sp. nov.

Stems usually solitary from a slender but evidently perennial root, simple or sparsely branched, 3.5–6 dm. high, very slender, glabrous throughout or sparsely incurved-puberulous on the younger parts; leaves alternate, linear or linear-filiform, 9–25 mm. long, 0.5–1.5 mm. wide, cuspidulate, short-petioled, 1-nerved, the margins often inflexed; peduncles 5–10 mm. long; racemes loosely many-flowered, the axis sometimes becoming 25 cm. long; bracts subulate, 1.5 mm. long, caducous; pedicels glabrous, 1.5–2 mm. long; sepals bearing 3–6 pairs of stipitate glands, sometimes also ciliolate with eglandular hairs toward apex, the upper sepal 2 mm. long, the lower sepals (connate nearly to apex) 1.5 mm. long; wings magenta-purple, broadly and obliquely cuneate-obovate, 3.8–4.5 mm. long, 2.8–3.2 mm. wide, subsessille or short-clawed, emarginate at apex, glabrous, about 5-veined, the veins loosely anastomosing, not at all prominulous; upper petals magenta-purple; keel yellow-tipped, becoming 4 mm. long; capsule 3.8 mm. long, 2.4 mm. wide, slightly shorter than the mature wings; seed densely pilose, 2.8 mm. long; aril sparsely pubescent on the sides, 0.8 mm. high.

Sabana del Cerro, near Cerro Pelado, between Zarzal and Nagua, Oriente, July, 1922 (*Léon 10860;* type No. 1,049,889, U. S. National Herbarium).

Nearly related to *Polygala cubensis* Chod., which is an annual with shorter sepals (1.1–1.3 mm. long), and somewhat smaller wings shorter than the capsule. In its slender but evidently perennial root resembling *P. Wrightii* Chod., which is densely incurved-puberulous and has the sepals ciliate with eglandular hairs. Much more material of the Cuban representatives of this group (section *Adenotricha* of subgenus *Hebeclada*) must be accumulated before the specific characters can be established satisfactorily.

### **Maytenus saxicola** Britton & Wilson, sp. nov.

A glabrous shrub, 4 m. high, with rather stiff, somewhat flexuose twigs. Leaves elliptic to elliptic-ovate, rigid-coriaceous, 3–6 cm. long, 1.5–3.3 cm. broad, obtuse or rounded at the apex, a cute at the base, dark green above, paler beneath, the midvein elevated on both sides, the lateral veins often rather indistinct, the margin minutely crenulate; petioles 5 mm. long or less; pedicels slender, up to 7 mm. long; capsule globose-obovoid, 8 mm. long, 7–8 mm. in diameter.

On rocks, Sierra Maestra, Oriente (*Léon, Clement and Roca 10221*).

### **Rhamnidium bicolor** Britton & Wilson, sp. nov.

A shrub, with slender puberulent twigs. Leaves opposite, elliptic or ovate-elliptic, 8 cm. long or less, repand-crenate, membranous, the apex acuminate, the base rounded or subtruncate, the venation ascending, densely and finely reticulate-veined on both sides, the upper surface green and glabrate, the under side whitish puberulent, the petioles 6–10 mm. long; stipules obliquely linear-lanceolate, nearly as long as the petioles; inflorescence axillary, glabrous; peduncles nearly as long as the petioles; flowers subglomerate; pedicels very short; sepals triangular-ovate, 2.5 mm. long, acute; glandular-dotted; petals orbicular-obovate, 1.5 mm. long, about 1.5 mm. broad.

High Sierra Maestra, Oriente (*Léon 11025*). Other specimens from the Sierra Maestra (*Léon 10952*), in foliage only, have entire leaves, somewhat larger, and may represent another species.

**Ouratea xolismaefolia** Britton & Wilson, sp. nov.

A glabrous shrub, with slender terete twigs. Leaves oblong, elliptic, or elliptic-obovate, coriaceous, 3 cm. long or less, the midvein prominent, the lateral venation delicate and nearly obscure, the apex rounded or emarginate, the base narrowed or cuneate, the petioles 1–2 mm. long; pedicels slender, 5–6 mm. long, sepals elliptic to oval, 3 mm. long; petals obovate, 4–4.5 mm. long, 3 mm. broad, rounded or truncate at the apex; anthers 3 mm. long.

High Sierra Maestra, Oriente (*Léon 10911*).

**Taonabo monticola** Britton & Wilson, sp. nov.

A glabrous shrub, 1 m. or more tall, with light brown twigs. Leaves elliptic-obovate, rigid-coriaceous, 2–5 cm. long, 1.3–2.5 cm. broad, rounded at the apex, acute at the base, indistinctly veined, the midvein impressed above; petioles 4 mm. long; peduncles 2–3 cm. long; sepals 5, the outer oval to suborbicular, 5.5–6 mm. long, 5–5.5 mm. broad, glandular-ciliate, the inner 4.5–5 mm. broad, rigidly and sharply acute, without marginal cilia; fruit (immature?) ovoid, 9.5 mm. in diameter.

Sierra Maestra, Oriente (*Léon 10839*, type; *10837*; *11193*).

**Taonabo Leonis** Britton & Wilson, sp. nov.

A glabrous shrub, with light-gray twigs. Leaves obovate, 2.5–5 cm. long, 1.4–2.7 cm. broad, rounded or truncate and often slightly emarginate at the apex, acute at the base, indistinctly veined, dark green above, paler beneath, the petioles 2–3 mm. long; peduncles 3–7 mm. long, reflexed; sepals 5, the outer oval, 4.7–5 mm. long, 4 mm. broad, rounded at the apex, glandular-ciliate, the inner elliptic, 3–3.5 mm. long, acute, without glandular cilia.

Vicinity of Pico Turquino, Oriente (*Léon 10910*).

**Haemocharis angustifolia** Britton & Wilson, sp. nov.

A tree 20–30 m. tall, with slender grayish brown twigs, pubescent with strigillose hairs. Leaves oblong or oblong-obovate, 2–5.5 cm. long, 0.5–1.3 cm. broad, obtuse or rounded at the apex, acute at the base, light green and glabrous above, paler beneath and pubescent; flowers about 3 cm. in diameter; sepals oval or suborbicular, 4.5–6 mm. long, 4–6 mm. broad, pubescent on the back with appressed hairs; petals obovate, 1.2–1.3 cm. long, 6–7 mm. broad, rounded at the apex, pubescent; filaments filiform, glabrous; ovary villous.

Sierra Maestra, Oriente (*Léon, 11072*).

**Begonia lomensis** Britton & Wilson, sp. nov.

Suffruticose, the stems 3–4.5 dm. high, rusty pilose. Leaves obliquely cordate-ovate to obliquely suborbicular, 1.5–4 cm. long, 1–2.7 cm. wide, acute, glabrous above at maturity, rusty pilose or nearly glabrous beneath, coarsely toothed, the petioles 4–20 mm. long, pilose; stipules lanceolate, acuminate, entire, 4–6 mm. long, 1.5–2 mm. broad; inflorescence long-peduncled; staminate flowers; pedicels slender, up to 7.5 mm. long, glabrous; sepals 2, orbicular, 7–8 mm. long, 8–9 mm. wide; petals 2, obovate, 4 mm. long, 3 mm. wide; stamens 20 or more; capsule long-pedicelled, the body 8–9 mm. long, 5–6 mm. wide, the wing about 9 mm. broad, obtuse or acutish.

Farallones de la Loma Regino, Oriente (*Léon 10731*).

**Ginoria montana** Britton & Wilson, sp. nov.

A glabrous unarmed shrub, with slender ascending branches. Leaves lanceolate, coriaceous, 2.5–4.3 cm. long, 0.7–1.7 cm. broad, obtuse at the apex, acute at the base, faintly reticulate-veined; petioles slender, 2 mm. long; cymes sessile or nearly so; flowers immature, long-pedicelled; calyx-lobes spreading, appendaged below the sinuses; stamens about 20.

Sierra Maestra, Oriente (*Léon 11009*).

**Psidium** (?) **cacuminis** Britton & Wilson, sp. nov.

Glabrous, with straight slender twigs. Leaves oblong, thick-coriaceous, 4–7 cm. long, reticulate-veined, sparingly punctate, bright green and shining above, pale green beneath, the apex rounded or obtuse, the base narrowed, the stout petioles about 6 mm. long; fruit oblong, solitary and nearly sessile in upper axils, nearly 2 cm. long.

Pico Turquino, Oriente (*Léon 10749*).

### **Calyptranthes montana** Britton & Wilson, sp. nov.

A much-branched shrub, with slender glabrous branches, the twigs rusty-brown and somewhat pubescent when young. Leaves lanceolate, coriaceous, 9–30 mm. long, 6–11 mm. broad, obtusely acuminate at the apex, acute at the base, rusty brown and pubescent when young, glabrous at maturity, the lateral veins rather prominent on both sides; petioles 0.9 mm. long or less; inflorescence 1–3-flowered, the peduncles filiform, 7 mm. long or less; buds globose-ovoid, 1.5 mm. in diameter.

Sierra Maestra, Oriente (*Léon 10805*).

### **Eugenia cati** Britton & Wilson, sp. nov.

A glabrous shrub or small tree, the twigs slender. Leaves elliptic to elliptic-obovate, chartaceous, 7 cm. long or less, rather sparingly punctate, dark green above, pale beneath, not very conspicuously veined, the apex rounded or obtuse, the base mostly narrowed, the petioles 3–7 mm. long; flowers glomerate in the axils; calyx-lobes suborbicular, about 3 mm. broad.

In woods, Loma del Gato, Cobre Range of Sierra Maestra, Oriente (*Léon, Clement and Roca 10045*, type; *10588*).

### **Eugenia ginoriaefolia** Britton & Wilson, sp. nov.

Glabrous; twigs slender. Leaves ovate to elliptic, chartaceous, 3–7 cm. long, dark green and shining above, rather prominently veined, pale beneath, densely punctate, the apex obtuse, the base obtuse or narrowed, the petioles only 3 mm. long or less; flowers glomerate at the nodes of twigs, sessile; calyx-lobes about 2 mm. broad, densely glandular, glabrous; petals elliptic to oval, about 3 mm. long, 1.8–2.2 mm. broad, obtuse or acutish at the apex; filaments filiform, glabrous, the anthers elliptic.

Sierra Maestra, Oriente (*Léon 10812*).

### **Eugenia lomensis** Britton & Wilson, sp. nov.

Shrub 2–3 m. high, with slender pubescent twigs. Leaves lanceolate or elliptic, coriaceous, 3.5–7 cm. long, 1.7–3 cm. broad, acuminate at the apex, acute at the base, glabrous or nearly so above, the midrib and lateral veins impressed, pubescent beneath, the midvein prominent; petioles 2.5 mm. long or less; fruit subglobose, 9 mm. in diameter, black, slender-peduncled, solitary or clustered in the axils of the leaves.

Foothills of the Sierra Maestra, Oriente (*Léon 10794*, type; *10962*).

**Eugenia brevipetiolata** Britton & Wilson, sp. nov.

A glabrous shrub, with rather thick brownish gray twigs. Leaves oval to suborbicular, 5–8 cm. long, 4–6.5 cm. broad, rounded at both ends, dark yellowish green above, paler beneath, the midrib impressed above, prominent beneath, the lateral veins slender, slightly elevated on both surfaces; petioles stout, 2–3 mm. long; buds subglobose, 6 mm. in diameter, solitary or few together in the axils of the leaves, glabrous.

Sierra Maestra, Oriente (*Léon 11046*).

**Eugenia rigidula** Britton & Wilson, sp. nov.

Shrub 1 m. tall, with slender brownish pubescent twigs. Leaves lanceolate to ovate-lanceolate, rigid-coriaceous, 1–2.8 cm. long, 4–11 mm. broad, acute at the apex, rounded at the base, sparingly pubescent on both sides when young, glabrous at maturity, the petioles 1 mm. long or less; young fruits subglobose, 4–5 mm. in diameter, pubescent with appressed whitish hairs.

Edge of woods, Sierra Maestra, Oriente (*Léon, Clement and Roca 10634*).

**Anamomis reticulata** Britton & Wilson, sp. nov.

Shrub or tree, the young twigs slender, brown, puberulent, the branches gray. Leaves obovate, coriaceous, 3–4.5 cm. long, 1–2.5 cm. broad, rounded at the apex, cuneate at the base, yellowish-green above, paler beneath, sparingly pubescent on both sides when young with short appressed hairs, glabrous at maturity, reticulate-veined; branches of the inflorescence appressed-pubescent; flowers undeveloped.

Sierra Maestra, Oriente (*Léon 10968*).

**Graffenrieda rufescens** Britton & Wilson, sp. nov.

Shrub 3 m. tall, the branches, twigs, calyx and under surface of the leaves densely scurfy with brownish scales. Leaves elliptic, 4.5–10 cm. long, 2.4–4 cm. wide, acuminate at the apex, acute at the base, 3-nerved, dark green and glabrous above, the petioles 1–2 cm. long; inflorescence much-branched; flowers short-pedicelled; calyx-tube 3–3.5 mm. long, 8-ribbed, its lobes semiorbicular, 1 mm. long or less; petals suborbicular or orbicular-obovoid, 3.5 mm. long, 3–3.5 mm. wide, yellow.

Sierra Maestra, Oriente (*Léon 11047*).

**Miconia plumieriaefolia** Britton & Wilson, sp. nov.

Shrub, the twigs, petioles and branches of the inflorescence clothed with a dense brownish white stellate scurf. Leaves

3-nerved, oblong or oblong-lanceolate, coriaceous, 10.5–15 cm. long, 2.5–3.8 cm. broad, green and glabrous or nearly so above, densely ferruginous-pubescent beneath with short stellate hairs, reticulate-veined, the lateral veins 2–3 mm. distant, nearly at right angles to the midrib, the petioles 1.5–2 cm. long; branches of the inflorescence loosely articulate; pedicels 2–4.5 mm. long; flowers undeveloped; calyx-lobes shortly triangular-ovate.

Sierra Maestra, Oriente (*Léon 10925*).

**Rapanea microphylla** Britton & Wilson, sp. nov.

A glabrous shrub, with short and slender twigs. Leaves obovate or oblong-obovate, coriaceous, 8–20 mm. long, pinnately few-veined, punctate, the apex rounded, the base connate, the petioles 2–3 mm. long; fruits nearly sessile, subglobose, shining, about 3 mm. in diameter.

Pico Turquino, Sierra Maestra, Oriente (*Léon 10714*).

**Symplocos Leonis** Britton & Wilson, sp. nov.

Shrub, the twigs dark brown, strigillose. Leaves elliptic, subcoriaceous, 4–8.5 cm. long, 2–4 cm. broad, rounded or obtusely acute at the apex, acute at the base, dark green, glabrous and indistinctly reticulate-veined above, the midrib impressed, paler, reticulate-veined and pubescent with appressed hairs especially on the midvein beneath, or nearly glabrous; petioles about 5 mm. long; inflorescence pubescent with ferruginous hairs; calyx-lobes elliptic, 1.4 mm. long, 0.9 mm. broad; petals 5, broadly oval, 3–3.5 mm. long, 2.5 mm. broad, glabrous; filaments distinct nearly to the base; fruit ellipsoid, 8.5 mm. long, 5.5 mm. in diameter, pubescent with scattered appressed hairs.

Sierra Maestra, Oriente (*Léon 10738*, type; *10907*).

**Plumiera montana** Britton & Wilson, sp. nov.

A tree up to 10 m. high or higher, glabrous throughout. Leaves oblanceolate, 15 cm. long or less, membranous when dry, the lateral venation rather widely spreading, the apex rounded, the base cuneate, the slender petioles 1–3 cm. long; flowers several or numerous; pedicels rather stout, 1.5 cm. long or less; calyx about 5 mm. long; corolla (white?) its slender tube about 2 cm. long, about one-half as long as the narrowly oblanceolate, rounded lobes; pod about 12 cm. long.

Sierra Maestra, Oriente. Type from banks of Yara River (*Léon 11060*).

**Marsdenia bicolor** Britton & Wilson, sp. nov.

A slender vine, with puberulent stems. Leaves oblong-elliptic to elliptic, 5–6.5 cm. long, 1.5–3.2 cm. broad, green above, whitish beneath, glabrous on both surfaces, the lateral veins indistinct; calyx-lobes ovate, 4 mm. long, about 2 mm. broad, acute or acuminate, slightly pubescent; corolla 1.5 cm. long, 1.5–1.8 cm. wide, glabrous, its lobes triangular, 6 mm. long, 5.5–6 mm. wide.

Sierra Maestra, Oriente (*Léon 10787*, type; *10788*).

**Sebesten Leonis** Britton & Wilson, sp. nov.

A tree up to 15 m. high, the young twigs sparingly pubescent, soon glabrous and gray. Leaves thick-coriaceous, glabrous or the short and stout petioles sparingly pubescent, shining, elliptic, oblong or obovate-elliptic, 5–9 cm. long, the venation impressed above, prominent beneath, the apex rounded, the base obtuse or rounded, the petioles only 8 mm. long or less, the upper surface dark green, the under surface light green; flowers several in terminal clusters; calyx subcylindric, nearly 2 cm. long, densely puberulent, its teeth very short and broad; corolla funnelform, its tube about 3 cm. long, enlarged upward, the widely spreading limb about 4 cm. broad, about 6-lobed; fruit ovoid, about 2 cm. long, its summit beaked.

Loma de Naranjo, Sierra Maestra, Oriente, at 600 m. elevation (*Léon 11021*).

**Varronia longipedunculata** Britton & Wilson, sp. nov.

A shrub with slender branches, the young twigs puberulent. Leaves elliptic or oblong, chartaceous, 7 cm. long or less, scabrate above, puberulent on the veins beneath, entire or sparingly repand, the apex obtuse or acute, the base mostly narrowed, the puberulent petioles 6–12 mm. long; peduncles solitary, slender, puberulent, longer than the leaves; flowers several in a terminal globose head about 1.5 cm. in diameter; calyx-lobes triangular, 1.5 mm. long, acute; corolla-lobes broadly obovate, 7.5 mm. long, 4.5 mm. broad.

Sierra Maestra, Oriente (*Léon 10964*).

**Salvia scopulorum** Britton & Wilson, sp. nov.

A shrub, about 3 m. high, the branches densely pubescent with short spreading hairs. Leaves ovate, coriaceous, crenulate, 3–5 cm. long, 1.5–3 cm. broad, acute to abruptly short-acuminate at the apex, rounded and often more or less subcordate at the base, dark green above, paler beneath, pubescent on both sides, the petioles 12 mm. long or less; calyx 10–11 mm. long, finely pubescent; corolla red, 1.8 cm. long or more, pubescent.

Farallones de Regino, Estribo Turquino, Oriente, 1600 m. alt. (*Léon 11010*).

### **Rondeletia naguensis** Britton & Wilson, sp. nov.

A shrub about 2 m. high, the young twigs and inflorescence densely strigose. Leaves elliptic, subcoriaceous, 4–10 cm. long, sparingly strigose on the veins beneath when young, soon glabrous, the apex obtuse or acute, the base obtuse or narrowed, the venation inconspicuous, the strigose petioles 6–12 mm. long; flowers in peduncled heads, the peduncles 2–4 cm. long; bractlets obovate, about 3 mm. long; calyx-lobes oblanceolate, 3.5–4 mm. long, densely pubescent with appressed hairs; capsule subglobose, 5.5 mm. in diameter, appressed-pilose.

Banks of a stream, Loma de Quintin, Nagua, Oriente (*Léon 10971*).

### **Rondeletia calophylla** Standley, sp. nov.

Branchlets slender, pilose-strigose; stipules deltoid-acuminate, 1.5 to 2.5 mm. long, erect, persistent; petioles stout, 2 mm. long, strigillose; leaf blades ovate, sometimes broadly so, 2 to 3.5 cm. long, 1 to 2.5 cm. wide, acute or sometimes obtuse, broadly rounded or subcordate at base, thick-coriaceous, dark green above, lustrous, scaberulous or glabrate, the venation prominulous-reticulate, much paler beneath and brownish, glabrate or scaberulous along the nerves, the costa prominent, the lateral nerves few and distant; inflorescence terminal on the main branches and on leafy lateral twigs, few-flowered, lax, the flowers pedicellate; calyx globose, densely whitish-strigillose; calyx lobes 5, oblong or linear-oblong, 2 mm. long, obtuse, glabrate, suberect; corolla densely white-strigillose outside, the tube 4 mm. long, the 5 lobes rounded, 2 mm. long; capsule subglobose, 3–4 mm. broad, glabrate; seeds broadly winged.

Type (in the U. S. National Herbarium) collected in the Sierra Maestra, Oriente, July, 1922, (*Léon 10741*).

In the key to the species of *Rondeletia* in the North American Flora, this plant runs at once to the group *Odoratae*, but it is not closely related to any of the species placed there, or to any other Cuban species previously known to the writer.

### **Guettarda cryptantha** Standley, sp. nov.

Shrub, the branches grayish, the branchlets slender, densely pilose with subappressed fulvous hairs; stipules 8–10 mm. long, oblong-lanceolate, long-acuminate, appressed-pilose; leaves opposite, the petioles stout, 2–3 mm. long, appressed-pilose, the blades elliptic or ovate-elliptic, 2.5–6 cm. long, 1.2–3 cm. wide, rounded at base, obtuse or rounded at apex, coriaceous, dark-green above, lustrous, at first pilose with very slender whitish appressed hairs but later glabrate, the venation depressed, paler and brownish beneath, thinly scaberulous-pilosulous and with longer subappressed hairs along the veins, the costa stout and prominent, the lateral veins 5–7 pairs, subarcuate, anastamosing, remote from the revolute margin; inflorescence few-flowered, closely sessile, terminal and axillary, subtended by large, densely pilose, oval bracts; hypanthium densely sericeous-pilose with long whitish hairs, the calyx 5–7 mm. long, cleft into 3 or 4 spatulate-obovate, obtuse, densely sericeous lobes; corolla brownish-red, the tube stout, 10–12 mm. long, densely pilose with long whitish ascending hairs, the 4 lobes rounded-oval, 4 mm. long, glabrous within.

Type collected on Loma del Gato, Cobre Range of Sierra Maestra, Oriente, altitude 900–1000 meters (*Léon, Clement and Roca 10301;* herbarium of the New York Botanical Garden).

**Guettarda cobrensis** Standley, sp. nov.

Shrub 3 meters high, the branches dark reddish brown, the branchlets thick, densely covered with minute appressed fulvous hairs, the internodes short; stipules oblong-ovate, 4 mm. long or more, acuminate, thin, brown, pubescent like the branchlets and with few long subappressed hairs; leaves opposite, the petioles stout, 4–6 mm. long, minutely and densely appressed-pilose, the blades oval or broadly oval, 3–6 cm. long, 2–4.5 cm. wide, rounded at apex, deeply cordate at base, thick-coriaceous, yellowish-green, concolorous, often somewhat bullate, glabrous above, the venation depressed, beneath bearing a few short appressed hairs along the coarse prominent costa, but elsewhere glabrous, the lateral veins stout and prominent, 5 or 6 on each side, subarcuate, ascending at an angle of 45–60°, the intermediate veins inconspicuous, the margin subrevolute; peduncles about 1 cm. long, pubescent like the branchlets, the flowers usually 3, sessile; fruit globose, 1 cm. in diameter, minutely tomentulose.

Type collected at edge of woods, Loma del Gato, Cobre Range of Sierra Maestra, Oriente, altitude 800 meters (*Léon, Clement and Roca 10271;* herbarium of the New York Botanical Garden).

Related to *G. crassipes* Britton, in which the leaves are densely long-pilose beneath along the costa.

**Stenostomum apiculatum** Britton & Standley, sp. nov.

Branchlets thick, resinous, densely leafy, sericeous-strigose; stipules united, persistent, the sheath 5 mm. long, densely strigose; petioles stout, 5–12 mm. long, densely strigillose; leaf blades elliptic, 4.5–7 cm. long, 2.5–4 cm. wide, obtuse or acute at base, obtuse at apex and apiculate-acuminate, coriaceous, green above, lustrous, glabrous, the costa depressed, paler beneath and brownish, sparsely strigillose, the veins prominent, the lateral ones about 9 pairs, arcuate, distant, the margin plane or subrevolute; peduncles slender, about 3 cm. long, the 2 branches 2–2.5 cm. long, 10–12-flowered; calyx and hypanthium 1–1.5 mm. long, glabrate, the calyx with very short, obtuse teeth; corolla 7 mm. long, densely strigillose outside; filaments very short, the anthers oblong-linear, equaling the corolla tube; stigma 4-lobate.

Type (in the U. S. National Herbarium) collected in the Sierra Maestra, Oriente, July, 1922 (*Léon, 10806.*)

**Psychotria Leonis** Britton & Wilson, sp. nov.

Shrub, the twigs and branches of the inflorescence puberulent. Leaves elliptic to oval, 3–5 cm. long, 1.5–3 cm. broad, acute to short-acuminate at the apex, acute at the base, glabrous above, pubescent beneath when young with short appressed hairs, the primary veins indistinct above, prominent beneath; petioles 1.3–1.5 cm. long, puberulent; panicles few-flowered; calyx funnel-shaped, shallowly toothed, the teeth triangular, acute; buds narrowly ellipsoid, puberulent; mature flowers and fruits not seen.

Sierra Maestra, Oriente (*Léon 10789*).

**Lobelia cacuminis** Britton & Wilson, sp. nov.

Suffrutescent, the stems 3–4 m. high, nearly glabrous. Leaves chartaceous, oblanceolate, 7–13 cm. long, 2.5–4.5 cm. wide, acuminate at the apex, cuneate at the base, rather coarsely dentate, the petioles 1.5–3 cm. long; midrib flat above, prominent beneath, the lateral veins ascending; inflorescence many-flowered; pedicels slender, 10–12 mm. long, pubescent; calyx-lobes narrowly lanceolate, 3–4 mm. long; mature corolla not seen; young fruits 1 cm. in diameter.

Pico Turquino, Oriente (*Léon 10862*).

**Senecio Leonis** Britton & Wilson, sp. nov.

Vine, the slender stems glabrous. Leaves ovate, triangular-ovate or occasionally lanceolate, 1.5–4.5 cm. long, 0.9–2.7 cm. wide, often with one or more prominent teeth at or above the base, palmately-veined, glabrous on both sides; petioles 0.5–1.5 cm. long; heads long-peduncled, the peduncles pubescent; involucre subcylindric-campanulate, 5–6 mm. high, its bracts oblong, glabrous, their tips acute or acuminate; pappus white, 4 mm. long; achene about 1 mm. long.

Climbing on shrubs, Loma del Sabicu, Oriente (*Léon 10751*).

**Chaptalia montana** Britton, sp. nov.

Leaves oblanceolate-spatulate, thin, 4–7 cm. long, lyrate-pinnatifid, the terminal lobe large, elliptic-obovate, obtuse, apiculate, the lateral ones few, small, rounded, the upper surface green and glabrate, the under grayish-lanate; scape filiform, 1.5–2.5 dm. long; head erect; involucre subcampanulate, its bracts linear, acuminate, lanate below, the inner ones about 7 mm. long; achenes fusiform, 5.5–6 mm. long, the slender beak longer than the body; pappus white.

Sierra Maestra, Oriente (*Léon 10802*).

### 65. UNDESCRIBED SPECIES FROM TRINIDAD

**Bactris savannarum** Britton, sp. nov.

Trunk slender, up to 10 m. high, erect, copiously armed, like the leaf-rachis, with nearly white, deflexed spines 1–5 cm. long, which turn darker in age. Leaves about 1 m. long or longer, petioled, the numerous, unarmed segments 2–4 dm. long, about 4 cm. wide or less, light green, paler beneath than above, the base attenuate, the apex acuminate or acute, some of the upper ones of young leaves confluent; spathe narrowly oblong, 2–3 dm. long-acuminate, densely appressed-bristly, the bristles rather soft; inflorescence about as long as the spathe, its axis and slender branches densely brown-villous; flowers numerous, nearly white, about 4 mm. long; fruit orange, depressed-globose, small for the genus, about 8 mm. in diameter, vertically striate; fruiting calyx nearly flat, about 5 mm. broad, its lobes rounded, striate.

Aripo Savanna and its forest borders, Trinidad (*Britton, Broadway and Hazen 269*, type; Trinidad Herbarium *9850, Broadway*); Professor L. H. Bailey has kindly sent us two photographs of this palm taken by him in 1921.

**Pilea aripoensis** Britton, sp. nov.

Stems filiform, 4–7 cm. long. Leaves membranous, spatulate, entire, 1-nerved, 12 mm. long or less, the apex rounded, the base cuneate, the filiform petiole somewhat shorter than the blade, the raphides linear, undulate, transverse, prominent upon the upper surface.

Hanging from wet dark banks, Heights of Aripo, Trinidad (Trinidad Herbarium *10,008*, *Broadway*).

### **Inga ierensis** Britton, sp. nov.

A tree up to 16 m. high, the petioles, leaf-surfaces and peduncles strigillose. Petioles slender, 2–3 cm. long; rachis-glands suborbicular, semiglobose; leaflets in 2 pairs, ovate-elliptic, chartaceous, shining, 7–10 cm. long, pinnately veined, the apex rather abruptly short-acuminate, the oblique base narrowed or obtuse, the strigulose petiolules 2–3 mm. long; peduncles about 6 cm. long or less; legume broadly linear, compressed, glabrous, shining, up to 10 cm. long, about 2 cm. wide, finely striate, abruptly short-tipped, the margins continuous or deeply constricted.

Forests, northern mountain range, Trinidad. Type from the Maracas Valley (*Britton and Hazen 1627*). In fruit April 10, 1920.

### **Serjania ierensis** Britton, sp. nov.

A vine up to 7 m. long, the branches slender, glabrous. Leaves about 6 cm. long, biternate, the short, slender petioles 1.5 cm. long or less, sparingly pubescent; leaflets coriaceous, glabrous, 4 cm. long or less, serrate, finely reticulate-veined, shining, those of the terminal segment acute or acuminate, those of the lateral segments rounded or obtuse; peduncles about as long as the leaves, glabrous; tendrils very slender, 2–4 cm. long; panicles puberulent nearly as long as the peduncles; samaras glabrous, about 15 mm. long, the wing finely reticulate-veined, about 4 times as long as the body and only partially enclosing it.

Dry thickets, Trinidad. Type from Palo Seco (*Britton and Hazen 1172*). In fruit March 30, 1920.

### **Clusia intertexta** Britton, sp. nov.

Forming impenetrable masses with interlocking aerial roots. Leaves orbicular-obovate, 10–14 cm. long, thick-coriaceous, rounded, the base subcuneate, the lateral veins many, about 4 mm. apart, prominent on the upper surface, the very stout petioles 1 cm. long or less; inflorescence several-flowered, its branches stout; bracts 2–3 cm. long; buds globose, glabrous; fruit (immature) oblong-ovoid, beaked, about 2.5 cm. long; stigmas 6.

Forest, Heights of Aripo, Trinidad (Trinidad Herbarium *9786*, *Broadway*), January 10–26, 1922.

### **Clusia aripoensis** Britton, sp. nov.

A tree, with slender twigs. Leaves narrowly obovate, subcoriaceous, 7–8 cm. long, the apex obtuse, the base cuneate, the rather closely pinnate venation prominent on the under side, almost wholly obscure above, the rather slender petioles 1–2 cm. long, stigmas 5; young fruit obovoid, 2.8 cm. long, 2 cm. in diameter.

Forest, Heights of Aripo Trinidad (Trinidad Herbarium *9785*, *Broadway*), January 10–26, 1922.

### **Stylogyne tenuifolia** Britton, sp. nov.

A tree up to about 10 m. in height. Leaves elliptic, membranous, 8–20 cm. long, glabrous, the base narrowed, the apex rather abruptly acuminate, the midvein impressed above, prominent beneath, the stout petioles 5–12 mm. long; inflorescence lateral and terminal, 5 cm. long or less, short-paniculate; bractlets oblong-lanceolate, 2–3 mm. long, deciduous; pedicels nearly filiform, 5–10 mm. long; calyx-segments broadly ovate, rounded, about 2 mm. long; corolla about twice as long as the calyx; fruit globular, white, 6–7 mm. in diamater.

Forests at higher elevations in the northern mountain range, Trinidad. Type from Mt. Tocuche (*Britton, Hazen and Mendleson 1341*); collected also by Mr. Broadway on the Heights of Aripo (Trinidad Herbarium, *9837*, *9840*).

### **Prestonia Fendleri** N. E. Brown, sp. nov.

Stem climbing, the flowering parts with internodes 4.5–12 cm. long, 1–2 mm. thick, thinly puberulous with minute curved hairs on the youngest parts, becoming glabrous and brown with age. Leaves with petioles 6–15 mm. long and blades 5–10 cm. long and 3–7 cm. broad, elliptic, subequally and broadly rounded at both ends, with a small abrupt point 1–2 mm. long at the apex, with about 5 ascending curved primary veins on each side of the midrib, inarching at their tips and forming loops near the margin. Racemes axillary, the axis 1–2 cm. long in the example seen, bearing 15 or more flowers on the upper half, flowerless below, thinly and minutely puberulous. Bracts minute, less than 1 mm. long. Pedicels 12–15 mm. long, slender, puberulous. Sepals 5 mm. long and 1.5–2 mm. broad, lanceolate, acute, thinly puberulous. Corolla pubescent at the top of the tube inside, otherwise glabrous; tube 15–17 mm. long and about 4 mm. in diameter, cylindric, with the mouth, where the lobes pass from it, raised into an erect ring 1 mm. high; inside this ring arise 5 linear erect exserted processes (coronal-lobes) 4 mm. long; lobes about 12 mm. long and 7 mm. broad, somewhat rhomboid, or obliquely subtruncate. Stamens inserted near the top of the tube, glabrous; filaments 2 mm. long; anthers sagittate, 4.5 mm. long, exserted. Ovary surrounded by an obtusely 5-lobed fleshy disk.

Trinidad, without precise locality, *Fendler 628*.

### **Cordia ierensis** Britton, sp. nov.

A tree up to 10 m. high, with slender, finely appressed-pubescent twigs. Leaf-blades elliptic to ovate, thin, 2 dm. long or less, scabrate-puberulent, the apex abruptly acuminate, the base obliquely obtuse or narrowed, the petioles 2 cm. long or less; panicle about 8 cm. broad, broader than long, many-flowered, its branches slender, densely appressed-pubescent; flowers sessile, the buds obovoid, rounded, densely appressed-pubescent, about 2 mm. long.

Forests, Trinidad. Type from Morne Bleu (*Britton, Freeman and Bailey, 2277*). In bud March 13, 1921. This is, as determined by Mr. N. E. Brown at Kew, the *Cordia panicularis* of Grisebach, not of Rudge.

### **Aegiphila trinitensis** Britton, sp. nov.

A shrub, with slender, glabrous branches, the bark nearly white, the young shoots brown, short, minutely puberulent. Leaves short-petioled, the blades ovate, thin, small for the genus, 4 cm. long or less, the apex acute or acuminate, the base narrowed; panicles small, short-peduncled, strigose, several-many-flowered, 2–3 cm. broad; calyx obconic, truncate, puberulent; corolla white, about 8 mm. long.

Hillsides and thickets in moist districts, Trinidad. Type from St. Ann's (*Mrs. W. E. Broadway*). In flower May 10, 1919. This is the species recorded by Grisebach from Trinidad, as *Aegiphila laevis*.

### **Anguria elliptica** Britton, sp. nov.

A slender, glabrous, high-climbing vine, with very slender tendrils 15 cm. long or less. Petioles about 2 cm. long; leaf-blades simple, oblong-elliptic, thin, entire, about 8 cm. long, pinnately veined, the apex abruptly acute, the base obtuse; peduncles slender, longer than the leaves; staminate flowers scarlet, spicate; spikes about 3 cm. long; calyx-lobes subulate, 1 mm. long; corolla-lobes spatulate-obovate or obovate, 4 mm. long, 2–2.6 mm. broad, rounded or subtruncate and mucronate at the apex, the margin minutely ciliate; anthers 4.5 mm. long, straight.

Forests in wet or moist districts, Trinidad; type from Arima (*Britton 2084*). In flower March 4, 1921.

### 66. UNDESCRIBED SPECIES FROM PORTO RICO

**Scleria doradoensis** Britton, sp. nov.

Perennial? Culms slender, rather stiff, glabrous, erect, tufted, 3–4 dm. high. Leaves glabrous, scabrate, shorter than the culm, about 2 mm. wide, the apex attenuate; inflorescence terminal, glomerate-spicate, 5–7 cm. long; glomerules 6–8, few-flowered, not nodding; bracts about 3 mm. long, brown-ciliate; achene white, subglobose-obovoid, very obtusely trigonous, verrucose-tuberculate, 1.5 mm. long, 12-porose underneath just above the trigonous base; hypogynium none.

White sand near Dorado (*Britton, Britton and Brown 7064*).

**Scleria Stevensiana** Britton, sp. nov.

Perennial? rootstocks short or none; culms very slender, tufted, slightly scabrous above, weak, 4–5 dm. long. Leaves soft, scabrous-margined, 4 mm. wide or less, panicles 2 or 3, axillary, the lower stalked, the upper one nearly sessile, about 3 cm. long; bracts narrowly linear-subulate, 2.5 cm. long or less; spikelets several or numerous; achene depressed-globose, about 1.5 mm. in diameter, apiculate, glabrous, shining, faintly reticulated, nearly white, with 3 vertical brown bands; hypogynium lobes lanceolate, acuminate, glabrous.

Lares (*Stevens and Hess 4944*).

**Lagenocarpus portoricensis** Britton, sp. nov.

Culm stout, erect, trigonous, glabrous, about 8 dm. high. Leaves 8–12 mm. wide, nearly as long as the culm, smooth, long-attenuate, with numerous transverse veinlets; panicle narrow, puberulent, about 3 dm. long and 5 cm. thick, the lower half of staminate spikelets on nearly erect branches, the upper half of pistillate; bractlets aristate; staminate spikelets about 4 mm. long, short-stalked; scales subtending the achene obovate, subtruncate, ciliolate, mucronate; achene, with its beak, ovoid, 3 mm. long, brown with three darker blotches, the beak about as long as the body.

Wet sandy situations between Manati and Vega Baja (*Underwood and Griggs 946*, type); collected also by Sintenis near Dorado. Recorded by C. B. Clarke and by Urban as *L. tremulus* Nees.

**Rynchospora Blauneri** Britton, sp. nov.

Perennal by short rootstocks; culms filiform, weak, clustered, glabrous, 3–5 dm. long; leaves filiform, glabrous, shorter than the culms; spikelets narrowly oblong, 3 mm. long, few together in 2 or 3 distant compact clusters subtended by a filiform bract 3–5 cm. long; scales ovate-oblong, acute, light brown; bristles none; achene obovate, light brown with darker brown margins, smooth, about 1 mm. long; tubercle conic, acute, about one-third as long as the achene.

Sierra de Luqiullo (*Blauner 247*, in herbarium of Columbia University, collected in 1852–53). Referred by Clarke to *R. divergens.*

**Rynchospora luquillensis** Britton, sp. nov.

Perennial by rootstocks; culms very slender, smooth, erect, about 2 dm. high. Leaves narrowly linear, about 1 mm. wide, flat, smooth, shorter than the culm; inflorescence a small terminal cluster of few spikelets; spikelets narrowly oblong, about 4 mm. long; scales oblong, brownish, acute; bristles about 6, retrorsely barbed, a little longer than the achene; style elongated; achene narrowly obovate, smooth, brown, about 2 mm. long; tubercle subulate, about as long as the achene.

Sierra de Luquillo (*Brother Hioram 364.*)

## 67. AN UNDESCRIBED SIPHOCAMPYLUS FROM HAYTI

**Siphocampylus pinnatisectus** Gleason, sp. nov.

Stem herbaceous, erect, slender, glabrous. Leaves alternate, broadly oblong in general outline, 5–7 cm. long, 3–3.5 cm. wide, narrowed at base into a petiole, glabrous, deeply pinnatisect into a terminal and 5–7 pairs of lateral linear lobes, each lobe and the rhachis about 2 mm. wide, with 2–4 sharp salient teeth or the smaller entire, sharply acute or submucronate, with a single midvein and faint lateral veinlets; flowers in the upper axils, few in number, appearing subcorymbose by the shortened internodes, on minutely puberulent pedicels 1 cm. long; hypanthium obconic, acute at base, 3 mm. high; calyx-lobes narrowly linear-triangular, acuminate, erect, separated by narrow acute sinuses; corolla red, about 25 mm. long, narrowly tubular, somewhat curved ventrally, constricted at base, gradually enlarged upward, 3 mm. in diameter at the throat, its lobes all depressed, 3–4 mm. long.

Type, *Nash and Taylor 1701*, collected on an open sunny hillside, between La Brande and Mt. Balance, Hayti, at altitude of 3150 ft., August 15, 1905.

*Siphocampylus pinnatisectus* differs from all other West Indian members of the genus in its deeply pinnatisect leaves.

CONTRIBUTIONS FROM THE NEW YORK BOTANICAL
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# ALTERNATION OF SEXES AND INTERMITTENT PRODUCTION OF FRUIT IN THE SPIDER FLOWER (*CLEOME SPINOSA*)

BY

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# ALTERNATION OF SEXES AND INTERMITTENT PRODUCTION OF FRUIT IN THE SPIDER FLOWER (*CLEOME SPINOSA*)[1]

A. B. STOUT

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Irregularities in the formation of reproductive organs, such as are seen in the phenomena of intersexualism in both plants and animals, have two points of special interest. First, they involve a particular type of sterility of various grades and degrees of expression, which in plants often affects the production of fruit and seeds and becomes a matter of practical importance in respect to crop production and in the breeding of various economic plants. A second point of interest is in the bearing which the phenomena of intersexualism have on questions of sex differentiation, the alternation of sex, and the evolutionary tendencies in reproduction.

In its general significance, several points regarding sterility from intersexualism are clear. In plants it tends to the alternative development of one or the other kind of sex organs, giving, in comparison to the fundamental condition of hermaphroditism, a one-sided sterility. There is incomplete development or abortion of one or the other of the sex organs which is discriminating and which results in alternative development, with, however, many grades in the relative development. Thus, in plants, the so-called "sterile" intersexes are, in general, individuals that are predominantly male and often highly functional as such. These individuals are sterile only in the sense that they are fruitless. Also the so-called "self-sterile" individuals and varieties of plants, as is well shown in the cultivated grapes in which sterility from intersexualism is well marked, are predominantly female and able to function feebly or not at all as males. They are productive of fruit only when properly pollinated from male or hermaphroditic individuals. Very seldom, if ever, is complete sexual impotence for a plant as a whole seen as a condition of intersexualism, as is frequently the case in sterility from hybridity.

But in many cases of intersexualism in animals, to which attention has recently been especially directed, the complete sterility of individuals is very frequent. Here, however, the condition arises in dioecious forms and involves the partial change of an organ from one sex to the other after

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[1] Contribution from the New York Botanical Garden, No. 239.

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differentiation has been partly achieved. This often results in a more or less complete sexual impotence or sterilization, a condition which has naturally been very generally regarded as abnormal and pathological. This is, however, not the case in those species of plants which are prevailingly dioecious or monoecious, for here, as well shown in the muskmelons, there is a tendency to produce flowers that are fully functional as hermaphrodites.

Whether, however, intersexualism results in complete sterility, as it frequently does in dioecious animals, or in one-sided sterility, as is the rule in hermaphroditic plants, the physiological basis for these variations in sex is to be regarded as most fundamental in the determination and expression of sex.

It is, furthermore, to be recognized that the mixture of sexes, with blending and changes in the character of the organs, often results in a wide range of variation in the morphological character of the different sex organs produced by a single individual. In many plants, the flowers on a single individual may be staminate, pistillate, and hermaphroditic, with also many intergrading types, thus exhibiting many grades of sexual impotence with marked differences in the ability to produce fruit.

These cases of partial variability in sex are of special interest, for here the various conditions of alternative impotence with corresponding irregularities in the production of fruit are all seen among the flowers of a single individual. In such cases there is also opportunity to observe whether the variations are irregular and sporadic or whether they are related to a definite period in development or are otherwise periodic. It is with special reference to these questions that the changes in the character of the flowers of *Cleome spinosa* L. are here reported as decidedly alternative and repeatedly cyclic, resulting in the intermittent production of fruit.

## Observations on Cleome spinosa

This species is most favorable material for a study of variation in the sex of flowers in relation to the development of the plant as a whole. It has long been known as having mixed flowers, yet the species has not become dioecious. All the individuals of the species are apparently quite alike in respect to the general range of variations in the sex of the flowers. The species is a quick-growing herbaceous annual. The first flowers open on the main raceme when the plant is relatively small—about two feet tall —and while the lateral branches are scarcely visible. The main raceme continues to elongate, producing flowers daily, often for a period of from eight to twelve weeks. Meanwhile a dozen or more lateral branches develop, and these may in turn branch. All the branches grow rapidly and produce flowers in abundance. When autumn arrives, well-grown plants are five or more feet tall with a spread of branches of as many feet in diameter. There has been a long period of bloom, often covering as many as ninety days, and this has been for the most part coincident with the period of rapid vegetative development. By far the greater amount of the vegetative growth of the plant takes place after the blooming begins. The first fruits are ripe and shed their seeds when the plant is only about half grown. The period of vegetative vigor overlaps that of the flowering and reproductive vigor in a decided degree and to an extent seldom seen in plants. Only during the last few days of bloom do vegetative growth and vigor noticeably wane.

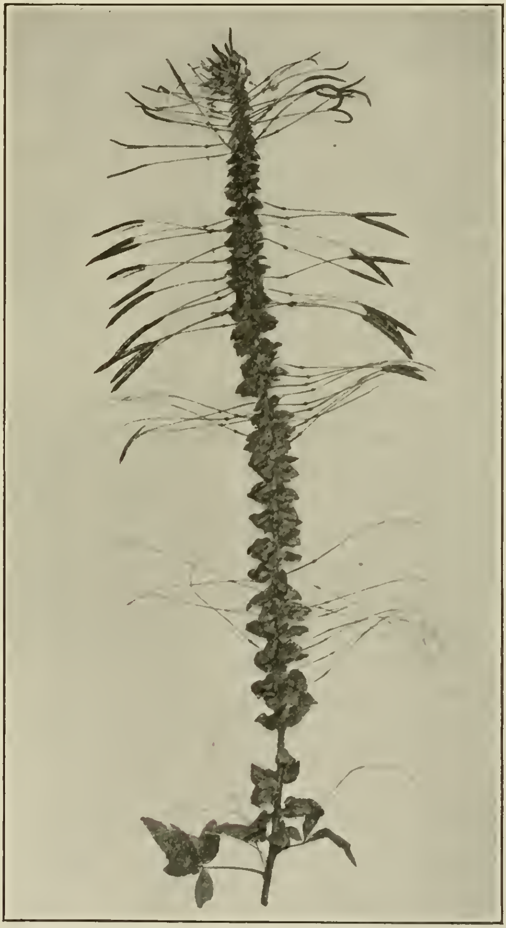

FIG. 1. Main raceme of a plant of *Cleome spinosa* at the close of the blooming period, showing the intermittent production of fruit. This raceme was about 3½ feet long. The pods on the lower half have dehisced.

