REDISCOVERY OF *CRATAEGUS PISIFERA* (ROSACEAE: MALEAE)

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ABSTRACT

Field searches in 2021 resulted in rediscovery of the pea-fruited hawthorn, *Crataegus pisifera* Sarg. (*C. succulenta* var. *pisifera* (Sarg.) Kruschke), a Vermont endemic known with confidence only from the type collections made in 1901. Collections made throughout the 2021 growing season from the type locality and from new populations nearby confirm its continued presence on the Vermont landscape. Additional morphological characterization is presented and deviations from the original description are discussed. Mature fruits in late October measured 7.2–11.2 mm in diameter, averaging 9.2 mm, larger than the immature fruits described in the literature. Thus, fruit diameter fails to separate *C. pisifera* from closely related *C. succulenta* varieties. We present a key, the first range map, and the first published illustrations of this long-lost species; we also include a second-step lectotypification that clarifies which of two available herbarium sheets is the one to be regarded as the lectotype.

RESUMÉ

Des recherches sur le terrain en 2021 ont permis de redécouvrir l'aubépine à fruit de pois, *Crataegus pisifera* Sarg. (*C. succulenta* var. *pisifera* (Sarg.) Kruschke), une endémique du Vermont connue avec certitude uniquement grâce aux collections types effectuées en 1901. Les collections effectuées tout au long de la saison 2021 dans la localité type et dans de nouvelles populations à proximité confirment sa présence continue dans le paysage du Vermont. Une caractérisation morphologique supplémentaire est présentée et les déviations de la description originale sont discutées. Les fruits matures à la fin octobre mesuraient 7,2–11,2 mm de diamètre, avec une moyenne de 9,2 mm, ce qui est plus grand que les fruits immatures décrits dans la littérature. Ainsi, le diamètre des fruits ne permet pas de séparer *C. pisifera* des variétés étroitement apparentées de *C. succulenta*. Nous présentons une cle, la première carte de l'aire de répartition et les premières illustrations publiées de cette espèce disparue depuis longtemps. Nous incluons également une lectotypification de deuxième étape qui clarifie laquelle des deux feuilles d'herbier disponibles est celle qui doit être considérée comme le lectotype.

KEY WORDS: Hawthorn, endemic microspecies, Vermont botanical history, second step lectotypification

INTRODUCTION

The first decade of the 20th century saw many new species of *Crataegus* described in North America, including about 25 based on collections from Vermont described by C. S. Sargent, Director of the Arnold Arboretum and author of The Silva of North America and other major publications on woody plants of North America. While many of those are now placed in synonymy, some are commonly accepted in current use, either at specific or infraspecific rank, e.g., *C. brainerdii* Sarg., *C. dissona* Sarg , *C. egglestonii* Sarg., *C. jesupii* Sarg., *C. faxonii* Sarg., and *C. pringlei* Sarg. Among this latter group is *Crataegus pisifera* Sarg., described from material collected in Cornwall, Addison County, Vermont (Sargent 1905a).

Since its publication, *Crataegus pisifera* has been a controversial taxon, interpreted in varied ways by different authors. Eggleston (1908, 1913) cited specimens from the type locality in synonymy with *C. neofluvialis* Ashe. His interpretation was followed by Palmer (1937, 1946, 1950, 1952), but Gleason and Cronquist (1963, 1991) passed over it in silence. It was accepted as a variety of *C. succulenta* Schrad. ex Link by Kruschke (1955), Seymour (1969a, 1969b), Phipps et al. (2014), and Gilman (2015). Haines (2011) revived it to the rank of species. However, Abbott in Abbott et al. (2017) placed it in synonymy of a broadly construed *C. succulenta*.

Discovery and Rediscovery

In early autumn 1900, Sargent visited Vermont, collecting hawthorns in Rutland, Middlebury, Charlotte, and Burlington. His visit of 8 September with Ezra Brainerd, President of Middlebury College and an expert in the flora of Vermont, inspired Brainerd to collect numerous hawthorns later that autumn and in spring of 1901. It was during this effort that Brainerd first noted the unusual plant later named *C. pisifera* at a site in the town of

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Cornwall, Addison County. An undated note of conveyance to Sargent mounted with the lectotype (Phipps 2007) stated: "I collected this with [W.W.] Eggleston, May 28 [1901]. You will find a specimen in my package with mature fruit. I thought it a form of *C. succulenta*." These specimens and a few others subsequently collected by Eggleston (see Exsiccatae), all from the same locality, are until now the only ones ever collected of *C. pisifera*.

While preparing new floristic accounts for New England (Haines 2011) and Vermont (Gilman 2015) we realized that modern knowledge of the genus in New England was sparse and we put substantial effort toward relocating *C. pisifera*. However, the literature, insofar as a locality was mentioned, referred only to the town of Cornwall without further localization, hampering our search. No oral tradition, which is strong among botanists and naturalists interested in some groups, e.g., ferns or orchids, has ever developed for hawthorns in Vermont, and local knowledge of many significant hawthorns lapsed during the middle and latter part of the 20th century. Furthermore, Cornwall has an area of nearly 28.5 sq. miles (7406 ha), is generally rural in character, and its land use is predominantly agricultural (CPC 2018)—i.e., it has abundant suitable habitat for hawthorns—so random searches seemed unlikely to recover *C. pisifera*. However, with the recent (ca. 2018) internet posting of specimen images by the C. V. Starr Virtual Herbarium at the New York Botanical Garden (NY), additional information came to our attention. Two sheets of *C. pisifera* collected by Eggleston were labeled in his own hand: "Cornwall, Iron Bridge." We also recently reinspected the syntype at A labeled in Brainerd's hand, "south of Iron Bridge" and realized the value of that datum as well.

At present there are no metal truss bridges in Cornwall, and review of the contemporary topographical map (USGS 1894) and published resources on Cornwall town history (CPC 2013) failed to identify any such bridges ca. 1900. However, there have only been two substantial bridges in the town (CPC 2013): a wooden covered bridge across Otter Creek, which forms the southeastern boundary of the town, and a bridge across the Lemon Fair River in the northwestern part of the town. The Otter Creek bridge was present ca. 1900 and could not have been the iron bridge referred to on the specimens. The Lemon Fair bridge, present since the late 1790's (Matthews 1862), may have been a metal truss bridge in the early 1900's—no direct evidence of its construction was found—but it was rebuilt in 1936 as a concrete bridge and replaced again in 2010 (CPC 2013). At the last rebuild, the eastern approach was re-aligned, significantly altering the landscape on the south side of the bridge.

Because it seemed to be the best candidate location to recover *C. pisifera*, a search was undertaken near the Lemon Fair bridge at flowering time on 22 May 2021. The search disclosed two hawthorns in bloom, one on each side of the river. Not within the immediate environs of the bridge, these shrubs are each located ca. 200' distant from the bridge (Fig. 1).

