

A Taxonomic Revision of *Collinsonia* (Lamiaceae) Based on Phenetic Analyses of Morphological Variation

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ABSTRACT. *Collinsonia* (Lamiaceae) is a small genus restricted to eastern North America with four species commonly recognized: *C. canadensis*, *C. serotina*, *C. tuberosa*, and *C. verticillata*. Considerable taxonomic confusion exists within subgenus *Collinsonia* (all taxa except *C. verticillata*). Principal components and canonical variates analysis were performed on a macro-morphological dataset of 23 variables scored for 118 specimens of subgenus *Collinsonia*. Results from field and herbarium observations and from the phenetic analyses indicate that specimens of *C. serotina* with four stamens (hereafter referred to as *C. anisata*) represent a distinct species. Specimens of *C. serotina* with two stamens are intermediate between *C. canadensis* and *C. anisata* and are tentatively recognized as *C. punctata*; further study is needed to determine their origin and evolutionary status. *Collinsonia tuberosa* and *C. canadensis* show considerable phenetic overlap and are here merged under *C. canadensis*. Four species of *Collinsonia* are now recognized: *C. anisata*, *C. canadensis*, *C. punctata*, and *C. verticillata*.

KEYWORDS: *Collinsonia*, Lamiaceae, morphology, phenetic analysis, Southeast U.S. endemic.

Collinsonia L. (Lamiaceae) is an eastern North American genus of perennial herbs with its center of diversity in the southeastern United States. Four species are commonly accepted: *C. canadensis* L., *C. serotina* Walter, *C. tuberosa* Michx., and *C. verticillata* Baldwin ex Elliott. Despite previous taxonomic work on the genus and extensive floristic work in the southeastern United States, the geographical patterns of morphological variation in *Collinsonia* are still poorly known.

Collinsonia was first described by Linnaeus (1737) in *Hortus Cliffortianus* and later included in *Species Plantarum* (Linnaeus 1753) and *Genera Plantarum* (Linnaeus 1754). Rafinesque (1817, 1825) distinguished three new genera, *Diallosteyra* Raf., *Hypogon* Raf., and *Pleuradenia* Raf., based on minute differences in calyx shape or stamen number, but these genera were not widely accepted. Bentham (1876) placed *Collinsonia* in tribe Mentheae ("Satureieae"), in a small, unnamed subgroup of Origaninae ("Menthoideae") with the mostly eastern Asian genera *Elsholtzia* Willd., *Keiskea* Mig., *Mosla* (Benth.) Buch.-Ham. ex Maxim., *Perilla* L., and *Perillula* Maxim (corrected nomenclature follows Sanders and Cantino 1984). Briquet (1895–1896) assigned *Collinsonia* to subfamily Lamioideae ("Stachyoideae"), tribe Mentheae ("Saturejeae"), and subtribe Collinsoniinae ("Perillinae") with the genera *Micheliella* Briq., *Mosla*, *Perilla*, and *Perillula*. The major differences between Bentham's (1876) and Briquet's (1895–1896) classifications of *Collinsonia* and its relatives were Briquet's transfer of *Elsholtzia* and *Keiskea* to the tribe Pogostemoneae and his separation of *Collinsonia* into two genera, *Collinsonia* and *Micheliella*. *Micheliella* sensu Briquet consisted of *M. anisata* (Sims) Briq. and *M. verticillata* (Elliott) Briq., both with four stamens, whereas *Collinsonia* consisted of only those species with two fertile stamens.

Wunderlich (1967) recombined *Collinsonia* and *Micheliella* into the single genus *Collinsonia* but retained *Keiskea* and *Elsholtzia* in a separate tribe, Elsholtzieae. In the last major reorganization of the Lamiaceae, Cantino et al. (1992) assigned *Collinsonia* to subfamily Nepetoideae and tribe Elsholtzieae with the genera *Elsholtzia*, *Keiskea*, *Mosla*, *Perilla*, and *Perillula*. Tribe Elsholtzieae sensu Cantino et al. (1992) is the same as Bentham's unnamed subgroup of subtribe Origaninae. A phylogenetic analysis of chloroplast restriction site variation (Wagstaff et al. 1995) supported the tribe Elsholtzieae as it is presently delimited. In a cladogram based on *rbcL* sequences (Kaufmann and Wink 1994), *Collinsonia* occupied a basal position within Nepetoideae, but no other genera of Elsholtzieae were included in this analysis. Harley et al. (2003) included *Keiskea* as a synonym of *Collinsonia*, citing the lacinate lower corolla lobe of *Collinsonia* sensu stricto as the only morphological distinction between the two genera. Phylogenetic analysis of nuclear ribosomal ITS sequence data, however, did not support the merger of *Collinsonia* and *Keiskea* into one genus (Peirson 2003; Peirson et al. 2004); *Keiskea* grouped more closely with *Perilla* than with *Collinsonia*.

Shinners (1962) published the only taxonomic treatment of the genus. He provided a brief synopsis of *Collinsonia* based on herbarium studies but performed no quantitative analyses and studied no natural populations. Shinners recombined the two genera and synonymized most of the approximately 35 specific names within *Collinsonia*. Shinners defined species boundaries within the genus, providing a key to the four species that he recognized (*C. canadensis*, *C. serotina*, *C. tuberosa*, and *C. verticillata*), but no species descriptions. He divided *Collinsonia* into two subgenera, *Collinsonia* and

Micheliella, based in part on Briquet's division of the genus. He designated the spring-blooming *Collinsonia verticillata* as the sole species of subgenus *Micheliella*, its subverticillate to opposite leaves and flowers, lack of subtending floral bracts, and basally enlarged and flattened pedicels being the primary distinctions between it and subgenus *Collinsonia*. *Collinsonia anisata* was not included in subgenus *Micheliella* but instead placed in synonymy with *C. serotina*. Shinnners downplayed the differences in stamen number in the genus, citing a specimen of *C. serotina*, *Godfrey and Kral 54288* (FSU), on which some flowers have two stamens and others on the same plant have four. The three fall-blooming species, *C. canadensis*, *C. serotina*, and *C. tuberosa*, were designated as subgenus *Collinsonia*, which has strictly opposite leaves, cream to yellow flowers, subtending floral bracts, pedicels not enlarged at the base and either two or four fertile stamens.

Despite Shinners' synopsis of the genus, considerable taxonomic and nomenclatural confusion involving subgenus *Collinsonia* persists. Numerical phenetic analyses (Duncan and Baum 1981) and field and herbarium observations were employed here to assess the morphological variation within subgenus *Collinsonia*. *Collinsonia verticillata* is clearly distinct, differing from the other species in blooming period and several morphological traits, and was therefore not included in the phenetic analyses. It was, however, included in the field and herbarium studies and taxonomic treatment. For this classification, a primarily phenetic species criterion (De Queiroz 1998; Sneath and Sokal 1973) was used to determine the boundaries of species.

MATERIALS AND METHODS

Field Studies and Specimen Collections. Field studies were conducted in 2001 of 22 natural populations of *Collinsonia*, representing all four commonly recognized species. Voucher specimens for each population were deposited in the Bartley Herbarium of Ohio University (BHO). Live specimens from some populations were transplanted to the Ohio University greenhouse or botanical garden for growth under similar conditions. Fresh flowers of several plants per population were preserved in 70% EtOH. Information regarding habitat and intrapopulational variation was recorded.

Herbarium Studies. Over 1,350 herbarium specimens of *Collinsonia* were examined from the following herbaria: BHO, BM, BRIT, CHARL, FLAS, FSU, GA, GH, K, KNK, KY, MICH, MISS, MU, MUHW, NCU, NLU, NO, NY, OXF, PH, TENN, UNA, USCH, VPI (abbreviations follow Holmgren et al. 1990). All original descriptions of the taxa were obtained, and exhaustive attempts were made to locate all extant type specimens by contacting the relevant herbaria. Unfortunately, only some of the type specimens could be located; the existence and whereabouts of many type specimens remain unknown. When original type material could not be located and was presumed destroyed, a neotype was designated.