At the close of the growth of the plant, about September 15th to October 5th as grown at the New York Botanical Garden, the main branch of a plant from the point where the flowers are first produced appears as shown in figure 1, the raceme being about three feet in length. Lateral branches are similar but frequently somewhat shorter. It is to be noted that the pods are in groups separated by sections of the stem upon which no fruit was formed. Fruit formation is therefore decidedly *intermittent.*

This habit of producing fruit intermittently was observed by the writer in groups of plants grown in ornamental planting in the Botanical Garden during previous years. For the purpose of making special observations on the conditions involved in the intermittent production of fruit, a crop of 128 plants was grown in 1921. These plants were examined frequently throughout the entire period of bloom, and records were taken for each individual plant as to the character of the flowers opening at a particular time. At the end of the season, observations on the distribution of fruit in regard to the record for the flowers was made. Controlled self- and cross-pollinations were made on many plants.

Every one of the 128 plants produced many pods and the seeds were numerous, but without exception there was decided intermittency in the production of fruit. On several plants there was considerable irregularity in the distribution of pods, but for most plants the pods were in several groups quite as shown in figure 1.

The study of the flowers from day to day together with the results of controlled pollination showed that the intermittent production of fruit is due to repeated cyclic changes in the morphological character of the flowers, which in the course of the cycles give many grades of intersexes. The flowers of any individual plant varied from perfect or fully hermaphroditic flowers to flowers that were functional only as males or only as females, with also innumerable intergrades as to the relative abortion of pistils or stamens. As a rule, however, the loss of sex is decidedly *one-sided.* When the flowers are hermaphroditic or are female, fruit is produced provided pollination is accomplished; when the flowers are male only, no fruit is produced. The plants pass through alternating periods when the flowers are predominantly hermaphroditic or are female, during which they are productive of fruit, to periods when the flowers are predominantly or only male and fruitless.

The sex character of the flowers, therefore, varies in cycles, which variation makes the intermittent production of fruit a necessary result. The main raceme shown in figure 1 bloomed for a period of 107 days, and on it were produced about 250 flowers. During this time there were for this particular raceme five periods when hermaphroditic and female flowers were produced, with intervening periods when the flowers were staminate only.

In selecting material to illustrate these changes in sex, flowers opening on the same raceme at the same time were taken, the selection being made at a time when the variation was marked. It is, however, seldom that the variation on any one date represents the complete range observed for a plant during a complete cycle. As is shown in the figures, the sex organs (pistils and stamens) when fully developed are large and conspicuous, and it is easy to observe variations in the degree of their development. The petals were removed from the flowers shown in Plate VI.

The three flowers shown in figure 2, Plate VI, were situated in a raceme in the succession shown and illustrate the range seen for the plant on the particular date when the photo was made; all the flowers were fully and very uniformly male; but the pistils were either normal and functional as in *a*, decidedly aborted and functionless as in *c*, or less conspicuously aborted as in *b*. On the particular date the flowers were varying in respect to femaleness. On other dates, however, maleness was quite as variable.

Maleness is well developed in all the flowers shown in figure 3, although the filaments vary in length and there is one stamen fully aborted in *b* and one in *c*. The pistils vary from the highly developed and functional as at *a* to the extremely aborted as in *d*. Figure 4 represents flowers of the same plant a few days later, showing extreme abortion in stamens of some flowers and some variation in the size of pistils, although all pistils were functional.

The pistils of the various flowers shown in figure 5 are either well developed (*a*, *b*, and *c*), or decidedly aborted (*d*, *e*, and *f*). The development of stamens is very irregular, and the extremes are seen for a single flower in the various grades as to length of filament and size, development, and dehiscence of anthers. Such irregularities as these are frequently seen, and for numerous plants the condition was more or less present throughout the period of bloom, with, however, no pod production for the flowers that had only aborted pistils.

Figure 6 shows two typical flowers of a plant on a date when the flowers could function only as females.

The four flowers shown in figure 7 show grades of abortion in both pistils and stamens and illustrate very well how the abortion tends to be one-sided, affecting first stamens and then pistils.

The many controlled pollinations that were made revealed that there was in these plants no limitation to fertility through physiological incompatibilities in fertilization. Every plant was highly productive of seed whenever pollen of dehiscing stamens was used on well-developed pistils either in self- or in cross-pollinations. Rudimentary pistils always failed to set seed. Pistils over 2 cm. in length usually produced seed.

Examination of pollen and tests for germination were made of pollen from all sorts of anthers. In large, well-developed anthers, 95% or more of the pollen grains appeared to be normal, and on a sugar-agar medium as many as 80% often germinated, producing tubes as long as 750 $\mu$. In such rudimentary stamens as at *d*, figure 4, only a few shriveled, empty, partly developed pollen grains were present which did not even swell up when placed in water. In the large-sized but indehiscent anthers of short stamens as in *c*, figure 4, varying percentages of the pollen appeared to be normal, but in no case did the pollen of such indehiscent anthers germinate when removed and placed on the same medium which gave good germination for the pollen of normally dehiscing stamens. There were many anthers that were partly dehiscent, that is, they opened to some extent, and the pollen thus shed was often viable in tests and productive of seed in controlled pollinations.

As a rule, the loss of sex for individual flowers was one-sided. When the pistil was rudimentary the stamens tended to be well developed as at *c*, figure 2. When the stamens were aborted the pistil was usually of good size as at *c*, figure 4. Occasionally, however, the pistil in flowers with aborted stamens was undersized as at *d*, figure 4, but cases of complete or extreme abortion of all stamens and of the pistil in the same flower were not observed.

The entire lot of plants were grown throughout under very uniform conditions which favored continued vegetative vigor, and only one generation has been critically studied. Development under conditions which affect differently the vegetative vigor and the length of the growing period may influence and possibly decidedly change the behavior in respect to cyclic changes, quite as such conditions are known to affect the sex of certain plants, particularly of *Arisaema triphyllum* (Pickett, 1915; Schaffner, 1922), from year to year. Definite evidence regarding the direct or indirect influences of environment and the somewhat synchronous changes of sex in the spider flower remains to be obtained.

At the close of the season, when the vigor of plants perceptibly wanes, all parts of the flower, corolla, pistils, and stamens alike, are uniformly undersized. Whether the last flowers that are produced on a plant that reaches old age before being killed by freezing temperatures are as a rule predominantly pistillate or staminate was not determined with certainty. On many such plants the last flowers were decidedly weak in maleness, but for other plants such flowers were decidedly male or bisexual.

## SUMMARY

In the cultures of *Cleome spinosa* grown for this observational study there was wide variation in the morphological character of the flowers in regard to the relative development of the two kinds of sex organs. The entire range of variations was seen among the flowers of a single plant, giving bisexual flowers, flowers that were functional only as males or as females, and many intergrading types. The variation from one extreme to the other was repeatedly cyclic, which condition results in the intermittent production of fruit.

All of the 128 plants grown under special observation were quite similar; all exhibited the extreme ranges of flower forms or intersexes; in all the production of fruit was more or less intermittent; none was exclusively staminate or pistillate.

## Discussion

The alternative loss of maleness and femaleness in the flowers of *Cleome spinosa* and the recurring periodic changes in the sex of the flowers are to be regarded as phenomena of internal and biogenetic regulation closely related to those influences which determine the development of the plant as a whole.

It is, of course, well recognized that in plants as contrasted with animals there is continually the formation of really *new* organs from a persistent embryonic complex of cells and that this continues until the maturity and death of the plant as a whole. Internal and biogenetic relations of correlation and self-regulation, operating independently or in response to external influences, are hence repeated successively in determining the character of the new organs in the same fashion as they operate once for all in the animal. When there is in addition a long flowering period which overlaps and is coincident with the period of the most vigorous vegetative development, as is the condition in this robust annual *Cleome spinosa*, the conditions are most favorable for a study of the factors influencing the differentiation of sex.

The fact that the loss of sex organs in the flowers of the spider flower is very decidedly one-sided and qualitative is of special significance. When the stamens are aborted the pistil is as a rule functional, and in many cases it is well developed; when the pistil is aborted the stamens are often highly developed and functional. Here, as is the rule in plants, intersexualism does not lead to sterility of the plant or of a flower as a whole. Not a flower was found in which the pistil and all the stamens were extremely aborted, and rather rarely was the abortion of one sex accompanied by the decided abortion of the other sex in the same flower. Abortion of pistils was frequently accompanied by irregular abortion among the various stamens of a flower, but the same irregularity in maleness was also seen for flowers in which there was no abortion of the pistil (see the flowers of fig. 4). While the expression of sex in at least half of the flowers of a plant is decidedly one-sided and alternative, it is not mutually exclusive, for on every plant many bisexual flowers are produced.

It should be noted that the influences operate primarily and almost discriminatingly on the organs of sex. The pedicels, sepals, and petals are often uniformly well developed for all the types of flowers; but undersized flowers were to be seen (*c* of fig. 3, and *d* of fig. 4) in which the flower as a whole is undersized. Such cases, if more general, would suggest a direct relation to waning vigor and decreased food supply such as may be considered to be the direct cause of undersized flowers and of loss of sex in gynomonoecious forms at the end of a period of bloom. That the conditions are more intricate in Cleome is evident, for in a marked degree the extreme variations in sex are independent of any other visible change and the various grades of intersexes are present from the beginning of bloom.

Furthermore, the influences that affect the sex of a single flower often extend to groups of flowers. Thus there is a period of maleness, which is followed by a period of femaleness or of bisexualism, and this in turn is followed by maleness. Flowers in the same condition as to sex are grouped along the raceme. There is a series of cyclic changes all occurring during the period of continuous bloom.

These qualitative changes in sex in flowers of *Cleome spinosa* do not involve the transformation of organs of one sex into organs of the other sex after differentiation has begun, as is the case in many of the intersexes reported in animals (Goldschmidt and Poppelbaum, 1914; Goldschmidt, 1916; Banta, 1916; Lillie, 1917; Sexton and Huxley, 1921). Here the change is accomplished, as it is in dioecious plants, by the abortion of one or the other kind of sex organs. The relative position of each in the flower as a whole is maintained, but the differentiation giving male and female flowers (along with bisexual flowers) is as complete as is seen in many species of dioecious plants. The differential determination of sex in repeated cyclic alternative changes as they occur in *Cleome spinosa* shows to what degree the internal correlative differentiations in development may be extended to the organs of sex after the plant as a whole has passed from the exclusively vegetative to the reproductive stage. At the time of the transition to the reproductive stage, the change is not necessarily complete and discontinuous, nor are the flowers produced in succession necessarily of the same grades of sex. Even when the flowers appear to be morphologically the same there may be a decided cyclic change in their physiological character, as is the case with *Brassica chinensis* and *B. pekinensis* (Stout, 1922). The contrast between these species of Brassica and *Cleome spinosa* illustrates well the different types of sterility that may develop in plants and the different expressions of cyclic regulation of them. In these Brassicas there is frequently rather decided abortion of flowers at the time of transition from vegetative to reproductive organs; in Cleome no indication of such abortion is present, the first flowers to appear being often fully developed as hermaphrodites. In the Brassicas there is a somewhat extended period of flower formation with flowers all morphologically bisexual—but in which the physiological relations in fertilization may vary in a very definite and single cycle; in *Cleome spinosa* there is no variation in the physiological nature of stamens and pistils that are at all functional in so far as these may be tested by the relations of fertilization, but there is the cyclic alternation in the morphological development of the organs of sex. This comparison illustrates two rather widely different expressions of sex in its relation to fertility and sterility.

The conditions in *Cleome spinosa* favor the view that, as held by Yampolsky (1920), there is a general tendency away from hermaphroditism toward dioecism among the higher plants. In the persistence of perfect flowers in greater or less numbers along with those which are more or less purely staminate or pistillate, *Cleome spinosa* is like most species which are in the transition stages toward dioecism. The alternate appearance of male, female, and hermaphroditic flowers in a raceme of course favors crossing, and when this alternation tends to be synchronous on all the branches of a plant, selfing is largely prevented except in the case of the hermaphroditic flowers.

In the spider flower, with its long flowering period and its alternation of maleness and femaleness in the racemes, it is evident that practically the whole vegetative feeding power of every plant is drawn upon for seed production. The conditions are markedly different, and we may consider them more highly adaptive to the demands of reproduction, than is the case in strictly dioecious plants in which seed production is confined to one of each pair of male and female plants. We may, perhaps, characterize the sex conditions in *Cleome spinosa* as effecting a sort of *super-dioecism* in that the conditions favor both reproduction and crossing for each individual.

Certain points regarding the determination of sex in the flowers of *Cleome spinosa* are clear. The conditions illustrate well the fact that the morphological differentiations of sex are fundamentally an extension of the phenomena of somatic differentiations. The expressions of differential qualities in leaves, stems, and flowers, with further differentiation of calyx, corolla, pistil, and stamens, with still further differentiations of tissue within each, are all recognized as one-sided, qualitative, and alternative expressions in protoplasmic units that are alike and which still remain alike in fundamental constitution. Even the physically qualitative division of germ plasm in the reduction divisions is found in regeneration experiments and in parthenogenesis not to be a direct and absolute condition in the alternation of generations. The theory of sex chromosomes decidedly fails in general application to plants, and even in animals, where its application seems most marked, sex is often intergrading and reversible, showing that there is alternative expression rather than alternative inheritance.

In *Cleome spinosa* it is evident that there are rather special and perhaps very specific stimulating and inhibiting influences which regulate the development of the sex organs. Whether these influences are substantive or more of the nature of stimuli, their action is cyclic and decidedly alternative. The results clearly show that sex of flowers is determined progressively as they are formed in response to regulation by internal biogenetic conditions.

New York Botanical Garden

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## EXPLANATION OF PLATE VI

Each group of flowers is from the same raceme on the same date. Petals have been removed. The scale in inches shows the reduction from natural size.

Fig. 2. Three sister flowers uniform as to maleness but highly variable in femaleness.

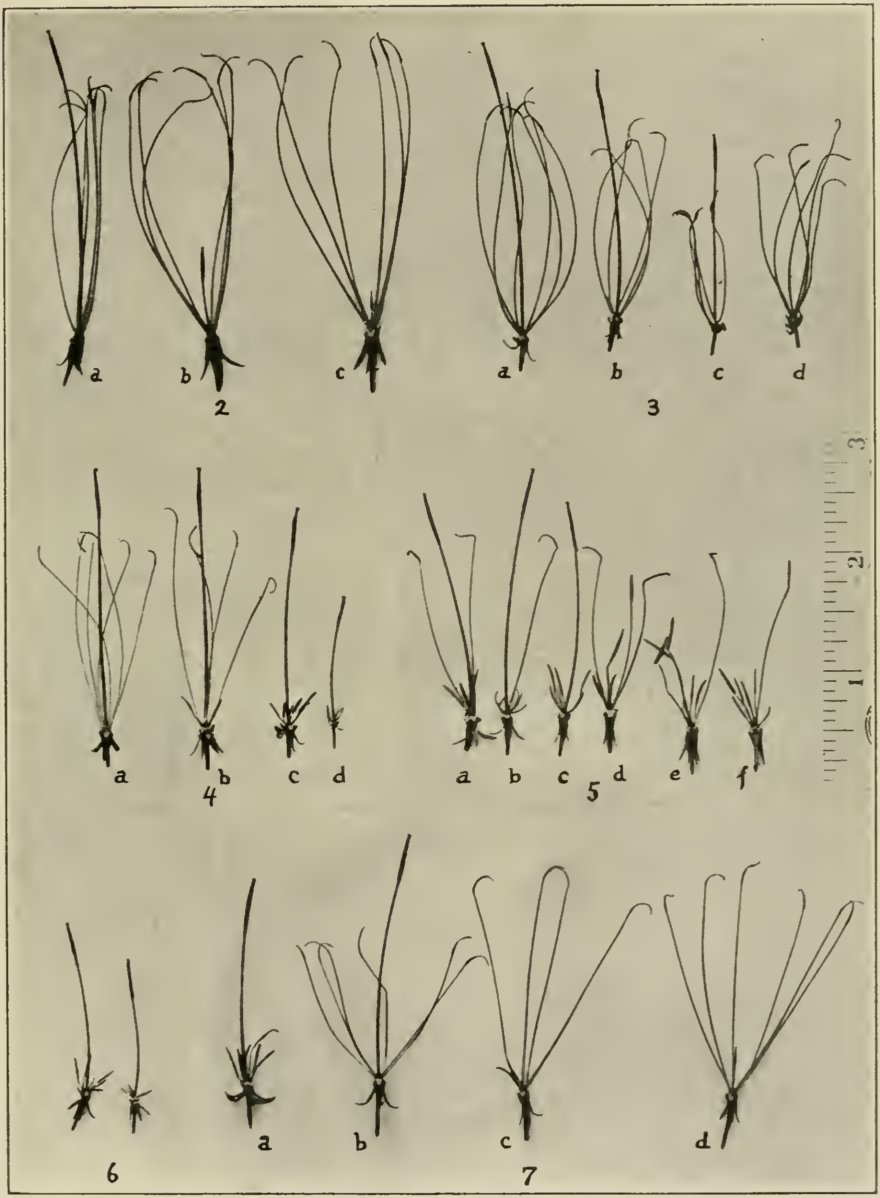
Fig. 3. The stamens of the four flowers vary as to length; one stamen in *b* and one in *c* are aborted; all others are highly functional. Pistils are functional in *a*, *b*, and *c*, but aborted in *d*.

Fig. 4. Four flowers from same plant as those of figure 3, several days later. Pistils vary as to length but all are functional. Stamens all excellent in *a*, two much aborted and indehiscent in *b*, all indehiscent in *c*, and all much aborted and containing no pollen in *d*.

Fig. 5. Pistils variable; in *a*, *b*, and *c*, fully functional; in *d*, *e*, and *f*, rather aborted. Stamens highly variable in each flower irrespective of the condition of the pistil.

Fig. 6. All stamens much aborted or rudimentary. Pistils somewhat undersized but functional.

Fig. 7. Abortion of stamens only, as at *a*, or of pistil, as at *c* and *d*, with a flower (*b*) fully hermaphroditic; all in bloom at the same time on the same raceme. Illustrates well the marked one-sided abortion of sex organs.



STOUT: ALTERNATION OF SEXES

CONTRIBUTIONS FROM THE NEW YORK BOTANICAL GARDEN
No. 240

# STERILITY IN LILIES

A. B. STOUT

NEW YORK
1923

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GARDEN

# STERILITY IN LILIES

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THE tendency of many species of lilies to produce seed irregularly, sparingly, or even not at all, is well exemplified in the old familiar Tiger Lily of our flower gardens. This species has been in cultivation in Europe since 1804; it thrives and blooms abundantly over a wide area; it has been observed in cultivation and also apparently wild in its native home (China and Japan) by persons interested in discovering whether fruits were formed. Yet the author is aware of only two references to the pods and seeds of this species, and the accuracy of these is somewhat doubtful. On the other hand, its fruitlessness has repeatedly been observed wherever it has been grown. The Tiger Lily is one of the most striking examples that can be cited of a plant which blooms in abundance but is propagated only by vegetative means.

## The Law of Compensation

A ready explanation has long been offered by gardeners and botanists for the condition of sterility found in such plants as the lilies. It has been generally believed that they are physically unable to develop seeds because the bulbs and bulblets use the available food. The tiny embryos were assumed to be virtually starved to death. This explanation of the condition has seemed so obvious and so correct that it has received the sanction of the most critical authorities, and is stated in Darwin's law of compensation and in Goebel's law of correlation. But this simple and apparently very satisfactory explanation we now know to be entirely wrong, at least in its application to the condition of sterility in the lilies. Obviously the best evidence of the truth of this statement is the fact that these usually fruitless plants have been shown to be fully able to produce capsules and seeds. Such evidence is in most cases readily obtained.

## Sterility Due to Incompatibility of Pollen

For a period of about fifteen years Focke persisted in attempts to obtain seed of *L. bulbiferum*. He secured bulbs from various parts of northern and western Germany and made many cross-pollinations of their flowers, but obtained at best only a few poor capsules. Finally, bulbs were secured from Switzerland and with the use of pollen of plants grown from them pods and seeds in abundance were matured on the hitherto fruitless plants.[1]

The writer has had much the same experience with other species of lilies. A fine large cluster of *L. croceum*, all descended from a single bulb, growing in the New York Botanical Garden, completely failed to set seed for eight consecutive years. The numerous flowers that appeared each year were self- and cross-pollinated, but there was never even a slight enlargement of any of the ovaries. In 1921, plants of *L. elegans* bloomed at the same time as the cluster of *L. croceum*, and their pollen was used in pollinations. Fine large pods then developed, and these contained many viable seeds. In 1922 these plants of *L. croceum* also yielded pods and seed by cross-pollination with another strain of the same species. Hence these plants were fully able to mature fruit, and their pollen was likewise able to function in certain reciprocal crosses.

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[1] Several papers by W. O. Focke bearing on phenomena of self-incompatibility were published between the years 1887 and 1893.

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SELF-STERILE, BUT PRODUCING PODS WHEN CROSSED

FIGURE 17. This plant of *Lilium speciosum* is fully self-incompatible, but yields fine pods to pollen from certain other plants of the same species, which presumably indicates their origin from different seeds. This, of course, does not insure compatibility, as plants known to be of distinct seed-origin are often incompatible. Self-incompatibility is also met with when large plantings of fruit trees of the same variety are made. Unless two or more distinct varieties of different seed origin are inter-planted, no fruit is produced.

SEED OF THE SEEDLESS TIGER LILY

FIGURE 18. While the Tiger Lily has thus far failed to yield pods to intra-specific pollination, many have been obtained to pollen of *L. maximowiczii,* as is proved by the two fine pods on the plant at the right. To the pollen of *L. warleyense* only imperfect pods were developed, as shown in the two upturned but partly developed pods on the left. The Tiger Lily is evidently able to produce seed and its usual sterility is due to physiological incompatibility of the pollen used, and is not in any way connected with the fact that the plant habitually reproduces by means of bulbs.

In an effort to discover compatible fertilizations that would produce seed on the Tiger Lily, bulbs of this species have been secured from widely separated localities, some even coming directly from apparently wild plants in China. All plants grown from these have, so far as tested, failed to yield fruits either by self-pollination or by cross-pollination between the different strains. Capsules also failed to form when pollen of such species as *L. canadense, L. supurbum, L. henryi, L. speciosum, L. auratum,* and *L. humboldtii* was used. To pollen of *L. warleyense*, the ovaries of the Tiger Lily began to enlarge and become upturned (see Fig. 18), but the capsules did not develop fully and yielded no seeds. But when pollen of *L. maximowiczii* was used fine pods were readily obtained (see Fig. 18). Potted plants, plants grown in the open, old plants of vigorous vegetative growth, and plants from bulblets blooming for the first time have all produced fine pods from the flowers thus pollinated. Yet on these same plants complete failure resulted from all attempts to produce seed by self-pollination.

It is clear that these usually sterile plants are able to form fruit and seeds and that their pollen is potent, provided there are compatible relations in fertilization. The bulb and the bulblet-forming habits of growth, and of vegetative propagation do not render seed production impossible. The sterility is that of physiological incompatibility in fertilization, a well-marked type which is also seen in numerous species that naturally reproduce exclusively by seeds, and is by no means peculiar to plants that reproduce vegetatively.

In the course of experimental studies with species of Lilium now in progress at the New York Botanical Garden, controlled pollinations have been made for plants of twenty-eight species. In every species thus far studied seed production is decidedly limited by incompatibility in fertilization.

The phenomena of incompatibility are well illustrated by the results obtained with *L. regale,* a splendid and beautiful lily recently introduced from China. Of the ten plants tested, nine were self-incompatible and one was self-compatible. Cross pollination between plants sometimes succeeded and sometimes failed. The same sort of results were also obtained with plants of *L. speciosum, L. candidum, L. henryi, L. parvum, L. tenuifolium, L. humboldtii, L. kelloggii, L. warleyense, L. longiflorum,* and *L. auratum.*

No capsules have yet been obtained on plants of *L. hansonii, L. parryi, L. maximowiczii,* and *L. chalcedonicum,* but in all cases except that of *L. hansonii,* only a few plants have been tested, and these were all obtained from a single source.

### Cross-Incompatibility

It is to be noted that crosses between different plants of a species in which there is self-compatibility are also frequently incompatible. One is, however, not at all certain that any two plants of a variety of lily are really of different seed origin, for they both may be the daughter bulbs of a single parent plant, and thus belong to a single clone. If the original plant grown from seed was entirely self-compatible, then one may expect the members of the clone to fail to set seed in crosses. The condition is similar to that encountered in fruit-growing, when an entire orchard of a self-incompatible variety of apple or cherry fails to set fruit unless proper cross-pollination with another variety is provided for. Without doubt it is often the extensive vegetative propagation of a single self-incompatible plant that makes it difficult to secure compatible crosses from apparently different plants of certain varieties of the day lilies and the true lilies.

Seedlings of *L. longiflorum* have been grown to the flowering age in the course of the studies here reported. Many of these were self-incompatible, a few set seed with their own pollen, and many crosses with other plants failed. Such ranges of variation in regard to the compatibilities of sister plants of seed origin are very common in many species.

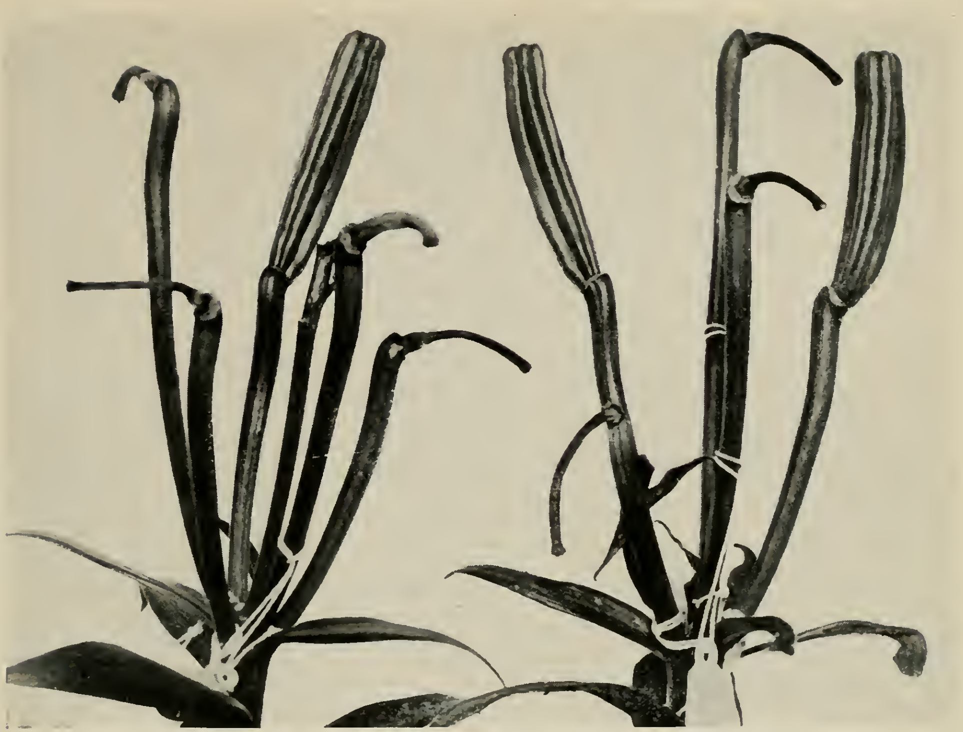
### Other Types of Sterility

There are other types of sterility in the lilies besides that of incompatibility. In certain hybrid varieties. *L. batemanniae,* for example, there appears to be complete impotence, a type of sterility that is very characteristic of hybrids; the spores, both in pistils and stamens, are aborted and functionless in any relation. A one-sided abortion characteristic of intersexes has also been noted in at least one species.

### How to Obtain Seed

The principal condition limiting seed production in the lilies is that of incompatibility. When seed is desired from plants that are yielding no seeds because of this condition, it is simply necessary to obtain other stocks of the same species and interplant so that cross-pollination may be effected by insects, or by hand. If the new stock is cross-compatible, seed will readily be produced, but if it is not, seed will not be formed until stock which is compatible is secured. Usually compatible clones may readily be obtained, and often a single planting of commercial bulbs contains such a mixture of stocks, but for certain species and especially for *L. tigrinum, L. hansonii,* and *L. candidum,* it seems somewhat difficult to secure compatible fertilization.

One of the principal sources of failure in establishing a planting of lilies in one's garden is the poor physical condition of bulbs when received. Especially is this true when bulbs are imported. In many species the dormant



RESULTS OF POLLINATION ARE QUICKLY EVIDENT

FIGURE 19. Both of these plants of *L. longiflorum* are self-incompatible and four crosses with other species likewise failed. The three growing pods are from other more successful crosses. The photograph was taken about two weeks after the last pollination was made.

period is very short or is entirely absent. With the death of the top there is usually continued development of the daughter bulbs, and growth of feeding roots. Without doubt the best means of securing healthy and vigorous bulbs, of many species at least, is to grow them locally either from seed or by vegetative propagation, and to transplant so that the bulbs are only out of the ground for a short time, when they are most nearly dormant.

Such excellent varieties as the Easter Lily, the Madonna Lily, Henry's Lily, the Lance-leaved Lily (*L. speciosum*), and the Regal Lily are readily grown from seed. Frequently blooms may be had on seedlings in two years—certainly they may be had in three years. The growing and breeding of lilies from seed presents many interesting possibilities, not only to the commercial growers of bulbs but to the amateur gardener as well.

In lilies the bulb habit of growth does not in the least affect seed production. To obtain seed one must either grow self-compatible plants or grow strains that are cross-compatible. When this is done, seed in abundance may readily be obtained except in the relatively few cases of impotence from intersexes or hybridity.

CONTRIBUTIONS FROM THE NEW YORK
BOTANICAL GARDEN—No. 241

# NOTES ON ROSACEAE—XIV

PER AXEL RYDBERG

NEW YORK
1923

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# Notes on Rosaceae—XIV

PER AXEL RYDBERG

## ROSES OF THE PRAIRIES AND PLAINS

The area here treated comprises the states between the Mississippi River and the Rockies and north of Oklahoma, with the exception of Missouri, in which so many southern plants are found and in which the Ozark Mountains have a different flora from the plains. As a key to the groups has already been published in a preceding paper,* I shall here omit the same, and I shall omit also the general discussion of any species already treated there, only citing specimens collected in the region now under consideration.

## I. SYNSTYLAE

Leaflets glabrous or slightly pubescent on the veins beneath, dark green and shiny above. 1. *R. setigera.*
Leaflets velutinous-pubescent beneath, rather dull above. 2. *R. rubifolia.*

### 1. ROSA SETIGERA Michx.

KANSAS: Cherokee County, 1896, *Hitchcock 676.*

### 2. ROSA RUBIFOLIA R. Br.

KANSAS: Manhattan, 1892, *Clothier.*

## II. CANINAE

### 3. ROSA RUBIGINOSA L.

KANSAS: Riley County, 1896, *J. B. Norton 677*; 1897, *Clothier 1107.*

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* See Bull. Torrey Club 45: 45–66. 1920.

## III. CAROLINAE

Leaflets not subcoriaceous.
  Infrastipular prickles decidedly curved, short, stout. 4. *R. palustris.*

  Infrastipular prickles straight (rarely slightly curved), slender.
    Leaflets decidedly pubescent beneath. 5. *R. Lyoni.*
    Leaflets glabrous or pubescent only on the veins beneath.
      Leaflets not glandular-dentate, the teeth usually simple. 6. *R. carolina.*
      Leaflets glandular-dentate, often with double teeth. 7. *R. serrulata.*
Leaflets subcoriaceous, densely pubescent beneath. 8. *R. rudiuscula.*

### 4. ROSA PALUSTRIS Marsh.

This has been reported only in the Mississippi and Minnesota River valleys, where the more pubescent western form has been found.

### 5. ROSA LYONI Pursh

KANSAS: Cherokee County, *Hitchcock 978.*
IOWA: Iowa City, 1916, *Wylie.*
Also reported from Minnesota.

### 6. ROSA CAROLINA L.

This has been reported from Minnesota and Kansas, but no specimens have been seen. It is found also in Wisconsin and Missouri.

### 7. ROSA SERRULATA Raf.

This has been reported from Iowa, but no specimens are now at hand.

### 8. ROSA RUDIUSCULA Greene

This belongs to the *Carolina* and not to the *Cinnamomea* group, having the hypanthium bristly and with the achenes inserted in the bottom only. The infrastipular prickles are small and scarcely stronger than the bristles. It also has spreading and deciduous sepals; and the leaflets are thicker and firmer than in *R. carolina* and *R. Lyoni.* The flowers are usually corymbose and the plant has the general aspect of *R. suffulta.* Dr. Greene in the original publications cited several specimens that do not belong to the species.

MISSOURI: Vale, 1906, *Bush 3916;* Little Blue, *Bush 208* (TYPE); Dodson, Jackson County, *Bush 160;* railroad north of Morley, 1893, *Eggert*; Grain Valley, *6998*.

IOWA: Amaxa, 1909, *M. P. Somes 3825*.

INDIANA: White County, southeast of Wolcott, *Deam 32712;* Laporte County, *32395*.

## IV. CINNAMOMIAE

- Infrastipular prickles wanting; branches unarmed or bristly, not prickly.
  - Inflorescence corymbose, terminating the stem (or rarely the branches); plant mostly suffruticose; stem very bristly, usually dying back to the ground (except in *R. polyanthema* and *R. Bushii*); leaflets 9–11.
    - Leaves glabrous or nearly so.
      - Leaflets obovate, pale and glaucous on both sides. — 9. *R. subglauca.*
      - Leaflets elliptic or oval, dark-green above.
        - Leaflets mostly 2–5 cm. long, not glaucous beneath, acute at the apex; plant 3 dm. high or more; flowers several. — 10. *R. arkansana.*
        - Leaflets rarely more than 2 cm. long, mostly rounded at the apex, somewhat glaucous beneath; plant 1–2 dm. high; flowers 1–3. — 11. *R. Lunellii.*
    - Leaflets densely pubescent, especially beneath.
      - Plant 3–6 dm. high, usually dying back to the ground.
        - Sepal erect in fruit; plant not glaucous.
          - Upper stipules and bracts not densely glandular; leaflets 1.5–4 cm. long; plant 3–5 dm. high. — 12. *R. suffulta.*
          - Upper stipules and bracts densely glandular; leaflets seldom more than 1.5 cm. long; plant 1–3 dm. high. — 13. *R. alcea.*
        - Sepals reflexed in fruit; plant glaucous. — 14. *R. conjuncta*
      - Plant shrubby, not dying back; branches from the upper axils soon overtopping the inflorescence. — 15. *R. polyanthema*
  - Inflorescence of few, either solitary or corymbose, flowers ending lateral branches; plant shrubby leaflets; 5–7 (or rarely 9 on the shoots).

Stem densely bristly even in age; stipules, petioles, and rachis often glandular-granuliferous; flowers solitary.
Hypanthium decidedly pear-shaped or elliptic, acute at the base, with a distinct neck at the top.
Leaflets conspicuously glandular-granuliferous, but scarcely at all hairy beneath, rounded-oval, often double-toothed. 16. *R. Engelmanni.*
Leaflets densely pubescent only rarely slightly glandular beneath, mostly elliptic, simple-toothed. 17. *R. acicularis.*
Hypanthium subglobose, almost without a neck; leaflets glandular-granuliferous as well as pubescent beneath. 18. *R. Bourgeauiana.*
Stem unarmed or when young slightly covered with more or less deciduous prickles; flowers solitary or few.
Leaflets decidedly and finely pubescent beneath. 19. *R. blanda.*
Leaflets glabrous on both sides, glossy. 20. *R. subblanda.*
Infrastipular prickles present.
Hypanthium globose; neck usually obsolete.
Stipules, petiole, and rachis copiously glandular; leaflets often double-toothed with gland-tipped teeth. 21. *R. Fendleri.*
Stipules, petiole, and rachis not conspicuously glandular, the first ones sometimes slightly gland-toothed.
Leaflets glabrous or nearly so. 22. *R. Woodsii.*
Leaflets finely puberulent beneath.
Young shoots armed with stout flat prickles; fruit about 15 mm. broad. 23. *R. terrens.*
Young shoots merely bristly; fruit rarely more than 10 mm. broad. 24. *R. Macounii.*
Hypanthium elongate, pyriform or elliptic, with a distinct neck. 25. *R. pyrifera.*

### 9. ROSA SUBGLAUCA Rydberg

This is related to *R. arkansana* Porter and *R. suffulta* Greene; from the former it differs in the decidedly obovate leaflets, rounded at the apex and more coarsely toothed; from the latter in the glabrous leaves; and from both in the glaucous foliage.

SASKATCHEWAN: Six miles east of Battle River, August 15, 1906, *Macoun & Herriot 70942, 70943*; Breakmore, July 18, 1906, *70941*; Brandon, *12589*.

A specimen from Decatur County, Iowa, collected by T. J. and M. F. L. Fitzpatrick may also belong here.

### 10. ROSA ARKANSANA Porter

This species was described from the Arkansas Cañon near Cañon City. The type is a glabrous plant and so described. The more common *R. suffulta* of the plains is densely pubescent. This was mistaken for *R. arkansana* by Watson, who has been followed by most American botanists. *R. arkansana* is found in the prairie region as well, but is much more local. It seems to be confined to the river valleys, while *R. suffulta* prefers the prairies and plains. *R. Rydbergii* Greene is nothing but *R. arkansana*. The peculiar hue of the upper surface of the leaves, so much emphasized by Dr. Greene, is due to some disease, probably bacterial. Some of the leaves or some part of them have retained their natural color on the upper surface. Best regarded it as a variety of *R. blanda*.

MINNESOTA: Winona, 1882, *Hasse Herbarium*.
NORTH DAKOTA: Fargo, *Bolley 129, 130*.
KANSAS: Comance County, 1897, *Carleton 254*.

### 11. ROSA LUNELLII Greene

This is closely related to *R. arkansana* and perhaps only a depauperate form of the same. It is, however, a much smaller plant and more glaucous, and the leaflets are more rounded at the apex.

MANITOBA: Brandon, 1887, *Fowler;* 1898, *E. S. Thompson*.
NORTH DAKOTA: Leeds, 1907 and 1908, *Lunell*.
SOUTH DAKOTA: Hermosa, 1892, *Rydberg 678a*.
NEBRASKA: Long Pine, 1893, *W. R. Dudley*.

### 12. ROSA SUFFULTA Greene

The first record of this species is in Hooker's Flora Boreali-Americana, where Borrer referred it to a variety of *R. stricta*. Crépin made it a variety of *R. blanda* and Watson confused it with *R. arkansana*. Dr. Greene was the first to see that it was not *R. arkansana* and proposed the name *R. pratincola*, overlooking the fact that this name had been used before. Discovering this fact twelve years later, he substituted the name *R. heliophila*. C. K. Schneider discovered the same fact a year later, but not knowing of Greene's last name, proposed *R.*

*arkansanoides.* All these names are superfluous, however, for the plant is the same as *R. suffulta* Greene. Besides these names several varietal names have been proposed. *R. dulcissima* Lunell is apparently based on a more luxuriant and less bristly form of this species.

### 13. ROSA ALCEA Greene

This species stands somewhat in the same relationship to *R. suffulta* as *R. Lunellii* does to *R. arkansana.* The plant is described as having prickly hypanthium, but this is not always the case. The upper part of the plant, especially the upper stipules and the bracts, are densely glandular, the glands often extend to the pedicels and hypanthium, the stalks of the glands sometimes become indurate and hence the hypanthium is prickly in fruit. This is sometimes also the case in *R. suffulta,* which form was described as *R. pratincola setulosa* by Cockerell.

SASKATCHEWAN: Milk River Ridge, 1895, *Macoun 10541;* Moose Jaw, *Spreadboro 10625;* also *Macoun 10539;* Regina 1903, *Fowler;* Indian Head, *1;* Prince Albert, *Macoun 12767* (?).

SOUTH DAKOTA: Deadwood, *Carr 150.*

### 14. ROSA CONJUNCTA Rydberg

This is related to *R. suffulta* and *R. subglabra* on the one hand, and to *R. virginiana* on the other. It differs from the last in the lack of glandular hairs on the hypanthium; in the pale green leaves with sharper toothing; in the absence of infrastipular spines; and in the insertion of the achenes, which is on the inside walls as well as in the bottom of the hypanthium. From *R. subglauca* it differs in the leaves pubescent beneath and in the reflexed sepals. It resembles *R. suffulta* in habit and pubescence, but the leaflets are more acute at the apex and cuneate at the base and glaucous, and the sepals are reflexed or spreading after anthesis. As the plant has been confused with *R. suffulta* and *R. arkansana,* this latter character caused the error in Britton's Manual, in which *R. arkansana* (which then included *R. suffulta*) was described as having spreading sepals. I am responsible for the error. *R. conjuncta* might be a hybrid of *R. suffulta* and *R. Lyoni* or some other species of the *Carolina* group, but none of the species of that group or of the *Cinnamomea* group (except the high northern *R. subglauca*) has the glaucous foliage of *R. conjuncta*. Hence it must be regarded as a distinct species.

### 15. ROSA POLYANTHEMA Lunell

This species resembles *R. suffulta* in the leaf-form and inflorescence, but the plant is shrubby, the upper branches soon overtopping the inflorescence. It is known only from the type locality and vicinity.

### 16. ROSA ENGELMANNI S. Wats.

In describing this species Dr. Watson included some eastern specimens which belong to *R. acicularis*. This has caused much confusion. Some botanists have regarded *R. Engelmanni* as a variety of *R. acicularis*, some as a mere synonym. *R. Engelmanni* is a purely Rocky Mountain species. The most eastern station from which the writer has seen the same is in the Black Hills of South Dakota. The specimens referred to it from Minnesota, Michigan and northern New York belong to *R. acicularis*. In *R. Engelmanni* the leaflets are much more rounded, without pubescence, but distinctly glandular-granuliferous beneath, usually double-toothed and with gland-tipped teeth. In *R. acicularis* on the contrary the leaflets are inclined to be elliptic, conspicuously pubescent but scarcely glandular beneath and with simple teeth.

Most of the specimens seen of *R. Engelmanni* are from Colorado and a few are from southern Wyoming. The only specimens from the region here treated are the following, but even these are not from the prairies and plains but from the mountains or wooded hills.

SOUTH DAKOTA: Spearfish Cañon, Black Hills, *Murdock 4136*; Rochford, *Rydberg 676* (in part); Custer, *Rydberg 676* (in part).

### 17. ROSA ACICULARIS Lindl.

Within the region the species is found only in the northern wooded part. Among other specimens may be mentioned:

MINNESOTA: Sandy Lake, *Sandberg 793*.

### 18. ROSA BOURGEAUIANA Crépin

Within the region it is found only in the northeastern wooded region.

MINNESOTA: Duluth, *Rydberg 8004*; St. Louis River, Carlton County, *Sandberg 130;* Two Harbors, *E. P. Sheldon.*

### 19. ROSA BLANDA Ait.

This species is confined within the region to the hardwood groves in the northern part. I can see no difference between the specimens from North Dakota, on which *R. gratiosa* Lunell was based, and those from the Eastern States.

MINNESOTA: Lake Minnetonka, *Sandberg, 798;* Thompson, Carlton County, *Sandberg 397;* Minneapolis, 1895, *E. P. Sheldon;* Lake Itasca, *G. B. Aiton.*

NORTH DAKOTA: near St. John, Rolette County, 1912, *Lunell* (*R. gratiosa*); Pleasant Lake, Benson County, 1912, *Lunell;* Turtle Mountains, 1912, *Lunell*; Bottineau, 1890, *Waldron.*

MANITOBA: Oak River, *Macoun & Herriot 70937;* six miles east of Forest, *Macoun & Herriot 70940.*

### 20. ROSA SUBBLANDA Rydberg

It is questionable if this species should be included among the prairie roses, as the following specimens are referred to it with considerable doubt.

IOWA: Grinell, 1877, *M. E. Jones.*

### 21. ROSA FENDLERI Crépin

This species is related to *R. Woodsii* and often confused with it. It is distinguished by the glandular stipules, petioles, and leaf-rachis. Watson distinguished it from *R. Woodsii* by the entire instead of lobed sepals. In both species they are either entire or lobed. *R. neomexiana*, *R. arizonica*, *R. puberulenta* and *R. granulifera* have been confused with it, but these all have curved prickles, while in *R. Fendleri* they are longer and more slender, straight or nearly so. *R. Fendleri* is a common species in the Rockies, ranging from Montana to northern Mexico. It extends eastward also into the plains and prairies and was redescribed from North Dakota by Lunell as *R. poetica.*

MINNESOTA: Montevideo, *Moyer 581.*

NORTH DAKOTA: Bismark, 1912, *Lunell.*

SOUTH DAKOTA: Hermosa, *Rydberg 677.*

NEBRASKA: McCalligan Cañon, Deuel County, *Rydberg 100.*

### 22. ROSA WOODSII Lindl.

This was published in 1820 in Lindley's Monograph. Five years later Lindley published an illustration in the Botanical Register of what he supposed to be the same, but evidently he was mistaken. In the Botanical Register (*pl. 976*) Lindley gave the following remarks:

> It was subsequently named and published by the writer of these remarks . . . but the specimens which were examined for the purpose, were so imperfect that, upon a comparison of the characters ascribed to the species with fresh specimens, they were ascertained to be materially erroneous; the stipulae, which were stated to possess the remarkable peculiarity of being convolute like those of *R. carolina*, proving to be, in fact, like those of *R. lucida.*
>
> But in M. de Candolle's Prodromus a new character is proposed for this plant. M. Seringe, by whom the article Rosa was prepared, had an opportunity of examining specimens in De Candolle's Herbarium. And yet our original error is still retained by Mr. Seringe, who has added to it more than one of his own. He defines the leaflets to be shining, while in fact they are the reverse; the sepals to be naked, which are covered with glands; and the lower pair of leaflets to be placed at a distance from the others, and fringed with glands, a peculiarity which we believe does not exist. *
>
> We cannot dismiss this subject without expressing our regret that the general brilliancy of M. de Candolle's Prodromus should be tarnished by an article so inaccurately compiled as the genus Rosa is, in the 2d volume of that work.

These cutting remarks of Lindley's were wholly unwarranted, for Seringe did not assign any new characters that were not found in Lindley's original publication, and it was the latter himself that assigned new characters. Let us recite a few lines from Lindley's own description in his Monograph, page 22.

> *Leaves* without pubescence; stipules very narrow and acute, convolute and fringed with glands . . . *Leaflets* 7–9, shaped like those of *R. rubella*, shining, flat, simple, acute, paler beneath . . . *Fruit* naked, ovate, with short, connivent, entire *sepals* which are free from glands as is the peduncle.

From this it is evident that *Rosa Woodsii* of the Botanical Register is not the same as the original one described in Lindley's Monograph. This carelessness on Lindley's part has caused a great deal of confusion, and it is hard to know what the original *R. Woodsii* was. Some have suggested *R. humilis*, but as the pedicels, hypanthium and sepals were without glands and the latter connivent, this suggestion is far from the truth.

