WHAT *IS* SUKSDORF'S HAWTHORN? REVISION OF THE WESTERN NORTH AMERICAN 20-STAMEN BLACK-FRUITED HAWTHORNS (*CRATAEGUS* SERIES *DOUGLASIANAE*, ROSACEAE SUBTRIBE MALINAE)

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ABSTRACT

An agamic complex of 20- and 10-stamen, black-fruited hawthorns (*Crataegus* subg. *Sanguineae*, sect. *Douglasianae*) occurs in western North America, with a 10-stamen taxon disjunct in the upper Great Lakes basin. Here, we recircumscribe the 20-stamen taxa at the core of this complex (*C.* ser. *Douglasianae*). This is needed in order to distinguish between a presumptively ancestral diploid and its allo- and autopolyploid derivatives, all differing in breeding system, distribution, morphology, and pattern of genetic variation. The earliest name for these 20-stamen taxa, *Crataegus gaylussacia* A. Heller, was given to distinctive plants of Marin and Sonoma counties in California that have recently been shown to be autotriploids. In *Flora North America*, however, this name was applied to all 20-stamen, black-fruited hawthorns. We recircumscribe *C. gaylussacia*, and also recircumscribe and typify a slightly younger name, *C. suksdorfii* (Sarg.) Kruschke, with a specimen from southern Washington with the diminished pollen fertility found in allopolyploid, apomictic black-fruited hawthorns occurring east of the Cascades, from northern California north to southernmost Alaska. Finally, we recognize the diploid, self-incompatible, sexual black-fruited hawthorns found west of the Cascades from northern California to southwestern Washington as **Crataegus rhodamae-loveae** sp. nov. Together with the 10-stamen, black-fruited hawthorns in predominantly tetraploid, apomictic, and self-fertile *C. douglasii* Lindl. and its segregates (discussed in detail in a companion paper), these species are linked by whole genome duplications associated in most cases with hybridization, with members of red-fruited *C.* subg. *Americanae*, and with each other. We suggest that this complex provides a model for understanding other such groups of *Crataegus* species that are related by whole genome duplications resulting from the fertilization of unreduced gametes (facilitated by but not necessarily dependent on occurrence of gametophytic apomixis), often together with hybridization. We note that an earlier effort at DNA barcoding these and other hawthorn species that provided limited support for our taxonomic decisions here also demonstrated some limited utility of the original plant DNA barcoding loci in groups like *Crataegus*. The taxonomic decisions we advocate will warrant consideration when other groups of hawthorns are revised in the light of data like those employed here.

Key Words: Apomixis, Biogeography, Classification, Microsatellites, Morphology, Pollen, Polyploidy, Species Concepts, Typification

ABSTRACT

Un complejo agámico de espinos negros de 20 y 10 estambres (*Crataegus* subg. *Sanguineae* sect. *Douglasianae*) se da en el oeste de Norteamérica, con un taxón de 10 estambres disjunto en la cuenca alta de los Grandes Lagos. Aquí, recircunscribimos los taxones de 20 estambres en el núcleo de este complejo (*C.* ser. *Douglasianae*). Esto es necesario para distinguir entre un diploide presuntamente ancestral y sus derivados allo- y autopoliploides, todos ellos diferentes en sistema de reproducción, distribución, morfología y patrón de variación genética. El nombre más antiguo para estos taxones de 20 estambres, *Crataegus gaylussacia* A. Heller, se dio a plantas de los condados de Marin y Sonoma en California, que recientemente se ha demostrado son autotriploides. En la Flora de Norte América, sin embargo, este nombre se aplicó a todos los espinos de 20 estambres y frutos negros. Recircunscribimos *C. gaylussacia,* y también recircunscribimos y tipificamos un nombre más moderno, *C. suksdorfii* (Sarg.) Kruschke, con un espécimen del sur de Washington con la fertilidad del polen disminuida propio de los espinos de fruto negro alopoliploides y apomícticos que ocurren al este de las Cascadas, desde el norte de California hacia el norte hasta el extremo sur de Alaska. Por último, reconocemos como **Crataegus rhodamae-loveae** sp. nov. los espinos de fruto negro diploides, autoincompatibles y sexuales que se encuentran al oeste de las Cascadas, desde el norte de California hasta el suroeste de Washington. Junto con los espinos de 10 estambres y fruto negro en *C. douglasii* Lindl., predominantemente tetraploide, apomíctico y autofértil, y sus segregados (discutidos en detalle en un artículo complementario), estas especies están vinculadas por duplicaciones del genoma completo asociadas en la mayoría de los casos con la hibridación, con miembros de *C.* subg. *Americanae* de fruto rojo, y entre sí. Sugerimos que este complejo proporciona un modelo para entender otros grupos de especies de Crataegus que están relacionados por duplicaciones del genoma completo resultantes de la fertilización de gametos no reducidos (facilitada por, pero no necesariamente