A review of floristic manuals and generic treatments was conducted to produce an initial list of gross morphological characters used to distinguish the species (viz., leaf shape, stem size, calyx size and stamen number). Specimens were examined and provisionally grouped into Shinners' taxa according to these features. Intermediates and apparent hybrids were initially included with the species they most closely resembled and whose geographic

range was most similar. The delimited groups were examined more closely, and a preliminary list of 73 macromorphological characters was assembled for use in the phenetic analyses. Ten specimens or operational taxonomic units (OTU's) of each species in subgenus *Collinsonia* were selected to represent the morphological variation and geographical range of each species and were scored for the 73 characters. Length and width measurements were made with a ruler or an ocular micrometer attached to a dissecting microscope. Pubescence and glandularity were measured using an ocular grid, and leaf angles were calculated using a protractor and then converted to radians.

Each OTU was represented by a single measurement per variable. Leaf measurements were taken from the largest leaf that could be scored for all leaf characters. Degree of leaf pubescence and glandularity on the lower one-third of the abaxial surface of the leaf were recorded as the number of trichomes or punctate glands per ocular grid square at specific magnifications. Major veins were avoided, as they were more pubescent than the surrounding leaf surface. Number of leaf teeth per side was scored for the side that had more leaf teeth if the two sides differed in number. Flowers (at full anthesis) were chosen from the middle portion of the inflorescence. Corolla, calyx, and pedicel characters were measured on the same flower. Bracts were measured from the upper third of the inflorescence or wherever their size was consistent. Anther and filament were chosen from the anterior pair of stamens, and the larger of the two anther thecae was measured. Whenever multiple measurements were possible, the largest value was recorded. Trichome length was recorded from the longest "normal" hair. Extreme outliers were not measured.

Phenetic Analyses. The initial dataset (30 OTU's \times 73 variables) was divided into three separate datasets, representing vegetative, inflorescence, and floral variables and was subjected to several iterations of canonical variates analysis (CVA) using Number Cruncher Statistical Software (NCSS, Hintze 1999). Characters were evaluated for their usefulness in separating the taxa, and those characters with variable-variate correlation values of less than 0.25 (absolute value) were discarded (as described in Ballard et al. 2001). Canonical variates analysis was repeated. The most highly correlated characters ($R^2 > 0.90$) were identified, and at least one character from each correlated set was removed during each iteration of CVA until a final character list of 22 continuous characters and one two-state character was distilled (Table 1).

Eighty-eight additional specimens of *Collinsonia* were selected for the final phenetic analysis. Specimens were selected to represent fully the morphological and geographic variation in the genus. OTU's were scored for the 23 variables, with each OTU represented by a single measurement per variable (in the manner described previously). Unavoidably 25 OTU's (approximately 22% of the total) contained at least one missing variable. Two ordination techniques were used for the final analyses. Principal components analysis (PCA) and canonical variates analysis (CVA) were carried out with Number Cruncher Statistical Software (NCSS, Hintze 1999).

PCA does not take into account a priori group assignments and was thus used to examine phenetic variation independent of taxon assignment. To test whether taxa delimited on the basis of stamen number are phenetically cohesive in the absence of this character, stamen number was removed from the PCA. Specimens with missing data were not included, which ultimately reduced the dataset to 93 OTU's \times 22 variables. PCA was performed on a standardized set of variables. The PCA acted upon a correlated dataset (scale-invariant correlation matrix), and varimax rotation was used to analyze the data. Components with eigenvalues greater than 1.0 were extracted and interpreted.

Unlike PCA, CVA uses combinations of weighted variables to maximize the variation between pre-selected groups relative to the variation within groups and provide the greatest separation of group centroids (Sneath and Sokal 1973). Based on the results of the PCA, four taxon groups were used in the CVA: *C. canadensis*, *C. serotina* with two stamens, *C. serotina* with four stamens, and *C. tuberosa*. As in the PCA, stamen number was not included among the variables in the CVA. CVA does not accommodate specimens

TABLE 1. Characters used in final phenetic analyses of morphological variation in *Collinsonia* subgenus *Collinsonia*. Variables 1 through 22 are continuous and variable 23 is two-state. All lengths were measured to the nearest 1.0 mm, 0.1 mm or 0.01 mm depending on scale. Leaf apex angle was measured to the nearest 1° and then converted to radians. Glandularity and pubescence were recorded as the number of trichomes or punctate glands per grid square on the ocular micrometer at the stated magnification.

Stem and leaf characters

1. Stem pubescence—between lowest 2 leaves (6×)
2. Stem width—between 1st and 2nd nodes (mm)
3. Leaf blade length (mm)
4. Leaf apex angle (°)
5. Leaf teeth—number per side
6. Leaves glandularity—lower surface (3×)
7. Leaf pubescence—lower surface (3×)

Inflorescence and floral characters

8. Bract length—upper third of inflorescence (mm)
9. Bract width—upper third of inflorescence (mm)
10. Calyx length (mm)
11. Middle calyx lobe length—upper lip (mm)
12. Middle calyx lobe base width—upper lip (mm)
13. Lower calyx tooth base width (mm)
14. Lower calyx tooth midpoint width (mm)
15. Length of inner calyx trichomes (mm)
16. Corolla length (mm)
17. Corolla tube length (mm)
18. Length of inner corolla trichomes (mm)
19. Filament length (mm)
20. Anther thecae length (mm)
21. Style length—including stigma (mm)
22. Length of longer stigma lobe (mm)
23. Number of functional stamens (2 or 4)

with missing values, so only 93 of the 118 specimens in the expanded dataset were analyzed. CVA was applied to unstandardized variables of the expanded dataset (93 OTU's × 22 variables).

RESULTS

Field Studies. Observations revealed that all species of *Collinsonia* showed considerable vegetative plasticity under field conditions, even within single populations. *Collinsonia canadensis* varied greatly in overall stature; flowering plants ranged in height from approximately 10 cm to more than 1 m. Leaf size and shape were also highly variable. Plants of *C. tuberosa* observed in Alabama, *Peirson* 395 (BHO), were fairly small with weak stems and small leaves. A number of the plants grew prostrate along the ground. Several rhizomes from this population were transplanted to the greenhouse. The following summer, the transplanted specimens of *C. tuberosa*, while still somewhat smaller, appeared nearly identical to *C. canadensis* plants growing in the greenhouse. The *C. tuberosa* plants were considerably larger with stouter stems and larger leaves; the plants no longer had a reclining habit.

Calyx and corolla characters, with the exception of flower color, were constant within populations. In *C.*

canadensis, flower color ranged from very pale yellow to darker yellow, sometimes with purple markings. Variation in flower color was most obvious in *C. verticillata* where flowers ranged from almost pure white to deep pink within single populations. Flower size and shape were largely consistent within populations and did not change with the robustness of the plant. Stamen number too did not fluctuate within any populations of *Collinsonia* studied (with the exception of occasional deformed flowers).

Field observations revealed little phenotypic variation (aside from leaf size and plant stature) within populations of *C. serotina* with four stamens. An additional distinguishing character revealed by the field studies, not mentioned by Shinnars (1962), was the scent of the plants. All observed plants of *C. serotina* with four stamens had an anise-like odor, contrasting sharply with the lemon-like odor present in the rest of the genus. Plants of *C. serotina* with two stamens were quite similar to *C. canadensis* in general vegetative features, but their calyx and corolla morphology (aside from stamen number) were more suggestive of *C. serotina* with four stamens. The plants possessed the lemon-like scent of *C. canadensis*.

Herbarium Studies. Results obtained from examination of herbarium specimens were generally consistent with results from field observations. Variation in vegetative traits was noted for all taxa. A general trend of increasing pubescence from more northern to more southern latitudes was noted. Specimens labeled as *C. tuberosa* were generally much smaller than specimens of normal *C. canadensis*. Closer inspection revealed that a number of these specimens of what is considered "typical" (not in the nomenclatural sense) *C. tuberosa* were in fact damaged. The plants had either been browsed or otherwise had damaged apical meristems. Herbarium studies also uncovered specimens of *C. canadensis* from northern, glaciated areas that were nearly identical to specimens of *C. tuberosa* from farther south (e.g., *Brumbach* 4905, FLAS). Considerable variation was observed among specimens of *C. serotina* with two stamens along the Gulf Coast, and some herbarium specimens (e.g., *Faircloth* 3029, NCU and *Jones* 2587, NCU) could not easily be assigned to a species. Shinnars' unusual plant (*Godfrey and Kral* 54288, FSU), with both two and four stamened flowers, came from one of these Gulf Coast populations. Examination of this specimen revealed that only one flower possessed four stamens, of which two were somewhat reduced in size. The presence of exerted sterile stamens was occasionally observed in *C. canadensis* as well.