Others have suggested *R. blanda* Ait., but the true *R. blanda* is a boreal plant and not found on the Missouri, and the leaves are dull and pubescent beneath. The *R. Woodsii* of the Botanical Register might sooner be a form of that species. The only species that agrees with the description of the original *R. Woodsii* is the one that Torrey called *R. foliosa leicocarpa* and in my flora of Colorado I called *R. Macounii*, the same as Greene has described as *R. Sandbergii* and Lunell as *R. deserta*. I also think *R. fimbriatula* Greene belongs here. It is a shrub belonging to the Rocky Mountain region but extends eastward to the Missouri River. Watson referred it partly to *R. Woodsii*, partly to *R. Fendleri*. Watson assigned also new characters to *R. Woodsii*, viz. lobed sepals. Notice that Lindley originally described them as "entire." The lobing or not-lobing of the sepals is a character of no value in the *Cinnamomea* group. In other groups as for instance, the *Carolina* and *Canina* groups, it is a fairly reliable character. *Rosa Maximiiliani* Nees belongs to this species.

NORTH DAKOTA: Pleasant Lake, Benson County, 1912, *Lunell* (*R. deserta* Lunell); Little Missouri River, *Moyer 702*.

SOUTH DAKOTA: Missouri River, north of White River, *Hayden 254;* White River, *Stearns*.

NEBRASKA: Cheyenne County, *Rydberg 101*.

KANSAS: Rawlins County, *Hitchcock 978a*.

### 23. ROSA TERRENS Lunell

This species differs from all the species of the *Cinnamomiae* of eastern North America in the stout prickles especially on the shoots. The prickles are fully as stout as those of the sweet brier. It is only known from the type collection.

### 24. ROSA MACOUNII Greene

It has been shown that the pubescent plant illustrated by Lindley in the Botanical Register under the name *R. Woodsii* has had a very confused nomenclatorial history. Watson thought it was the original *R. Woodsii* and stated that it was the same as *R. Maximiliani* Nees. At the time when I noticed the discrepancy in Lindley's treatments, I thought that Watson's statement was correct and adopted the name *R. Maximiliani* for the present species. The name was used in that sense in my

Flora of Colorado. Later I have had access to Prince Maximilian's Reise and found that the plant described there was the glabrous plant or the true *R. Woodsii.* In my Flora of Colorado I made another mistake, adopting the name *R. Macounii* for the glabrous plant, depending upon the impression I had received from Greene's rather vague description. After having seen Greene's type, though this does not represent the common form of the species as I know it, I came to the conclusion that the name *R. Macounii* should be adopted for the species here treated, being the oldest available name. *R. grosseserrata* E. Nelson was a mixture, but the type evidently belongs to the large-leaved form of this species not uncommon in the Central Rockies. *R. subunda* Lunell represents a depauperate form and *R. naiadum* the more common form of the plains and prairie region.

MINNESOTA: Montevideo, *Moyer 372.*

NORTH DAKOTA: Kuhn, La Mouse County, *Brenckle;* Minot, Lake Ibsen, Jamestown, Tower, and Butte, *Lunell* (without numbers).

SOUTH DAKOTA: Hermosa and Hotsprings (Black Hills), *Rydberg 677;* Wolf Creek, *Visher 2189;* Bear Creek, *Visher 2032;* Mobridge, *Moyer 691*, Big Stone Lake, *542*

NEBRASKA: Chadron, *J. M. Bates;* Lawrence Fork, *Rydberg 102;* Banner County, *Rydberg 98;* Hay Springs, *MacDougal 102;* Nattick, Thomas County, *Rydberg 1848.*

### 25. ROSA PYRIFERA Rydberg

This is a species of the Northern Rocky Mountains, first mentioned by Watson in a note under *R. Fendleri.*[*] It differs in the pear-shaped fruit and the more numerous, rather corymbose flowers. A few rather dubious specimens have been collected in the plains and prairie region. These have fruits which are inclined to be ellipsoid, rather than pyriform. Among them may be noticed.

SOUTH DAKOTA: Mobridge, *Moyer 688.*

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[*] Proc. Am. Acad. 20: 345. 1885.

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# THE VEGETATIONAL HISTORY OF THE MIDDLE WEST

HENRY ALLAN GLEASON

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# THE VEGETATIONAL HISTORY OF THE MIDDLE WEST

HENRY ALLAN GLEASON

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## PART I

THE DYNAMIC VIEWPOINT.—Many years have elapsed since Engler published his famous and fundamental "Leitende Ideen," which he had adopted as a basis for his discussion[1] of the Tertiary and Pleistocene development of the vegetation of the earth. Here, in thirty-six concise paragraphs, he summarized the general principles controlling the distribution of species and of species-groups. The first two of them serve as a summary for all:

"1. Die gegenwärtige Verbreitung der Pflanzen ist nicht blos bedingt durch die jetzt auf der Erde herrschenden klimatischen Bedingungen und die Bodenverhältnisse.

"2. Ein wahres Verständniss der Verbreitung der Pflanzen ist nur dann möglich, wenn man die allmälige Entwicklung derselben zu ermitteln sucht."

Engler was apparently inspired to his studies of vegetational history and development, at least in part, by the classic essays of Asa Gray.[2,3,4] His lead was followed by numerous European botanists, who, assisted by the co-operation of palaeontologists and glacial geologists, have in the past two decades contributed greatly to the knowledge of the phytogeographical history of central and western Europe. Later American botanists, on the other hand, neglected such lines of investigation almost completely and their phytogeographical activities were confined, as is natural in relatively new regions, to descriptions of floras and the determination of modern distribution. It remained for Adams[5,6] to revive developmental biogeography in America and to show that the distribution of a species can be satisfactorily explained only through the location of its origin and the nature of its subsequent migrations.

GENERAL CONTROL OF DISTRIBUTION.—The distribution of plants, as shown by Engler's principles quoted above, depends, in general terms, on modern environment and earlier developmental history. Both

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[1] Engler, Adolph. Versuch einer Entwicklungsgeschichte der Pflanzenwelt, insbesondere der Florengebiete, seit der Tertiärperiode. Leipzig, 1879.

[2] Gray, Asa. The flora of Japan. Scientific Papers 2: 125–141. (1859) 1889.

[3] Gray, Asa. Sequoia and its history. Scientific Papers 2: 142-173. (1872) 1889.

[4] Gray, Asa. Forest geography and archaeology. Scientific Papers 2: 204–233. (1878) 1889.

[5] Adams, C. C. Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull. 3: 115–131. 1902.

[6] Adams, C. C. Postglacial origin and migrations of the life of the northeastern United States. Journ. of Geog. 1: 303–310, 352–357. 1902.

of these are intimately concerned with migration, the latter factor portraying its progress and the former its limitation. Neither factor alone can account completely and satisfactorily for the present range of any species. This is the resultant of its range at any period in the past and its opportunities for subsequent migration; one exposure in the long film of an activity which has been continued since the origin of the species. If logs in the glacial drift show that *Pinus Strobus* formerly existed in central Illinois and experiment proves that it can thrive there now, historical evidence must be used to show why it left: modern conditions may show whether and why it is not returning.

Vegetational History and Human History.—The history of the vegetation of the Middle West, as of every other portion of our continent, is a history of repeated migrations of diverse floristic elements, arriving in the region from various directions, persisting there for various lengths of time, and finally retreating under the pressure of environmental changes which made their position no longer tenable. This history has been complicated by the extinction of old and the differentiation of new species, by the mingling of species of originally different history, and by the persistence of isolated relics of early migrations. In all these respects, vegetational history exhibits a striking parallelism to human history. Thus Europe has witnessed during the last two millenniums the extinction or absorption of the early Iberians, the persistence of the Basques, the arrival and retreat of the Moors and Turks, and an enormous evolution in culture. Furthermore, the underlying causes of vegetational and human history are similar, even though the human species exhibits an exceedingly complex relation to its environment. The geography of man has long been recognized as merely the present condition of his history, and the relations of both to natural conditions and processes have been well summarized.[7] Unfortunately, no such summary exists for plants.

Outline.—It has therefore been necessary to preface this history of plant life in the Middle West, presented in Part IV., by a discussion of the conditions and nature of plant migrations in Part II., and by a resumé of the evidence used in determining past migrations in Part III.

## Part II. The General Nature of Plant Migrations

A great body of literature dealing with the migration of plants has appeared in the last century and a half. This has been so well summarized by Clements[8] that it needs no further discussion here. Most

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[7] Semple, Ellen C. Influences of geographic environment. New York, 1911.

[8] Clements, Frederic E. The development and structure of vegetation. Studies in the vegetation of the state III. Botanical Survey of Nebraska VII. Lincoln, 1904.

of it deals with the migration of individual species, and Clements' exposition of the whole subject is without doubt the best general treatment extant.

Invasion, Migration, Ecesis.—Following Goeze, he considers the general movement of species or associations under the term *invasion,* and recognizes that this consists of two distinct processes. One of these, to which he restricts the term *migration,* involves merely the movement of the plant by means of its reproductive bodies or vegetative processes. The mechanics of such movement, the methods of seed dispersal or vegetative propagation, while exceedingly diverse, are already well understood and require no discussion here. The second process, which he terms *ecesis,* includes the actual establishment of the plant in a new location. Ecesis depends entirely upon the environmental conditions of the new location in their relation to the physiological requirements of the seedlings. The details of these relations are for most plants entirely and for all plants mostly unknown, and are to be determined by the methods of experimental ecology. Migration, in Clements' use of the term, is completely unsuccessful in the failure of ecesis, and ecesis, to be effective and complete the process of invasion, must be carried to the maturity of the plant and the production of a second generation of disseminules. The distinction between the two processes is fundamental, and Clements' clear analysis has done much to systematize the knowledge of the subject.

The term *invasion,* which Clements applies to the whole phenomenon of movement, is in many cases scarcely appropriate. His own definition and the general meaning of the word both imply a movement of plants into an area not before occupied by them, that is, an extension of their range. As a matter of fact, the migration of plants is almost or quite as frequently out of an area previously occupied as into a new one, and then involves a retreat or restriction of their range, a result to which the term invasion can not be properly applied. The term migration, in the sense of Clements, is distinctly a process of one generation. Ecesis involves the development of a second generation of individuals, but scarcely applies to the whole population of a species. Yet these processes, participated in by a whole population and continued regularly through successive generations, may lead to broad results far more inclusive than those chiefly considered by Clements. For the purposes of this article, the migration of plants is understood as any general movement by which the range of a species is changed.

Efficiency of Plant Dispersal.—The efficiency of plant dispersal is well understood. Each normal individual produces one or many crops of seeds or other reproductive bodies and these are dispersed thoroughly over the surrounding territory to an extent dependent upon their structure and their environment. At the margin of the present range of a species, whether that margin is the boundary of an association in which it occurs or the general margin of its whole range, seeds are annually dispersed in all directions, inward through its present range and outward and beyond it as well. Examples of this are well known and need not be cited. Except in comparatively infrequent cases, where the ability to produce seeds or other reproductive bodies is lost, the potentiality of continuous and extensive migration is constantly present. The slow rate of actual normal migration is not due to inefficiency of the migratory devices of the plant, nor, except as mentioned above, to deficient seed production, but to the inhibiting effect of environmental factors in the area beyond the present distribution of the species. This is particularly true toward the center of the range. Every swamp is annually and abundantly planted with seeds of upland species, while the swamp plants are simultaneously distributed over the upland, and in neither case do any of them grow, except under the most unusual circumstances.[9] Even at the margin of the specific range, where reduced or intermittent seed production might be expected, Griggs has shown that many species are able to propagate themselves freely.[10]

There is for each species a general limit of distance over which its seeds may be dispersed. The number of seeds arriving on any area diminishes with increasing distance from the parent plant; in fact, for small distances, the number seems to vary inversely as the square of the distance. Since only a small portion of the seeds germinate and grow to maturity, most young plants of the second generation are located relatively close to the parent.

MIGRATION AND SUCCESSION.—Actual migration, therefore, requires a change in the existing environment for its inception. (The abnormal type of migration, due to the acquisition of new means of dispersal by which previous environmental barriers are crossed, is mentioned in a later paragraph.) A migratory advance postulates the development of individuals in territory not previously occupied and requires an environmental change of sufficient extent not merely to permit the growth of the migrants, but to permit it against the competition of the previous inhabitants. A migratory retreat requires a detrimental

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[9] Brewster, William. Occurrence of the skunk cabbage in an unusual place. Rhodora 11: 63, 64. 1909.

[10] Griggs, Robert F. Observations on the behavior of some species at the edges of their ranges. Bull. Torrey Club 41: 25–49. 1914.

change, either in physical conditions or in their control by plant life or in parasites and enemies, sufficient to prevent the establishment of new plants in the immediate vicinity of the parent, so that the species disappears from the habitat with the death of existing individuals. Succession results when migration is so complete and is shared by individuals of so many species that the nature of the vegetation is fundamentally changed. The close relation between succession and migration have been noted elsewhere,[11] and the nature of the causal environmental changes have been discussed in detail by Clements.[12] Instances are of course well known in which species migrate into an association and become an integral part of it without causing succession. Thus in parts of New Jersey *Daucus Carota* has entered the hemlock-maple forest, and in northern Michigan *Rumex Acetosella* has become widely distributed through the aspen association. Such a result may be termed taxonomic succession, as distinguished from the ecologic succession previously mentioned.

Rate of Migration.—The simple production, movement, and establishment of reproductive bodies, constituting together the method of migration, is not the only factor concerned in the process. The rate of migration depends upon one or the other of two conditions: the rate of environmental change and the migration-capacity of the plant. The latter condition may in turn be resolved into two components; the mobility of the plant, depending on the structure of its migrating parts and its ability to utilize the necessary environmental agencies, and the length of its juvenile period, which must be completed before a new crop of disseminules is produced to continue the march. Migration-capacity may be formulated in general terms as mobility divided by length of juvenile period. Hence those plants which combine excellent structural devices for dispersal with a short vegetative cycle, such as the dandelion (*Taraxacum*), migrate more rapidly than others with less mobility, as lamb's-quarters (*Chenopodium*), or with a long vegetative period, as the maple (*Acer*), while slowest of all are those plants which lack both favoring features, as the oak (*Quercus*). The actual rate of migration is fixed by the slowest of the two general conditions. If environmental change is slow, migrating species may keep even with it and continually scatter their seeds forward into territory where they can not yet grow. If environmental change is rapid, the slower species may not be able to keep even with it and consequently follow

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[11] Gleason, H. A. The structure and development of the plant association. Bull. Torrey Club 44: 463–481. 1917.

[12] Clements, Frederic E. Plant succession, an analysis of the development of vegetation. Carnegie Inst. Washington, Publ. 242. 1916.

at a distance far behind other more mobile forms. Thus in the slow extinction of a pond by the deposition of peat, there is no break in the time-continuity of the contracting zones of vegetation around it, since mobility exceeds the rate of environmental change. But if a pond is drained artificially, producing in a single year an effect similar to that of a century of peat formation, the more mobile species enter first on the freshly exposed area and some years may elapse before all the remainder have appeared. So also the sudden cessation of prairie fires on parts of the prairies led to the immediate advance of the forest, and the more mobile species composed the bulk of the early invaders. In general, migration connected with physiographic succession keeps pace with the environmental changes, so that associations are well marked and the correlation between zonation and succession is prominent. Even such a slow environmental change as the advance or retreat of a continental glacier may have been too rapid for some species, while certainly slow enough for others. Numerous species were doubtless destroyed completely with the advance of the glaciers and others during their retreat, from inability to keep pace in their migration with the changing conditions of the environment.

The most rapid rate of migration is found in the anthropochorous species which utilize human activities for their dispersal. Such not only move with extreme rapidity, but by the nature of their dispersal are able to cross barriers quite impassable for other species. Our own country has been occupied during the past century by hundreds of such species which have crossed an ocean to reach us and have spread hundreds of miles over the land in a very short time. Yet most of these same species are stopped completely by an area of undisturbed natural vegetation, which they are unable to colonize.[13]

The Time Factor and Migration.—The present status of migration depends upon its rate, as discussed in the preceding paragraph, and on the elapsed time since migration began. The more rapidly moving species may be at the limit of their present potential range and wait upon further environmental change, while the slower ones may be far from their actual limit, although progressing toward it at their best speed. The condition is well illustrated in the belts of forest which parallel the rivers of Kansas and Nebraska, in which, in general, the more mobile species have extended farthest to the west.[14] It is also prominent throughout the prairie region of the Middle West, where

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[13] Gleason, H. A. & F. T. McFarland. The introduced vegetation of the vicinity of Douglas Lake, Michigan. Bull. Torrey Club 41: 511–521. 1914.

[14] Kellogg, R. S. Forest belts of western Kansas and Nebraska. U. S. Dep. Agr. Forest Bull. No. 66. 1905.

there is a continuous movement of the more mobile forest species into the land originally occupied by prairies.

The time factor naturally begins with the origin of the species concerned. Those of relatively recent origin have had little time in which either to extend or to contract their original ranges. Since major environmental changes are usually slow in their accomplishment, recent species have in general had also relatively little opportunity to use their migratory abilities. Such species are therefore restricted more closely to the site of their origin.

It is probably true, however, that many of our species have not had a single point or even a limited area of origin. The bulk of later Tertiary plants, as far as palaeontological evidence indicates, are of genera still existing, and many of the comparatively few known species of Pleistocene plants are either identical with or closely similar to existing species. Such evidence deals especially with woody plants, but what is true of them is doubtless true of herbaceous plants as well. The distinction between such Pleistocene plants and their modern representatives may depend largely on a break in the record, on a period from which fossils are lacking. Probably if a complete series of specimens were at hand, showing comprehensively the maples of the eastern states, for example, from the Pliocene to the present time, it would be seen that some of the earlier forms are absolutely continuous with our present species and that the slight morphological distinctions between them are only the result of continuous slow variation throughout the centuries. According to this view, many modern species had no localized origin and are not the offshoot of any parent, but represent the mass development of a species, which, under our present taxonomic ideas, came to a stop at the beginning of a break in our geological record of it and reappeared as a new species at the beginning of our next experience with it. During the long history of such a species, most of which is unknown to us, it may have migrated repeatedly in various directions, occupied larger or smaller areas, been separated into disjunct regions and again united, or one part of its population exterminated, and its range as we see it today represents merely the present condition of this long development. We are never sure of the prehistoric stages in this history, through the imperfections in the fossil record, but in certain cases we can arrive at some idea about them by circumstantial evidence.

Such a consideration does not account for the multiplication of species. Whether that is caused by mutation, natural selection, or hybridization, it seems certain that their perpetuation to the present time has depended greatly upon their ability to migrate as changes of environment demanded.

SIGNIFICANCE OF THE MARGIN OF RANGE.—The margin of the range of a species, then, does not always represent the boundary of the territory in which the species can or will live under present conditions, but merely the distance which it has travelled so far in its march to this goal. Instances are not lacking, of course, in which this migration has been completed and further extensions or retractions of the range wait upon future climatic changes. As one illustration, the distribution of *Pinus ponderosa* along the eastern foothills of the Rocky Mountains may be cited, where it has been clearly shown[15] that the species is now at the margin of its potential range. On a smaller scale, a sharply marked boundary between two associations indicates completed migration in that restricted area of the species on both sides of the boundary to the limits permitted by the present environment.

ADVANCING AND RETREATING MIGRATIONS IN THE MIDDLE WEST.—Both advancing and retreating migrations are now in progress in the states of the Middle West. In most cases these movements are too slow to come under direct observation, and reported extensions of ranges are generally due to incomplete or faulty early observations. Still the rapid spread northward of *Prosopis glandulosa* from Texas across Oklahoma into Kansas,[16] the westward migration of trees along the rivers of Nebraska,[14,17] and the recent discovery of young trees of *Quercus palustris* in southeastern Nebraska[18] may be cited as instances of visible migration. In general, migration is shown chiefly by the rôle of the species in succession. If, at or near the edge of its range, it participates in succession as an invading species, it is advancing; if it is not able to hold its own in competition, if the associations of which it is a member are regularly succeeded by others of which it is not a part, a retreating migration is indicated. This is illustrated in Michigan and Wisconsin by the regular succession of coniferous associations by deciduous forests, indicating the retreat of the conifers and the advance of the deciduous trees.[19]

EFFECTS OF CHANGES IN PHYSIOLOGICAL REQUIREMENTS.—There is no reason why changes in the physiological requirements of a species

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[15] Dodds, Gideon S., Francis Ramaley, & W. W. Robbins. Studies in mesa and foothill vegetation, I. Univ. Colorado Studies 6: no. 1, 11–49. 1908.

[16] Bray, William L. Distribution and adaptation of the vegetation of Texas. Bull. Univ. Texas 82. 1906.

[17] Bessey, C. E. Are the trees advancing or retreating upon the Nebraska plains? Science II., 10: 768-770. 1899.

[18] Pool, Raymond J. Pin oak in Nebraska. Torreya 20: 50-52, 1920.

[19] Whitford, H. N. The genetic development of the forests of northern Michigan: a study in physiographic ecology. Bot. Gaz. 31: 289–325. 1901.

might not have the same effect as a change of environment in causing migration. It is well known that plant breeders have developed new races of cultivated plants which thrive in climates different from that of the original home of the species. Possibly the rapid spread of American Opuntias in parts of Australia may be explained in this way. Under natural conditions, such changes in physiological requirements are usually correlated with changes in structure, and the latter are used as a basis for taxonomic differentiation. Whenever such evolutionary changes appear, new areas may be opened to the new species and eventually occupied by them. So such genera as *Eupatorium* and *Vernonia,* originating probably in northern South America, have migrated northward into the cold-temperate zone, as evolution has changed their physiological requirements and morphological structure. So have bromeliads migrated away from the humid tropical forests, entered the deserts of southern Mexico, and established themselves as epiphytes on the cacti;[20] so have the cacti migrated out of the desert region, where they probably originated, and established themselves as epiphytes in the tropical forest.

MIGRATIONS AS RELATED TO CONTINUITY OF SUITABLE HABITATS.—The range of every species is discontinuous. Throughout its whole area only particular habitats are occupied, leaving others to different species and associations. In each habitat, the space is shared with other associated species. These phenomena are in general of ecological rather than geographical interest, but are still of importance in their relation to the direction of migration. Within the habitat, so far as the association is continuous, even the least mobile species may migrate freely and ultimately attain a uniform distribution.[11] But from one habitat to another, the means of dispersal must be sufficient to carry the species across the intervening gap, which becomes a barrier to the less mobile forms. During the long course of time, accidents of dispersal may carry many species across a barrier, but accidents are probably not as efficient as frequently supposed. Mink Grove and Lynn Grove, two isolated areas of forest in Champaign County, Illinois, had large trees in them when first observed by white men nearly a century ago, and their age is doubtless 150 years at a minimum. Although these groves lie but a few miles from the nearest strips of forest along streams, in which species of *Hicoria* and *Quercus* are abundant, not an individual of these genera has reached them. Extensive migrations of plants, proceeding at a relatively rapid rate, therefore take

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[20] MacDougal, D. T. Botanical features of North American deserts. Carnegie Inst. Washington, Publ. 99. 1908.

place along routes where suitable habitats are nearly continuous, such as river valleys for mesophytic species or interfluvial uplands for xerophytic forms. There is every reason to believe that the postglacial migration of the deciduous forests into the Middle West followed the river courses almost exclusively. From these earlier migrations along the line of least resistance, a slower type of migration gradually extends the range out upon other habitats. This follows regularly the physiographic development of an area, as Cowles has shown,[21] and may also be induced by the reaction of an association upon the environment in the margin of a contiguous association beyond it.[11] So the forests of the Middle West, entering the region along the nearly continuous habitats of the river courses, where they migrate rapidly, have also spread at right angles to them, but more slowly, until in some cases those of different river systems have become united.

Each important change in the climate or the configuration of the land, due to geological causes, has created new migration routes and destroyed old ones, interrupting migrations then in process and initiating new ones, which may progress in different directions and be participated in by plants of different origin. There is evidence of several such migrations in the Middle West, which are discussed in Part IV.

The Interpretation of Isolation.—Actual geographical isolation of a species, in the ordinary sense, is effective only when an outlying habitat is separated from the general range by a distance greater than the migration-capacity of the plant. Instances of this are too well known to need citation. Only two explanations are possible for such a condition. Either the species has had two separate and independent origins, or else the vicissitudes of migration have brought it about. Even if the possibility of the former alternative is admitted, the latter is the more plausible in the majority of cases. It implies that the two disjunct bodies of the species were at some time one, either in a territory from which both portions have migrated and which is no longer occupied, or through the existence of connecting links between the two which have now disappeared. Both cases have been caused by a retreating migration.

Environmental changes which permit the advance or compel the retreat of one species are quite likely to affect others similarly, since associated species demand in general the same environment. Migration is therefore concerned with numerous species simultaneously.

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[21] Cowles, H. C. The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification of plant societies. Bot. Gaz. 31: 73–108, 145–182. 1901.

Whole floras migrate together, the hardiest and most mobile species first, the others in their train. They establish successional series in the region which they enter, and build up new associations in the new territory. These are analogous to the associations of their original range, but differ in the absence of the slower moving species and in the presence of laggards from the retreating flora.

Just as portions of a single species may be isolated during its migrations, so may areas of one type of vegetation be completely surrounded by an advancing flora and left isolated from the main body. These are known as relic colonies. The cause of such isolation is the failure, up to the present time, of sufficient environmental change to cause their extinction, or, in ecological terms, it is the relative slowness of the succession in certain habitats unfavorable to most of the advancing species. These habitats remain with their original vegetation upon them, while elsewhere it is displaced. Such relic colonies are of common occurrence wherever migrations are recent. Every movement of vegetation has certainly left relic colonies behind it, but their perpetuation to the present time depends absolutely on the continuation of an environment not only favorable to the relic species but distinctly unfavorable to the invaders.

ADJUSTMENTS IN DISTRIBUTION.—The distribution of a species and the distribution of vegetation must both be regarded as subject to continual adjustment. Boundaries extend and contract, associations advance and retreat with every geographical fluctuation of the environment. Even within the limit of a single association, every minor environmental variation, whether geographical or seasonal, is marked by the entrance or disappearance of some species, or by changes in the numerical proportion of the others. This may account for the conditions recently reported on Mt. Marcy,[22] where twenty-one species formerly reported by Peck have apparently disappeared and seven " rather conspicuous plants, which such a careful botanist could scarcely have missed, have apparently come into the flora."

GENERAL RESULTS OF CONTINUED MIGRATIONS.—Obviously the general result of continued migrations is the mingling of floras of diverse origin, while great climatic changes or important geological episodes tend toward the segregation of floras and the consequent initiation of new migrations. Regions affected by Pleistocene glacia-

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[22] Adams, C. C., Geo. P. Burns, T. L. Hankinson, Barrington Moore, & Norman Taylor. Plants and animals of Mount Marcy, New York. Ecology 1: 71-94, 204-233, 274-288. 1920.

tion, such as the area here discussed, fall in this group, and in them floras of different origin are still relatively distinct and adjustments of range are actively in progress. On the other hand, in regions which have enjoyed relatively uniform environmental conditions for a long period of time, migrations are more generally completed and vegetation is in more nearly a static condition, except in those successional series which are related to continuous physiographic processes such as baseleveling. This is now the case in parts of the tropics, and was formerly the case over wide areas of the North Temperate zone in the later Cretaceous and earlier Tertiary periods, when the flora and vegetation of North America and Eurasia were remarkably uniform.

SUMMARY OF PART II.—1. Migration of a species depends on an environmental change within or beyond its range.

2. The rate of migration depends on the rate of environmental change or the migration-capacity of the plant.

3. The present status of migration, as shown by the range of the species, depends on its rate and on the time available for it.

4. The present range of a species is not necessarily final, even without further environmental change.

5. Migration proceeds most rapidly along routes with nearly continuous habitats.

6. Species of similar environmental demands migrate together.

7. Isolated areas of a species or of vegetation are to be interpreted as results of retreating migration.

8. Long continued uniformity of environment leads to floristic uniformity; recent environmental changes to floristic segregation and to new migrations.

## PART III. THE EVIDENCE OF PLANT MIGRATIONS

The entire distance which may have been travelled by the native plants of the Middle West in their migrations since the close of the last glaciation seldom exceeds 500 miles. Since the time available for this movement may be 10,000 to 40,000 years, this requires an average annual migration of only 66 to 264 feet. In the case of trees, a juvenile period of 20 years would still necessitate a movement during one generation of not more than a mile. The discovery of migrations still in progress is accordingly removed from direct observation, except in the case of a few species, and any conclusions must depend entirely upon historical or indirect evidence.

Historical Evidence of Migrations.—Historical evidence may occasionally be used with considerable success, especially where civilization has existed for a long period of time and written records preserve trustworthy accounts of some of the original features of the vegetation. Thus Graebner[23] has been able to demonstrate that certain heaths of northern Germany were originally beech forests. Tansley[24] has also made frequent use of historical records. For the Middle West, such data cover little more than a single century and are correspondingly restricted in value. There are, however, numerous early books of travel which give fairly accurate accounts of the plant life. Their descriptions of prairie fires, of the former extent of prairies, and of the oak openings are in many cases excellent and may probably be relied upon completely. They generally lack detail and seldom mention many species by name, but are nevertheless better for phytogeographical purposes than the floras compiled by early botanists. In almost every county seat copies of the original land survey maps may be consulted. On many of them various features of the vegetation are shown, such as the occurrence of swamps, prairies, and barrens. In some cases the nature of the forest may be approximated by reference to the accompanying field books, since the surveyors' monuments were usually located with relation to certain described trees.

Succession as Evidence of Migration.—For migrations still in progress, the most valuable line of contemporary evidence is found in the successional relations of the species toward the margin of their ranges. Even there, succession can not generally be observed directly, but numerous other considerations offer convincing evidence of the nature of the process, such as the relation of the associations to physiographic development, the reaction of the plant cover on the environment, the presence and relative abundance of seedlings, or the relative age of individuals. These have been used so freely by ecologists and such a body of accepted data has been published that they need no discussion here. Nevertheless, a timely warning against the too general application of their principles of succession has been sounded by Harvey[25] and deserves careful consideration. When, at or near the margin of a range, a species or the members of a flora of uniform geographical distribution participates in successions as invading species, they are

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[23] Graebner, P. Die Heide Norddeutschlands und die sich anschliessenden Formationen in biogischer Betrachtung. Die Vegetation der Erde, vol. 5, Leipzig, 1901.

[24] Tansley, A. G. Types of British vegetation. Cambridge, 1911.

[25] Harvey, Leroy H. Some phytogeographical observations in Lake County, Michigan. Mich. Acad. Sci. Rep. 21: 213–217. 1920.

extending their range. Similar behavior toward the center of the range may indicate only a general closing-up process, representing the later slower stages of a migration and not implying any general extension of range in the ordinary sense of the word.

The known successional tendencies of the three major types of vegetation of the Middle West have frequently been described, especially the tendency of the deciduous forests to succeed the prairies toward the west and the coniferous forests toward the north. Project this tendency into the future and it points to a still wider extension of this type of forest, with a corresponding restriction of prairie and coniferous forest. Project it into the past and it reveals a former condition of restricted deciduous forest and of a larger extent of prairie and coniferous forest. Obviously, such reasoning must not be carried too far, and its results must always be checked by the existence of relic species or relic colonies, as discussed in a following paragraph.

The stratigraphic sequence of fossils has been used with great success as one line of evidence in Europe.[26] While similar evidence has already yielded important results in America, the necessary data for extensive generalizations are usually lacking or deficient. The careful examination of the structure of peat has scarcely more than begun in this country, and the pioneer work of Dachnowski[27] may lead to important results.

Geological events must have necessitated certain migrations and by their very nature give a general idea of them. Thus it is incredible that beech-maple forests could have occupied northern Michigan during the maximum advance of the Wisconsin glaciers, which reached some 400 miles farther south. A northward movement of these trees and their associated species to their present location must have taken place after the retreat of the ice, but the details of this migration must be discovered by other lines of evidence.

DETERMINING MIGRATION CENTERS.—Adams[5] has advanced certain criteria for determining the migration-center of animals, which are in many cases equally applicable to plants. They are, with two omissions, as follows:

1. Location of greatest differentiation of a type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms.

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[26] Lewis, F. J. The plant remains in the Scottish peat mosses. Part I. The Scottish southern uplands. Trans. Roy. Soc. Edinburgh 41: part 3, 699-723. 1905.

[27] Dachnowski, Alfred P. Peat deposits and their evidence of climatic changes. Bot. Gaz. 72: 57–89. 1921.

4. Location of maximum size of individuals.
5. Continuity and convergence of lines of dispersal.
6. Location of least dependence on a restricted habitat.
7. Continuity and direction of individual variations or modifications radiating from the center of origin along the highways of dispersal.
8. Direction indicated by biogeographical affinities.

The Five Elements in the Flora of the Middle West.—Applying his principles to the vegetation of the Middle West, it is found to be composed of five elements, not of equal importance, centering respectively in the southern Appalachian Mountains, in the southern Coastal Plain and the Mississippi Embayment, in the Ozark Mountains, in the plains of Kansas and Nebraska, and in Canada east of the Great Lakes. Four of these lie beyond the glaciated region far enough to have suffered little or not at all from the advance of the ice, and there is no reason to believe that they did not occupy these positions continuously through the later glacial period. The last one is in the glaciated region, and must have been developed since the retreat of the ice from a temporary refuge farther south. For the first four, we are probably safe in assuming that all subsequent migrations of their floral elements have been on lines essentially radial, either from or toward these centers, as ranges may have extended or retreated. For the fifth, we are undoubtedly correct in assuming a general northward shift of the whole flora following the ice retreat.

Glacial vs. Modern Climate.—The close similarity between the interglacial and the modern floras, so far as evidence is at hand, indicates that the glacial climate differed from the modern not so much in kind as in degree. It may be expected accordingly that migrations of the deciduous forests took place first in a northward direction from their Appalachian center and later westward into the Middle West, and that any eastward migration of a prairie flora took place toward the north of our area, where there is still a marked distinction between winter and summer rainfall and a generally smaller total amount, rather than at the south where rainfall is more abundant and more evenly distributed throughout the year.

Further evidence may be drawn from the topography of the region. Large and sharply marked moraines may indicate a rapid advance of the glacial ice. Wide stream valleys leading from the moraines, with great outwash deposits, may indicate rapid melting of the ice under relatively high temperatures, and consequently in the adjacent region a flora and vegetation correlated with such climate. Such evidence has been used chiefly in connection with the Wisconsin glaciation, where it seems that the temperature at the time of maximum ice advance was high and probably not unlike that of the present time. The immature development of the drainage systems over the Wisconsin drift, particularly toward the west, may also be due not merely to youth but also to an early postglacial climate drier than that of the present day.

If a considerable number of species are now confined to an area immediately beyond a moraine and seldom or never occur within it, their distribution may be explained in several ways. First and most obviously, present conditions of soil and climate may exclude them. But if the general vegetation and climate of the two regions are similar and if habitats apparently identical, as judged by the vegetation, exist on both sides of the moraine, this explanation is less plausible. Secondly, their migration up to the present time may have extended merely to the moraine, which they will later cross. But it is difficult to understand why the boundary of the range of numerous species should be so nicely adjusted to the moraine. The third explanation, which is here accepted, is that they occupied this area before or during the formation of the moraine, have occupied it ever since, and are not at present extending their range.

Relic Colonies.—Lastly, and most important of all, past migrations may be judged by relic colonies. Unfortunately, they can be used only for the more recent movements, since the relics of earlier migrations have been completely destroyed. Many such colonies still exist, isolated by recent migrations, or did exist long enough to be recorded before being sacrificed to agriculture, and afford the most valuable evidence of the past range of the floras which they represent. They even give valuable clues to migrations of still earlier date, during which the flora of the colonies entered the region, and therefore show at once an early advance followed by a later retreat.

Although the probability of extreme migrations, except in the case of very mobile species, is very slight, the time available is very long and has certainly been sufficient for the improbable to happen many times. Therefore, in general, isolated stations of a single mobile species shed little light on its past history. But isolated colonies of several or many species, provided with diverse methods of dispersal, represent a different condition. It is entirely beyond the limits of probability or coincidence to presume that a dozen or more species, normally growing together in one section of the country, should also be found together in another remote section beyond the normal limits of dispersal of any of them. Isolated colonies of this character are common phenomena in the Middle West and can have but one significance, that at some time in the past these colonies were more numerous and separated by narrow intervals within the normal migration-capacity of the species, or were entirely continuous over the whole area. Stated in more general terms, the present occurrence of relic colonies indicates the past extent of the vegetation of which they are a type. For the same reason, isolated stations of a single relatively immobile species indicate a former more nearly continuous distribution, and evidence from this source is of greater importance when the species in question is regularly associated with some peculiar or unusual habitat.

A combination of evidence from successional tendencies and relic colonies indicates both the direction and the extent of prehistoric migrations. The full extent may not be indicated, because the isolated colonies may have disappeared completely from the more remote parts of their original range. In such cases isolated stations of single species may give some not entirely untrustworthy idea of it. The farther back in time plant migrations are traced, the fewer relic colonies may be expected and the more dependence must be placed on individual species.

No one of these various lines of evidence is sufficient in itself to build up a history of vegetational movements in the Middle West. All of them must be used together and the deductions from all woven into a history which accounts for present conditions satisfactorily and is plausible in itself. The development of this history must be commenced with the present, where the latest migrations are shown by successional relations. The extent of these recent events may be estimated and checked by relic colonies, which in turn point to earlier migrations. These must be checked by glacial topography, by inferences concerning glacial climates, and by the distribution of plants along the moraines. Still farther back, plant distribution and migrations must be deduced from fossils, from the location of the moraines, from the known physiological requirements of the plants, and through the use of Adams' criteria.

The vegetational history which follows in Part IV has been constructed in this way. Observed conditions and recorded vegetational changes during the historical period have given evidence on migrations then in progress and permitted deductions as to those of the later prehistoric period. Conclusions as to the preceding stages have been reached through use of the various lines of evidence outlined above and carried back with decreasing detail and assurance to the advance of the Illinoian glaciers.

SUMMARY OF PART III.—1. Migrations in progress now or in the recent past are indicated by historical evidence or by observation of successions.

2. Former migrations are indicated by the occurrence and distribution of relic colonies and species, by ecological and taxonomic evidence as stated by Adams, by glacial history and topography, by fossils, and by inferences as to former climate.

3. Evidence from all available sources must be combined to build a plausible and possible chain of events, leading on to and culminating in the known present distribution of plants.

4. Conclusions as to early stages of plant distribution and migration are reached in reverse order of their occurrence, that is, from present to past. The accuracy of each conclusion depends on the accuracy with which the conditions of the following stage have been interpreted. Each earlier stage must therefore be discussed in less detail and with greater probability of error.

## PART IV. THE DEVELOPMENT AND HISTORY OF VEGETATION IN THE MIDDLE WEST

PREGLACIAL.—From the close of the Carboniferous Period to the Lower Cretaceous or Comanchean Period, the area now comprised between the Missouri Valley and the Appalachian Mountain system was continuously land. The pteridophytic and gymnospermous flora which occupied it can be partly reconstructed from the fossils of those ages, but its migrations are unknown. During the Lower Cretaceous the first representatives of the angiosperms must have arrived in our area, since the fossil remains of such plants are preserved in contemporary deposits still farther west, and through the Upper Cretaceous angiosperms constituted the dominant vegetation. It is not probable that herbs were prominently developed; angiosperms consisted chiefly of woody plants of families and genera still in existence in the area and of other groups now primarily or exclusively tropical. This flora is undoubtedly continuous with the forest flora of the Tertiary, usually designated the arctotertiary flora, and through it with the forests of the present.

While there may have been differentiation of floristic types in the Cretaceous, correlated with local climatic conditions, the first of the great vegetational segregations which is still of importance in our region began at the close of the Cretaceous with the uplift of the Cordilleran complex of mountains.[28] Intercepting the moisture-laden winds from the Pacific and restricting the rainfall of the lands immediately east of them to moisture derived from the Gulf of Mexico, the elevation of these mountains led to the development of semiarid conditions over the Great Plains, which soon had an effect on the

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[28] Harvey, Leroy H., Floral succession in the prairie-grass formation in southeastern South Dakota. Bot. Gaz. 46: 81-108. 1908.

character of the vegetation. The result was the grassland type which still prevails in that region.

This result naturally required thousands of years for its accomplishment, but the *modus operandi* may be summarized as involving five processes: (1) the disappearance of the arborescent flora; (2) the great increase in the number of individuals of the herbaceous species; (3) competition for space among the herbs, leading to the eventual dominance of the grasses, as the group best suited by growth-form and ecological requirements to the new conditions; (4) the development by evolution of new and characteristic species and genera, and (5) the immigration, usually accompanied by specific or generic evolution, of other species from the Sonoran deserts at the south and the Great Basin deserts at the west.

How far toward the east the prairie vegetation may have extended in Tertiary time and how many advances and retreats it may have made in response to climatic variation are unknown. We may believe, however, that the present climatic center of the Prairie Province in western Kansas and Nebraska and eastern Colorado has been occupied by this vegetation continually since its origin, and that amoeba-like arms have been pushed out many times in many directions and withdrawn again. It is also probable that the arctotertiary forests have continuously occupied the Ozark uplift, since it still harbors many old species, although not so many as the Appalachian uplift of the same latitude, from which it was isolated during the Tertiary by the oceanic waters of the Mississippi Embayment. This isolation and the proximity of the Ozarkian region to prairie and Sonoran floras on the west have led to a considerable differentiation between the Ozarkian and Appalachian forest centers, as has already been noted in Part III.

Fossil evidence indicates that the arctotertiary flora included both angiosperms and gymnosperms and had little or no latitudinal differentiation, at least as far north as 70°. The second great floristic development affecting our region was the general segregation of these two groups into a northern flora, with gymnosperms predominating, and a southern flora, in which angiosperms were dominant. This probably began only with the approach of the first glacial period and may not have been completed until the ice age was well under way. The processes were essentially the same as those outlined above for the prairie vegetation, but in this case involved also the permanent disappearance from both floras of a number of species belonging to genera whose modern representatives are tropical. The former presence of *Ficus, Artocarpus, Sabal,* and other genera of similar climatic requirements in northern latitudes has frequently been taken to indicate a tropical or subtropical climate in those regions. The writer sees no reason for believing that such genera could not have produced species adapted to a temperate climate then, just as *Phoradendron, Diospyros,* and *Tripsacum* have at present, so that the actual shift of climate northward may have been only a few hundred miles.

These three floristic and vegetational types have since maintained their identity, and the history of the vegetation of the Middle West is concerned almost exclusively with them. A fourth floristic element, the Coastal Plain flora of the southeastern states, was likewise segregated from the arctotertiary forests, probably during the late Tertiary or Pleistocene, and enters the southern portion of our region, but has probably never occupied a more extensive territory than at present. The Coastal Plain flora has been considerably modified by the immigration, accompanied by evolution, of numerous tropical forms, entering the region via Texas or the Florida peninsula. Some of these have extended still farther north and have invaded other floras as well.

Early Glacial Stages.—There is no present evidence concerning the migrations of vegetation during the Nebraskan and Kansan glacial advances, at least one of which entered our area, or during the corresponding Aftonian and Yarmouth interglacial stages, and the earliest evidence at hand deals with its location during the Illinoian period at the time of maximum advance of the ice.

The southern boundary of Illinoian glaciation extends in a generally southwesterly direction across Ohio and Indiana and lies on the northern slope of the Ozark uplift in southern Illinois. It then turns northward, following in a general way the present course of the Mississippi river to the Wisconsin border, displacing the river westward in eastern Iowa, but passing to the east of the driftless area in northwestern Illinois. Its deposits in Wisconsin are almost wholly covered by those of a later period and its further extent in the Middle West is unknown.

The pre-Illinoian flora of the territory covered by this ice sheet must have been destroyed or have migrated south, west, or in both directions. The immediate problems are to ascertain the distance beyond the glacial boundary to which it was forced and the location of the extraglacial floras during the time of maximum ice advance. Several features of present distribution seem to cast some light on the questions.

*The Mississippi Embayment.*—The Mississippi embayment of southern Indiana, Illinois, and Missouri is occupied by a large number of species which reach here their northern limits in the extensive floodplains of the Ohio, Wabash, and Mississippi rivers, without migrating farther to the north along these floodplains into glaciated territory.

Noteworthy among them are *Taxodium distichum,** *Rhamnus caroliniana, Gleditsia aquatica, Nyssa aquatica, Ilex decidua, Catalpa speciosa, Fraxinus profunda, Celtis mississippiensis, Quercus Phellos, Leitneria floridana,* and a host of other shrubs and herbaceous species. Soil conditions can not be cited as the cause of this range, because the soils in which these plants grow is all alluvial, washed down by the streams from the glaciated region, and parallels them without any essential difference for miles within the glacial boundary. Neither can climate be cited, since two of them, *Taxodium distichum* and *Catalpa speciosa,* are commonly, and others occasionally, cultivated 200 to 300 miles north of their natural limits.

*Northern Limits of Southern Plants.*—The rocky hills of the Ozark uplift in southern Illinois also carry a number of southern plants which reach here their northern limits, such as *Pinus echinata, Batodendron arboreum, Ulmus alata, Azalea nudiflora, Bumelia lycioides, B. lanuginosa,* and many others. These also have failed to utilize the extensive strip of similar habitats along the rocky bluffs of the Mississippi river for further migrations into the glaciated region. Still other species have interesting ranges correlated in some way with the glacial boundary. Thus *Heuchera parviflora* occupies isolated areas along the boundary only, with the exception of its stations in the lower Allegheny mountains. *Trichomanes Boschianum* preserves an outpost in southern Illinois, where it has recently been discovered by Cowles. *Sullivantia Sullivantii* occurs only along the glacial boundary from Ohio to Illinois and reappears in the driftless area 300 miles to the north. *Saxifraga Forbesii* is strictly limited to two stations along the glacial boundary in southern Illinois and southeastern Missouri. *Phlox Stellaria* is chiefly confined to certain limestone cliffs along the glacial boundary in Illinois and not far beyond it in Kentucky.

Undoubtedly there are species which reach their northern limit near the glacial boundary because of climatic conditions. This might be true of *Phoradendron flavescens,* whose host trees are abundant north of the boundary, but which has not crossed itself. But with numerous species with coincident range margins at this line, and several species with isolated stations near it, an easier explanation is that they remained here during the glacial period and have not migrated northward since then, indicating that the northern boundary of the arctotertiary forests lay parallel with and close to the ice margin.

There is at present no evidence whether this forest flora at that time extended westward toward the Ozarks, leaving northern Missouri

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* A single colony accurs in Knox County, Indiana, within the glaciated area.

and Iowa to a prairie flora of western affinity, or northward along the western boundary of the ice fields, restricting the prairie to a location farther west. Extensive forest beds overlie the Kansan drift in northeastern Iowa, as shown by McGee,[29] who states that more wood is preserved in these beds than at present grows in the area, but the time-position of these forests may be either Yarmouth, Illinoian, or Sangamon.

*The Migration of the Conifers.*—The conifers of the present northeastern forests, or their ancestral prototypes, migrated southward before the ice and must have been reduced to a narrow strip between the ice margin and the deciduous forests. There is no evidence whether this flora extended west as far as southern Illinois or existed in the unglaciated region of northwestern Illinois. It is noteworthy that *Pinus Strobus* does not occur on the exposures of St. Peter's sandstone near the confluence of the Mississippi and Illinois rivers, but its absence proves nothing. The only species of essentially boreal affinity now existing in southern Illinois are *Sullivantia Sullivantii* and *Saxifraga Forbesii,* and it is not necessary to presume that they were ever accompanied by coniferous forests. Such forests may have existed anywhere along the glacial margin, or may have been restricted to some especially favorable area, such as the re-entering angles in Ohio and Indiana, or to the mountains of Pennsylvania and adjacent states. The prominent development of vegetation of this affinity in the southern Allegheny mountains may have arisen during a later glacial advance or may have persisted since the Illinoian.