In addition to plants at the Lemon Fair locality, a much larger population and numerous outlying individuals of an apparently identical hawthorn were also located in an expanded search in the neighboring town of Bridport, about 9.3 km (5.8 miles) west of the Lemon Fair bridge. This population extends along Market Road West and Basin Harbor Road, and also into old field/pasture conditions in the vicinity of the West Branch of Dead Creek, especially in the SE quadrant of the Market Road West / Basin Harbor Road intersection. The population along Market Road West includes some 90+ large individuals, but the size of the overall population is not yet known pending field investigations remote from roadsides. Another individual was observed on Middle Road (also known as Crown Point Road).

METHODOLOGY

To determine the identity of these plants from the presumptive type locality, and nearby, we undertook to characterize their morphology in comparison with the lectotype and syntypes of *C. pisifera* and with Sargent's original description.

Sequential collections were made from a selection of plants on 22 May, 27 May, 19 July, 6 September and 23 October 2021. Care was taken to collect material for analysis from the same individuals over these dates. Collections were made by Gilman (*21005*, *21006*, *21007*) from Market Road West in Bridport (Fig. 2a) and (*21008* and *21048*) from Cornwall; one collection was made by Haines (*s.n.*, 27 May 2021), from the same plant in Cornwall as *Gilman 21048*, and another by Haines (*s.n.*, 27 May 2021) from a plant on Middle Road in

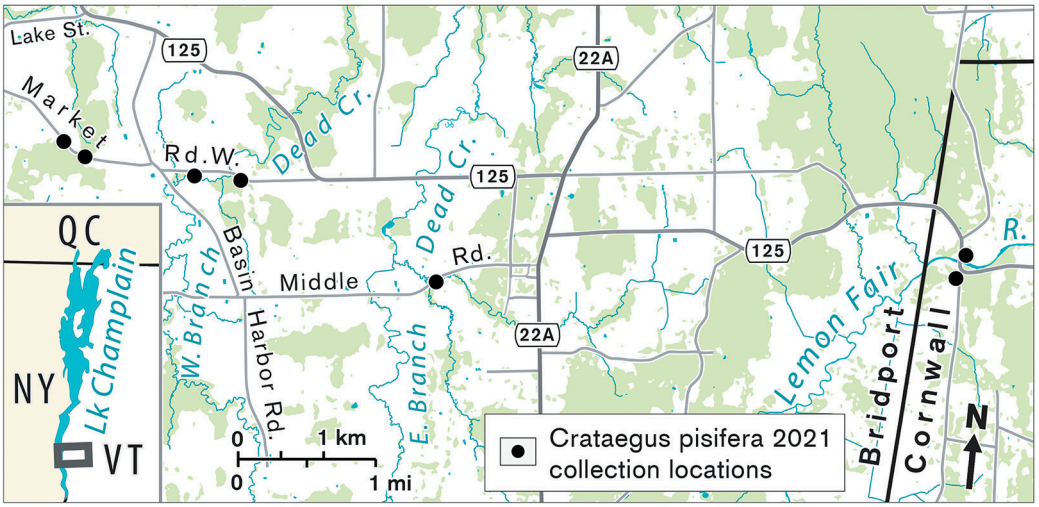


Fig. 1. Locations of 2021 collections of *Crataegus pisifera* in the towns of Bridport and Cornwall, Vermont. The type locality was near the Vt. Rte. 125 bridge over the Lemon Fair River in Cornwall. Map credits: Tom M. Ruehli, cartographer. Forest cover: USDA Forest Service, 2016 tree canopy cover (CONUS), Salt Lake City, UT. Streams: USDA/NRCS National Hydrology dataset. Roads and boundaries: © Openstreetmap contributors

Bridport. Observations of some field characters, e.g., plant growth form, branching pattern, and height, were made specifically on the September site visit.

We examined the lectotype (A) and other syntypes (see Exsiccatae) for discrepancies with newly collected material and we deconstructed the original description (Sargent 1905a) to make comparisons of the current collections to 81 characters listed there (Table 1). Measurements were taken of many quantifiable characters that were listed by Sargent without measure, using a digital caliper (Gyros Digi-Science Accumatic; Gyros Precision Tools Inc., Monsey, NY) or binocular dissecting scope. Qualitative characters were visually assessed.

RESULTS AND DISCUSSION

Our comparisons of the current plants to character states given in the original description (Sargent 1905a) are given in Table 1, with some additional comments. Most characters were found to be present and identical to, or within the range of, what was presented in the original description with two notable exceptions. Stamen number, originally reported as 20, was found to range only from 11 to 18 with an average of 15, and fruit size, originally reported as 6–8 mm in diameter, was found to range from 7.2 to 11.2 mm in diameter with an average of 9.2 mm. Other fruit characters, related to ripening, were also found to vary from the original description and from the lectotype and syntype specimens because our specimens were collected about a month later and were fully ripe.

***Stamen number.*—**We found a variable number of stamens in our plants (Figs. 2b, 2c), with an average of 15, but Sargent (1905a) described *C. pisifera* as having 20 stamens. His statement was in line with his general practice of acknowledging stamen number in multiples of five, although he sometimes acknowledged variability in stamen number in descriptions (e.g., that of *C. egglestonii*). In the Manual of North American Trees (Sargent 1905b), his careful analysis of stamen insertion in whorls of five or ten, with the first (outer) whorl usually having ten stamens in five pairs opposite the sepals, and subsequent (inner) whorls with five stamens each, comports with the modern understanding of androecia throughout much of the Rosaceae (Kalkman 2004; Ronse De Craene 2010), and his common use of stamen number in multiples of five in keys throughout his hawthorn publications indicate the importance that he assigned to this character. Nevertheless, in the generic description of *Crataegus*, Sargent (1905b) stated that stamen number is "often variable in number in

Fig. 2. Flowers. **A.** Mature plant (*Gilman 21006*) in full anthesis, 22 May 2021. **B.** Inflorescence (*Gilman 21009*) showing small, pink anthers. **C.** Variable stamen count (*Gilman 21009*); lower flower has 15 stamens, upper flower has 11.

Table 1. Character states described by Sargent (1905a) with observations on recent collections.

