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MONOGRAPH OF THE NORTH AMERICAN SPECIES OF *CORYDALIS*¹

GERALD BRUCE OWNBEY²

INTRODUCTION

My attention was attracted to the genus *Corydalis* of the family Fumariaceae some years ago, since it seemed to offer many unsolved problems in the systematic interpretation of various species. The genus had received no special attention from any American botanist since the time of Engelmann and Gray, and the proposal of nearly forty new names for members of the genus in America by Fedde during the early years of the present century had made it imperative that their proper status be determined so that scientific literature no longer would be encumbered with superfluous nomenclatorial terms.

A great volume of herbarium material has been available, in the study of which I have attempted to make full use of classical methods. In addition, it was felt that field studies would help in the understanding of some of the more difficult species. With this in view a six-weeks field trip was made through the western United States during the summer of 1946.

I have attempted to view all species in the light of modern concepts of speciation. Population studies of one species have confirmed the presence of minor measurable differences between inbreeding colonies of this species, even those not widely separated geographically. I also have had opportunity to grow several species under greenhouse conditions and to test the stability of minor variants. Further work along these lines doubtless would do much in clearing up obscure problems not amenable to standard methods of the herbarium taxonomist.

¹An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

²Instructor in Botany, University of Minnesota, Minneapolis.

HISTORY OF THE GENUS

Linnaeus¹ included all of the species of fumariaceous plants known to him in the single polymorphous genus *Fumaria*. The subsequent subdivision of this heterogeneous group of plants was left to later authors who attempted to revive names of pre-Linnaean botanists in something resembling their original sense.

The nomenclatorial complications of the generic name *Corydalis* have been investigated by Sprague², from whose account the following discussion largely is abstracted. The name has been used in two distinct senses as follows:

(1) *Corydalis* [Knaut, Meth. Pl. 153. 1716; Dill. Cat. Pl. App. 129. t. 7. 1719]; Medik. Phil. Bot. 1:96. 1789. This is *Cisticapnos* Adans. Fam. Fl. 2:431. 1763 (*Cysticapnos* Gaertn. Fruct. Sem. Pl. 2:161. t. 115. 1791), and is based upon *Fumaria vesicaria* L. This monotypic genus sometimes is united with *Corydalis* Vent., but in the opinion of students of the family, such as Hutchinson and Fedde, it should be retained separately. As the fruit of *Cysticapnos* is inflated and bladder-like, it seems probable that sufficient grounds exist for segregating the species generically from *Corydalis*.

(2) *Corydalis* Vent. Choix de Pl. t. 19. 1803. [*Capnoides* Tourn. Inst. Rei Herb. 423. t. 237. 1719]; *Capnoides* Adans. Fam. Pl. 2:431. 1763. Ventenat treated only a single species, *Corydalis fungosa* (*Adlumia fungosa* Greene), which is now universally recognized as a separate genus. The generic name, however, must be credited to Ventenat, even though the single species is referable to *Adlumia*, since the author states in a footnote that his generic concept is founded upon that of Tournefort, who described and figured *Corydalis sempervirens* (as *Capnoides sempervirens*).

Because of the widespread acceptance of the name *Corydalis* in its modern sense, perhaps occasioned by its adoption by de Candolle in his monumental works^{3,4}, the International Botanical Congress of Vienna conserved it over *Capnoides* Adans., *Cisticapnos* Adans., *Neckeria* Scop., and *Pseudofumaria* Medik. The conservation of *Corydalis* has insured its permanent use, and has precluded the revival of any other generic name which otherwise might supersede it.

GENERAL MORPHOLOGY

The aerial parts of *Corydalis* are succulent, and annual or biennial in all of our species. The glaucous foliage and finely dissected leaves give a characteristic aspect to the plants.

In distinguishing sections and species, greatest importance is attached to the morphology of the outer petals, stigma, fruits, seeds, and underground parts. An account of the peculiarities of structure and the special terms used in referring to them is given, therefore, in the following discussion.

¹Linnaeus, Sp. Pl. 2:700. 1753.

²Sprague, in Kew Bull. Misc. Inf. 1928:351. 1928.

³DeCandolle, Reg. Veg. Syst. Nat. 2:113. 1821.

⁴DeCandolle, Prod. Syst. Nat. 1:126. 1824.

Root: The nature of the root is an important diagnostic character in delimiting sections. In annual, winter annual, and biennial species of Section EUCORYDALIS, an ordinary tap root is present. This often is quite succulent and may be somewhat lignified when the plant reaches maturity. The roots of the perennial species must also be classified as tap roots, although they become fleshy at a very early seedling stage. In *C. pauciflora* of Section PES-GALLINACEUS the mature root is tuberous and ordinarily bifurcate. In Section RAMOSO-SIBIRICAE, the seedlings develop a tuberous swelling the first year. This grows to large proportions during succeeding years and often is crushed and flattened by pressure of the soil.

Stem: A rhizome is present only in perennial species of Section RAMOSO-SIBIRICAE. This gives rise apically to the annual stems.

The hollow, annual stems are succulent in all of our species, although sometimes semi-ligneous at the base. They are monopodial in growth except in Section EUCORYDALIS where they predominately are sympodial. The nodes are somewhat abbreviated toward the base.

Leaves: In our species of Section RAMOSO-SIBIRICAE only a single leaf is produced annually until the plants reach flowering age. The number produced in Section PES-GALLINACEUS is unknown, but presumably is low. In all members of Section EUCORYDALIS a basal rosette of leaves is developed prior to the development of the flowering stems. Leaves are produced alternately, the later ones often being progressively reduced in size and intergrading imperceptibly into the floral bracts. The larger stem leaves are petiolate and pinnate except in *C. pauciflora* where they are simple and ternately divided. The primary segments are themselves once or twice pinnatifid or incised. The petioles are somewhat expanded at the base, especially those of the larger cauline leaves. A few sheath-like cataphylls sometimes are present at the base of the stem.

Inflorescence: The inflorescence is a terminal raceme or panicle, the flowers being crowded at first but becoming more distant during and after anthesis through elongation of the floral axis. The floral bracts offer very little in the way of diagnostic characters. For the most part they are successively smaller from the base to the apex of the floral axis. The uppermost are often extremely minute.

Flowers: *Corydalis* flowers are bilaterally symmetrical. They are dimerous, having two inconspicuous sepals, two laterally placed outer petals, one of which is spurred, and two inner, dorsi-ventrally placed petals opposite the sepals. There is some cohesion but no true fusion of the petal margins at the base. The stamens are arranged in two phalanges of three each, which are opposite the outer, lateral petals. Morphology of all the parts presumably is conditioned to some extent by compression in the bud. Floral structure is quite uniform throughout the genus.

The very much reduced, rudimentary sepals are scarious and fugacious, and function as protective organs only in the early bud stage. Although they are of little diagnostic value, they are described in detail for each species treated in this paper.

The presence of a single spurred petal and the polyspermous fruit are paramount characters in distinguishing the genus *Corydalis* from closely allied genera. The relative size and shape of the spur vary in different species. In measuring the length for this study the distance from the point of attachment of the pedicel to the tip of the spur is taken. The free end of the petal is carinate. This carina is referred to in the following descriptions as the *hood*. It is often provided with a medial exterior fold, the *crest*, and an expanded border of greater or lesser width, the *wing margin*.

The unspurred outer petal is similar to the spurred one with respect to the hood, crest and wing margin. When the flowers are fully developed, the petal sometimes is geniculate immediately posterior to the hood. In Section RAMOSOSIBIRICAE there is a distinct basal gibbosity which probably represents a rudimentary spur.

The two asymmetric inner petals are connate at their apices and enclose the anthers and stigma at anthesis. They consist of an outer broader portion, the *blade*, and a narrower basal portion, the *claw*. Medially, on the outer surface, there is a longitudinal fold which lies between the margins of the outer petals in the bud. In addition, on the exterior basal half of the blade adjacent to the spurred petal, there is another simple longitudinal fold or fleshy protuberance. Morphology of the inner petals ordinarily is not of diagnostic importance below the sectional level.

Each *stamen phalange* consists of three stamens whose filaments are united laterally. The anther of the central stamen is dithecal; those of the outer stamens are monothecal. The phalange opposite the spurred petal is provided with a nectiferous *stamen spur* which extends into the petal spur and is adnate to it for the greater portion of its length. No morphological characters of value in distinguishing species are to be found in the androecium.

Both the stigma and style are persistent. The style is slender, short, and not distinctive in character. The flattened stigma, however, often is quite characteristic. Stigmatic surfaces are located on papillary projections numbering from four to eight in our species. As the projections are somewhat delicate, an unopened flower or large bud should be selected for examination. In these, germinating pollen does not obscure details of structure as it does in older flowers. The nature of the stigma is of considerable diagnostic value, especially in defining sectional lines.

Teratological flowers of the type termed "peloric" have been reported from time to time. I myself have observed two instances of this phenomenon in which both outer petals were spurred.

Cleistogamy in *Corydalis* has been recognized for many years. In *C. micrantha* and *C. pseudomicrantha* the potentiality for cleistogamy is present at all times. In other species it is rare, non-existent, or unrecognized. The problem of self-fertility is well worth investigation. The flowers of all species studied show evidence of germination of the pollen which is clustered around the stigma. Under

such conditions it is difficult to determine just how much self-pollination actually is occurring. Opportunity for cross-pollination is not lacking as witnessed by the large number of insects, both as to individuals and species, that visit *Corydalis* having brightly colored flowers.

Fruit: The young fruit is enclosed by the stamen phalanges at anthesis, and is oriented so that the placentae are opposite the inner petals in the dorsiventral plane and the flattened stigma in the transverse plane. When mature, it is a few- to many-seeded, bicarpellate capsule varying in shape from narrowly linear to broadly elliptical, oblongoid or obovoid, and sometimes flattened at the base. Dehiscence is accomplished by separation of the two valvate portions from the two placentae. In Section RAMOSO-SIBIRICAE the valves roll up elastically from the base and the seeds are scattered to a considerable distance from the parent plant.

All American species of the genus fall into two well-defined groups with respect to disposition of the fruit on the pedicel. In Sections RAMOSO-SIBIRICAE and PES-GALLINACEUS the body of the fruit is geniculate at the base and is reflexed to a marked degree upon erect or spreading pedicels. In Section EUCORYDALIS the fruit is not geniculate and is not reflexed except by actual curvature of the pedicel.

The ovules are campylotropous. At a very early stage a comb-like or sheathing caruncle appears near the point of attachment of the funicle. At maturity the caruncle covers a greater or lesser portion of the seed. The testa is seen to be essentially smooth to variously reticulate or muricately decorated when viewed under magnification. The nature of these decorations, as well as gross size of the mature seed, is of importance in specific diagnosis.

A pathological condition in which the fruits become swollen, spongy and sterile is not uncommon in *C. Caseana* and *C. aurea*. Upon examination such abnormal fruits are found to contain an insect larva. The egg of the adult insect apparently is lodged in the young fruit at flowering time; the resultant larva passes through the early stages of its existence enclosed within the tissues of its host. Faulty interpretation of the peculiar fruit developed under these conditions has led to some confusion in terminology.

GENERIC RELATIONSHIPS

It is not within the scope of this paper to discuss the relative merits of the many genera of the family Fumariaceae. Hutchinson⁵ lists eighteen genera from Europe, Asia, Africa and North America, and Fedde⁶ proposes one additional genus from Asia. In North America only four genera are represented, namely, *Fumaria*, *Dicentra*, *Adlumia*, and *Corydalis*. All of our species of *Fumaria* are weeds introduced from Europe.

The genus *Corydalis*, the largest of the family, includes a heterogeneous aggregate of species all of which, however, have certain fundamental characters in common. The petals are free or essentially so, and the corolla is zygomorphic,

⁵Hutchinson, in Kew Bull. Misc. Inf. 1921:97. 1921.

⁶Fedde, in Engler & Prantl, Nat. Pflanzenf. ed. 2. 17b:121. 1936.

having a single spurred petal. These two characters distinguish the genus clearly from *Adlumia*, which has petals united below, both of the outer ones barely saccate at the base, and, furthermore, it is of climbing habit. The genus *Dicentra* has both outer petals equally spurred, but does not differ fundamentally in any other respect from *Corydalis*. The fruit of *Corydalis* is a 2- to many-seeded, dehiscent, bivalvate capsule, while *Fumaria* has an indehiscent, one-seeded fruit.

The distinctions between extra-American genera of the Fumariaceae and *Corydalis* are of like magnitude to those of the American genera. An important element in the family is its naturalness and the equal systematic value of the features characteristic of its included genera.

EVOLUTIONARY TENDENCIES AND INTERSPECIFIC RELATIONSHIPS

A discussion of evolutionary tendencies often is speculative. The initial assumption generally made is that distant or close genetic relationships are indicated

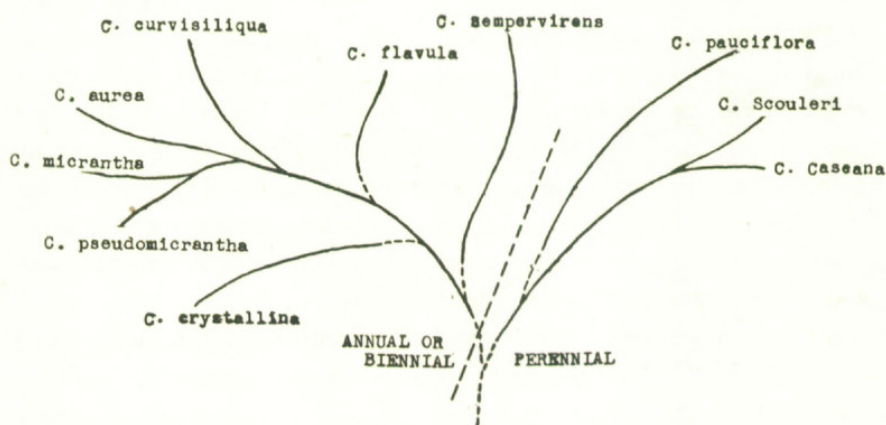


Fig. 1. Suggested interspecific relationships.

by greater or lesser morphological similarities. This assumption ordinarily is justifiable providing due consideration is given to such modifying factors as parallel evolution. Discussions of this nature also are of value in bringing into perspective the probable direction of evolution within the group, and serve to emphasize not only inter-relationships of species, but the characters which are undergoing basic change. This makes possible a prediction of the type of subsequent change to be expected.

Annual species usually are assumed to have arisen from perennial species by compression of the life cycle into a single year. Many genera have both perennial and annual species, *Corydalis* being such a genus. Presumably, one or more lines of perennial species have given rise to the annuals which now predominate in America.

Among perennial species of *Corydalis* are some with rhizomes and some with tuberous roots, one of which type may have given rise to the other at some time in the past. Also, among perennials are species with pinnate leaves and those with sim-

ple, ternately divided leaves. The upper stem leaves of the pinnate-leaved species are much reduced, and, strictly speaking, are simple. Historically, a species with simple leaves could then be derived from one with compound leaves by a fore-shortening of the axis or by a reduction of compound leaves to their terminal segments. It is not improbable that this has occurred in *Corydalis*.

Among both perennial and annual species are those with paniculate and those with racemose inflorescences. The racemose type could be derived from a paniculate type by reduction of branching.

In some annual species, such as *C. aurea*, both sympodial and monopodial growth is found. Racemes in both types are terminal. After flowering of the primary raceme in the sympodial type, growth in length is taken over by the uppermost axillary shoot. This in turn gives rise to a terminal raceme. The evolutionary significance of the sympode is not clear. I believe, however, that it should be looked upon as derived from the monopodial type. It may represent only an adaptation for continued growth provided conditions remain favorable.

CONCEPT OF SPECIES AND SUBSPECIES

I have attempted to portray the species as natural, biological units, the members of which are more closely related genetically to one another than to members of other species. Closeness of genetic relationship is manifested by relatively close morphological similarities. Comparative morphology, then, remains the most immediately usable criterion of genetic relationship. The individuals of each species are potentially interfertile, or at least their historical progenitors were interfertile. Further, each species occupies a "natural" distribution determined by factors inherent within it.

Great morphological variability in some species of *Corydalis* makes over-all statements of distinguishing characteristics of species and subspecies misleading if unqualified. There apparently is a corresponding amount of genetic diversity in some of these plastic or polymorphic species. *C. aurea*, for example, is relatively uniform throughout the northern part of its range. In southwestern United States it breaks up into innumerable forms or ecotypes. According to recent concepts, these may be looked upon as expressions of genetic differences due to isolation of small segments of the whole. Under such circumstances there is said to be a potential loss of heterozygosity and its accompanying morphological variability, together with potential evolution of the isolated segments along lines divergent from that of the species proper. This appears to be a satisfactory explanation of the condition in *C. aurea*, but experimental data to support this view are insufficient. Although colony-to-colony variation can be demonstrated statistically in *C. flavula*, this does not carry over into any recognizable regional pattern of variability. I hope to have opportunity to discuss this question more fully in a future study.

Another type of variability common to many plant species is most striking in *C. sempervirens* and *C. micrantha*. The conditions under which the particular

plant grows affect gross size and form to a marked degree. For example, plants subjected to abnormally dry conditions often are dwarfed; those growing in shade have fewer branches, more delicate-textured leaves and more slender stems. When plants of *C. micrantha* grow closely crowded together they are less branched and a higher percentage of normal flowers is developed.

The probability of interspecific hybridization in nature is limited to *C. aurea*, *C. micrantha* and *C. curvisiliqua*. These species seem to be closely related, and the possibility or even probability of hybridization among them must be considered. Evidence for this is at present inferential and is based upon plants of intermediate character collected in southern Missouri, Oklahoma, and Texas. Controlled crosses between these species are necessary to supply affirmative or negative evidence of potential hybridization in nature.

In adopting the category of subspecies, I have attempted to maintain its usage in the strictest sense. According to this usage, each subspecies has a discrete or nearly discrete distribution of its own within that of the species as a whole. One may have potential overlap in situations where the habitats favored by the subspecies themselves overlap or intergrade. In instances where two or more elements of the species have been isolated historically by some barrier subsequently removed, the elements may again intermingle along their zone of contact providing they are still interfertile.

The second attribute of a subspecies in *Corydalis* is minor but perceptible morphological differentiation. The subspecies are not always mutually exclusive on morphological grounds, but each has a norm of variability which differs from that of other subspecies. It sometimes becomes a matter of judgment as to whether to describe two closely related elements as species or subspecies. There is no hard-and-fast rule which will be universally applicable due to the fundamental nature of speciation.

CHROMOSOMAL COMPLEMENTS

The basic chromosome number in *Corydalis* is 8 in species, all European, so far reported, with a single exception having a probable basic number of 7. There is evidence of the occurrence of polyploidy in two species, but the data are too scanty to justify generalization.

| Species | Reported by | n | 2n |
|-------------------|-----------------------|---|-----|
| <i>C. bulbosa</i> | Maude ⁷ | — | 24 |
| <i>C. cava</i> | Tischler ⁸ | 8 | — |
| <i>C. lutea</i> | Kellet ⁹ | — | 56? |
| <i>C. pumila</i> | Nemec ¹⁰ | — | 16 |

⁷Maude, in New Phyt. 39:18. 1940.

⁸Tischler, in Biol. Centralbl. 48:343. 1928; Planta 8:696. 1939.

⁹Kellet, acc. to Darlington & Janaki, Chromos. Atlas Cult. Pl. p. 69. 1945.

¹⁰Nemec, acc. to Tischler, in Planta 8:695. 1929.

In two American species which I examined, the diploid number has been tentatively established as 16. I hope that a further report on American species will be possible when data from material now under study are compiled.

ALKALOIDAL PROPERTIES

The alkaloidal properties of a large number of fumariaceous and papaveraceous species have been reported by Manske¹¹. American species of *Corydalis* investigated have been *C. Caseana* (ssp. *Caseana*), *C. Scouleri*, *C. aurea* (ssp. *aurea*), *C. aurea* ssp. *occidentalis* (as *C. montana*), *C. micrantha* (ssp. *australis* ?), *C. crystallina* and *C. sempervirens*. It is of interest to taxonomists that each species was found to contain a particular set of alkaloids, some of which are common to other species but not in the same combinations.

Manske has drawn certain conclusions about interspecific relationships which are substantiated on morphological grounds. For example, from a chemical standpoint, he agrees that *C. micrantha* and *C. crystallina* are species distinct from *C. aurea*. However, he treats *C. aurea* ssp. *occidentalis* (*C. montana*) as a distinct species, a view that I am not able to support on the basis of comparative morphology. Manske's work has gone a long way in confirming for this group an assumption that perhaps is sometimes unwarranted, that is, that physiological differentiation may accompany morphological differentiation, even in lower systematic categories. It would be of great interest to the taxonomist to know whether changes in alkaloidal properties are present in widely separated geographical segments of a species in which little or no morphological differentiation is present.

ECONOMIC IMPORTANCE

In so far as is known, the species of *Corydalis* are not of great economic importance. According to collectors' notes, the plants are utilized by the Zuñi Indians of the Southwest, but to what extent or purpose is unknown to me. As a forage for livestock, they are of no importance both because of their relative scarcity and the apparent unpalatability of the foliage. On account of their high alkaloidal content, it is probable that they are distasteful to livestock as well as toxic if eaten in quantity.

Many species of *Corydalis* have been grown in gardens as much for their value as curiosities as for their intrinsic decorativeness. Of the American species, *C. Caseana* ssp. *Brandegei* and ssp. *Cusickii* are especially recommended for trial. Both are handsome plants in nature, but greatly restricted in habitat. *C. Scouleri*, *C. aurea*, and *C. sempervirens* have been under cultivation in European gardens in the past.

¹¹Series of papers in Can. Jour. Res. Ser. B, beginning with 7:258-264. 1932, and still continuing.

GEOGRAPHICAL DISTRIBUTION

The genus *Corydalis* is confined almost exclusively to the northern hemisphere. Its center of diversity is in Eurasia, there being several times the number of species there as are found in North America. In North America, the greatest number of species are concentrated in eastern Oklahoma and adjacent Texas, Arkansas, and Missouri, all species found there being placed in Section EUCORYDALIS. The closest affinities of each of the sections represented in North America are, however, with their Asiatic and European counterparts, and not with each other. Problems of the limits of distribution of the American species are discussed individually in the taxonomic section which follows.

ACKNOWLEDGMENTS

I am greatly indebted to the Missouri Botanical Garden and to its director, Dr. G. T. Moore, for the use of its library and herbarium facilities during the course of this study. I am especially grateful to Dr. J. M. Greenman and Dr. R. E. Woodson for their help and guidance.

I wish to extend my thanks to the curators of the several herbaria who have permitted me to study the material located at their institutions. However, in order to conserve space in this paper it has been necessary to omit detailed lists of specimens examined with the exception of the material from Mexico, Canada, Alaska, and that of *C. micrantha* ssp. *texensis* first described in this paper. The disposition of all numbered and many unnumbered collections viewed in the course of this study may be ascertained by reference to the Index to Exsiccatae. For the information of curators of herbaria and other interested persons, citation of authenticated specimens for each county listed may be found in the original manuscript which is deposited in the library of Washington University, St. Louis, Missouri. Following is a list of the herbaria, together with the abbreviations adopted. Material at each of these herbaria has been viewed and annotated by me.

CA—Herbarium, Colorado Agriculture and Mechanics College.

CAS—Herbarium, California Academy of Sciences.

CIUC—Clokey Herbarium, University of California.

D—Dudley Herbarium, Leland Stanford University.

DU—Herbarium, Duke University.

G—Gray Herbarium, Harvard University.

IH—Intermountain Herbarium, Utah State Agricultural College.

M—Herbarium, Missouri Botanical Garden.

NMA—Herbarium, New Mexico College of Agriculture and Mechanic Arts.

NY—Herbarium, New York Botanical Garden.

RM—Rocky Mountain Herbarium, University of Wyoming.

T—Herbarium, Tulane University.

UA—Herbarium, University of Arizona.

- UC—Herbarium, University of California.
 UM—Herbarium, University of Minnesota.
 UO—Herbarium, University of Oklahoma.
 US—United States National Herbarium.
 UT—Herbarium, University of Texas.
 WS—Herbarium, State College of Washington.

TAXONOMY

CORYDALIS Vent. Choix de Pl. *t.* 19. 1803, *nom. conserv.*, exclusive of *Corydalis fungosa* Vent.; not Medik.

[*Capnoides* Tourn. Inst. Rei Herb. 423, *t.* 237. 1719].

Fumaria L. Sp. Pl. 2:700. 1753, in part.

