LOBELIA SPLENDENS HUMB. & BONPL. EX WILLD., A POORLY UNDESTOOD MEMBER OF THE LOBELIA CARDINALS COMPLEX

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In a beautifully illustrated book recently published by the University of California Press, Mason (1) uses the name *Lobelia splendens* Willd. for the Californian representative of the North American cardinal-flower, *Lobelia cardinalis* L. Mason's usage is consistent with that of Asa Gray, who more than 80 years ago published the treatment of Gamopetalae in the *Botany of California* (2), and is consistent with that of Jepson (3), but differs from that of both authors who have published general revisions of *Lobelia* within the last few years (4). Inasmuch as these authors also differ between themselves as to the proper delimitation of the taxon which is typified by *Lobelia cardinalis*, a further note on this taxon seems in order.

Section *Lobelia*, to which *L. cardinalis* belongs, is a group of about 20 species characterized by having markedly roughened, foveate-reticulate seeds. All the native species in eastern continental North America (exclusive of the sub-tropical region of Florida) are members of this section. Within the section differentiating characters, both qualitative and quantitative, are abundant; recognition of individual species is usually possible after casual inspection, without any necessity for measurement, critical comparison or subjective judgment. There is often much intra-specific variation (as in *L. spicata*, *L. siphilitica* and *L. puberula*), but the species themselves are ordinarily distinct from all their congeners in habit, appearance and a variety of morphological characters.

(1) Mason, Herbert L. A Flora of the Marshes of California. Univ. of Calif. Press, Berkeley & Los Angeles. [x], 878 pp., illus. 1957.

(2) Gray, A. Bot. Calif. 1:619. 1876, and in Synop. Fl. North Amer. 2 (1): 3. 1878.

(3) Jepson, Willis Linn. Man. Fl. Pl. Calif. 976. 1925.

(4) McVaugh, Rogers. Campanulaceae (Lobelioideae). North Amer. Flora 32A: 35-99, 1943. Wimmer, F. E. Campanulaceae-Lobelioideae II. Teil. Pflanzenreich IV. 276b (Heft 107): 408-695. 1953.

In the two recent revisions of this part of the genus **Lobelia** (5), there is good general agreement on delimitation of species, except in the treatment of the taxon which I call **L. cardinalis** (recognizing 2 subspecies of which one is further divided into 4 named varieties) and Wimmer calls **Grex Cardinales** (comprising the 4 species **L. cardinalis** L., **L. graminea** Lam., **L. splendens** Willd and **L. cordigera** Cav.).

The present paper is written to reiterate my conviction that there is no justification for the recognition of more than 1 species in the **Cardinales**. The several populations which comprise this group are very closely related, as shown by their morphology, their uniformity in chromosome number, the ease with which they may be hybridized and the partial fertility of the offspring, their similar habitats coincident flowering seasons over a wide range of ecological conditions and nearly 40° of latitude. Their status as a biological entity is completely misrepresented unless they are treated as a single wide-ranging species. Section **Lobelia** includes approximately 20 well —differentiated species—groups, of which the **Cardinales** comprise a single one; it seems illogical to divide the latter into several species on the basis of relatively trivial characters, the like of which have generally been used as indicators of infra-specific differences in Section **Lobelia**. One example of this may be cited:

Lobelia spicata Lam. is made up of 5 readily recognizable populations that are morphologically distinct and that are geographically segregated as well. These were discussed in detail in my early papers (6), and were accepted without change or comment by Fernald (7), by Gleason (8), and by Wimmer (9). In recent years they have been regarded by most authors as of infra-specific (i. e. in this case varietal) rank. The recognition of these varieties involves a number of morphological characters, including pubescence, shape and number of the cauline leaves, presence or absence of a distinctive basal rosette, shape of the hypanthium and fruit, anther-color, and auriculate or non-auriculate condition of the calyx-lobes.