Character states from the original description	Recent observations (✓=observed, ⦸=not observed)
LEAVES	
1. Rhombic to ovate on vigorous shoots	✓
2. Acute or acuminate	✓
3. Gradually narrowed to the cuneate entire base	✓ Some are slightly rounded to base
4. Finely doubly serrate above	✓
5. With straight glandular teeth	✓
6. Slightly divided above the middle into numerous short acute lobes	✓
7. Nearly fully grown when the flowers open during the last week of May, [and at that time]:	✓
8. Thin	✓
9. Yellow-green	✓ Yellow-green to bright green
10. Lustrous	✓
11. Smooth	✓
12. Glabrous above with the exception of a slight pubescence along the midribs	✓
13. Pale below	✓ Paler than adaxial surface but not whitened or notably bicolor
14. Clothed below along the base of the veins with short, persistent hairs	✓ Pubescence along abaxial veins is present but obscure
15. At maturity coriaceous, [and at that time]:	✓
16. Conspicuously reticulate venulose	✓
17. Dark yellow-green and lustrous on the upper surface	✓
18. Pale on the lower surface	✓ Paler than adaxial surface but not whitened or notably bicolor
19. 5–7 cm[1] long	✓ (4.2–)5.4(–6.3) cm
20. 4–5 cm wide	✓ (3.1–)3.9(–5.0) cm
21. With stout yellow midribs deeply impressed on the upper surface	✓
22. With 5 or 6 pairs of slender primary veins extending obliquely to the points of the lobes	✓ Short shoot leaves usually with 4–5 pairs of primary veins
PETIOLES	
23. Stout	✓
24. Wing-margined to the middle	✓ Wings narrow and inconspicuous
25. Puberulous on the upper side when young	✓
26. Becoming glabrous	✓
27. Sometimes slightly tinged with rose color	✓ Especially near the base
28. 1–1.5 cm in length	✓ Spring 8.6 mm, fall 10.3 mm[2]
FLOWERS	
29. 1.3–1.5 cm in diameter	✓ (1.24–)1.5(–1.68)[3] cm
PEDICELS	
30. Slender	✓
31. Elongated	✓ (7.0–)10.7(–16.5) mm
32. Slightly villous	✓
CORYMBS	
33. Wide	✓
34. Compound	✓
35. Many-flowered	✓ (10–)15(–20)[4]

[1]Erroneously printed in original publication as mm.
[2]Both spring and fall numbers, Gilman *21005*, n=3; + *21006* n=4, +*21008*, n=3; total n=10; only short leaves were measured which may account for shorter lengths than Sargent reported.
[3]Haines *s.n.,* n=5; Gilman *21005*, n=10; *21006*, n=10 *21008*, n=10, total n=35.
[4]Typical terminal inflorescences, Gilman *21005*, n=10; *21006*, n=10; *21007*, n=10; *21008*, n=10.

Table 1. continued

Character states from the original description	Recent observations (✓=observed, ⃠=not observed)
BRACTS/BRACTLETS	
36. Oblong-ovate to linear	✓
37. Acute	✓
38. Glandular	✓
39. [Bractlets] fading to brown	✓
40. [Bractlets] often persistent until the flowers open	✓
CALYX	
41. Tube narrowly obconic	✓
42. Lobes wide	✓ Widest at base
43. Lobes acuminate	✓
44. Lobes incisely glandular-serrate	✓ Nearly pectinate glandular
45. Lobes glabrous on the outer surface	✓
46. Lobes pubescent on the inner surface	✓ Sparsely pubescent with long hairs
47. Lobes reflexed after anthesis	✓
STAMENS	
48. [Number] 20	⃠ (10–)14 (–19)[5], in 2–3 whorls
49. Anthers minute	✓ 0.7–0.8 mm; when measured dry[6] they are smaller, 0.4–0.7 mm
50. Anthers light pink	✓
STYLES	
51. Styles 2 or 3	✓ Usually 2
FRUIT	
52. Ripening at the end of September	⃠ Ripens end of October
53. Remaining on branches until the following spring	⃠ Very few persistent to Mar 2022
54. Pedicels slender	✓
55. Pedicels erect or spreading	✓
56. In many-fruited clusters	✓
57. Hard	⃠ Soft at full maturity
58. Subglobose	✓
59. Crimson	✓ Very bright, perhaps slightly more scarlet than crimson in life
60. Lustrous	✓
61. Marked by occasional pale dots	⃠ Dots are not noticeable
62. 6–8 mm diameter	⃠ Sep (*21006* + *21048*) *n*=51 average 7.67 mm; Oct (*21006* + *21048*) *n*=139, average 9.17 mm range 7.5–11.2 mm
63. Calyx prominent	✓
64. Calyx cavity deep	✓
65. Calyx cavity narrow	✓
66. Calyx lobes wide	✓
67. Calyx lobes coarsely serrate	✓ Nearly pectinate-glandular
68. Calyx lobes light red below the middle	✓
69. Calyx lobes pubescent on the upper side	✓
70. Calyx lobes persistent on ripe fruit	✓
71. Flesh thin	⃠ Early September not measured; October 2.58 mm, rather thick
72. Flesh dry	⃠ October moist although not juicy
73. Flesh mealy	⃠ October flesh soft, smooth
74. Nutlets 2 or 3	✓ Usually 2; 28 fruits yielded 53 nutlets[7]
75. Nutlets full and rounded at the end	✓
76. Nutlets ridged on the back	✓

[5]Haines *s.n.,* n=10; Gilman *21005*, n=10, *21006*, n=10, *21007*, n=10; *21008*, n=10.
[6]Dry anther measurements, Gilman *21005*, n=3; *21006*, n=4; *21008*, n=3, total n=10.
[7]*Gilman 21048*, *n*=28

Table 1. continued

Character states from the original description	Recent observations (✓=observed, ⦸=not observed)
77. Ridge broad	✓
78. Ridge slightly grooved	✓
79. Nutlets irregularly penetrated on inner faces by broad, shallow cavities	✓ Of 35 inspected, 23 have shallow concavities, 9 are plane, and 3 have deep concavities[8]
80. Nutlets 5–6 mm[9] long	✓ (4.3–)5.1(–6.7)[10]
81. Nutlets about 4 mm[11] wide	✓ (3.2–)4.0(–5.6)[12]

[8]*Gilman 21048*, *n*=35.
[9]Erroneously printed in the original description as cm.
[10]*Gilman 21006*, *n*= 53.
[11]Also erroneously printed in the original description as cm.
[12]*Gilman 21006*, *n*=53.

the same species by imperfect development." The developmental path leading to such variability in *Crataegus* was investigated by Evans and Dickinson (1996), who concluded that variability of stamen number in the species they studied was due to the failure of some stamens in the first whorl to develop (i.e., reducing the number downwards from ten). We note that flowers on our plants have up to 18 stamens, indicating development of at least three whorls, as is necessary in a 20-stamen flower. For this reason, we conclude that the original description is generally correct but is erroneous in not noting that most flowers have fewer than 20 stamens.

Fruit size.—A defining feature of *Crataegus pisifera* encapsulated in its species epithet is the small size of the fruit, listed in the original description as 6–8 mm. Later, different authors cited different size ranges, e g , Haines (2011) as 5–9 mm and Phipps (2014) as 4–6 mm, but even so, the fruits have always been cited as smaller than those of *C. succulenta* s.str. Our collections from two individuals (*Gilman 21006* and *21048*) made on 6 September ranged from 6.3 to 8.9 mm and in diameter, averaging 7.5 mm, in line with the original description (Figs. 3a, 3b). However, fruits collected from the same individuals on 23 October (Figs. 3c. 3d) were significantly larger, ranging from 7.2–11.2 mm and averaging 9.2 mm in diameter (Fig. 4) and, therefore, do not accord with the original description. In choosing the lectotype of *C. pisifera* Phipps (2007) noted that the fruits had been collected in July, and that fruit sizes were larger on some of the paratypes. He further commented that "perhaps this differentium is not as reliable as earlier believed." Inspection of label dates for all available original material indicates that fruits of a syntype collected by Brainerd (A, barcode 00017188) were collected on 28 September, while those on the sheet chosen by Phipps (2007) as the lectotype (A, barcodes 00816467 and 00816468), dated in Eggleston's hand from 26 July, were likely gathered by Eggleston, not by Brained. Because the Brainerd syntype (barcode 00017188) comports more fully with Sargent's protologue we propose, below, a second-step lectotypification and designate that sheet as the lectotype. Our collections of 23 October were made four weeks later than Brainerd's latest collection.