*The Migration of Deciduous Forests.*—During the long Sangamon interglacial stage which followed the retreat of the Illinoian glaciers, deciduous forests undoubtedly migrated to the north and probably also to the west. The full extent of this migration can at present only be surmised, since it must be ascertained wholly by fossil evidence, and this is in most cases lacking. Nevertheless, logs of both angiospermous and coniferous species are found frequently in the soil layer between the Illinoian drift and the superposed Wisconsin soil in various parts of Illinois. Leverett[30] has noted that the coniferous remains must not be considered evidence for the maintenance of such forests throughout the interglacial stage, since they probably were deposited at the end of it, just before the approach of another glacier. The notable discoveries in the vicinity of Toronto, summarized by Chamberlin and

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[29] McGee, W. J. The pleistocene history of northeastern Iowa. U. S. Geol. Surv. Ann. Rep. II1: 189-599. 1891.

[30] Leverett, Frank. The Illinois glacial lobe. U. S. Geo. Surv, Mon. 38. 1899.

Salisbury,[31] indicate that deciduous trees may have migrated during the Sangamon stage to distances some 500 miles beyond their present range.

There must have been other vegetational movements during the Iowan glaciation and the succeeding Peorian interglacial stage, but no evidence concerning them has been found, and none is expected from the region under discussion, except from fossils which may eventually be discovered in the Peorian soils. The Peorian stage may have had a relatively warm and arid climate, since during this time extensive deposits of loess were made over wide areas in the Middle West. This type of climate may have persisted into or even through the Wisconsin glaciation.

Wisconsin Glacial Period.—The close of the Peorian interglacial stage saw the advance of the Wisconsin glaciers, which as the last glacial invasion have left the greatest impress on the nature and location of the present vegetation. Originating in the Labradorian center, the ice sheet flowed in a southwesterly direction into our area, wholly covering the state of Michigan and partially covering Ohio, Indiana, Illinois, and Wisconsin. Toward the periphery, the ice sheet was divided into more or less well-marked lobes, with re-entering angles between them. The ice margin along the eastern boundary of Ohio reached nearly to the northern extremity of West Virginia, extended across Ohio in a generally southwesterly direction to a point not far north of Cincinnati, westward across Indiana in about latitude 39° 30′, westward into Illinois, and thence northward on about longitude 89° to latitude 45° in Wisconsin. Here the boundary again turned west, and another lobe extended south into the north-central portion of Iowa. Throughout this area there is an extensive development of moraines, the chronological relations of which have been discussed in admirable detail by Leverett[30,32,33] and Alden.[34] These moraines mark successive stages in the retreat of the ice, and it is to be hoped that the application of De Geer's methods to the region will eventually yield an approximate time-scale for their history, an event which will be of the highest importance in developing a clear idea of the consequent migrations of vegetation. At the same time, a continued study of the

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[31] Chamberlin, T. C. & R. D. Salisbury. Geology. New York, 1907

[32] Leverett, Frank. Glacial formations and drainage features of the Erie and Ohio basins. U. S. Geol. Surv. Mon. 41. 1902.

[33] Leverett, Frank, & Frank B. Taylor. The pleistocene of Indiana and Michigan and the history of the Great Lakes. U. S. Geol. Surv. Mon. 53. 1915.

[34] Alden, Wm. C. The quaternary geology of southeastern Wisconsin, with a chapter on the older rock formations. U. S. Geol. Surv. Prof. Paper 106. 1918.

peat deposits[27] is certain to yield precise information concerning the nature of the flora.

Outside the margin of the Wisconsin ice lay the five floristic groups of plants already mentioned, the prairie flora to the west, the Ozarkian forests to the southwest, the coastal plain flora of the Mississippi Embayment to the south, and the deciduous forests of the Appalachian and Piedmont regions to the southeast, while the coniferous forests of the present northeastern states were limited to a belt paralleling the glacial margin. There is no reason to believe that the general space relation of these five groups has ever been altered, although they must have suffered many fluctuations in their distribution and extent during the preceding glacial advances.

With the retreat of the ice, the new glacial soil was thrown open to migration and speedily covered by plants. Adams has given a picturesque account[6] in general terms of the waves of vegetation which swept on to the north as the ice margin retreated. But postglacial migration was by no means as simple as he has described it, particularly because of the opportunities for migration in easterly and westerly directions as well as toward the north. It is also obvious that the advantage in migration lies with the floristic type located nearest to the new land. Hence it is important to locate the five floristic types as accurately as possible for the time of maximum advance of the Wisconsin ice.

DISTRIBUTION OF PLANT LIFE DURING THE WISCONSIN.—When it is considered that the past distribution of plants can in general be interpreted only through circumstantial evidence, it becomes hazardous to venture any opinion on the actual details of plant distribution during this period. Nevertheless certain modern conditions are of interest in this connection.

The glacial drift of southern Illinois beyond the Shelbyville moraine, which marks the southern boundary of the Wisconsin glaciation, is characterized by a large number of more or less xerophytic species. Among these may be mentioned *Ambrosia bidentata, Ascyrum hypericoides, Chamaecrista nictitans, Crotalaria sagittalis, Crotonopsis linearis, Diodia teres, Diospyros virginiana, Galium pilosum, Parsonsia petiolata, Passiflora lutea, Plantago aristata, Plantago virginiana, Quercus marylandica,* and *Quercus stellata.* Few of these are native anywhere within the Wisconsin drift limits, although several of the weedy species have within recent years migrated northward and are now found rather uniformly throughout Illinois. They may be described collectively as xerophytic selections from a southern flora. The same region is also marked by a few rather peculiar xerophytic selections from a western or southwestern flora, not found elsewhere in the state, such as *Geoprumnon mexicanum* and *Megapterium missouriense,* but it must be noted that these are much fewer than the southern element, and also much fewer than species of the same western element in western Illinois.

Some of the most noteworthy mesophytic trees are nearly or quite absent from the same region, such as *Fagus grandifolia, Cynoxylon floridum, Liriodendron Tulipifera,* and *Magnolia acuminata,* although some of them extend much farther north in almost the same longitude and all of them, crossing Illinois at its southern end, extend westward as far as the Ozark mountains.

The Ozarkian flora at the present time barely reaches Illinois. A few species occur on the rocky hills of the Ozark uplift, such as *Solidago Drummondii* and *Solidago Radula; Trillium viride* occurs northeast of St. Louis, but in general the flora is poorly developed east of the Mississippi, although strongly marked only a few miles west of it. Even such a mobile species as *Vernonia Baldwini,* common in the vicinity of St. Louis, is scarcely known on the Illinois side. There is no evidence as to the date when this flora appeared in Illinois, and no reason to believe that it ever extended farther east or took a more prominent part in the plant life of the region.

In western Illinois, beyond the Wisconsin drift, north of the low range of hills which divided the Illinoian till into two portions (see Leverett's map[30]), and mostly west of the Illinois river, there are a number of intensely xerophytic western species, such as *Bouteloua hirsuta, Bouteloua oligostachya, Schedonnardus paniculatus, Opuntia fragilis, Mentzelia oligosperma, Lesquerella argentea,* and *Cristatella Jamesii.* They are not merely xerophytes, but are limited to peculiar and extreme habitats. They have not been reported east of the terminal moraine, even from similar habitats on the sand dunes of Lake Michigan. *Schedonnardus paniculatus,* with a single station in Illinois, and *Cristatella Jamesii,* with two known stations in Illinois and one in eastern Iowa, present excellent examples of discontinuous distribution, since their nearest stations to the west are 300 to 500 miles away. Such distances are much beyond the normal range of their migration and these eastern stations must be regarded as the relics of a former nearly continuous range across eastern Nebraska and Iowa. This in turn implies a climate some time in the past much drier than at present. There are also in this part of the state a few xerophytic southern plants, such as *Quercus marylandica* and *Crotonopsis elliptica,* but their successional relations indicate a later arrival in the region.

It has been indicated that coniferous plants during the Illinoian glaciation must have been confined to a narrow strip paralleling and adjacent to the ice margin. The same conditions must have obtained during the Wisconsin. The lack of relics of this flora along the Shelbyville and Bloomington moraines is striking. From Edgar County, Illinois, where the terminal moraine enters the state from Indiana, west and north to La Salle County, almost no boreal relics occur. The absence of pines may well be explained by the soil conditions, but the swamps and bayous of the rivers are also without *Larix* and *Thuja* and any of the ericads of the peat bogs of the north; even *Caltha palustris* and *Spathyema foetida* are almost unknown along the glacial boundary until well towards the northern end of the state, although most of these plants are found freely along the moraine in similar latitudes in Ohio and some in Indiana. At the north they reappear: *Abies balsamea* occurs in northeastern Iowa, and *Pinus Strobus* is abundant from southwestern Wisconsin northward. Even *Primula Mistassinica* occurs in northwestern Illinois.

All of these facts of modern distribution may be explained by postulating a glacial climate during the Wisconsin considerably drier than at present and not much different in temperature, so that the vegetation of extra-glacial Illinois assumed a xerophytic aspect. Under this view, we may assume that the Ohio valley in southern Indiana and Illinois was occupied by its present forest flora, possibly not so luxuriantly developed; the Illinoian drift to the north of it by a xerophytic forest of southeastern affinity with a slight admixture, decreasing toward the west, of a prairie element; western Illinois was exclusively prairie, of a type similar to that now prevailing possibly 400 miles farther west. A narrow and interrupted strip of coniferous forest followed the glacial boundary, especially in places where greater topographic relief afforded better shelter. Toward the east, across Indiana and Ohio, the strip became broader and included more species. Toward the north it broadened out again in the driftless area in the shelter of the deep rocky ravines, with the additional protection of the projecting Des Moines lobe of ice extending southward to the west of them. It is doubtful if any conifers or associated species occurred west of this lobe. Tundra vegetation, less affected by the environmental conditions, grew on the thin soil overlying the ice back of the glacial margin. In general, the climatic conditions and vegetation may have been shifted in this latitude 300 to 400 miles east of their present location. The presence of an old flora in the Ozarks indicates that this shift did not extend much farther toward the south.

There is also some geological evidence of a climate during Wisconsin time well suited to a xerophytic vegetation. Various rivers of the region, notably the Wisconsin, the Green, and the Illinois, which rise within the Wisconsin drift and flow out to the west or southwest, occupy, beyond the Wisconsin terminal moraine, valleys entirely out of proportion to the size of the present rivers and choked with immense quantities of glacial outwash. This may indicate unusually rapid melting, due to a mild (and presumably also a dry) climate.

During this period, forest belts of the more mesophytic species may have existed along the Mississippi, Wabash, Illinois, Missouri, Cedar, and Des Moines rivers in the eastern portion of this semi-arid region, just as they do today in a similar climate in Nebraska and Kansas.

Climate in the Early Post-Wisconsin.—Whether or not the conclusion is accepted that a mild and semi-arid climate existed in the Peorian and persisted through the Wisconsin stages, it seems almost certain that such a climate characterized at least a portion of the time involved in the post-Wisconsin glacial retreat. Palaeontological and geological evidence for such a condition is scanty, and is concisely summarized by various authors in a recent volume.[35] Alden [35a] believes "that during the deposition of the post-Wisconsin loess the climate in the northern interior may have been somewhat drier than at present, but was not greatly different." Knowlton says [35e] "There is some little palaeobotanical support for the contention that there was a slightly warmer period following the close of the glacial epoch." Tyrrell concludes[35f] that the glacial climate of the Canadian northwest was "succeeded by a dry continental climate, under neither of which conditions was a forest growth possible." Basing his opinion on the occurrence of certain animal remains, Hay believes [35d] "that after the retreat of the ice-sheet a warmer period ensued," at the culmination of which "the region along the southern shores of Lakes Ontario, Erie, and Michigan enjoyed a climate similar to that now prevailing in Tennessee

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[35] Die Veränderungen des Klimas seit dem Maximum der letzen Eiszeit. Eine Sammlung von Berichten . . . herausgegeben von dem Exekutivkomitee des 11. Internationalen Geologenkongresses. Stockholm, 1910. Including:

[35a] Alden, Wm. C. Certain geological phenomena indicative of climatic conditions in North America since the maximum of the latest glaciation. 353–363.

[35d] Hay, O. P. On the changes of climate following the disappearance of the Wisconsin ice sheet. 371–374.

[35e] Knowlton, F. H. The climate of North America in late glacial and subsequent post-glacial time. 367–369.

[35f] Tyrrell, J. B. Changes of climate in northwestern Canada since the glacial period. 389–391.

and Arkansas." Similar opinions have also been expressed by Coleman, Matthew, Dawson, Leverett, Upham, and Davis.

The same period was early recognized in Scandinavia by Blytt[36] and has been generally accepted by most European phytogeographers. Of the numerous papers on the subject published in the same volume, those of Andersson [35b-c] seem especially conclusive. He decides that during the early postglacial stages the climate of Scandinavia had winters similar to those of the present, while the summers were longer and about 2.5° C. warmer. Later the climate became wetter, while remaining equally warm, while for the modern period there is evidence of a slow lowering of the temperature. It is also worthy of note that Andersson lays great stress on the value of relic colonies as evidence of past distribution.

The term xerothermic period has long been used by Europeans for this period of mild and drier climate, and may well be extended to the same type of climate, probably contemporaneous, in America.

A xerothermic period, occurring in comparatively recent times, and without any subsequent geological episodes to modify greatly the trend of plant migrations, would certainly have left an impress on the distribution of vegetation which would still be visible. Among the effects which might be expected is a great extension of the prairie flora toward the east, taking advantage of the favorable climate. This should now be evidenced by relic prairie colonies and by isolated stations of western species at the east and by a deficiency of hydrophytic and mesophytic boreal relics at the west. Both of these results are actually demonstrable at the present time, as will be shown below. A third effect should be seen in the migrations of the deciduous forests from the southeastern center, in which the more mesophytic species would be limited at first to a northward migration only, passing to the east of the area affected by xerothermic conditions, while the more xerophytic species would migrate both north and west, accompanied by other species of edaphically moist floodplains, such as now form the westernmost groves of Kansas and Nebraska. Present distribution indicates that this was also a fact, although it is less clearly evident at the present time.

Tundra and Coniferous Forest Migration.—The northern boundary of the tundra vegetation overlying the glacial ice extended toward the north with the retreat of the ice. At its southern boundary,

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[35b] Andersson, Gunnar. Das spätquartäre Klima, eine zusammenfassende Uebersicht. xii-lvi.

[35c] Andersson, Gunnar. Swedish climate in the late-quaternary period. 247-294.

[36] Blytt, Axel. Dia Theorie der wechseluden kontinentalen und insurlaren Klimate. Engler's Bot. Jahrb. 2: 1-50. 1881.

the tundra persisted until destroyed by the warmer climate or by the succession of the coniferous forests. In general, tundra withstands a climate slightly warmer than its optimum better than the competition of forest species, which quickly destroy it by shading.[22] As in all such retreating migrations, relic colonies were isolated, surrounded by the advancing forests, and persisted for a longer or shorter time until finally completely overgrown by the spruces and firs. Naturally those endured the longest which occupied habitats least favorable to forest growth. We may presume that the sand dunes along the shores of the postglacial lakes and such isolated rock outcrops and cliffs as Starved Rock in Illinois and the Dells of the Wisconsin River were for a long time occupied by tundra plants, just as they are now occupied by relics of the coniferous forests. The xerothermic period and ordinary successional processes have long since destroyed the last vestige of tundra vegetation in these latitudes, and the southernmost species are now found scarcely farther south than Lake Superior. On Isle Royale[37] associations still exist which bear a general resemblance to the arctic tundra and contain a few species of distinctly northern distribution. As the tundra migrated northward into cooler and moister regions, and the cooling influence of the ice was felt farther beyond its margin, the belt of tundra broadened, that is, it migrated toward the north faster than it retreated from the south, until it now occupies an area some hundreds of miles wide.

The boreal coniferous forests which had occupied a narrow or interrupted strip along the glacial margin during the Wisconsin stage also migrated northward following the retreat of the glaciers, surrounding the relic colonies of tundra and eventually replacing them by succession. The pioneers in the movement were probably then as now the xerophytic species advancing along the rock outcrops and till of the upland, and the bog species proceeding along the drainage lines and the glacial lakes. These forests also advanced toward the north faster than they retreated from the south, and consequently occupied a strip of increasing breadth. This led to their present dominance over a large area north and east of the Great Lakes and to their temporary dominance, which is still continued in many habitats, in northern Minnesota, Wisconsin, and Michigan. Their northward movement brought the conifers into climates progressively cooler and relatively moister. This led not only to a greater number and size of individuals, but also permitted a northwestward migration into northern Minnesota and Manitoba. This northwestern prolongation was eventually extended,

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[37] Gleason, H. A. The ecological relations of the invertebrate fauna of the Isle Royale, Michigan. Rep. Mich. Geol. Survey 1908: 57-78. 1909.

with the complete disappearance of the land ice, as far as Alaska. Since the morainal strip of boreal vegetation was, in the Middle West at least, always narrow, frequently interrupted, and probably completely absent about the Des Moines lobe, and composed chiefly of a xerophytic selection of species, the western end of the forest belt was composed, during its advance to its present location, of a comparatively meager flora. Each mile of advance to the northward saw the widening of the belt and the junction of portions previously isolated, and consequently permitted a westward migration of species from the eastern states, which were little affected by the xerothermic climate. This westward migration has by no means been completed and is probably even now in progress through the forests of Quebec and Ontario, but the boreal flora of the upper Lake region is still poor in comparison with that of Quebec, New Brunswick, and the New England states. The northwestern extension across Manitoba to Alaska shows a progressive diminution in the number of species concerned, as graphically shown by Transeau's[38] map.

When these forests reached the eastern foothills of the Rocky Mountains in Alberta, they were again in contact with the closely related species of the Pacific Conifer Province, from which they had long been separated. It will be interesting to learn from future studies what exchange of species now took place; whether widely distributed species common to both regions, such as *Populus tremuloides,* had been in both since their segregation; whether the numerous Pacific plants of the St. Lawrence valley are preglacial members of the northeastern flora, or migrated eastward at this comparatively recent stage. It is not too much to expect that all of these matters are possible of solution.

In this migration of boreal plants, numerous relic colonies were left behind. Many of them have since disappeared before the encroachment of surrounding vegetation or the changes in climate, but thousands still exist. As is generally the case with relic colonies, they occupy for the most part extreme habitats, either xerophytic rock hills and sand dunes, clothed with *Pinus Strobus* and *Pinus Banksiana,* or bogs, characterized by *Larix laricina* and *Thuja occidentalis.* It is especially noteworthy that in Ohio, where the influence of xerothermic conditions was reduced by the eastern position, the hydrophytic colonies persist farther south than the xerophytic. In Illinois the condition is reversed, and neither of the two hydrophytic trees is reported from Iowa. Tamarack bogs are found in Illinois only along the borders of deep lakes in the immediate vicinity of Lake Michigan, while *Pinus Strobus*

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[38] Transeau, Edgar N. Forest centers of eastern America. Amer. Nat. 39: 875-889. 1905.

occurs not far from the Mississippi and in one county in southeastern Iowa. The occurrence of boreal relics in the driftless area of northeastern Iowa has already been noted.

Ponds were abundant on the Wisconsin drift in Illinois half a century ago, and were notable for the complete lack of such hardy boreal plants as *Comarum palustre, Dulichium arundinaceum,* and *Menyanthes trifoliata.* They were mostly shallow and easily drained and have long since disappeared. They were also characterized by the absence of deep peat deposits, indicating that they had never been occupied by boreal vegetation and were of comparatively recent origin. The carefully prepared reports of the Illinois soil survey present interesting figures concerning them. Ten counties of central Illinois contain only 1,986 acres of deep peat, or 0.04% of their area, and of this 1,779 acres lie in the floodplain of the Illinois River. Three counties of north-central and northern Illinois contain 0.15% of deep peat, one county in the Kankakee valley 0.83%, while three counties of northeastern Illinois contain 4.67%. Even in southern Michigan, far within the boundary of the Wisconsin deposits, only the deeper lakes are bordered by tamarack bogs. This lack of hydrophytic boreal relics toward the southwestern angle of the Wisconsin glaciation is best explained by the assumption of the xerothermic period, as already noted, during which hydrophytic habitats were obliterated toward the west, except in the deepest depressions or in local areas affected by subsurface water,[39] thereby restricting the relic colonies chiefly to the xerophytic types.

EARLY MIGRATION OF THE PRAIRIE FLORA.—An advance of the prairie vegetation toward the east and northeast followed immediately behind the coniferous forests, displacing the rearguard of the forest by successional processes. There is now no place in the Middle West where grassland is succeeding forest, and it becomes difficult to picture the detailed steps by which such succession proceeded. In bogs, as the climate grew warmer, and the ingress of water was reduced with increasing distance from melting ice, the gradual drying may have inhibited the growth of seedlings and permitted the entrance of prairie species. This process is now seen in modified form in southern Michigan, where partial drainage of tamarack bogs leads to the displacement of the usual bog shrubs by *Dasiphora fruticosa.* On uplands, the exposure of the marginal trees to warm and dry winds during the summer, with consequent injury through excessive transpiration, may

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[39] Gates, F. C. A bog in central Illinois. Torreya 11: 205-211. 1911.

have had the same effect,[40] while severe winter-killing among young plants may have resulted from deficient snow cover.[41,42]. Certainly the fewest boreal relic colonies are now found in southern Wisconsin and southeastern Minnesota,[43] where such atmospheric conditions are still more or less in effect.* Geographically the advance of the prairies was favored by the slow withdrawal of the eastern ice northward and the rapid retreat of the western ice northeastward, thereby opening to invasion first Illinois and then Indiana. A slight change in the nature of the ice retreat might have affected the future vegetational development of the region very greatly.

The distance to which the prairie vegetation migrated northward is not definitely known. Very likely it reached in central Michigan as far as the jack pine plains, which still contain numerous prairie species, and if this is true must have reached similar or even higher latitudes in Wisconsin. There is no present reason to believe that prairies were developed on the north shore of Lake Erie. Deciduous forests in Minnesota now occupy a narrow strip between the prairie and the coniferous forests, and it is probable that their entrance was about equally at the expense of the two earlier types of vegetation. If this is true, the prairies did not extend much beyond their present range in that state.

The eastern migration of the prairie proceeded as a wedge-shaped extension between the coniferous vegetation at the north and the deciduous forests at the south and reached limits considerably beyond the eastern margin of modern continuous prairies. Numerous relic colonies formerly occurred, before they were destroyed by agriculture, in eastern Indiana, northwestern Ohio, and southern Michigan[44] (see also Cooper's description of an oak opening in his novel of the same name). Vegetation closely simulating typical prairie exists along the Scioto River near Columbus, Ohio. Bonser[45] has described a marshy tract near Sandusky, Ohio, which still contains some western species, notably *Vernonia fasciculata*. This so-called prairie has doubtless

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* Contrast maps in references 37 and 42.

[40] Shimek, B. The prairies. Bull. Lab. Nat. Hist. Univ. Iowa $6^2$: 169-240. 1911.

[41] Gates, F. C. The relation of snow cover to winter killing in *Chamaedaphne calyculata*. Torreya 12: 257-262. 1912.

[42] Gates, F. C. Winter as a factor in the xerophily of certain evergreen ericads Bot. Gaz. 57: 445–489. 1914.

[43] Livingston, B. E. A study of the relation between summer evaporation intensity and the centers of plant distribution in the United States. Plant World 14: 205–222. 1911.

[44] Gleason, H. A. A prairie near Ann Arbor, Michigan. Rhodora 19: 163-165. 1917.

[45] Bonser, Thomas A. Ecological study of Big Spring Prairie, Wyandot County, Ohio. Ohio Acad. Sci. Special Paper 7. 1903.

preserved its hydrophytic environment since an early period, being watered by springs, and consequently contains a considerable number of boreal species, notably *Betula pumila*. *Opuntia humifusa* occurs near the same place. Species of distinctly western affinities do not occur on Presque Isle, near Erie, Pennsylvania,[46] and the abundant development of boreal species and the typically Alleghenian aspect of the flora in northeastern Ohio make it reasonably certain that extensive prairies were not developed east of Cleveland.

The unglaciated areas of southern Ohio, Indiana, and Illinois, and the Ozark region of southern Missouri are now populated with a forest flora that presents indications of great antiquity, and in their greater topographical relief offer better opportunities for forest species to endure unfavorable atmospheric conditions. It seems reasonably certain that the prairies did not encroach on this area at any time. Probably the southern boundary of the glaciated area marked the division between forest and prairie, and probably forest belts followed even then the courses of the rivers northward well into the prairie region. The forest belts of the Mississippi may have been derived from the southern species of the Mississippi embayment; at the present time several of them follow the course of this river northward, such as *Gleditsia aquatica* and *Hicoria Pecan*. No evidence is now at hand concerning the possible extent of the prairie into the Ozark region of southwestern Missouri and northwestern Arkansas. What relation the xerothermic period may have had to the barrens of Tennessee, the prairie belt of central Alabama, the prairies of eastern Arkansas, and the coastal prairies of Louisiana must be left to the deductions of observers who have had personal experience with the vegetation of these areas.

In further support of the idea of a xerothermic period, it need only be recalled that the discontinuous distribution of such plants as *Opuntia fragilis* and *O. humifusa*, *Sporobolus heterolepis*, *Cristatella Jamesii*, and *Callirrhoe triangulata* can be adequately explained only by assuming a former period of climate sufficiently drier than the present to permit their continuous migration. This, with the existence of relic prairie colonies at the east and the prevailingly xerophytic nature of the relic boreal colonies at the west, seems to be sufficient evidence of the actuality of a post-Wisconsin xerothermic period.

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[46] Jennings, Otto E. A botanical survey of Presque Isle, Erie County, Pennsylvania. Annals Carnegie Mus. 5: 289–421. 1909.

The eastward advance of the prairies was either accompanied or followed by some specific evolution among the species participating, as indicated by such plants as *Phymosia remota,*[47] *Synthyris Bullii,* and *Tetraneuris herbacea.* These plants are now confined to the eastern arm of the Prairie Province, but in each case have their nearest related species much farther west.

There is no reason to suppose that the xerothermic period came to a sudden close, which would require an equally sudden geological event in explanation. In fact, it may have been most pronounced during the Wisconsin glaciation and diminished in intensity ever since, but not sufficiently to check the rapid advance of the prairies behind the retreating coniferous forests. Neither can the time of maximum advance of the prairies be correlated at present with the postglacial stages of the Great Lakes.

EARLY MIGRATIONS OF THE DECIDUOUS FORESTS.—At some time an amelioration of the climate began. This change was probably less connected with temperature, which has doubtless changed but little in our area since the Wisconsin glaciation, than with rainfall and atmospheric humidity. The total rainfall probably increased considerably, but the increase fell chiefly during the winter months and changed the climate from one of summer rains, such as is now characteristic of the prairies farther west, to one of fairly equable rainfall. This change first made itself felt in the east and gradually progressed toward the west. At the present time, each hundred miles west of the Wabash River along the fortieth parallel shows a marked diminution in winter rainfall.

The effect of this climatic change was the retardation and eventual cessation of the old successional relation between coniferous forest and prairie, soon followed by a break in the equilibrium along the southern and eastern margins of the prairies, leading to an advance of the deciduous forests northward and westward.

Two general routes were followed in this forest migration, a northward and westward route from the forests along the southern edge of the prairies and a northward and then northwestward route from those lying east of the easternmost extension of the prairies. Many species were common to both regions and participated in both migrations; others were localized and show by their present distribution that they entered the Middle West by only one of these routes. Both took place simultaneously, and in some places both migrations eventually met,

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[47] Clute, W. N. The rarest American Plant. Amer. Botanist 26: 127–129. 1920.

so that races of similar ultimate ancestry but of different recent history are again growing together.

*The Southern Migration.*—The southern migration was participated in chiefly by oaks and hickories of the drier uplands, and by oaks, elms, ashes, walnuts, maples, hackberry, cottonwood, honey locust, coffee tree, buckeye, and sycamore of the lowlands. Following as closely behind the prairies as environmental change would permit, these plants established two successional series, a xerarch series on the uplands, leading to the establishment of an oak-hickory forest, and a hydrarch series along the stream valleys, leading to the development of marginal belts of hydrophytic or mesophytic forest. The hydrarch series migrated more rapidly up the stream courses, since the species concerned could take advantage of local conditions of favorable moisture, while the xerarch series found its most favorable route along the broken topography of the river bluffs, between the prairies above and the hydrarch forests below. The two types of forest thus advanced upon the prairies together along the river courses leading southward into the Ohio valley and eastward into the Mississippi, and the present outposts of this migration are still to be seen in Kansas, Nebraska, the Dakotas, and Manitoba on the west and in Michigan and Wisconsin on the north.

Some of the mesophytes were left far behind in this advance, and the beech, sugar maple, tulip tree, and basswood are not particularly important members of the climax forest or even totally absent from Illinois west. In such cases a temporary climax developed in ravines and on floodplains and was composed chiefly of a selection of species persisting from the earlier successional stages. The slower trees have been migrating, nevertheless, and with the greater success the farther east. Beech is common in the Ohio valley: it has scarcely moved up the Mississippi, but has followed the Wabash well into Indiana, and the Miami, Muskingum, and Scioto until Ohio is occupied by it completely. There is reason to believe[48] that large areas of forest were developed on the uplands in which the most mesophytic tree was the red oak, *Quercus rubra.*

*The Northern Migration.*—The northern migration proceeded from the deciduous forests which had had a glacial center of preservation in the Allegheny Mountains from Pennsylvania southward. These species, now constituting the well known Alleghenian element in the flora of New York and New England, have been during and since the

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[48] Gleason, H. A. An isolated prairie grove and its phytogeographical significance. Bot. Gaz. 53: 38–49. 1912.

glacial period more or less mixed with boreal elements, and this condition has been increased by their postglacial migration into a country from which the coniferous forests were retreating and leaving numerous relics behind, without an intervening prairie stage. Moving slowly northward behind the glaciers, which occupied the Ontario basin long after migration routes farther west were open, a portion of the species concerned finally turned to the west and northwest and entered Michigan, Wisconsin, and Minnesota, while others, such as *Quercus Prinus,* moved scarcely west of the Appalachian region.

It has not been possible so far to form an opinion as to the particular postglacial stage of the Great Lakes when this westward turn took place. It may have been in a narrow strip between the prairies and the coniferous forests, following the former to the north and broadening out only after reaching relatively high latitudes, in which case it could have occurred at an early postglacial stage, or it may be a more recent movement, even as late as the Nipissing stage, in which case it might have passed to the north of Lake Erie and entered Michigan by crossing the Detroit and St. Mary's rivers.

*The Combined Effects.*—The two migrations together may be compared to a vast U, with its base in the southern Alleghenies, one side extending as far west as the Ozarks, and the other passing northwest to Minnesota. The northern migrants have shown little tendency to move southward, especially toward the western part of their route, while the southern ones have moved steadily northward until their outposts have entered the area of the northern arm in Michigan and Wisconsin, where oak, sassafras, and sycamore occur in the same area with sugar maple, beech, and white pine. The base of the U has gradually closed over Ohio and part of Indiana, chiefly through immigration from the south. As a result there is little difference between the forests of southern Michigan and those of any part of glaciated Indiana. The valley of the Grand River in central Michigan is a well marked division line between forests of the two types, according to observations of B. E. Quick, and above it the deciduous forests are derived mostly from the northern migration.

*Migration and Evolution.*—The forest migration was accompanied by specific evolution also, and various species have been described from the forest region of the Middle West. In most cases their probable evolution is in doubt, from lack of careful study, but Dr. F. W. Pennell has kindly supplied certain cases among the Scrophulariaceae in which the ancestry of the species or varieties seems reasonably certain. Thus *Agalinis paupercula* of the glaciated region is considered as derived from *A. purpurea; Aureolaria Pedicularia* (L.) Raf. (*Dasystoma Pedicularia*) has given rise to the variety *ambigens* (Fernald) of the Middle West. In other cases, the parent species, existing through the glacial period south of the ice margin, has followed both routes of migration and in so doing has become segregated into a pair of closely related forms, one of which took the southern route leading northward from the Ohio valley and the other the northern route along the Alleghenies and the Great Lakes. Thus *Trillium nivale, T. declinatum,* and *Cynoglossum virginianum* of the southern portion of the Middle West are paired with *Trillium undulatum, T. cernuum,* and *C. boreale* respectively of the northern portion.

Changes in the prairie flora took place at the same time. Distinctly western species withdrew entirely from the eastern extension or, like *Cristatella Jamesii* and others already mentioned, left relics behind in especially favorable xerophytic habitats. Relic colonies were isolated throughout the region, many of which still persist. These were subject to slow but persistent succession by the forests; many must have been obliterated, while others were greatly reduced in size.

*Prairie and Boreal Relics.*—The nature and location of these prairie relics and of the boreal relics in the same area may yet give a clue for the better understanding of the period and route of the northern migration of deciduous forests. There is in general a great difference in environment between forested and unforested habitats, such as a prairie and either a coniferous or a deciduous forest. Differences also exist between the two types of forest, but these are of less importance and to many species of little significance. Boreal relics, therefore, have not commonly persisted in the prairie, but remained in definite colonies. Similarly, prairie relics have been confined largely to colonies and have not persisted as scattered plants within the invading deciduous forests.[49] So, wherever the deciduous forests have succeeded the coniferous forests directly, numerous boreal species persisting to the present time bear evidence of the fact. These are of common occurrence in southeastern Michigan and indicate that the prairies were not universal there, but are rare or lacking in Illinois and Indiana, showing that the coniferous forests had disappeared before the advent of the deciduous trees from the south. Relic colonies, as has been pointed out before, remain in habitats not necessarily favorable to themselves, but unfavorable to the invaders. Consequently, prairie and boreal relics sometimes occupy the same station, into which they have been

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[49] Vestal, Arthur G. Local inclusions of prairie within forest. Trans. Illinois Acad. Sci. 11: 122–126. 1918.

forced by the invasion of the deciduous forests. Such conditions are visible at the Dells of the Wisconsin, the dunes at the head of Lake Michigan, and in various places in southern and southwestern Michigan. The conclusion from both conditions is that in the western and central part of our area successions between the coniferous forests and the prairie were mostly completed before the arrival of deciduous trees, while toward the east the deciduous forests arrived before the prairies or during their advance upon the boreal associations.

DEVELOPMENT OF THE PRAIRIE-GRASS FORMATION. The prairie flora also changed considerably during this advance of the deciduous forests. Scores of species, which had been inhabitants of sand dunes, rocky soil and barrens, or the more xerophytic upland woods. migrated faster than the trees and became firmly established in the prairie associations. The only restrictions on this movement were that the plants should be herbs, dying to the ground every year and thereby escaping the effect of the arid xerothermic winter, and adapted to compete for space with grasses, which were the dominant plants of the prairies. Among these emigrants were numerous southeastern grasses which, having the same vegetative form, mingled easily with the western species and became dominant with them.

As the xerothermic period finally drew to a close, the western species were at a disadvantage. They were unable to withstand a large increase in moisture, while the species of eastern derivation could exist with a much greater rainfall. The latter accordingly became more and more abundant, until they practically dominated the prairies. In fact, the four most important grasses of the Illinois prairies, *Andropogon furcatus, A. scoparius, Sorghastrum nutans,* and *Spartina Michauxiana,* are all of eastern origin. The western species became reduced in number of individuals or restricted to extreme habitats where edaphic conditions compensated for the increased rainfall.

Here we have the origin of the flora of the eastern arm of the Prairie Province, early recognized by Pound and Clements as distinct from that of the western plains, and designated by them the prairie-grass formation. Just as the original western prairies were segregated from the arctotertiary forests by climatic differentiation, so the xerothermic period produced an analogous vegetation thousands of years later from the same stock. In the later case, however, the process was one of selective migration, rather than of extermination and evolution, and most of the southeastern species now characteristic of the prairie-grass formation still live also in the forested region of the southeastern states. Nevertheless, the movement was doubtless accompanied by evolution in many instances: *Asclepias Meadii,* a typically prairie species, seems to be a derivative of *Asclepias amplexicaulis* of a more eastern range; a varietal evolution from *Agalinis tenuifolia* illustrates the same geographical relation, according to Dr. F. W. Pennell, and other similar cases might be cited.

The numerous ponds of the eastern arm of the Prairie Province were also formed at this time, in response to increasing rainfall in a region physiographically immature. They were of necessity colonized almost completely by species of southeastern origin, since true hydrophytes were not found in the western vegetation.

EXTENT OF FOREST MIGRATION IN THE PREHISTORIC PERIOD. The northern arm of the forest advance lay chiefly or wholly in a region not reached by the prairies. There is no reason to believe that it has suffered any retardation to the present time, except as caused within the past century by commercial developments in lumbering and agriculture.

The southern migration, on the other hand, was quite different in nature, due to a less favorable climate and to the character of the vegetation encountered. It has already been noted that it followed the water courses, most of which, as tributaries of the Mississippi, offer convenient highways leading from the center of forest preservation into the area of xerothermic prairies. It has also been noted that the longitudinal advance following the streams was more rapid than the lateral advance at right angles to them. The forests therefore soon assumed the form of long branching strips, following the rivers from their mouths toward their sources. Through the slow lateral advance these strips were widened and eventually became confluent across the interfluvial prairies, frequently isolating portions of the prairie in the process.

The nature of the forest advance was determined by the location of sufficient environmental change to permit the migration. Since the unfavorable environment was chiefly due to conditions of rainfall and atmospheric humidity, the advance followed the lines of topographic relief, where some shelter was offered from the drying winds and the subsurface water stood at a greater height, and the water courses where edaphic moisture compensated for low rainfall. The rolling surface of the moraines offered favorable conditions for trees of the xerarch series, and they were soon colonized by forests of oak and hickory, reaching the moraines by the intersecting streams and spreading across from one stream valley to another. On the other hand, the wide alluvial bottom lands of the larger rivers, notably the Missouri, Mississippi, and Illinois, seem to have resisted forest invasion, and on them the forests were limited to relatively narrow strips along the channel and the abandoned oxbows, alternating with strips of prairie. This condition, recorded by numerous early observers, is so unlike our modern experience with floodplain vegetation in the Middle West that it at once stimulates inquiry into the circumstances of more recent forest development.

In a forest advance along the bluffs of a river flowing from north to south through a region of prevailingly westerly winds, the greatest protection against atmospheric conditions will be found on the western lee side of the river, rather than on the windward eastern side. Actual conditions throughout the Middle West, however, show an unexpected distribution, in that by far the largest areas of forest were originally found on the eastern side of such streams. This has been discussed in an earlier article,[50] in which the explanation was offered that the irregular distribution is due to prairie fires, which, driven before a westerly wind, have gradually destroyed much of the forests on the western side but have had little effect on those to the east of the stream. The period of great forest migration must therefore have closed with the advent of the Indian and the prairie fire.

The extent of forest advance before that time can only be approximated by a study of the present distribution of morainal forests and of the relative amounts on different sides of streams. Planimeter measurements have been made of maps showing forest distribution in two parts of Iowa and in three counties in Illinois and have given results of remarkable but not necessarily significant uniformity. In Shimek's[51] map of the Lake Okoboji region, Iowa, 26.5% only of the forests are on the west side of the lakes, and 73.5% on the east side. McGee's[29] map of northeastern Iowa shows for the Wapsipinicon River 27.9% on the west and 72.1% on the east, and for the Cedar River 29.7% on the west and 70.3% on the east. Tracings of the original land surveys of Champaign, Piatt, and Moultrie Counties, Illinois, show forests on the west side of the streams amounting to 31%, 31.6%, and 29.8%, and on the east side 67.3%, 67.4%, and 70.2% respectively. In Champaign County 1.7% and in Piatt County 1% of the forest area is in isolated groves apart from any river system. If we may assume that forest was originally developed equally on both sides of the streams, the total area would be increased by amounts ranging from 36% of the present area in Piatt County to 44% along the Wapsipinicon River. The lakes of the Okoboji region would have additional forest on the west side amounting to 47% of the present total, and if they were carried completely around the lakes the increase would be still greater.

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[50] Gleason, H. A. The relation of forest distribution and prairie fires in the Middle West. Torreya 13: 173–181. 1913.

[51] Shimek, B. The plant geography of the Lake Okoboji region. Bull. State Univ. Iowa. Bulletins from the laboratories of natural history 72. 1915.

The extent of migration up the streams beyond the present limit of forest can be considered with less accuracy. The original land surveys frequently show small areas of forest isolated from the main body along the head waters of a stream. Also, the upstream end of the forest belts is regularly wide and blunt. Modern observation shows that in the same area establishment of new forest is rapid as far upstream as there is a differentiation of upland, bluff, and floodplain. If the interruped belts were made continuous and were extended upstream according to the topography, there appears to be room in Champaign County for at least 28 more miles of forest belt, comprising probably 14 square miles. There is also evidence that the moraines were forested wholly or in part in prehistoric time. Fragments of the forests still persist in sheltered places in Champaign County, and well developed morainal forests occupy considerable areas of McLean County. In Champaign County, about 50 square miles of land is morainal and may have been forested.

The land survey maps indicate 44,846 acres of forest in Champaign County, and this figure is apparently somewhat too small, since the surveyors frequently referred to trees up to two feet in diameter standing on land designated on the map as prairie. Increasing this amount by 64 square miles makes a possible total of nearly 86,000 acres of prehistoric forests, almost twice the present extent, and increases the proportion of forest, from 7.1% to 13.5% of the total area. While the accuracy of this estimate can not be proved, we may safely conclude that the forested area was at one time greatly larger than its present extent through Illinois and Iowa, and doubtless also through the prairie region of Wisconsin and Indiana.

Second Period of Prairie Dominance. The advance of the forest would in time have given a continuous forest covering to the Middle West, except on those limited habitats where tree growth is impossible for edaphic reasons. The forest would have extended west to the climatic limit of tree growth and tongues would have projected beyond the principal area along the habitats where special environmental conditions compensated for the unfavorable climate. This advance came to a sudden conclusion with the arrival of the American Indian and the consequent introduction of prairie fires. This stage in the history of the Middle West has been discussed in an earlier paper[50] and needs only brief recapitulation here.

Prairie fires were set annually by the Indians in the autumn months to drive game from the open prairies into the forest, where it was more easily stalked. Sweeping eastward before the prevailingly westerly winds of that season, the fires destroyed seedling trees at the west margin of the forest, preventing further advance in that direction. It is doubtful if they penetrated far into the forest, but by destroying the undergrowth and killing the more susceptible species, they gradually reduced the forest to the open parklike condition known as oak openings. Here the herbaceous vegetation was composed largely of prairie grasses, which furnished additional material for fires and led to the annual extension of the prairie through the eventual death of the remaining trees. The forest was thus slowly pushed back to the river bluffs, where the greater topographic diversity favored its persistence, or, where the bluffs were low and with gradual slopes, was completely destroyed on the west side of the streams. Fires even crossed the smaller streams, attacked the forests of the eastern side, and by burning through them isolated areas of forest toward the headwaters of the stream from the main body below. This condition is shown in several places on the original land surveys of central Illinois, and examination of them indicates that the separation was always in places of low relief, leaving forests isolated where the bluffs were steeper or higher.

On the eastern side of the forest, protected against fires driven by the prevailing winds, encroachment by the prairie was less rapid and doubtless in many cases negligible. It is probable that the forest advance was completely stopped in some places, but may have continued slowly in others.

Along the moraines, which are generally characterized by a gently rolling topography, the forests were destroyed completely, except in those few favored situations where ponds or swamps on the west side acted as an effective barrier to the fires.

Another effect of prairie fires was the production of the so-called barrens, areas characterized by a sparse growth of "scrub" oak (apparently *Quercus velutina* in most cases), hazel, and wild plum. The exact cause of the barrens is unknown, but descriptions from early literature and accounts of personal observers in Illinois, Indiana, and Iowa agree that these three species of plants were the principal, if not the only, woody species present, and that they seldom exceeded four or five feet in height. They seem to represent a late stage in the degeneration of the forest, where seedlings were established and the young plants burned to the ground frequently without completely destroying the root system. This developed further each year, reached a large size, and sent up sprouts annually which persisted a year or two longer before the next fire again killed them to the ground.

During this same period, a few new isolated groves were established on the prairies, but always in areas well protected from the fires. Two such have been examined in Champaign County, Illinois, are mentioned before in this paper, and described in more detail elsewhere[50]. They are composed exclusively of mobile species and have been in existence such a short time that they have not yet changed the nature of the prairie soil[52].

SECOND PERIOD OF FOREST ADVANCE.— Settlement of the forested regions of the Middle West began about the opening of the nineteenth century, progressed steadily westward, and reached the Missouri River in fifty years. Actual settlement of the prairies was long avoided, vast areas were still untouched at the time of the Civil War, and prairie fires did not cease being a menace in parts of Illinois until 1860 and in Iowa until somewhat later. As soon as fires ceased, the advance of the forest was renewed, and at a rate probably more rapid than the original, since considerable improvement of climate may have taken place since the first advance was stopped by fires.

Early literature contains many accounts of this spread of the forested area, which was rapid enough to attract the attention of travellers. It seems to have progressed in several different ways. The lateral advance of the forest at right angles to the streams and the longitudinal advance along the streams continued as before. Willows, cottonwoods, and some hydrophytic shrubs moved rapidly up the rivers and creeks, and were followed by elms, maples, and ashes. Thirty years after the first prairie settlements were made in Macon and Moultrie counties, Illinois, these fringing forests had extended one or two miles up the smaller streams. Isolated colonies of mobile species, especially willow, *Salix humilis,* and wild plum, *Prunus americana,* were established well out on the prairie, grew into thickets, and frequently received further additions of forest species, carried in by the birds which visited them or by wind. Large areas of barrens were converted into forest as by magic, when the fires that had maintained them were stopped and the oak sprouts became trees.

The total afforestation during this period was considerable and in some cases almost unbelievable, and may best be indicated by a few examples. Thus the driftless area of northwestern Illinois and southwestern Wisconsin, which now gives the impression of having been heavily forested, was 80-90% prairie a century ago,[53] and was described by Keating[54] as presenting "the waved appearance of a somewhat ruffled

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[52] Hopkins, C. G., J. G. Mosier, E. Van Alstine, & F. W. Garrett. Champaign County soils. Ill. Agr. Exp. Sta. Soil Report 18. 1918.

[53] Schockel, Bernard H. History of development of Jo Daviess County. Illinois State Geol. Surv. Bull. 26. 1916.