After consideration of a taxonomic system including several species with **varieties** defined on the basis of combinations of characters like the above, it seems inconsistent to recognize as **species** similar populations, that are defined on the basis of even fewer and weaker

(5) McVaugh, op. cit. 66-82; Wimmer, op. cit. 410-447.

(6) In *Rhodora* 38: 305-322, 1936, and in *North Amer. Flora* 32A: 71-73. 1943.

(7) In *Gray's Manual*, ed. 8. 1356. 1950.

(8) *New Britt. & Brown Illus. Flora* 3. 322. 1952.

(9) *Pflanzenreich* IV. 276b (Heft 107): 438-442. 1953.

morphological characters. The "species" recognized by Wimmer in the **Cardinales**, for example, are based primarily upon width of cauline leaves, width of corolla-lobes, and presence or absence of pubescence.

In my early work on **Lobelia cardinalis** in eastern North America (10), I unfortunately failed to study the Mexican and Central American materials that resemble **L. cardinalis**. I thus failed to recognize the high degree of similarity which exists among all populations of these distinctive plants. I did point out, however, that the plants from Kansas and Texas westward belonged to a major taxon with narrower leaves and shorter flowers than the cardinal flower of eastern North America. Referring to the authority of Asa Gray (2), I used the name **Lobelia splendens** Willd. for these plants of western United States.

After study of the **Cardinales** throughout their whole range, I became convinced that but a single species was involved. In 1940 (11) and again in 1943 (12) and in 1951 (13), I recognized as **L. cardinalis** subsp. **cardinalis** the relatively uniform and wide-ranging population which is confined to eastern North America, west to Minnesota, Iowa, eastern Oklahoma and eastern Texas. I recognized at the same time a second major subspecies, subsp. **graminea** (Lam.) McVaugh, which represents the species in all its range in western North America, from western Missouri, Colorado and southern California, south throughout México and Central America. (It has since been collected in Colombia: Antioquia, 1 km. S. of Hoyo Rico, elev. 2600 m., 26 Sept. 1948. **F. A. Barkley 18A112**, herb. MICH). It was proposed also to subdivide subsp. **graminea**, recognizing 4 varieties based on characters of the pubescence, the inflorescence and the cauline leaves. At the present time there seems no reason to doubt the validity of any of these conclusions, except that at least one of the varieties [var. **multiflora** (Paxt.) McVaugh] appears to have been too inclusive as originally described, and ill-founded from the standpoint of nomenclature.

Fortunately there is abundant cytogenetical evidence to support the morphological study on which my earlier classification was based. Dr. Wray M. Bowden, of the Canadian Department of Agriculture at Ottawa, has grown many collections of **L. cardinalis** subsp. **cardinalis** and subsp. **graminea**, including material of var. **graminea**, var. **pseudosplendens** McVaugh and var. **phyllostachya** (Engelm.) McVaugh, as well as some additional taxa for which he has not yet published names.

(10) *Rhodora* 38: 259, 276-278. 1936.

(11) *Ann. Mo. Bot. Gard.* 27:347-349. 1940.

(12) *North Amer. Flora* 32A: 80-82. 1943.

(13) *Fl. Texas* (ed. C. E. Lindell) 3: 362-366. 1951.

Dr. Bowden is in complete agreement with my view that *L. cardinalis* includes two major subspecies (with perhaps two other subspecies as yet undescribed), and that subsp. *graminea* includes not only the varieties named above but almost certainly some additional geographical varieties or subvarieties. He has kindly permitted me to quote his opinions and anticipate to this extent the publication of the results of his work. He has made numerous artificial crosses, involving many of the known infraspecific taxa, and has grown many F^1 hybrids. All plants were diploid, $2n = 14$. The artificial F^1 hybrids were obtained by controlled hybridization; the crosses were easily made, and seed was abundantly set. Some of the F^1 plants were selfed; these were found to be partly fertile and some F^2 hybrids were grown. There are differences in chromosome structure among the different subspecies and varieties, as shown by univalents in some cells in MI stages of meiosis in the pollen mother cells of the F^1 hybrids. The following is from Dr. Bowden's letter of March 7, 1958:

"I have not made all the possible different crosses of all subspecies and varieties of *L. cardinalis* but I am sure from the crosses attempted that when plants of (different) subspecies or varieties occur in close proximity, they can cross since all attempts to make artificial crosses in the *L. cardinalis* complex always resulted in hybrid seed, the seed germinated, the plants were strong, (and) were [of those tested] at least partly fertile".

Because of the existence of several "puzzling" populations which are intermediate between other varieties or subspecies, it is likely that introgressive hybridization has occurred or is occurring in nature where two or more infraspecific taxa have grown together in the past or are growing together at present. Opportunities for such hybridization are probably greatest in the area from Kansas to Arkansas and Texas (where the ranges of subsp. *cardinalis* and var. *phyllostachya* are essentially contiguous), and in eastern and southern México (where var. *phyllostachya*, var. *multiflora* [sensu Mc Vaugh], var. *graminea* and possibly var. *pseudosplendens*, and also various anomalous and intermediate plants are found).

The varieties of subsp. *graminea* appear to be most clearly marked (perhaps because of greater distances between individual localities where the plants can grow) on the Pacific side of the North American continent, from Panamá to Arizona. In the southern part of this range the species is chiefly represented by var. *graminea*; farther north, especially from Jalisco and Durango northward, var. *pseudosplendens* predominates. In both these varieties the leaves are narrow (8-14 times as long as wide), but in var. *graminea* they tend to be entire or nearly so, whereas

in var. **pseudosplendens** they are usually markedly dentate. Var. **pseudosplendens** is characterized by the relatively few-flowered raceme (the flowers usually 20 or fewer) on a naked peduncle, the upper foliage leaves larger than the lowest bracts and well below them.

Californian material does not fit readily into any of the described varieties. It grows in the mountains of Los Angeles, San Bernardino and San Diego Counties, and apparently an isolated population or series of small populations has evolved in this region. An excellent illustration was published by Mason (1) in 1957. The plants are relatively narrow-leaved, but the leaves are broader (6-10 times as long as wide) than those of var. **pseudosplendens** which they otherwise resemble in having dentate margins. The upper leaves are reduced and bractiform, so that ordinarily the "peduncle" of var. **pseudosplendens** is not developed. The flowers are like those of the other varieties of subsp. **graminea** in having short filaments (18-24, or rarely 28 mm.). The anther-tube in Californian specimens is longer on the average than in other varieties; it is usually 4-5 mm. long. (almost as long as in subsp. **cardinalis**, as against 3.5-4.5 mm. in most of the varieties of subsp. **graminea**). A specimen from San Bernardino (**Parish 3808**) was referred by Wimmer (14) to **L. cardinalis** var. **cardinalis**, but this appears to be an error; on a specimen of this number, which I have examined (in U. S. Nat. Herb.), the filaments were 19-20 mm. long. only. Some other California collections are referred by Wimmer to **L. graminea** var. **pseudosplendens** viz. **Abrams 2937**, **Gander 2893**, **Dunn s. n.**

In distinguishing **L. cardinalis** from **L. graminea**, **L. splendens** and **L. cordigera** Wimmer does not use the character of filament-length consistently although he gives the appropriate measurements in some of his descriptions. For his **L. splendens** he gives the filament-length as 26-30 mm.; on one of the specimens cited however, the filaments are only 22-24 mm. long (**Pringle 2287**, at MICH, NY, US).