Since our later fruits average nearly 2 mm larger, we feel the original description should be emended. Our later fruit collection also results in different character states for the fruit (Table 1, #'s 52, 57, 72, 73, 74): the pomes are soft, not hard; the flesh is thick, not thin; it is moist (although not juicy), not dry; and it is soft and smooth (comparable, e.g., to banana), not mealy. Gilman's personal observation is that the flavor is bland, neither acidic nor sweet, and faintly apple-like. The original description noted that fruits persist through winter, but a visit in March 2022 showed that most fruits were either dropped or predated, with only a very few remaining attached.

Leaves.—While the current plants have leaves that match the description and type, we also undertook to compare the length:width ratio of short-shoot blades as emphasized by Phipps (2014) in his short description of *C. pisifera*. We calculate an average ratio of 1.4:1, well within the range (1.3–1.6:1) stated there. *Crataegus pisifera* differs, sometimes subtly, in leaf blade outline from *Crataegus succulenta,* but it is important to mention that some plants of *C. succulenta* have a nearly identical leaf blade outline and cannot be separated

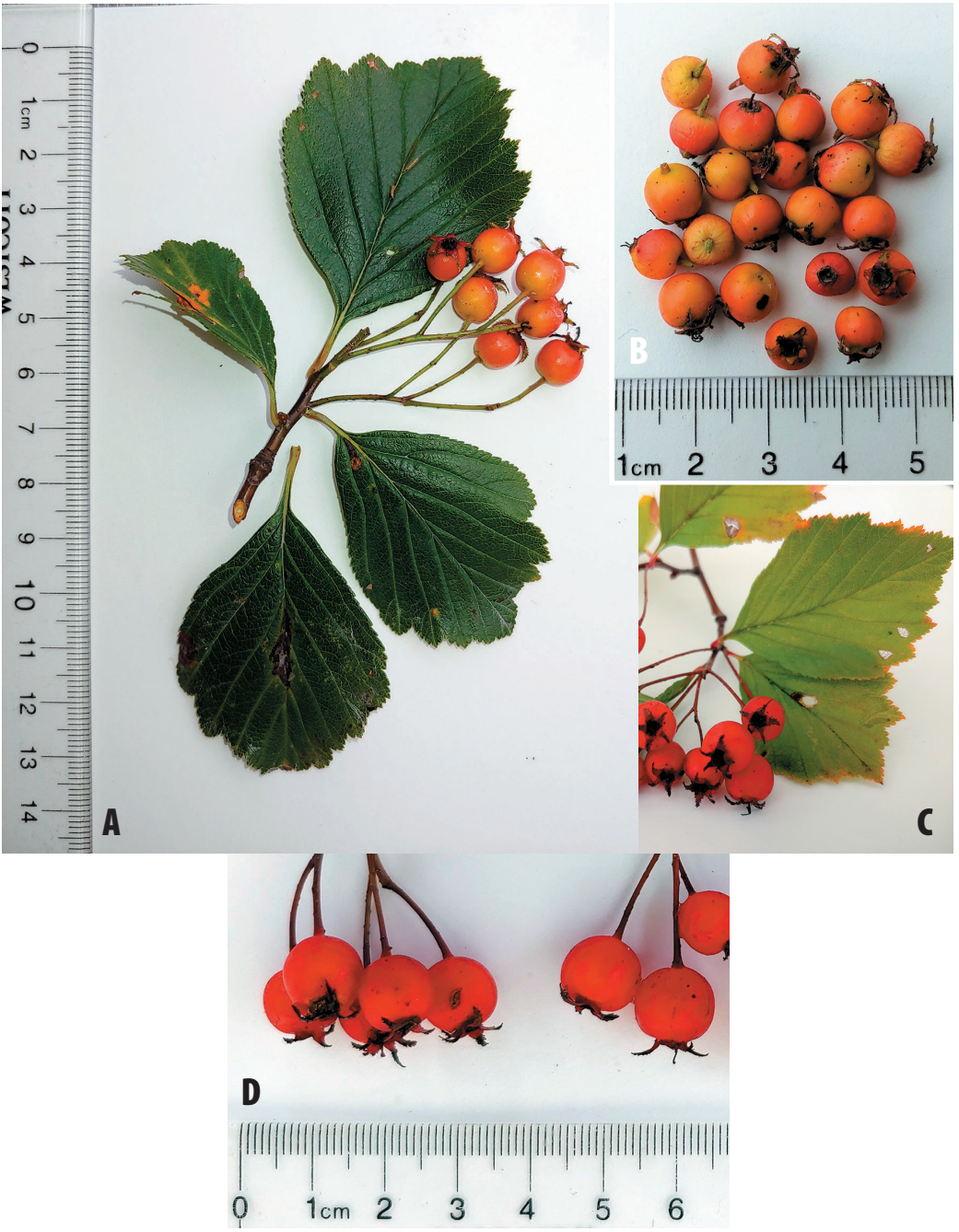
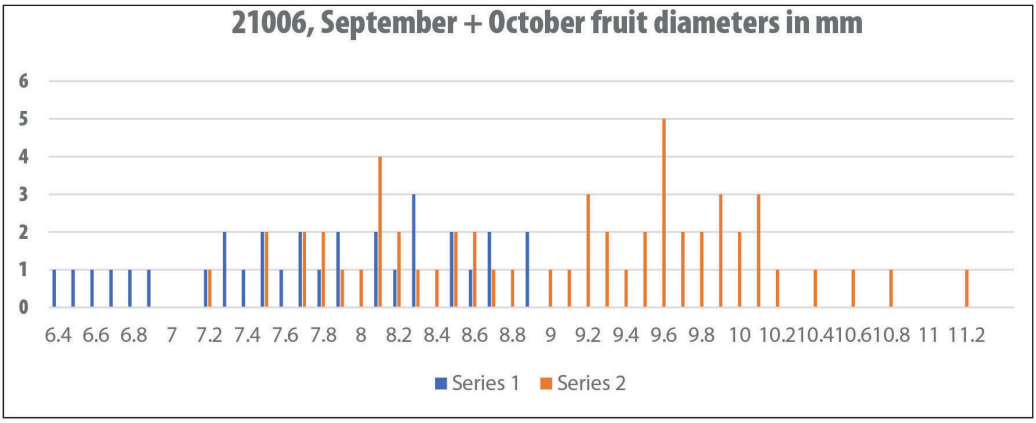
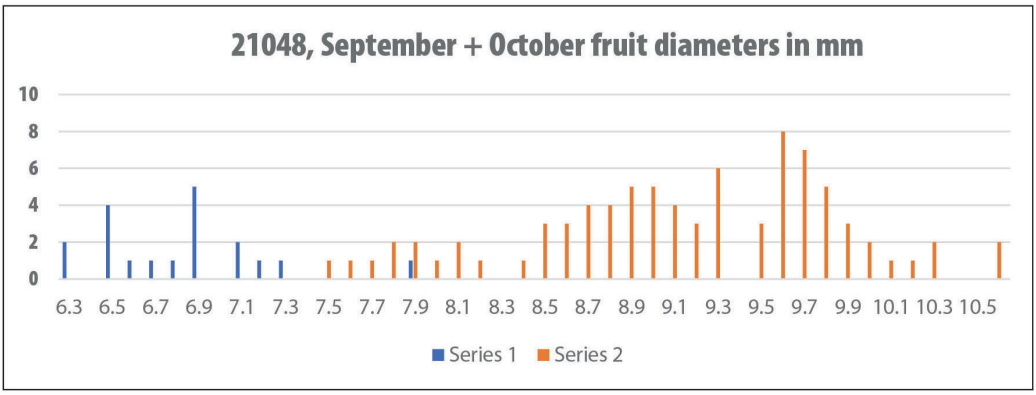