Phenetic Analyses. The first three principal components axes in the PCA (Fig. 1) account for approximately 62% of the variation. The first principal component (PC1) almost completely separates *C. serotina* with four stamens from the other taxa based primarily

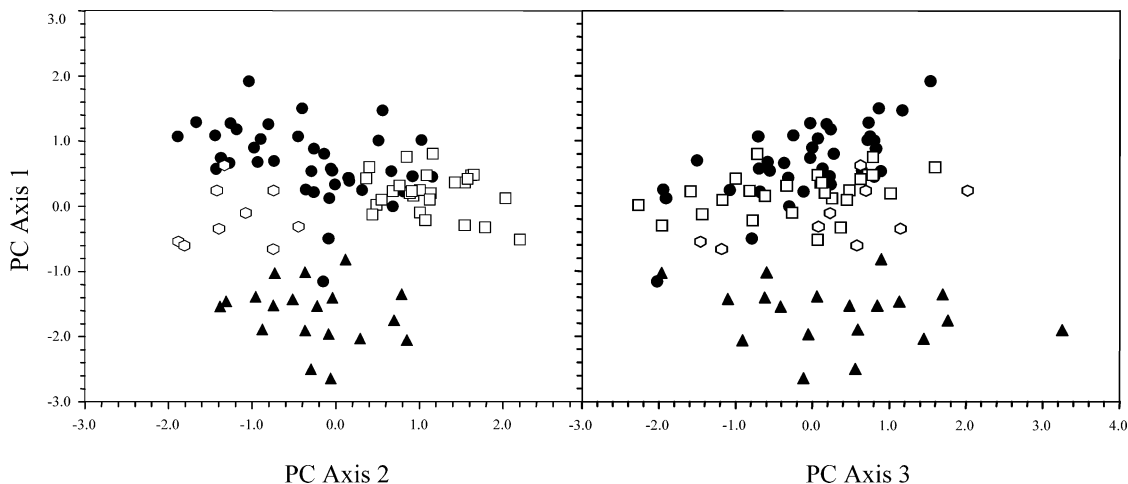


FIG. 1. Principal components analysis (PCA) of 22 standardized morphological variables from 93 specimens. Four taxon groups were assigned: *Collinsonia canadensis* (closed circle), *C. tuberosa* (open square), *C. serotina* with 2 stamens (open hexagon) and *C. serotina* with four stamens (closed triangle).

on bract and calyx characters (Table 2). One outlier of *C. canadensis* falls within the variation of *C. serotina* with four stamens. Further examination indicates that it is indeed *C. canadensis* but has abnormal floral and calyx morphologies. *Collinsonia serotina* with two stamens falls between *C. canadensis* and *C. serotina* with four stamens, while *C. canadensis* and *C. tuberosa* show virtually no separation along PC1. Overall size and leaf teeth number tend to segregate *C. canadensis* and *C. tuberosa* along PC2, although the taxa show consid-

erable overlap. PC3 accounts for no separation of the taxa.

The CVA (Fig. 2) shows strong separation of *C. serotina* with four stamens from the other taxa along CV1. Variable-variate correlations (Table 3) indicate that bract and calyx features account for much of the variation along this axis. As in the PCA, *Collinsonia canadensis* and *C. tuberosa* show no separation along CV1, and *C. serotina* with two stamens is positioned intermediate between *C. canadensis* and *C. serotina* with four stamens. CV2 accounts for complete segregation of *C. canadensis* and *C. tuberosa*, while *C. serotina* with two stamens is within the variation present in *C. canadensis*. Stem width, blade length, number of leaf teeth, and leaf glandularity account for most of the separation along CV2. CV3 partially separates *C. serotina* with two stamens from the other taxa. Overall, this analysis sharply separates *C. serotina* with four stamens and fully segregates the other three taxa, placing *C. serotina* with two stamens intermediate between the former and *C. canadensis*.

TABLE 2. Variable loadings onto principal component axes for 22 continuous characters used in principal components analysis. Values greater than 0.25 (absolute value) indicated in bold.

Variable	PC1	PC2	PC3
1	-0.057688	0.423717	0.164570
2	-0.158102	-0.734811	0.168546
3	-0.055846	-0.891463	0.238441
4	-0.603080	0.279601	0.086517
5	-0.196754	-0.861695	0.123744
6	0.214706	0.478745	-0.195713
7	-0.211340	-0.433535	0.020203
8	-0.798992	-0.112169	0.334600
9	-0.826154	-0.102727	0.290748
10	-0.797307	-0.269578	0.328777
11	-0.503451	-0.454919	0.307379
12	-0.865662	-0.187832	0.235657
13	-0.806285	-0.159732	0.226333
14	-0.897445	-0.152504	0.206112
15	-0.751563	-0.252132	0.257463
16	-0.419475	-0.314996	0.723259
17	-0.414956	-0.268748	0.737452
18	-0.522276	-0.333089	0.105785
19	-0.182406	-0.257496	0.805962
20	0.686368	-0.014554	0.133556
21	-0.224813	-0.006998	0.850685
22	-0.049712	0.068686	0.059674

DISCUSSION

Specimens of *C. serotina* with four stamens show consistent and marked separation from the other taxa in both ordinations, despite stamen number not being included in the analyses. Moreover, all of our observations indicate that number of stamens is a reliable diagnostic character. Although Shinnors noted variation in this character in one specimen (*Godfrey and Kral 54288*, FSU), we found only one flower on this specimen with four stamens, of which two stamens were somewhat reduced in size. Examination of herbarium specimens revealed that *C. serotina* with four stamens

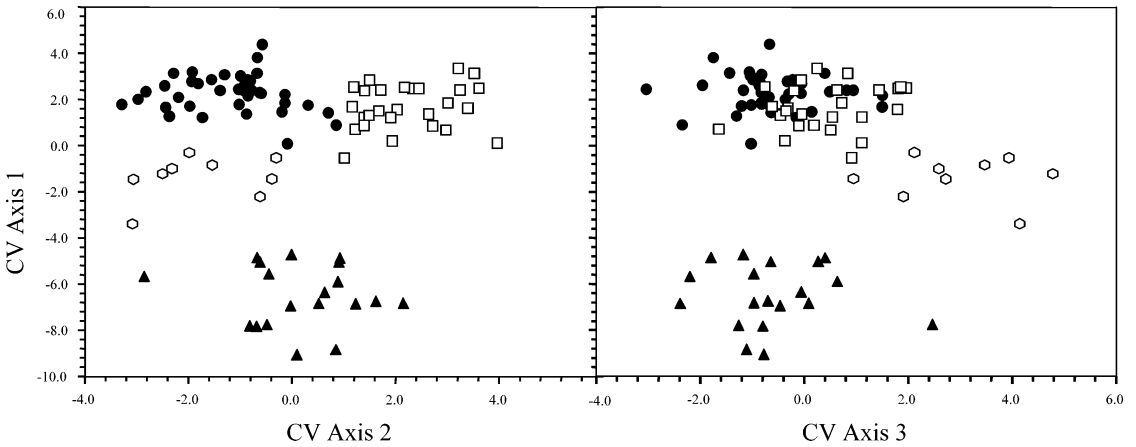


FIG. 2. Canonical variates analysis (CVA) of 22 unstandardized morphological variables from 93 specimens. Four taxon assignments were used in the analysis: *Collinsonia canadensis* (closed circle), *C. tuberosa* (open square), *C. serotina* with two stamens (open hexagon) and *C. serotina* with four stamens (closed triangle).

ranges through the coastal plain from southern Mississippi to central Georgia and extends into the piedmont regions of Alabama and Georgia. This represents a considerable constriction of range from previous circumscriptions of the species. Results of the phenetic analyses, the difference in stamen number, and the anise-like odor of *C. serotina* with four stamens (versus lemon-like in the rest of the genus) indicate that it is a distinct species.