The name **L. splendens** Willd., was based originally on cultivated plants in the Berlin garden (15). The colored plate represents a narrow-leaved, smooth, large-flowered plant with broad corolla-lobes, quite unlike the majority of wild plants in southern México, the supposed source of the cultivated material. Except for two recent collections, I have seen but few wild plants that resemble **L. splendens**, and it is probable that this particular population is restricted in range. The following specimens resemble the original illustration of **L. splendens** in aspect and in flower-size; they are characterized by stout stems, linear or

(14) Op. cit. 413.

(15) Willd. Hort. Berol. pl. 86. 1809.

lanceolate and nearly entire leaves, few-flowered spikes and coarse, large flowers (filaments 26 - 30 mm. long; lobes of the lower lip of the corolla 8 - 10 mm. wide, as against 3.5 - 5 mm. wide in most varieties of *L. cardinalis*): **Estado de México**: east of Toluca. **Barkley et al. 623**, 10 August 1947 (MICH); **Morelos**: Lagunas de Zempoala, **Rowell 2035**, 29 July 1949 (MICH).

It appears that from the standpoint of nomenclature the name *Lobelia splendens* should be restricted to plants like those described above, which are known in nature from few localities, all in the general region of México City. It should not be used for plants from California or elsewhere in the United States, or from northern México. If the cardinal flowers from these localities are thought to be conspecific with *L. cardinalis* L., there are subspecific and varietal names available; if they are thought to represent species distinct from *L. cardinalis*, there are at least two names (*L. graminea* and *L. cordigera*) which are older than *L. splendens*, which apply to the Latin American complex of the *Cardinales*, and which can precisely typified.

It is in the area near México City, especially in the states of Michoacán, Morelos, México and Puebla, and in the Distrito Federal, that much additional field work is needed to aid in the clarification of the taxonomic status of *L. splendens* Willd., *L. fulgens* Willd., *L. cordigera* Cav., and the assemblage which I called, in my earlier papers, var. *multiflora* (Paxton) McVaugh. The last three names have been applied to almost any densely pubescent plant with subentire leaves 6 - 8 times as long as wide; it is now apparent that the mere presence or absence of pubescence does not furnish a reliable criterion, and the so-called var. *multiflora* probably includes anomalous elements which may belong to different varieties or subspecies. It is hoped that collectors will make an effort to secure mature seeds, as well as herbarium specimens, particularly from plants which appear to be unusually large-flowered, with narrow leaves and smooth stems, or from similarly large-flowered plants, with broadly lanceolate leaves and pubescent stems. Dr. Bowden has well along toward completion a revision of the entire complex of the *Cardinales*, and he informs me that he would be pleased at any time to receive additional material, and especially seed-samples for garden testing, of any of the Mexican populations. (16).

As pointed out recently in a study of *Prunus serotina* (17), the distribution of that species is similar in many respects to that of *Lobelia*

(16) Communications should be addressed to Dr. Wray M. Bowden, Botany and Plant Pathology Laboratory, Science Service, Department of Agriculture, Ottawa, Canada.

(17) McVaugh, Rogers. Suggested phylogeny of *Prunus serotina* and other wide ranging phylads in North America. *Brittonia* 7:320-322, and maps, pp. 327-328, 1952.

cardinalis. Each is represented in eastern North America by one relatively uniform subspecies, and in western North America by a variable complex of varieties. In both the **Lobelia** and the **Prunus** the area of greatest taxonomic complexity appears to be in the general region of México City, and divergence into distinct varieties appears to increase northward along the axes marked respectively by the Sierra Madre Oriental and the Sierra Madre Occidental. Similar patterns of distribution are well known in many genera represented both in southern México and in temperate North America (e. g., **Ostrya**, **Arbutus**, **Platanus**, **Tilia**, **Cephalanthus**), and investigation of the historical factors which have contributed to these patterns is greatly to be desired. In **Lobelia**, at least, taxonomic and cytogenetic studies which are in progress will clarify the status of one such widely distributed group of plants, and may ultimately be useful in working out the history and relationship of other groups which are more difficult to collect and more difficult to handle experimentally.