Capnoides Adans. Fam. Pl. 2:431. 1763, *nom. rejic.*

Neckeria Scop. Introd. Hist. 313. 1777, *nom. rejic.*

Pseudo-Fumaria Medik. Phil. Bot. 1:110. 1789, *nom. rejic.*

Pistolochia Bernh. Syst. Verz. Pfl. 57. 1800; not Raf.

Borckhausenia Gaertn. ex Mey. & Scherb. Oekon.-Tech. Fl. Wett. 3:4. 1801.

Odoptera Raf. Cat. 15. 1824.

Capnites Dumort. Fl. Belg. 117. 1827.

Bulbocapnos Bernh. in Linnaea 8:469. 1833.

Sophorocapnos Turcz. in Bull. Soc. Nat. Mosc. 21¹:570. 1848.

Cryptoceras Schott & Kotschy, in Oester. Bot. Wochenbl. 4:121. 1854.

Corydallis Aschers. Fl. Prov. Brand. 2:9. 1864.

Capnodes Ktze. Rev. Gen. 1:13. 1891.

Annual, biennial or perennial herbs from a tap root, tuberous root or rhizome; stems monopodial or sympodial; leaves simple or pinnate, the pinnae deeply once or twice divided and incised; inflorescence a panicle or raceme, terminal, bracteate; flowers bilaterally symmetrical; sepals 2, scarious, often fugacious; petals 4, free or somewhat coherent at the base, in two whorls of two petals each; outer petals dissimilar, one spurred, the other sometimes gibbous at the base, both more or less distinctly keeled or hooded at the apex; inner petals similar, connate at the apices, clawed; stamens in two groups or phalanges opposite the outer petals, each phalange with three anthers, the outer two of which are monothecal, the central dithecal; phalange opposite the spurred petal having a distinct glandular spur which is adherent to the inner surface of the petal spur except at the tip; stigma persistent, flattened, sometimes 2-lobed, with 4–8 papillary stigmatic surfaces; style distinct, slender; fruit a bicarpellate, many-seeded capsule, with two sterile valves and two persistent placentae; seeds having a distinct chalazal appendage or caruncle, smooth or variously decorated under magnification.

Standard Species: *C. SEMPERVIRENS* (L.) Pers. Syn. Pl. 2:269. 1807.

KEY TO THE SECTIONS

- A. Perennial from a rhizome or tuberous root; leaf blades pinnate or simple; flowers never yellow; fruits oblongoid to obovoid, reflexed upon erect or spreading, straight pedicels; stigma approximately rectangular or triangular, as long as broad or longer.
- B. Rank-growing, hydrophilous species of western United States; rhizome and roots large and fleshy; leaf blades pinnate, the pinnae

- once or twice pinnatifid or incised; flowers pink or white; stigma rectangular, or if triangular, narrowest at the apex.....Section I. RAMOSO-SIBIRICAE (p. 198)
- BB. Low-growing species of the far north; roots small, tuberous, usually bifurcate; leaf blades simple, once ternately divided, the segments incised; flowers blue or purplish-blue; stigma triangular, broadest at the apexSection II. PES-GALLINACEUS (p. 207)
- AA. Annual or biennial, with a somewhat succulent root; leaf blades pinnate, the pinnae once or twice pinnatifid or incised; flowers yellow (except in sp. 4); fruits narrowly to broadly linear, never reflexed upon the straight or curved pedicels; stigma approximately rectangular, broader than long (except in sp. 4).....Section III. EUCORYDALIS (p. 209)

SECTION 1. *Ramoso-sibiricae* (Fedde) G. B. Ownbey, stat. nov.

Ramoso-sibiricae Fedde, in Engler & Prantl, Nat. Pflanzenf. ed. 2. 17b:131. 1936, as subsection.

KEY TO THE SPECIES AND SUBSPECIES

- A. Stem leaves about 3; primary axis of inflorescence with about 25 flowers; flowers pink, the inner petals not tipped with deep red or purple; outer petals having no wing margin, the hood generally having a very high crest; stigma approximately triangular, narrowest at the apex, about as broad as long; fruit obovoid; seeds about 3.5 mm. in diameter, distinctly papillose under magnification; coastal Washington, Oregon, and Vancouver Island.....1. *C. Scouleri*
- AA. Stem leaves 3-5; primary axis of inflorescence often with 50 or more flowers; flowers pink to white, the inner petals always tipped with deep red or purple; outer petals usually having a well-developed wing margin, the hood with a low or obsolescent crest; stigma approximately rectangular, longer than broad; fruit oblongoid, elliptical, rarely obovoid; seeds about 2.5 mm. in diameter, obscurely papillose under magnification.
- B. Plants about 10 dm. tall; wing margin of the outer petals lacking or narrow, the unspurred outer petal acute; California.....2. *C. Caseana*
ssp. *Caseana*
- BB. Plants 8-20 dm. tall (except ssp. 2b); wing margin of the outer petals moderately to very highly developed, the unspurred outer petal not acute.
- C. Outer petals rounded, sometimes mucronulate, the wing margin scarcely folded back upon the hood.
- D. Plants mostly 10-15 dm. tall; flowers pink or white; outer petals mucronulate; Colorado.....2a. *C. Caseana*
ssp. *Brandegei*
- DD. Plants mostly 4-10 dm. tall; flowers white; outer petals occasionally barely retuse, not mucronulate; Utah.....2b. *C. Caseana*
ssp. *brachycarpa*
- CC. Outer petals emarginate, the wing margin folded back upon the hood.
- D. Inflorescence not profusely branched; spurred petal 18-24 mm. long; wing margin very highly developed, not erose; northeastern Oregon and southern Idaho.....2c. *C. Caseana*
ssp. *Cusickii*
- DD. Inflorescence profusely branched; spurred petal 16-20 mm. long; wing margin moderately developed, minutely erose; northern Idaho.....2d. *C. Caseana*
ssp. *hastata*

As here understood, this section includes only two species, *C. Scouleri* of coastal Oregon, Washington, and Vancouver Island, and *C. Caseana* of widespread but sporadic occurrence in many mountainous districts of western United States.

Under *C. Caseana* are included several variants which hitherto have been regarded as distinct species. These variants are essentially identical with respect to coloration of the flowers and detailed morphology of the inner petals, stigmas, fruits, and seeds. They differ appreciably in what are better considered as minor characters, such as the development of a wing margin on the outer petals, length of spur, and length of pedicel. The leaves and gross size of the plants vary to some extent among the different elements of the species, but the taxonomic value of these must be discounted as about the same type and degree of variability are found in other species of the genus.

Corydalis Caseana is an excellent example of the type of morphological divergence commonly met with when component parts of a species are isolated geographically. The subspecies might be thought of as incipient species whose modified genetic make-up and consequent morphological divergence have not yet reached the species level. In another sense they might be thought of as remnants of a species which through isolation have lost a large portion of the genetic variability present in the ancient stock.

The members of this section have well-defined habitat requirements, any deviation from which is sufficient to prevent survival. The plants grow in or near a continuous source of fresh, running water, in springs, along small creeks, and in the case of ssp. *Brandegei* also in wet, open, subalpine forests. All require considerable sunlight for best development, but at the same time will tolerate some shade. Plants growing in the sun tend to have smaller, more firmly textured leaves. *C. Scouleri* grows at elevations of sea level to about 2500 feet. The subspecies of *C. Caseana* grow at elevations of 3000–11,000 feet.

The time required for these plants to reach flowering size is not known. At one locality I have seen seedlings of at least three size classes. These classes very likely correspond to age intervals of one year, yet the largest of the seedlings was still relatively small. It therefore seems probable that these plants do not attain flowering size until they are four years or more old.

1. *C. SCOULERI* Hook. Fl. Bor. Am. 1:36. t. 14. 1829.

Corydalis macrophylla Nutt. apud Torr. & Gray, Fl. N. Am. 1:69. 1838; Torr. & Gray, l. c. 665. 1840, as syn.

Capnodes Scouleri Ktze. Rev. Gen. 1:15. 1891.

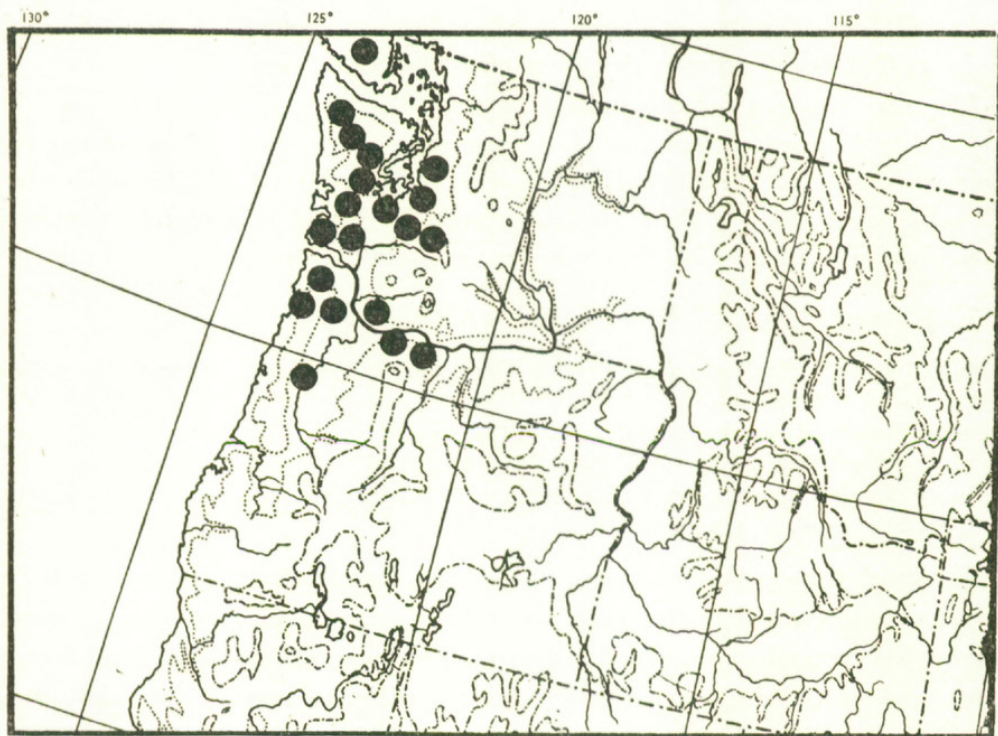
Corydalis Allenii Fedde, Rep. Spec. Nov. 10:478. 1912.

Capnoides Scouleri Thorner ex Fedde, in Engl. & Prantl, Nat. Pflanzenf. ed. 2. 17b:133. 1936, nom. nud. in synon.

Perennial from a rhizome; stems 1 or more, usually 5–10 dm. tall, branched above; stem leaves widely divergent, about 3, very long-petiolate; blades pinnately, more or less ternately, compound, 1 dm. or more long and broad, the primary segments once or twice pinnatifid or incised, the ultimate segments variable, sometimes broadly elliptical or less commonly ovate or obovate with rounded apices, or sometimes narrowly elliptical with acute apices, but more often intermediate, 1–8

cm. long, 0.5–4.0 cm. broad, minutely apiculate; inflorescence not strongly monopodial, consisting of 1 or more simple racemes or sparingly branched panicles arising from the axils of the stem leaves, each raceme usually with fewer than 25 flowers; bracts obscure, the lowermost narrowly elliptical, the upper much reduced, linear; pedicels erect, 2–5 mm. long; sepals ovate or broadly lanceolate, lacinate or toothed, 1–2 mm. long, deciduous at anthesis; flowers light to deep pink, the inner petals not tipped with purple; spurred petal usually somewhat arcuate, 20–25 mm. long, the lanceolate spur 14–20 mm. long, the regular crest moderately to very highly developed, extending to and beyond the acute tip of the hood, wing margin absent; uns spurred outer petal 12–15 mm. long, naviculate, the crest similar to that of the spurred petal; inner petals usually 9–11 mm. long, the blade much broader at the apex, the slender claw equalling the blade in length; stamen spur one-half to two-thirds the length of the petal spur, bent or hooked at the apex; stigma roughly triangular, the width at the lower lobes about the same as the length along the medial line; style slender, about 3 mm. long; fruit obovoid, 10–15 mm. long, 4–5 mm. broad; seeds black, about 3.5 mm. in diameter, conspicuously papillose under magnification.

This species is limited in distribution. It is found in wet, cool habitats of northwestern Oregon, northward to Vancouver Island. Morphologically, it is most easily distinguished from *C. Caseana* by its generally highly developed crest and absence of a wing margin on the outer petals. The obovoid fruits most typical of



Map 1. Distribution of *Corydalis Scouleri* Hook.

this species are rarely approached in *C. Caseana*, and its approximately triangular stigma may be contrasted with the nearly rectangular stigma found in that species. Finally, the seeds of *C. Scouleri* are considerably larger and more distinctly papillose.

Within the species there is considerable morphological variability, especially with respect to the leaves. The very small, narrowly elliptical ultimate leaf segments found on some specimens are in part the basis for Fedde's proposed segregate, *C. Allenii*, which I cannot maintain on valid grounds. *C. Scouleri* also is variable with regards to its flowers, particularly in length of spur, amount of curvature of the spurred petal, development of the crest, and gross size. When considered against the background of the species as a whole these variants lose their systematic significance. As possible examples of population variability potentialities of the species from locality to locality they are of considerable interest.

Moist, shady woods, especially along water courses; Vancouver Island, western Washington and northwestern Oregon at elevations of sea-level to about 3500 feet. Flowers about April 15 to June 15; fruits about May 15 to July 30.

BRITISH COLUMBIA: Vancouver Island.

WASHINGTON: Clallam, Clark, Grays Harbor, Jefferson, King, Mason, Pacific, Pierce, Thurston, and Wahkiakum counties.

OREGON: Benton, Clackamas, Clatsop, Columbia, Hood River, Marion, Multnomah, Tillamook, and Washington counties.

2. *C. CASEANA* Gray ssp. *Caseana* G. B. Ownbey, stat. nov.

Corydalis Caseana Gray, in Proc. Am. Acad. 10:69. 1874.

Corydalis Bidwelliae Watson, Bot. Calif. 2:429. 1880.

Capnodes Bidwellianum Greene, Fl. Fran. 280. 1891.

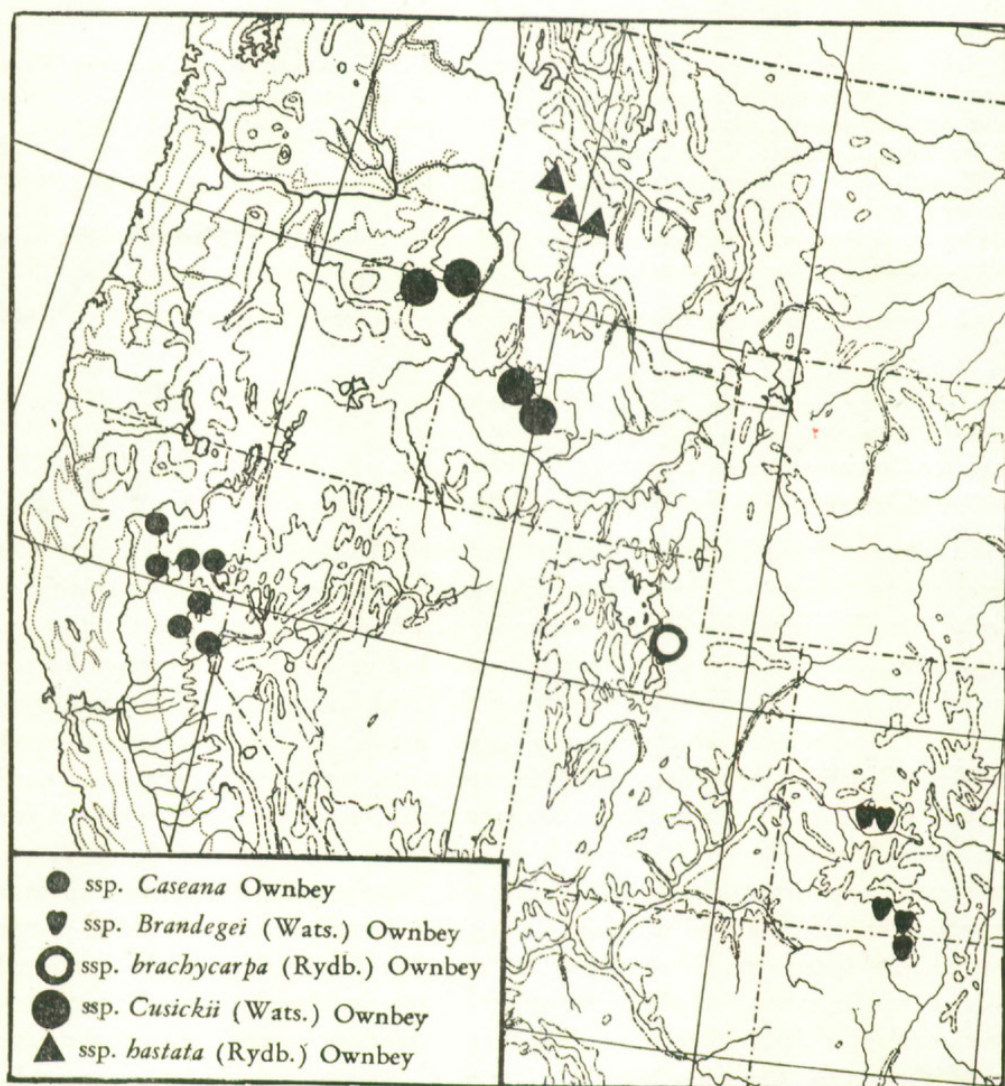
Capnodes Caseanum Greene, l. c. 1891.

Capnodes Caseanum Ktze. Rev. Gen. 1:14. 1891.

Glaucous perennial; stems 1-several, generally 10 dm. or less in height; stem leaves about 5, pinnate, the primary segments again once or twice pinnatifid or deeply incised; ultimate segments narrowly to broadly elliptical, mostly 1-2 cm. long, apiculate; inflorescence paniculate, consisting of a strong numerous-flowered central axis and 1 to several shorter, fewer-flowered lateral axes, these often again branched at the base; bracts inconspicuous, usually narrowly elliptical, rarely broader in outline, the lowermost about 10 mm. long, greatly reduced upward; pedicels semi-erect, 3-5 mm. long; sepals variable, sometimes with a broad base and a very long-attenuated central lobe, sometimes orbicular and denticulate at the margin, sometimes otherwise, 2-4 mm. long, rarely persisting through anthesis; flowers light pink or probably also white, the inner petal tips reddish-purple; spurred petal often curved, usually 16-22 mm. long, rarely longer, the spur gradually to rapidly tapered to the blunt apex, 12-16 mm. long, the hood crested, the crest regular or denticulate, rarely obsolete, extending to and beyond the acute tip of the petals, the wing margin, if present, narrow, regular or more or less denticulate and not folded back toward the hood; unspurred outer petal 10-12 mm. long, the crest and margin similar to that of the spurred petal; inner petals

usually 9–10 mm. long, the claw 3–5 mm. long; stamen spur one-half to three-fourths the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong, 10–15 mm. long, 3–4 mm. broad; seeds dark brown to black, minutely papillose under magnification, about 2.5 mm. in diameter.

Morphologically, the subspecies is best distinguished by its narrow or obsolete wing margin, its generally narrower, curved spurred petal, and acute apices of the outer petals. It is probably most closely similar to ssp. *Brandegei* from which it differs appreciably in the smaller gross size of the plants, smaller flowers, and narrower petal margins. The variant named *C. Bidwelliae* by Watson is of no



Map 2. Distribution of *Corydalis Caseana* Gray.

systematic importance. Leaflet size, petal margin, crest and slenderness of the spur upon which Watson's proposed species was based vary to some extent even at a single locality.

This plant has been collected as far south in California as Truckee, by Sonne, but there are no recent collections from this area.

Very moist, often shady situations, in springs and on gravel bars, in and along streams; southeastern Shasta County southward and eastward to Placer County, California, at elevations of about 4000–6000 feet. Flowers from about June 1 to July 30; fruits from about July 1 to September 1.

CALIFORNIA: Butte, Lassen, Placer, Plumas, Sierra, and Tehama counties.

2a. *C. CASEANA* Gray ssp. **Brandegei** (Wats.) G. B. Ownbey, stat. nov.

Corydalis Brandegei Watson, Bot. Calif. 2:430. 1880.

Capnoides Brandegei Heller, Cat. N. Am. Pl. 55. 1898.

Glaucous perennial; stems 1–several, 5–15, mostly 10–15, dm. or more in height; stem leaves about 5, the lowermost sometimes 10 dm. long, pinnate, the pinnae once or twice pinnatifid or deeply incised, the ultimate segments mostly elliptical, 1–5 cm. or more long, apiculate; inflorescence paniculate, consisting of a central numerous-flowered axis and often 1–several fewer-flowered secondary axes, these sometimes again branched; bracts inconspicuous, narrowly elliptical to linear, much reduced and minute upward; pedicels semi-erect, about 5 mm. in length, up to 10 mm. in fruit; sepals 2–3 mm. long, ovate or orbicular, the margin irregularly toothed; flowers light pink to white, the inner petals tipped with deep red or purple, inverted, the spur often nearly upright along the raceme; spurred petal 18–25 mm. long, the spur 12–16 mm. long, the hood crested, the crest low and regular, extending to and beyond the rounded apex of the petal to form a short beak, the wing margin broad, scarcely folded back toward the hood; unspurred outer petal about 12 mm. long, the crest and wing margin similar to that of the spurred petal; inner petals 10–12 mm. long, the claw 4–5 mm. long; stamen spur about two-thirds the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong, 15–18 mm. long, about 5 mm. broad; seeds dark brown to black, about 2.5 mm. in diameter, minutely papillose under magnification.

This subspecies is distinguished most easily on the basis of the wing margin, which is broad, regular, not retuse at the apex, and not appreciably folded back upon the hood as in ssp. *Cusickii* and ssp. *bastata*. It sometimes appears so when the flowers are distorted in pressing. The manner in which the low, regular crest extends beyond the rounded apex is characteristic. Occasionally the spur is nearly erect and the fruits, when mature, reflexed nearly to the pedicels. This situation is found especially in plants from the southern portion of the range.

Subspecies *Brandegei* is very abundant in Colorado from the summit of Wolf Creek Pass, Mineral County, for approximately 4 miles down the west side, at elevations of about 10,000–10,800 feet. Only a few plants are present on the

east side of the pass. At this site the flowers are uniformly pinkish-lavender in color. At similar elevations in Kebler Pass, Gunnison County, the plant also is abundant, especially on the west slope for at least two miles from the summit. The plants are essentially identical to those at Wolf Creek Pass except with respect to flower color. Here there is a preponderance of very light, nearly white-flowered individuals.

Very moist, subalpine situations, especially along water courses, at elevations of about 8,000–11,000 feet; Gunnison and Delta counties, Colorado, southward to northern Rio Arriba County, New Mexico. Flowers from about June 10 to August 10; fruits from about July 10 to September 10.

COLORADO: Archuleta, Conejos, Delta, Gunnison, Hinsdale, and Mineral counties.

NEW MEXICO: Rio Arriba County.

2b. *C. CASEANA* Gray ssp. ***brachycarpa*** (Rydb.) G. B. Ownbey, stat. nov.

Capnoides brachycarpum Rydb., in Bull. Torr. Bot. Club 34:426. 1907.

Corydalis brachycarpa Fedde, Rep. Spec. Nov. 10:315. 1912.

Glaucous perennial; stems 1–6, 4–10 dm. tall; leaves 3–5, the lower ones long-petiolate, pinnate, the pinnae once or twice pinnatifid or incised; ultimate leaf segments elliptical, acute at both ends, usually 1–3 cm. long and 0.4–1.0 cm. broad, minutely apiculate; inflorescence paniculate, consisting of a stout central axis and often one or more secondary axes; bracts linear, the lower ones about 15 mm. long, much reduced above; pedicels stout, spreading to semi-erect, about 5 mm. long at flowering time, up to 10 mm. or more long at fruiting time; sepals ovate or broadly lanceolate, more or less undulate or toothed at the margin, 3–5 mm. long, sometimes persisting through anthesis; flowers white, the inner petals tipped with deep red or purple; spurred petal 18–22 mm. long, the spur straight, gradually narrowed to the blunt apex, 9–12 mm. long, the wing margin broad, undulate, stiff, not appreciably folded back toward the hood, rounded at the apex, occasionally barely retuse, the crest obsolescent or lacking; unspurred outer petal 12–14 mm. long, the margin and crest similar to that of the spurred petal; inner petals 9–11 mm. long, the claw about 4 mm. long; stamen spur one-half to two-thirds as long as the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong in outline, about 12 mm. long and 4 mm. broad; mature seeds not seen.