Fig. 3. Fruits. **A., B.** 4 September 2021 (*Gilman 21006* and *21048*); **C.,D.** 23 Oct 2021 (both *Gilman 21006*).



September (blue): *n*=32, range 6.4–8.9 mm, n=32, avg=7.8
October (red): *n*=56, range 7.2-11.2, n=56, avg 9.1



September (blue), *n*=19, range 6.3-7.9, average 6.9
October (red), *n*=83, range 7.5-10.6, average 9.2

Fig. 4. Seasonal variation of fruit sizes, as measured on pomes of *Gilman 21006* and *Gilman 21048*. September (blue): *n*=32, range 6.4–8.9 mm, avg 7.8 mm. October (red): *n*=56, range 7.2–11.2 mm, avg 9.1 mm.

without reproductive material. Most short-shoot leaves of *C. pisifera* have decidedly rhombic leaf blades, with a straight or barely convex taper to the base from the widest point of the leaf blade. The apical portion of the leaf blade (from the widest point to the apex) is equal to or shorter than the basal portion of the leaf blade (from the base to the widest point). Therefore, some leaves are asymmetrically rhombic with a suggestion of a nearly truncate apex (Fig. 5). *Crataegus succulenta*, on the other hand, has short shoot leaves with blades that have convex taper to the base, giving the overall base a more rounded aspect and the blades are more commonly broad-elliptic to elliptic-orbicular or elliptic-ovate. The apical portion of the leaf blade is usually equal to or longer than the basal portion.

Additionally, Phipps (2007) noted that the leaf lobing of *C. pisifera* is unusual among taxa closely allied to *C. succulenta*, although he did not explicitly state how so. We note that the lobes tend to be shorter and broader and have more obtuse to acute tips than those of *C. succulenta*, which have lobes that tend to be a bit more drawn out and have acute to narrow-acute tips. These differences are especially accurate in the region of *C. pisifera* but do work for many collections outside of the range of *C. pisifera*.

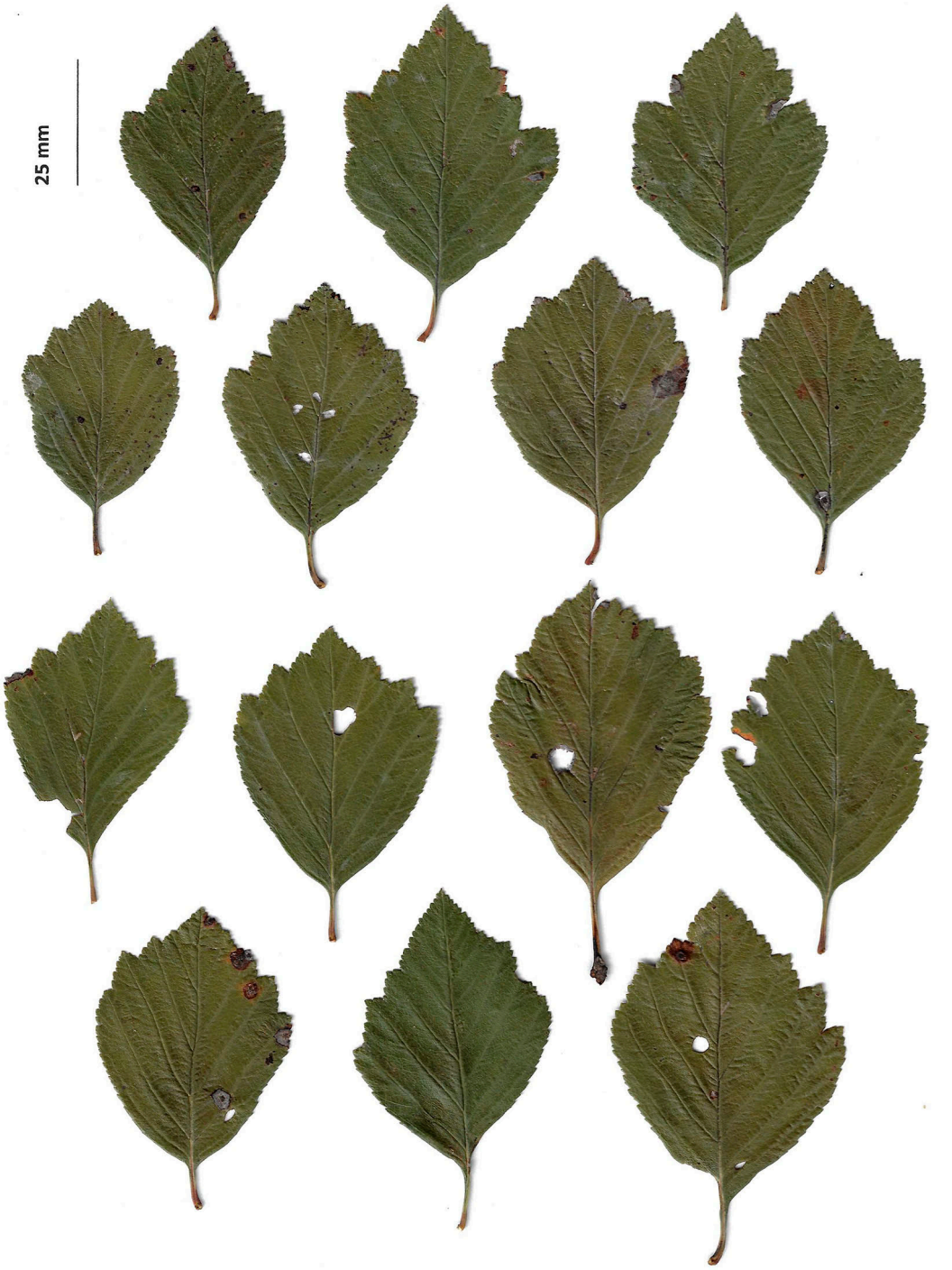


Fig. 5. Leaf shapes. Short-shoot leaves from *Gilman 21006* in top two rows and *Gilman 21048* in bottom two rows. Note the occasional occurrence of exaggerated proximal lobes.