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dependiente de la existencia de apomixis gametofítica), a menudo junto con la hibridación. Señalamos que un esfuerzo anterior de mediante código de barras de ADN de estas y otras especies de espino, proporcionó un apoyo limitado a nuestras decisiones taxonómicas, al igual que sucede en grupos de plantas como *Crataegus*. Las decisiones taxonómicas que defendemos merecerán consideración cuando se revisen otros grupos de espinos a la luz de datos como los empleados aquí.

INTRODUCTION

In western North America the common, native hawthorns are either red-fruited species of *Crataegus* subgenus *Americanae* El-Gazzar or black-fruited ones belonging to *C.* subg. *Sanguineae* Ufimov. European red-fruited *C. monogyna* (*C.* subg. *Crataegus*) is naturalized and invasive (Christensen et al. 2014; EDDMapS 2016). The only other member of *C.* subg. *Crataegus* also naturalized in western North America, *C. laevigata* (Poiret) de Candolle, is known only from the San Juan Islands of Washington (Phipps 2015). Together, all of these species fall into two kinds, comprising individuals with either around 20 stamens per flower, or around 10 stamens per flower (Christensen 1992; Dickinson et al. 1996; Evans & Dickinson 1996; Phipps 2015; Phipps & Muniyamma 1980; Ufimov & Dickinson 2020). In *C.* subg. *Sanguineae,* there are two North American sections, *C.* sect. *Douglasianae* C.K. Schneid. discussed here, and *C.* sect. *Salignae* T.A. Dickinson & Ufimov that is restricted to the southern Rocky Mountains and adjacent areas of the Great Basin (Dickinson et al. 2021; Ufimov & Dickinson 2020). Until recently, the two stamen number morphotypes in *C.* sect. *Douglasianae* have been treated as Suksdorf's hawthorn, *C. suksdorfii* (Sarg.) Kruschke, and Douglas hawthorn, *C. douglasii* Lindl., respectively, both in *C.* ser. *Douglasianae* (C.K. Schneid.) Rehder (Dickinson et al. 2008). However, in the online *Jepson Manual* for California (Phipps 2013) and in *Flora North America* Vol. 9 (Phipps 2015), an earlier name for a California hawthorn (*C. gaylussacia* A. Heller) was applied to all *Douglasianae* with 20 stamens per flower. Here we show that a narrower circumscription of *C. gaylussacia*, resurrection of a recircumscribed *C. suksdorfii*, and description of one new species are warranted on the basis of differences within this group in biogeography, ploidy level, breeding system, and morphology. Molecular data are also available that are relevant to these proposed changes, and a set of microsatellite data are reanalyzed and found to support this revised taxonomy.

Taxonomic history.—Understanding the black-fruited hawthorns of the western North America has been a process, by Europeans and Euro-Americans and -Canadians over the past 200–250 years, of sequentially unpacking the diversity present in these widespread, often locally abundant plants (Table 1). As also noted in Table 1, indigenous peoples of western North America have a much longer history of analyzing this diversity, and in an apparently much more pragmatic context (food, tools, etc.; Turner 2014a; Turner 2014b; Turner 2014c; Zarrei et al. 2015). This unpacking process is exemplified by the way closer examination of North American hawthorns in general revealed, during the nineteenth and early twentieth centuries, striking differences in floral architecture not known in European hawthorns. Notably, this consisted of discovering the discontinuous variation in stamen number per flower referred to above, with variously around 20 (as in virtually all Eurasian *Crataegus* species), or else 5–10 stamens per flower (Table 1). Over time, these and other differences formed the basis for an extensive infrageneric classification (Lo et al. 2007; Loudon 1838; Palmer 1925; Phipps 2015; Phipps et al. 1990; Sargent 1907b; Schneider 1906; Ufimov & Dickinson 2020) that now is largely supported at the level of subgenera, sections, and series by phylogenetic inferences from DNA sequence data (Albarouki & Peterson 2007; Dai et al. 2009; Liston et al. 2021; Lo et al. 2009a; Lo et al. 2007; Verbylaitė et al. 2006; Zarrei et al. 2014; Zarrei et al. 2015).