The finding that *C. serotina* with two stamens is phenotypically intermediate between *C. canadensis* and *C. serotina* with four stamens is supported by field and

herbarium observations and phenetic analyses. *Collinsonia serotina* with two stamens occurs scattered along the Gulf Coast from eastern Louisiana to Florida, with one disjunct population in south-central South Carolina. It is particularly well represented in the Tallahassee area of the Florida panhandle. *Collinsonia canadensis* and *C. serotina* with four stamens occur throughout this region, although the range of *C. serotina* with two stamens along the Gulf Coast is slightly broader than that of the latter. The intermediacy of *C. serotina* with two stamens and the overlap in range of the three taxa suggest the possibility of a hybrid origin of *C. serotina* with two stamens. However, a population observed in Tallahassee contained only *C. serotina* with two stamens; there were no *C. canadensis* or *C. serotina* with four stamens in the immediate vicinity. *Collinsonia serotina* with two stamens could represent a series of independent hybridizations along the gulf coast, a morphologically stabilized species of hybrid origin now occupying a specific niche and range, a relictual Gulf Coast endemic, or something else altogether. Further studies including chromosome counts (chromosome numbers are known only for *C. canadensis*), pollen viability analyses, and molecular phylogeographic analyses will be required to examine these hypotheses and determine the evolutionary status of these populations.

Based on our assessment of some specimens that Shinnars annotated, it appears that he included some unusual variants of *C. canadensis* in his circumscription of *C. serotina* (Shinnars 1962). Three specimens of somewhat distinctive, larger-flowered *C. canadensis* from North Carolina (one of which Shinnars annotated as *C. serotina*) were included in our analyses. They grouped closer to *C. canadensis* than to either group of *C. serotina*. Based on field and herbarium observations and results of the phenetic analyses, our circumscrip-

TABLE 3. Variable-variate correlations for 22 continuous characters used in final canonical variates analysis. Values greater than 0.25 (absolute value) indicated in bold.

Variable	CV1	CV2	CV3
1	-0.006636	0.106555	0.097235
2	-0.134872	-0.350820	0.209169
3	-0.139846	-0.743842	0.194962
4	-0.215529	0.215406	-0.160412
5	-0.171377	-0.556766	-0.071089
6	0.135495	0.348464	0.244921
7	-0.104297	-0.183618	0.499777
8	-0.403294	0.051604	0.309559
9	-0.462245	0.078783	0.164551
10	-0.341801	-0.199845	0.059736
11	-0.201446	-0.372013	0.078131
12	-0.444456	-0.021145	0.013558
13	-0.315504	-0.090107	-0.062983
14	-0.566876	0.045058	0.132208
15	-0.341309	-0.026161	0.119259
16	-0.190941	-0.174204	0.085389
17	-0.175839	-0.153079	0.066426
18	-0.147128	-0.153971	0.112862
19	-0.127578	-0.156456	0.043336
20	0.214388	-0.158046	-0.119704
21	-0.116212	-0.016202	0.160890
22	0.029064	-0.044498	0.151827

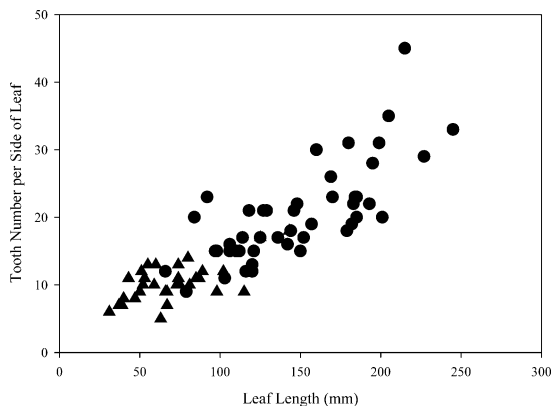


FIG. 3. Scatterplot of two morphological characters scored for specimens of *Collinsonia canadensis* (closed circle) and *C. tuberosa* (closed triangle).

tion of *C. serotina* is considerably narrower than that of Shinners.

While *C. canadensis* and *C. tuberosa* segregated fully along one axis of the CVA, the PCA revealed substantial phenetic overlap. The main discriminating characters between the two taxa are stem width, leaf length, tooth number per leaf, and leaf glandularity (Tables 2, 3). A plot of leaf length versus tooth number (Fig. 3) reveals that *C. canadensis* and *C. tuberosa* represent partially overlapping ends of a continuum and could be considered conspecific. A UPGMA cluster analysis of the expanded dataset (118 OTU's \times 23 variables) displayed considerable intermingling of *C. canadensis* and *C. tuberosa* specimens (Peirson 2003). Degree of glandularity on the abaxial surface of the leaves, while also a distinguishing factor in the CVA, tends to increase for all species within subgenus *Collinsonia* with decreasing latitude. Minor differences in leaf shape and flower color have been used by some authors to distinguish the two taxa, but field and herbarium studies revealed that the distinctions are unreliable. Their floral morphologies are essentially identical, and the taxa flower at the same time.

Examination of herbarium specimens and field observations showed that the morphological variation in *C. canadensis* is considerable and encompasses that described for *C. tuberosa*. The fact that a number of *C. tuberosa* specimens were found upon closer inspection to be damaged suggests one possible cause of the small stature that characterizes *C. tuberosa*. Two specimens of *C. canadensis* (both from the same population in Athens Co., Ohio) were used in the phenetic analysis. One was a voucher collected from the population and the other was one of several specimens grown from seeds from the population. The seedlings were transplanted to the botanic garden in the spring, and one was collected in full bloom later in the summer. Its overall appearance was very similar to *C. tuberosa*

specimens from the southeastern United States. It grouped closer to *C. tuberosa* than to the other specimens from the same population in the ordinations. After a year in the greenhouse, transplanted specimens of *C. tuberosa* from a calcareous cove forest in Alabama, while still smaller, appeared nearly identical to transplanted *C. canadensis*. Edaphic factors may strongly influence growth form and habit in *Collinsonia*. Although not quantitatively tested, physiological stress seems to play a role in the variability within *C. canadensis* sensu lato. Phenetic results, herbarium studies, and limited field and common garden observations suggest that *C. canadensis* and *C. tuberosa* comprise one widely distributed and phenotypically plastic species.

Taxonomic Conclusions and Nomenclature. These results indicate that *Collinsonia* is composed of four morphologically distinct taxa. The four species here recognized are *C. verticillata* Baldwin ex Elliott, *C. canadensis* L., *C. anisata* Sims, and *C. punctata* Elliott. The taxonomic circumscription of *C. verticillata* remains unchanged. The circumscription of *C. canadensis* is broadened to encompass the variants formerly recognized as *C. tuberosa*. The plants previously recognized as *C. serotina* sensu lato are separated into two species. *Collinsonia anisata* represents what was previously considered *C. serotina* with four stamens. *Collinsonia punctata* encompasses what had been considered *C. serotina* with two stamens.

The epithet "*serotina*" was applied by Walter to a specimen from the Carolinas, for which he provided only a scanty description. The specimen in the Walter Herbarium at the British Museum is in poor condition and possesses no floral material; its identity could not be determined with certainty. In addition, Walter's brief description provides no aid in determining which species he was describing. An additional complicating factor concerns the validity of "type specimens" in the Walter Herbarium. The history of the specimens at the British Museum was discussed by Fernald and Schubert (1948). Shinners (1962) accepted Walter's name but summarily dismissed the "type specimens" in the Walter Herbarium, which Walter may never even have seen. Shinners did not designate any type specimen. Others have questioned the validity of Walter type specimens and names as well (Ward 1977; Cantino 1981). For these reasons, we do not consider the specimens in the Walter Herbarium at the British Museum to be type specimens. Because there are no recognized type specimens and the protologue is ambiguous, the name *C. serotina* is hereby rejected as an ambiguous name. The name *Collinsonia anisata* describes plants with four fertile stamens and a strong anise odor. This is the earliest name that unambiguously applies to this species. The type specimen of *C. punctata* Elliott is conspecific with the plants from the Gulf Coast region that we have referred to as *C. serotina* with 2 stamens.

TAXONOMIC TREATMENT

COLLINSONIA L., Sp. Pl. 1: 28. 1753 and Gen. Pl. (ed. 5) p. 16. 1754.—TYPE: *C. canadensis* L., Sp. Pl. 1: 28. 1753.

Diallosteyra Raf., Neogenyt. p. 2. 1825.—TYPE: *D. punctata* (Elliott) Raf., Neogenyt. p. 2. 1825.

Hypogon Raf., Fl. Ludov. p. 41. 1817.—TYPE: *H. verticillatum* Raf., Fl. Ludov. p. 148. 1817.