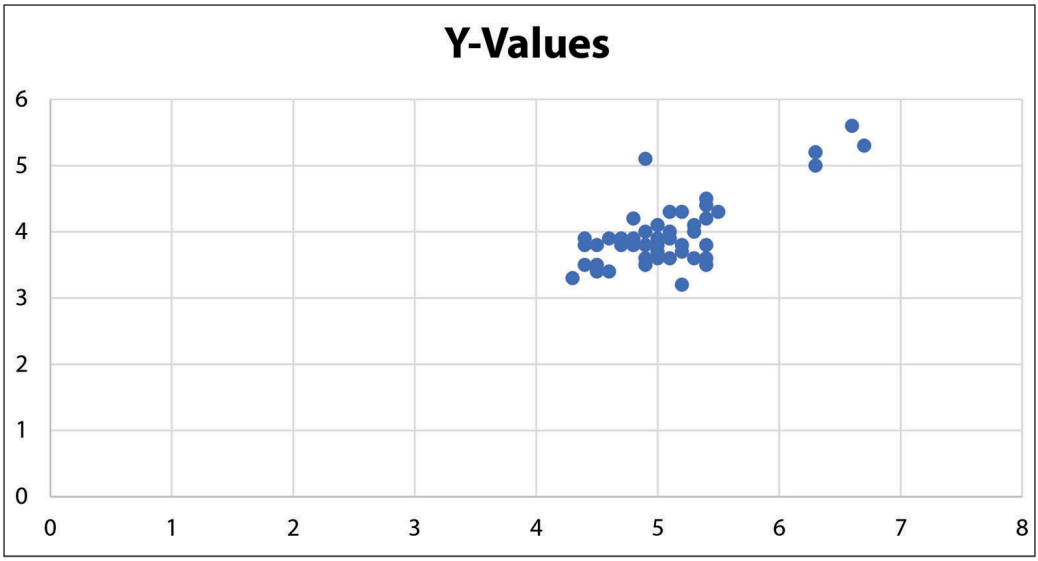


Fig. 6. Pyrene sizes from *Gilman 21006*, collected on 23 Oct 2021. X axis= length in mm, Y axis=width in mm. *n*=53 (less five duplicates = 48 dots shown). Range of lengths 4.3–6.7 mm, average 5.1 mm; range of widths 3.2–5.6, average 4.0 mm.

Pyrenes.—Pyrenes are as reported by Sargent, except that not all have the "broad, shallow cavities" of the original description. Of 35 inspected by Haines, nine were plane, 23 had shallow cavities, and three had deep concavities. Twenty-eight pomes chosen for inspection by Gilman (*Gilman 21006*) yielded only 53 pyrenes, indicating likely three instances of abortive pyrenes, and four instances of atypically large pyrenes (6.1–6.7 mm) (Fig. 6). It is these larger pyrenes that have deep cavities. We suggest their large size is a consequence of more resources being available to a surviving pyrene, and that the large size allows room for a deeper cavity to develop.

Synonymy with taxon neofluvialis and the [non]occurrence of neofluvialis in Vermont.—Eggleston (1913) placed *C. pisifera* in the synonymy of *C. neofluvialis* Ashe, a position adopted later by Palmer, who transferred *C. neofluvialis* to varietal status under *C. succulenta* Schrad. ex Link in the third edition of the Flora of Vermont (Dole 1937). However, Eggleston (1913) made no statement of his reasons for doing so. He had collected putative specimens of *C. neofluvialis* in North Carolina, where that species was originally collected and described (Ashe 1899), but those collections (housed at GH) have been determined by Phipps as *C. succulenta* s.str. (*Eggleston 4136*, GH! [HUH 01649185], duplicate at US [00510467; image!]; *Crayton & Eggleston 4388*, GH! [HUH 01649169], duplicate at VT!)]. Furthermore, a specimen from the Biltmore Herbarium (no collector, GH! [HUH 10649177]) that Eggleston had annotated as *C. neofluvialis* was also later determined by Phipps as *C. succulenta* s. str. *Crataegus neofluvialis* had been described (Ashe 1899) as having 10–15 stamens and with fruits 6–9 mm in diameter, in line with *C. pisifera,* although it has leaves more obviously narrowed to a cuneate base. From these facts, we conjecture that Eggleston likely observed (as we did) a stamen number fewer than 20 in *C. pisifera*, and that he emphasized stamen number and fruit size, but discounted leaf shape in his decision to ally *C. pisifera* with *C. neofluvialis*. Eggleston also overlooked characters that current *Crataegus* authors consider important and that do not accord between the two, such as pubescence of the abaxial leaf surface (only along veins vs. across the surface), anther color (pale vs. anthocyanic) fruit color (crimson vs. greenish, orange, or rosy cheeked [Ashe 1899]), and average pyrene number (2–3 vs. 3–5).

The repeated synonymy of *C. pisifera* with *C. neofluvialis* has resulted in incorrect attribution of *C. neofluvialis* to Vermont in some publications since Dole (1937). Ironically, both taxa were attributed to the state by Seymour (1969a, 1969b) and by Phipps (2014) although until now only the original collections of *C. pisifera*

were known and no other putative *C. neofluvialis* specimens from Vermont have been seen. Seymour's (1969a, 1969b) segregation of the two was based on stamen number (*C. neofluvialis* 10, *C. pisifera* 20), an obvious error. Phipps (2014) distinguished the two based on leaf lobing which we concur is a significant difference, and we presume that including Vermont in the range of *C. neofluvialis* in his treatment was a trivial error.

Other specimen(s) so annotated.—We have seen a syntype of *C. gemmosa* Sarg., collected in 1901 by Sargent at Grand Rapids, Michigan (A [HUH 00017819]!) that has been annotated by Phipps as *C. pisifera*. However, we disagree with that determination. Although the specimen has relatively smaller fruits than normal for *C. gemmosa*, its infructescences are quite pubescent, and even the pomes show some pubescence at their bases and summits, very much unlike the almost completely glabrous inflorescences, infructescences, and pomes of *C. pisifera*.

With this analysis of the current populations in concert with historical material, we contend that *C. pisifera* (Fig. 7) is a globally rare taxon restricted to a small area of Addison County, Vermont, that the Lemon Fair bridge is the Iron Bridge locality of Eggleston's labels, and that the population has persisted more than 115 years (1904–2020) although lost to local knowledge. Our rediscovery of this local endemic and the extended range and the larger populations reported here add to its significance (Wesley Knapp, NatureServe, pers. comm.).