Subspecies *brachycarpa* is a well-marked unit. It is best distinguished morphologically on the basis of the broad, spreading wing margin of the outer petals which are commonly neither acute-tipped nor emarginate, but rounded, at the apex. The broad margin is very well developed even in the bud. The plant possibly is closest to ssp. *Cusickii*, but in addition to the above-mentioned differences, it is only about one-half as large. The leaves are very similar to those of ssp. *Cusickii* as found in Oregon.

The name *brachycarpa* is something of a misnomer if it was intended to call attention to a fruit difference between this and other members of the complex.

The normal fruits, although perhaps smaller than those ordinarily found in other subspecies, are in no way significantly different. It is probable that the name was applied because of a misinterpretation of the swollen fruits very commonly found on living plants. All such fruits examined were found to contain an insect larva, the adult counterpart of which has not been identified. The stimulation of growth of pathogenic tissue results in a globose, spongy, abnormal, sterile fruit. A similar situation is not uncommon in *C. aurea*.

This subspecies is of very limited distribution, and it is possible that the adult population numbers no more than a few hundred individuals.

On gravel bars along stream courses at elevations of about 8500–10,000 feet; Wasatch Mountains, Salt Lake and adjacent Utah counties, Utah. Flowers from about July 1 to July 30; fruits from about July 30 to August 30.

UTAH: Salt Lake and Utah counties.

2c. *C. CASEANA* Gray ssp. **Cusickii** (Wats.) G. B. Ownbey, stat. nov.

Corydalis Cusickii Watson, Bot. Calif. 2:430. 1880.

Capnoides Cusickii Heller, Cat. N. Am. Pl. 55. 1898.

Corydalis Hendersonii Fedde, Rep. Spec. Nov. 12:278. 1913; not Hemsl.

Corydalis idahoensis Fedde, l. c. 16:195. 1919.

Glaucous or green perennial; stems 1–several, 8–15 dm. tall; leaves 4–6, pinnate, the pinnae once or twice pinnatifid or deeply incised; ultimate leaf segments usually narrowly, sometimes broadly, elliptical, apiculate, 1–5 cm. long, 0.5–1.5 cm. broad; inflorescence paniculate, consisting of a stout central axis bearing numerous flowers and 1–several shorter, fewer-flowered secondary axes; lowermost bracts very narrowly to broadly elliptical or obovate, often 15 mm. long, much reduced and usually linear above; pedicels spreading, 5–10 mm. long at flowering time, often up to 15 mm. long at fruiting time; sepals ovate to lunate, often toothed or lacinate, 2–4 mm. long; flowers white or tinged with pink, the inner petals tipped with deep red or purple, the apices of the outer petals widely divergent; spurred petal 18–24 mm. long, the spur generally straight, 10–14 mm. long and not rapidly tapering to the blunt apex, the crest, when present, low and inconspicuous, the wing margin extremely broad, deeply notched at the apex and folded back upon the hood; unspurred outer petal 12–15 mm. long, the margin similar to that of the spurred petal; inner petals 9–11 mm. long, the slender claw about 4 mm. long; stamen spur straight, one-half to three-fourths the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style 3–4 mm. long; fruit oblong-elliptical, 10–15 mm. long, 4–5 mm. broad; seeds dark brown, minutely papillose under magnification, about 2.5 mm. in diameter.

The highest development of the wing margins of the outer petals found anywhere within the species is present in ssp. *Cusickii*. This and the long pedicels are its most distinctive features. The wing margin and emarginate apex is emulated on a much lesser scale by ssp. *bastata*. Both ssp. *brachycarpa* and ssp. *Brandegei* have broad margins, but they never are greatly emarginate at the apex and the

margins are stiffer and never appreciably folded back upon the hood when the flowers are fresh.

This plant was described by Watson from material collected by Cusick in the Wallowa and Blue mountains of northeastern Oregon. It still is collected occasionally in the Wallowa Mts. and is present in some abundance above Cornucopia. It has been collected a few miles above Sumpter in the Blue Mts. and if it is at all abundant in this area it is at this point or further south. In Idaho, a variant with broader bracts, generally broader leaflets, and less-branched inflorescence is common in some localities. The Idaho form was described as *C. Hendersonii* by Fedde. It is found along the tributaries of the South, Middle and North Forks of the Boise River and the South Fork of the Payette River at known elevations of 5000–7500 feet. It does not often occur along the larger streams. On a hillside about 6 miles northeast of Rocky Bar, Elmore County, there is a pure stand covering approximately one-half acre. The plant here reaches its maximum development.

Growing in and along springs and small streams at elevations of about 5000–7500 feet; mountains of southwestern Idaho and northeastern Oregon. Flowers from about June 15 to July 30; fruits from about July 1 to August 15.

IDAHO: Boise, Camas, Elmore, and Valley counties.

OREGON: Baker and Union counties.

2d. *C. CASEANA* Gray ssp. ***hastata*** (Rydb.) G. B. Ownbey, stat. nov.

Capnoides hastatum Rydb., in Bull. Torr. Bot. Club 34:426. 1907.

Corydalis hastata Fedde, Rep. Spec. Nov. 10:315. 1912.

Corydalis Cusickii var. *hastata* Fedde, l. c. 12:279. 1913.

Glaucous or green perennial; stems 1–several, 10–18 dm. tall; main stem leaves 3–5, the lower ones widely divergent from the stem, the blade deltoid, pinnate, the pinnae once or twice pinnatifid or deeply incised; ultimate leaf segments broadly elliptical, ovate- or obovate-elliptical, rounded or acute at the ends, usually 1.5–4 cm. long and 0.5–1.5 cm. broad, minutely apiculate, of very thin, tissue-like texture when dry; inflorescence paniculate, delicately and profusely branched, consisting of a main axis and several more or less branched secondary axes; bracts often foliose, ovate to obovate, somewhat reduced above; pedicels about 5 (5–10) mm. long, semi-erect or spreading; sepals about 2 mm. long, usually with an elongate, lanceolate medial lobe and two basal auricles which are often somewhat toothed at the margins; flowers pale pink to white, the inner petals tipped with deep red or purple; spurred petal 16–20 mm. long, the spur 10–12 mm. long, straight or incurved, gradually narrowed toward the broad, blunt apex, the wing margin moderately well developed, reflexed toward the hood, commonly erose, retuse at the apex, the low crest extending over the apex of the hood into a short beak; unspurred outer petal 10–12 mm. long, the margin and crest similar to that of the spurred petal; inner petals 7–9 mm. long, the stout claw about one-third the total length; stamen spur two-thirds to three-fourths as long as the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style 2–3

mm. long; fruit oblong, 12–16 mm. long, about 4 mm. broad; mature seeds dark brown, minutely papillose under magnification, about 2.5 mm. in diameter.

Although characterized by numerous morphological differences of greater or lesser value, this plant must be included with *C. Caseana* in the broad sense. It is best distinguished morphologically on the basis of the broadly spreading deltoid leaf blades, the broadly elliptical ultimate leaf divisions, and the profusely branched inflorescence. In floral characters it most closely resembles ssp. *Cusickii*, but differs from it in having considerably smaller flowers with shorter inner petals and outer petals with a much narrower, usually erose wing margin which, as in that subspecies, is reflexed upon the hood and usually is emarginate at the apex. Only in ssp. *Caseana* is the wing margin narrower. The sepals are, indeed, as noted by Rydberg in his original diagnosis, somewhat characteristic. Sepals in *Corydalis* are, however, a very much reduced organ, and there is everywhere considerable variability in outline. I believe that the sepals of ssp. *bastata* cannot justifiably be given much weight as a distinguishing feature.

This subspecies is of limited and as yet not definitely circumscribed distribution. It is found in Idaho from southwestern Shoshone County, southward and eastward to northern Idaho County, probably only at medium elevations. It is especially abundant along Orogrande Creek, Clearwater County. It has been reported from the upper reaches of the Selway River (Moose Creek Trail), but its presence there should be confirmed.

Very wet situations, in and along streams at elevations of about 3000–4000 feet; mountains of northern Idaho. Flowers from about June 15 to July 30; fruits from about July 15 to August 30.

IDAHO: Clearwater, Idaho, and Shoshone counties.

SECTION II. PES-GALLINACEUS

Sect. PES-GALLINACEUS Irmisch, in Abh. Nat. Ges. Halle 6:273. 1862.

CORYDALIS §. II. *Capnites* DC. Reg. Veg. Syst. Nat. 2:115. 1821.

Pistolochia Bernh. Syst. Verz. Pfl. 57. 1800.

Bulbocapnos Bernh. in Linnaea 8:469. 1833.

KEY TO THE SPECIES

A single representative in North America..... 3. *C. pauciflora*

3. *C. PAUCIFLORA* (Steph.) Pers. Syn. Pl. 2:269. 1807; Cham. & Schlecht. in Linnaea 1:560. 1826, not Edgew.

Fumaria pauciflora Steph. ex Willd. Sp. Pl. 3²:861. 1803.

Corydalis pauciflora γ *parviflora* Regel, in Bull. Soc. Mosc. 34³:136. 1861.

Capnodes pauciflorum Ktze. Rev. Gen. 1:14. 1891.

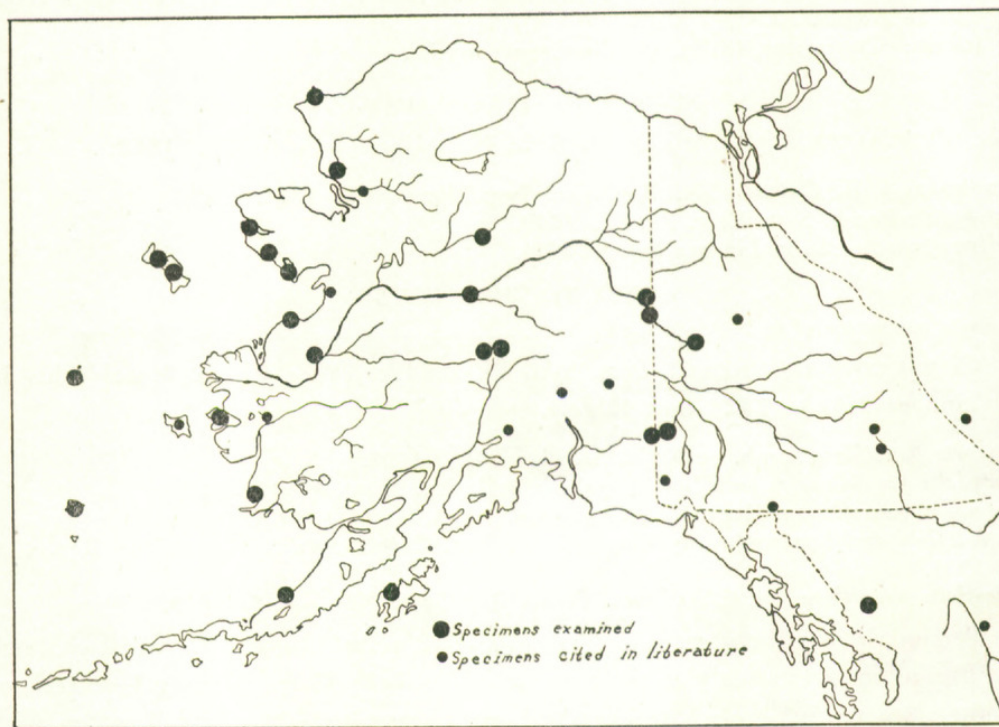
Capnoides pauciflorum Cov. in Brooks et al. Rec. Cape Nome & Norton Bay Reg. 170. 1901.

Corydalis pauciflora var. *Chamissonis* Fedde, Rep. Spec. Nov. 16:48. 1919.

Perennial; root deep-set, tuberous, usually bifurcate, having a central channel, the fibrous rootlets mostly at the base, accessory buds at the summit 1–several, or lacking; stems usually 1–3, unbranched, erect, mostly 8–20 cm. tall, often with 1–2 basal cataphylls; basal leaves none; stem leaves 2–5, long-petioled, simple, the

blades ternately divided, the segments again incised into 2-4 (usually 3) lobes, the ultimate lobes elliptical; peduncles stout, terminal, with 3-5 inverted flowers crowded at the summit; bracts ovate to obovate, 4-10 mm. long, 3-5 mm. broad, the lowermost larger; pedicels stout, erect, 4-10 mm. long at flowering time, up to 20 mm. long at fruiting time; sepals scarious, fugacious, 1-2 mm. long and broad, variously toothed; flowers blue, often tinged with purple; spurred petal 17-20 mm. long, the hood short and inconspicuous, the low, regular crest extending to or nearly to the obtuse apex of the petal, the wing margin narrow, the spur 7-10 mm. long, abruptly incurved near the blunt apex; spurless outer petal 10-12 mm. long, nearly as broad basally as apically, the apex 1-2 mm. longer than that of the other petals, the crest similar to that of the spurred petal, the margin reflexed; clawed inner petals 8-10 mm. long, the slender claw occupying one-half or more of the total length, the blade obovate; stamen spur clavate, two-thirds to three-fourths the length of the petal spur; stigma triangular, broadest at the 4-lobed apex; fruits reflexed, about 12 mm. long and 5 mm. broad, elliptical to obovate; seeds turgid, black, shiny, essentially smooth under magnification.

This distinctive species is well known to students of boreal floras. It is the only Asiatic species of *Corydalis* whose distribution extends across the Bering Straits into America. It is beyond the scope of this paper to discuss names proposed for variant forms of the species found in Asia. An excellent discussion of the application of the name to the American plant is to be found in Hultén's recent work (*Flora of Alaska and Yukon* 5:810. 1945).



Map 3. Distribution of *Corydalis pauciflora* (Steph.) Pers.

In tundra; islands of the Bering Sea and Straits eastward throughout Alaska to the Yukon and northern British Columbia at elevations of sea level to about 3500 feet; also widely distributed in Asia. Flowers from about June 1 to July 15; fruits from about July 1 to August 1.

ALASKA: Ft. St. Michaels, Norton Sound, 1865-66, *Bannister* (G, US); Nome, July, 1890, *Blaisdell* 67 (UC); Seal Islands, 1875, *Bryant* (US); Anvik, near the Mission, Lower Yukon River, June 11, 1924, *Chapman* 1 (NY); Mission premises, Anvik, without date, *Chapman* 28 (G); near Chinik, Seward Peninsula, July 3, 1900, *Collier* (US); St. Paul I., Bering Sea, July 9, 1899, *Coville & Kearney* 1810 (US); Port Clarence, July 12, 1899, *Coville & Kearney* 1966 (US); Hall I., Bering Sea, July 14, 1899, *Coville & Kearney* 2033 (G, US); McKinley Park Sta., Mt. McKinley Nat. Park, June 4, 1932, *Dixon* 17 (UC); roadside, Igloo Creek, same locality, June 13, 1932, *Dixon* 25 (UC); White River Valley, near the boundary, 1909, *Eaton* (US); St. Matthew I., July 8-13, 1916, *Hanna* (US); on hillside, Goodnews Bay, July 14, 1919, *Harrington* 57 (US); St. Paul I., June 30-Aug. 20, 1910, *Heath* (D); Nome, 1914, *Hill* 65 (US); wet brook banks, Karluk, June 14, 1901, *Horne* (NY); St. Paul I., Aug. 1, 1897, *Kincaid* (UC); St. Paul I., without date, *MacIntyre* (G); St. Paul I., July, 1892, *Macoun* (NY); St. Paul I., July, 1891, *Macoun* (M, G, US); St. Paul I., June 29, 1914, *Macoun* (NY, US); Cape Lisburne, Aug. 13, 1931, *Mason* (M, UC, NY, G); Iviktook Lagoon, St. Lawrence I., July 10, 1931, *Mason* (UC); Old Man Creek, a branch of the Koyukuk, 4 mi. above camp, near Caribou Mt., July 6, 1901, *Mendenhall* (US); between Yukon River, Nation River, and International Boundary, 1930, *Mertie* 60 (US); damp moss in small gulch, open land near Teklanika River, Mt. McKinley Nat. Park, 3600 ft. alt., June 24, 1928, *Mexia* 2040 (UC); Golovin Bay, 1881, *Muir* 168 (G); moist thicket near headquarters, Mt. McKinley Nat. Park, May 31, 1939, *Nelson & Nelson* W-2206 (RM); Nelson I., July 6, 1921, *Palmer* 194 (US); St. Paul I., June 10, 1890, *Palmer* 178 (US); near Karluk, Kodiak I., June 1, 1897, *Rutter* (D); same locality, May 23, 1897, *Rutter* 92 (D); same locality, June 13, 1903, *Rutter* 179 (US); same locality, June 14, 1903, *Rutter* 206 (M, US); Mt. McKinley Nat. Park, June 13-22, 1937, *Scamman* 620 (G); Camp Retreat, June 28, 1886, *Stoney* (US); Anvil Mt., vicinity of Nome, June 29, 1918, *Thornton* 319 (US); damp hillside near creek, Tanana, June 14, 1914, *Thousen* 6 (DU); St. Paul I., July 9, 1899, *Trelease & Saunders* 3872 (M); Hall I., July 4, 1899, *Trelease & Saunders* 3873 (M); St. Matthew I., July 15, 1899, *Trelease & Saunders* 3874 (M); St. Paul I., July 28, 1895, *True & Prentiss* 12 (NY, G, US); Noatak, July, 1929, *Wagner* (US); vicinity of Port Clarence, July 16, 1901, *Walpole* 1457 (US); same locality, July 18, 1901, *Walpole* 1467 (US); St. Paul I., July, Aug., 1879, *White* (G).

BRITISH COLUMBIA: Mountains near head Iskut River, Cassiar Dist., July 30, 1910, *Preble & Mixter* 619 (US).

YUKON: Across Bonanza Creek, Dawson, June 19, 1914, *Eastwood* 307 (G, US); 24-mile house, Dawson, June 25, 1914, *Eastwood* 380 (CIUC, G, US).

SECTION III. EUCORYDALIS

Sect. EUCORYDALIS Prantl, in Engler & Prantl, Nat. Pflanzenf. 3²:144. 1889.

Corydalis §. III. *Capnoides* DC. Reg. Veg. Syst. Nat. 2:122. 1821.

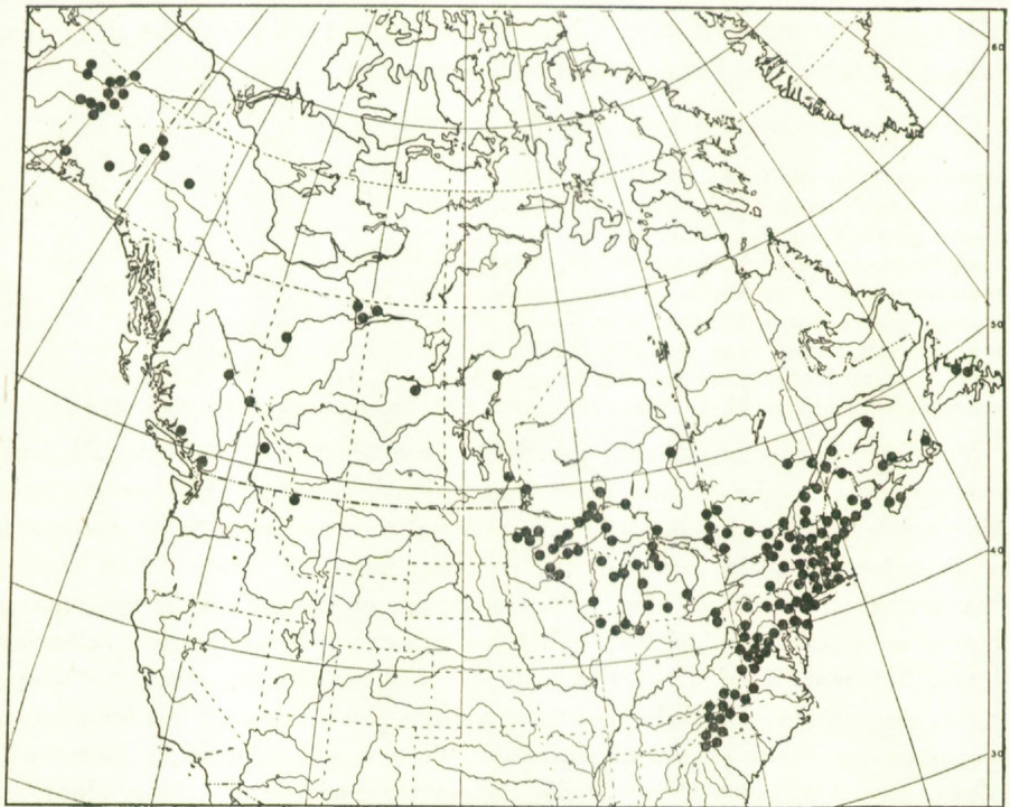
KEY TO THE SPECIES AND SUBSPECIES

- A. Flowers pink, the petals tipped with yellow, the hood not crested, the claw of the inner petals much longer than the blade; stigma not distinctly 2-lobed, with 4 papillary stigmatic surfaces; fruits erect, very slender, usually 30-35 mm. long; seeds about 1 mm. in diameter; Georgia to Newfoundland, British Columbia, and Alaska..... 4. *C. sempervirens*
- AA. Flowers pale to bright yellow throughout, the claw of the inner petals equalling or shorter than the blade; stigma 2-lobed, each lobe having 3 papillary stigmatic surfaces; seeds 1.5-2.0 mm. in diameter.

- B. Spurred petal 7-9 mm. long, the hood having a high, undulate or toothed crest, the spur incurved, about 2 mm. long; fruits broadly linear, usually straight, pendent on very long pedicels; central to eastern United States..... 5. *C. flavula*
- BB. Spurred petal 10-22 mm. long (in normal flowers), the spur not appreciably incurved, usually 4-8 mm. long; fruits erect, on relatively short pedicels (except in sp. 9).
- C. Spurred petal 16-22 mm. long, the hood with a very high crest, the wing margin very broad; fruits densely beset with transparent, clavate pustules; southwestern Missouri to central Texas.. 6. *C. crystallina*
- CC. Spurred petal 10-18 mm. long, the wing margin moderately broad to narrow; fruits essentially glabrous, although sometimes obscurely granulose along the sutures.
- D. Plants often bearing cleistogamous flowers; spurred petal of normal flowers 10-15 mm. long, the hood with a low, regular, undulate or obsolescent crest; seeds about 1.5 mm. in diameter, nearly smooth under magnification.
- E. Normal-flowered racemes not greatly exceeding the leaves, often short; spur usually somewhat globose at the tip; fruits often stout, commonly 10-15 mm. long; central United States..... 7. *C. micrantha*
ssp. *micrantha*
- EE. Normal-flowered racemes often greatly exceeding the leaves, elongated; spur not globose at the tip; fruits slender, 15-30 mm. long.
- F. Stems usually weak and not strongly striate when dry; foliage green to glaucous; fruits 15-20 mm. long; south-central to southern United States..... 7a. *C. micrantha*
ssp. *australis*
- FF. Stems usually stout and strongly striate when dry; foliage glaucous; fruits 25-30 mm. long; coastal south Texas..... 7b. *C. micrantha*
ssp. *texensis*
- DD. Plants seldom bearing cleistogamous flowers (except in sp. 10); spurred petal mostly 14-18 mm. long; seeds about 2 mm. in diameter, essentially smooth to variously decorated under magnification.
- E. Seeds distinctly muricate or muriculate under magnification; central Texas to southern Kansas.
- F. Hood crestless or with a moderately well-developed crest; fruits 26-34 mm. long, usually abruptly acute; seeds distinctly muricate under magnification; central and western Texas..... 8. *C. curvisiliqua*
ssp. *curvisiliqua*
- FF. Hood with a well-developed crest; fruits 20-25 mm. long, gradually tapered; seeds muriculate under magnification; north Texas to southern Kansas..... 8a. *C. curvisiliqua*
ssp. *grandibracteata*
- EE. Seeds never muricate though sometimes muriculate at the margin under magnification.
- F. Racemes usually surpassed by the leaves; hood sometimes crested; fruits spreading or pendent, usually 18-24 mm. long; seeds with no ring margin; northern United States to Alaska and southward in the Rocky Mountains to Mexico..... 9. *C. aurea* ssp. *aurea*
- FF. Racemes usually surpassing the leaves (except in sp. 10); hood usually not crested; fruits erect, often incurved; seeds usually having a ring margin.

local variants, however, have been observed. Plants collected by Bartlett at Medford, Mass., have exceptionally stout, incurved fruits, and a collection made by Ehlers at Prentis Bay, Michigan, has unusually small flowers. It is doubtful if either of these variants is of nomenclatorial consequence.