Micheliella Briq., in Engl. & Prantl, Nat. Pflanzenf. 4(3a) p. 325. 1897.—TYPE: *M. verticillata* (Elliott) Briq., Nat. Pflanzenf. 4(3a) p. 325. 1897.

Pleuradenia Raf., Neogenyt. p. 2. 1825.—TYPE: *P. praecox* (Walter) Raf., Neogenyt. p. 2. 1825.

Branched or unbranched perennial herbs with aromatic foliage and a short, thickened rhizome. Stems 1–5 mm in diameter, terete to nearly quadrangular, occasionally with slightly swollen nodes. Stems glabrous to moderately pubescent below, with unbranched (rarely branched) hairs, glabrous to densely non-glandular or glandular pubescent above. Glandular trichomes short-stalked with bulbous orange to yellow head. Leaves 3–22 cm long, 2–13 cm wide, opposite to subverticillate, petiolate or uppermost leaves sessile; lamina broadly elliptical to ovate or somewhat rhombic, coarsely serrate- to crenate-margined, glabrous to sparsely pubescent on the adaxial surface, glabrous to moderately pubescent (especially along the midrib and larger veins) and sparsely to moderately glandular punctate on the abaxial surface; petiole 7–60 mm long, glabrous to densely non-glandular or glandular pubescent. Inflorescence a terminal raceme or panicle, flowers 2 or 6 (as a pair of reduced cymes) at each node of the inflorescence; bracts present or absent, sessile, lanceolate to narrowly cordate, entire-margined, gla-

brous to sparsely pubescent and punctate-dotted, 1–20 mm long, 1–20 mm wide, sometimes dramatically decreasing in length and width in upper portion of inflorescence; axes glabrous to densely non-glandular or glandular pubescent and punctate. Pedicel 3–6 mm long, sparsely to moderately non-glandular or glandular pubescent and punctate; bracteoles absent. Calyx 2–7 mm long at anthesis, zygomorphic, campanulate, 10-nerved, sparsely to moderately pubescent and glandular punctate externally, moderately pubescent along internal margin; teeth 5, lance-subulate to lanceolate, deltoid or occasionally oblong, posterior and anterior teeth sometimes upturned in fruit, posterior 3 forming a lip, anterior 2 free to rim of calyx tube. Corolla 8–17 mm long, cream, light yellow or lavender, zygomorphic, glabrous to glandular pubescent and punctate externally, moderately pubescent internally on the throat, tube straight, lobes 5; anterior lobe lacinate and much larger than other lobes, spreading and elongate; other 4 lobes short and rounded. Fertile stamens 2 (posterior pair reduced to staminodes or rarely absent) or 4, exerted well beyond corolla; filament 9–16 mm long, widely divergent, glabrous; anther thecae divaricate, barely separate to slightly confluent at dehiscence; pollen 6-colpate (further details under *C. canadensis*). Style gynobasic, 12–21 mm, glabrous, equally or unequally 2-lobed apically. Ovary 4-lobed, 0.7–1.2 mm long, 0.7–1.2 mm wide. Nectary disk asymmetrical, a large, nectar-secreting lobe equaling or surpassing the ovary. Nutlets 1–3 (the other ovary lobes aborting), globose to subglobose, ca. 2 mm in diameter, smooth surfaced, glabrous or pubescent, brown.

Vernacular Names: Horsebalm, Richweed, Stoneroot.

KEY TO SPECIES

1. Flowers 6 (as a pair of reduced cymes) at each node in lower portion of the unbranched inflorescence; floral bracts absent; leaves generally 4, opposite to subverticillate; flowers light pink to lavender; flowering late spring 1. *C. verticillata*
1. Flowers 2 at each node of the simple or branched inflorescence; floral bracts present; leaves generally more than 4, strictly opposite; flowers cream to pale yellow; flowering late summer through fall 2
 2. Fertile stamens 4; plants with anise-like scent 2. *C. anisata*
 2. Fertile stamens 2; plants with lemon-like scent 3
 3. Calyx 2–5 mm long; calyx teeth lance-subulate to narrowly lanceolate; flowers 8–13 mm long 3. *C. canadensis*
 3. Calyx 4.5–7 mm long; calyx teeth broadly lanceolate; flowers 12–17 mm long 4. *C. punctata*
1. COLLINSONIA VERTICILLATA Baldwin ex Elliott, Sketch Bot. S.C. & Ga. 1: 36. 1817.—*Micheliella verticillata* (Elliott) Briq., in Engl. & Prantl, Nat. Pflanzenf. 4(3a): 325. 1897.—TYPE: USA. Georgia: hab. Milledgeville, *D. Boykin* (holotype: CHARL!; possible isotypes: GH (2 sheets)!).
Collinsonia verticillata var. *purpurascens* Baldwin ex Elliott, Sketch Bot. S.C. & Ga. 1: 37. 1817.—TYPE: USA. South Carolina: Pickens Co., wooded slopes on E side of Eastatoc Creek, *C.L. Rogers* 70191 (holotype: presumed destroyed; neotype (here designated): MICH!; isoneotypes: FLAS!, FSU!, GA!, GH!, KY!, MISS!, NLU!, NY!, TENN!, VPI!)

Unbranched perennial herb to 5 dm tall. Foliage with lemon-like scent. Stems 2–3 mm in diameter, sparsely to densely pubescent below, with unbranched hairs (rarely branched and appearing lanate), moderately to densely glandular pubescent above. Leaves 9–

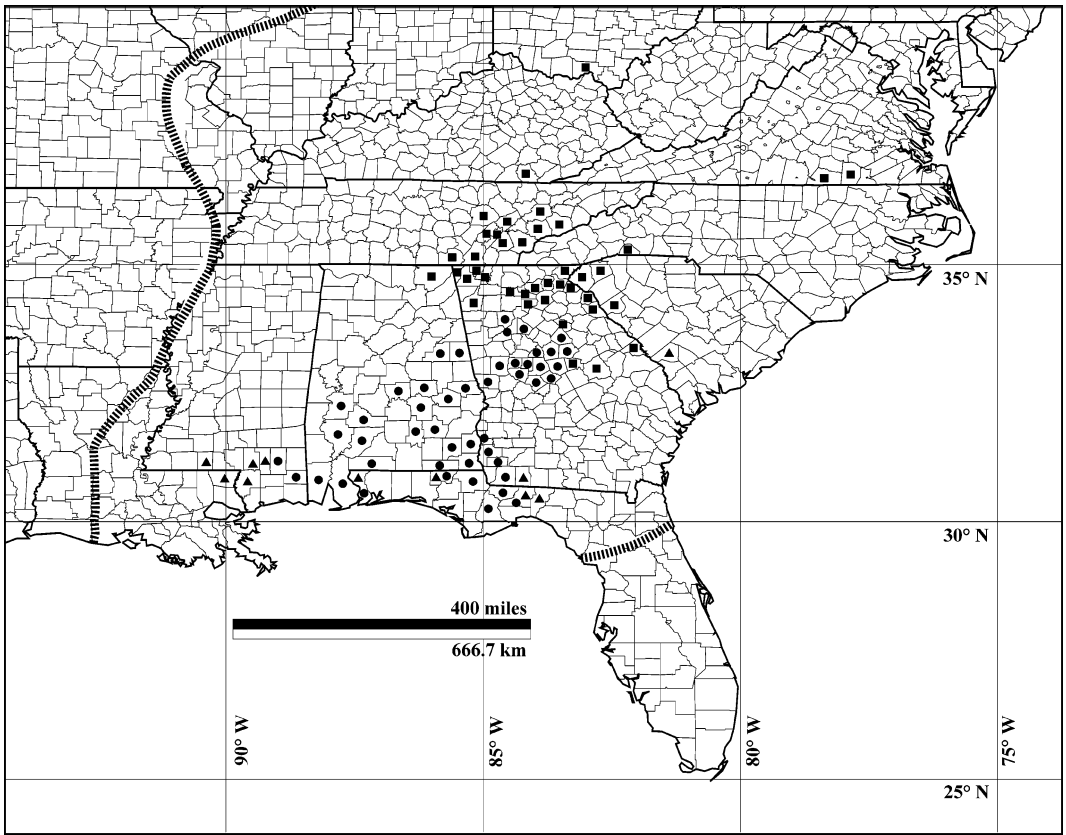


FIG. 4. Distribution of *Collinsonia anisata* (closed circles), *C. punctata* (closed triangles) and *C. verticillata* (closed squares). Western and southern range of *C. canadensis* indicated by dashed line.