The relationships of *Crataegus pisifera* remain to be resolved and, because its relationship to *C. succulenta* s. str. is not resolved, we prefer for the moment to regard it at species rank, the rank at which it was originally described, pending additional investigation. Notwithstanding our revision of some character states there are sufficient differences in leaf color, leaf lobing, pubescence of foliage, inflorescences, infructescences and fruits, as well as in stamen number variability, and nutlets to distinguish from its close congeners (see Key). The term microspecies has not been directly applied to *C. pisifera*, but it has been invoked in discussions of hawthorns (e.g., Majeský et al. 2017; Dickinson 2018, inter alia), and the morphological evidence presented here shows *C. pisifera* to fit that definition although, approaching this taxon at present, we also agree with Phipps (2014), who emphasized the study of infraspecific variation. As noted above, in the Flora of North America—the first continent-wide review of the genus in more than 160 years—Phipps followed his own advice and recognized *C. pisifera* as a variety of *C. succulenta*. Our recent rediscovery of *C. pisifera* presents an opportunity to re-examine it with new material and new tools. In particular, its ploidy level, which would shed light on its breeding system, should be investigated.

KEY TO NEW ENGLAND HAWTHORNS WITH CONCAVITIES IN PYRENES

1. Androecium with one cycle of stamens (i.e., stamens numbering mostly 5–10 per flower).
   2. Inflorescence glabrous.
      3. Sepals prominently glandular-serrate to glandular-pinnatifid with elongate calyx teeth, the longest teeth (0.3–)0.5–1.5 mm long; flowers with 4 or 5 styles _____ **C. bicknellii**
      3. Sepals entire to glandular-serrate, the longest teeth (when present) 0.1–0.5(–0.6) mm long; flowers with 2–4 styles.
         4. Leaf blades adaxially with abundant strigae during flowering, the hairs persisting at least along the main veins and/or in patches between the veins until early summer; short shoot leaves with blades elliptic to elliptic-obovate or obovate, the apical margins usually with weak to strong concave taper to the apex (infrequently some blades with straight taper), mostly cuneate at the base; flowers small to medium, 15–18 mm in diameter; anthers anthocyanic _____ (in part) **C. scabrida**
         4. Leaf blades adaxially glabrous or with very sparse strigae during flowering and then soon glabrous; short shoot leaves with blades broad-rhombic to broad-ovate or triangular-ovate, the apical margins usually with convex to straight taper (infrequently some blades with weak concave taper), broad-cuneate to broad-rounded at the base; flowers large, 19–22 mm in diameter; anthers usually non-anthocyanic _____ (in part) **C. handyae**
   2. Inflorescence sparsely to densely villous during flowering, usually some hairs persisting at least into early fruit.
      5. Pyrenes with a definite depression occupying most of each half of the inner face; bracts of leaf opening strongly tinged with red to orange-red and conspicuous; inflorescence relatively large, with (8–)10–31 flowers; sepals conspicuously glandular-serrate to glandular-pinnatifid; leaf blades mostly rhombic to obovate, those on short shoots with often with inconspicuous lobes _____ **C. macracantha**
      5. Pyrenes plane on the inner faces or some faces with irregular and shallow erosions; bracts of leaf opening yellow-brown or weakly tinged with red, less conspicuous; inflorescence mostly of small to medium size, with 3–16(–19) flowers; sepals glandular-serrate; leaf blades rhombic or elliptic to ovate, suborbicular, or elliptic-ovate (rarely oblong-obovate), those on short shoots with inconspicuous to evident lobes.

6. Inflorescence moderately villous; hypanthium moderately villous; young branchlets sparsely villous; flowers 18–19 mm wide; pomes obloid to obovoid, sparsely villous; leaf blades elliptic to rhombic or rhombic-ovate, usually widest near the middle, the margins with +/- straight taper to the apex ____ **C. laurentiana**
6. Inflorescence sparsely pubescent; hypanthium glabrous or sparsely pubescent; young branchlets glabrous; flowers 14–18 mm wide (or 19–22 mm in *C. handyae*); pomes globose to subglobose (rarely to short-obloid), glabrous; leaf blades vary variable in shape, but usually with one or more features: somewhat oblong in outline; broadest above or below the middle; and/or the margins with concave taper to the apex.
7. Flowers large, 19–22 mm in diameter; anthers usually non-anthocyanic; leaf blades adaxially glabrous or with very sparse strigae during flowering and then soon glabrous ____ (in part) **C. handyae**
7. Flowers small to medium, 14–18 mm in diameter; anthers anthocyanic; leaf blades adaxially with abundant strigae during flowering, the hairs persisting at least along the main veins and/or in patches between the veins until early summer.
8. Branch thorns long, slender, and straight or nearly so, (35–)45–60 × 1.9–2.1 mm ____ **C. ideae**
8. Branch thorns variable, usually shorter, more stout, and slightly curved, 22–45(–65) × (1.9–)2–2.9 mm.
9. Most leaf blades on short shoots elliptic to elliptic-obovate to oblong-obovate, with concave taper to the apex; hypanthium usually glabrous ____ (in part) **C. scabrida**
9. Most leaf blades on short shoots ovate to rhombic-ovate or broad-ovate, with convex or straight taper to the apex; hypanthium usually sparsely villous near the base ____ **C. egglestonii**

1. Androecium with two or three cycles of stamens (i.e., stamens numbering mostly 12–20 per flower).
10. Flowers 20–23 mm wide, with (4–)5 styles and anthers (1.6–)1.8–2.3 mm long ____ **C. umbratilis**
10. Flowers 13–20.5(–22) mm wide, with 2 or 3 styles and anthers 0.7–1 mm long.
11. Flowers with sparsely glandular-serrate sepals and mostly 3 styles; the apex of some branchlets and thorn bases with bloom in later season; inflorescences tending to be smaller, with 6–13 flowers ____ **C. brainerdii**
11. Flowers with prominently glandular-serrate to glandular-pinnatifid sepals and mostly 2 styles; branchlets and thorns without bloom; inflorescences tending to be larger, with (7–)12–20 flowers.
12. Pyrenes with deep excavations on the inner surfaces, mostly 6–7 mm long; inflorescences definitely villous (glabrous to sparsely villous in rare forms); leaf blades on short shoots with convex taper to the base, the apical portion usually equal to or longer than the basal portion (the portions defined as what is positioned above and below the widest point of the blade), with acute to narrow-acute lobes ____ **C. succulenta**
12. Most pyrenes plane to shallowly and irregularly eroded on the inner surfaces, only rare ones with deep excavations, 4.2–5.4(–6.7) mm long; inflorescences usually glabrous to sparsely villous; flowers 13–15(–16) mm in diameter; leaf blades on short shoots with straight to barely convex taper to the base, the apical portion usually equal to or shorter than the basal portion, with obtuse to acute lobes ____ **C. pisifera**

TYPIFICATION AND EXSICCATAE

Crataegus pisifera Sarg., Rhodora 7:163–164. 1905. *Crataegus succulenta* Link var. *pisifera* Kruschke, Milwaukee Public Mus. Publ. Bot. 3:159. 1965. Type: U.S.A. VERMONT. Addison Co.: Cornwall, S of Iron Bridge, 28 May & 28 Sep 1901, *E. Brainerd 15d* (Lectotype, **second-step chosen here**): A [00017188]). See Fig. 8. Lectotype, first-step, Phipps 2007: Cornwall, 26 Jul 1901, *E. Brainerd 15d* (A [00016467, 00016478]).