[54] Keating, William H. Narrative of an expedition to the source of St. Peter's River . . . performed in the year 1823 . . . under the command of Stephen H. Long. Philadelphia, 1824.

ocean; it is covered with a dry short grass," while the higher knobs, now concealed by the forest, rose from the midst of the prairie and were visible thirty miles. A little later we find farmers near St. Louis complaining that the rapid growth of trees had seriously restricted the natural pastures.[55] The Mississippi and Illinois rivers at that time had long strips of prairie in their floodplains, which are now completely forested, except where under cultivation. The dune region at the head of Lake Michigan, which is now well forested with oak, was then "treeless, except for a few stunted pines." Forested areas in Indiana were developed, within the memory of men now living, from barrens over which a man on horseback had been visible for six miles (personal communication from Mr. C. C. Deam). The rapid development of forests on the sand dunes of the Illinois River has been noted elsewhere.[56]

This great forest advance of the nineteenth century proceeded by ordinary successional processes and affected hundreds of square miles. It ceased only with the complete occupation of the prairie land for agriculture. Since then, that is, during the last 50 years, forest succession has been limited to sand dunes, roadsides, and railway lines. Every roadside in the Middle West is a potential forest and would speedily become so in fact except for constant effort in keeping the thickets and young trees cut down.

Coastal Flora of the Great Lakes.— The extensive sandy beaches of the Great Lakes are characterized by a number of species which do not occur or are rare elsewhere in the Middle West. The geographical origin of many of these species is indicated by their distribution elsewhere or by the range of their nearest relatives. Thus *Iris lacustris* is closely related to *Iris cristata; Solidago Houghtonii* to *S. Riddellii* and *S. ohioensis,* and both were probably derived by immigration from the south, accompanied by specific evolution. *Cirsium Pitcheri* may have a similar origin. *Corispermum hyssopifolium,* for similar reasons, appears to have entered the region from the west. Besides these, there is a considerable group of species which are distributed along the northern shores of the Atlantic, sometimes in Europe as well as America, are not ordinarily found inland, but appear along the shore of the Great Lakes. This group includes *Ammophila arenaria, Elymus arenarius, Juncus balticus, Halerpestes Cymbalaria, Cakile edentula, Prunus pumila, Lathyrus maritimus, Chamaesyce polygonifolia, Hud-*

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[55] Peck, J. M. A gazetteer of Illinois. Philadelphia, 1837.

[56] Gleason, H. A. The vegetation of the inland sand deposits of Illinois. Bull. Illinois State Lab. Nat. Hist. 9: 21–174. 1910.

*sonia tomentosa*, and *Tanacetum huronense*. Two other species, *Salix syrticola* and *Solidago Gillmani*, are endemic to the Great Lakes, but the distribution of their nearest relatives indicates that they are of the same ultimate geographical origin.

The most plausible explanation for the occurrence of these species so far inland from their maritime range is that they migrated along the shores of the Champlain Sea during the Algonkian or Nipissing stages of the Great Lakes, and entered the lake region along the Kirkfield or North Bay outlets.[33] This explanation agrees with the present center of abundance of the lake shore species near the north end of Lake Huron and, since the ice fields were not far away during this period, with their prevailingly northern maritime distribution.*

SUMMARY OF PART IV AND CONCLUSION.— 1. The principal vegetational and floristic elements of the Middle West were differentiated during the Tertiary Period and have continuously maintained their present relative position.

2. Each glacial advance has induced extensive migrations toward the south and west, but in them the coniferous and arctic floras have been greatly narrowed and the deciduous forests have lived uninterruptedly in the Ohio valley.

3. Extensive readjustments of distribution have taken place in each interglacial stage. During the Sangamon, most or all of the Middle West was probably occupied by deciduous forests.

4. Climate in the Middle West beyond the Wisconsin glaciation was semi-arid during the time of maximum ice advance, thereby restricting the boreal floras greatly toward the west.

5. A xerothermic period followed the retreat of the Wisconsin ice, and caused the eastward migration of prairies as far as Ohio, succeeding the coniferous forests as the latter migrated north.

6. A gradual increase in rainfall was accompanied by a westward migration of deciduous forests. This was composed of two elements, one moving from the Ohio valley and one from the Allegheny Mountains. At the close of this period, forests occupied a much greater proportion of the Middle West than at present.

7. With the arrival of the Indian and prairie fires, prairies again began to encroach on the forests and reduced the forested area to its condition at the beginning of the last century.

8. During the nineteenth century extensive afforestation took place, continuing until the land was placed under cultivation.

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* Since this paper went to press, D. C. Peattie has discussed this subject in more detail in Rhodora 24: 57-70, 80-88. 1922.

The writer has no doubt that further study of the problem of glacial and postglacial vegetational history, based on additional facts of modern distribution, on better knowledge of plant migration and the ecological requirements of species, and on new evidence from fossils, and carried on by investigators with different viewpoints and different personal experiences, will lead to many important modifications of the outline here presented. The field is large, almost untouched, and of compelling interest, and it is hoped that it will attract the attention of students not only in the region here discussed, but elsewhere through the country as well.

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# EVOLUTION AND GEOGRAPHICAL DISTRIBUTION OF THE GENUS VERNONIA IN NORTH AMERICA

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# EVOLUTION AND GEOGRAPHICAL DISTRIBUTION OF THE GENUS VERNONIA IN NORTH AMERICA

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The genus Vernonia, with its vast assemblage of over 500 species, ranges through the western hemisphere from Argentina to Manitoba, occupying a region of great climatic variation and habitats of great ecological diversity. In preparing manuscript for the treatment of the genus in the "North American Flora," 123 species have been recognized north of Colombia and Trinidad. Within this number a few stand comparatively isolated from all the others, while many are so closely related in form and structure and so similar in distribution that they must be closely akin genetically. Over 30 species-groups may be distinguished in this way. Within these minor groups evidences of specific evolution correlated with geographic distribution are frequently seen, while most of the groups, considered each as a whole, present strong evidence in favor of their relation to, and probable origin from, each other. It is therefore possible to build up a general scheme of evolution and migration within the genus in which the two lines of evidence, structural and geographic, complement and support each other.

There can be little doubt that the ancestral home of the genus, as far as North American species are concerned, is tropical South America. This is shown by the presence there of a large number of species of greater structural diversity than exist on the North American continent, and also by the fact that many South American species are of a structure which clearly indicates their primitive nature.

Within the genus as a whole, the more fundamental structural differences, which have been used in the division of Vernonia into its many sections and subsections, relate chiefly to the structure of the achenes, the pappus, and the involucral scales. Nothing can now be said concerning the possible evolution of these groups. Of those distinguished by Bentham and Hooker in "Genera Plantarum" and accepted by Hofman in "Die natürlichen Pflanzenfamilien," four have reached North America.

1. The section Stengelia, of the East Indies, with veiny, foliaceous involucral scales, is represented by a single species, *V. anthelmintica* (L.) Willd., sparingly introduced into a few islands of the West Indies. Certain Mexican species which bear a superficial resemblance to this section appear to belong rather to the section Lepidaploa, and their similarity to Stengelia is better explained by convergent evolution.

2. The section Tephrodes, of the paleotropical region, with terete achenes, is represented by a single species, *V. cinerea* (L.) Less., widely introduced

as a weed in tropical America and recently reported from extreme southern Florida. Its further migration through the agencies of commerce is to be expected.

3. The section Stenocephalum, with coriaceous, spine-tipped involucral scales, represented by several species of tropical South America, has a single little-known and recently discovered species, *V. jucunda* Gleason, in the mountains of southern Mexico. If we assume from the negative evidence at hand that the section is actually absent from Central America, we may infer an early migration of the section northward, followed by extinction in Central America and the isolation of the single species in Chiapas.

4. The section Lepidaploa, with membranous involucral scales and ribbed achenes, includes 120 species of North America and many more in South America.

Within this large section there is still well-marked evidence of evolutionary development in structure, illustrated most plainly by the character of the inflorescence. One type of inflorescence may be assumed *a priori* as the most primitive, and from it by successive small changes all the other types may be derived. Since the center of evolution and migration for the genus is considered to be tropical South America, where this primitive type is largely developed, and since the succeeding stages in the modification of the inflorescence occur progressively farther to the north, structure and distribution complement each other, and it may be assumed with little hesitation that migration and structural evolution have proceeded simultaneously; that the tropical species, while not necessarily the oldest in time, are at least the most primitive in structure, and that the outlying species of the temperate part of North America are both young in age and advanced in evolution. It can not now be stated whether there is a similar correlation between structure and distribution among the species of South America.

In the section Lepidaploa, the inflorescence is either a scorpioid cyme or some other type of cluster obviously derived from it by certain apparent modifications in the original structure. In such an inflorescence each head is morphologically terminal; a lateral branch, arising at the first node below the involucre, terminates in a second head and bears another lateral branch which behaves in the same way. There is thus produced a more or less elongate sympodial axis, morphologically indeterminate in its development, and with its series of truly terminal heads apparently lateral and secund along it. Since the successive lateral branches arise from nodes, which are normally marked by leaves, it may be assumed at once that the leafy scorpioid cyme is the primitive inflorescence, while those species in which the bracteal leaves are suppressed stand relatively higher in the scale of evolution.

Each segment of such an inflorescence then consists of a basal internode with a leaf at its summit and a head beyond it. The structure of the bracteal leaves varies greatly, but in general they maintain the form and pubescence of the cauline leaves and differ from them chiefly in size. The head is pediceled if separated from the bract by an obvious internode, and the inflorescence is then a scorpioid raceme. If this internode is reduced, the head is sessile and the cluster becomes a scorpioid spike. The clusters may be straight or flexuous, long or short, crowded or loose, with heads ranging from 2 to 25 in number. As a result of the straightening of the sympodial axis, the heads appear lateral and are usually placed about 90° around the axis from the bracteal leaf.

The leafy scorpioid cyme is found in 57 species, ranging throughout the West Indies and on the continent extending north into southern Mexico. Species with leafless cymes, 63 in number, occur commonly on the continent from Panama to New England. From this region four have crossed the narrow gulf east of Yucatan and entered Cuba; one has reached the Bahamas from Florida; one is endemic to St. Vincent, and another reaches Trinidad and the neighboring islands. In general, the distribution of the latter group is continental, of the former Antillean.

Perhaps the simplest type of the primitive leafy inflorescence is found in the species-group Graciles, in which the cymes are stemlike and quite undifferentiated from the truly vegetative portion of the stem, with bracteal leaves closely resembling the cauline in size and shape. Species of this group are almost entirely South American, ranging, according to Ekman, from Colombia to eastern Brazil. One species only, *V. gracilis* H. B. K. var. *tomentosa* Ekman, of Bequia, occurs in our range.

A second group, with almost equally simple inflorescence, composed of long, irregular, branching cymes, with long internodes and leaflike bracts, is the Argyropappae, of tropical South America, Central America, and southern Mexico. The South American origin of the group may be assumed. From there, *V. remotiflora* Rich. has been introduced into St. Thomas; *V. acilepis* Benth. is endemic to Costa Rica, and *V. argyropappa* Buek extends from Peru to Mexico. Two offshoots of the latter have arisen in Mexico, *V. hirsutivena* Gleason in Yucatan and *V. ctenophora* Gleason in Campeche, differing in minor structural details.

It will be observed that these two groups, simplest in structure, are distributed primarily in South America and that only a part of their species reach North America, although among these are three endemic species and one endemic variety.

A third group of similar primitive structure as to inflorescence is the Schiedeanae, of Central America and southern Mexico. While its members differ sharply from the preceding group in their large heads, the peculiar development and specialization of the involucral scales, and the absence of foliar resin dots, they retain the simple cymes and broad, heavy leaves, and may possibly be derived from it. *V. vernicosa* Klatt, with narrow acuminate scales, appears to be the simplest and is endemic to Costa Rica. *V. Seemanniana* Steetz follows in Costa Rica, with broad, obtuse scales, and the greatest modification is found in *V. Schiedeana* Less., ranging from Honduras to Vera Cruz, with involucral scales broadly dilated at the tip. The progressive specialization in structure, correlated with increasing distance to the north, is here clearly shown.

There now follow seven species-groups with 33 species, all West Indian, all clearly related, and all exhibiting a remarkable correlation between structure and distribution.

The most primitive of these, from which the other six are directly or indirectly derived, is the Arborescentes, ranging from the Windward Islands to Jamaica. The wide range and primitive structure probably indicate an early arrival in the region. The most primitive species, *V. icosantha* DC., has stems bearing leaves of normal size to the apex and terminating in a single sessile head. At the base of this head the two primary cymes arise; they are straight, elongate, with prominent internodes, sparingly branched or simple, and bear numerous heads. The chief distinction in the inflorescence between it and the Graciles is the regular presence of paired primary cymes. In *V. sericea* L.C.Rich., of the Virgin Islands and Porto Rico, the cymes are shorter and more frequently branched. *V. borinquensis* Urban, of Porto Rico, has exceedingly flexuous, many-headed, freely branched cymes, the branches invariably arising at the base of a head. *V. arborescens* (L.) Sw., of Jamaica, has numerous frequently congested cymes and reduced bracteal leaves. *V. permollis* Gleason, of Jamaica, completes the group, with congested cymes and an unusual development of foliar pubescence. The general tendency of the group is toward the production of cyme-branches and supernumerary cymes, making a congested inflorescence in which the bracteal leaves are reduced.

The Longifoliae, a group of three species, is related through *V. longifolia* Pers., of the Lesser Antilles, to *V. icosantha*. Superficially the two species are much alike, but the inflorescence in the former shows a distinct difference. The primary cymes are short, compact, divergently spreading at an angle of 60–90°, crowded, bearing only 2–5 heads on short internodes with bracteal leaves considerably smaller than the heads. Secondary cymes arise just below the primary in the upper leaf axils. They are essentially leafless for the first 2–5 cm., and then bear toward the summit either the usual crowded heads or a terminal head subtended by two short cymes. This whole inflorescence terminates completely the growth of this portion of the stem, but during the next vegetative season new branches appear from the next lower axils in order, grow out at a divergent angle, soon surpass the old cymes of the previous season, and at the next blooming season bear their cymes in turn. The plant has therefore a method of continuing its vegetative growth beyond one season, and as a result reaches a considerably larger size. *V. Shaferi* Gleason, of Montserrat, is closely similar, and represents an island endemic. *V. albicaulis* Pers., of the Virgin Islands and Porto Rico, preserves the same inflorescence but differs in its obtuse or broadly rounded leaves.

It is a comparatively short distance across open water to the north of Porto Rico, the home of *V. albicaulis*, to the southern islands of the Bahamas. In these southernmost islands occurs *V. bahamensis* Griseb., the most primitive member of the species-group Bahamenses. The fundamental difference between this group and the Longifoliae is again found in the inflorescence. Here the cymes, after the flowering period, continue their elongation into the vegetative shoots of the next season. Not every cyme necessarily elongates, but there are regularly 2–4 such branches at the apex of each year's growth. Toward their base, paired scars mark the location of former heads and bracteal leaves, while above them scars in spiral arrangement indicate the former position of foliage leaves. All these Bahaman species are therefore bushy, widely spreading, freely branched shrubs. It is particularly worthy of note that they all have broad obtuse to retuse leaves; that *V. bahamensis*, the species most nearly resembling *V. albicaulis* in leaf form, is the species of the southernmost islands, and that the particular specimen in herbaria which most closely approximates the leaves of the Porto Rican plant in size was collected on South Caicos Island, almost the extreme southeastern island of the group. *V. arbuscula* Less. and *V. obcordata* Gleason occur farther to the northwest in the Bahamas. *V. complicata* Griseb., of eastern Cuba, differs only in minor characters. It is difficult to imagine a more striking instance of correlation between structure and distribution than is presented by this group in its relation to the Longifoliae.

The last three species-groups illustrate the following course of development in the inflorescence:

1. The cyme is a special branch with reduced bracteal leaves and elongate axis.
2. The cyme and leafy branches differ merely in position, and the inflorescence is compact.
3. The cyme becomes the leafy branch at the conclusion of the blooming season, and the inflorescence is compact and reduced.

The fourth species-group of the seven, the Racemosae, includes five species of Hispaniola and Cuba. They are probably derived from *V. sericea* of the Arborescentes, which is located near by in Porto Rico; *V. racemosa* Delp. was considered by Ekman a variety of *V. sericea*, and, like it, most of the species have leaves pubescent on the lower surface. In this group the two upper primary cymes are short, with only 2–5 heads. Below them, every leaf axil for a considerable distance down the stem produces similar short lateral cymes. The whole makes an elongate subcylindric inflorescence, quite different from the broad, spreading type of the preceding groups. Secondary vegetative branches apparently do not exist. Within the group, evolution is seen in the progressive reduction of the leaf surface, of the cymes, and of the number of flowers in the head. While *V. racemosa* of Hispaniola has lanceolate leaves, and cymes of 2–5 many-flowered heads, the next three, one of Hispaniola and two of Cuba, have progressively narrower and more revolute leaves and smaller and fewer heads. The group culminates in a fifth species, *V. corallophila* Gleason of Cuba, with linear leaves revolute to the midvein, 11-flowered heads, and 1-headed cymes which appear as single axillary heads.

A fifth species-group, the Gnaphaliifoliae, also appears to be derived from *V. sericea* or some species similar to it. There is the usual terminal head, subtended by two primary cymes, and numerous other cymes arise from the upper axils. They are usually flexuous, spreading or ascending, and only occasionally branched. Such structures point unmistakably to an origin within the Arborescentes, with which they share many structural features and from which they are indeed rather weakly separated. The three species are all Cuban. In this group axillary branches do not continue the vegetative growth, but the whole herbaceous stem dies and is replaced by new growth from the perennial base.

All groups heretofore described in this general series have acute or acuminate involucral scales. The sixth, the Acuminatae of Jamaica, have obtuse scales, and also differ from the Arborescentes in their resinous-dotted, non-papillose leaves and in their flattened and twisted pappus bristles. Nevertheless, the simplest species of this group bears a general resemblance to *V. arborescens;* has been placed adjacent to that species by Ekman, and may have been derived from it. I fail completely to see any resemblance between this group and the Fruticosae, as has been claimed by Ekman. *V. acuminata* Less. is the common species of lower elevations. *V. pluvialis* Gleason, the high-mountain derivative, presents an inflorescence of short, much congested cymes, aggregated in subcapitate clusters.

The seventh and last group of this series, the Fruticosae, includes one species of Hispaniola and eight of Cuba, particularly of the mountains of the eastern part. Many of these are poorly known, some by a single collection, and the number of species may easily be subject to increase or decrease as further collections are accumulated for study. From the inflorescence standpoint, they exhibit the simplest scorpioid cymes to be found in the West Indies. They are mostly straggling vinelike plants with indeterminate growth. At some distance above the base the main axis ends in a terminal head, while immediately beneath it a lateral branch, diverging at a small angle, continues the sympodial axis and bears heads in the same way. The heads are separated by internodes about equal to those of the sterile section of the stem in length, they are subtended by bracteal leaves which in almost all species are virtually indistinguishable from the cauline in size and shape, and furthermore the cyme axis is frequently prolonged after flowering into a leafy, sterile stem. In their leaf habit and papillose pubescence they approach *V. gnaphaliifolia;* in other features they have no near relatives in the West Indies and apparently none in South America. Nevertheless, they offer no new structural features to separate them from the preceding species-groups. In the lack of sufficient material, the evolution within the group can not now be discussed.

It is not necessary to presume that only one ancestral stock of Vernonia migrated into the West Indies. The seven species-groups just described, constituting probably one evolutionary stock, have spread over the whole region and developed into many species. Other stocks may also have immigrated from South America, been isolated in certain islands, and developed endemic species. Certainly two species-groups now exist whose relations can not be explained, and which should probably be considered as entirely distinct evolutionary lines. These are the Buxifoliae and the Sagraeanae.

The Buxifoliae include three species of the mountains of Hispaniola. They are characterized by glabrous achenes, heads in subcapitate clusters, and an unusually large number of involucral scales, arranged in a beautifully spiral imbrication.

The Sagraeanae include ten species, nine in Cuba and one in Hispaniola, with an outlying variety in Dominica, characterized by large glabrous achenes and usually by large many-flowered heads. Ekman would relate the group to the Bolivian *V. robusta* Rusby, which differs in achenes, hispid in the furrows, and in the number of setae of the pappus, about 25, instead of 40–70; also to the Bolivian *V. obtusata* Less. (*V. subacuminata* Hieron.) which has densely hirsute achenes. There is a superficial resemblance to these Bolivian plants in their heavy, rugose, reticulately veined leaves, and to *V. robusta* also in their large heads. On the ground that specialized involucral scales, few-flowered heads, and rigid, coriaceous, or tomentose leaves are characters which indicate an evolutionary advance, *V. Sagraeana* DC. and *V. viminalis* Gleason may be regarded as the most primitive species, and *V. Wrightii* Sch.-Bip. and *V. purpurata* Gleason as the most advanced.

We have now disposed of all leafy-bracted scorpioid species of North America except two, *V. yunquensis* Gleason and *V. segregata* Gleason. These Cuban species are poorly known and the former is represented in herbaria only by the type specimen. While each of them exhibits certain points of resemblance to other West Indian species, it is not possible to draw any conclusions as to their relationships.

The general affinities of the 57 species of the leafy-bracted groups may be summarized by the diagram (fig. 1), from which it may be seen that without exception the more advanced groups lie progressively farther from South America, that no group is common to the West Indies and the continent of North America, except as introduced, and that, with very few exceptions, the more advanced species of each group also lie farther away from the center of origin, either in horizontal or in altitudinal distance.

The 63 species in which the bracteal leaves are suppressed show certain fundamental differences among themselves in the structure of the inflorescence, as a result of which five well-marked evolutionary stages may be distinguished. In the first of these the cymose structure is obvious, each cyme is more or less elongate with secund heads, and branches occur at such intervals that the scorpioid structure is not obscured. In the second, secondary branches are developed at the bases of a great many heads, so that three successive nodes without branches rarely occur. The result is a large branching cluster which bears little superficial resemblance to the simple scorpioid cyme, although undoubtedly derived from it. In the third, the heads are suppressed at those nodes where secondary branches are developed. Since these appear at virtually every node, only terminal heads are produced on the cymes, and the whole cluster appears to be dichotomously branched. The fourth stage represents a much greater step forward. Here the basal internodes of the inflorescence are much shortened or almost suppressed, while the number of heads is greatly reduced. Since the terminal internodes retain a normal length, the whole inflorescence appears subumbellate. While in the first three stages new vegetative branches may arise from below the inflorescence, so that the stem may live several years and reach a large size, in the fourth type, as well as in the fifth, the appearance of the inflorescence prevents further growth

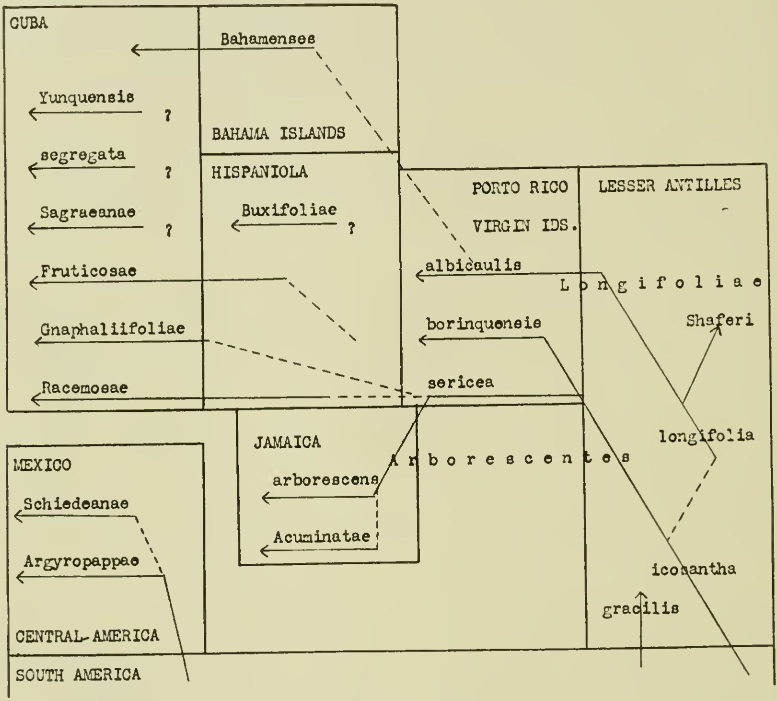

FIG. 1. Migration and evolution of the leafy-bracted Vernoniae of North America. Solid lines show distribution by their location, migration by the direction of the arrow. Dotted lines show probable connection by evolution between species-groups.

of the stem, and new vegetative parts appear only from the perennial base of the plant. In the fifth and last stage, only a few terminal and subterminal heads retain the umbellate arrangement, while from the upper stem axils similar clusters arise, producing a broad, flat-topped or hemispheric cluster with all the heads peduncled. These five stages are shown diagrammatically in figure 2.

FIG. 2. Modifications of the inflorescence in the bractless Vernoniae of North America *A*. Stage 1, *Vernonia scorpioides*, lateral branch with two terminal cymes. *B*. Stage 2, *canescens*, lateral portion of the inflorescence. *C*. Stage 3, *havanensis*, portion of a terminal inflorescence. *D*. Stage 4, *Karvinskiana*, terminal inflorescence, with a few primary branches omitted. *E*. Stage 5, *texana*, complete terminal inflorescence. All figures diagrammatic as to position of branches or cymes, but accurate as to character of branching and proportion.

Other evidences of evolution appear within the last two stages, leading to the segregation of several species-groups.

The five stages are again well correlated with their geographical distribution. The first occurs in South America and is represented in our region by a single species of St. Vincent, *V. pallescens* Gleason, and by two which extend across the Isthmus of Panama into southern Central America, *V. scorpioides* (Lam.) Pers. and *V. brachiata* Benth. The second includes several species of northwestern South America, some of which extend into Central America also, and several others ranging as far north as southern Mexico. Species of the third stage have crossed the narrow channel from Yucatan and are now limited to western Cuba; the fourth is confined to Mexico, and the fifth has four species in northern Mexico and 31 in the United States and the Bahamas.

The species-group Stellares, representing the second stage, includes the commonest species of the mountains of Colombia, Central America, and southern Mexico. The Colombian species *V. canescens* H.B.K. and *V. mollis* H.B.K. retain the primitive character of acuminate involucral scales; the former also extends north into Mexico, and the latter is doubtfully admitted into the North American flora. Of the remaining five with acute to rounded scales, *V. patens* H.B.K. occurs in both continents, while the others are strictly North American. The most advanced morphologically is *V. morelana* Gleason, which alone does not occur south of Mexico.

The third stage includes the species-group Menthaefoliae, undoubtedly closely related to the Stellares, but now isolated in western Cuba and the Isle of Pines, except for a few specimens from central and eastern Cuba as well, where they may have been recently introduced.

The fourth stage includes three well-marked species-groups, which are nevertheless closely related. The Umbelliformes include 9 species, mostly quite closely related and in some cases separated with difficulty. The simplest species (and the commonest in herbaria) have small heads, with short involucres and seldom more than 15 flowers; the more advanced have larger heads and taller involucres. One of these, *V. Conzattii* Robinson, with its abruptly rounded and mucronate involucral scales, marks a transition to the group Mexicanae, with three species in the higher mountains of southern Mexico. Here the scales are extraordinarily specialized, being 3–8 mm. wide, loosely spreading, at least at the tip, and prominently reticulately veined. The two closely related species of the Alamanianae have also large scales but lack the reticulate venation. The general evolutionary tendency of the series is apparently toward large heads and specialized scales, and this is correlated geographically with an ascent to higher levels in the mountains.

Passing now to the 35 species of the fifth stage of evolution, as shown by the inflorescence, we find the most primitive members in the Texanae, a group of four species, three in northern Mexico and one in Texas. Since the inflorescence has already passed to the paniculate stage, equally characteristic of the other species of the United States, evidence for the primitive character of the group must be sought in other characters. The leaves in all four species are more or less pitted beneath and the outer pappus bristles are poorly differentiated from the inner in width, both of which features occur also in the Umbelliformes. The most important primitive character, however, lies in the involucre, and has not been mentioned before because it is shared by virtually all the groups hitherto discussed. Here the scales are relatively few in number and poorly imbricated. The inner scales are progressively more exposed than the middle and outer ones, contrasting plainly with the numerous regularly imbricated scales of most other species of the United States. Of the four species in the group, *V. texana* (A. Gray) Small, is best known and occurs in Texas, Louisiana, and Arkansas.

From the area of the Texanae, migration accompanied by specific evolution has proceeded in two directions, northward through the prairie region and eastward along the coastal plain. In each direction one or more of the primitive structures have been lost, until in Michigan and Massachusetts they have disappeared completely.

In northern Texas occurs the group Lindheimerianae of three species, two of which are suspected to be hybrids. *V. Lindheimeriana* Gray & Engelm., which is undoubtedly a good species, retains the primitive involucre and narrow outer bristles of the Texanae, from which it seems to be derived, and differs chiefly in its tomentose leaves and scales.

The Fasciculatae, extending from Texas and New Mexico northward and eastward to Manitoba and Ohio, retain the pitted leaves and present to a still greater degree the narrow, undifferentiated outer bristles of the pappus. They have lost the primitive involucre and have developed long heads with numerous scales imbricated with great regularity. It is noteworthy that the more southern species, as *V. marginata* (Torr.) Raf., still show a tendency toward acumination of the scales, as in Texanae, which character is lost to a large extent in *V. fasciculata* Michx., ranging from Nebraska to Ohio, and completely in *V. corymbosa* Schw., distributed along the Red River of the North in Minnesota, the Dakotas, and Manitoba, where it marks the extreme northern limit of the genus.

The peculiar local species, *V. Lettermanni* Engelm., of Arkansas and adjacent Oklahoma, bears a strong superficial resemblance to *V. fasciculata* and is possibly an evolutionary development from it. It retains the glabrous leaves with pitted lower surfaces and the congested heads with closely imbricated scales, like the latter species, but has broader, well differentiated outer pappus bristles.

The group Interiores takes its name from *V. interior* Small, which is undoubtedly the basic species. Common in central and northern Texas, where it overlaps the range of the ancestral Texanae, it extends north to Nebraska, and thence east to the Mississippi River. The involucre in this species has only partially lost its primitive structure; the outer pappus is narrow but nevertheless plainly differentiated; the leaves are broad, without pits, and characterized by multilocular hairs forming a more or less tomentose pubescence. *V. Baldwini* Torr. is an Ozarkian derivative, with broader outer pappus bristles, and with the acuminate involucral scales recurved at the tip and pubescent on the inner face. The species is probably of recent origin, and specimens from the overlapping ranges of *V. Baldwini* and *V. interior* are frequently intermediate in character. *V. aborigina* Gleason, known so far only from the original collection in southeastern Oklahoma, appears to be a giant form of *V. Baldwini*. It retains most of the morphological characters of that species, but is much larger in all its dimensions, with about twice as many flowers in each head. *V. missurica* Raf., the last of the group, has the widest distribution of the four, ranging from Texas, where it is not particularly common, north and east to Michigan, and becoming exceedingly abundant in Iowa, Illinois, and Indiana. It is characterized by larger, more compact inflorescence, fully differentiated pappus, and regularly imbricated involucre. Many specimens from the southern part of its range retain the sharply acute, relatively narrow involucral scales of *V. interior*, while those from farther east have fewer, broader, and obtuse or apiculate scales. The species also occurs to a limited extent and with slightly different structure along the Gulf Coast as far east as Alabama.

The origin of two other western species is in doubt. *V. Bolleana* Sch.-Bip., of northwestern Mexico, seems to bear no close relation to any other known species. *V. crinita* Raf., of the Ozarkian region, is characterized by filiform involucral scales, and may represent an extreme development from the Interiores.

The eastward migration along the coastal plain from Texas led to the present development of seventeen species. They are not easily divided into distinct species-groups, a feature possibly indicative of recent immigration and evolution. The most primitive group is the Angustifoliae, ranging from Louisiana east to the Atlantic, thence north to the Carolinas and south into Florida and the Bahamas. The group retains the primitive involucre, narrow leaves, and low stature of the Texanae, and the type species of that group was originally described as a variety of *V. angustifolia* Michx. Some of the species have an inflorescence approaching umbelliform and rather suggestive of *V. liatroides* DC. or other species of northern Mexico. *V. angustifolia* has the widest distribution, almost coextensive with that of the group. The other four, each of restricted distribution and lacking the acuminate scales of the simpler species, seem to represent recent evolutionary developments. Of these, *V. Blodgettii* Small, in southern Florida, marks the re-entrance of the group into the tropics, and leads to the closely related *V. insularis* Gleason of the nearby Bahamas.

The group Pulchellae is obviously closely related to the Angustifoliae, as shown by narrow leaves and general vegetative habit, but differs in the absence of resin glands on the achenes and in the prolongation of the involucral scales into filiform appendages. The three species, *V. pulchella* Small, *V. recurva* Gleason, and *V. scaberrima* Nutt., are all of limited distribution in the coastal plain of Georgia and the Carolinas.

The species-group Glaucae lies generally to the north of the Angustifoliae and has probably been derived from it. Here the heads are larger, the pappus is tawny or almost white, and the involucral scales are long-acuminate or almost filiform. The leaves are large in proportion to the height of the stem, and the greatest expanse of foliar surface is toward the base of the stem. While this feature is apparent in *V. glauca* (L.) Willd., an Alleghenian species ranging northward to Pennsylvania, it is still further developed in *V. acaulis* (Walt.) Gleason and *V. georgiana* Bartlett, two coastal plain species with distinctly basal leaves.

Two other species with prolonged filiform scales constitute the group Noveboracenses. *V. noveboracensis* (L.) Michx. has attained a wide distribution over the Piedmont region of the eastern states from Mississippi to Massachusetts, occasionally invading the coastal plain also. There it has given rise to a localized species, *V. Harperi* Gleason, characterized by larger heads with more numerous flowers.

*V. gigantea* (Walt.) Britton is closely related to *V. concinna* Gleason, of the Angustifoliae, and like that species is confined to the southeastern portion of the coastal plain.

The last species-group of the southeastern states is the Altissimae. *V. ovalifolia* T. & G. is a variable species of the southeastern coastal plain, and appears to be the most primitive species of the group in their evolution from the Angustifoliae. Although some of its variants approach *V. concinna*, it is generally distinguished by the broader, regularly imbricated involucre and the broad leaves. *V. flaccidifolia* Small is a well-marked species of the southern Appalachian region. *V. altissima* Nutt., the last species of the group, has a wide distribution from Georgia and Alabama north and west to New York and Missouri. Typical forms of the species avoid the coastal plain and are characteristic of the woodlands of the central states, but the variety *laxa* Gleason occurs along the Gulf Coast. In its western extension *V. altissima* comes in contact with several species of the western migration route, and many intermediate forms occur which are probably to be considered as hybrids.

Considering the 35 species with paniculate inflorescence as a whole, we see that the species with primitive involucre invariably lie far to the south or southwest, and that those with the broadest and most obtuse scales, as well as those with the most filiform scales, lie always well to the north or northeast. It is also worthy of note that only seven of the 35 have attained a wide distribution, while the other 28 occupy small or localized ranges. These seven are *V. fasciculata* Michx., *V. interior* Small, *V. missurica* Raf., *V. angustifolia* Michx., *V. glauca* (L.) Willd., *V. noveboracensis* (L.) Michx., and *V. altissima* Nutt., representing six species-groups. This fact alone may indicate the comparatively recent immigration and incomplete evolution of the genus in the northern portion of its range.

The general relations of the 63 species of the genus in which the bracteal leaves are suppressed is exhibited in a diagram (fig. 3).

In the evolution of the genus in North America, no general plan or tendency is apparent, except in the one feature of inflorescence. In every case it is found that species structurally aberrant from the general type occupy outlying ranges or peculiar habitats. The evolution in structure may be summarized as follows:

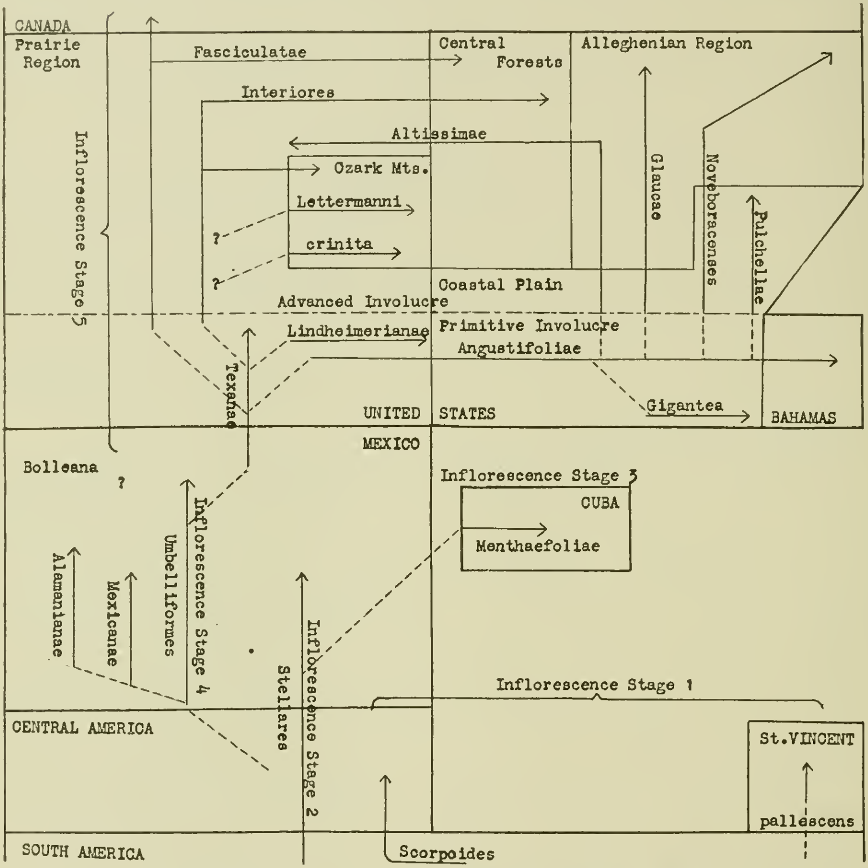

FIG. 3. Migration and evolution of the bractless Vernoniae of North America. Solid lines show distribution by their location, migration by the direction of the arrow. Dotted lines show probable connection between species-group.

1. From elongate cymes to short, compact, freely branching cymes or capitate clusters.

2. From small, acute or acuminate involucral scales to broad, blunt, or veiny scales, or to narrow, prolonged, or filiform scales.

3. From a medium number (13–21) of flowers in each head to a large number (55–89, or even more), or to a reduced number (as low as 5).

4. From lanceolate, acuminate leaves to linear, 1-nerved, or revolute leaves, or to blunt, broad, rigid or coriaceous leaves.

In the leafy-bracted forms, comprising 57 species, there is a general tendency toward the congestion of the inflorescence by repeated branching or toward its reduction by shortening the cymes. The former is most apparent in the species-group Arborescentes, the latter in the Racemosae and Acuminatae. There is a great reduction in the number of flowers in the outlying members of the Acuminatae, Sagraeanae, and Racemosae. Specialization of the involucre by the development of broad, blunt scales occurs in the Schiedeanae, and of narrow, prolonged scales in the Sagraeanae, while the Buxifoliae have increased the number and the regularity of imbrication of the scales. Leaves have shown a tendency to become broad and blunt from the Arborescentes through the Longifoliae and into the Bahamenses, or narrow, one-nerved, and revolute from the Arborescentes into the Racemosae. Montane species have been developed in the Acuminatae and the Buxifoliae, and in both cases are characterized by crowded, few-flowered heads and by small and broad leaves.

Among the 63 species with bractless cymes there is less diversification in structure, except in the inflorescence, which has already been discussed. In the Stellares there is a gradual progression from narrow, acuminate involucral scales to short and blunt ones. A similar tendency occurs among the Interiores and Altissimae, and reaches a climax in the series from the Umbelliformes to the Alamanianae and Mexicanae, with their highly specialized, broad or veiny scales. On the other hand, there is a notable tendency toward prolongation of the scales in *V. crinita* and in the Glaucae, Pulchellae, and Noveboracenses. Excepting the Stellares, all these groups show likewise a tendency to larger heads, reaching a maximum in the Mexicanae, Alamanianae, and *V. crinita*. Forms with unusually small heads rarely occur, and are most characteristic of the single species, *V. gigantea*. Two groups only have developed montane forms, the Alamanianae and Mexicanae, and in their unusually large, many-flowered heads differ remarkably from the montane forms of the West Indies.

Neither is there any correlation between structure and habitat. The variation between the montane species of the West Indies and Mexico has already been mentioned. The relatively arid conditions of the Bahamas are reflected in the thick, firm leaves of the Bahamenses and *V. insularis*, but those of the former, with broad-leaved ancestors, are broad and blunt, while the latter, originating from the Angustifoliae of the Gulf States, preserves the linear leaves. The Racemosae, of arid situations in Cuba and Hispaniola, and *V. texana*, likewise a xerophyte, have narrow leaves, but the hydrophytic *V. fasciculata* has narrow leaves also, while the xerophytic *V. Baldwini* has broad leaves. The xerophytic Bahamenses have assumed the form of bushy shrubs, while *V. texana* has remained an herb, although growing in a region where the shrub form is common.

Three processes seem to have been concerned in the general history of the genus, by which it has reached its present distribution and differentiation. Physiological evolution, scarcely indicated by structure, has enabled the genus to migrate into new environments beyond its original home; migration has brought it to its present distribution and is doubtless still continuing: structural evolution, favored by geographic isolation, has differentiated the present species, but is very little correlated with their physiology or ecology, although proceeding simultaneously with their migration. A single structural tendency appears to be general and possibly orthogenetic, that of the shortening and branching of the cymes.

## SUMMARY

1. Three sections of the genus are represented in North America by a single species each; one section is represented by 120 species.
2. In this section the chief differentiation of groups rests on the structure of the inflorescence; minor differentiation of species-groups is based on the achenes, the involucre, the pappus, and the character of the pubescence.
3. Of the two subsections, one is chiefly Antillean, the other continental, while both are developed in continental South America.
4. Characters which are held to represent primitive conditions in one group may indicate advanced evolution in another, and such characters have no apparent correlation with environment.
5. In every case, those groups which appear to be the simplest in morphological structure occur to the south, while the more complex groups appear progressively farther to the north. In most groups the same statement holds for the individual species.
6. The geographical arrangement of the species-groups and species follows well-known migration routes and supports the conclusion that evolution and migration have proceeded together.

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# Notes on Fabaceae—I

PER AXEL RYDBERG

## HOMALOBUS Nutt.

For several years I have worked on genera of the Fabaceae for the North American Flora. Two parts containing the tribe Psoraleae have already been published, and the manuscript for the Indigoferae and a large part of the Galegeae is ready. My work has taken me to *Astragalus* and related genera. I have heard a rumor that M. E. Jones has been working on an illustrated revision of *Astragalus*, and I wish that this had been published so that I could have availed myself of it in my studies. It would perhaps have helped me to avoid some of the errors which are so likely to creep in.

There is little room for critical notes in the Flora, and yet notes of this character are necessary for a proper understanding of my disposition of genera and for a just appreciation of the amount of work that I have done on the group. It is my intention, therefore, to publish a series of preliminary notes in order to thresh out any unavoidable criticism, which might come from certain quarters, before my final monograph is published. If I should criticise any fellow botanist in this undertaking I do it in order to bring out the facts.

Just before the present paper was completed there appeared an article by J. F. Macbride, entitled: A revision of *Astragalus*, subgenus *Homalobus*, in the Rocky Mountains.* Now it may perhaps seem superfluous for me to go into details and publish another paper on the same subject so soon. So far as generic and specific limits are concerned, I do not think that either Macbride or Jones can ever agree with me. It surprises me, however, that so many of my species, even some that had been sneered at by Jones, have been accepted by Macbride. That he should have reduced some of my species to varieties I might have expected, since I do not see where to draw lines between species and varieties and prefer a binomial name to a trinomial

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* Contr. Gray Herb. II. **65**: 28–39. 1922.

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for the sake of convenience. He has not treated me more harshly in this respect than he has others; for he has reduced to varieties or synonyms the species of other botanists, such as *Astragalus lingulatus* Sheld., *A. exiliflorus* A. Nels., *Homolobus caespitosus* Nutt., *H. canescens* Nutt., *H. brachycarpus* Nutt., *A. amphidoxus* Blankinship, *H. dispar* Nutt., *H. junceus* Nutt., *A. junciformis* A. Nels., *A. diversifolius* Gray, *A. strigosus* Coult. & Fish., *A. Palliseri* Gray, and *A. acerbus* Sheld. In this way he has reduced half of Nuttall's species, all of A. Nelson's and all but one of Sheldon's. Is such a reduction warranted?

I once criticised Brand for his work on the Polemoniaceae, because he did not try to find what the types really represented. May I not now have the right to criticise Macbride for the same laxities? In his paper on *Homalobus* he reduced my *H. microcarpus*, *H. proximus*, and *H. Salidae*, although he admitted that he had not seen the types; he reduced also my *H. Clementis*, *H. stipitatus* and *H. uniflorus*, without including the types among the specimens cited, thus implying that he did not have them before him. The same can be said about Sheldon's *Astragalus lingulatus* and *A. acerbus*. Except in the case of *A. lingulatus* the types of all these species are readily accessible to anyone who may wish to see them.

As I have not found it necessary to change essentially my grouping of the species from that published in my Flora of the Rocky Mountains, I shall keep the same groups as there. I shall also omit the keys except in cases where the species are from the Pacific coast. Keys would be superfluous, since my own are found in my Flora of the Rocky Mountains and since Macbride has given a good one in the paper cited above.

### A. CAESPITOSI

1. HOMALOBUS CAESPITOSUS Nutt. This is the most common and best known of the group, and its nomenclature has not been much confused. Occasionally the leaves are two- or three-foliolate instead of simple. *H. canescens* Nutt. is only a more silvery form of the species. Gray, who merged *Homolobus* in *Astragalus*, recognized the identity of the two, retaining the specific name *caespitosus*, although there was an earlier

*Astragalus caespitosus* Pallas. On this account Sheldon substituted the name *A. spatulatus.* In the meantime O. Kuntze had transferred all species of *Astragalus* to *Tragacantha.* M. E. Jones* has made *A. caespitosus* a variety of *A. simplicifolius* (Nutt.) A. Gray, probably because he did not understand the latter species, which is discussed below. Macbride has followed Jones.