In shallow, often dry soil, rock ledges, crevices, and talus, and on burned or otherwise disturbed areas, at elevations of about 500–5000 feet; northeastern Georgia to Maine and Newfoundland, thence westward to Montana and British Columbia and northwestward to Alaska. Flowers throughout the summer months from about May 15 to September 15; fruits from about June 1 to September 30.



Map 4. Distribution of *Corydalis sempervirens* (L.) Pers.

GEORGIA: Rabun County.

SOUTH CAROLINA: Pickens County.

NORTH CAROLINA: Alexander, Buncombe, Burke, Caldwell, Forsythe, Haywood, Henderson, Jackson, Macon, Mitchell, Transylvania, Watauga, and Wilkes counties.

TENNESSEE: Carter County.

KENTUCKY: Bell and Harland counties.

VIRGINIA: Augusta, Bedford, Carroll, Giles, Lee, Madison, Loudoun, Page, Pulaski, Rappahannock, Rockingham, Shenandoah, and Smyth counties; Shenandoah National Park.

WEST VIRGINIA: Grant, Mineral, Monroe, Pocahontas, Preston, Raleigh, and Webster counties.

MARYLAND: Allegany, Frederick, and Garrett counties.

PENNSYLVANIA: Adams, Bedford, Bucks, Elk, Fayette, Indiana, Lancaster, Luzerne, Lycoming, Monroe, Montgomery, Northampton, Perry, Philadelphia, Union, Westmoreland, and York counties.

NEW JERSEY: Bergen, Essex, Hunterdon, Ocean, Passaic, Sussex, and Warren counties.

NEW YORK: Albany, Dutchess, Essex, Franklin, Greene, Herkimer, Jefferson, Nassau, Orange, Putnam, Rensselaer, St. Lawrence, Saratoga, Tompkins, Warren, Washington, and Westchester counties.

CONNECTICUT: Fairfield, Hartford, Middlesex, New Haven, and New London counties.

RHODE ISLAND: Providence County.

MASSACHUSETTS: Berkshire, Essex, Franklin, Hampden, Hampshire, Middlesex, Norfolk, Suffolk, and Worcester counties.

VERMONT: Addison, Caledonia, Chittenden, Orange, Rutland, and Windham counties.

NEW HAMPSHIRE: Carroll, Cheshire, Coos, Grafton, and Hillsboro counties.

MAINE: Aroostook, Cumberland, Franklin, Hancock, Knox, Lincoln, Oxford, Penobscot, Sagadahoc, Somerset, Washington, and York counties.

OHIO: Lake and Portage counties.

INDIANA: Lake and Starke counties.

ILLINOIS: Cook, LaSalle, and Ogle counties.

MICHIGAN: Cheboygan, Crawford, Emmet, Ingham, Keweenaw, Leelanau, Mackinac, Marquette, Muskegon, and St. Clair counties.

WISCONSIN: Adams, Ashland, Bayfield, Brown, Oneida, Polk, Sauk, Sawyer, Shawano, and Vilas counties.

MINNESOTA: Aitkin, Beltrami, Carlton, Cass, Chisago, Clearwater, Cook, Itasca, Lake, Millelacs, and St. Louis counties.

MONTANA: Flathead County; Glacier National Park.

NEWFOUNDLAND: gravelly railroad embankments, Grand Falls, July 4, 1911, *Fernald & Wiegand 5455* (NY, G); sandy terraces, n. bank of river above the falls, Bishop's Falls, valley of Exploits River, July 28 & 29, 1911, *Fernald & Wiegand 5456* (G); dry woods, Buchan (?) Junction, July 13, 1930, *Jaussan* (G); railway, Gambo, July 14, 1893, *Wagborne 21* (UA).

NOVA SCOTIA: DIGBY CO.—clearing at border of deciduous woods, Wentworth Lake, Sept. 4, 1921, *Fernald & Long 23866* (G). INVERNESS CO.—dripping cliffs, Big Intervale, July 17, 1941, *Roland 41416* (G). LUNENBURG CO.—recently burned clearing w. of Bridgewater, Aug. 18, 1921, *Fernald & Long 23865* (G).

PRINCE EDWARD ISLAND: PRINCE CO.—dry clearings, Alberton, July 11, 1912, *Fernald & St. John 7502* (WS, NY, G, US).

NEW BRUNSWICK: KENT CO.—Bass River, June 10, 1869, *Fowler* (G).

QUEBEC: BROME CO.—Mt. Elephantis, Brome, July 30, 1902, *Pease 606* (G); dry mountain ledge, Bolton, July 25, 1926, *Knowlton* (G). CHAMBLY CO.—St. Hubert: Tourbieres, environs de Montreal, June, 1913, *Victorin 206* (M, WS, US). CHARLEVOIX CO.—vicinity of Cap à L'Aigle, July 27, 1905, *Macoun* (G). GASPÉ CO.—alluvial woods, York River, July 29, 1905, *Williams, Collins & Fernald* (G). KAMOURASKA CO.—dry, quartzite hills, Ste. Anne, July 14, 1922, *Fernald & Pease 25088* (G). LAKE ST. JOHN DIST.—carrière de granit, Roberval, July 20, 1921, *Victorin 15757* (G). MEGANTIC CO.—dry, serpentine slopes and crests of Caribou Hill, Black Lake, Aug. 26, 1915, *Fernald & Jackson 12098* (G). NISSISQUOI CO.—rocky places, Philipsburg, June 22, 1910, *Edmondson 4995* (G). MONTMAGNY CO.—Grosse-Ile, l'estuaire du Saint-Laurent, July 31, 1935, *Victorin, Rolland-Germain, Rousseau & Meilleur 40082* (G). PONTIAC CO.—Ile-des-Soeurs, Lake Timiscaming, June 26, 1918, *Victorin 8365* (US). RICHMOND CO.—dry ledge, Cleveland, July 30, 1923, *Chamberlain & Knowlton* (M, G). RIMOUSKI CO.—dans un champ près du chemin du cap à l'Orignal, Aug. 19, 1927, *Rousseau 26971* (CIUC). TERREBONNE CO.—sur les gneiss laurentiens, St. Jerome, July 4, 1930, *Victorin & Rolland-Germain 33122* (RM, G). TWO MTS. CO.—La Trappe, Oct. 9, 1926, *Louis-Marie* (G). CO. UNCERTAIN—on rocks along Matamek River, n. shore, July 26, 1927, *Bowman 247* (G); Lac Kamatose, sur le ballast de la route, 101 milles au nord de Mont-Laurier, Aug. 23–25, 1941, *Victorin, Rolland-Germain & Dominique 260* (G).

ONTARIO: ALGONA DIST.—thin soil, e. ridge, Havilland Bay, 47° 00' N., 84° 45' W., Aug. 12, 1935, *Taylor, Hosie, Fitzpatrick, Losee & Leslie 1310* (US). CARLETON CO.—Cascades, vicinity of Ottawa, July 31, 1920, *Victorin 10055* (WS). FRONTENAC CO.—

Battersea, June 13, 1898, *Edmondson 1106* (NY); Kingston, May 30, 1901, *Fowler* (G, US); Barriefield, June, 1897, *Boyd* (M). KENORA DIST.—Minaki, July 25, 1915, *Thompson 30* (M). LEEDS CO.—Jones Falls, June 7, 1895, *Fowler* (US). MUSKOKA DIST.—crevices of rocks, Lake Joseph, Muskoka, Aug. 20, 1881, *Burgess* (M); Lake Muskoka, Aug. 16–18, 1898, *Topping* (US). NIPISSING DIST.—common on sunny rocks, Twin Islands, Timagami region, July 24, 1926, *Anderson & Anderson 26039* (M, NY, G); Cache Lake, Algonquin Park, July 4, 1900, *Macoun* (US); open, grassy woods, Sturgeon Falls near Lake Nipissing, Aug. 14, 1937, *Nelson & Nelson 2395* (RM). PARRY SOUND DIST.—Island 74 in French River, July 5, 1939, *Dewey 1* (US); in soil pockets on granite ridge, s. side of French River Harbor, n. w. part of Parry Sound, Sept. 6, 1932, *Grassl 3766* (NY). RENFREW CO.—bluffs, Bonne Chere Mts., July 20, 1899, *Umbach* (US). THUNDER BAY DIST.—Mungo Park Point, Nipigon Lake, 1912, *Pulling* (G); crevice of altered lava, rocky knoll, flat e. of Schreiber, Aug. 21, 1937, *Hosie, Losee & Bannan 1412* (G); dry ledges, S. Slate Island, July 6, 1933, *Pease & Bean 23,549* (G); black loam along Amadis River, 1912, *Pulling* (G); diabase crevices, Shangoia Island, Sibley Tp., 48° 20' N., 88° 50' W., July 6, 1936, *Taylor, Losee & Bannan 505* (D). TIMISKAMING DIST.—Moose River Basin, 1903, *Bell* (G).

MANITOBA: SELKIRK DIST.—Elk Island, Lake Winnipeg, July 20, 1887, *Macoun* (NY). DIST. UNCERTAIN—Piguionay (mile 214), route of Hudson Bay Railway, July 8, 1917, *Emerton* (G); Lake Winnipeg Valley, 1857, *Bourgeau* (G).

SASKATCHEWAN: north shore, Athabaska Lake, July 26, 1920, *Laing 174* (US); exposed rocky slopes, Charlot Pt., Lake Athabaska, about 59° 36' N., 109° 13' W., June 12, 1935, *Raup 6088* (G); in clay and sandy soil, Sulphide Lake (Lac la Ronge), Oct. 3, 1941, *Studer 4-16* (CIUC).

ALBERTA: ATHABASKA DIST.—Egg Lake, Athabaska Delta, July 18, 1920, *Harper 53* (US); Smith Landing, June 13, 1903, *Preble & Cary 13* (US); Granite Hill, Gov. Hay Camp district, Slave River, about 59° 31' N., 11° 28' W., Wood Buffalo Park, Mackenzie Basin, Aug. 14, 15, 1928, *Raup 2443-a* (G); short distance e. of Sand Point, n. shore of Lake Athabaska, about 58° 57' N., 110° 42' W., 700 ft. alt., Sept. 1, 1932, *Raup & Abbe 4531*. PEACE RIVER DIST.—Notikewin, Peace River region, roadside in poplar woods, 57° N., 118° W., July 12, 1931, *Moss 2255* (WS).

BRITISH COLUMBIA: CARIBOO DIST.—Hargreaves Ranch, 2900 ft. alt., Mt. Robson, Aug. 19–26, 1943, *Scamman 3272* (G, US); in brush on rocky slope, Campbell Island in Summit Lake, 31 mi. n. of Prince George, Aug. 1, 1941, *Weber 2600* (WS, M, NY, G, US). COAST DIST.—Bute Inlet, without date, *Anderson* (WS). KOOTENAY DIST.—Revelstoke, May 27, 1890, *Macoun* (US); deserted log road, Revelstoke, July 6, 1905, *Shaw 830* (NY, G, US). NEW WESTMINSTER DIST.—Cheak Kamis, June 25, 1920, ex herb. *Anderson* (WS); Mons, P. G. E. Railway, June 20, 1916, *Macoun* (NY, G).

YUKON: n. side of Moose Creek near Clark's Peak, 3500 ft. alt., Mayo District between Stewart and MacMillan Rivers, Aug. 7, 1939, *Bostock 60* (G); Klondyke, Aug. 23, 1898–1901, *MacLean* (UC, G); Moosehide Mt., Dawson, July 14, 1902, *Macoun* (NY); Bonanza Creek, Aug. 11, 1899, *Tarleton 178a* (NY); Dawson, July 17, 1898, *Williams* (NY).

ALASKA: edge of airfield, Franklin, Fortymile dist., July 16, 1941, *Anderson & Gasser 7320* (RM, G); dry ground, The Birches, 55 mi. below Tanana, on the Yukon River, July 8, 1902, *Brooks* (G); roadside near Knik, Oct., 1913, *Chaney 151* (M); Eagle to Valdes trail, June 30, 1902, *Collier 72* (US); headquarters, Mt. McKinley Nat. Park, June 28, 1932, *Dixon 45* (UC); Hot Springs on the Tanana River, July 28, 29, 1909, *Hitchcock* (US); Rampart, July 26, 1901, *Jones 67* (US); Mt. McKinley Nat. Park, summer, 1932, *Kaye 1501* (UC); Dall River Trail, 3 mi. above Dall City, Ft. Hamlin, Yukon River, to Bergman, Koyukuk River, June 29, 1901, *Mendenhall* (US); n. of superintendent's office, 3000 ft. alt., Mt. McKinley Nat. Park, July 23, 1928, *Mexia 2106* (M, UC, D, NY, G, US); exposed hillsides above spruce woods, e. side of Wonder Lake, near center of n. boundary of Mt. McKinley Nat. Park, Aug. 14, 1928, *Mexia 2240* (M, UC, D, NY, G, US); McKinley Park Station, July 31, 1922, *Murie* (US); rocky soil near Park Headquarters, Mt. McKinley Nat. Park, June 22, 1939, *Nelson & Nelson W-2151*

(RM); open woods just below Park Headquarters, Mt. McKinley Nat. Park, July 3, 1939, *Nelson & Nelson 3622* (RM, G); roadside near Park Headquarters, Mt. McKinley Nat. Park, July 16, 1939, *Nelson & Nelson 3833* (M, RM, IH, NY, G); Fairbanks, June, 1927, *Palmer 1769* (US); recent clearings and open woods, Goldstream Creek and Pedro Dome, 51 mi. n. of Fairbanks, 65° N., 147° 30' W., 800–2000 ft. alt., June 13, 1926, *Porsild & Porsild 135* (G); open, forested bottom lands, Kokrines Mts., n. side of divide, towards Melozitna River, 65° 20' N., 154° 30' W., 800–4000 ft. alt., June 23–July 5, 1926, *Porsild & Porsild 739* (G); hill s. of Mitchell Creek, 3000 ft. alt., Copper River region, Aug. 6, 1902, *Poto 121* (US); Anchorage area, May 23, 1943, *York 4* (M); sandy hillside near Palmer, July 5, 1943, *York Pa208* (M); Mt. McKinley Nat. Park, 63° 43' N., 149° 15' W., July 5–7, 1936, *Scamman 213* (G); Livengood, about 80 mi. n.-n.w. of Fairbanks, June 19–21, 1940, *Scamman 1735* (CIUC, G); Gens de Large (Chandler River) & Koyukuk rivers, 1899, *Schradler* (US).

5. *C. FLAVULA* (Raf.) DC. Prod. Syst. Nat. 1:129. 1824.

Fumaria flavula Raf. in Desv. Jour. Bot. 1:224. 1808.

Corydalis aurea α *flavula* Wood, Am. Bot. & Fl. 34. 1870.

Corydalis flavidula Chapm. Fl. S. U. S. Suppl. 1:604. 1883, sphalm.

Capnodes flavulum Ktze. Rev. Gen. 1:14. 1891.

Neckeria flavula Millsp. Fl. W. Va. 327. 1892 (W. Va. Agr. Exp. Sta. Bull. 2).

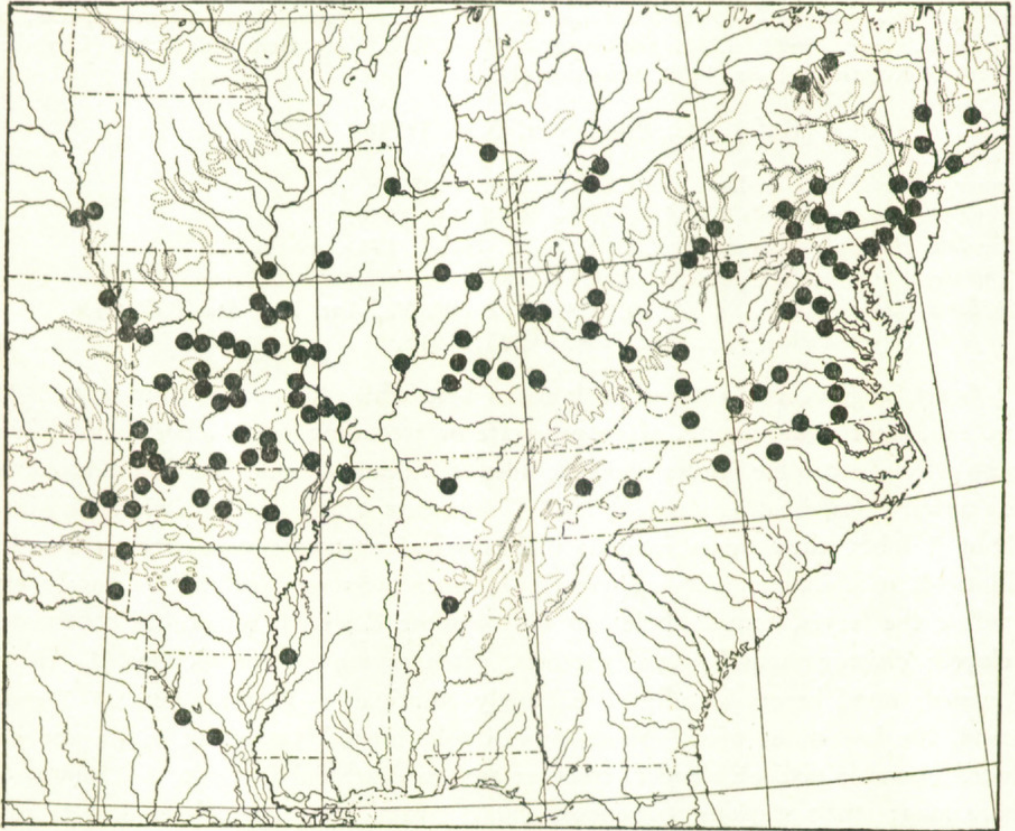
Corydalis Geyeri Fedde, Rep. Spec. Nov. 10:311. 1912.

Green or glaucous winter annual; stems 1–several, sympodial, commonly 15–30 cm. tall, erect while young, often prostrate or ascending when older; basal leaves long-petioled; cauline leaves short-petioled to almost sessile, hardly reduced in size upward; leaf blades pinnate, with 5–7 segments which are again pinnatifid into about 5 lobes, these again incised; ultimate leaf segments narrowly to broadly elliptical, subapiculate, varying greatly in size; racemes equalling or barely exceeding the leaves, commonly 6- to 10- or more flowered, sometimes poorly developed; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; floral bracts broadly to narrowly elliptical, 6–12 mm. long, 3–7 mm. broad, the lowermost often foliose or variously incised, becoming entire and reduced upward; pedicels slender, erect at anthesis, reflexed in fruit, 6–15 mm. or more long; sepals scarious, fugacious, about 1 mm. long, lanceolate; flowers pale yellow, somewhat crowded; spurred petal 7–9 mm. long, the hood crested, the crest high, undulate or toothed, the wing margin well developed, also undulate or toothed, the incurved spur about 2 mm. long; spurless outer petal 6–8 mm. long, the crest and wing margin as in the spurred petal; clawed inner petals 5–7 mm. long, the claw 2–3 mm. long, the blade approximately twice as broad near the apex as at the distinctly lobed base; stamen spur less than 1 mm. long, less than one-half the length of the petal spur; stigma broader than high; fruits reflexed or variously disposed, 14–22 (often 18–20) mm. long, straight, essentially glabrous; seeds about 2 mm. in diameter, black, shiny, on magnification seen to be concentrically, submuricately decorated on the narrow, acute ring margin.

This species is easily distinguished by the small, crested flowers, the very short, incurved spur, and long, reflexed pedicels. Cleistogamous-flowered plants are col-

lected occasionally, and these often have much broader and larger ultimate leaf segments and weaker, more diffusely branched stems. Such plants can be determined accurately by fruit characters alone.

Moist, loose soil, wooded slopes and bottom lands, at elevations up to about 2000 feet; Connecticut and New York to North Carolina westward to northern Louisiana, eastern Oklahoma, Kansas and Nebraska. Flowers in early spring from about March 15 to May 15; fruits from about April 1 to June 1.



Map 5. Distribution of *Corydalis flavula* (Raf.) DC.

CONNECTICUT: Middlesex County.

NEW YORK: Nassau, Onondaga, Rockland, Ulster, and Yates counties.

NEW JERSEY: Camden, Hunterdon, Mercer, and Somerset counties.

PENNSYLVANIA: Allegheny, Franklin, Huntingdon, Lancaster, Montgomery, Perry, Philadelphia, Snyder, Washington, and York counties.

DELAWARE: Newcastle County.

MARYLAND: Allegany, Baltimore, Carroll, Cecil, Hartford, Howard, Montgomery, and Prince Georges counties.

VIRGINIA: Albemarle, Alexandria, Bedford, Botetourt, Buckingham, Dinwiddie, Fairfax, Fauquier, Greensville, Henrico, Mecklenburg, Prince George, Prince William, Pulaski, Roanoke, Shenandoah, Stafford, Warren, and Wythe counties.

WEST VIRGINIA: Berkeley, Cabell, Fayette, Monongalia, Ohio, and Raleigh counties.

NORTH CAROLINA: Durham, Forsythe, Halifax, and Madison counties.

KENTUCKY: Fayette, Shelby, and Woodford counties.

TENNESSEE: Blount, Davidson, Knox, and Obion counties.

ALABAMA: Tuscaloosa County.

MISSISSIPPI: Sharkey County.

LOUISIANA: Natchitoches and Rapides parishes.

ONTARIO: Essex County, Point Pelee and Pelee Island.

MICHIGAN: Kalamazoo County.

OHIO: Clermont, Franklin, Hamilton, Ottawa, Ross, Scioto, and Warren counties.

INDIANA: Floyd, Lawrence, Marion, Montgomery, Orange, and Perry counties.

ILLINOIS: Hancock, Jackson, Mason, Pike, St. Clair, Union, Wabash, and Will counties.

MISSOURI: Barry, Boone, Butler, Callaway, Camden, Clay, Cooper, Franklin, Howell, Jackson, Jasper, Jefferson, Lawrence, McDonald, Madison, Maries, Marion, Montgomery, Morgan, Oregon, Ozark, Perry, Pettis, Phelps, Pulaski, St. Clair, St. Francois, Ste. Genevieve, St. Louis, Shannon, Texas, Warren, and Washington counties.

IOWA: Pottawattomie County.

NEBRASKA: Sarpy County.

KANSAS: Atchinson and Wyandotte counties.

OKLAHOMA: Adair, Cherokee, LeFlore, McCurtain, and Muskogee counties.

ARKANSAS: Carroll, Cross, Garland, Jackson, Searcy, Van Buren, and Washington counties.

6. *C. CRYSTALLINA* Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867; Bot. Gaz. 11:189. 1886.

Corydalis aurea β. ? *crystallina* Torr. & Gray, Fl. N. Am. 1:665. 1840.

Corydalis crystallina Engelm. ex Torr. & Gray, l. c. 1840, as syn.

Capnodes crystallinum Ktze. Rev. Gen. 1:14. 1891.