18 cm long, 7–10 cm wide, subverticillate to opposite, petiolate; lamina broadly elliptical to ovate, rounded to slightly truncate at base, rounded to broadly acuminate at apex, coarsely serrate-margined, glabrous to sparsely pubescent on the adaxial surface, glabrous to moderately pubescent on the abaxial surface (especially along midvein and larger axillary veins); petiole 15–30 mm long, moderately to densely glandular pubescent. Inflorescence a terminal panicle, flowers 6 at each node of the inflorescence (a pair of reduced cymes); bracts absent; axis moderately or densely glandular pubescent and punctate, pubescence occasionally appearing lanate. Pedicel ca. 6 mm long, enlarged and flattened at base, sparsely to moderately glandular pubescent and punctate. Calyx 5–6 mm long at anthesis, moderately glandular pubescent and glandular punctate externally, teeth lance-subulate to lanceolate. Corolla ca. 16 mm long, pale pink to lavender, sparsely to moderately pubescent and punctate externally. Fertile stamens 4; filament 12–16 mm long. Style 12–20 mm. Ovary ca. 1.0 mm long, ca. 1.0 mm wide. Nutlets 1–3, pubescent.

Phenology. Flowers late April through late May.

Distribution (Fig. 4). Confined to the southern Ap-

palachian Mountains in Alabama, Georgia, Kentucky, North Carolina, South Carolina, and Tennessee, with disjunct populations in southern Ohio (Scioto County) and southern Virginia (Brunswick and Mecklenburg Counties). Small (1903, 1933) and Lowe (1921) attributed *C. verticillata* to Mississippi, but Jones (1976) did not. No specimens of *C. verticillata* from Mississippi were observed. Soukup (1993) speculated that the Ohio populations of *C. verticillata* might be “new arrivals” to the state, having first been located in the 1960’s (Braun 1964).

Reproductive Biology. Fone (1987, 1989) and Fone and Wyatt (1989) examined the relationships between inflorescence form, plant size and a number of other factors and their effects on seed production in *C. verticillata*. They found that pollination limitation was the most significant factor in low seed production.

2. *COLLINSONIA ANISATA* Sims, Bot. Mag. 30. 1809.—*Hypogon anisatum* (Sims) Raf., Fl. Ludov. p. 148, 1817.—*Michieliella anisata* (Sims) Briq., in Engl. & Prantl, Nat. Pflanzenf. 4(3a) p. 325, 1897.—TYPE: USA. South Carolina (lectotype designated by Shinnars (1962): Bot. Mag. t. 1213. 1809)

- Collinsonia anisata* var. *major* Benth. in DC., Prodr. 12: 254. 1848.—TYPE: USA. Florida: locality unknown, *Hooker 1846* (lectotype (here designated): K!; syntype (Georgia, locality unknown, *Nuttall*): K!)
- Collinsonia verticillaris* Raf., Fl. Ludov. p. 41. 1817.—TYPE: USA. Mississippi: Perry Co., slopes of Milky Creek in Camp Shelby Training Area 11, T3N, R11W, Sect. 36., 7 Oct. 1996, *S. W. Leonard 9655* (holotype: presumed destroyed; neotype (here designated): MICH!; isoneotypes: GA!, NCU!, NY!)
- Hypogon verticillatum* Raf., Fl. Ludov. p. 148. 1817.—TYPE: USA. Mississippi: Perry Co., slopes of Milky Creek in Camp Shelby Training Area 11, T3N, R11W, Sect. 36., 7 Oct. 1996, *S. W. Leonard 9655* (holotype: presumed destroyed; neotype (here designated): MICH!; isoneotypes: GA!, NCU!, NY!)
- Branched to occasionally unbranched perennial herb to 6 dm tall. Foliage with anise-like odor. Stems 2–4 mm in diameter, sparsely to densely pubescent below, with unbranched hairs, moderately to densely glandular pubescent above. Leaves 8–20 cm long, 6–13 cm wide, opposite, petiolate or uppermost leaves sessile; lamina narrowly elliptic to broadly ovate, rounded to cuneate at base, rounded/mucronate to acuminate at apex, coarsely serrate- to crenate-margined, glabrous to sparsely pubescent on the adaxial surface, sparsely to moderately pubescent (especially along the midvein and larger axillary veins) and often moderately glandular punctate on the abaxial surface; petiole 7–40 mm long, moderately to densely non-glandular or glandular pubescent. Inflorescence a terminal raceme or panicle, flowers 2 at each node of the inflorescence; bracts present, broadly cordate below, lanceolate to lance-elliptic above, sparsely pubescent and punctate dotted, 2–20 mm long, 2–20 mm wide, often dramatically decreasing in length and width in upper portion of inflorescence; axes moderately to densely non-glandular or glandular pubescent and punctate. Pedicel 5–6 mm long, moderately non-glandular pubescent or glandular pubescent and punctate. Calyx 5–7 mm long at anthesis, moderately pubescent and glandular punctate externally, teeth broadly lanceolate to oblong. Corolla 14–17 mm long, cream to light yellow, moderately pubescent and punctate externally. Fertile stamens 4; filament 10–15 mm long. Style 14–20 mm. Ovary ca. 1.2 mm long, ca. 1.2 mm wide. Nutlets 1–3, glabrous.
- Phenology.** Flowers late August through mid-October.
- Distribution (Fig. 4).** Confined to the coastal plain and piedmont regions of the southeastern United States in Alabama, Florida, Georgia, and Mississippi.
3. *COLLINSONIA CANADENSIS* L., Sp. Pl., 1: 28. 1753.—TYPE: USA. Virginia to Canada (lectotype designated by Stearn (1957) in *Intro. Linneaus' Sp. Pl.* 47: Hort. Cliff. t. 5. 1738)
- Collinsonia angustifolia* Raf., Med. Fl., 1: 114. 1828.—TYPE: USA. Ohio: Athens County, east side of Cable Lane within Athens city limits, 29 August 2001, *J. Peirson 383* (holotype: presumed destroyed; neotype (here designated): BHO!)
- Collinsonia canadensis* L. var. *cordata* Pursh, Fl. Am. Sept., 1:20. 1813.—TYPE: USA. South Carolina: Pickens Co., Table Rock State Park, 27 Oct. 2004, *A. Darr 2022* (holotype: presumed destroyed; neotype (here designated): USCH 93426!; isoneotypes: MICH!, USCH!)
- Collinsonia canadensis* L. var. *ovata* Pursh, Fl. Am. Sept., 1:20. 1813.—TYPE: USA. North Carolina: Graham Co., south of Robbinsville, 27 Aug. 1955, *Wilbur 4653* (holotype: presumed destroyed; neotype (here designated): MICH!)
- Collinsonia cuneata* Wender., Schrift. Ges. Bef. Gesammt. Naturw. Marb. 2: 242. 1831.—TYPE: USA. Michigan: Van Buren Co., southwest of Bangor, 12 Sept. 1959, *E. G. Voss 9120* (holotype: presumed destroyed; neotype (here designated): MICH!)
- Collinsonia decussata* Moench, Meth. p. 379. 1794.—TYPE: USA. North Carolina: Burke Co., east of Enola, 9 Sept. 1958, *C. R. Bell 15111* (holotype: presumed destroyed; neotype (here designated): MICH!)
- Collinsonia ovalis* Pursh, Fl. Am. Sept., 1:20. 1813.—TYPE: USA. South Carolina: Orangeburg Co., 13 Sept. 1939, *Godfrey 8219* (holotype: presumed destroyed; neotype (here designated): GH!; isoneotype: NY!)
- Collinsonia praecox* Walter, Fl. Carol. p. 65. 1788.—*Pleuradenia praecox* (Walter) Raf., Neogenyt. p. 2. 1825.—TYPE: USA. South Carolina: Chester Co., 6 Sept. 1982, *Newberry 1912* (holotype: presumed destroyed; neotype (here designated): NCU!)
- Collinsonia scabriuscula* Aiton, Hort. Kew. (ed. 1), 1: 47. 1789.—*C. scabra* Pers., Syn. Pl. 1: 29. 1805.—*P. scabra* (Pers.) Raf., Neogenyt. p. 2. 1825.—TYPE: unknown locality, Hort. Fothergill 1776 (holotype: BM!)
- Collinsonia scabriuscula* Aiton var. *puberula* Benth., in DC., Prodr., 12: 253. 1848.—TYPE: USA. Alabama: Clair City, in rupestribus montanis, Sept. 1843, *Rugel* (lectotype (here designated): GH!; isosyntype (Louisiana, New Orleans, 1832, *T. Drummond*): GH!)
- Collinsonia tuberosa* Michx., Fl. Bor.-Am., 1: 17. 1803.—*Collinsonia canadensis* var. *tuberosa* (Michx.) A.W.Wood, Cl. Bk. Bot. p. 544. 1861.—TYPE: USA. Carolina (isotype: P; photo of isotype: GH!)
- Collinsonia urticifolia* Salisb., Prodr. p. 75. 1796.—TYPE:

USA. Pennsylvania: Philadelphia Co., Olney, 26. Aug 1922, R. R. Dreisbach 2-185 (holotype: presumed destroyed; neotype (here designated): MICH!)