2. HOMALOBUS BRACHYCARPUS Nutt. Gray, Watson, Sheldon, Jones, and Macbride have regarded this as a synonym of *H. caespitosus.* Nuttall distinguished it by its shorter, broader and more abruptly acute pod and by its smaller size. I take it to be the same as the plant described and figured by Watson in King's Report under the name *Astragalus simplicifolius* Gray, although the leaves of Nuttall's specimens are narrower than those figured by Watson. Evidently Jones has followed Watson in his interpretation, for he has shown the close relationship between what he called *A. simplicifolius* and *A. caespitosus*, and afterwards went so far as to make the latter a variety of *A. simplicifclius.* The plant described and figured by Watson, however, is not the same as *Phaca simplicifolia* Nutt.; if it is not *H. brachycarpus* it is without a name. The duplicate of Nuttall's type of *H. brachycarpus* in the Torrey Herbarium strongly resembles Watson's plant but is somewhat taller and has narrower leaves. That in the Gray Herbarium is different and is exactly like the type of *H. canescens*; it does not agree with the description of *H. brachycarpus.* The following specimens belong to the latter:—

WYOMING: hills on the Platte, *Nuttall*; northwestern Wyoming, *Jones 68*; Big Horn Mountains, *Tweedy 136*; Laramie Plains, 1897, *Osterhout*; Fort Steele, *Tweedy 4193*; Pine Bluffs, *A. Nelson 2877*; Natrona, *A. Nelson 142*; Laramie, *A. Nelson 31, 7289*; Fort Bridger, *Lauderdale.*

UTAH: Unitah Mountains, *Goodding 1285*; Wasatch Mountains, *Watson 289.*

3. HOMALOBUS SIMPLICIFOLIUS (Nutt.) Rydb. There are several points in the original description of Nuttall's *Phaca simplicifolia* that do not fit Watson's plant, such as the following: "scapes 1–2-flowered, scarcely exserted;" "legumes glabrous,

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* Proc. Calif. Acad. II. 5: 647. 1895.

coriaceous, sessile, somewhat triquetrous, pointed, scarcely longer than the calyx;" "flowers ochroleucous:" In Watson's plant the scape is three- to seven flowered, usually as long as, or longer than, the leaves; the pod is decidedly flat; and the corolla is purple. All the characters given by Nuttall fit *A. exiliflorus* A. Nelson, but I do not think that the two are identical. There is, however, a plant of southern Wyoming and northern Colorado that agrees fully with Nuttall's type. This resembles Nelson's species but is smaller and has shorter leaves. In this respect it approaches *H. brachycarpus*, being distinguished from that species by its narrower and more pungent leaves and by its shorter, unmottled, and rather turgid pod, thicker nearer the lower suture than the upper, hence Nuttall's expression, "somewhat triquetrous." Nuttall's specimen in the Gray Herbarium has leaves only, so that Watson had no opportunity to compare the pods. The following specimens belong to this species:—

WYOMING: Rocky Mountains, *Nuttall; Fremont;* Ham's Fork, *C. C. Curtis*; Green River, *Jones*; Hanna, *Payson & Payson 1694*.

COLORADO: Canon City, *Brandegee.*

4. HOMALOBUS EXILIFOLIUS (A. Nels.) Rydb. See notes under the preceding species. The following specimens belong here:—

WYOMING: Freezeout Hill, *Elias Nelson 4493*; Fort Steele, *Tweedy 4194*.

5. HOMALOBUS LINGULATUS (Sheld.) Rydb. This is known only from the original collection, and its description is much like that of the preceding species, the only essential difference being the glabrous calyx. The mature fruit is unknown. When the plant is better understood it may prove to be the same as *H. exilifolius*, in which case the species should bear Sheldon's specific name, which antedates Nelson's by five years.

6. HOMALOBUS UNIFLORUS Rydb. It is possible that this may represent an aberrant form of *H. brachycarpus*, i.e. *Astragalus simplicifolius*, as understood by Watson. The pod, however, is different, being lanceolate in outline, more tapering at the apex, 6–7 mm. long and 2–3 mm. wide. It is, therefore,

more like that of the true *H. simplicifolius*.* The following specimens may be cited:—

WYOMING: Evanston, *A. Nelson 2971* (flower); Carter, *M. E. Jones* (fruit).

### B. TENELLI

7. HOMALOBUS TENELLUS (Pursh) Britton. The description of *Astragalus tenellus* Pursh, dating from 1814, was drawn (according to Pursh himself) from flowering specimens of the present species and the fruit of some other *Astragalus*, both of which had been collected by Lewis. When Pursh found that his description had been based on a mixture, he redescribed the flowering specimens, associating them with a fruiting plant collected by Bradbury on the Upper Missouri and giving the species the new name *Ervum multiflorum*, on account of its *Ervum*-like pods. A fragment of Bradbury's plant in the Torrey Herbarium is clearly identical with the flowering specimens collected by Lewis: hence there is no doubt that *Astragalus tenellus* (so far as the flowering specimens are concerned) and *Ervum multiflorum* are the same.

8. HOMALOBUS DISPAR Nutt. Nuttall first described this species in 1818 under the name *Orobus dispar*, from specimens that he collected at Fort Mandan. To those who consider *H. dispar* and *H. tenellus* identical, this note will be of no interest. It is here presented, however, for the benefit of those who are willing to admit their distinctness as species or varieties. Since Nuttall and Bradbury were members of the same expedition and often collected together, one might perhaps assume that *Orobus dispar* and *Ervum multiflorum* were the same. They are not. Nuttall's specimen in the Torrey Herbarium agrees with his description in having broader leaflets than *H. tenellus* and broader short-stipitate pods. Of *Phaca nigrescens* Hook., which was described in 1830 from specimens collected by Richardson, there is likewise a duplicate in the Torrey Herbarium. This belongs to *H. dispar*, while a specimen collected by Nuttall on the Platte River, which was named *Homalobus nigrescens* by him and *Astragalus multiflorus* by Hooker, is like *A. tenellus* Pursh. Macbride states correctly that "Nuttall's

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* See also Bull. Torrey Club **34**: 49. 1917.

specimen in the Gray Herbarium has narrowly linear leaflets and the stipe of even very immature pods is quite as long as the calyx." These statements do fit Nuttall's specimens of "*H. nigrescens*" in the Torrey Herbarium but not his description of *H. dispar*. The specimens in question were collected on the Missouri, but I do not know the date; there is no evidence that they came from Fort Mandan.

9. HOMALOBUS STIPITATUS Rydb. Although *H. tenellus* is much more common than *H. dispar*, the two species have nearly the same range; *H. stipitatus* is confined to the northeastern part of this range. All the specimens in the New York Botanical Garden Herbarium are cited under the original description and need not be repeated here.

10. HOMALOBUS STRIGULOSUS Rydb. Macbride has reduced this to *Astragalus tenellus* forma *strigulosus*. An additional specimen is here recorded:—

UTAH: Jugtown, *Jcnes 5400*.

### 11. **Homalobus Standleyi** sp. nov.

*Astragalus tenellus* var. *Clementis* Macbride, Contr. Gray Herb. II. **65**: 35 (in part). 1922.

A perennial, with a caespitose caudex; stems 2–3 dm. high, sparingly strigose; stipules deltoid, about 2 mm. long, connate; leaves 3–5 cm. long; leaflets nine to fifteen, elliptic or oblong, 5–10 mm. long, 2–3 mm. wide, glabrous above, strigose beneath; racemes lax, 4–7 cm. long, including the short peduncle; bracts lance-subulate, 1–2 mm. long; calyx strigose, the tube 2 mm. long, the teeth subulate, fully 1 mm. long; corolla white or tinged with purple, the keel purple-tipped; banner 6 mm. long, obovate, slightly retuse; wings 5 mm. long; keel-petals 5 mm. long, with a rounded apex; pod about 1 cm. long, 3 mm. broad, strigose, elliptic-oblong, acute at each end, short-stipitate, the stipe shorter than the calyx-tube.

TYPE collected at Ponchuelo Creek, New Mexico, July 4, 1908, *Standley 4181* (herbarium of the New York Botanical Garden).

This is closely related to *H. strigulosus* but differs in the white or purple-tinged (not ochroleucous) corolla, with a decidedly purple-tipped keel, and in the narrower pods with much shorter stipes. Macbride thought that this belonged to *H. Clementis* Rydb. and, on account of the similarity of the pod to that of *H. strigulosus*, made *H. Clementis* a variety of *Astragalus tenellus*. He had evidently not seen the type or a duplicate of the type of *H. Clementis*, but had seen specimens of *Baker 489* from Marshall Pass, Colorado, which evidently belong to *H. Clementis*. In our specimen of this number the pods are very immature, but a closer examination would have shown Macbride that Baker's plant and *Standley 4181* were not the same. In the type of *H. Clementis* the pods are half broader than in *H. Standleyi*, distinctly black-hairy and tapering at both ends, but the stipe if any is only a fraction of a millimeter long, i. e. the pod is subsessile; the corolla also is much larger. *Baker 489* also has black-hairy pods.

12. HOMALOBUS ACERBUS (Sheld.) Rydb. Macbride reduced this species to *Astragalus tenellus* forma *acerbus*, but had evidently seen no specimens of it. M. E. Jones has referred the type of *A. acerbus* in the Columbia Herbarium to *A. wingatanus* and expressed his views in print.* as follows: "*Astragalus acerbus* seems to be identical with *A. Dodgeanus* Jones, and the latter is not surely separable from *A. wingatensis* [*wingatanus*]." In *H. tenellus* and its closer relatives the corolla is ochroleucous (not a very important character); the racemes, together with the peduncles, seldom overtop the leaves to any extent; the pods are decidedly veiny; and the plants are inclined to blacken in drying. In *H. acerbus*, on the other hand, the corolla is white or purple-tinged; the racemes are twice to four times as long as the leaves; the venation of the pods is indistinct; and the plants show no inclination to blacken. The following specimens belong here:—

COLORADO: Glenwood Springs, 1893, *Saunders*; DeBeque, *Osterhout 4282*; Grand Junction, 1895, *M. E. Jones*.

13. HOMALOBUS DODGEANUS (M. E. Jones) Rydb. At present I have no authentic specimens of this species before me but, according to my memory, it is very closely related to *H. acerbus*, and Jones, as shown above, regards the two as identical. In fact Jones's own specimens, determined by him as *Astragalus Dodgeanus*, from Grand Junction, collected May 22, 1895, represent *H. acerbus* and are here listed under that species.

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* Proc. Calif. Acad. II. 5: 636. 1895.

The type came from Thompson's Springs, Utah. The decidedly oblique pods and black-hairy calyx of *H. Dodgeanus* would make the species distinct enough, if these features should prove constant; otherwise the two species should perhaps be united. In this case Jones's specific name should be retained.

14. HOMALOBUS CLEMENTIS Rydb. See my notes under *H. Standleyi* above. Notwithstanding Macbride's remarks and his reduction of this species to a variety of *Astragalus tenellus*, I still consider it nearest to *H. wingatanus* and worthy of recognition. In both *H. wingatanus* and the allied *H. lancearius* the pod is acute at each end, as in *H. Clementis*, and a minute stipe is sometimes produced. In *H. lancearius*, in fact, this stipe may be fully as long as in *H. Clementis*. The following specimens may be cited:—

COLORADO: Saugre de Cristo, *Clements*; Marshall Pass, *Baker 489*; without locality, *C. H. Hall.*

15. HOMALOBUS WINGATANUS (S. Wats.) Rydb. To the specimens listed by Macbride the following may be added:—

COLORADO: Mancus, *Eastwood.*

UTAH: Monticello, *Rydberg & Garrett 9151, 9228.*

16. HOMALOBUS LANCEARIUS (A. Gray) Rydb. This species is still known with certainty only from the type collection: Beaver Dam, Arizona, 1877, *Palmer 114*. A flowering specimen from Allen Canyon in southeastern Utah, *Rydberg & Garrett 9309*, resembles the type very much but is doubtful in the absence of fruit. In the original description of *Astragalus lancearius*, Gray called attention to the fact that the species strongly resembled *A. filipes* in habit and in flowers, but that the pod was perfectly sessile. On this account it would have to be placed in the *Tenelli* group, probably near *H. wingatanus* and *H. acerbus*. Jones* claimed that the species was the same as *Astragalus recurvus* Greene, which on account of its completely two-celled fruit is a species of *Hamosa*. Later he† retracted his statement, adding that *A. lancearius* was "a good species but near *A. Rusbyi* Greene." The first part of his conclusion is correct but the latter part is far from the mark.

17. HOMALOBUS EPISCOPUS (S. Wats.) Rydb. Under *Astragalus Coltoni* Jones, Macbride makes the following statement:

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* Proc. Calif. Acad. II. **5**: 636. 1895.

† Contr. West. Bot. **8**: 12. 1898.

"Rydberg's reduction . . . of this species to *A. episcopus*, a plant with strictly sessile pods, is not understandable." The explanation of this reduction is as follows. In the herbarium of Columbia University there is a sheet labelled: "Coll. United States Department of Agriculture. *Astragalus Episcopus*, S. Watson, n. sp. Locality Utah. Collector, Capt. Bishop, 1872." The specimens on the sheet are more or less broken up into pieces but the habit is very similar to that of *A. Coltoni*, as represented by our specimens collected at Castle Gate by Jones. The plants are in flower, but the color of the corolla can not be determined. There is also a broken immature pod, showing a stipe nearly 1 cm. long. On the same sheet is a pocket containing two pods; one of these is mature and of exactly the same shape as the pods of *A. Coltoni* (except that the stipe is broken off), while the other is very young but shows a stipe 7 mm. long. On the pocket is written in what I take to be Watson's hand, "*Astragalus episcopus*, Wats. S. Utah. Capt. Bishop, 1873. pods." These specimens in the Columbia University Herbarium clearly belong to the same species as *A. Coltoni*. Macbride's statement that the pod of *A. episcopus* is "sessile" does not agree either with the type specimen or with Watson's description, which reads: "pod narrowly oblanceolate, compressed, 1¼ inches long, 2½ lines broad, acute at each end, very shortly stipitate, reflexed." Watson's description, however, agrees in every respect with the Columbia University specimens, except the words "very shortly;" for the stipe is rather long. As Watson also describes the flowers as being "purple or yellowish," he might have had a mixture, and if the specimens in the Columbia Herbarium were included in his conception of the species, this was certainly the case. The specimen in the Gray Herbarium is also fragmentary but shows a plant related to *H. lancearius*; its pod, however, is larger, 3 cm. long, and 5–6 mm. broad, tapering at both ends and very shortly stipitate, and the corolla is larger, being fully 12 mm. long.

18. HOMALOBUS VEXILLIFLEXUS (Sheld.) Rydb. This was originally described as *Astragalus pauciflorus* Hook.; since, however, there is an older *A. pauciflorus* Pallas., Hooker's specific name is not tenable in *Astragalus* and hence not in *Homalobus*. As the plant is well known no specimens need be cited.

*H. miser* (Dougl.) Rydb. should be withdrawn, at least provisionally. My conception of it was partly based on Gray's interpretation of the species, when he included under it *Lyall 7*, a specimen in flower only. Jones and Piper have referred this specimen to *Astragalus microcystis* A. Gray, a species of *Phaca*. I do not feel certain that their identification is correct or that Lyall's specimen really represents *Astragalus miser* Dougl. Since Gray placed the species among the *Homalobi* and since I at that time identified certain slender specimens in fruit with Lyall's plant, I admitted *H. miser* as valid. I now think that the true *A. miser* is still to be identified.

### C. BOURGOVIANI

This group bears the name of *Debiles* in my Flora of the Rocky Mountains. It is desirable to change the name, however, since *Astragalus debilis* (Nutt.) A. Gray, as will be shown below, is an imperfectly known species.

19. HOMALOBUS BOURGOVII (A. Gray) Rydb. The habit and the black-hairy calyx and pod make this plant resemble a good deal *Astragalus alpinus* L. and *Phaca elegans* Hook., both now belonging to other genera. Except for the somewhat ridged valves of the pod the plant is a true *Homalobus*. In the alpine regions of the Canadian Rockies there grows a low, almost acaulescent form, with minute leaflets. This looks very unlike the ordinary form, but all grades between the two extremes are found.

### 20. **Homalobus retusus** sp. nov.

A perennial, with a slender caespitose rootstock; stems decumbent or ascending, 1–2 dm. long; stipules lanceolate or the lower ovate or triangular, connate, 1–2 mm. long; leaves 5–8 cm. long; leaflets nine to eleven, oblong to oval, often retuse or emarginate, 5–12 mm. long, 2–4 mm. wide, glabrous above, sparingly strigose beneath; peduncles 6–10 cm. long, slender; racemes short, five- to ten-flowered, bracts lanceolate, 2 mm. long; calyx black-hairy, the tube 2 mm. long, the teeth subulate, 1 mm. long; corolla purplish; banner 8–9 mm. long, obovate; wings 7–8 mm. long, the blade obliquely oblanceolate, with a long basal auricle; keel-petals slightly shorter, with a rounded apex; pod black-hairy, sessile, 8 mm. long, 3.5 mm. wide.

TYPE collected at Fort Selkirk, Yukon, July 20, 1899, *Tarleton 128, a & b* (herbarium of the New York Botanical Garden). The following specimens in flower may belong here:—

YUKON: Ranch Valley, *Gorman 1082;* White Horse, *Macoun 58429.*

When I transferred *Astragalus debilis* (*Phaca debilis* Nutt.) to *Homalobus*, I thought that the specimens above cited belonged to it and drew the characters of the pod from them. I have since found that they represent a species close to *H. Bourgovii*. M. E. Jones identifies *Phaca debilis*, with *Astragalus Bodini* Sheld., which is a true *Phaca* related to *P. microcystis*. A duplicate of the type of *P. debilis*, which is in the Torrey Herbarium, somewhat resembles *P. Bodini* in habit, but the calyx is not black-hairy and the leaflets are emarginate. Macbride admits *Astragalus debilis* as a member of the subgenus *Homalobus*, citing the following two species from Colorado: North Park, *Osterhout 3*, and Upper Platte, *Geyer 3*. The latter I have not seen but Osterhout's plant clearly belongs to *P. Bodini*. Osterhout had labelled it "*Astragalus debilis*," apparently following Jones's interpretation. Until the fruit is discovered, I fear that *P. debilis* can not be fully interpreted.

*Astragalus grallator* S. Wats. is regarded by M. E. Jones as an abnormal form of *A. Haydenianus*, and I am inclined to agree to this view. In this case the species should be removed from *Homalobus*. The specimen of *A. grallator* in the Torrey Herbarium, so named by Watson, is a similar abnormal form of some other species.

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# THE TAXONOMIC AND MORPHOLOGIC STATUS OF OPHIOGLOSSUM ALLENI LESQUEREUX

ARTHUR HOLLICK

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# The taxonomic and morphologic status of Ophioglossum Alleni Lesquereux

ARTHUR HOLLICK

(WITH PLATES 10-12)

About fifty years ago Lesquereux described, without any accompanying illustration, an imperfect fossil plant specimen from the Miocene Tertiary shales of Florissant, Colorado, under the name *Ophioglossum Alleni.*[*] The description was as follows:

> Leaf, elliptical, narrowed by a curve to the acute base; shorter and broader than in *O. vulgatum* L., of our time, with the same areolation.
>
> The leaf is about 3 cent. long (point broken), a little more than 2 cent. broad, marked in the middle by the remnant of a fruiting pedicel . . .

Subsequently the same author redescribed and figured the specimen under the name *Salvinia Alleni*,[†] and remarked: "By its form, its areolation, its size, all its characters, indeed, it is remarkably similar to *Salvinia reticulata* Heer."[‡] His amended description was as follows:

> Leaves oval, rounded in narrowing to the base; lateral veins, none visible, areolae large, irregularly square or equilateral, inordinately distributed.
>
> Leaf about three and a half centimeters long, twenty-two millimeters broad, of a thin substance, with a thick middle nerve and irregularly quadrate meshes, formed of very distinct black nervilles, the primary ones more or less in right angle to the middle nerve, with oblique, generally parallel veinlets between them . . . .

Later he listed and figured two other, more perfect specimens,[§] with the following brief comment:

> The species is common and has been obtained in large well-preserved specimens by the different collectors. The leaves are merely variable in size, obtuse or slightly emarginate at the apex, topped by the point of the excurrent nerve.

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[*] U. S. Geol. Survey Terr., Sixth Ann. Rept. 1872: 371. 1873.

[†] U. S. Geol. Survey Terr. Rept. vol. 7 (The Tertiary Flora): 65. *pl. 5, f. 11.* 1878. Reproduced on PLATE 10, FIG. 1.

[‡] Flora Tertiaria Helvetiae 3: 156. *pl. 145, f. 16.* 1859. Reproduced on PLATE 10, FIG. 4.

[§] U. S. Geol. Survey Terr. Rept. vol. 8 (The Cretaceous and Tertiary Floras): 136. *pl. 21, f. 10, 11.* 1883. Reproduced on PLATE 10, FIGS. 2, 3.

In 1894 I had occasion to examine the figures and descriptions of this and other fossil species described under, or referred to, the genus *Salvinia*, and in a paper on the subject I referred Lesquereux' species to the genus *Tmesipteris** and incidentally compared it with *Salvinia reticulata* (Ettingshausen) Heer, above mentioned, which Heer had suggested was, apparently, specifically identical with a fragmentary leaf or pod originally described by Ettingshausen under the genus *Dalbergia*;† but the resemblance to a pod did not impress me at the time.

In 1913, Professor T. D. A. Cockerell,‡ in a discussion of the fauna and flora of the shales in which the species was originally discovered and from which the specimens subsequently collected were obtained, remarked:

> The so-called *Tmesipteris alleni* (Lx.) Hollick, although common, can not be referred to any genus known to those who have examined it. It has nothing whatever to do with *Tmesipteris*, nor does it belong to *Salvinia* or *Ophioglossum*. as placed by Lesquereux. It may be known for the present as *Carpolithes alleni* (Lx.).

Thus it was given its fourth generic appellation—one that suggested similarity in appearance to a carpel or capsule or pod-like organism of some kind.

In 1919 Florin,§ in a paper on fossil Salvinias, expressed an opinion similar to that expressed by Cockerell—to the effect that the taxonomic status of Lesquereux' species was too uncertain to warrant its reference to any well-defined genus—and relegated it to the comprehensive fossil genus *Phyllites*, under the name *P. alleni* (Lesquereux) Florin (loc. cit. p. 254). The fifth generic name was thus applied in connection with the species—a name, apparently, meant to indicate that the author intended to suggest that it probably represented a foliar organ.

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* Fossil Salvinias, including description of a new species. Bull. Torrey Club **21**: 253–257. *pl. 205*. 1894.

† *Dalbergia reticulata* Ettingshausen, Beitrag zur Kenntniss der Fossilen Flora von Tokay. Sitzb. K. Akad. Wiss. [Wien.] Math.-Naturwiss. Cl. **11**$^4$: 813. *pl. 4, f. 5*. 1853. Reproduced on PLATE 10. FIG. 5.

‡ The Fauna of the Florissant (Colorado) Shales. Am. Jour. Sci. **36**: 498–500. 1913.

§ Eine Uebersicht der Fossilen *Salvinia*-Arten, mit besonderer Berücksichtigung eines Fundes von *Salvinia Formosa* Heer in Tertiär Japans. Bull. Geol. Inst. Upsala **16**: 249–260. *pl. 11*. 1919.

Recently Professor Cockerell* called attention to the fact that, in connection with certain specimens of the species, there could be detected a peculiar protuberance or body, apparently attached to the midrib, near the middle, in regard to one of which he remarked (loc. cit. pp. 211–212):

> It looks like a small berry, with the contents extruded. . . Probably the riddle would never have been solved but for the discovery of a younger specimen . . . This . . . shows that we have to do neither with a leaf, frond nor pod, but with a cladode. Attached to the midrib is an indistinct mass, presumably a thin bract, upon which can be seen a dark object . . . which seems to agree very closely with the flower of *Ruscus* . . . The genus Ruscus [has] . . . lanceolate to ovate sharply pointed cladodes . . . . At first sight the venation seems quite different from that of the fossil, *but if we imagine the Ruscus cladode broadened and abbreviated until the principal veins are nearly or quite transverse instead of longitudinal, the correspondence is exact.*†

Based upon this course of reasoning a new genus was evolved, and Lesquereux' multi-generic species became *Brachyruscus Alleni* (Lesquereux) Cockerell (loc. cit. p. 212)—the sixth binomial under which it was described and discussed. Incidentally it may also be noted that this last change of name definitely transferred the species from the Pteridophyta to the Spermatophyta and changed it from a frond, a leaf, or a fruit to a cladode. The question whether or not this last change of name should be accepted as the final word in regard to its probable taxonomic and morphologic status did not, however, appear to be answered conclusively or satisfactorily, based as it was on a frank appeal to the imagination to supply the necessary evidence. Also the naïvely worded footnote on page 212 appeared to be more or less of the nature of a challenge. In any event the statements and conclusions set forth in the paper certainly called for a critical examination of all of the available facts and their faithful presentation, without any attempt to connect them with any preconceived theory and without any appeal to the imagination to supply any features in the specimens that might be poorly preserved or lacking.

During a recent visit to the United States National Museum I was enabled to examine some fifty specimens of the species in

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* A new genus of fossil Liliaceae. Bull. Torrey Club **49**: 211–213. *f. 1.* 1922.

† The italicising is mine.

question, all of them from the type locality at Florissant, Colorado. Among these I had no difficulty in finding a dozen or more that showed, either distinctly or indistinctly, the presence of some kind of a body, as described by Professor Cockerell. Nine were selected for illustrating the critical characters, all of which were photographed and are reproduced, natural size, on PLATE 10, FIGS. 6–11, and on PLATE 11, FIGS. 1–3; and the latter three were also enlarged so as to show the characters more clearly. The three enlargments are reproduced on PLATE 11, FIGS. 1a–3a. The salient characters that they may be seen to reveal are: (1) a system of reticulate nervation, with the nerves of uniform rank throughout; and (2) either an indistinct thickening or a well defined, flattened spheroidal body (occasionally two), located toward the middle of the foliaceous organ.

The general appearance of the specimens, however, strongly suggests that they represent a flattened pod, or a detached carpel of a pod, rather than a foliaceous organ, to which are attached either immature, or imperfect, or mature and perfect seeds. In certain of the specimens, as in those represented on PLATE 11, FIGS. 1, 1a, and 3, 3a, the seedlike bodies are apparently in the superior position and are impressed on the exposed surface of the specimens. In others, as represented on PLATE 11, FIGS. 2, 2a, they appear to occupy the inferior position and are more or less masked by the overlying tissue. The superior position is also indicated in the specimens depicted on PLATE 10, FIGS. 10, 11, and the inferior position in FIGS. 6–9 on the same plate. The latter figures also appear to represent more or less immature or imperfect specimens; and in the specimen represented by FIG. 8 the overlying tissue near the middle was carefully chipped away from what appeared to be some kind of a body beneath, but nothing was revealed except some obscurely defined ridge and furrow markings that appear to represent a slight thickening or expansion of the median nerve or rib.

On PLATE 12, FIG. 1, is shown a pressed capsule of *Staphylea trifolia* Linnaeus, and in FIG. 2 the exterior of a detached carpel of *Koelreuteria bipinnata* Franchet. In each may be seen the surface inequalities due to the underlying seeds. FIG. 3 represents the exterior of a carpel of *Koelreuteria paniculata* Laxman; FIG. 4, the interior with seeds attached to the alate expansion of the midrib; FIG. 5, the latter flattened by pressure; FIG. 6, the same with seeds detached. FIG. 7 is a reproduction of Cockerell's figures illustrating his description of *Brachyruscus*, and FIG. 8, a drawing of a cladode of *Ruscus aculeatus* Linnaeus, with infloresence attached. A comparison between the last two figures hardly seems to suggest, even with the assistance of an earnest effort of the imagination, that there could be any near relationship between the specimens that they represent; and, in any event, it is evident that, if the description and figures of *Brachyruscus* correctly describe and depict the specimen selected by the author as the type of the genus, *Brachyruscus Alleni* Cockerell can not possibly be either congeneric or morphologically identical with *Ophioglossum Alleni* Lesquereux. The author has, however, provided for this contingency to a certain extent, in the footnote previously mentioned, which should be read in this connection.

Incidentally, on PLATE 12, FIG. 9, is a drawing of a bract of *Dobinia vulgaris* Hamilton, showing the character of the nervation and a fructification attached to the midvein, in order that it may perhaps be recognized and accepted, in preference to the cladode of *Ruscus*, as the morophological equivalent and a possible family relative of *Brachyruscus*.

In view of the facts here presented if anyone should deem it necessary to coin a seventh generic name for *Ophioglossum Alleni*, based upon its resemblance to capsules or carpels of species of certain genera included in the Staphyleaceae and Sapindaceae, the responsibility will rest on him, not on me. The already established name, which is descriptive of what the species appears to morphologically simulate and which is therefore properly applicable, is *Carpolithes Alleni* (Lesquereux) Cockerell.

## Explanation of plates 10–12

### PLATE 10

SALVINIA ALLENI (Lesquereux) Lesquereux
[= *Ophioglossum Alleni* Lesquereux]

FIG. 1. U. S. Geol. Survey Terr. Rept. Vol. 7 (The Tertiary Flora): *pl. 5. f. 11.* 1878.

*10* FIG. 2. Idem. Vol. 8 (The Cretaceous and Tertiary Floras): *pl. 21, f.* 1883.

FIG. 3. Idem. *f. 11.*

SALVINIA RETICULATA (Ettinghausen) Heer

FIG. 4. Flora Tertiaria Helvetiae **3**: *pl. 145, f. 16.* 1859.

DALBERGIA RETICULATA Ettinghausen

FIG. 5. Sitzb. K. Akad. Wiss. [Wien] Math.-Naturwiss. Cl. **11**$^4$: *pl. 4, f. 5.* 1853.

SALVINIA ALLENI (Lesquereux) Lesquereux

Reproductions of photographs, natural size, of specimens from the type locality at Florissant, Colorado.

FIG. 6. Showing indications of immature or imperfectly developed fructification. U. S. Nat. Mus. No. 36693.

FIG. 7. Idem. U. S. Nat. Mus. No. 36690.

FIG. 8. Idem., with overlying tissue removed. U. S. Nat. Mus. No. 36692.

FIG. 9. Showing indications of more maturely developed fructification. U. S. Nat. Mus. No. 36694.

FIG. 10. Showing mature fructification. U. S. Nat. Mus. No. 36691.

FIG. 11. Idem. U. S. Nat. Mus. No. 36688.

## PLATE 11

SALVINIA ALLENI (Lesquereux) Lesquereux

Reproductions of photographs of specimens from the type locality at Florissant, Colorado, showing mature fructifications.

FIG. 1. Natural size. U. S. Nat. Mus. No. 36695.

FIG. 1a. Same specimen, × 2.

FIG. 2. Natural size, U. S. Nat. Mus. No. 36689.

FIG. 2a. Same specimen, × 2.

FIG. 3. Natural size. U. S. Nat. Mus. No. 50277.

Fig. 3a. Same specimen, × 2.

## PLATE 12

STAPHYLEA TRIFOLIA Linnaeus

FIG. 1. Capsule, natural size, compressed, showing inequalities due to included seeds; distal end upward. From a specimen in the herbarium of the New York Botanical Garden, collected at Knoxville, Tennessee, in April, 1878, by Albert Ruth, No. 358.

KOELREUTERIA BIPINNATA Franchet

FIG. 2. Carpel, natural size, compressed, showing outer surface with inequalities due to included seed; distal end downward. From a specimen in the herbarium of the New York Botanical Garden, collected in Central China, 1885-88, by Angust Henry, No. 7591.

KOELREUTERIA PANICULATA Laxman

Carpel, natural size, under varied conditions; distal ends downward. From a tree in the grounds of the U. S. Department of Agriculture, Washington, D. C., collected in August, 1922, by Arthur Hollick.

FIG. 3. Outer surface.

FIG. 4. Inner surface, with seeds attached to a late expansion of the midrib.

FIG. 5. Same, flattened by pressure.

FIG. 6. Same, with seeds detached.

BRACHYRUSCUS ALLENI (Lesquereux) Cockerell

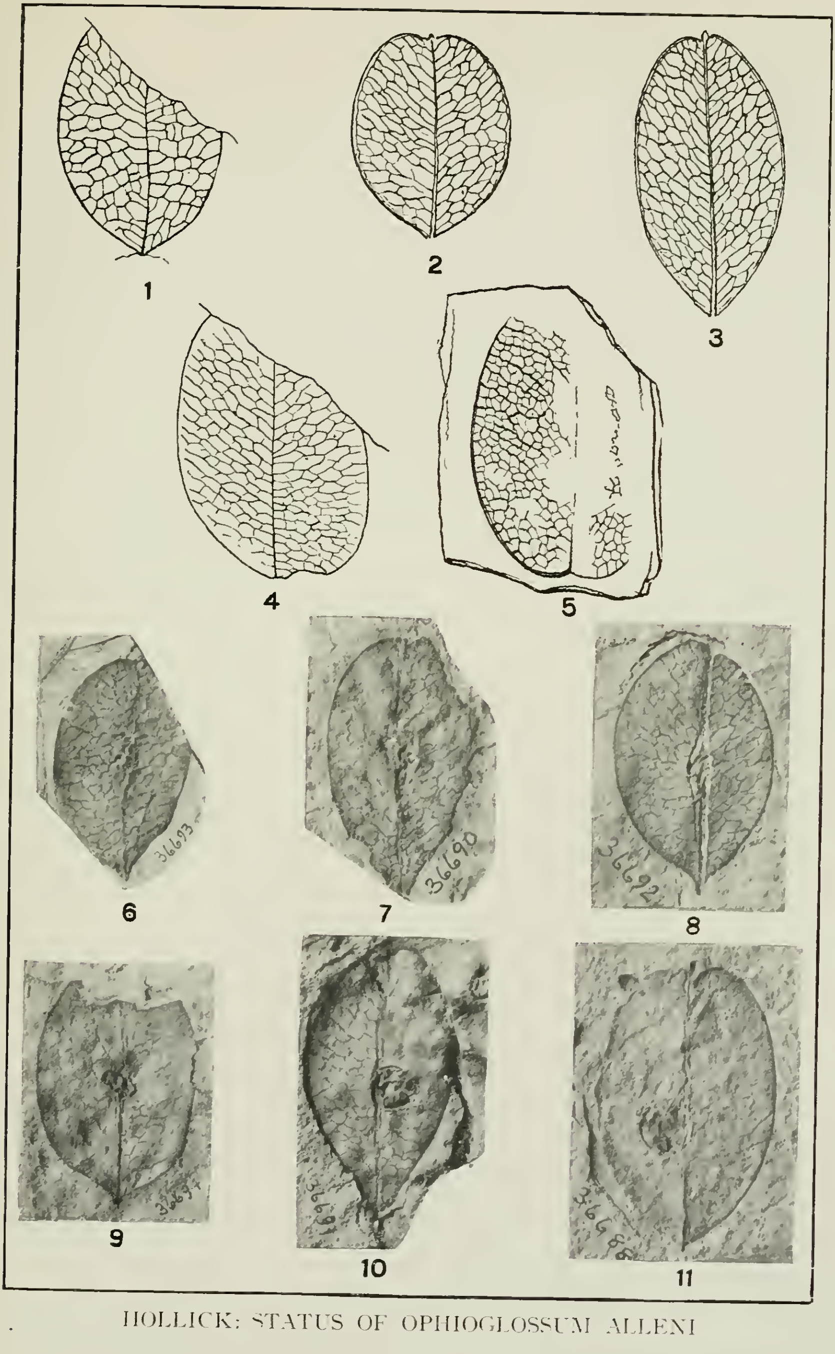
FIG. 7. Bull. Torrey Club **49**: *f. 13, A-D.* 1922.

RUSCUS ACULEATUS Linnaeus

FIG. 8. Cladode, natural size, upper surface, showing inflorescence attached to the median nerve; distal end upward. From a cultivated specimen in the herbarium of the New York Botanical Garden, collected at Montpellier, France.

DOBINEA VULGARIS Hamilton

FIG. 9. Bract, natural size, upper surface, showing fructification; distal end upward. From a specimen in the herbarium of the New York Botanical Garden, collected in Nepal, India, probably in 1821, by Nathaniel Wallich.

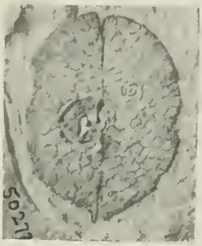


HOLLICK: STATUS OF OPHIOGLOSSUM ALLENI

1

2

2a

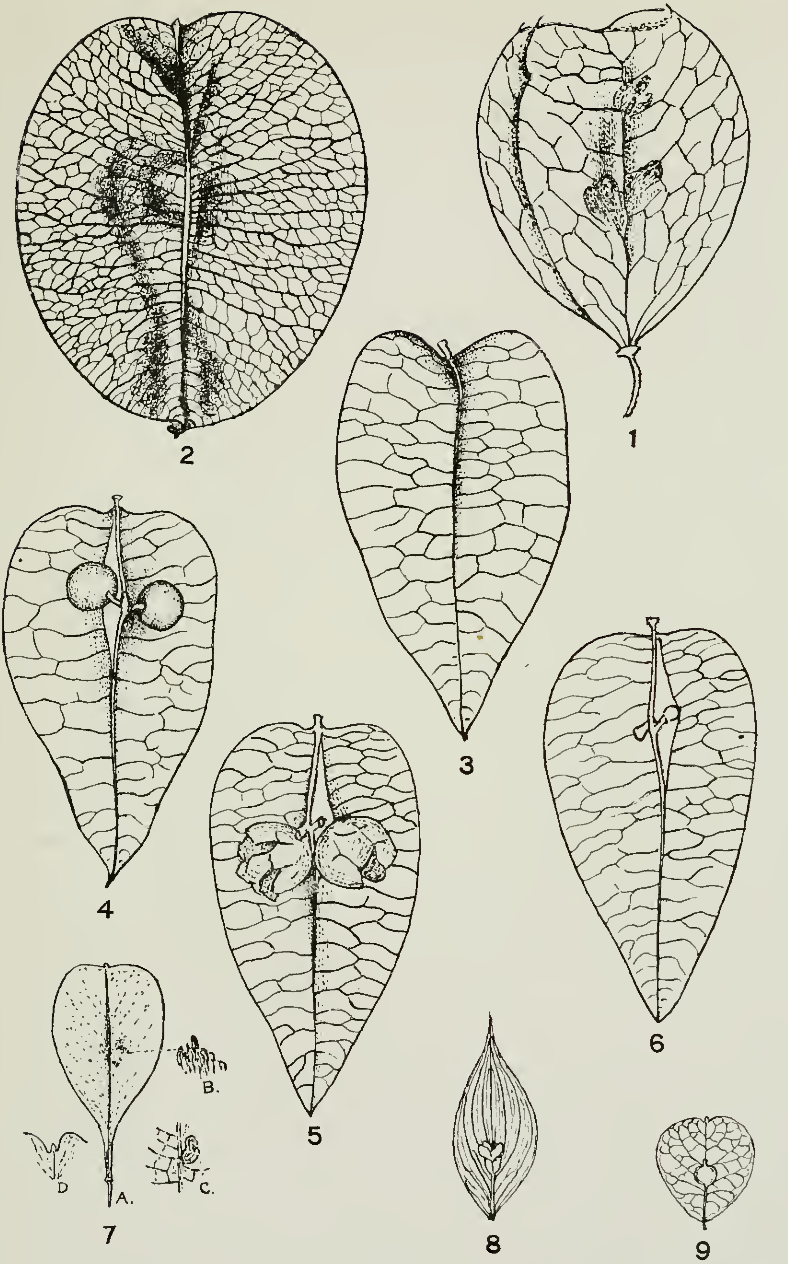


3

1a

3a

HOLLICK: STATUS OF OPHIOGLOSSUM ALLENI



HOLLICK: STATUS OF OPHIOGLOSSUM ALLENI

CONTRIBUTIONS FROM THE NEW YORK BOTANICAL
GARDEN—No. 246

# STUDIES IN TROPICAL ASCOMYCETES—II. AN INTERESTING XYLARIA FROM PORTO RICO

BY

FRED J. SEAVER

NEW YORK
1923

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# Studies in tropical Ascomycetes—II. An interesting Xylaria from Porto Rico

FRED J. SEAVER

(WITH PLATE 18)

During a recent collecting trip to Porto Rico* the writer had the opportunity of visiting one of the most interesting and fruitful collecting grounds for fungi to be found on the island, the Luquillo Mountains. This trip was made possible through the efforts of Mr. E. M. Bruner, Forester of Porto Rico, who placed at our disposal the Forest Ranger's cabins, located at an elevation of about 1200 feet. This camp consisted of two cabins, one of boards with metal roof and the other a rough building with thatched roof. The cabins were provided with cots, utensils, and charcoal stoves for cooking. Mr. Bruner acted as host and supervised the house-keeping activities during our stay here. The party consisted of Dr. and Mrs. Britton, Mr. Bruner, Professor Dale of the University of Porto Rico, and the writer.

The trip from San Juan to Mameyes was made by automobile and the ascent from this point to the Forester's camp on foot or by horse. Arriving at the camp soon after noon on Friday, February 23, the remainder of the afternoon was spent in the vicinity of the camp site.

Saturday, February 24, an expedition was planned to the top of El Yunque, for a long time supposed to be the highest peak in Porto Rico but now known to be exceeded by several others. The ascent was made much easier by reason of the trail of broken stone which had been constructed under the supervision of Mr. Bruner for a greater part of the distance. Soon after the expedition started, it began to rain, as it nearly always does at this elevation, and a slow drizzle continued during the remainder of the day, making the climb at places very slippery and disagreeable. We succeeded, however, in reaching the top

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* Jour. of the New York Bot. Gard. **25**: 99–101. 1923.

JAN - 1925

at an elevation of about 3500 feet. Here the soil and atmosphere were saturated so much so that it was impossible to find a dry place where one could sit to rest or eat. The trunks of the trees and even the leaves were loaded with mosses and hepatics, and there seemed to be scarcely room for a fungus to grow, although a number of specimens of *Aschersonia* in fruit (*Hypocrella*) were found and in some abundance.

The view, which must be remarkable under favorable conditions, was entirely missed by us on account of the atmospheric conditions. In spite of the fact that we were under the tropical sun, had it not been obscured by the clouds and fog, a cold chill wind swept over the mountain top which compelled us to look for a sheltered spot where we could eat our lunch in comparative comfort.

Not finding the conditions especially favorable for mycological collecting at this elevation the writer preceded the party down the trail in order to have time to hunt leisurely for things of a mycological nature. Many interesting collections were made, most of which have not been studied critically. One which was of more than usual interest was a species of *Xylaria* which is made the subject of the present paper. These specimens were found opposite the overhanging rock about midway between the summit and the Forester's cabin to the left of the trail going down.

On account of the density of the forest and the general gloominess of the day it was difficult to detect the presence of minute fungi. However, on picking up what appeared to be a dead stick a seed the size of an ordinary marble was found attached to its base. On closer examination the object, which proved to be a large fungus, was at first thought to be a fine *Cordyceps*. It finally turned out to be a *Xylaria*. On further search other plants were found until fifty or a hundred specimens had been collected, each growing from a seed of what proved to be that of the mountain palm, *Euterpe globosa* Gaert. A number of fungi, such as certain species of *Sclerotinia*, grow exclusively on seeds. Also a number of species of *Cordyceps* grow on underground fungi which have much the same general appearance, but so far as the experience of the writer has gone this is the only species of *Xylaria* encountered which has the general appearance of a *Cordyceps* with the habitat of the *Sclerotinia*.

The species has been found only in the one locality in Porto Rico. The host on which the fungus preys, however, occurs from Cuba to Hispaniola and Porto Rico and in the Lesser Antilles from Saba to Grenada. Assuming that the fungus is restricted to the one host, as it seems to be, its possible range of distribution then is as indicated above. The only economic bearing which the fungus could have is in connection with the destruction of the seeds of the host. How important this can be cannot be stated.

Our material from Porto Rico agrees quite closely, so far as we can judge from the description, with *Xylaria palmicola* Winter,* described from Brazil. No specimens of the South American species have been seen and the host of that species is not named. The fact that the host of the Porto Rican species does not occur in South America, so far as we know, leads the writer to regard ours as distinct. The species is dedicated to Mr. Bruner and a description appended.

### **Xylaria Bruneriana**, sp. nov.

Stromata growing upon and their mycelium filling the seeds of their host and apparently absorbing the greater part of their contents, reaching a height of 10–12 cm. and a diameter of 2–4 mm., consisting of a sterile stem and a fertile club-shaped head, the latter comprising about one fourth of the whole stroma and considerably thicker; stem cylindrical, slightly tapering above and becoming twisted (especially when dried); perithecia subglobose, about 500 μ in diameter; asci subcylindric, eight-spored, reaching a length of 140 μ, the ascus wall being very transparent and often almost invisible; spores unequal-sided, rather sharp pointed, 16 × 6–7 μ, often slightly flattened, hyaline, becoming dark brown.

On fallen seeds of the mountain palm, *Euterpe globosa* Gaert., El Yunque, February 24, 1923.

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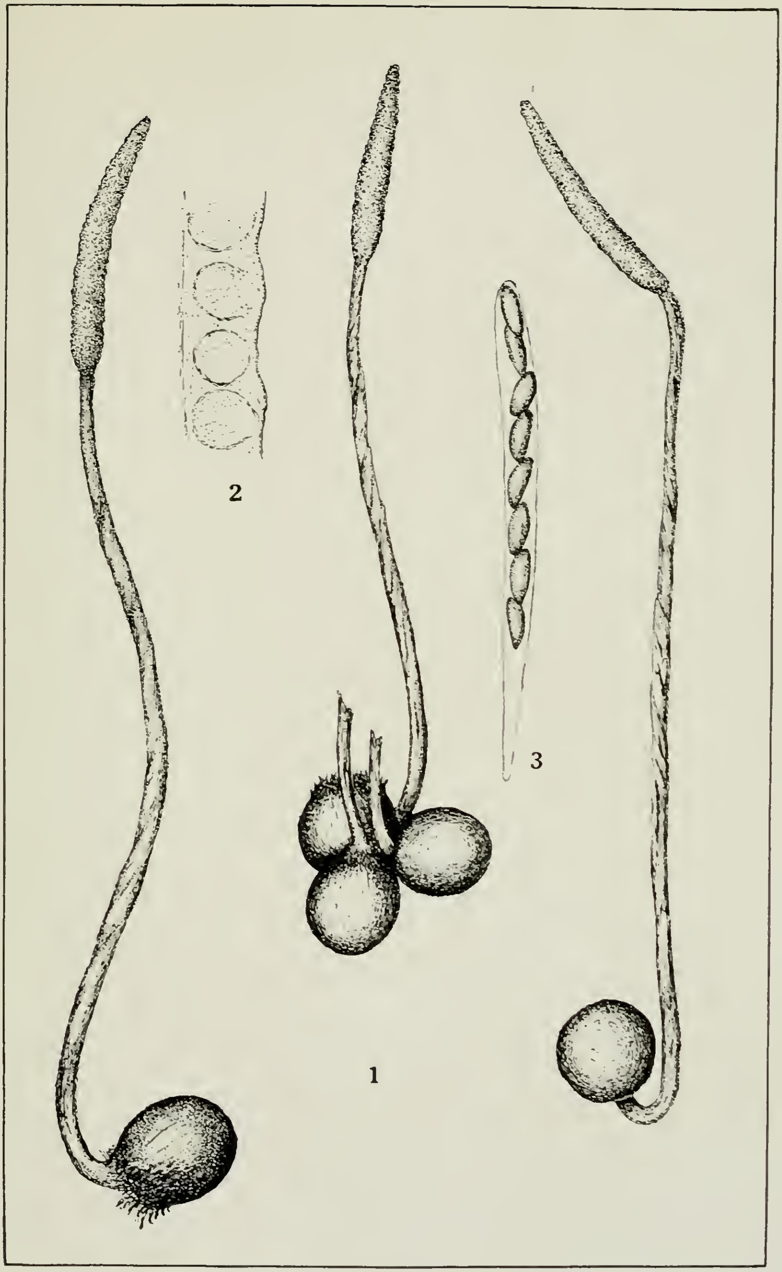
* Grevillea **15**: 89. 1887.

## Description of plate 18

### XYLARIA BRUNERIANA Seaver

FIG. 1. Several plants about natural size.
FIG. 2. Diagram of a section of the fertile head.
FIG. 3. Ascus with spores, drawn with the aid of the camera lucida.