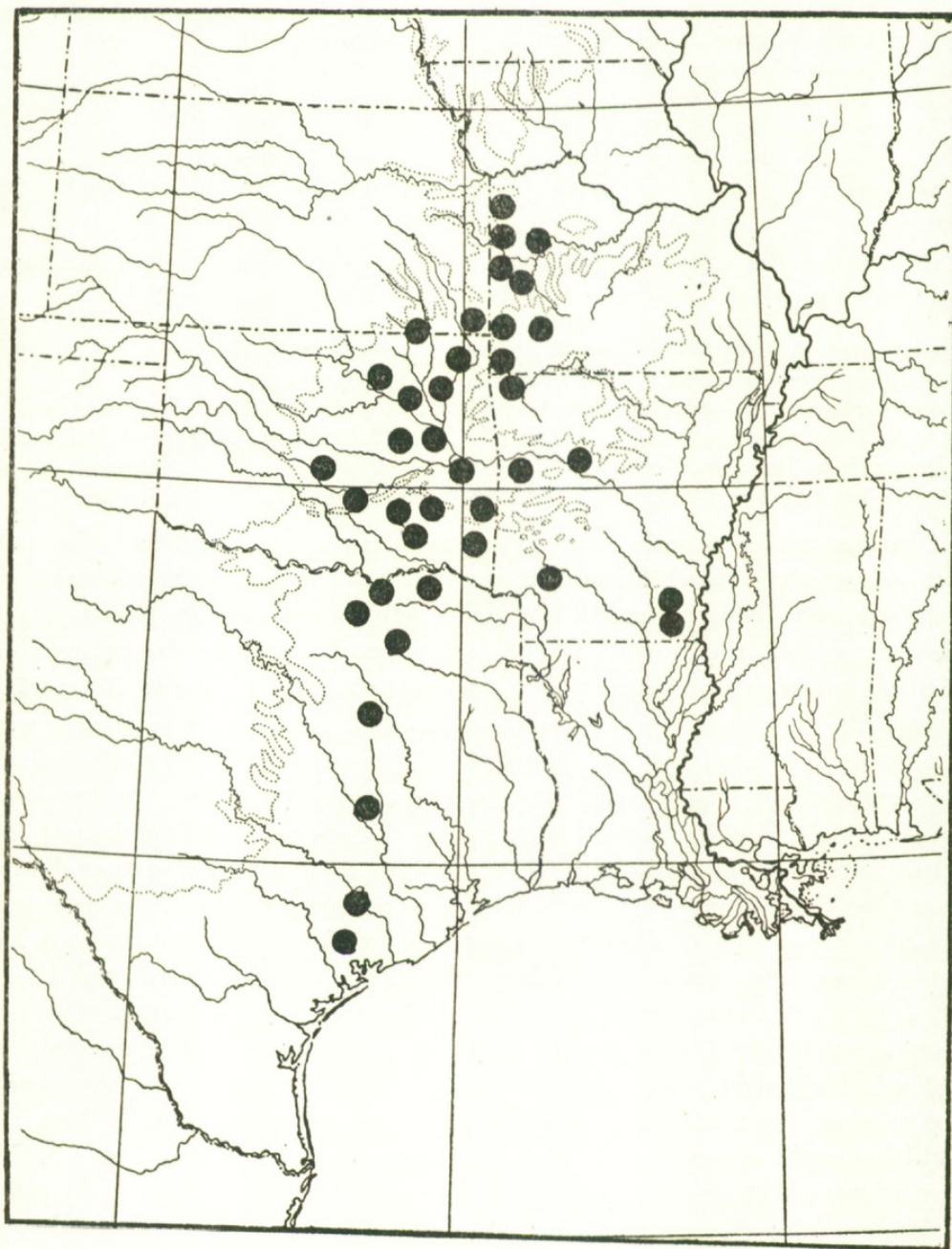
Capnoides Halei Small, in Bull. Torr. Bot. Club 25:137. 1898, as to most of Hale's collection from Louisiana.

Corydallis crystallina var. *strictissima* Fedde, Rep. Spec. Nov. 10:479. 1912.

Glaucous winter annual; stems 1—several, often sympodial, 20–40 cm. tall, erect or ascending; basal leaves long-petioled; cauline leaves short-petioled to sessile, somewhat reduced upward; leaf blades pinnate, the segments pinnatifid and once again incised, the ultimate lobes broadly lanceolate to linear-lanceolate, subapiculate; primary racemes surpassing the leaves, 8- to 18- (ordinarily 12- to 15-) flowered, the later secondary racemes fewer-flowered; bracts ovate to ovate-acuminate, 5–12 mm. long, 3–6 mm. broad, usually much reduced upward; pedicels stout, erect, about 1 mm. long; sepals scarious, fugacious, 2 mm. or less long, broadly ovate to cordate, somewhat attenuate, the margin sometimes incised, especially at the base; flowers bright yellow, crowded at first, becoming more distant at anthesis; spurred petal 16–22 mm. long, the hood always crested, the crest very high, undulate or toothed, the wing margin very broad, reflexed upon the hood, the spur 6–8 mm. long, the blunt tip distinctly globose; spurless outer petal 12–14 mm. long, about 3 mm. longer than the inner petals, the wing margin wide, not reflexed upon the hood, enclosing the margins of the spurred petal in the bud, the crest as in the spurred petal; inner petals oblanceolate, 9–11 mm. long, the narrow claw 4–5 mm. long, the blade about twice as wide at the tip as at the base, the basal lobes small; stamen spur 3.5–5.0 mm. long, clavate, curved or bent near the apex; stigma about twice as broad as high; style long and slender; fruits erect, 14–18 mm. long, stout, straight or moderately incurved toward the floral axis, densely beset with transparent, clavate pustules which often break open at

maturity or, rarely, glabrate; seeds black, about 2 mm. in diameter, distinctly submuricately decorated under magnification, having no ring margin.

This species is distinguished from all other species of *Corydalis* by the peculiar type of pubescence of the fruit. The pustules sometimes appear ligulate when desiccated or, as is often the case, when they rupture at maturity. The crest and margins of the hood of the outer petals are more highly developed than in any other yellow-flowered species.



Map 6. Distribution of *Corydalis crystallina* Engelm.

C. crystallina var. *strictissima* is a habitat variant and of no systematic value. The type was collected by F. L. Harvey in "Orchards, grain fields, etc., Northwest Arkansas," and was distributed as Curtiss's North American Plants 125*. Fedde cites the collection but gives the number erroneously as 125a. Too, he previously had described *C. micrantha* var. *diffusa*, a synonym of *C. micrantha* ssp. *australis*, on the basis of the true Curtiss's North American Plants distribution #125a, collected by Curtiss himself in Duval County, Florida.

Prairies, fields, open woods, and wasteland; southwestern Missouri to central Texas. Flowers in early spring from about April 1 to May 15; fruits from about April 15 to June 1.

MISSOURI: Bates, Benton, Cass, Greene, Henry, Jasper, Lawrence, McDonald, Newton, St. Clair, and Vernon counties.

ARKANSAS: Ashley, Benton, Carroll, Drew, Franklin, Nevada, Pope, Sebastian, and Washington counties.

KANSAS: Cherokee and Montgomery counties.

OKLAHOMA: Atoka, Cleveland, Craig, Haskell, Latimer, LeFlore, McCurtain, Mayes, Muskogee, Okmulgee, Osage, Pittsburg, Pontotoc, Pushmataha, Rogers, and Tulsa counties.

TEXAS: Brazos, Colorado, Denton, Fannin, Grayson, Kaufman, Lamar, Navarro, Tarrant, Van Zandt, and Victoria counties.

7. *C. MICRANTHA* (Engelm.) Gray ssp. *micrantha* G. B. Ownbey, stat. nov.

Corydalis aurea var. *micrantha* Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867.

Corydalis micrantha Gray, in Bot. Gaz. 11:189. 1886, in part.

Neckeria micrantha MacMillan, Metasp. Minn. Valley. 255. 1892.

Capnoides micranthum Britton, in Mem. Torr. Bot. Club 5:166. 1894.

Corydalis micrantha var. *pachysiliquosa* Fedde, Rep. Spec. Nov. 10:380. 1912.

Corydalis monilifera var. *ferruginifera* Fedde, l. c. 11:498. 1913.

Glaucous or nearly green winter annual; stems 1-several, usually 15-25 cm. tall, erect or ascending, sparingly branched; basal leaves crowded, long-petioled; cauline leaves short-petioled to nearly sessile, gradually reduced upward; leaf blades pinnate, the 5-7 primary segments pinnatifid and again incised, the ultimate lobes oblong-elliptical or obovate, subapiculate; normal-flowered racemes usually present, slightly exceeding the leaves, 6- to 16-flowered, not surpassed by the fewer-flowered secondary racemes; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; bracts elliptical, the lowermost 5-8 mm. long and 2-4 mm. broad, the upper much reduced, often minute on cleistogamous-flowered racemes; pedicels erect, the lower usually 2-4 mm. long, gradually decreasing in length upward; sepals scarious, fugacious, 1.5 mm. or less long, ovate, often undulate or toothed at the margin; flowers pale yellow, often somewhat crowded throughout anthesis; spurred petal 11-15, usually 12-14 mm. long, the hood crested, the crest low, undulate or rarely obsolescent, the wing margin well developed, the spur 4.5-6.0 mm. long, the apex distinctly globose; spurless outer petal 9-11 mm. long, semi-geniculate, the crest low; inner petals 7-9 mm. long, oblanceolate, the claw 3-4 mm. long, the blade twice as broad at the apex as at the obscurely lobed base; stamen spur 3-4 mm. long, about three-fifths the length of

the petal spur, straight or curved, sometimes clavate; stigma 2-lobed, rectangular, twice as wide as high; fruits erect, commonly 10–15 mm. long, rarely longer, often shorter in cleistogamous-flowered racemes, straight or moderately incurved; seeds about 1.5 mm. in diameter, black, shiny, turgid, concentrically but moderately decorated under magnification, obtuse at the border, with no ring margin.

The subspecies of *C. micrantha* are all characterized by very small seeds and can be distinguished from all other yellow-flowered species by them alone. Subspecies *micrantha* usually can be distinguished from ssp. *australis* by its less elongated racemes, generally smaller flowers, globose tipped spur and generally shorter, stouter fruits. The two subspecies intergrade in all of these characters, especially in southern Missouri and Oklahoma, but in most cases the disposition of a given specimen is not difficult. In southern Missouri a form is also found which is characterized by larger, more showy flowers, longer pedicels, and relatively short fruits. This large-flowered form has been confused by various authors with *C. aurea*. As flower size is not considered a good criterion for separation of the segregates of *C. micrantha*, this form seems better left with the typical subspecies.

A dwarf form of ssp. *micrantha* was collected by Reverchon at Columbia, Brazoria Co., Texas. This locality is far removed from the expected range of the subspecies and it seems likely that data on the label are mixed. Its presence there should be verified.

Although encountered occasionally in other species of *Corydalis* the cleistogamous condition reaches its highest development in *C. micrantha*. It occurs at random throughout the range of the species. A single plant may have only normal flowers, only cleistogamous flowers, or both cleistogamous and normal flowers. In the last instance, the cleistogamous flowers are produced only on the smaller, less well-developed secondary branches. Plants having only cleistogamous flowers are quite different in aspect, usually being much more profusely and delicately branched. The racemes are short, weak, and ordinarily have 1–5 small, undeveloped, self-fertilized flowers and ultimately the same number of fruits crowded near the apex. The disposition of such specimens is likely to prove difficult for one who is unfamiliar with this type of variation.

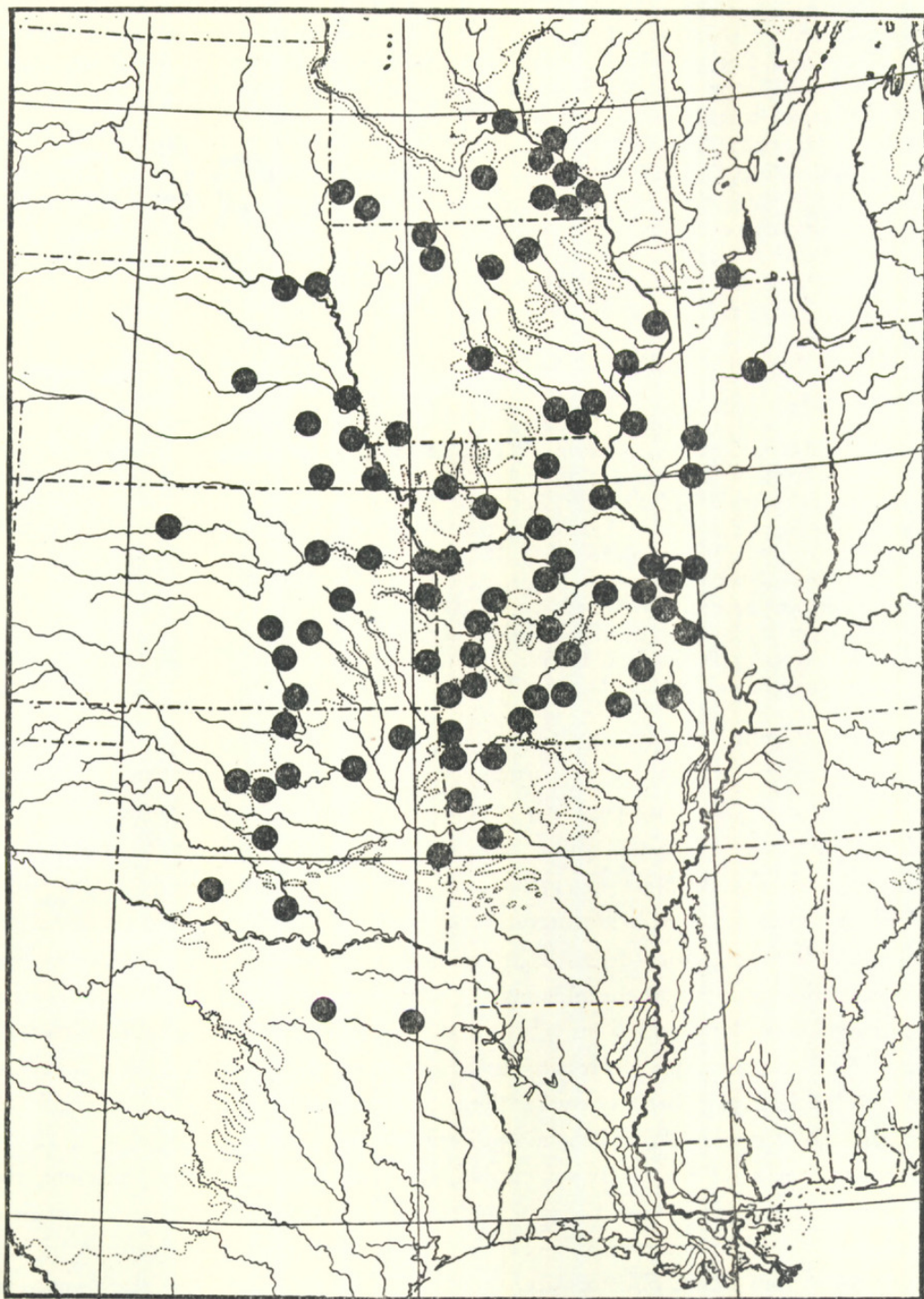
The conditions which institute cleistogamy are not entirely understood. It is notable, however, that plants growing in the shade or those which are crowded together so that they shade each other are predominantly cleistogamous. Also, age of the plant is of some significance, as the later racemes are often entirely cleistogamous on plants which at first produced only normal flowers.

Along bluffs, rocky hills, open woods, and river banks, often in disturbed soil; southern Minnesota to Illinois, Kansas, and northern Texas. Flowers in early spring from about April 1 to May 15; fruits from about April 15 to June 1.

MINNESOTA: Fillmore, Goodhue, Hennepin, Murray, Nobles, Olmsted, Pipestone, Steele, and Winona counties.

WISCONSIN: Pepin and Rock counties.

IOWA: Dickinson, Emmet, Floyd, Henry, Jackson, Muscatine, Page, Palo Alto, Polk, Van Buren, Wapello, and Wright counties.



Map 7. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *micrantha* Ownbey.

ILLINOIS: Henderson, LaSalle, Menard, Peoria, and St. Clair counties.

MISSOURI: Adair, Boone, Camden, Cass, Cedar, Christian, Dade, Daviess, Gasconade, Greene, Henry, Iron, Jackson, Jasper, Jefferson, Lawrence, Livingston, McDonald, Marion, Miller, Moniteau, Phelps, Polk, Pulaski, Ralls, Randolph, St. Charles, St. Clair, Ste. Genevieve, St. Louis, Shannon, Stone, Texas, Wayne, and Webster counties.

ARKANSAS: Benton, Carroll, Logan, and Washington counties.

SOUTH DAKOTA: Clay County.

NEBRASKA: Cass, Cedar, Gage, Lancaster, Nance, Otoe, Richardson, and Sarpy counties.

KANSAS: Bourbon, Chase, Cowley, Geary, Harvey, Lyon, Miami, Osborne, Riley, Sedgwick, Shawnee, and Wyandotte counties.

OKLAHOMA: Carter, Comanche, Kay, Kingfisher, LeFlore, Logan, McClain, Murray, Oklahoma, Payne, Rogers, and Tulsa counties.

TEXAS: Brazoria, Dallas, and Upshur counties.

7a. *C. MICRANTHA* (Engelm.) Gray ssp. ***australis*** (Chapm.) G. B. Ownbey, stat. nov.

Corydalis aurea var. *australis* Chapm. Fl. S. U. S. Suppl. 1:604. 1883.

Corydalis micrantha Gray, in Bot. Gaz. 11:189. 1886, in part.

Capnoides Halei Small, in Bull. Torr. Bot. Club 25:137. 1898, as to the Curtiss collections from Jacksonville, Florida, but not as to most of Hale's specimens from Louisiana.

Capnoides campestre Britton, Man. ed. 2. 1065. 1905.

Corydalis curvisiliqua var. *tenerior* Fedde, Rep. Spec. Nov. 10:365. 1912.

Corydalis micrantha var. *diffusa* Fedde, l. c. 380. 1912.

Corydalis micrantha var. *leptosiliqua* Fedde, l. c. 11:497. 1913.

Corydalis campestris Buchholz & Palmer, in Trans. Acad. Sci. St. Louis 25:115. 1926.

Corydalis Halei Fernald & Schubert, in Rhodora 48:207. 1946.

Green or somewhat glaucous annual; stems 1-several, usually 20-40, occasionally up to 60 cm. tall, the earlier usually stouter, semi-erect, the later ascending; basal leaves crowded, long-petioled; cauline leaves short-petioled or nearly sessile, reduced upward; leaf blades pinnate, the 5-7 primary segments pinnatifid and again incised, the ultimate lobes longer than broad, approximately ovate, sub-apiculate; normal-flowered racemes usually present, much surpassing the leaves, 10- to 20-flowered, not surpassed by secondary racemes; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; bracts elliptical, usually less than 8 mm. long and 4 mm. broad, the upper much reduced; pedicels erect, the lower 3-6 mm. long, decreasing in length upward; sepals scarious, fugacious, 1.5 mm. or less long, broadly ovate, the margin undulate or toothed especially at the base; flowers pale yellow, becoming distant during anthesis; spurred petal 12-14 mm. long, the hood nearly always crested, the crest low, regular or undulate, the wing margin well developed, the spur 4-6 mm. long, the tip blunt, never distinctly globose; spurless outer petal 9-11 mm. long, geniculate, the crest low; inner petals 8-10 mm. long, oblanceolate, the claw 3-4 mm. long, the blade twice as broad near the apex as at the obscurely lobed base; stamen spur 2.5-3.5 mm. long, about three-fifths the length of the petal spur, usually straight, sometimes bent near the tip, clavate; stigma 2-lobed, rectangular, twice as wide as high; fruits erect, 15-20, rarely 25 mm. long, slender, straight or moderately incurved; seeds

about 1.5 mm. in diameter, black, shiny, concentrically but moderately decorated under magnification, obtuse at the border, with no ring margin.

Subspecies *australis* is best distinguished by its elongate normal-flowered racemes, its short, saccate spur which is never clearly globose at the tip, its slender, erect fruits, and its minute, nearly smooth seeds.

The peculiarities of this plant were first recognized by Chapman who in 1883 published a short and accurate description of it in the first supplement to his 'Flora' under the name *Corydalis aurea* var. *australis*. In 1886 Gray (Bot. Gaz. 11:189), in his study of *C. aurea* and its allies, concluded that Chapman's variety belonged with *C. micrantha* and reduced it to synonymy under that species. In conformance with Gray's treatment Chapman, then, also treated his variety as a synonym of *C. micrantha* in the third edition of his 'Flora' issued in 1897. The following year Small redescribed Chapman's plant as *Capnoides Halei*...

Small's description of *Capnoides Halei* was drawn on the joint basis of Hale's collection from Louisiana and Curtiss's collections from Florida. Hale's plants (s. n. in Herb. N. Y. Bot. Gard.), are all *C. crystallina* except for one small specimen which is referable to the subspecies described above. It is evident from the general aspect of the plants of *C. crystallina* that they are those referred to by Small in comparing the "new" species with *Capnoides curvisiliquum* (*Corydalis curvisiliqua*) when he distinguished it from that species by "... its more slender habit, and especially by the more coarsely dissected leaf-blades."

Also cited by Small was Curtiss 4515 from Jacksonville, Florida, and with the exception of the sentence quoted above, it is from these Florida specimens that the description is drawn. They, therefore, should be designated the authentic type if the species were maintained.

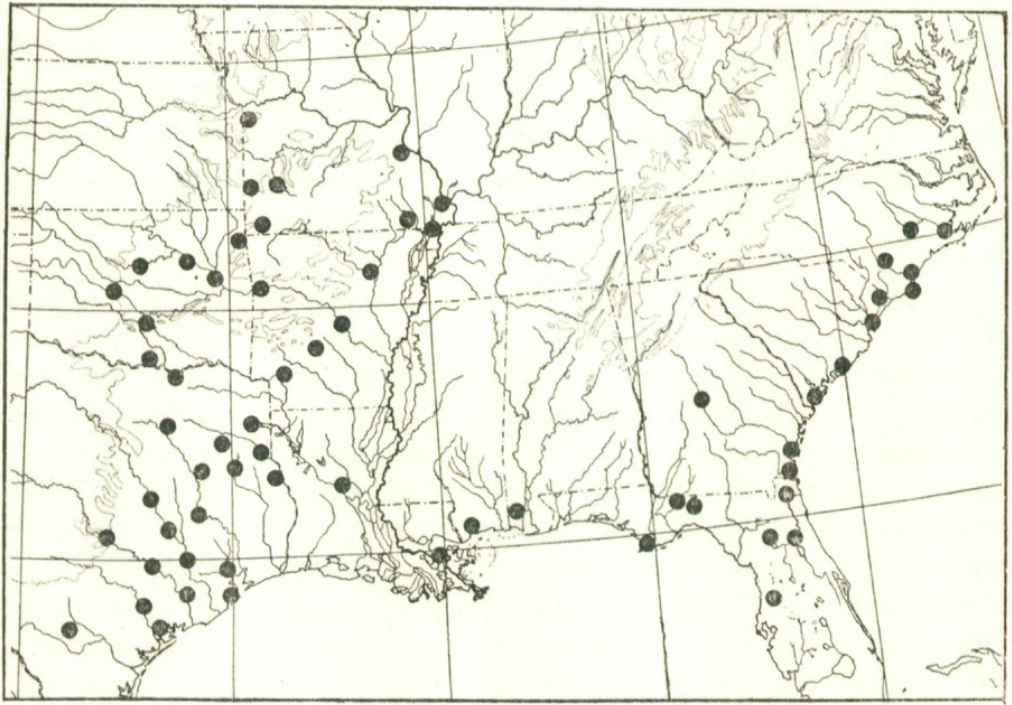
This entity has been the subject of a recent paper by Fernald and Schubert (Rhodora 48:207. 1946) who, recognizing its distinctness, have revived Small's name, and transferred it to *Corydalis*. I do not believe, however, that the differences between this and ssp. *micrantha* are of specific level, and am therefore taking up Chapman's earlier varietal name *australis* in its new rank of subspecies. In support of this view it may be mentioned that seeds of ssp. *micrantha* and ssp. *australis* are identical in size and decoration of the testa, that the flowers are similar in that both have a low crest, and that the geographical distribution of the two subspecies taken as a whole is not unnatural. Even greater variability in habit, together with similar minor morphological variability of the floral organs and fruits, is found in other species of *Corydalis* such as *C. aurea* and *C. Caseana*.

Plants of ssp. *australis* from coastal North Carolina, South Carolina, and Georgia are appreciably smaller and more strict in habit than those from other parts of the range of the subspecies. The flowers also are noticeably smaller, the hood is not crested, and the fruits are very slender and often moniliform.

The center of diversity of this subspecies is eastern Oklahoma and southeastern Missouri, and plants intermediate between this subspecies and ssp. *micrantha* and

C. curvisiliqua are not uncommonly collected in this area. The disposition of a given specimen, however, ordinarily is not difficult.

In disturbed, often sandy soil, abandoned fields and waste areas, along roadsides, and in open woods; from southern Missouri and eastern Kansas to Texas, Florida, and North Carolina. Flowers in early spring, about February 15 to April 30; fruits from about March 1 to May 15.



Map 8. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *australis* (Chapm.) Ownbey.

NORTH CAROLINA: Bladen, Brunswick, Craven, Jones, Lenoir, and New Hanover counties.

SOUTH CAROLINA: Beaufort, Charleston, Georgetown, and Horry counties.

GEORGIA: Camden, Glynn, and Pulaski counties.

FLORIDA: Alachua, Duval, Franklin, Hernando, Leon, Marion, Nassau, Putnam, and St. John counties.

ALABAMA: Mobile County.

MISSISSIPPI: Harrison County.

LOUISIANA: Jefferson, Natchitoches, Orleans, and Rapides parishes.

TEXAS: Anderson, Austin, Bastrop, Bell, Brazos, Burleson, Caldwell, Clennan, Dallas, DeWitt, Frio, Galveston, Gonzales, Grayson, Gregg, Harris, Henderson, Jackson, Kaufman, McLennan, Nueces, Rusk, San Augustine, Smith, Tarrant, Travis, Upshur, Victoria, Waller, Washington, and Wharton counties.

OKLAHOMA: Carter, Cleveland, Creek, Logan, Murray, Muskogee, Oklahoma, Payne, and Pottawatomie counties.