Branched or unbranched perennial herb to 8 dm tall. Foliage with lemon-like odor. Stems 1–5 mm in diameter, with slightly swollen nodes, glabrous to densely pubescent below, with unbranched hairs, glabrous to moderately non-glandular or glandular pubescent and punctate above. Leaves 3–22 cm long, 2–13 cm wide, opposite, petiolate or uppermost leaves sessile; lamina elliptic to ovate or somewhat rhombic, cordate/truncate to rounded or cuneate at base, rounded/mucronate to acuminate at apex, coarsely serrate- to crenate-margined, glabrous to sparsely pubescent on the adaxial surface, glabrous to moderately pubescent and sparsely to moderately glandular punctate on the abaxial surface; petiole 7–60 mm long, glabrous to densely pubescent (sometimes glandular pubescent in upper portion of the stem). Inflorescence a terminal raceme or panicle, flowers 2 at each node of the inflorescence; bracts present, lanceolate to lance-elliptic, glabrous, 1–3 mm long, ca. 1 mm wide, not appreciably decreasing in length and width in upper portion of inflorescence; axes moderately non-glandular or glandular pubescent and punctate, occasionally glabrous in lower portion of inflorescence. Pedicel 3–4 mm long, sparsely to moderately non-glandular or glandular pubescent and punctate. Calyx 2–5 mm long at anthesis, sparsely to moderately pubescent and glandular punctate externally, teeth lance-subulate to narrowly lanceolate. Corolla 8–13 mm long, cream to yellow, glabrous and glandular punctate externally. Fertile stamens 2 (posterior pair reduced to staminodes or rarely absent); filament 9–16 mm long; pollen 6-colpate, tectate-perforate, psilate to weakly suprareticulate, apocolpia dome-shaped, mesocolpia protruding, colp margins thickened. Style 12–21 mm. Ovary 0.7–1.0 mm long, 0.7–1.0 mm wide. Nutlets typically 1, occasionally 2, glabrous. Chromosome numbers, $2n = 50, 52$.

Phenology. Flowers August through mid-October. A phenotypically unusual specimen from St. Helena Parish, Louisiana, was collected in full bloom in early July (Allen 9760, FLAS). Relocation of this population should be attempted. Skinner (1976) identified three species of bumblebees (*Bombus*) as the principal pollinators of *C. canadensis*.

Distribution (Fig. 4). Widely distributed from northern New England and southern Ontario to the Gulf of Mexico and from the east coast to just west of the Mississippi River. Fernald (1950) and Gleason and Cronquist (1991) reported *C. canadensis* from Arkansas; Lang (1966) also reported it from Arkansas. No specimens from Arkansas were observed.

Cytology. Two studies provided haploid chromosome numbers of 25 (Keener 1979) and 26 (Gill 1981).

Palynology. Trudel and Morton (1992) and Wagsstaff (1992) found the hexacolpate pollen of *C. canadensis* to be unique among the North American Labiatae, having an almost smooth tectum with only minute perforations.

4. *COLLINSONIA PUNCTATA* Elliott, Sketch Bot. S.C. & Ga., 1: 36. 1817.—*Collinsonia canadensis* var. *punctata* (Elliott) A.Gray, Syn. Fl. N.A., 1: 351. 1878.—*Diallostera punctata* (Elliott) Raf., Neogenyt. p. 2. 1825.—TYPE: USA. Unknown locality, hab. in umbrosis (holotype: CHARL!).

Branched or unbranched perennial herb to 8 dm tall. Foliage with lemon-like odor. Stems 2–4.5 mm in diameter, with slightly swollen nodes, moderately to densely pubescent below, with unbranched hairs, moderately to densely non-glandular or glandular pubescent and punctate above. Leaves 13–22 cm long, 8–13 cm wide, opposite, petiolate or uppermost leaves sessile; lamina elliptic to ovate, cordate/truncate to rounded or cuneate at base, rounded/mucronate to acuminate at apex, coarsely serrate- to crenate-margined, glabrous to sparsely pubescent on the adaxial surface, sparsely to moderately pubescent and sparsely to moderately glandular punctate on the abaxial surface; petiole 17–50 mm long, moderately to densely pubescent (sometimes glandular pubescent in upper portion of the stem). Inflorescence a terminal raceme or panicle, flowers 2 at each node of the inflorescence; bracts present, lanceolate to lance-elliptic, glabrous, 3–6 mm long, ca. 1–3 mm wide, not appreciably decreasing in length and width in upper portion of inflorescence; axes moderately non-glandular or glandular pubescent and punctate. Pedicel 3–6 mm long, sparsely to moderately non-glandular or glandular pubescent and punctate. Calyx 4.5–7 mm long at anthesis, sparsely to moderately pubescent and glandular punctate externally, teeth broadly lanceolate. Corolla 12–17 mm long, yellow, glabrous and glandular punctate externally. Fertile stamens 2 (posterior pair reduced to staminodes); filament 10–16 mm long. Style 14–20 mm. Ovary ca. 1.0 mm long, ca. 1.0 mm wide. Nutlets 1–2, glabrous.

Phenology. Flowers late August through mid-October.

Distribution (Fig. 4). Confined primarily to the Gulf Coast from eastern Louisiana to the Florida panhandle with one location in south-central South Carolina.

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APPENDIX 1

Specimens used as OTU's in the phenetic analyses of subgenus *Collinsonia*. The alphanumeric code for each OTU is given in brackets. Taxon names and assignments are those accepted in the Taxonomic Treatment.

Collinsonia amisata. U.S.A. Alabama: Autauga Co., Kral 61108 (BRIT), [SER9]; Alabama: Baldwin Co., McDaniel 7203 (FSU), [SER23]; Alabama: Baldwin Co., Peirson 391 (BHO), [SER33]; Ala-

bama: Baldwin Co., *Peirson* 391 (BHO), [SER39]; Alabama: Clarke Co., *Kral* 45004 (GA), [SER11]; Alabama: Elmore Co., *Haynes* 6056 (NCU), [SER25]; Alabama: Elmore Co., *Haynes* 6056 (BRIT), [SER26]; Alabama: Elmore Co., *Peirson* 387 (BHO), [SER34]; Alabama: Lee Co., *Earle and Baker* (MU), [SER5]; Florida: Gadsden Co., *Faircloth* 1571 (GA), [SER20]; Florida: Gadsden Co., *Peirson* 388 (BHO), [SER37]; Florida: Gadsden Co., *Peirson* 388 (BHO), [SER38]; Florida: Jackson Co., *Anderson* 5475 (FSU), [SER15]; Florida: Jackson Co., *Knight* 527 (FSU), [SER24]; Georgia: Butts Co., *Howell* 1658 (GA), [SER19]; Georgia: Decatur Co., *Mitchell* 1319 (FSU), [SER21]; Georgia: Decatur Co., *Godfrey* 71552 (FSU), [SER22]; Georgia: Fulton Co., *Harper* 1276 (GH), [SER2]; Georgia: Harris Co., *Jones* 21360 (GA), [SER13]; Georgia: Harris Co., *Jones* 21123 (BRIT), [SER7]; Georgia: Upson Co., *Chronquist* 4695 (GA), [SER4]; Mississippi: Perry Co., *Leonard* 9655 (BRIT), [SER10]; Mississippi: Perry Co., *Leonard* 9655 (FSU), [SER16].