XYLARIA BRUNERIANA Seaver

CONTRIBUTIONS FROM THE NEW YORK BOTANICAL GARDEN
No. 247

# NOTES ON FABACEAE—II

PER AXEL RYDBERG

NEW YORK
1923

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# Notes on Fabaceae—II

Per Axel Rydberg

## HOMALOBUS Nutt. (*con.*)

### D. Campestres

This group differs from the *Tenelli* not only in the narrow strictly sessile pod but in the acute keel-petals, a character which as far as I know separates it from all the other groups of *Homalobus*.

21. Homalobus campestris Nutt. This was described from specimens collected on the "Colorado of the West," meaning some of the tributaries of the Green River. One specimen of Nuttall's is in the Torrey Herbarium and is in flower. The calyx is 5 mm. long, more or less black-hairy; the lobes are subulate, decidedly longer than broad; nearly every leaf has one or two pairs of lateral leaflets, and the terminal leaflet is represented by the flattened, somewhat falcate prolongation of the rachis. The corolla is evidently ochroleucous, without a trace of purple. Gray, in transferring this species to *Astragalus*, evidently confused it with some other member of the group, describing the leaves as having often nine to thirteen leaflets and the corolla as being yellowish white, usually tinged with purple. He also regarded *H. tenuifolius* Nutt. as a depauperate form and evidently had in mind *H. hylophilus* Rydb., *H. oblongifolius* Rydb. and their allies. As *Astragalus campestris* was preoccupied, Greene substituted the name *A. convallarius*. Jones at first made the plant *A. serotinus campestris*,* but cited under this name specimens belonging to other species, one of them, *6015n*,

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* Proc. Calif. Acad. II. 5: 668. 1895.

[The Bulletin for July (**50**: 231–260 *pl. 13, 14*) was issued July 27, 1923.]

being *H. humilis.* Later* he changed the name to *A. decumbens convallarius.* Even at that time, however, he had a misconception of certain species; for, on a later page of the same article, he changed *Astragalus junceus* (Nutt.) Gray to *A. diversifolius roborum* and labeled with this name specimens belonging to *H. campestris.*

Macbride† united *A. campestris* and *A. junceus*, regarding "the relative length of the calyx-lobes and the presence or absence of black pubescence" as "trivial variations" and of "no practical taxonomic value." Perhaps they are so and perhaps *H. campestris*, *H. junceus* and *H. junciformis* should be only one species, but he has used one of these characters, the longer calyx-lobes, together with the presence of lateral leaflets, as a character to separate his *A. campestris diversifolius* (Gray) Macbr. from the typical form of the species. These characters are just those that characterize the type.

Only two of the specimens cited by Macbride under the variety *diversifolius* are found in New York herbaria: the first of these is Nuttall's, from the "sources of the Platte," Wyoming, which represents the type collection of *H. orthocarpus* Nutt.; and the second is *Baker 242*, from Cedar Edge, Colorado, which matches the type of *H. campestris* in every respect. Evidently Macbride has misinterpreted *A. diversifolius* A. Gray (see below). Of the specimens in the Gray Herbarium, *Canby 84*, from Helena, Montana, is *H. junceus;* so also are *Watson 92* and *Nelson & Macbride 1292*, both from Idaho. The rest represent the typical *H. campestris*, except *Macbride & Payson 3183*, in flower only, from Clyde, Idaho, which may be *H. orthocarpus.* In the herbaria of the New York Botanical Garden and Columbia University, the following specimens of *H. campestris* are found:—

WYOMING: *Nuttall.*

UTAH: Glenwood, *Ward 227;* Hooper, *Leonard 98;* Tropic, *Jones 5312h;* Mandan, *Mulford 118;* Salt Lake City, *Garrett 984;* Pavant Mountains, *Eggleston 10149.*

COLORADO: Cedar Edge, *Baker 242;* Como, *Crandall;* Middle Park, *Patterson;* Glenwood Springs, *Osterhout;* White River, *Mrs. Dun.*

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* Contr. W. Bot. **10:** 58. 1902.

† Contr. Gray Herb. II. **65:** 35. 1922.

22. HOMALOBUS JUNCEUS Nutt. The duplicate of the type in the Torrey Herbarium is in fruit but shows a white-hairy calyx with very short calyx-lobes and leaves with no or very small lateral leaflets. Sheldon thought that this and *Astragalus diversifolius* represented but one species and applied the latter name to it, as the earlier *A. junceus* was preoccupied by *A. junceus* Ledeb. Since, however, *A. diversifolius* is a synonym of *H. orthocarpus*, *A. junceus*, if transferred to *Astragalus*, would be without a name. This species is much more common than *H. campestris*. I shall therefore not enumerate any specimens. Most of those cited by Macbride under *A. campestris* belong here. Jones, as already noted, named the species *A. diversifolius roborum*.

23. HOMALOBUS JUNCIFORMIS (A. Nels.) Rydb. The status of this species is somewhat problematical, since it has the short calyx-lobes of *H. junceus* and the black-hairiness of *H. campestris*. It is stouter than either, with larger flowers and broader leaflets. Standley regarded it as identical with *H. orthocarpus*, but that species has smaller flowers and a much broader pod. The mature pod of *H. junciformis* is unknown, but the young pod suggests a similarity to that of *H. junceus*. Jones* made *H. junciformis* a synonym of *A. diversifolius*, evidently not being acquainted with the true *A. diversifolius*. The only specimens of *H. junciformis* seen are:—

WYOMING: Fort Steele, *A. Nelson 4839;* Point of Rocks, *A. Nelson 3081;* Leucite Hills, *A. Nelson 4668*.

24. HOMALOBUS ORTHOCARPUS Nutt. The duplicate of the type in the Torrey Herbarium shows only the upper part of the plant, but Nuttall states that the lower leaves bear several leaflets, while the upper are more or less reduced to the rachis. This fact furnished Gray the name *Astragalus diversifolius*, when he found that *A. orthocarpus* was preoccupied by *A. orthocarpus* Boiss. In *H. orthocarpus* the calyx is white-hairy, the lobes are deltoid and not much longer than broad, while the pod is much broader than in the related species, in the duplicate of the type being about 2 cm. long and 4 mm. wide. In the herbarium of the New York Botanical Garden the only specimen like the type is *Goodding 1084* from Juab, Utah, which has been

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* Contr. West. Bot. **10:** 68. 1902.

referred to *A. episcopus* Wats. According to Macbride *A. episcopus* has sessile pods; one might suppose from this that the latter species was a synonym of *H. orthocarpus;* but it is not, since it really has a short-stipitate and glabrous pod. There is also a specimen collected at Salida, Colorado, *Johnston & Hedgecock 634*, which resembles Goodding's very much, but it is in flower only and therefore doubtful. So also is *Macbride & Payson 3183* from Idaho, to which reference has already been made.

25. HOMALOBUS DECUMBENS Nutt. The specimen in the Torrey Herbarium consists of two pieces, a small plant with five attached branches and a single loose branch; the former bears one mature pod and two small racemes in bud; the separate branch bears five immature pods. All the pods are minutely pubescent and decidedly arcuate, and the mature pod is nearly 2.5 cm. long and 3 mm. wide; the calyx lobes are subulate and less than half as long as the tube. The only specimens in the herbarium of the New York Botanical Garden similar to the type are *Hall & Harbour 142*, in part, from Colorado, and *Goodding 1429* from Wood's Creek, Wyoming. The pods of the latter are very young and scarcely show any indication of being arcuate. The specimens in the Gray Herbarium bearing the same number have a better developed pod, and I would refer them to *H. microcarpus*.

A specimen in flower, from Mammoth Hot Springs, Wyoming, named by the collectors *A. decumbens*, viz., *Aven & Elias Nelson 5649*, resembles this species in habit but is more canescent. Macbride has cited this specimen under *A. divergens*, but I rather think that it belongs either here or under *H. tenuifolius* Nutt.

26. HOMALOBUS SEROTINUS (A. Gray) Rydb. Gray described *Astragalus serotinus* as having glabrous or minutely pubescent pods, and Macbride says in his key, "pods glabrous or nearly so." There are three sheets of Cooper's collection in the New York herbaria, and in all three the pods are minutely strigose. The species varies much in the width of the leaves. When they are very narrow the plant resembles much in habit *H. campestris*, but the tip of the keel is always purple and the leaflets more numerous and glabrate above.

WASHINGTON: Okanogan River, *Cooper;* Peshasti, *Sandberg & Leiberg 473;* Loomis, *Griffiths & Cotton 343;* without locality *Vasey 273.*

OREGON: Wallowa County, *Sheldon 8065.*

MONTANA: Big Fork, *Umbach 621.*

ALBERTA: Tunnel Mountain, *McCalla 2134.*

BRITISH COLUMBIA: Nicola Valley, *Dawson 4269.*

27. HOMALOBUS STRIGOSUS (Coult. & Fish.) Rydb. This resembles *H. Palliseri* in habit but differs in the pubescent pod and longer calyx-lobes. Jones* claims that it is the same as *H. serotinus.* It is true that the two resemble each other very much in general appearance, but the calyx-lobes in *H. strigosus* are almost twice as long and the leaves are cinereous on both sides. Macbride regards it as a variety of *H. serotinus.*

ALBERTA: Vermillion Range, *Moodie 1238,* in part.

MONTANA: Park County, *Tweedy;* St. Ignatius Mission, *MacDougal 290;* Columbia Falls, *Williams 1003,* Helena, *Kelsey;* Tobacco Mountain, *Butler;* Deer Lodge River, *Cooper.*

WYOMING: Mammoth Hot Springs, *Mearns 1329;* Alcova, *Goodding 146;*† Sheridan and Buffalo, *Tweedy 3168;* Big Horn, *Tweedy 2355.*

IDAHO: Beaver Canon, *Watson 91;** Howe, *Macbride & Payson 3106,*† in part; Mammoth Hot Springs, *Nelson & Nelson 5648;*† Salmon, *Payson & Payson 1762.*

28. HOMALOBUS TENUIFOLIUS Nutt. The duplicate of Nuttall's type in the Torrey Herbarium is a small plant about 7 cm. high and bears two racemes, one with six flowers and the other with a single pod. The calyx is 2 mm. long, including the lobes, which are about 0.5 mm.; the corolla is about 4 mm. long, and the pod, 14 mm. long and 3 mm. wide, is strigose; the leaflets are narrowly linear-subulate. In the herbarium of the New York Botanical Garden there is only one specimen in fruit like it, *Tweedy 259.* The others are larger and would be referred to *H. decumbens* if they were not so canescent and if the pods were not straight. Gray, as already noted, thought that the species was a depauperate form of *H. campestris.* Coulter and Nelson seem to include it in that species, while Macbride united it with

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* Proc. Calif. Acad. II. **5:** 668. 1895.

† Referred by Macbride to *A. divergens* Blankinship.

*A. divergens* Blankenship. It would have been more logical to reduce it to a variety of *A. serotinus*. It is not more distinct from that species than *A. strigosus* or *A. Palliseri*. None of the specimens cited by Macbride and seen by me belong to *H. tenuifolius* except *Parry 81* and *A. Nelson 9648*. See under *H. strigosus* and *H. decumbens*.

WYOMING: Rocky Mountains, *Nuttall; Parry 81;* Mount Leidy, *Tweedy 259;* Medicine Bow, *A. Nelson 9648*.

MONTANA: Lima, *Rydberg 2706;* Red Rock, *Shear 5043*.

COLORADO: Lake City, *Pease; Hall & Harbour 142*, in part.

29. HOMALOBUS DIVERGENS (Blankinship) Rydb. In habit the plant resembles the preceding, but the leaflets are much broader and shorter. I have not seen the type, but Blankinship's illustration (except the pod) represents the plant I have in mind. In the original diagnosis the pod is described as stipitate and is so figured. In all the specimens I have seen it is sessile. Blankinship might have had a mixture containing pods of some other species, as for instance the alpine form of *H. Bourgovii*. Not having seen the type, it was not so strange that I, under these circumstances, redescribed the plant as *H. camporum*.* This is the name it would bear, if by chance *Astragalus divergens* should be different from our present conception.

WYOMING: Leckie, *Merrell & Wilcox 537, 585;* Steamboat Mountain, *A. Nelson 7085;* Laramie Hills *198;* Bird's Eye, *Nelson 9559*.

MONTANA: Helena, *Rydberg 2708*.

IDAHO: Beaver Canon, *Rydberg 2707*.

UTAH: Alta, *Jones 1210*.†

30. HOMALOBUS HUMILIS Rydb. Macbride has transferred this to *Astragalus*, under the name *A. Carltonii*, as there was an older *A. humilis* Bieb.

UTAH: Bullion Creek, *Rydberg & Carlton 7147;* Delano Peak, *7219* and *7219a;* Mt. Ellen, *Jones 5670;* Panguitch Lake, *6015n* (this with narrow leaflets).

31. HOMALOBUS OBLONGIFOLIUS Rydb. Macbride regarded this as a variety of *H. hylophilus*. As far as I know the plant

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* Bull. Torrey Club **32:** 666. 1906.

† This Macbride refers to *A. Carltonii* Macbride, i. e. to *H. humilis*, but the pod is that of *H. divergens* and *H. tenuifolius*.

is confined to Colorado. Macbride cites two specimens from Wyoming, *Nelson 869* and *Payson 2068*. The former, as represented in the Columbia University Herbarium is typical *H. hylophilus*, having glabrous pod and broad leaflets. The other number I have not seen.

COLORADO: Cerro Summit, *Baker 409;* Nederlands, *Clokey 3284;* Leadville, *Jones,* Teller, *C. S. Sheldon 108;* Marshall Pass and Leadville, *Jones;* Pinkham Creek, *Goodding 1472,* Delta, *N. F. T. Nelson 181;* without locality, *Parry*, in 1864.

32. HOMALOBUS PAUCIJUGUS Rydb. This resembles *H. tenuifolius* in habit and pod but differs in the few leaflets. As there is an older *Astragalus paucijugus* Schrenk, Macbride renamed my species *A. Garrettii*.

33. HOMALOBUS DECURRENS Rydb. This was also renamed *A. Rydbergii* by Macbride, on account of *A. decurrens* Boiss.

COLORADO: Golden, *Jones 528; Greene;* Estes Park, *Osterhout 2222;* Lake Eldora, *Clokey 3201;* Jefferson County, *3808;* Larimer County, *Osterhout A;* Stove Prairie and Como, *Crandall;* Gray Back, *Rydberg & Vreeland 5960;* Tolland, *Johnston & Hedgecock 664;* without locality, *Hall & Harbour 142*, in part; Central City, *Sccvell.*

34. HOMALOBUS MICROCARPUS Rydb. This was reduced by Macbride to a synonym of *A. decumbens.* There would have been more reason for reducing it to, or for making it a variety of, *H. divergens*, since the general habit, the form of the leaflets and the shape of the pod approach that species, but the whole plant is greener, more luxuriant and more erect. One specimen, *Watson 287* from the Uintah Mountains, Utah, may belong here. It has the small pod and the flowers of *H. microcarpus* but is taller, with very long peduncles, 10–14 cm. long, longer leaves, up to 15 cm. long, and more numerous leaflets, the pod is hairy with short black hairs. Macbride erroneously referred the specimen to *Astragalus serotinus* var. *Palliseri*, which has glabrous pods.

COLORADO: east of Rabbit-Ear Range and on the forks of Poudre River and Big South, *Crandall;* Como, *Crandall & Cowen 131;* North Park, *C. F. Baker;* Steamboat Springs, *Osterhout 2774;* Empire, *Tweedy 5642;* without locality, *Hall & Harbour 143; Parry 435.*

WYOMING: Woods Creek, *Goodding 1429.*

35. HOMALOBUS HYLOPHILUS Rydb. This is the most common species of the group in the Northern Rockies, extending as far south as northern Utah and the Black Hills, but not being found in Colorado. Jones* claims that this is a shade form of *A. decumbens convallarius*, due mainly to his misinterpretation of *A. convallarius*, which latter was based on *Homalobus campestris* Nutt.

36. HOMALOBUS PALLISERI (A. Gray) Rydb. Macbride reduced this to a variety, *A. serotinus Palliseri* (Gray) Macbride. It is more closely related to *H. hylophilus*, having the same glabrous pod, but the leaflets are much narrower and the calyx-lobes shorter. There are, however, specimens of *H. hylophilus* which have nearly as narrow leaflets as those of *H. Palliseri*. The Montana specimens of *H. Palliseri* have longer pods and in that respect approach *H. hylophilus*.

ALBERTA: Rocky Mountains, *Bourgeau;* headwaters of the Saskatchewan, *S. Brown 923;* Banff, *S. Brown 80; VanBrunt 6; Canby 41; Barber 105, 279.*

BRITISH COLUMBIA: Carbonate, *Shaw 227, 241;* Green, *3210;* Kettle River, *J. M. Macoun 63152, 63756;* Lake Osoyoos, *70440;* Canmore, *J. Macoun 15;* Maligne River, *Spreadborough 19310;* Armstrong, *E. Nelson 133.*

WASHINGTON: Concomilli, *Griffiths & Cotton 319;* Ophir, *Elmer 528;* Walla Walla, *Brandegee.*

MONTANA: Spanish Basin, *Flodman 636;* Bozeman, *Wilcox 115;* Old Hollowtop, *Rydberg & Bessey 4489;* Bridger Mountains, *4494;* Old Sentinal, *MacDougal 168, 172;* Terminus, *Watson 88.*

37. HOMALOBUS DETRITALIS (M. E. Jones) Rydb. This has been placed in the present group but probably does not belong here. In general habit it resembles the *Simplicifolii*, but the leaves have five leaflets. Whether it has the acute keel-petals characteristic of the *Campestres* or not I do not know, as I did not look for that character when I saw the type some years ago.

### E. STENOPHYLLI

Pod glabrous, except the stipe.
  Leaflets narrowly linear.

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* Contr. West. Bot. **10:** 69. 1902.

Leaflets few, the terminal one wanting or continuous with the rachis; calyx-lobes lanceolate, 1.5–2 mm. long. 38. *H. Coltoni.*
Leaflets many, the terminal one present; calyx lobes triangular, 1 mm. long or less.
Leaflets slightly strigose beneath or glabrous throughout. 39. *H. stenophyllus.*
Leaflets strigose-cinereous on both sides.
Stipe of the pod fully half as long as the body, ocrolla ochroleucous or white. 40. *H. MacGregorii.*
Stipe about one third as long as the body; corolla purple. 41. *H. canovirens.*
Leaflets linear-oblong to oval, glabrous above, strigose beneath. 42. *H. Antiselli.*
Pod strigose throughout.
Leaflets linear; raceme elongate lax.
Body of the pod 2–2.5 cm. long abruptly contracted at the base, straight. 43. *H. filipes.*
Body of the pod 2.5–3 cm. long, gradually tapering at each end, slightly arcuate. 44. *H. inversus.*
Leaflets elliptic; raceme short dense. 45. *A. gaviotus.*

38. **Homalobus Coltoni** (M. E. Jones) Rydb. comb. nov.
*Astragalus Coltoni* M. E. Jones, Zoe **2**: 237. 1891.
*Homalobus episcopus* Rydb. Bull. Torrey Club **40**: 53, in part. 1913. Not *A. episcopus* S. Wats., 1875.

*Astragalus Coltoni* was based on specimens from Castle Gate, Utah. It has the habit of *H. junceus* and *H. campestris*, but the pod has a slender stipe, the corolla is purplish, the wings are nearly as long as the banner and the keel is rounded at the apex. It is therefore more closely related to *H. stenophyllus*. I had mistaken it for *H. episcopus* (see my notes under that species on pages 184–5).

UTAH: Castle Gate, *Jones*, in 1890 and 1894; southern Utah, *Bishop*, in 1872.

NEW MEXICO: Carrigo Mountains, *Matthews*, in 1892.

39. HOMALOBUS STENOPHYLLUS (T. & G.) Rydb. This is the best known species of the group and was the first one published, the original name being *Astragalus leptophyllus* Nutt. As that name was preoccupied, *A. stenophyllus* was afterwards substituted. Torrey & Gray suggested that the species might belong in the genus *Homalobus*. The type was collected in flower, and the fruit remained unknown for some time. The type is

perfectly glabrous, except for the more or less black-strigose calyx, but sometimes the upper part of the stem and the lower surface of the leaflets are slightly strigose. This is the case with *S. Watson 283*, which was mistaken for *S. filipes*. Watson's description of that species also applies to *H. stenophyllus*.

BRITISH COLUMBIA: Nicola Valley, *G. M. Dawson 4269*, in 1877; also *J. Macoun*, in 1889.

OREGON: Andrews, *Griffiths & Morris 523;* Hoover Creek, *Leiberg 140;* Juniper Springs, Malheur County *2264;* between Dayville and Mitchell, *Lawrence 1024;* east of Heffner, *582 A;* Blue Mountains, *895;* Burns, *Peck 3029;* without locality, *Nivius*.

IDAHO: Big Willow, Canyon County, *Macbride 161;* Mackay, *1414;* House Creek, *Nelson & Macbride 1761;* Shoshone, *1165;* Martin, *Macbride & Payson 3079;* Reynolds Creek, *Macbride 1029;* Big Butte, *Palmer 240*.

NEVADA: Quinn River Crossing, *Griffiths & Morris 172;* Palisade, *M. E. Jones*, in 1882; Pah-Ute Mountains, *S. Watson 283;* Trucke Pass, *Kenedy 1314;* Alleghany Creek, *Nelson & Macbride 2166;* Reno, *Jones*, in 1897; Montana headwaters of the Missouri, *Wyeth*.

WASHINGTON: Coulee City, *Henderson 2358*.

### 40. **Homalobus MacGregorii** Rydberg, sp. nov.

A perennial, with a cespitose caudex; stems strigose, striate; lower stipules triangular, scarious, connate, the upper ones more herbaceous, distinct; leaves 5–8 cm. long; leaflets thirteen to nineteen, linear, 10–15 mm. long, 1–2 mm. wide, strigose on both sides; peduncles 1–2 dm. long; racemes lax, 5–12 cm. long; bracts subulate, 2–3 mm. long, calyx strigose, the tube 4–5 mm. long, the teeth triangular, 1 mm. long or less; corolla ochroleucous or white; banner 12 mm. long, obovate; wings 11 mm. long, the blade obliquely oblanceolate, equalling the claw; keel-petals 10 mm. long, rounded at the apex, the blade broadly lunate with a rounded basal auricle; pod stipitate, the stipe 12–15 mm. long, slightly pubescent, the body glabrous, linear-elliptic, acute at each end, 2.5 cm. long, 5–6 mm. broad.

TYPE collected near Frazier Borax Mine, Mount Pinos, Ventura County, California, June 12–14, 1908, *Abrams & McGregor 219* (herbarium of the New York Botanical Garden).

This species is related to *H. stenophyllus* but the stem and leaves are strigose-canescent. It has been mistaken for *H. An-*

*tiselli* but the leaflets are much narrower and pubescent on both sides. Besides the type, the following specimens belong here.

SOUTHERN CALIFORNIA: Kenworthy, *H. M. Hall 1182;* San Bernadino Mountains, *Parish Brothers 1281.*

LOWER CALIFORNIA: Orcutt, in 1885; *856*, in 1883.

41. HOMALOBUS CONOVIRENS Rydb. *Astragalus Coltoni moabensis* M. E. Jones. This is also related to *H. stenophyllus*, but the leaves and stem are densely grayish strigose, the stipe much shorter, the corolla dark bluish purple.

UTAH: Western slope of La Sal Mountains, *Rydberg & Garrett 8536, 8564;* La Sal Mountains, *Jones*, in 1993.

COLORADO: Naturita, *Payson 336.*

42. **Homalobus Antiselli** (A. Gray) Rydb. comb. nov.

*Astragalus Antiselli* A. Gray, Bot. Calif. **1**: 152. 1880.

This species differs from the three preceding in the broader leaflets, glabrous above and strigose beneath. *A. Hasseanus* Sheld.* is without doubt the same.

CALIFORNIA: Santa Catalina Island, *Rixford*, in 1914; Sulphur Mountains, *Abrams & McGregor 40;* Santa Inez, *Mrs. Curran*, in 1885; Ventura, *Elmer 3616;* Santa Barbara, *S. F. P.* [*Peckham ?*]; *Torrey 92 bis;* Buenaventura, *Hasse*, in 1888.

43. HOMALOBUS FILIPES (Torr.) Heller. This is very closely related to *H. stenophyllus* and distinguished only by the strigose pod and strigose stem and leaves. The two species have been confused and may not be specifically distinct.

WASHINGTON: Fort Okanogan, *Pickering*, in U. S. Exploring Expedition; Grand Coulee, *Griffiths & Cotton 440;* Ritzville, *Sandberg & Leiberg 163;* Sprague, *Sandberg & Leiberg*, in 1893; Ellenburg, *Piper 2717;* Yakima Region, *Brandegee 732;* Crab Creek, *Saksdorf 281.*

OREGON: Alkali, *T. Howell*, in 1882.

NEVADA: West Humboldt Mountains, *Heller 10631.*

44. **Homalobus inversus** (M. E. Jones) Rydb. comb. nov.

*Astragalus inversus* M. E. Jones, Zoe. **4**: 276. 1893.

This is closely related to *H. filipes*, differing mostly in the longer, more tapering and slightly curved pod.

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* Minn. Bot. Stud. **1**: 124. 1894.

CALIFORNIA: Susanville, *Brandegee;* same locality, *Jones;* Lava beds, Modoc County, *M. S. Baker*, in 1893.

45. **Homalobus gaviotus** (Elmer) Rydb. comb. nov.

*Astragalus gaviotus* Elmer, Bot. Gaz. **39**: 54. 1905.

This species is referred with some doubt to this group as the flowers have not been seen. The pod is strigose, nearly straight on the upper suture, the stipe is shorter than in the other species, the raceme is short even in fruit and the leaflets broad.

CALIFORNIA: Gaviota, *Elmer 3759;* same locality, *Eastwood 55* (determined erroneously as *Phaca canescens* Nutt.).

CONTRIBUTIONS FROM THE NEW YORK
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# STUDIES OF LYTHRUM SALICARIA—I. THE EFFICIENCY OF SELF-POLLINATION

By A. B. Stout

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# STUDIES OF *LYTHRUM SALICARIA* I. THE EFFICIENCY OF SELF-POLLINATION

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# STUDIES OF *LYTHRUM SALICARIA* I. THE EFFICIENCY OF SELF-POLLINATION

A. B. STOUT

(Received for publication December 8, 1922)

The conditions that exist in species with trimorphic flowers permit the investigation of the problems regarding the nature of sex-differentiation and the degrees of compatibility between male and female organs under very favorable circumstances. In these forms the morphological adaptations for cross-pollination are often decidedly correlated with physiological incompatibilities which make cross-fertilization more certain by excluding the functioning of the chance self-pollinations which occur.

In general it is to be recognized that sexual fusions are favored by similarity of the gametes both in genetic constitution and in immediate origin, and that such conditions as trimorphism and self-incompatibility are to be regarded as, in a high degree, secondary and acquired. While these conditions secure the advantages of bringing together gametes of different origins and in greater or less degree of different genetic constitution, they decidedly limit and restrict free fertilization and full productivity.

The combination of morphological trimorphism with physiological incompatibilities as seen in species like *Lythrum Salicaria* may well be regarded as the highest degree of specialization in sex-determination and fertilization that exists in flowering plants. For this species there is the obvious morphological differentiation giving three lengths of pistils and three sets of stamens of lengths corresponding to those of the pistils, with the stamens bearing pollen differentiated as to size, color, and nature of the reserve food material in storage. For the individual, the flower of any particular plant has a pistil of one of the three lengths and a set of stamens for each of the other two lengths. This gives differentiation of forms as such, and in the single plant there is the differentiation that gives two kinds of stamens. Furthermore, this morphological differentiation is decidedly correlated with physiological differentiation. The noteworthy researches of Darwin (1865, 1877) showed that there is marked or even complete sterility to (1) self-pollinations, to (2) intra-form cross-pollinations, and to (3) the inter-form cross-pollinations that are illegitimate (*i.e.*, those that involve different lengths of pistil and stamen). Seed-production was hence found to be more or less limited to legitimate pollinations, which are necessarily crosses.

The specializations in these forms allow no doubts as to their significance such as have often been raised in regard to the colors of entomophilous flowers, for here the adaptations are morphological and depend directly

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on the agency of insects for their effectiveness in pollination. The relative lengths of the different sets of stamens and of the pistils are unquestionably provisions favoring crossing.

It is, however, obvious that such differentiations are not fundamental expressions of sexual antithesis, since they are all reciprocal in any pair of flowers. Any two plants of any two forms are cross-compatible or cross-incompatible according to whether the cross is legitimate or illegitimate. The differentiations, at least in respect to maleness, that in dimorphic plants are seen in individuals as such and which appear to have definite genetic value are here seen equally well in the two sets of stamens in a single flower. All this emphasizes the fact that the conditions are secondary and acquired in contrast to the more primitive condition of homomorphism and a more general compatibility of gametes.

The generally accepted view has been that the differentiations in this species are well established and very stable. The tendency has been to emphasize, as did Darwin, the evidence that here there is adaptation favoring crossing, and to pass the evidence, which has to some extent been noted, that the adaptations are incomplete. It is to be recognized that such evidence has a very direct bearing on questions of the origin of trimorphism, of the nature of sex-differentiations, and of whether there is still opportunity for further selection in the species either toward greater or toward less restriction of fertilization. It is evidence along these lines that the writer wishes to present in reports, of which this is the first, of investigations with the species.

## The Efficiency of Self-pollination for Plants Grown in Isolation

The writer's studies of *Lythrum Salicaria* were begun in 1917 in testing the self-compatibility of plants grown in isolation from other plants of the same or of related species. On such a plant hundreds of flowers open daily during a rather extended period of time and insect visitors can go from flower to flower, but with no chance, if the isolation is complete, of bringing pollen from other plants of *Lythrum Salicaria*. A large number of flowers are thus involved in the chance for self-fertilization (including here autogamy and geitonogamy), and the results can be obtained for the entire period of bloom. This test does not, however, determine the relative fertility of a plant to pollen of its two sets of stamens, nor does it reveal the need or the efficiency of particular species of insects in the self-pollination of the various forms, which may indeed give results that are highly variable from season to season or from year to year or according to location. However, if seed is produced there is positive evidence of self-compatibility, and the negative results may be tested further by controlled pollinations.

*Short-styled Plants Grown in Isolation.* Two large, well-developed plants several years old were dug from a mixed population growing at the New York Botanical Garden. One (*S no. 2*) was grown in the garden of the

Department of Botany at Columbia University, under the observation of Professor R. A. Harper, and one (*S no. 1*) at the University of Missouri under the care of Professor G. M. Reed. Both plants made vigorous growth and bloomed profusely, but neither plant produced a single capsule during the entire period of bloom of the season of 1917. In 1918 the plant at Missouri suffered severely from drought, and its failure to set any seed that year is not to be considered as adequate evidence of complete self-incompatibility.

The short-styled plant at Columbia University thrived and in the course of its season of bloom in 1918 produced 17 pods. Ten of these contained only mere rudiments of seeds, two contained one good seed (plump and apparently fully developed) each, three had two good seeds each, one had seven seeds, and one had eight. Sixteen of these 23 seeds germinated. In the following year (1919) this plant bloomed more abundantly than in the previous year and produced at least 5000 flowers, and during the entire season 161 pods matured. The seeds in 100 of these pods were counted; the number per pod ranged to 116, and the average was 23.67 (see table 1). This plant grew poorly in 1920, when its roots were separated to make two plants. In 1921 these thrived, and there was abundant bloom but only about 25 pods were produced. The irregular pod production by this plant may involve one or more of several conditions; possibly in 1919 insects may have brought pollen from a distance from plants of this species growing in city parks, or the irregularity may involve the presence or absence of certain insects that are most efficient in causing self-pollination.

*Long-styled Plants Grown in Isolation.* A long-styled plant (*L no. 1*) was grown at Baraboo, Wisconsin, under the care of Mr. William Toole, Sr., a well known pansy specialist. Plants of the variety *rosea* were also growing in the nursery at some distance away, so that some of the seed produced by the plant *L no. 1* may have been due to cross-pollination by insects. But another long-styled plant (*L no. 2*) was grown in what was certain isolation at Pleasantville, N. Y., under the care of Dr. M. A. Howe. Capsules were produced by both these plants. Of the 65 capsules on *L no. 1* in 1917, 16 contained no seeds, 17 contained one seed each, and the highest number of seeds in any capsule was 17. In 1917 a total of 53 capsules matured on the plant *L no. 2*. As shown in table 1, the number of seeds per capsule for this plant was also low, although all but three of the capsules contained some fully matured seeds.

In 1918 both plants produced capsules quite as in 1917, but the capsules on *L no. 2* were somewhat more numerous than in the previous year though still constituting a small proportion of the entire number of flowers.

The capsules produced by these two plants were distributed irregularly but rather indiscriminately throughout the flowering branches. Self-fertilization appeared to be effected with the same frequency and efficiency throughout the flowering period. No very decided seasonal differences appeared in respect to the proportional number of flowers which matured

Table 1. *Self-compatibility in Lythrum Salicaria to insect-pollination, and cases typical for the results obtained for controlled hand-pollinations*

|  | Number of Flowers Pollinated | Number of Pods Produced | Number of Pods used in Seed Counts | Distribution of Seed per Pod. Class Groups 1 to 10 |  |  |  |  |  |  |  |  |  |  |  |  |  | Average Seed for Pods with Seed |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  | 0 | –10 | –20 | –30 | –40 | –50 | –60 | –70 | –80 | –90 | –100 | –110 | –120 | –130 |  |
| Isolation, Insect-pollination |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| S. no. 1 | ? | 0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| S. no. 2. (1918) | ? | 17 | 17 | 10 | 7 |  |  |  |  |  |  |  |  |  |  |  |  | 3.28 |
| S. no. 2. (1919) | ? | 161 | 100 | 0 | 34 | 30 | 16 | 4 | 5 | 4 | 0 | 2 | 1 | 2 | 0 | 2 |  | 23.67 |
| L. no. 1 | ? | 65 | 65 | 16 | 47 | 2 |  |  |  |  |  |  |  |  |  |  |  | 2.96 |
| L. no. 2 | ? | 53 | 53 | 3 | 47 | 3 |  |  |  |  |  |  |  |  |  |  |  | 4.85 |
| M. no. 2 | ? | 3000 | 300 | 14 | 202 | 48 | 8 | 7 | 6 | 1 | 5 | 1 | 1 | 1 | 2 | 3 | 1 | 8.91 |
| M. no. 1. (1919) upper ⅓ | ? | many | 71 | 7 | 43 | 12 | 3 | 2 | 1 | 0 | 2 | 0 | 1 |  |  |  |  |  |
| middle ⅓ | ? | few | 31 | 3 | 16 | 3 | 0 | 3 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 1 |  |  |
| lower ⅓ | ? | few | 40 | 6 | 20 | 3 | 1 | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 2 | 1 |  |  |
| " total | ? | 1500 | 142 | 16 | 79 | 18 | 4 | 7 | 5 | 1 | 5 | 1 | 1 | 1 | 2 | 2 |  | 18.25 |
| Hand-pollination |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| M. no. 1. (1919) | 233 | 134 | 134 | 1 | 28 | 29 | 19 | 20 | 14 | 6 | 5 | 8 | 3 | 0 | 0 | 1 |  | 24.61 |
| M. *5–1* no. 13 | 103 | 0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| M. *3* no. 7 | 48 | 8 | 8 | 1 | 5 | 2 |  |  |  |  |  |  |  |  |  |  |  | 7.00 |
| M. *1* no. 48 | 35 | 6 | 6 | 0 | 1 | 2 | 2 | 1 |  |  |  |  |  |  |  |  |  | 20.33 |
| M. *1* no. 31 | 33 | 4 | 4 | 0 | 0 | 2 | 1 | 1 |  |  |  |  |  |  |  |  |  | 25.00 |
| M. *1* no. 56 | 60 | 9 | 9 | 0 | 0 | 4 | 3 | 0 | 1 | 1 |  |  |  |  |  |  |  | 28.33 |
| M. *5–1* no. 25 | 32 | 9 | 9 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 2 | 1 |  |  |  |  |  | 50.88 |
| M. *5–1* no. 35 | 32 | 5 | 5 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 |  |  |  |  | 49.50 |
| M. *1* no. 30 | 37 | 9 | 9 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 2 |  |  |  | 59.66 |
| M. *1* no. 57 | 40 | 44 | 44 | 0 | 1 | 7 | 3 | 2 | 7 | 3 | 3 | 12 | 5 | 1 |  |  |  | 63.15 |
| L. *4* no. 2 | 55 | 2 | 2 | 0 | 2 |  |  |  |  |  |  |  |  |  |  |  |  | 6.00 |
| L. *1* no. 66 | 68 | 2 | 2 | 0 | 2 |  |  |  |  |  |  |  |  |  |  |  |  | 6.00 |
| L. *2* no. 18 | 50 | 7 | 7 | 0 | 6 | 1 |  |  |  |  |  |  |  |  |  |  |  | 7.42 |
| L. *1* no. 8 | 49 | 22 | 22 | 0 | 11 | 10 | 1 |  |  |  |  |  |  |  |  |  |  | 8.90 |
| L. *5–5* no. 38 | 24 | 6 | 6 | 0 | 2 | 1 | 2 | 1 |  |  |  |  |  |  |  |  |  | 20.00 |
| S. *5* no. 5 | 14 | 4 | 4 | 0 | 1 | 2 | 1 |  |  |  |  |  |  |  |  |  |  | 14.00 |

capsules that could be referred definitely to differences in insect visitations or to the constitution of the plants.

*Mid-styled Plants Grown in Isolation.* A plant of this form (*M no. 2*) was sent to Mr. H. L. Skavlem, who grew it at Carcajou Point, Lake Koshkonong, Wisconsin. Mr. Skavlem states that by the middle of July this plant was "over four feet high with an abundance of bloom which continued for about six weeks." The plant bloomed from July 14, 1918, until the first week in September. There were about 35 well-developed main flower spikes ranging from 3 to 14 inches in length, and the total number of flowers produced was estimated at 8,000. This description would apply as well to any well-developed plant of any of the three forms.

This mid-styled plant was decidedly self-compatible in this isolation test. At least 3,000 capsules matured on it in 1917. A total of 300 capsules were examined and counts were made of the seeds present, with results as summarized in table 1. The number of seeds per capsule ranged to 121; twenty-eight capsules had more than 30 seeds each, but 202 capsules contained less than 11 seeds per capsule, and 14 contained only rudiments of seeds. The average number of seeds per pod for those that had good seeds was 8.91. In 1918 the self-compatibility of this plant was quite the same as in 1917.

In making the counts of seeds in 300 capsules (1917 crop) of this plant, position was taken into account. Each branch involved in the counts was divided into three sections of equal length, here designated as the lower third, middle third, and upper third. In the lower third of all branches there were 10 capsules with more than 30 seeds each. It is clear that the average number of seeds per capsule was lower toward the top of the branches of this plant, but smaller capsules and fewer seeds per capsule are, as a rule, to be expected toward the apex. Otherwise the plant was rather uniformly highly self-compatible, and capsules with seeds were produced in a considerable proportion of the flowers subjected to open pollination throughout the entire period of bloom.

Another mid-styled plant (*M no. 1*) was grown in my own home garden. This plant made a vigorous growth and produced in 1917 at least 6,000 flowers. At the close of the season it was found that relatively few of the flowers produced pods during the first two thirds of the period of bloom, but that later nearly every flower produced a pod.

In 1918 it was planned to test experimentally the behavior of this plant, and especially to determine if the marked difference in production of fruit involved changes in the innate ability of the plant to produce fruit or indicated merely some difference in insect-pollination. A large, well-developed long-styled plant was planted by its side. The two began blooming only one day apart. The long-styled plant was allowed to bloom, thus affording opportunity for free cross-pollinations by insects between the two, until the 17th of August, when the long-styled plant was cut down. During the time that both were in bloom nearly all flowers that opened on the mid-styled plant developed fine pods, showing that the feeble production of pods during the early part of bloom as observed in the previous year when the plant was in isolation was not due to an impotence of the pistils. During the rest of the season its performance was quite as in the previous year.

In 1919 the long-styled plant was kept cut down so that no flowers were produced by it, and a series of guarded self-pollinations were made on the plant *M no. 1*. Branches were enclosed in glassine paper bags. Whenever pollen from short stamens was used for pollinations, the flowers to be thus pollinated were opened early in the morning and the long stamens were removed, and then pollen from the short stamens was used later in the day when the anthers were dehiscing.

Legitimate cross-pollinations, using pollen of flowers brought in vials from the experimental plots over a mile distant, were made on 22 flowers during the first 18 days of bloom. The plant was in bloom 55 days. The results obtained for selfing are summarized in table 1 and are shown in more detail in table 2, in which, to facilitate ready comparison, the data are compiled for three periods.

TABLE 2. *Record for controlled pollinations of mid-styled plant no. 1 in summer of 1919*

| | 1st to 18th Day | 19th to 36th Day | 37th to 55th Day |
|---|---|---|---|
| Selfed with pollen of long stamens | | | |
| Failures—no pods | 70 | 35 | 9 |
| Pods produced | 18 | 46 | 70 |
| Seeds per pod—range and average | (0 to 117) av. 34 | (2 to 81) av. 32 | (3 to 82) av. 32 |
| Selfed with pollen of short stamens | | | |
| Failures | 33 | 57 | 47 |
| Pods | 1 | 1 | 1 |
| Seeds per pod | 37 | 10 | 1 |
| Legitimate cross-pollination | | | |
| Failures | 2 | | |
| Pods | 20 | | |
| Seed-range and average | (12 to 176) av. 98 | | |

Of the 140 flowers hand-pollinated with pollen from short stamens, only three produced pods yielding 1, 10, and 37 seeds respectively, but these may have been due to chance pollination with pollen from the long stamens at the time of their removal or with pollen of other flowers which were enclosed in the same bag. The results indicate that the plant remained decidedly if not completely self-incompatible to pollen of its own short stamens throughout the entire period of bloom.

When pollen of long stamens was used in hand-pollinations, the proportion of pods produced increased as the season advanced, and during the last 18 days of bloom there were but 9 failures out of 79 flowers pollinated. The results show conclusively that the self-compatibility in this plant involves fertilizations from the pollen of long stamens, and also that this compatibility actually increases toward the end of the period of bloom. The increase in compatibility affects, however, the number of pods that are formed rather than the number of seeds in a pod. The average number of seeds in the pods that were produced was almost the same for all periods, but the highest number of seeds in any pod was obtained during the first 18 days of bloom.

The 22 legitimate crosses made during the first 18 days gave 20 pods with seeds ranging in number from 12 to 176, with an average of 98 seeds per capsule. These results show conclusively, as do those of open cross-pollinations during the early part of the period of bloom in the previous year, that the pistils of the plant are highly potent during the period of marked self-incompatibility. The decided change in fruit-production is hence due to a change in the physiological relations between pistils and the pollen of long stamens. Pollen from both short stamens and long stamens was examined at frequent intervals throughout the entire period of bloom; there was very little abortion, the pollen was successfully germinated in artificial media, and the use of such pollen in legitimate crosses on several dates during the first 30 days of bloom was almost invariably highly effective in pod- and seed-production. There were in this plant no noticeable evidences of impotence of stamens and anthers, such as are to be seen in some plants of this species.

The branches left to open-pollination produced pods quite as in the year 1917. Several of the main branches were selected and divided into thirds, and seeds in all pods in the lower two thirds were counted; then an equal number of pods from the many pods in the uppermost third were taken at random for counts, the entire number, 142, being as near the number of pods secured from the selfing by hand in which the pollen of long stamens was used as was possible. As shown in table 1, the range for number of seeds per pod and the average were higher for the lower two thirds than in the last third, showing that the change in compatibility involves number of pods formed rather than number of seeds per pod. Comparison shows that the controlled pollinations in which pollen from long stamens was used were somewhat more successful than free open-pollinations, when judged by the average number of seeds produced.

A third mid-styled plant (*M no. 3*) was grown in isolation in the New York Botanical Garden at a distance of about one mile from the location of the plant *M no. 1*. This plant proved to be decidedly less self-compatible to open self-pollination than were *M no. 1* and *M no. 2*, but, as in *M no. 2*, there was quite the same proportion of pods produced throughout the entire season of bloom, no change in compatibility being evident as observed in the plant *M no. 1*.

*Summary*. In these tests seeds were obtained to illegitimate self-pollination of plants of all three forms. Mid-styled plants were most highly self-compatible in respect to the number of pods produced. The pods found were distributed irregularly over the entire period of bloom except for one plant (*M no. 1*), in which it was found that there was an actual change in the degree of self-compatibility to pollen from its own stamens. The results from year to year have been very uniform for all plants, except for the plant *S no. 2*. Its feeble production of pods in 1918, followed by the production of 161 pods in 1919, suggests that the plant is rather strongly self-compatible provided insects make the proper pollinations. It may readily be conceded that the kinds of insects that can most efficiently self-pollinate long-styled and mid-styled plants are not the ones which best self the short-styled plants.

Self-pollination does not appear to be uniformly as efficient in seed-production as are certain legitimate cross-pollinations, at least for the one mid-styled plant *M no. 1* (see table 2). Of the 22 flowers on it that were crossed during the first 18 days of bloom there were only two failures, the highest number of seeds for a capsule being 176 and the average 98. Whether such pollination would be more effective than selfing during the last part of the period of bloom was not tested.

### SELF-COMPATIBILITY TESTS BY THE BAGGING METHOD

A total of about 600 plants have been grown in pedigreed cultures from seed. A considerable number of these have been tested for self-compatibility in the following manner: branches were enclosed in glassine paper bags, and pollinations of flowers opening within were made from day to day. Long-styled plants and short-styled plants were selfed by using the pollen from mid-length stamens, and the mid-styled by use of the pollen of long stamens. In making pollinations, stamens with dehiscing anthers were removed with sterile tweezers and brushed on pistils, leaving an abundance of pollen. In cases of pseudo-proterogyny the fully protruding pistils of partially opened flowers were likewise treated along with pistils of more mature flowers. It appears that in the decidedly pseudo-proterogynous flowers the pistils protrude long before they are receptive to any kind of fertilization, and that highest seed production in compatible fertilizations occurs when pollination is made at or about the time that petals open and pollen is shed. On plants two or more years old, a total of as many as 500 or more flowers were often thus pollinated. On plants in the first year of growth from seed the number thus selfed was often much less.

These tests are undoubtedly less adequate than tests in isolation for revealing feeble grades of self-compatibility and in showing such changes in self-compatibility as are seen in the plant *M no. 1*, but hand-pollinations make certain that pollen in abundance is applied to the stigmas at the time when they are judged to be most receptive.

The general results summarized for each form without reference to lines of descent are as follows:

| | Fully Self-incompatible | Feebly Self-compatible | Medium Self-compatible | Highly Self-compatible |
|---|---|---|---|---|
| Mid-styled plants..... | 64 | 20 | 21 | 7 |
| Long-styled plants..... | 83 | 14 | 0 | 0 |
| Short-styled plants.... | 22 | 1 | 0 | 0 |

An attempt has been made to grade the plants according to whether the self-compatibility is feeble, medium, or strong, the judgment being based on the proportion of selfed flowers that gave pods and the number of seeds produced. Results typical for various grades are given in table 1. The tests made show that many plants of the species are without doubt entirely self-incompatible (*M 5–1 no. 13* in table 1 for example), and that others are highly self-compatible (*M 1 no. 57*), with various intervening amens grouping of which is neither definite nor accurate.