ARKANSAS: Benton, Crawford, Hempstead, Hot Spring, Jackson, and Pulaski counties.

MISSOURI: Barry, Carter, Cedar, Dunklin, Jackson, Jefferson, Madison, Mississippi, St. Clair, Scott, and Vernon counties.

KANSAS: Miami County.

7b. *CORYDALIS MICRANTHA* (Engelm.) Gray ssp. **texensis** G. B. Ownbey, ssp. nov.

Herbae annuae glaucae; caulibus 20–45 cm. longis saepe crassis post exsiccationem valde striatis; foliorum laminis pinnatis, segmentis primariis pinnatifidis incisus ultimis oblongo-acutis subapiculatis; racemis saepe crassis folia superantibus, bracteis ovato-attenuatis margine denticulatis infimis ca. 5 mm. longis 2 mm. latis superioribus aliquid minoribus; floribus flavis primo congestis in anthesim remotioribus, pedicellis erectis patulisve 2–4 mm. longis, sepalis fugaceis ca. 1.5 mm. longis ovato-attenuatis, petalo calcarato valde arcuato 12–15 mm. longo carinae cristo satis humili undulato margine bene manifesto supra cristum inflexo calcare obtuso haud globoso, petalo ealcarato exteriori ca. 10 mm. longo margine haud reflexo duobus interioribus 8–10 mm. longis oblanceolatis ungui 3–4 mm. longo, lamina apice quam basi multo latiori, calcare staminali ca. 2 mm. longo clavato, stigmate 2-lobato ca. bis longiori latiori; fructibus erectis vel incurvatis gracilibus 25–30 mm. longis; seminibus ca. 1.5 mm. diam. sub lente aliquid ornatis margine obtuso.

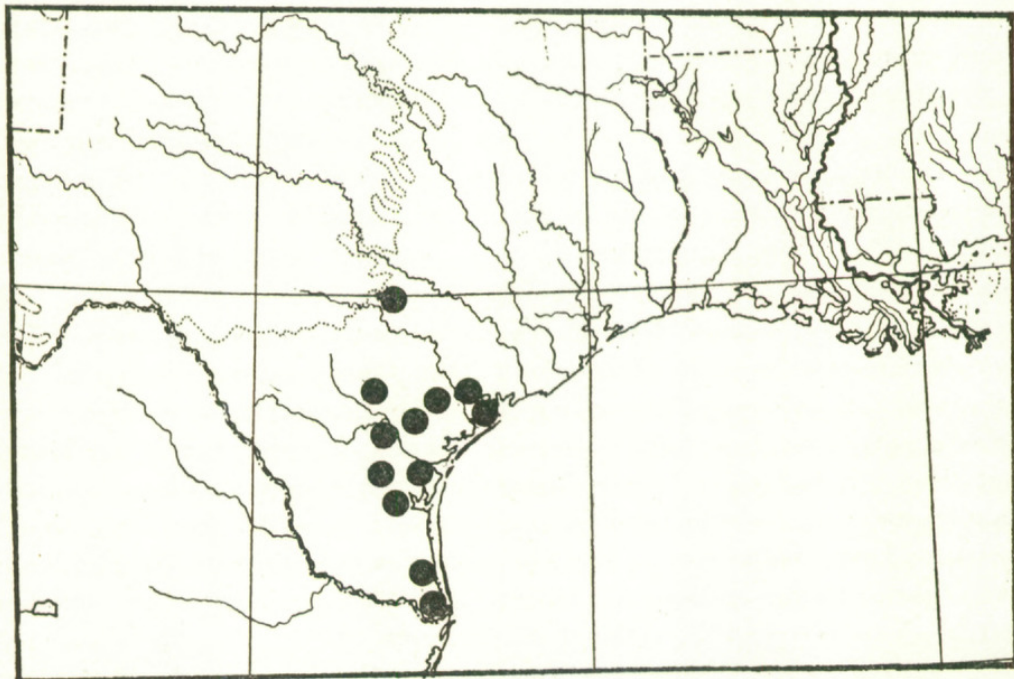
Glaucous annual; stems 20–45 cm. long, often stout and strongly striate when dry, prostrate-ascending; leaf blades pinnate, the primary segments pinnatifid and again incised, the ultimate lobes oblong-acute, subapiculate; racemes often stout, surpassing the leaves; bracts ovate-attenuate, denticulate at the margin, the lowermost about 5 mm. long and 2 mm. broad, the upper somewhat reduced; pedicels erect or spreading, 2–4 mm. long; sepals fugacious, about 1.5 mm. long, ovate-attenuate; flowers yellow, crowded at first, becoming more distant during anthesis; spurred petal strongly arcuate, 12–15 mm. long, the hood with a low undulate crest, the wing margin well developed, reflexed upon the hood, the blunt spur 5–7 mm. long, not globose; spurless outer petal about 10 mm. long, the margin not reflexed; inner petals 8–10 mm. long, oblanceolate, the claw 3–4 mm. long, the blade much broader at the apex than at the base; stamen spur about 2 mm. long, clavate; stigma 2-lobed, twice as broad as high; fruits erect or incurved, slender, 25–30 mm. long; seeds about 1.5 mm. in diameter, moderately decorated under magnification, obtuse at the border, with no ring margin.

This well-defined subspecies is endemic to the coastal plain of southern Texas. It is most closely comparable to ssp. *australis*, but is easily distinguished by its longer fruits and more strongly arcuate spurred petal. In habit and foliage it is very similar to *C. curvisiliqua* ssp. *curvisiliqua* with which it is often confused. It can be distinguished from the latter by its non-muricate seeds and shorter spur which is not globose at the tip.

Moist, often sandy soil, open ground of alluvial plains and uplands; south coastal Texas. Flowers in early spring from about February 20 to March 20; fruits from about March 1 to April 10.

TEXAS: ATASCOSA CO.—moist, alluvial ground, Campbellton, March 10, 1917, *Palmer 11239* (M, G, US). BEE CO.—Beeville, March 30, 1932, *Jones 29365* (M, TYPE). CALHOUN CO.—Bahia del Espiritu-Santo, ex herb. *Berlandier 548, 1799, 1933* (G). CAMERON

co.—Palm Grove, March 3, 1940, *Parks 1429* (M). GOLIAD co.—Goliad, Feb., 1927, *Williams 11* (UT). JIM WELLS co.—sandy loam, about 600 ft. alt., Romarsid Ranch, March 18, 1943, *Freeborn 338* (UT). KENDALL co.—Edge Falls, March 26, 1938, *Parks 29500* (G). KLEBERG co.—Riviera, Feb. 22, 1930, *Harrison* (US). LIVE OAK co.—sandy upland, 41 mi. n. of Alice, March 1, 1944, *Painter & Barkley 14461* (UT). NUECES co.—Corpus Christi, May, 1913, *Orcutt 5829* (M); Robstown, March 26, 1920, *High 91* (M). VICTORIA co.—Victoria, April 6, 1900, *Eggert* (M); sandy, open ground, Victoria, March 4, 1916, *Palmer 9064* (M, D, US); Victoria-Goliad, March 29, 1930, *Tharp* (UT). WILLACY co.—in open ground, sandy situations, March 21, 1937, *Runyon 1618*.



Map 9. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *texensis* Ownbey.

8. *C. CURVISILIQUA* Engelm. ssp. **curvisiliqua** G. B. Ownbey, stat. nov.

Corydalis aurea var. *curvisiliqua* Gray, in Proc. Acad. Phila. 1863:57. 1864, nom. nud.

Corydalis curvisiliqua Engelm. ex Gray, l. c. 1864, nom. nud. in synonym.; apud Gray, Man. Bot. ed. 5: 62. 1867; Bot. Gaz. 11:188. 1886.

Capnoides curvisiliqua Ktze. Rev. Gen. 1:14. 1891.

Neckeria curvisiliqua Rydb. in Univ. Nebr. Bot. Surv. Nebr. 3:24. 1894.

Glaucous winter annual or perhaps biennial; stems 1–several, the primary often erect, the 1–several secondary ascending, 10–40 cm. long, often somewhat branched; basal leaves long-petioled; cauline leaves short-petioled, reduced in size; leaf blades pinnate, the pinnae twice pinnatifid, rarely again incised, the ultimate segments oblong, obtuse or rounded; peduncles usually surpassing the leaves, the primary 6- to 18-, usually about 12-flowered; the secondary fewer-flowered; bracts ovate, 10 mm. or less long, 6 mm. or less wide, the lowest sometimes foliose, much reduced upward; pedicels stout, spreading, 2–3 mm. long; sepals scarious,

broadly ovate to ovate-attenuate, often more or less toothed or undulate at the margin, about 1 mm. long; flowers bright yellow, often strongly arcuate, crowded on the raceme at first, becoming more distant during anthesis; spurred petal 16–18 mm. long, with a very broad wing margin, the crest absent to well developed and undulate or toothed, the spur 7–9 mm. long, often somewhat globose at the blunt tip; spurless outer petal 12–15 mm. long, geniculate, about 3 mm. longer than the inner petals, the crest similar to that of the spurred petal; inner petals oblanceolate, 9–11 mm. long, the slender claws nearly half the total length; stamen spur clavate, bent near the apex, 4–6 mm. long; stigma 2-lobed, twice as broad as high; style slender; fruits slender, erect, moderately to strongly arcuate or incurved toward the floral axis, usually 26–34 mm. long; seeds about 2 mm. in diameter, black, muricate, with essentially no ring margin at maturity.

Subspecies *curvisiliqua* is most easily recognized by its extremely long, erect, incurved fruits, and its seeds which are distinctly muricate under magnification. The latter character is approached nowhere else in the genus, and, indeed, is the strongest character upon which the species is based. The tetragonal character of the fruits mentioned by Gray (Bot. Gaz. 11:189. 1886), although perhaps more pronounced here, especially in fresh material, is by no means unique.

Floral characters which are of value in recognizing this subspecies are the well-developed wing margins of the outer petals, the much-reduced, claw-like basal portion of the unspurred outer petal, and the well-developed spur which is about one-half the total length of the spurred petal. The degree to which the crest is developed is extremely variable; material from the type locality usually has no apparent crest. Some plants, however, have a moderately well developed crest. This diversity is general throughout the range of the subspecies.

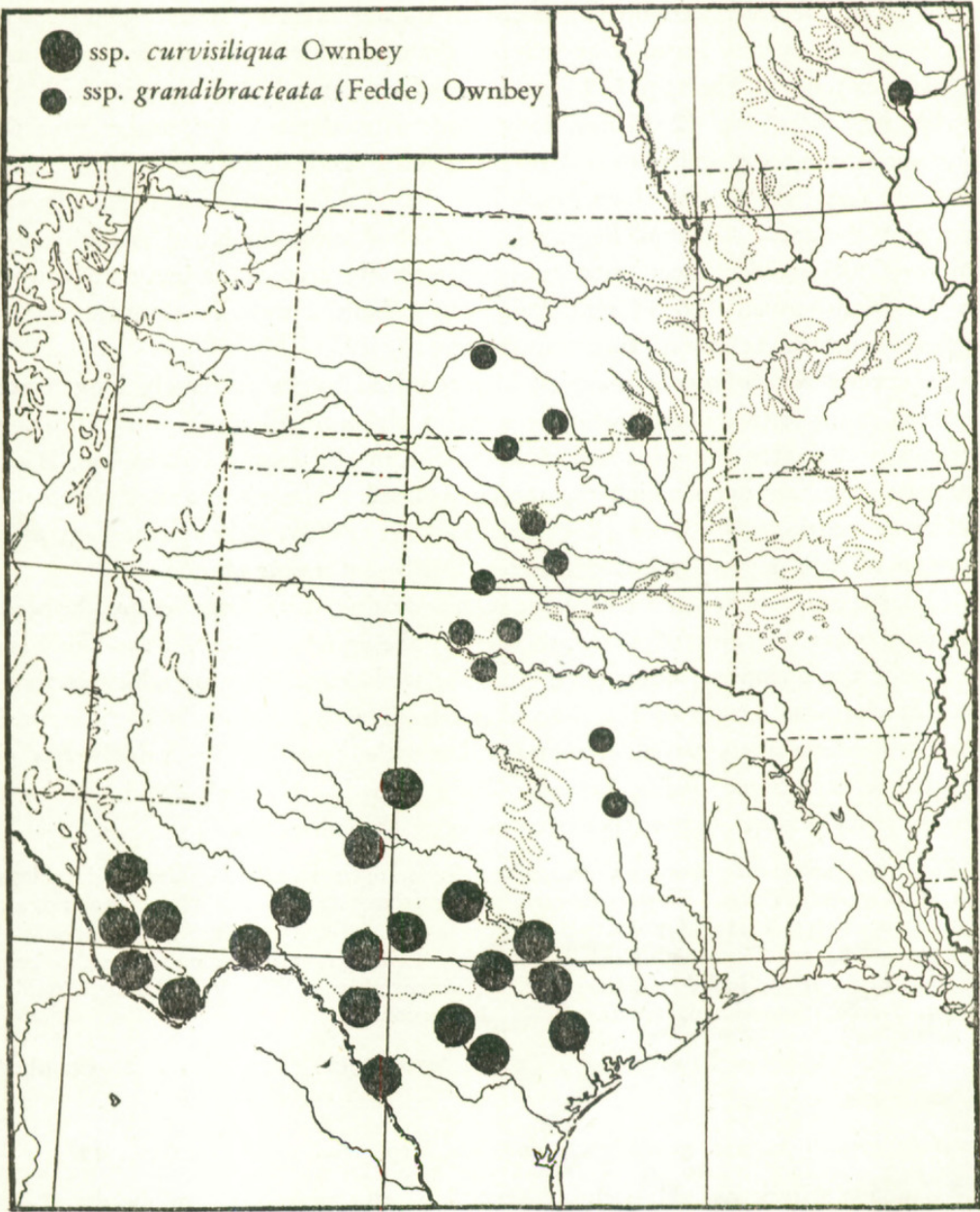
Disturbed soil, sandy bottoms, abandoned fields, open woods, hillsides, and valleys; central to western Texas. Flowers in early spring from about March 1 to May 1; fruits from about March 15 to May 15.

TEXAS: Bexar, Brewster, Caldwell, Comal, Crockett, Culberson, Edwards, Frio, Gillespie, Hays, Irion, Jeff Davis, Karnes, Kerr, Kinney, Llano, Maverick, Medina, Presidio, Taylor, Terrell, Tom Green, Travis, and Uvalde counties.

8a. *C. CURVISILIQUA* Engelm. ssp. ***grandibracteata*** (Fedde) G. B. Ownbey, stat. nov.

Corydalis curvisiliqua var. *grandibracteata* Fedde, Rep. Spec. Nov. 11:291. 1912.

Glaucous winter annual; stems 1–several, stout, ascending, commonly 20–30 cm. long; basal leaves numerous, moderately long-petioled; cauline leaves somewhat reduced, shorter-petioled; leaf blades pinnate, the primary segments pinnatifid and usually again incised, the ultimate segments elliptical to obovate; peduncles stout, surpassing the leaves; bracts conspicuous, usually ovate-acuminate, the lowermost usually 10–15 mm. long and 4–6 mm. wide, somewhat reduced upward; pedicels spreading, usually 2–3 mm. long; sepals ovate, variously toothed; flowers bright yellow; spurred petal 15–18 mm. long, having a well-developed wing margin, the hood crested, the crest conspicuous, regular or undulate, the stout spur 7–9 mm.



Map 10. Distribution of *Corydalis curvisiliqua* Engelm.

long, somewhat globose at the tip; spurless outer petal 12–15 mm. long, geniculate, the basal portion slender, claw-like, the crest similar to that of the spurred petal; inner petals oblanceolate, 9–11 mm. long, the claw slender, 4–5 mm. long; stamen spur about two-thirds the length of the petal spur; stigma twice as broad as high; style slender; fruits slender, erect, incurved toward the floral axis, 20–25 mm. long, gradually tapered apically; seeds about 2 mm. in diameter, black, having a narrow ring margin, distinctly muriculate under magnification.

This subspecies is best distinguished by its slender, lanceolate, erect, incurved fruits, its relatively large flowers, the usually highly developed crest and wing margin, and the large ovate floral bracts. The muriculate character of the seeds, so striking in *ssp. curvisiliqua*, is here reduced nearly to the condition found in *C. aurea ssp. occidentalis*. Hybridization between the two and with *C. micrantha ssp. australis* may account for the anomalous nature of many specimens. However, because of the greatest agreement in floral morphology with *C. curvisiliqua* and because its range is a northward extension of that species I believe that it is properly placed here.

The isolated occurrence of *ssp. grandibracteata* in Muscatine Co., Iowa, perhaps is best explained by a chance introduction of seeds.

Usually in sandy soil, open ground, alluvial plains, roadsides, prairies, and slopes; southern Kansas to northern Texas; eastern Iowa. Flowers from about April 15 to May 15; fruits from about May 1 to May 30.

IOWA: Muscatine County.

KANSAS: Chautauqua, Stafford, and Sumner counties.

OKLAHOMA: Alfalfa, Caddo, Canadian, Cleveland, Comanche, Grady, Kingfisher, Kiowa, Logan, McClain, Oklahoma, and Stephens counties.

TEXAS: Archer, Clay, Collin, Dallas, and Navarro counties.

9. *C. AUREA* Willd. *ssp. aurea* G. B. Ownbey, stat. nov.

Corydalis aurea Willd. Enum. Hort. Berol. 2:740. 1809.

Fumaria aurea Muhl. ex Willd. l. c. 1809, as syn.

Fumaria aurea Ker, Bot. Reg. 1:t. 66. 1815.

Odoptera aurea Raf. Cat. 15. 1824.

Corydalis montana Engelm. ex Gray, in Mem. Am. Acad. 4:6. 1849, nom. nud. in synon.

Corydalis aurea var. *typica* Regel, in Mem. Acad. St. Petersb. 4⁴:19. 1861 (Tent. Fl. Ussuri. 19. 1861); Bull. Soc. Mosc. 34³:145. 1861.

Corydalis aurea var. *parviflora* Regel, in Bull. Soc. Mosc. 34³:146. 1861.

Corydalis aurea β. *macrantha* Wood, Am. Bot. & Fl. 34. 1870.

Capnodes aureum Ktze. Rev. Gen. 1:14. 1891.

Neckeria aurea Millsp. Fl. W. Va. 327. 1892 (W. Va. Agr. Exp. Sta. Bull. 2).

Corydalis Wetherillii Eastw. in Bull. Torr. Bot. Club 29:524. 1902.

Corydalis wyomingensis Fedde, Rep. Spec. Nov. 10:312. 1912.

Corydalis tortisiliqua Fedde, l. c. 313. 1912.

Corydalis Gooddingii Fedde, l. c. 1912.

Corydalis hypocotiformis Fedde, l. c. 314. 1912.

Corydalis Engelmannii Fedde, l. c. 365. 1912.

Corydalis aurea var. *robusta* Fedde, l. c. 379. 1912.

Corydalis monilifera Fedde, l. c. 417. 1912.

Corydalis washingtoniana Fedde, l. c. 419. 1912.

Corydalis macrorrhiza Fedde, l. c. 479. 1912.

Corydalis Albertae Fedde, l. c. 11:196. 1912.

Corydalis Jonesii Fedde, l. c. 1912.

- Corydalis oregana* Fedde, l. c. 290. 1912.
Corydalis densicoma Fedde, l. c. 291. 1912.
Capnoides Wetherillii Heller, in *Muhlenbergia* 7:123. 1912.
Capnoides euchlamydeum Woot. & Standl. in *Contr. U. S. Nat. Herb.* 16:122. 1913.
Corydalis tortisiliqua var. *longibracteata* Fedde, l. c. 11:497. 1913.
Corydalis Engelmannii var. *exaltata* Fedde, l. c. 1913.
Corydalis isopyroides Fedde, l. c. 498. 1913.
Corydalis isopyroides var. *Mearnsii* Fedde, l. c. 12:37. 1913.
Corydalis wyomingensis var. *lativaginata* Fedde, l. c. 38. 1913.
Capnoides Engelmannii Cockerell, in *Univ. Colo. Stud.* 11:216. 1915.
Capnoides macrorrhiza Cockerell, l. c. 1915.
Corydalis euchlamydea Fedde, l. c. 18:32. 1922.

Glaucous winter annual or biennial from a more or less branched caudex; stems sympodial, prostrate-ascending, 10–50, usually 20–35 cm. long; basal leaves long-petioled; cauline leaves barely reduced in size upward, also usually long-petioled; leaf blades pinnate, with 5–7 pinnae, these pinnatifid into about 5 segments which are again incised; ultimate leaf segments broadly to narrowly elliptical, 1.5–several times as long as broad, greatly variable in gross size, subapiculate; peduncles short, terminal; racemes shorter than to barely exceeding the leaves, the primary 10- to 30-, usually 10- to 20-flowered, the secondary 4- to 12-flowered; bracts elliptical to linear, the lowest 4–10 mm. long and 1–2 mm. broad, rarely larger, often denticulate at the apex, much reduced upward; pedicels erect when young, generally reflexed or recurved in fruit, the lowermost 5–10 mm. long; sepals scarious, fugacious, broadly ovate or ovate-attenuate, irregularly toothed, 1–3 mm. long; flowers pale to bright yellow; spurred petal 13–16 mm. long, the hood usually not crested, the crest when present low and incised, the wing margin moderately to well developed, the spur straight or slightly incurved, 4–5 mm. long, the tip somewhat globose; spurless outer petal 9–11 mm. long, the hood and crest as in the spurred petal; inner petals 8–10 mm. long, the claw 3.5–4.5 mm. long, the blade somewhat broader and more distinctly winged distally; stamen spur 2–3 mm. long; stigma about twice as broad as high; fruits commonly 18–24, rarely up to 30 mm. long, usually slender, often erect when young, generally pendent at maturity, straight to moderately arcuate, often moniliform, the valves often torulose when dry; seeds nearly 2 mm. in diameter, black, shiny, turgid, obscurely decorated to nearly smooth under magnification, broadly acute at the edge, with no ring margin.

This subspecies is best distinguished on the basis of the generally weak racemes and slender, pendent or spreading fruits. The racemes ordinarily do not exceed the leaves except in early stages of growth. It intergrades at times with ssp. *occidentalis*, but in general can be distinguished without difficulty when the plant is in fruiting condition.

Contingent upon the broad view of the subspecies adopted here it has been necessary to reduce to synonymy a large number of specific and varietal epithets proposed by Fedde. For the most part, they are founded upon minor variant forms which are by no means mutually exclusive. A brief discussion of the proposed

biological basis for the type of variability found in *C. aurea* is given in the introductory material to this paper.

Corydalis aurea ssp. *aurea* is of north temperate and subarctic distribution. In the northern part of its range it is found at low elevations, but in the southern part it is confined largely to mountainous districts, and may grow at elevations of 11,000 feet or more. Consequent to its wide range and adaptation to a diversity of habitats, this subspecies has become quite polymorphic. It seems probable that a good deal of minor genetic differentiation has taken place in each of the isolated mountain ranges of the Southwest. Ultimately the many forms thus produced may be of nomenclatorial rank. At present their nomenclatorial recognition can add nothing to an understanding of the group.