Other original material seen: U.S.A. VERMONT. Addison Co.: Cornwall, without locale, 28 May 1901 & 26 Jul 1901, *W.W. Eggleston 2234, 2323* (A [000016465, 00016466, 00016467, 0001646828]); without locale, 28 May 1901, 26 Jul 1901 & 15 Sep 1904, *W.W. Eggleston 2234* (K [000756155-image!], P [P03326139-image!], SJFM, US [0301874-image!], VT [053284, 053285, 0247505]); Cornwall, Iron Bridge, 28 May 1901, 26 Jul 1901 & 15 Sep 1904, *W.W. Eggleston 2234* (NY [01043374-image!, 01043375-image!].

Recent specimens seen: U.S.A. VERMONT. Addison Co.: Bridport: Market Road West, 0.75 mi E of Lake Street, S side of road, 22 May 2021, 4 Sep 2021 & 23 Oct 2021, *A.V. Gilman 21005* (VT, NEBC); Market Road West, 1.0 mi E of Lake Street = 0.4 mi W of Basin Harbor Road, S side of road, 22 May 2021, 4 Sep 2021 & 23 Oct 2021, *A.V. Gilman 21006* (VT, NEBC); Market Road West, 0.2 mi E of Basin Harbor Road, S side of road, 22 May 2021, 4 Sep 2021 & 23 Oct 2021, S side of road, *A.V. Gilman 21007* (NEBC, VT); Market Road West, E of stream, 27 May 2021, *A. Haines s.n.* (DINH); S side of Middle Road, ca 0.75 mi W of village, *A. Haines s.n.* (DINH); Cornwall, S of bridge over Lemon Fair River, 22 May 2021, *A.V. Gilman 21008* (NEBC, VT); Vt. Rte. 125, E side of Road, N of bridge over Lemon Fair River, 19 Jul 2021, 4 Sep 2021 & 23 Oct 2021, *A.V. Gilman 20148* (NEBC, VT).

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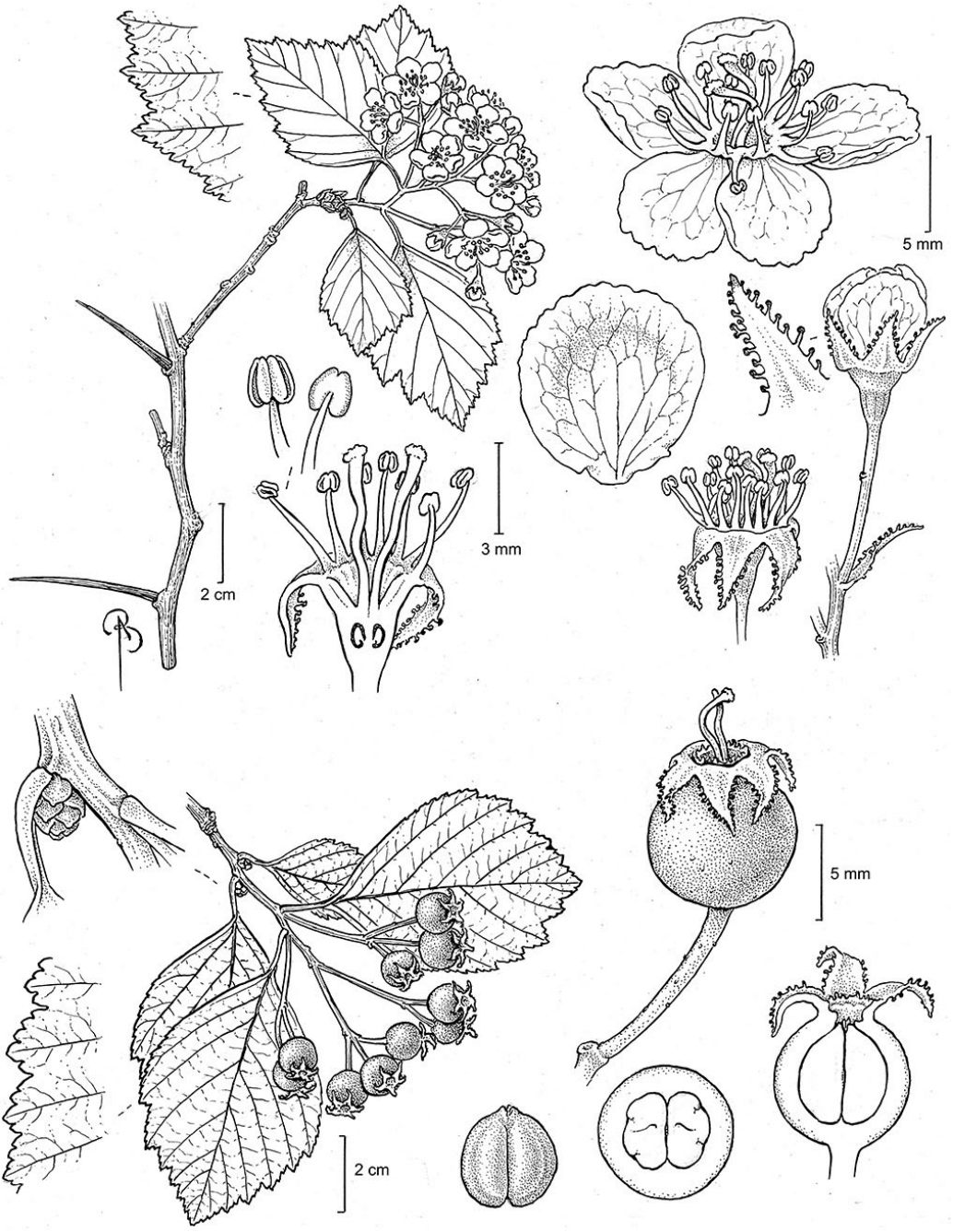

Fig. 7. Pea-fruited hawthorn, *Crataegus pisifera* Sarg. Based on topotypes (*Gilman 21008* and *21048*) from Cornwall, Vermont and on material (*Gilman* 2006) collected in nearby Bridport, Vermont. Drawn by Bobbi Angell, January 2022.

FIG. 8. Second stage lectotype of *C. pisifera* Sarg., *Brainerd 15d* (A [00017188]). Image courtesy of The Herbarium of the Arnold Arboretum of Harvard University.

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