Collinsonia canadensis. U.S.A. Alabama: Bibb Co., *Kral* 41090 (NLU), [TUB18]; Alabama: Blount Co., *Smith* (GH), [TUB27]; Alabama: Calhoun Co., *Nixon* 852 (BRIT), [TUB13]; Alabama: Cleburne Co., *Smith* 1219 (UNA), [TUB12]; Alabama: Etowah Co., *Peirson* 395 (BHO), [TUB31]; Alabama: Etowah Co., *Peirson* 395 (BHO), [TUB32]; Alabama: Jackson Co., *DiPietro* 525 (BRIT), [TUB21]; Alabama: Tuscaloosa Co., *Harper* 3538 (GH), [TUB7]; Connecticut: Litchfield Co., *Ahles* 89655 (GA), [CAN26]; Florida: Calhoun Co., *Godfrey* 76689 (FSU), [CAN28]; Georgia: Elbert Co., *Duncan* 10557 (MISS), [TUB16]; Georgia: Floyd Co., *Lipps* (TENN), [CAN3]; Georgia: Floyd Co., *Lipps* 68-212 (BRIT), [CAN18]; Georgia: Rabun Co., *Duncan* 10366 (BRIT), [CAN11]; Georgia: Rabun Co., *Milsted* 1307 (GA), [CAN14]; Georgia: Rabun Co., *Milsted* 276 (GA), [CAN16]; Georgia: Union Co., *Pyron and Duncan* 4 (GA), [CAN2]; Georgia: Whitfield Co., *Di Gioia* 52 (GA), [TUB9]; Georgia: Whitfield Co., *Harper* 1287 (GH), [TUB28]; Kentucky: Henry Co., *Gentry* 766 (NCU), [CAN38]; Kentucky: Jefferson Co., *Davies* 576 (NCU), [CAN23]; Kentucky: Powell Co., *Higgins* 1980 (NCU), [CAN12]; Louisiana: St. Helena Co., *Allen* 9760 (FLAS), [TUB15]; Louisiana: St. Helena Co., *Allen* 9760 (NLU), [TUB3]; Louisiana: St. Helena Co., *Allen* 9760 (NLU), [TUB5]; Louisiana: St. Helena Co., *Burke and Rekas* (FLAS), [TUB11]; Louisiana: St. Helena Co., *Thieret* 36958 (FSU), [TUB29]; Massachusetts: Franklin Co., *Day* 42 (GH), [CAN10]; Massachusetts: Worcester Co., *Maina and Gates* 19992 (BRIT), [CAN17]; Massachusetts: Hampden Co., *Seymour* (GH), [CAN6]; Massachusetts: Hampden Co., *Seymour* 513 (BRIT), [CAN9]; Mississippi: Covington Co., *Tracy* 8760 (GH), [TUB6]; Mississippi: Grenada Co., *MacDonald* 7873 (TENN), [TUB19]; Mississippi: Harrison Co., *Tracy* 4904 (GH), [TUB25]; Mississippi: Kemper Co., *McDaniel* 15699 (FSU), [TUB1]; Mississippi: Kemper Co., *McDaniel* 15699 (TENN), [TUB20]; Mississippi: Oktibbeha Co., *McDaniel* 26487 (FSU), [CAN13]; Mississippi: Pearl River Co., *Sargent* 8453 (BRIT), [TUB26]; North Carolina: Alamance Co., *Ramseur*

and Ham. 2025 (NCU), [TUB22]; North Carolina: Haywood Co., *Freeman* 58299 (NCU), [CAN7]; North Carolina: Jackson Co., *Mouzon* 170 (NCU), [CAN41]; North Carolina: Macon Co., *Coker Co. Harb. and Totten* (NCU), [CAN39]; North Carolina: Macon Co., *Radford* (NCU), [CAN40]; North Carolina: Madison Co., *Sather* 2033 (NCU), [SER31]; North Carolina: McDowell Co., *Wieg. and Manning* 2719 (GH), [CAN29]; North Carolina: Stanly Co., *Ahles* 19940 (NCU), [SER30]; North Carolina: Watauga Co., *Bouff. and Wood* 17616 (NCU), [SER32]; Ohio: Adams Co., *Wagstaff* 88-029 (BHO), [CAN35]; Ohio: Athens Co., *Hall* 2024 (BHO), [CAN1]; Ohio: Athens Co., *Peirson* 383 (BHO), [CAN47]; Ohio: Athens Co., *Peirson* 384 (BHO), [CAN46]; Ohio: Hocking Co., *Peirson* 385 (BHO), [CAN44]; Ohio: Hocking Co., *Peirson* 385 (BHO), [CAN45]; Ohio: Lorain Co., *Jones* 67-9-3-984 (BHO), [CAN32]; Ohio: Vinton Co., *O'Dell* 1362 (BHO), [CAN34]; Pennsylvania: Berks Co., *Brumbach* 4905 (FLAS), [CAN24]; Pennsylvania: Northampton Co., *Churchill* (GH), [CAN30]; South Carolina: Chester Co., *Newberry* 1912 (NCU), [CAN36]; South Carolina: Dorchester Co., *Ahles* 37875 (BRIT), [TUB14]; South Carolina: Orangeburg Co., *Godfrey* 8219 (GH), [TUB10]; South Carolina: Orangeburg Co., *Godfrey* 8219 (NY), [TUB24]; Tennessee: Anderson Co., *McNeilus* 89-837 (TENN), [CAN19]; Tennessee: Carroll Co., *Svenson* 420 (GH), [CAN5]; Tennessee: Davidson Co., *Shaver* (BRIT), [CAN8]; Tennessee: Grundy Co., *Kral* 43679 (BRIT), [CAN20]; Tennessee: Grundy Co., *Kral* 43679 (GA), [TUB30]; Tennessee: Hamilton Co., *Alex., Ever and Pearson* (NY), [TUB23]; Tennessee: Marion Co., *Pyne* 94-348 (TENN), [TUB17]; Tennessee: Montgomery Co., *Brown and Clebsch* (NCU), [CAN22]; Tennessee: Roane Co., *Furrt and Mahler* 4519 (NCU), [CAN15]; Tennessee: Roane Co., *Peirson* 396 (BHO), [CAN33]; Tennessee: Roane Co., *Peirson* 396 (BHO), [CAN42]; Tennessee: Roane Co., *Peirson* 396 (BHO), [CAN43]; Tennessee: Roane Co., *Woff and Dennis* 51048 (TENN), [TUB2]; Tennessee: Sequatchie Co., *Pyne* 93-266 (BRIT), [TUB4]; Tennessee: Sequatchie Co., *Pyne* 93-266 (BRIT), [TUB8]; Virginia: Giles Co., *Fogg* 12852 (GH), [CAN25]; Virginia: Montgomery Co., *Kral* 11538 (VPI), [CAN31]; Virginia: Wise Co., *Culbertson* 1969 (VPI), [CAN27]; West Virginia: Greenbrier Co., *Hunnewell* 7102 (GH), [CAN4].

Collinsonia punctata. U.S.A. Florida: Escambia Co., *Burkhalter* 10269 (FSU), [SER17]; Florida: Grady Co., *Faircloth* 3029 (NCU), [CAN37]; Florida: Jefferson Co., *Godfrey and Kral* 54288 (FSU), [SER12]; Florida: Jefferson Co., *Kral* 1707 (FSU), [SER28]; Florida: Leon Co., *Anderson* 19062 (FSU), [SER1]; Florida: Leon Co., *Anderson* 16985 (FSU), [SER14]; Florida: Leon Co., *Kral* 3705 (FSU), [SER18]; Florida: Leon Co., *Anderson* 14562 (FSU), [SER27]; Florida: Leon Co., *Peirson* 390 (BHO), [SER35]; Florida: Leon Co., *Peirson* 390 (BHO), [SER36]; Florida: Leon Co., *Kral* 3705 (BRIT), [SER6]; Mississippi: Lamar Co., *Jones* 2587 (GA), [SER29]; Mississippi: Lamar Co., *Jones* 2587 (NCU), [CAN21]; Mississippi: Pearl River Co., *Sargent* 8504 (BRIT), [SER8].