Among the many recognizable variants which in my opinion are not nomenclatorially important the following are mentioned briefly:

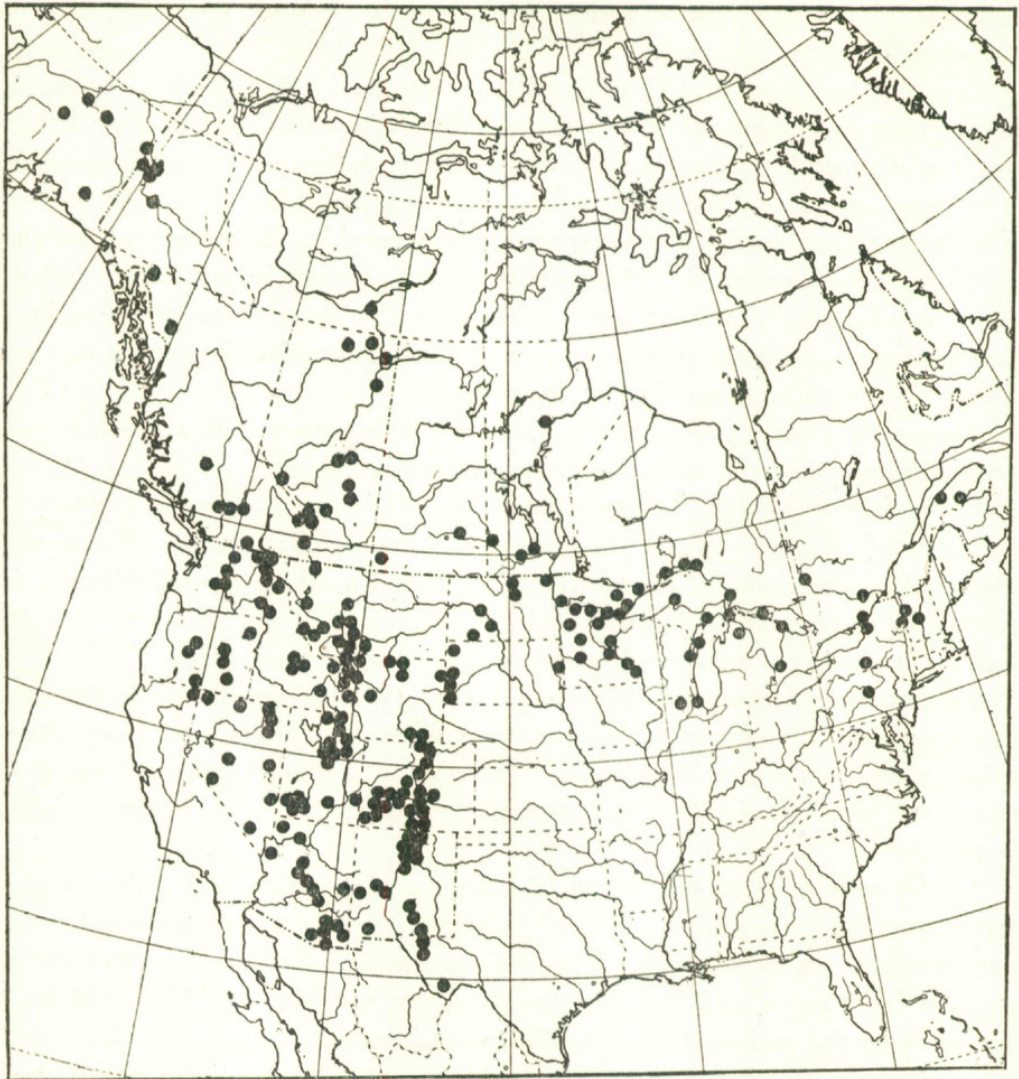
Plants from Rimouski County, Quebec, described as *C. aurea* var. *robusta* by Fedde, are of interest primarily because of their very foliose stems. Plants with similar foliage are found in southeastern Canada and northern United States as far west as the shores of Lake Superior and Lake Michigan. Fruit characters emphasized by Fedde do not set these plants apart from the subspecies proper.

At low elevations in Washington, Oregon, Idaho, Nevada, and Wyoming plants sometimes are found with stout stems, semi-erect fruits, and short, obtuse ultimate segments of the basal leaves. These are all better placed with ssp. *aurea* because of the unreliability and probable superficiality of the distinguishing characters.

In the mountains of Otero and Lincoln counties, New Mexico, is a variant having very large, foliose bracts. In fruit characters it is intermediate between ssp. *aurea* and ssp. *occidentalis*. This variant was described as *Capnoides eublamydeum* by Wootton and Standley, but I cannot see that the differences are in any way essential, and am therefore reducing the name to synonymy.

Particularly striking variant forms having weak, diffusely branched, leafy stems, weak, 1- to 4-flowered racemes, and very broad, incompletely divided ultimate leaf segments occur sporadically throughout the Southwest. Among many localities where plants of this description are found may be mentioned especially Crandall Canyon, Carbon County, Utah, the Charleston Mts., Clark County, Nevada, the Grand Canyon National Park, Arizona, the Santa Catalina and Chiricahua Mts., Arizona, the Black Range, Grant and Sierra counties, New Mexico, the Guadalupe Mts., Culberson County, Texas, and the Davis Mts., Jeff Davis County, Texas. The tendency for plants of this sort to be produced, therefore, is widespread. Viewed separately they often appear significantly different, but against the background of the subspecies proper their significance fades.

Although the outer petals of ssp. *aurea* ordinarily are not crested, an occasional exception to this generalization is met with in northern and western United States. The fact that the presence of a crest apparently is not tied up with any constant morphological difference, together with its erratic occurrence, leads me to believe that it does not warrant serious consideration.



Map 11. Distribution of *Corydalis aurea* Willd. ssp. *aurea* Ownbey.

Loose, open, often gravelly soil, lake shores, talus slopes, ledges, rocky hillsides and creek bottoms, gravel pits, road cuts, and burned-over areas; northeastern United States, northward and westward to Quebec, the Dakotas, Mackenzie, and Alaska, southward in the Rocky Mountains to Arizona, New Mexico and western Texas, at elevations of a few hundred feet in northern United States and Canada to over 11,000 feet in the Colorado Rockies. Flowers throughout the summer months, from about May 1 to August 30; fruits from about May 15 to September 15.

PENNSYLVANIA: Snyder County.

NEW YORK: Essex, Jefferson, and Tompkins counties.

VERMONT: Addison, Chittenden, Rutland, and Windsor counties.

NEW HAMPSHIRE: Grafton County.

ILLINOIS: Cook and Winnebago counties.

MICHIGAN: Alpena, Keewenaw, Mackinac, Montmorency, Oscoda, and Schoolcraft counties.

WISCONSIN: Brown and Door counties.

MINNESOTA: Aitkin, Becker, Beltrami, Carlton, Cass, Chisago, Clearwater, Cook,

Crow Wing, Dakota, Goodhue, Hennepin, Hubbard, Lake, Meeker, Ottertail, Polk, Pope, Ramsey, Renville, St. Louis, Todd, Wabasha, and Winona counties.

SOUTH DAKOTA: Brookings, Custer, Fall River, Harding, Lawrence, Meade, and Pennington counties.

NORTH DAKOTA: Benson, McLean, Morton, Pembina, and Rolette counties.

MONTANA: Carbon, Cascade, Chouteau, Deerlodge, Flathead, Gallatin, Jefferson, Lewis & Clark, Meagher, Missoula, Park, Powell, and Ravalli counties; Glacier National Park.

WYOMING: Albany, Big Horn, Crook, Fremont, Johnson, Lincoln, Park, Sheridan, Sublette, Teton, and Uinta counties; Yellowstone National Park.

COLORADO: Boulder, Chaffee, Clear Creek, Conejos, Custer, El Paso, Fremont, Gilpin, Grand, Gunnison, Hinsdale, Jefferson, Lake, La Plata, Larimer, Mineral, Montezuma, Montrose, Ouray, Park, Pueblo, Rio Grande, Saguache, San Juan, Summit, Teller, and Weld counties; Rocky Mountain National Park.

NEW MEXICO: Bernalillo, Catron, Colfax, Dona Ana, Eddy, Grant, Lincoln, Luna, Mora, Otero, Rio Arriba, Sandoval, San Miguel, Santa Fe, Sierra, Socorro, and Taos counties.

TEXAS: Brewster, Culberson, and Jeff Davis counties.

ARIZONA: Apache, Cochise, Coconino, Gila, Graham, Mohave, Pima, and Yavapai counties; Grand Canyon National Park.

UTAH: Beaver, Cache, Carbon, Daggett, Duchesne, Garfield, Iron, Salt Lake, San Juan, San Pete, Summit, Uintah, Utah, and Wasatch counties.

NEVADA: Clark, Elko, Esmeralda, Humboldt, Lincoln, Nye, and White Pine counties.

CALIFORNIA: Modoc County.

IDAHO: Bannock, Blaine, Bonner, Clark, Custer, Fremont, Kootenai, and Owyhee counties.

OREGON: Crook, Grant, Harney, Lake, and Willamette counties.

WASHINGTON: Chelan, Douglas, Ferry, Kittitas, Okanogan, Pend Oreille, Spokane, Stevens, and Whitman counties.

QUEBEC: BONAVENTURE CO.—Restigouche River, Matapedia, Aug. 1, 1936, *Victorin, Germain & Dominique 48996* (UO, UC, CIUC, G). RIMOUSKI CO.—Massacre Island, on conglomerate covered with moss, coniferous woods, Bic, Aug. 12, 1927, *Rousseau 26871* (US); same locality, June 30, 1927, *Rousseau 26401* (M, WS, G); humus in crevices of calcareous rock, July 8, 1905, *Collins & Fernald 85* (G, UC, NY, US). TEMISCAMING DIST.—Point-au-vent (Lake Temiscaming), June 25, 1918, *Victorin 8358* (M, G, US). WRIGHT CO.—Aylmer, May 26, 1901, *Fowler* (US).

ONTARIO: ALGOMA DIST.—waste ground by Algoma Central Railway, Gray (Mile 229), June 23, 1921, *Pease 18029* (G); ballast near Coppermine Point, Lake Superior, July 7, 1935, *Pease & Ogden 25161* (G). BRUCE CO.—Lion's Head, on damp calcareous rocks, June 11, 1932, *Victorin & Prat 45945* (RM, G). CARLETON CO.—vicinity of Ottawa, May 28, 1921, *Rolland 15761* (WS, NY, US). FRONTENAC CO.—Gardiner's Farm, near Kingston, June 10, 1897, *Langford* (M). LAMBTON CO.—on sides of sand hills, near Port Franks, May 24, 1906, *Dodge 1* (US). MANITOULIN CO.—dry cliffs, Gore Bay, Manitoulin Island, July 5, 1935, *Pease & Ogden 25190* (G, US). THUNDER BAY DIST.—rich shore of Lake Superior, about Lat. 48° 45' N., Long. 87° 15' W., 1 mi. n.e. of Schreiber, Aug. 16, 1937, *Hosie, Losee & Bannan 1413* (G); damp diabase ledge, Norma Creek, Thunder Cape, June 26, 1936, *Taylor, Losee & Bannan 504* (CIUC).

MANITOBA: MARQUETTE DIST.—Fort Ellice, along the line of the Grand Trunk Pacific Railway, June 27, 1906, *Macoun & Herriot* (G). PORTAGE LA PRAIRIE DIST.—Portage la Prairie, along the line of the Grand Trunk Pacific Railway, May 28, 1906, *Herriot* (G); Carberry, 1898, *Thompson* (M). DIST. UNCERTAIN—Piguitonay, Mile 214, route of Hudson Bay Railway, July 8, 1917, *Emerton* (G); Charleswood, June 5, 1915, *Thompson 97* (M).

SASKATCHEWAN: MOOSE JAW DIST.—newly burnt woods, Cypress Hills, June 15, 1884, *Macoun* (G). QU'APPELLE DIST.—moist woods, Qu'Appelle Valley, June 26, 1938, *Shevkenek 115* (G). DIST. UNCERTAIN—in rich, moist ground, usually in burnt-over ground, McKague, June 21, 1940, *Breitung 577* (M, IH, UT, NY).

ALBERTA: CALGARY DIST.—gravel banks and rocky hills, Shaganappi, vicinity of Calgary, 3400–3600 ft. alt., May 30, 1913, *Moodie 137* (NY, US). EDMONTON DIST.—burned area in woods, Edmonton, May 21, 1931, *Moss 2140* (WS). JASPER NAT. PARK—Jasper, 3472 ft. alt., Aug. 31–Sept. 2, 1943, *Scamman 3369* (G, US). MEDICINE HAT DIST.—moist, rocky woods, vicinity of Rosedale, 2200–2500 ft. alt., May 27, 1915, *Moodie 911* (M, CIUC, D, UT, NY, G, US). RED DEER DIST.—n. e. of Buffalo Lake, May 23, 1926, *Brinkman 2015* (US); Sarcee Reserve, June 15 to Aug. 15, 1905, *Goddard 489* (UC). ROCKY MTS. NAT. PARK—Bow River Valley, 4500 ft. alt., Banff, June 9–18, 1906, *Brown 62* (M, NY, G, US); roadside near the village, vicinity of Banff, 4500 ft. alt., June 19, 1899, *McCalla 2124* (NY, US). VICTORIA DIST.—grain field, Fort Saskatchewan, June 10, 1930, *Turner* (G). DIST. UNCERTAIN (probably ATHABASKA)—Athabaska Landing, July 28, 1914, *Hitchcock 12064* (US); Fort Chipewyan, Athabaska, June 5, 1903, *Preble & Cary 5* (US); muddy river bank along lower Firebag River near its mouth, June 3, 1935, *Raup 6033* (G); base of eastern slope of Caribou Mts., about 58° 57' N., 113° 55' W., and 58° 51' N., 113° 57' W., Wood Buffalo Park, Mackenzie Basin, July 17, 1930, *Raup 2439-a* (NY, US).

BRITISH COLUMBIA: CARIBOO DIST.—Alexis Creek, June, 1914, *Newcombe 19* (G). CASSIAR DIST.—above Discovery on road to Surprise Lake, July 10, 1930, *Setchell & Parks* (UC); near head of Ingenika River, Sept. 8, 1910, *Preble & Mixter 689b* (US); near head Iskut River, July 29, 1910, *Preble & Mixter 601* (US). KOOTENAY DIST.—near Goat Creek, 27 mi. n. of Natal, July 4, 1941, *Weber 2296* (M, RM, WS, NY, G); Kicking Horse Valley, vicinity of Field, 4000 ft. alt., June 20, 1906, *Brown 214* (M, NY, G, US). YALE DIST.—near Guichon Creek, 13 mi. s. of Savona, 50° 32' N., 120° 52' W., about 3500 ft. alt., June 23, 1941, *Hitchcock & Martin 7412* (M, RM, WS, UC, IH, NY, G); along Boleen Creek, about 1 mi. n.w. of Falkland, 2400 ft. alt., June 30, 1941, *Hitchcock & Martin 7485* (M, RM, WS, UC, IH, NY, G).

MACKENZIE: Fort Resolution, no date, *Onion, Kennicott & Hardisty* (NY).

YUKON: Fifty-Mile River, Aug. 4, 1899, *Bolton* (US); Dawson, June 3, 1914, *Eastwood 133* (WS, CIUC, G, US); recent burns, Fort Selkirk, June 13, 1899, *Gorman 1023* (NY, US); Klondyke, 1900, *MacLean* (US); Bonanza Creek, Aug. 11, 1899, *Tarleton 49b* (NY, US); Walker Gulch, July 16, 1899, *Williams* (NY); Lake Lebarge, June 23, 1899, *Tarleton 49a* (NY, US).

ALASKA: Eagle to Valdes trail, June 30, 1902, *Collier 73* (US); vicinity of Copper Center, 1908, *Heideman 66* (US); Hot Springs on the Tanana River, July 28, 29, 1909, *Hitchcock* (US); Yukon River country, no date, *Ketchum* (G); banks of railroad cut, Mt. McKinley Nat. Park, Aug. 2, 1939, *Nelson & Nelson 4010* (M, RM, NY, G); Fairbanks, June, 1927, *Palmer 1750* (US); Gopher Center, Copper River region, June 1, 1902, *Poto 14* (US).

9a. *C. AUREA* Willd. ssp. *occidentalis* (Engelm.) G. B. Ownbey, stat. nov.

Corydalis aurea var., Gray in Smiths. Contr. Knowl. 5:10. 1853 (Pl. Wright. 2:10).

Corydalis montana Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867.

Corydalis aurea var. *occidentalis* Engelm. apud Gray, l. c. 1867; Bot. Gaz. 11:188. 1886.

Capnoides montanum Britton, in Mem. Torr. Bot. Club 5:166. 1894.

Neckera aurea occidentalis Rydb. in Univ. Nebr. Bot. Surv. Nebr. 3:24. 1894.

Corydalis crassipedicellata Fedde, Rep. Spec. Nov. 10:364. 1912.

Corydalis bilimbata Fedde, l. c. 379. 1912.

Corydalis chihuahuana Fedde, l. c. 418. 1912.

Corydalis curvisiliquaeformis Fedde, l. c. 11:289. 1912.

Corydalis Jonesii var. *stenophylla* Fedde, l. c. 497. 1913.

Corydalis pseudomicrantha var. *Griffithsii* Fedde, l. c. 12:37. 1913.

Corydalis pachyloba Fedde, l. c. 38. 1913.

Capnoides pachylobum Greene ex Fedde, l. c. 1913, nom. nud. in synon.

Glaucous winter annual or biennial; stems often erect while young, usually 10–25 cm. or more long; basal leaves long-petioled; cauline leaves few, often some-

what reduced in size; leaf blades pinnate, having 5-7 pinnae, these pinnatifid and again incised; ultimate leaf segments usually oblong, 2-5 times longer than broad, subapiculate; peduncles usually stout; racemes surpassing the leaves at least in the early stages of growth, 5- to 20-, usually 8- to 12-flowered; bracts elliptical to linear, 10 mm. or less long, much reduced upward; pedicels erect, 1-5 mm. long; sepals scarious, fugacious, ovate, often toothed at the margin, 2 mm. or less long; flowers mostly bright yellow; spurred petal 14-18 mm. long, the hood usually not crested, the wing margin well developed, the blunt spur 5-9 mm. long, often somewhat globose at the tip; spurless outer petal 8-13 mm. long, geniculate, the hood and margin as in the spurred petal; inner petals 8-11 mm. long, the claw about one-half of the total length; stamen spur 3-6 mm. long; stigma about twice as broad as high; fruits 12-30, commonly 16-18 mm. long, erect, stout, curved upward and inward or obliquely along the floral axis, not moniliform; seeds about 2 mm. in diameter, black, acute at the edge, usually having a narrow marginal ring which is distinctly reticulate under magnification.

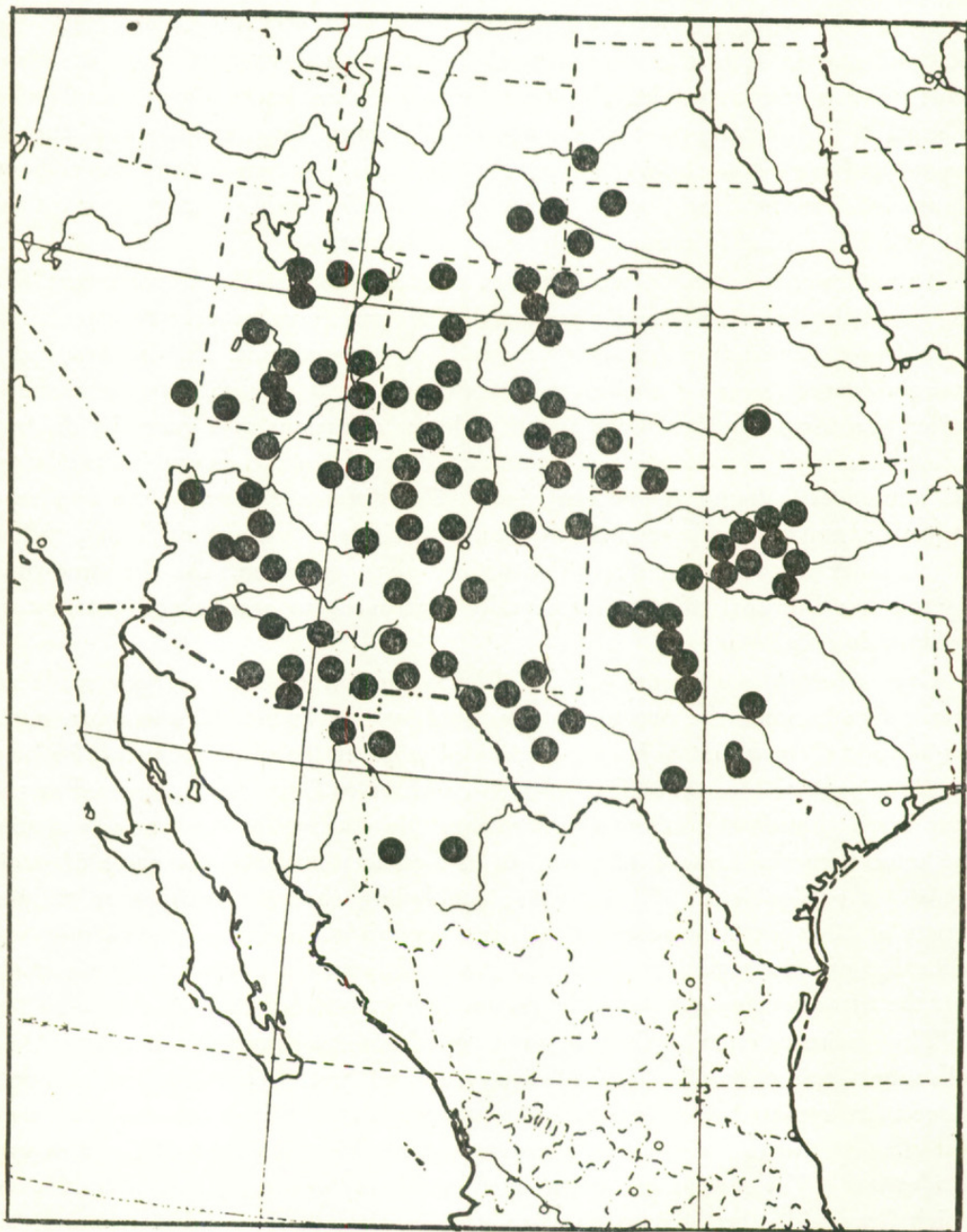
This subspecies is most often confused with *ssp. aurea*. The two are best distinguished by the more strongly monopodial growth form, stouter racemes, generally larger flowers and longer spurs, and, most important, the stouter, more strongly curved, erect or semi-erect fruits of *ssp. occidentalis*. In southwestern United States *ssp. occidentalis* is found at lower elevations as a general rule, but since the seeds of *ssp. aurea* often are washed down from the mountains the latter also sometimes is found at low elevations. The difference between the two represents a summation of several divergent tendencies which together form a rather reliable index to the proper disposition of any given specimen. At the same time the two are segments of a fundamentally heterogeneous species and true intermediates do exist.

Gray referred to this entity in the fifth edition of his 'Manual' but made no clear choice between the two names suggested by Engelmann, *C. aurea* var. *occidentalis* and *C. montana*, as he was undecided whether the plant represented a new species or variety. In 1866 Engelmann, in a letter to Gray (still preserved at the Gray Herb.), made the following statement: "If you retain *montana* as a species you must keep the name, I suppose, but as a variety of *aurea* the name of *occidentalis* is preferable . . .". In 1886, concluding that the entity was truly a variety of *C. aurea*, Gray accepted the name *occidentalis* and published *C. montana* as a synonym. In accordance with this point of view, there seems to be no doubt that the name *occidentalis* should be retained in its modified rank of subspecies.

The specimens cited by Gray in 1886 are of historical interest. Fendler's 1847 collections from Santa Fe, New Mexico, are cited first. These specimens appear to me to be typical but depauperate *C. aurea* *ssp. aurea*. The fact that they were first cited has led to their general acceptance as the historical type of *C. aurea* var. *occidentalis*. The second collection cited is Wright 1309 from El Paso, Texas, which Gray said is better representative of the entity. This is quite true, and this collection is typical of the subspecies as understood today. Next cited is Pringle

198 (later taken as the type of *C. chihuahuana* Fedde) which is again typical *ssp. occidentalis* as are Palmer's 1865 collections from Arizona (at least as to *Coues & Palmer 294*), and *Rusby 9* from the Burrow Mountains. The portion of *Hall & Harbour 31*, cited last, deposited in the Gray Herbarium, is true *ssp. occidentalis*; material bearing identical labels deposited in the Missouri Botanical Garden Herbarium and in the United States National Herbarium is *ssp. aurea*.

Loose, often sandy, dry soil, bottom-lands, prairies, plains, foothills and mesas, and



Map 12. Distribution of *Corydalis aurea* Willd. *ssp. occidentalis* (Engelm.) Ownbey.

along ditches, railroad embankments and washes, at elevations of about 1000–6500 feet; southwestern South Dakota and eastern Wyoming to western Oklahoma, Texas, northern Mexico, and Nevada. Flowers in spring at lower elevations, in summer at higher elevations, from about March 15 to July 30; fruits from about April 1 to August 15.

SOUTH DAKOTA: Fall River County.

NEBRASKA: Banner and Dawes counties.

KANSAS: Stafford County.

OKLAHOMA: Beckham, Blaine, Caddo, Canadian, Cimarron, Custer, Grady, Greer, Jackson, Jefferson, Kingfisher, Kiowa, Texas, and Tillman counties.

TEXAS: Childress, Comanche, Crosby, Culberson, Dickens, Fisher, Hall, Hudspeth, Jeff Davis, Kent, Lubbock, Nolan, Reeves, Scurry, and Sutton counties.

WYOMING: Albany and Platte counties.

COLORADO: Arapahoe, Archuleta, Baca, Boulder, Denver, Fremont, Garfield, Gunnison, Huerfano, La Plata, Larimer, Las Animas, Moffat, Montrose, Ouray, Pueblo, Rio Grande, and Weld counties.