In these tests mid-styled plants have been more highly sel loom; than plants of the other forms. This is true both in relative ed in produce fruit to selfing, and in the range to higher grades of several one plant, *M 1 no. 57*, every flower that was selfed produced a fective other pods were produced in other flowers that spontaneousl ceable while enclosed in a glassine bag.

Of the 97 long-styled plants tested in hand-pollinations, only 14 produced pods, and not one gave over 30 seeds in any pod. In all of these the self-compatibility was apparently of a weak grade.

Twenty-three short-styled plants were tested, and only one produced seeds.

The results obtained in the controlled self-pollinations with these plants agree in general with those obtained in isolation tests. A rather large proportion of mid-styled plants are self-compatible in some degree, and nearly half of the plants of this form produced pods containing viable seeds to selfing, and a few were highly self-compatible. There has been no difficulty in finding mid-styled plants to use as parents of self-fertilized lines of progeny. Relatively few long-styled plants produced pods to selfing, and in all such plants the self-compatibility was feeble, few pods being produced and these having few good seeds. Short-styled plants have as a class been decidedly self-incompatible, and of the seedlings tested only one has produced seeds to selfing. The high seed-production seen in the plant *S no. 1* in 1919 was not duplicated by the plant in 1918 nor in 1920 and 1921. There has not been opportunity to test this plant by controlled hand-pollinations as the plants grown from seed have been tested.

## SUMMARY

1. Many plants of *Lythrum Salicaria* are capable of producing capsules and viable seeds to illegitimate self-pollination brought about either by controlled hand-pollination or by insect-pollination in the field. The capacity for self-fertilization still lingers strongly in the species.

2. The proportion of self-compatible plants is greatest in the mid-styled plants, in which also the highest grades of self-compatibility are to be seen. Long-styled plants are, as a class, less self-compatible, and the short-styled plants are still less so. The three forms appear to differ in the capacity for self-compatibility.

3. There are wide variations in the degree of self-compatibility. In the most highly self-compatible form, the mid-styled, there are all gradations between complete self-incompatibility and the highest grade of self-compatibility.

4. The variations in the physiological condition of the sex organs, as

exhibited in selfing, suggests that wide variations may likewise be expected
mid-s[illegible] [illegible]ings even for those that are legitimate.
crossed [illegible] e noticeable case of end-bloom self-compatibility was found. This
the hi[illegible] mid-styled plant and involved only fertilizations from pollen of
Whethe[illegible] long stamens.
last par[illegible] physiological relations of the sex organs in plants of this tri-
[illegible] species exhibit quite the same range of variations as are seen in
many [illegible] omorphic species.

## Conclusion

For the species *Lythrum Salicaria* the evidence of wide variation in the degree of self-incompatibility is definite. The physiological differentiations of the sex organs are incompletely correlated with the apparent structural adaptations for cross-pollination; they are not fixed, constant, and fully achieved either in expression or in heredity, but are fluctuating and intergrading. They still present opportunity for further selection either toward greater or toward less restriction of fertilization.

The persistence of self-compatibility in various degrees of expression, and the apparent difference in respect to self-compatibility seen among the various forms, present strong evidence that self-compatibility was the antecedent condition in the species out of which the present complex of sex relations is still evolving, just as the sets of styles and stamens of different lengths have been developed out of an original homomorphic species.

New York Botanical Garden

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# The Physiology of Incompatibilities

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# THE PHYSIOLOGY OF INCOMPATIBILITIES[1]

A. B. Stout

In general survey, physiological incompatibilities in fertilizations include two groups of phenomena:

1st. There are the very general and characteristic failures of cross-fertilization *between* different species, long considered as the most adequate evidence of specific distinction; and

2d. There are those physiological limitations to free and general fertilization *within* species exhibited best in the failure of certain homomorphic hermaphrodites to self-fertilize, but also in the cross-incompatibilities among seed-grown individuals of the same species or race.

Certain aspects of the physiology of these incompatibilities are clear. They exist and are in operation when the sex organs and sex elements are in a condition for proper fertilization; the elements do not function in certain relations but do in others; fertilization is discriminative.

It is not, therefore, a question of what brings the spores or gametes to ripening, or of the mere production of those egg or stylar secretions or chemotactic influences which make fertilization possible. It is rather a question of a very special kind of development or physiological condition which discriminates between fertilizations when they are otherwise possible.

Inter-specific incompatibilities are very generally considered to involve species specificity. They are expressed in the interaction between egg secretions and sperms, in mechanical and chemical resistance of the cortical layers of eggs to the entrance of sperms, in the extrusion of sperm chromatin after fertilization, in the death of the heterogenetic hybrid, or in the sexual impotence of such hybrids. In all these ranges of expression the incompatibilities appear to be deep-seated and inherent in the physical and chemical differences in the organization of species.

Turning now to intra-specific incompatibilities, there is apparently a very different physical basis. Here there is self-incompatibility involving the germ cells of a single individual. Here also there is cross-incompatibility between individuals of the same parentage. Such cases are frequent among homomorphic hermaphrodites. They are so widely distributed in the families of flowering plants that it would seem that there must be some

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[1] Read in the symposium on "Sterility in Plants," at the joint meeting of Section G of the American Association for the Advancement of Science, the Botanical Society of America, and the American Phytopathological Society, at Cambridge, December 27, 1922.

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fundamental principle operating in their origin and development. In these higher plants there is the development of a nearly naked egg (free of a decided membrane) imbedded in the tissue of the ovule, and a highly specialized male gametophyte—the pollen tube—with its various growth relations in the style. While fertilization in these cases involves a series of physical and chemical relations, it is fundamentally an egg-and-sperm reaction.

It is to be noted that studies of the physiology of pollen germination have failed to reveal a specificity that is comparable or related to the compatibility or incompatibility found in homomorphic species. It has, however, long been known that in cases of self-incompatibility the pollen tubes often make feeble growth in the style, and more recently it has been shown that their rate of growth is not accelerated as the eggs are approached. This condition apparently persists when incompatible pollen is mixed with compatible pollen and the tubes of both grow side by side in the style. This indicates that the reactions are decidedly discriminative and suggests that they involve reactions of the pollen tubes to secretions of the eggs. There is, however, evidence that in many grades of self-incompatibility the injurious effects may be exhibited after what is apparently a successful fertilization.

One aspect of the development of self-incompatibility in the hermaphrodite is clear. Every such individual is itself the result of a compatible fertilization in which two cells fused, and the two elements of the resulting diploid organization show themselves compatible throughout the somatic life of the individual; but the two kinds of sex elements produced by it are incompatible, and this is of course irrespective of their germ-plasm complex. The incompatibility arises along with sex differentiation, which in seed plants begins with the development of pistils and stamens and is independent of any readjustments of the germ plasm in the reduction divisions.

The biogenetic nature of the development of self-incompatibilities is further indicated by the wide variations which exist in their expression in individuals. Between the extreme or alternative conditions there are many intergradations, and the extreme conditions are reversible in a progeny. This is the general rule of behavior in such pedigreed cultures as have been critically tested in this particular. Cross-incompatibilities exhibit quite the same ranges of expression, and here reciprocals may give directly opposite results.

But there is also conclusive evidence in certain species of cyclic changes in the self-compatibility of an individual. These are best seen in plants which have a somewhat extended and continuous period of bloom. In some species there is self-compatibility at the end of the period of bloom; in others the climax of self-compatibility is at the mid-period of the bloom, and for certain perennials there is some evidence of changes from year to year in relation to the age of the plant. It is to be noted that a mid-period self-compatibility is preceded and followed by self-incompatibility. There is alternative expression of extreme grades of compatibility and incompatibility in the series of flowers produced in succession on the same branch. The functions of fertilization are in such cases operating in a cycle of intensities.

It may here be reported that, in the species *Brassica pekinensis*, self-incompatibility of a plant as a whole or of a family of plants may be decidedly changed by a cultural treatment which reduces vegetative vigor. In a family of this species grown for three generations, less than 10 percent of the total of 326 plants were highly self-compatible and there was no hereditary effect of selection for self-compatibility. When a generation of this family was grown in small pots with decided reduction of vegetative vigor, of a total of 1,128 plants there were 734 (65%) that were highly self-compatible, and only 22 (less than 2%) were self-incompatible. Furthermore, a large proportion of the former were self-compatible in the earliest flowers that opened. The family was decidedly changed in regard to the number of plants that were self-compatible, and in the individuals the characteristic cycle was altered. Such results, together with the other behavior noted above, indicate that there is a direct and very decided physiological correlation between vegetative vigor and the functional properties of the organs concerned with fertilization.

This is at least suggestive that the physiological conditions which restrict and limit indiscriminate fertilization within species are not only subject to internal regulation, but that in some cases at least they are correlated with changes in vegetative vigor.

The situation gives hope that the cyclic expression of sexual affinities and the development of extremes of compatibility may be so regulated experimentally that the specific biogenetic factors and conditions operating in this highly specialized differentiation may be determined.

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# Genera of North American Fabaceae—I

P. A. RYDBERG

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# GENERA OF NORTH AMERICAN FABACEAE
## I. TRIBE GALEGEAE

P. A. RYDBERG

(Received for publication December 16, 1922)

The tribe Galegeae has been divided since Bentham's time into seven subtribes. Of these one has already been raised to tribal rank, Psoralieae, which is characterized by the glandular-punctate foliage and by the pods, which are one- or few-seeded, usually indehiscent but rarely breaking open irregularly across the middle, never valvate. Another subtribe should be removed as a tribe Indigofereae, having three characters seldom found elsewhere in Fabaceae and never combined in any of the tribes. These are malpighiaceous hairs (appressed hairs, 2-branched with branches forming a straight line, the hairs therefore apparently attached at their middle), appendaged connectives in the anthers, and lateral spurs on the keel-petals. It may be that Glycyrrhiza and one or two genera should be removed also and form another tribe, on account of the indehiscent (though several-seeded) glandular fruit and confluent anther cells.

After the removal of the two subtribes mentioned, the tribe may be characterized as follows:

Herbs, shrubs, or trees, or woody vines, without glandular dotted foliage (except in Glycyrrhiza). The leaves are odd-pinnate or abruptly pinnate, with or without stipels, very rarely with malpighiaceous hairs. The calyx is campanulate to tubular, 5-toothed or 5-lobed, rarely more or less 2-tipped. The corolla is papilionaceous, with 5 petals, the two keel-petals more or less adnate along the lower margins. The stamens are 10, diadelphous or monadelphous, the connective without appendages. The ovary is usually many-ovuled, more or less curved or bent upwards; the style slender and the stigma small. The fruit is several- or many-seeded, 2-valved, usually dehiscent.

As stated before, Bentham and Hooker acknowledged 7 subtribes. These authors were closely followed by Taubert in Engler and Prantl's Natürlichen Pfanzenfamilien. Taubert's key in translation reads as follows, after the Indigofereae and Psoralieae have been removed:

*α*. Seeds strophiolate. Flowers in 2's in the leaf-axils or forming a terminal raceme (compare Tephrosia and Fordia). *c*. BRONGNIARTIINAE.
*β*. Seeds not strophiolate.
  I. Inflorescence racemose, terminal, opposite the leaves, or on the branches paniculate, more rarely in the axils of the upper leaves or all peduncles or only the lower paired or clustered in the axils. Stipe inside the staminal sheath sometimes surrounded by a small cup-like disk. *d*. TEPHROSIINAE.

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II. Inflorescence always axillary. Stipe without disk at the base.
  Pod flat, when inflated at least the endocarp flat, 2-valved. *e.* ROBINIINAE.
  Pod inflated or bladdery, rarely flat, then 2-celled lengthwise.
    Style bearded above; pod inflated or bladdery, not dehiscent or opening only at the apex, more rarely 2-valved, never with a longitudinal partition. *f.* COLUTEINAE.
    Style naked, more rarely hairy like a brush around the stigma; pod 2-celled or nearly 2-celled lengthwise, seldom 1-celled. *g.* ASTRAGALINAE.

From this key it is evident that the subtribes are very artificial and that it has been very hard to find really good distinctive characters. It is also evident that these characters have been drawn without taking into consideration the American genera in full, in which they break down repeatedly.

While the strophiole is very well developed in the Brongniartiinae, in fact better so than in any other group in the Fabaceae, strophioles are present, although small, in several species of Cracca.

The Tephrosieae of Bentham (Tephrosiinae of Taubert) is in itself not a natural division, for Barbiera is not at all closely related to the rest, being distinguished by the long-clawed petals, the presence of 2 bractlets beneath the tubular calyx, and the style bearded along the upper side. In fact, it has no close relative in the whole tribe. The paired bractlets are found in Sesban and related genera and in Diphysa, which are all included in the Robinieae of Bentham (Robiniinae of Taubert).

Neither does Krauhnia seem to be closely related to Cracca or Galega, but apparently forms a natural group with several Asiatic genera, especially Millettia.

The position of the inflorescence, being either terminal or apparently opposite the leaves, a character very important in the minds of both Bentham and Taubert, seems to be of little value, for in many species of Galega and a few of Cracca (see explanation under Cracca) the inflorescence is axillary, just as in the Coluteinae and Astragalinae. The other character, the presence of the disk at the base of the staminal sheath, is also unreliable, for, while it is fairly well developed in Cracca and Krauhnia and their relatives, it is not at all in Barbiera.

The Robinieae of Bentham (Robiniinae of Taubert) is distinguished from the Coluteae and Astragaleae (Coluteinae and Astragalinae of Taubert) by the one-celled, two-valved, flattened, not inflated pod, but in the genus Diphysa, included in the first, the exocarp is strongly inflated, forming two lateral elongate bladders, and in Homalobus and Kentrophyta, segregates of Astragalus, the pod is decidedly compressed and fulfills all the characters ascribed to the Robinieae. In Bentham and Hooker's Genera Plantarum the following remarks are made: "In Astragalus paucis [legumen] planissimum est, sed membranaceum et perfecte septatum." This statement applies to Hamosa Med., a segregate of Astragalus found both in the Old

World and America, in which the pod is flat and 2-celled. In Atelephragma Rydb., another segregate found only in America, the septum is incomplete, while in Homalobus and Kentrophyta, both exclusively American, there is not a vestige of a partition and the fruit is exactly like the fruit of Poitoea, Coursetia, or Corynella, placed in the Robinieae.

Both Bentham and Hooker, and Taubert seem to have ignored or else knew imperfectly these segregates of Astragalus when characterizing their subtribes. In Benthamantha, also placed in the latter subtribe, the pod is also similar but with false transversal partitions. In Sesban and Daubentonia, both referred to Robinieae, the pod is hardly compressed, in the former terete or nearly so, in the latter 4-angled. There is therefore no definite line between these three subtribes as constituted by Bentham and Hooker and by Taubert, nor are the Brongniartiae or the Tephrosieae very distinct.

The classification must therefore be remodeled along other lines. I shall give here a tentative reclassification, which will probably be modified when more study has been made on the Astragalinae.

- Seeds strophiolate; embryo with a straight radicle; flowers 1 or 2 in the axils of the leaves or in terminal racemes or panicles; calyx subtended by a pair of deciduous bractlets; pods flat; trees or shrubs. Subtribe 3. BRONGNIARTIANAE.
- Seeds not strophiolate (rarely slightly so in species of Cracca); embryo mostly with an incurved radicle; flowers mostly racemose.
  - Bractlets 2 under the calyx; pods internally with more or less distinct false cross-partitions.
    - Calyx tubular, with long lobes; petals long-clawed, their blades cuneate at the base, that of the banner oblong, not spreading; pods flat, many-seeded, dehiscent; shrubs with odd-pinnate leaves. Subtribe 4. BARBIERIANAE.
    - Calyx campanulate, with short tooth-like lobes; petals short-clawed, at least the blades of the wings with basal auricles; blade of the banner sub-orbicular or broadly ovate; pods not flattened or if flat 2-seeded (Glottidium).
      - Exocarp of the pod not inflated; hypanthium obsolete, not differentiated from the calyx; shrubs or trees, with abruptly pinnate leaves. Subtribe 5. SESBANIANAE.
      - Exocarp of the pod inflated, forming two elongate bladders, one on each side of the pod; hypanthium well developed and differentiated from the calyx, obconic; shrubs and trees, with odd-pinnate leaves. Subtribe 6. DIPHYSANAE.
  - Bractlets under the calyx wanting; pods usually without cross-partitions, except in Benthamantha, Sphinctospermum, and Hebestigma.

- Base of the pistil or of its stipe usually surrounded by a more or less developed saucer-shaped disk within the staminal sheath; racemes terminal, or terminal and in the upper axils, or opposite the leaves, or if axillary, the leaflets with parallel oblique lateral veins.
  - Leaflets with parallel or indistinct lateral veins; pods obliquely striate; leaves without stipels; herbs or low shrubs. Subtribe 1. CRACCANAE.
  - Leaflets netted-veined; pods not obliquely striate; leaves mostly with stipels; trees or (ours) woody vines. Subtribe 2. MILLETTIANAE.
- Base of the pistil or its stipe not surrounded by a disk; racemes always axillary; leaflets not with parallel oblique lateral veins.
  - Pods flat, or if terete with prominent sutures, neither inflated nor with even a vestige of a longitudinal partition.
    - Flowers in fascicles, on short branches arising in the axils of fallen leaves; leaves abruptly pinnate; banner usually enveloping the other petals. Subtribe 7. CORYNELLANAE.
    - Flowers in axillary racemes; leaves odd-pinnate, except in some species of Coursetia and occasionally in Olneya; banner mostly spreading. Subtribe 8. ROBINIANAE.
  - Pods more or less inflated or completely or partially 2-celled, by the intrusion of one or both sutures.
    - Style bearded along the upper margin; pods always 1-celled and inflated. Subtribe 9. COLUTEANAE.
    - Style glabrous, or bearded only around the stigma.
      - Anther-cells not confluent; pods not prickly; plant not glandular-dotted. Subtribe 10. ASTRAGALANAE.
      - Anther-cells confluent at the apex; pods in ours prickly; plant glandular-dotted. Subtribe 11. GLYCYRRHIZANAE.

## SUBTRIBE 1. CRACCANAE

Herbs or shrubs, with alternate odd-pinnate leaves, persistent stipules, but no stipels, the leaflets usually with parallel oblique lateral veins. The flowers are racemose. The calyx is campanulate 5-lobed, but the upper lobes are often more or less united. The corolla is truly papilionaceous, the petals are more or less clawed, the banner is broad and spreading. The stamens are monadelphous or diadelphous, inserted on a more or less developed campanulate disk. The style is glabrous throughout or more or less hairy around the stigma. The legume is elongate, flat, 2-valved, usually obliquely striate. The seeds are reniform or transversely oblong, *i.e.*, their longer axis parallel to the axis of the pod.

The subtribe contains, besides the following three genera, a few confined to the Old World. Cracca is cosmopolitan of warmer regions, Peteria is endemic American, and Galega is Eurasian, introduced in the New World.

Stipules not spinescent; lateral veins of the leaflets prominent.
  Upper filaments wholly united with the staminal sheath, forming a closed tube; banner in ours glabrous. 1. GALEGA.
  Upper filament free, at least at the base; banner strigose on the back. 2. CRACCA.
Stipules spinescent; upper filament free; lateral veins of the leaflets obsolete. 3. PETERIA.

### 1. **Galega** [Tourn.] L. Sp. Pl. 714. 1753

Perennial herbs. The leaves are odd-pinnate, with semi-sagittate stipules. The flowers are in axillary or terminal racemes with narrow bracts and no bracteoles. The calyx has 5 subequal lobes. The corolla is white or light blue; the banner is obovate-oblong, narrowed below into a very short claw; the wings have an oblong blade with a prominent basal auricle, and a longer claw, and are adherent to the keel at the middle; the keel-petals are obtuse, more or less arcuate, longer than the wings, and united nearly their whole length. The filaments are monodelphous, *i.e.*, all united into a sheath. The ovary is sessile, many-ovuled; the style glabrous; the stigma small, terminal. The pod is linear, terete, 2-valved, sometimes constricted between the seeds. Seeds are transversely oblong, without strophiole.

ILLUSTRATION: Plate XXXIII *A*. *Galega officinalis* L., × 2/3; 1. calyx, 2. banner, 3. wing, 4. keel-petal, 5. staminal sheath, 6. pistil, × 2; 7. pod, × 1; 8. cross section of pod, 9. seed, × 2.

In the Species Plantarum, the genus Galega contained only one species, *Galega officinalis* L., which therefore is the type.

Synonyms:

Callotropis G. Don. Gen. Syst. **2**: 228. 1832. Type: *C. tricolor* (Hook.) G. Don., based on *Galega tricolor* Hook., which is supposed to be the same as *G. officinalis* L.

Accorombona Endl. Gen. 1427. 1841. This was a substitute for Callotropis G. Don., not Calotropis R. Br. 1809. Hence the same type.

The genus consists of 4 or 5 species native of southern Europe and the Orient. Of these, *G. officinalis* is sometimes cultivated as a forage plant and in olden times was used in medicine. It has been found occasionally in the western states from Kansas to Utah, as an escape from cultivation or introduced incidentally among seeds. The genus is closely related to Cracca, differing mainly in the monadelphous stamens. The racemes are mostly axillary, and therefore the genus is, according to Bentham and Hooker, anomalous in their subtribe Tephrosieae, but, as will be shown, this abnormality is found even in species of Cracca.

### 2. **Cracca** L. Sp. Pl. 752. 1753

Herbs, often woody below, or shrubs. The leaves are odd-pinnate, the leaflets striate, with veins oblique to the midrib and parallel; the stipules are setaceous, or broader and striate. The flowers are racemose, the racemes are either terminal, with or without smaller racemes in the upper axils, or apparently opposite the leaves, or rarely axillary. The individual flowers are usually in clusters of 2–6 at each node of the peduncle. The calyx is campanulate, furnished with a more or less developed disk; the lobes are five, either subequal or the lowest one longer, the upper two usually more or less united. The petals are clawed; the blade of the banner is suborbicular, more or less sericeous without; the blades of the wings are oblong or obliquely obovate, slightly coherent with the keel, with a more or less developed basal auricle; the keel-petals are more strongly lunate with a larger basal auricle. The stamens are usually partly monadelphous, the uppermost filament at first free from the staminal sheath at the base, adnate to it at the middle, and often separating from it later. The ovary is sessile, many-ovuled, the styles inflexed or incurved, somewhat horny at the base, most commonly glabrous, the stigma terminal. The pod is sessile, flat, 2-valved, many-seeded.

Illustration: Plate XXXIII *B*. *Cracca virginiana* L., × 2/3; 1. calyx, 2. staminal sheath, 3. pistil, 4. banner, 5. wing, 6. keel-petal, 7. pod, × 1; 8. pod in cross-section, 9. seed, × 2.

The genus was first established in Linnaeus' Flora Zeylanica 1747. The first species described both in this book and in Species Plantarum is *C. villosa*, which must be regarded as the type.

Synonyms:

Brissonia Neck. Elem. **3**: 36. 1790. No type was given, but the genus was based on "some species of Galega L." [Necker's reference indicated the 14th edition of Linnaeus' Systema Vegetabilium.] The first botanist to assign species in the genus was Desvaux (Jour. Bot. **3**: 78. 1814), who proposed *B. trapesicarpa*, *B. stipularis*, and *B. coronillaefolia*, but none of these are found in Linnaeus' work named above. De Candolle (Prod. **2**: 249. 1825) adopted Brissonia as a section under Tephrosia. Of this section apparently *T. toxicaria* Pers. should be regarded as the type.

Reineria Moench, Meth. Suppl. 44. 1802. Type: *R. reflexa*.

Thephrosia Pers. Syn. Pl. **2**: 328. 1807. It was based on 39 species, without definite type. The first species is *T. filifolia*, but the type ought to be sought in the second and larger division with pinnate leaves.

Kiesera Reinw. Syll. Pl. Nov. **2**: 11. 1828. Type: *K. sericea* Reinw., which is supposed to be the same as *Tephrosia candida* DC.

Apodynomene E. Meyer, Conn. Pl. Afr. Aust. 111. 1835. Type: *E. grandiflora* (Pers.) E. Meyer, based on *Tephrosia grandiflora* Pers. This is the first and best known species.

Catacline Edgew. Jour. As. Soc. Beng. **16**: 1214. 1847. Type: *C. sericea* Edgew.

Macronyx Dalz. Hook. Kew Jour. **2**: 35. 1850. Type: *M. strigosus*, which is close to if not identical with *Tephrosia tenuis* Wall. Perhaps this should be excluded from the synonyms of Cracca.

Balboa Liebm. Vidensk. Meddel. 1853: 106. 1854. Type: *Balboa diversifolia* Liebm., the only species.

Seemannantha Alef. Bonplandia **10**: 264. 1862. This was a substitute for Macronyx, and hence based on the same type.

Cracca is a large genus, probably containing about 150 species, found in warmer regions of both hemispheres. In North America (including Central America and the West Indies), there are 72 species, of which 65 are native and 7 introduced.

Taubert divided the genus into 4 sections: Brissonia, Reineria, Pogonostigma, and Requienia. Of these the last two, which are not represented in America, should be removed as distinct genera, having 1-seeded fruits.

The principal character by which Taubert distinguished the first two sections was the relative width and length of the calyx lobes. Some species, as for instance *C. leucantha*, which has long and narrow calyx-lobes, really belong to Brissonia instead of Reineria. A better distinction is the inflorescence, which is monopodial in the former and sympodial in the latter. In the monopodial inflorescence the terminal raceme is best developed, but many of the species bear also secondary racemes in the upper axils. In the sympodial inflorescence the terminal raceme develops first, but in the uppermost leaf-axils a branch is produced which in its turn develops a terminal raceme; this is repeated several times, and the racemes therefore appear to be opposite the leaves. In a few species, as for instance *C. rhodantha*, *C. foliosa*, *C. vicioides*, and *C. Brandegei*, the racemes are mostly at the nodes, but neither opposite the leaves nor strictly axillary; they are inserted in the axils but obliquely, *i.e.*, not in the plane determined by the stem and the rachis of the leaves. The monopodial or sympodial character is not perfectly clear.

Several of the species are used as a fish-poison by the natives of the region where they grow, others for poisoning arrows in Southern Africa; still others furnish a blue dye, somewhat resembling indigo.

### 3. **Peteria** A. Gray. Pl. Wright **1**: 50. 1852

Perennial herbs, somewhat woody at the base. The leaves are odd-pinnate with spiny stipules. The flowers are usually in terminal racemes. The calyx is cylindro-campanulate, gibbous at the base above; 5-lobed with the upper two lobes united high up. The corolla is ochroleucous or nearly white, the banner long-clawed with an oblong-obovate blade; the wings have an obliquely oblong blade, slightly auricled at the base, and a slender claw; the blades of the keel-petals are obliquely obovate, obtuse, with a broad, rounded basal auricle. The stamens are diadelphous, with the upper filament wholly free. The ovary is short-stipitate or sessile, many-ovuled, the style with a horny base, inflexed, glabrous, except at the apex, where there is a ring of hairs. The pod is linear, straight, compressed, 2-valved, many-seeded, with thick sutures.

The genus was based on a single species, *P. scoparia* A. Gray, and consists of three species of southwestern United States and northern and central Mexico. In habit the species resemble some species of Astragalus and its segregates, but the racemes are not axillary but terminal, or when an axillary branch is developed become apparently opposite the leaves as in Cracca. The spinescent stipules constitute also a distinctive character. The genus is evidently related to Cracca, but the hair-tufts around the stigma and the less distinct veining of the leaflets obscure the relationship.

ILLUSTRATION: Plate XXXIII *C. Peteria scoparia* A. Gray, × 2/3; 1. calyx, × 2; 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, × 1; 7. pod of *P. glandulosa*, × 2/3; 8. cross section of the same, × 2; 9. seed, × 2.

### SUBTRIBE 2. MILLETTIANAE

Trees or woody vines with alternate odd-pinnate leaves and persistent stipules, usually also with stipels. The calyx is campanulate, 5-toothed, but the lobes are often minute, or the upper 2 and the lower 3 more or less united, forming an upper and a lower lip. The corolla has short-clawed petals, the banner being broad, spreading or reflexed. The stamens are monadelphous or diadelphous, the upper filament free at least at the base. The pod is flat, 2-valved, elongate, several-seeded. Seeds mostly reniform.

Besides the following genus which is represented by native species in the eastern United States and eastern Asia, the subtribe consists of four or five Asiatic and perhaps two African genera.

### 4. **Kraunhia** Raf. Med. Rep. N. Y. II, 5: 352. 1808

High-climbing woody vines with odd-pinnate leaves, small stipules and stipels. The flowers are in terminal racemes, with deciduous bracts. The calyx is more or less 2-lipped, the upper lip with 2 broad teeth united to near the apex, the lower with 3 longer teeth. The corolla is blue or purple, rarely white, the petals are subequal in length; the banner has a suborbicular blade, reflexed, and with 2 callosities or appendages, the claw is short; the blades of the wings are obliquely obovate, falcate with a large basal auricle on the upper edge and often a smaller one on the lower; the keel-petals are clawed, united at the apex, the blade is lunate with a sharp basal auricle. The stamens are diadelphous, the upper stamen is free or slightly adherent at the middle. The ovary is stipitate, many-ovuled, glabrous; the style inflexed, glabrous; the stigma small. The pod is elongate, flat, 2-valved. The seeds are reniform, without strophiole.

ILLUSTRATION: Plate XXXIII *D. Kraunhia frutescens* (L.) Greene, × 2/3; 1. calyx, 2. stamens, 3. pistil, 4. banner, 5. wings, 6. keel-petals, × 1; 7. fruit, 8. the same in cross section, × 2/3.

The genus was established on *Glycine frutescens* L. without a diagnosis.

Synonyms:

Diplonyx Raf. Fl. Ludov. 101. 1817. Type: *D. elegans* Raf., which is regarded as the same as *Kraunhia frutescens* (L.) Greene.

Thysanthus Ell. Jour. Acad. Phila. **1**: 371. 1818. Type: *T. frutescens* (L.) Ell., based on *Glycine frutescens* L.

Wisteria Nutt. Gen. **2**: 115. 1818. Type: *W. speciosa* Nutt., based on *Glycine frutescens* L. Sprengel (Syst. 3: 255. 1826) corrected the spelling of the name to Wistaria, as the genus had been dedicated to Dr. Wistar.

The genus consists of 5 or 6 species, of which two are native of eastern and southern United States. It is evidently very closely related to the large Asiatic genus Millettia, the species of which are mostly trees or shrubs; only a few of them are climbing.

### SUBTRIBE 3. BRONGNIARTIANAE

Trees or shrubs, with alternate odd-pinnate leaves, stipules, and sometimes stipels. The flowers are axillary or in terminal racemes or panicles. The calyx is more or less 2-lipped, the tube short, the upper 2 lobes united high up, the lower 3 lobes also somewhat united. The corolla has a broad banner. The stamens are monadelphous or diadelphous. The pod is usually elongate, flat, 2-valved, several-seeded. The seeds are erect, *i.e.*, the longer axis of the seed is at right angles to the axis of the pod, with a well developed strophiole.

The subtribe consists of the following two genera and two from Australia. It is distinguished by the well developed strophiole. Its relationship is probably with the Robinianae.

| | |
|---|---|
| Calyx 5-lobed, the upper 2 lobes united two thirds their length, the lower 3 usually free to near the base; stamens diadelphous. | 5. BRONGNIARTIA. |
| Calyx 2-lipped, the upper 2 and the lower 3 lobes united to the apex; stamens monadelphous. | 6. HARPALYCE. |

### 5. **Brongniartia** H.B.K. Nov. Gen. & Sp. **6**: 465. 1823

Shrubs or trees, with odd-pinnate leaves. Stipules are present, but often caducous, the leaflets entire-margined, sometimes with minute stipels. The flowers are normally axillary in small 1- -7-flowered clusters. In some species, however, the upper floral leaves are reduced to the two stipules, which resemble a pair of bracts, and the inflorescence becomes falsely racemose. The individual flowers are subtended by a pair of bractlets, sometimes foliaceous, sometimes reduced to a pair of hair-tufts. The upper two calyx-lobes are united high up, the lower only slightly at the base. The corolla is red, brown, or purple; the banner is broad, its blade orbicular or broadly obovate, short-clawed; the wings are obliquely oblanceolate or obovate, more or less falcate, with a short fleshy claw and a rounded auricle; the blades of the keel-petals are broadly lunate, with a fleshy claw, united from the middle to the tip. The stamens are diadelphous, the alternate ones shorter; the ovary is short-stipitate, the style incurved, glabrous, the stigma minute. The pod is short-stipitate, flat, elongate, 2-valved, usually several-seeded, slightly wing-margined on the upper suture, the valves leathery.

ILLUSTRATION: Plate XXXIV *E. Brongniartia Benthamiana* Hemsl., × 2/3; 1. calyx, 2. staminal sheath, 3. pistil, 4. banner, 5. wing, 6. keel-petals, × 1; 7. pod, × 2/3; 8. seed of *B. sericea* Schlecht., × 1.

The genus was established on two species, *B. mollis* and *B. podalyrioides*, of which the first may be regarded as the type.

Synonyms:

Peraltea H.B.K. Nov. Gen. & Sp. **6**: 469. 1823. Type: *P. lupinoides* H.B.K., now known as *Brongniartia lupinoides*.

Megastegia G. Don, Gen. Syst. **2**: 468. 1832. Type: *M. speciosa* G. Don, regarded as the same as *B. thermoides*.

The genus consists of 37 species, natives of Mexico and Central America, and a few species from South America. One species, *B. oligosperma* Baill., is somewhat abnormal in the genus on account of its hairy few-seeded pods.

### 6. **Harpalyce** DC. Mem. Leg. 496. 1825

Trees or shrubs, with alternate odd-pinnate leaves and small stipules. The leaflets are entire-margined, petioluled, sprinkled beneath with yellow or orange glands or gland-like scales. The flowers are racemes. The calyx is 2-lipped, with the upper 2 and the lower 3 lobes united to the tip. The banner is rounded or obovate, short-clawed, the wings are very irregular, strongly curved, obtuse, the keel-petals more or less falcate, united to above the middle but the tips free and obtuse. The stamens are monadelphous, but the sheath is split to the base; the anthers are alternately longer and shorter. The ovary is sessile, the style arcuate, glabrous, the stigma minute, terminal. The pod is 2-valved, several-seeded, leathery or woody.

ILLUSTRATION: Plate XXXIV *F. Harpalyce Loeseneriana* Taub., × 2/3; 1. calyx, 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, × 1; 7. pod, 8. cross section of the same, × 1; 9. banner of *H. cubensis* Griseb., 10. wing, 11. keel-petal, 12. seed, × 2/3.

The genus was based on an unpublished illustration in Mocino and Sesse's Flore de Mexique of *Astragalus carnosus*. In De Candolle's Prodromus the type is given as *H. formosa* DC., based on the same.

The genus consists of 14 species, *viz.*, 7 from Mexico, 1 from Guatemala, 3 from Cuba, and 3 from Brazil. One species, *H. mexicana*, is abnormal in that the valves of the pod are woody. As the flowers of this species are unknown, it may belong to some other genus. The rest can be divided into three natural groups: (1) Cuban species, in which the petals are fleshy, the keel much longer than the other petals, and the pod is small and narrow; (2) Mexican species (including the one from Guatemala), in which the petals are membranous, the keel is scarcely longer than the banner, and the pod large and broad; (3) Brazilian species, similar to the Mexican but the pod narrower and more or less divided internally by false cross-partitions of spongiose tissue.

## SUBTRIBE 4. BARBIERIANAE.

Shrubs, with alternate odd-pinnate leaves, narrow stipules and stipels. The flowers are in axillary and terminal racemes, each subtended by a pair of bractlets. The calyx is cylindric, 5-lobed, the lobes subequal. The corolla is not truly papilionaceous, the petals with long slender claws; the blade of the banner is oblanceolate, not spreading; the wings have elliptic blades, the keel-petals oblanceolate or oblong, obtuse blades, scarcely falcate, and united above the middle. The stamens are diadelphous, the sheath is straight; the ovary is sessile, the style nearly straight to near the apex, hairy along the upper side above; stigma minute. The pod is flat, straight, 2-valved, transversely septate within.

The subtribe consists of a single genus and a single species.

### 7. **Barbieria** DC. Mem. Leg. 241. 1825

The generic characters are included in the subtribal description.

Illustration: Plate XXXIV G. *Barbieria pinnata* (Pers.) Baill., × 2/3; 1. calyx, 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, 7. pod, × 1; 8. cross section of the same; 9. seed, × 2.

The genus was based on *Clitoria polyphylla* Poir. or *Galactia pinnata* Pers. Its distribution extends from Porto Rico to Cuba, southern Mexico, Bolivia, and Brazil.

## Subtribe 5. Sesbanianae

Trees, shrubs, or herbs with abruptly pinnate leaves and caducous stipules but no stipels. The flowers are borne in axillary racemes. The calyx is round-campanulate, fully as broad as high, with very short teeth. The banner has a broad reflexed blade and a short claw; the keel-petals are strongly arcuate, united at the middle, but the claws and tips are free. The stamens are diadelphous; the staminal sheath is dilated below and the upper filament knee-bent near the base. The pod is 2-valved but often indehiscent, stipitate and beaked, compressed, usually with cross-partitions between the seeds, but not disarticulate.

On account of the abruptly pinnate leaves this subtribe, as well as the Corynellanae, is somewhat abnormal in the tribe but could not be transferred to the tribe Vicieae, to which it does not show any relationship in other ways. The structure of the flower is practically the same as in many genera of the subtribe Robinianae; the pod, however, is, in most of the genera, but slightly compressed and internally divided by false transverse partitions.

The subtribe consists of the five following genera, which are thus distinguished.

Pods flattened, neither 4-winged nor 4-angled.
  Pods many-seeded, linear, with thick margins; calyx not conspicuously oblique.
    Pod not torulose.
      Flowers middle-sized or small; banner suborbicular; blades of the broad keel-petals with an auricle; seeds subcylindric-oblong. 8. Sesban.
      Flowers large; banner elliptic; blades of the rather narrow keel-petals without a basal auricle; seeds reniform-oblong. 9. Agati.
    Pod torulose; banner suborbicular, equaling the other petals; blades of the broad keel-petals without a basal auricle; seeds reniform-oblong. 10. Daubentoniopsis.

| | |
|---|---|
| Pods 2-seeded, with thin margins, lance-elliptic; seeds oblong-reniform enclosed in the inner membranous layer of the valves; calyx decidedly oblique. | 12. GLOTTIDIUM. |
| Pod 4-angled, often 4-winged, not torulose. | 11. DAUBENTONIA. |

### 8. **Sesban** Adans. Fam. 2: 327. 1763

Herbs or shrubs with abruptly pinnate leaves and numerous leaflets. The flowers are borne in axillary racemes, with deciduous bracts, and a pair of deciduous bractlets under the flowers. The corolla is yellow or the banner dotted, streaked, or tinged with purple. The banner has often one or two callosities at the base of the suborbicular reflexed blade; the wings are short-clawed, the blades obliquely oblanceolate or oblong, with a basal auricle; the keel-petals have long claws, the blades are strongly and broadly lunate with a lateral auricle on the upper side. The pod is slender, terete or slightly compressed, short-stipitate, many-seeded, with cross-partitions between the seeds, 2-valved. Seeds cylindro-oblong, subtruncate at the ends.

ILLUSTRATION: Plate XXXIV *H*. *Sesban Sesban* (L.) Rydb., × 1/2; 1. calyx, 2. stamens, 3. pistil, × 2; 4. banner, 5. wing, 6. keel-petal, × 1; 7. pod, × 1/2; 8. cross section of pod; 9. seed, × 2.

The genus was established on *Aeschynomene Sesban* L. Scopoli (Introd. 308. 1777) changed the name to Sesbania, the latter being better Latin form.

Synonyms:

Darwinia Raf. Fl. Ludov. 106. 1817. Type: *D. exaltata* Raf., which has been known under the name *Sesbania macrocarpa* Muhl.

Monaplectra Raf. Fl. Ludov. 106. 1817. This was proposed instead of *Darwinia* in case the latter happened to be preoccupied.

The genus consists of perhaps 20 species of the warmer regions of both hemispheres. It is represented in North America by 4 native and 3 introduced species.

### 9. **Agati** Adans. Fam. 2: 326. 1763

Small trees, having abruptly pinnate leaves, with many entire leaflets and deciduous stipules. The flowers are large, borne in small axillary racemes, and with two deciduous small bractlets subtending the calyx. The calyx is in structure the same as in Sesban. The petals are comparatively narrower, the banner is without callosities, its blade oval in outline, and retuse at the apex; the blades of the wing- and keel-petals are obliquely lanceolate-lunate, tapering at the base without any distinct auricle. The staminal sheath and the pistil resemble also those of Sesban, except that they are more gradually arcuate. The pod is the same as in that genus.

ILLUSTRATION: Plate XXXV *I*. *Agati grandiflora* (L.) Desv., × 1/2; 1. stamens, 2. pistil, 3. banner, 4. wing, 5. keel-petal, × 1/2; 6. pod, × 1/4; 7. cross section of the same, × 1; 8. seed in position in the pod, × 1.

The genus was based on *Robinia grandiflora* L.

Synonym:

Resupinaria Raf. Sylva Tell. 115. 1838. Type: *R. grandiflora* Raf. or *Robinia grandiflora* L.

The genus is represented by *A. grandiflora* (L.) Desv. and one or two species closely related to it and perhaps not specifically distinct from it, natives of southern Asia and northern Australia, and by *A. tomentosa* (H. & A.) Nutt. from the Hawaiian Islands.

### 10. **Daubentoniopsis** Rydb., gen. nov.

Shrubs, having abruptly pinnate leaves, many entire caducous stipules, caducous bracts and bractlets. The flowers are in axillary racemes. The calyx is rounded campanulate, broader than high, its lobes very short. The corolla is yellow, the banner suborbicular, retuse, reflexed, with a short claw, without callosities; the wings are short-clawed, with obliquely oblong blades, without a distinct basal auricle; the keel-petals are also clawed with a lunate, nearly semicircular blade. The stamens are diadelphous, the staminal sheath dilated at the base. The ovary is stipitate, glabrous, the style arcuate, glabrous; the stigma minute. The pod is coriaceous, stipitate, somewhat compressed, linear, several-seeded, decidedly constricted between the seeds and with spongy transverse partitions. The seeds are oblong-reniform, about twice as long as high.

ILLUSTRATION: Plate XXXV *J. Daubentoniopsis longifolia* (Cav.) Rydb., × 1/2; 1. calyx, × 2; 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, × 1; 7. pod, 8. cross section of the same, × 2/3.

The genus is based on *Aeschynomene longifolia* Cav. Ic. 4: 8. 1797. It is intermediate between Sesban and Daubentonia, having exactly the flowers and seeds of the latter, but the pod is neither 4-angled nor winged. It is constricted around the seeds, but the exocarp is spongy. In Sesban the pod is hardly constricted, the calyx-teeth are more evident, the banner usually has a callosity, and the seeds are different.

The type of the genus, **D. longifolia** (Cav.) Rydb., has a rather peculiar history. It was first described by Cavanilles (*loc. cit.*), and independently by Ortega[1] under the same name. Cavanilles' species was transferred to Piscidia by Willdenow.[2] De Candolle,[3] when he established the genus Daubentonia, included it in that genus, but from the short description given it is evident that he had in mind a yellow-flowered Daubentonia of the southern United States and northern Mexico. In his Prodromus[4] he repeated his error, and besides described on page 265 a *Sesbania longifolia* based on *Aeschynomene longifolia* Ortega. His description fits Cavanilles' plant. When Watson[5] merged Daubentonia into Sesbania, he, influenced by De Candolle's misconception, thought himself forced to give the yellow-flowered Daubentonia a new name, *S. Cavanillesii* S. Wats., as there was already a *S. longifolia* (Ort.) DC. Unfortunately, however, he based this name on *Aeschynomene longifolia* Cav., and technically he gave a new name

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[1] Ort. Dec. 70. 1797–1800.

[2] Sp. Pl. 3: 920. 1803.

[3] Mem. Leg. 286. 1823.

[4] Prodr. 2: 267. 1825.

[5] Bibl. Ind. 258. 1878.

to the species of Daubentoniopsis instead. Pollard,[6] following De Candolle's and Watson's interpretation of Cavanilles' plant, was of the opinion that this, being the first one described, should retain the specific name *longifolia*, and therefore proposed the name *S. mexicana* Poll. for Ortega's plant. As the two are the same, he merely added a new synonym to our species of Daubentoniopsis. The yellow-flowered Daubentonia is still nameless.

### 11. **Daubentonia** DC. Mem. Leg. 285. 1823

Shrubs or trees, having abruptly pinnate leaves, with many leaflets and deciduous stipules. Flower in axillary racemes, resembling closely those of Sesban, but the calyx-lobes are still smaller, the calyx-tube being merely undulate on the margins, slightly ciliate at the teeth. The banner is without callosities, and the wings and keel-petals are without basal auricles. The pod is more or less 4-angled, but somewhat compressed. The endocarp is membranous and constricted around the seeds, the exocarp more or less spongy, the sutures are thick, each produced into two sharp ridges or wings. The seeds are reniform.

ILLUSTRATION: Plate XXXV *K*. *Daubentonia punicea* (Cav.) DC., × 1/2; 1. calyx, × 2; 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, 7. pod, 8. cross section of the same, × 1.

The type of the genus is *D. punicea* (Cav.) DC., based on *Piscidia punicea* Cav.

The genus consists of about half a dozen species, of which 3 are natives of South America, one of the southern United States and northern Mexico, **Daubentonia Drummondii** Rydb. (*Daubentonia longifolia?* T. & G. Fl. N. Am. **1**: 293. 1838), and 1 or 2 of Mexico. I have based it on *D. longifolia?* T. & G., rather than on *D. longifolia* DC., in part as to description, for that name really belongs to *Daubentoniopsis longifolia*, as stated before. One of the South American species, *D. punicea*, has also been found introduced in Florida and Mississippi.

### 12. **Glottidium** Desv. Jour. Bot. **1**: 119. 1813

Annual herbs, having abruptly pinnate leaves, with many leaflets and deciduous stipules. The flowers are in axillary racemes or panicles. The calyx and corolla are almost exactly like those of Sesban, the banner with callosities, the wings and keel-petals of the same shape as those of that genus. The pod, however, is different, broad, stipitate, compressed, 2-valved, and 2-seeded, the valves at last separating in two layers, the endocarp very thin and papery, the exocarp firmer, somewhat inflated, but not bladdery as in Diphysa.

ILLUSTRATION: Plate XXXV *L*. *Glottidium vesicarium* (Jacq.) Harper, × 2/3; 1. calyx, 2. stamens, 3. pistil, 4. banner, 5. wing, 6. keel-petal, × 2; 7. pod, × 2/3; 8. pod in cross section, × 1; 9. seed, × 2/3.

The genus is monotypic and was based on *Aeschynomene platycarpa* Michx., which is the same as *Glottidium vesicarium* (Jacq.) Harper.

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[6] Bull. Torrey Bot. Club **24**: 154. 1897.

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