UTAH: Duchesne, Emery, Garfield, Grand, Millard, Piute, Salt Lake, San Juan, Sevier, Uintah, Utah, and Washington counties.

NEVADA: Lincoln County.

ARIZONA: Apache, Cochise, Coconino, Gila, Graham, Maricopa, Mohave, Navajo, Pima, Pinal, Santa Cruz, and Yavapai counties.

NEW MEXICO: Catron, Colfax, Dona Ana, Eddy, Grant, Hidalgo, Luna, McKinley, Quay, Rio Arriba, Sandoval, San Juan, San Miguel, Socorro, Taos, Torrance, and Valencia counties.

CHIHUAHUA: Sept., 1934, *Dobie 13* (UT); Casas Grandes, June 2, 1899, *Goldman 433* (G, US); St. Diego, 6000 ft. alt., April 18, 1891, *Hartman 600* (NY, G, US); Chihuahua, spring, 1936, *LeSueur Mex-516* (UT); Majalca, June 24, 1936, *LeSueur 1207* (M, G); vicinity of Chihuahua, about 4250 ft. alt., April 8–27, 1908, *Palmer 4* (M, NY, G, US); valley near Chihuahua, March 22, 1885, *Pringle 198* (UC, NY, G, US—Isotypes of *C. chihuahuana* Fedde); 14 mi. s. e. of Minaca, 6500 ft. alt., July 25, 1937, *Shreve 8012* (UA); near Colonia Garcia in the Sierra Madres, 7300 ft. alt., July 25, 1889, *Townsend & Barber 163* (M, UC, NMA, NY, G, US—Isotypes of *C. crassipedicellata* Fedde); Santa Eulalia plains, 1885, *Wilkinson* (D).

DURANGO: San Ramon, April 21 to May 18, 1906, *Palmer 72* (M, UC, NY, G, US); Otinapa, July 25 to Aug. 5, 1906, *Palmer 399* (M, NY, G, US).

SINALOA: By spring water in shady canyon, near Platano, Sierra Monterey, March 9, 1940, *Gentry 5869* (M, UA, NY, G).

SONORA: Babispe, 5330 ft. alt., Dec. 24, 1890, *Hartman 358* (G); no definite locality, 1890, *Lloyd 369* (G).

STATE UNCERTAIN: Mexico, no date, *Coulter 664* (M, NY, G).

10. *C. PSEUDOMICRANTHA* Fedde, Rep. Spec. Nov. 11:499. 1913 .

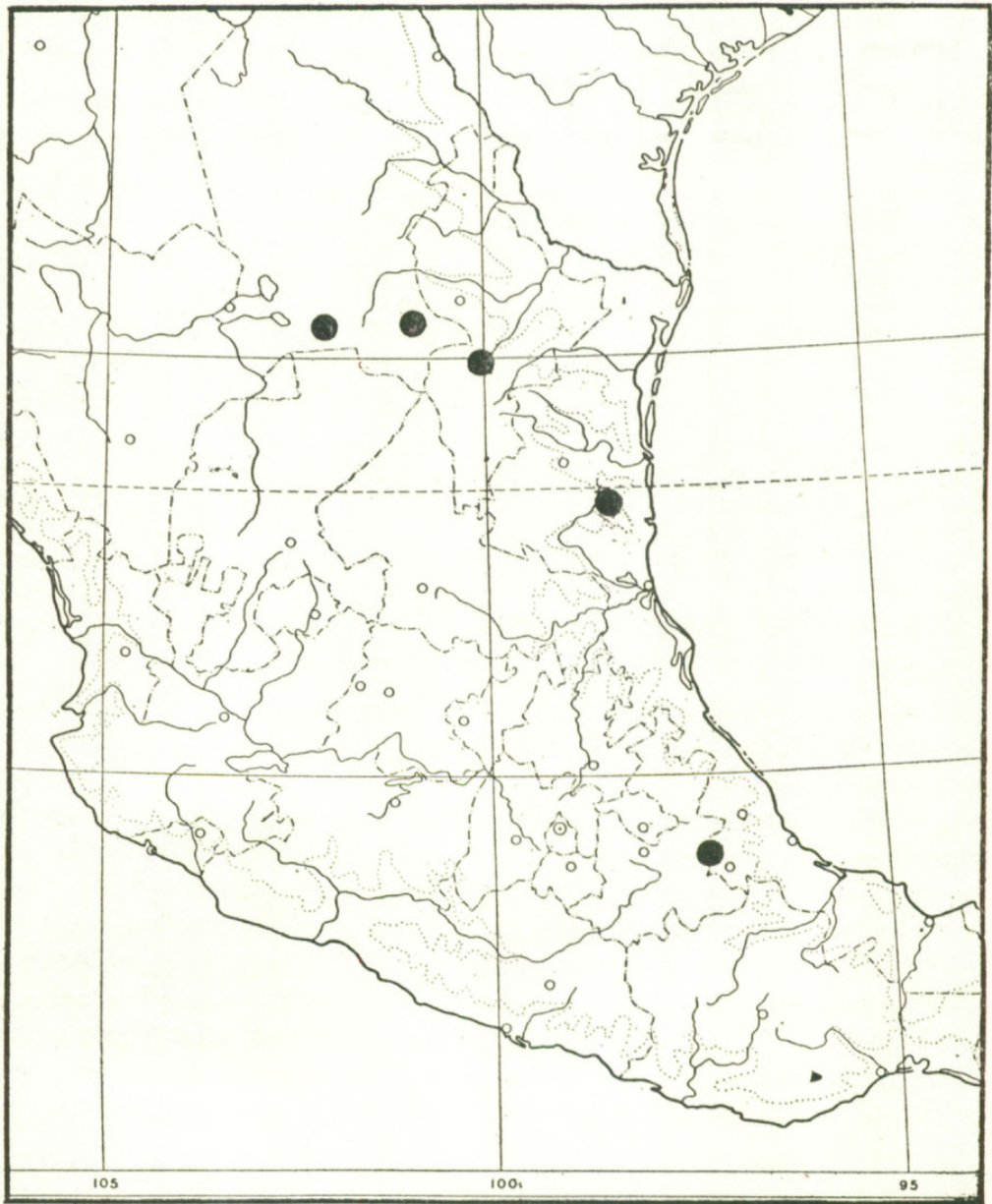
Glaucous or green biennial (or annual?); stems 1–several, sympodial, usually 20–40 cm. long, prostrate-ascending; basal leaves crowded, long-petioled; cauline leaves short-petioled, hardly reduced upward; leaf blades pinnate, the primary segments pinnatifid and again incised, the ultimate lobes elliptical, subapiculate; normal-flowered racemes, when present, 6- to 12-flowered; cleistogamous-flowered racemes abundant, 1- to 5-flowered; bracts elliptical to obovate, 2–8 mm. long, 1–5 mm. broad, often minute on cleistogamous-flowered racemes; pedicels erect, the lower 1–3 mm. long, shorter upward; sepals about 1 mm. long and 0.5 mm. broad, ovate-attenuate; flowers pale yellow, inconspicuous, crowded at anthesis; spurred petal 10–12 mm. long, the hood crestless, the wing margin narrow, the spur 3–4 mm. long, not globose at the tip; spurless outer petal 8–9 mm. long, slender, usually straight; inner petals 7–8 mm. long, narrowly oblanceolate, the

claw about two-fifths the total length; stigma 2-lobed, rectangular, twice as broad as high; fruits erect, commonly 25–30 mm. long, slender, straight or moderately curved; seeds about 2 mm. in diameter, black, submuricately decorated under magnification especially at the often distinct ring margin.

This subspecies is best distinguished by its slender, erect and usually straight fruits, in contrast to those of *C. aurea* ssp. *aurea* which are mostly pendent and curved. The presence of cleistogamous flowers suggests an affinity with *C. micrantha* but size and decoration of the seeds indicate that it is more properly maintained as a distinct species.

Mountains of southern Coahuila to Vera Cruz, Mexico, at elevations of about 7000–9500 feet. Flowers and fruits throughout the spring and summer months.

COAHUILA: Saltillo, Sept., 1898, *Palmer* 356 (G, US); Sierra de Parras, 8000–9000 ft. alt., July, 1910, *Purpus* 4602 (M, UC, G, US, TYPE).



Map 13. Distribution of *Corydalis pseudomicrantha* Fedde.

NUEVO LEON: Sierra Madre Oriental; lower San Francisco Canyon, about 15 mi. s. w. of Galena, 7500–8000 ft. alt., June 12, 1934, *Mueller & Mueller 773* (UT, G).

TAMAULIPAS: Canyon de Garrapata, April, 1926, *Runyon 1021* (G, US).

VERA CRUZ: Boco del Monte, Aug., 1908, *Purpus 3073* (M, UC, NY, G, US).

INTRODUCED SPECIES

C. lutea DC, a European species, was collected at Elk Rock, Multnomah County, Oregon, M. W. Gormon 4076, June 2, 1917 (WS, D); J. C. Nelson & M. W. Gormon 1259, same date (G). Gormon made the following comment on the label: "Com. Probably esc. from cultivation. Native of S. Eur. where it runs wild as a weed." This apparently is the only recorded instance of a native European or Asiatic species having escaped from cultivation in the United States. Doubtless it has happened other times, as many Eurasian species are attractive horticultural curiosities and have been grown in this country. Sporadic occurrence of such species or of weedy species accidentally introduced is to be expected.

C. lutea has the following characteristics: Leaves thrice ternately compound or incised, the ultimate segments elliptical; flowers yellow, the spur about one-fourth the total length of the spurred petal; fruit about 10 mm. in length, long-pedicellate.

EXCLUDED SPECIES

Corydalis biaurita Hornem. Hort. Hafn. 2:668. 1815 = *DICENTRA* sp.

C. bracteosa Spreng, Syst. Veg. ed. 16. 3:162. 1826 = *DICENTRA* sp.

C. canadensis Goldie, in Edinb. Phil. Jour. 6:329. 1822 = *DICENTRA CANADENSIS* (Goldie) Walp.

C. Cucullaria Pers. Syn. Pl. 2:269. 1807 = *DICENTRA CUCULLARIA* (L.) Bernh.

C. eximia Link, Enum. Hort. Berol. 2:218. 1822 = *DICENTRA EXIMIA* (Ker) Torr.

C. formosa Pursh, Fl. Am. Sept. 2:462. 1816 = *DICENTRA FORMOSA* (Andr.) DC.

C. fungosa Vent. Choix de Pl. t. 19. 1803 = *ADLUMIA FUNGOSA* (Ait.) Greene.

C. ochotensis Turcz. Reported from Sitka, Alaska, by Regel, in Bull. Soc. Mosc. 34³:142. 1861. This species actually does not occur in America.

C. paeoniaefolia Pers. Syn. Pl. 2:269. 1807. Listed as a questionable synonym of *C. Scouleri* Hook., Torrey and Gray, Fl. N. Am. 1:69. 1838. This Asiatic species actually is not found in America.

C. tenuifolia Pursh, Fl. Am. Sept. 2:462. 1816 = *DICENTRA* sp.

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The collector's numbers are printed in *italics*, or if the collection is unnumbered, it is indicated by a dash following the collector's name. The numbers in parentheses are those assigned to the species and subspecies in this revision.

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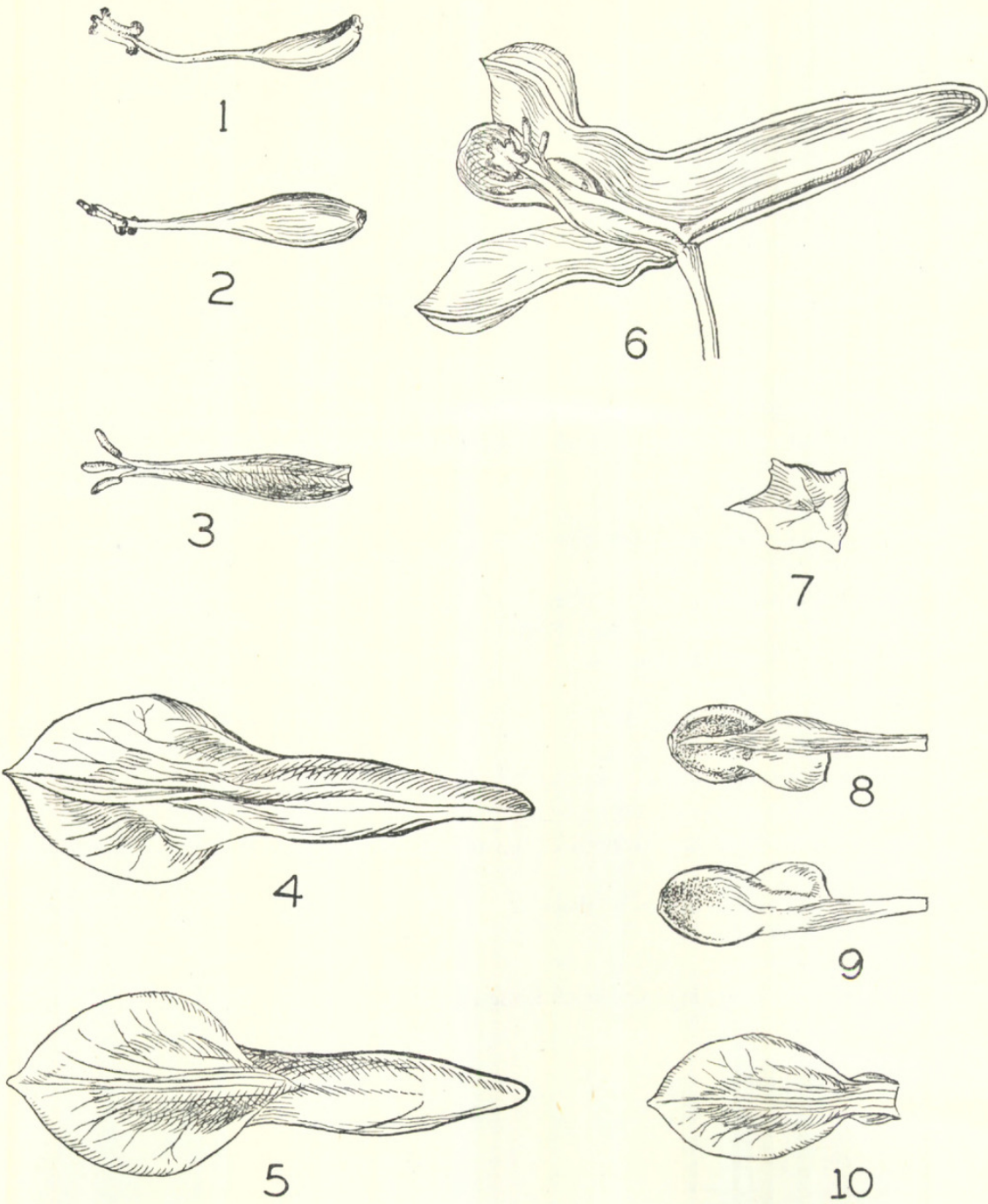
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EXPLANATION OF PLATE

PLATE 28

Generalized floral morphology of *Corydalis* drawn from *C. Caseana* Gray ssp. *Brandegei* (Wats.) Ownbey.

- Fig. 1. Dorsal view of gynoecium.
- Fig. 2. Lateral view of gynoecium.
- Fig. 3. Unspurred stamen phalange.
- Fig. 4. Exterior view of spurred petal.
- Fig. 5. Interior view of spurred petal.
- Fig. 6. Internal structure of flower showing arrangement of parts.
- Fig. 7. Sepal.
- Fig. 8. Exterior view of clawed inner petal.
- Fig. 9. Interior view of clawed inner petal.
- Fig. 10. Interior view of unspurred outer petal.



OWNBEY—MONOGRAPH OF CORYDALIS

EXPLANATION OF PLATE

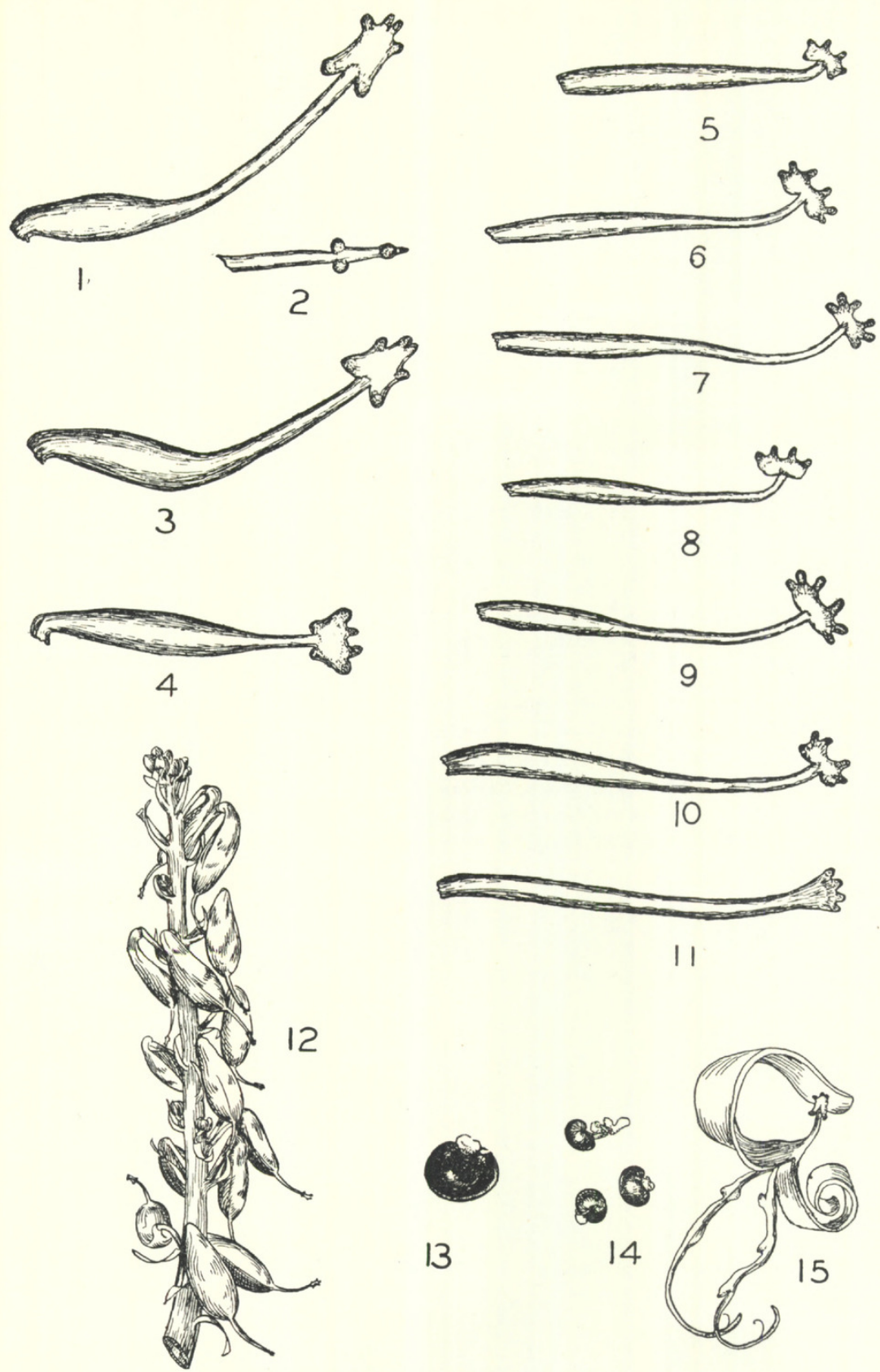
PLATE 29

Figs. 1-11. Gynoecia of species of *Corydalis* at flowering time; drawn especially to show morphology of the stigma. Each drawing is representative of all subspecies of the species; \times about 8.

- Fig. 1. *C. Caseana* Gray.
- Fig. 2. *C. Caseana* Gray; side view of stigma.
- Fig. 3. *C. Scouleri* Hook.
- Fig. 4. *C. pauciflora* (Steph.) Pers.
- Fig. 5. *C. micrantha* (Engelm.) Gray.
- Fig. 6. *C. curvisiliqua* Engelm.
- Fig. 7. *C. aurea* Willd.
- Fig. 8. *C. flavula* (Raf.) DC.
- Fig. 9. *C. crystallina* Engelm.
- Fig. 10. *C. pseudomicrantha* Fedde.
- Fig. 11. *C. sempervirens* (L.) Pers.

Figs. 12-15. *C. Caseana* Gray; drawings representative of Sections RAMOSO-SIBIRICAE and PES-GALLINACEUS.

- Fig. 12. Raceme in fruit; \times about 1.
- Fig. 13. Seed; \times 4.
- Fig. 14. Seed; \times 2.
- Fig. 15. Fruit, showing manner of dehiscence; \times 4.



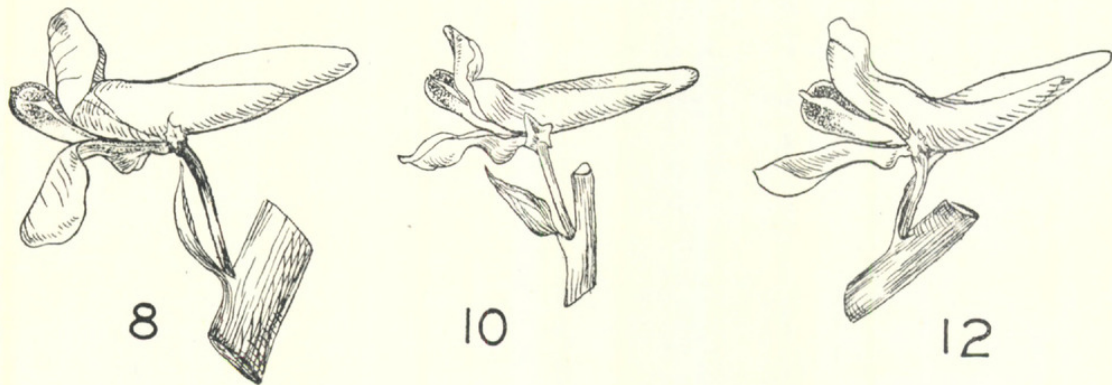
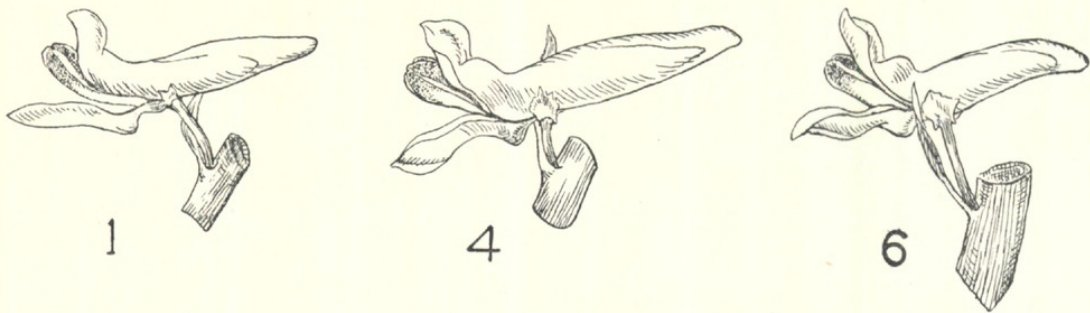
OWNBEY—MONOGRAPH OF CORYDALIS

EXPLANATION OF PLATE

PLATE 30

Flowers of the subspecies of *Corydalis Caseana* Gray and of *Corydalis Scouleri* Hook. An interior view of the unspurred outer petal is shown in each case to illustrate differences in structure; $\times 1\frac{1}{2}$.

- Figs. 1-3. *C. Caseana* Gray ssp. *Caseana* Ownbey.
- Figs. 4-5. *C. Caseana* Gray ssp. *Brandegei* (Wats.) Ownbey.
- Figs. 6-7. *C. Caseana* Gray ssp. *brachycarpa* (Rydb.) Ownbey.
- Figs. 8-9. *C. Caseana* Gray ssp. *Cusickii* (Wats.) Ownbey.
- Figs. 10-11. *C. Caseana* Gray ssp. *hastata* (Rydb.) Ownbey.
- Figs. 12-13. *C. Scouleri* Hook.



EXPLANATION OF PLATE

PLATE 31

Corydalis pauciflora (Steph.) Pers.

Fig. 1. Raceme in fruit; \times about $1\frac{1}{2}$.

Fig. 2. Habit of plant; \times about $1\frac{1}{2}$.

Fig. 3. Stigma; \times 8.



Ownbey, Gerald B. 1947. "Monograph of the North American Species of *Corydalis*." *Annals of the Missouri Botanical Garden* 34, 187–259.

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