Variation in ploidy level and breeding system.—Discussions of taxonomic complexity in North American *Crataegus* initially drew upon evidence of polyploidy obtained from pollen fertility data (Standish 1916) and then from sectioned material of root tips and developing pollen mother cells (Longley 1924; Moffett 1931). These results bolstered the arguments of Brown (1910), Camp (1942), Rickett (1936), and others that apomixis, hybridization, and polyploidy were responsible for the very large numbers of hawthorn species described 1890–1910. Later, chromosome squash methods were employed by Gladkova, Muniyamma, Ptak, and others (Dickinson et al. 1996; Dickinson & Phipps 1986; Gladkova 1968; Muniyamma & Phipps 1979b; Ptak 1986; Smith & Phipps 1988). These studies confirmed the subtribe Malinae base chromosome number

TABLE 1. Taxonomic history of the principal black-fruited hawthorns (*Crataegus sect. Douglasianae* C.K. Schneid.) of western North America. Prior to the eighteenth century, knowledge of the plants of western North America was held by the indigenous peoples of the region. They developed this knowledge over more than 13,000 years of occupation following deglaciation (Turner 2014b) and it can be recovered in the ethnobotany of modern indigenous peoples of the Pacific northwest and adjacent areas. Names and uses have been compiled, and in the case of the hawthorns the names repeatedly emphasize their shrubby habit ("bush"), thorniness, and fruits ("berries") (Turner 2014c; Zarrei et al. 2015). The remainder of this table summarizes the modern documentation of these hawthorns, beginning with eighteenth century European exploration of the region.

Name	Documentation	Evidence	Notes
?Psidium[struck out], an Pyrus? Pyrus? Crataegus? Mespilus?	Torner Collection of Sessé and Mociño Biological Illustrations, Number 1959, courtesy of the Hunt Institute for Botanical Documentation Carnegie Mellon University, Pittsburgh, Pa. (2005).	Twenty stamens per flower, calyx lobes relatively short, leaves like those of *C. suksdorfii* sensu stricto, thorns straight, apparently relatively short by comparison with other structures. Recorded at Nootka Island by the artist Atanasio Echeverría y Godoy for the Sessé and Mociño Expedition (1787–1803).	Probably allopolyploid *C. suksdorfii* sensu stricto
"Deep purple haw. Columbia R. April 29th 1806."	Lewis & Clark specimen first described in *Flora Americae septentrionalis* (Pursh 1814); PH/APS Special Collection- Lewis and Clark; Deep purple Haw.	12 or 13 stamens per flower. Collected on the Walla Walla R., Walla Walla Co. OR (Reveal et al. 1999)	*C. glandulosa* Moench (Pursh 1814); *C. douglasii* Lindl. (Meehan 1898; Reveal et al. 1999)
***C. punctata* β? *brevispina* Douglas, MSS apud Herb. Hort. Soc. Lond.**	*Flora boreali-americana* (Hooker 1832); Kew 000370425! (pubescent; Fig. 10). Also Kew 00042062! (Douglas) and 00042063! (Scouler).	"Two varieties are in Mr. Douglas's collection from the North-West coast; both, indeed, with short thorns; one is glabrous in every part, the other has the peduncles, calyces, and underside of the leaves downy." (Hooker 1832).	The pubescent form (Fig. 10) labeled (by Nuttall?) as *C. sanguinea* Pall. β. *douglasii* Torr. & A. Gray and "near the confluence of the Columbia 1825" is probably diploid *C. rhodamae-loveae* sp. nov. whereas, as noted by Nuttall (1846), the glabrous one corresponds to *C. douglasii* Lindl. (below). Steudel (1840) listed *C. brevispina* Dougl. as a synonym of *C. punctata* Jacq. but with no other information, making Douglas' name invalid (K. Gandhi pers. comm.).
***C. douglasii* Lindl.**	Lindley (1835); Kew 000442061! Also Kew 000442065!, 000442066! (Douglas specimens of *C. douglasii*).	Flowers shown with 10 stamens per flower (Plate 1810), matching type specimen and Douglas collections.	Hypanthium glabrous or sparsely pubescent, calyx lobes 2–3 mm long with some marginal teeth.
***C. sanguinea* β. *Douglasii* Nutt.**	*Flora North America* (Torrey & Gray 1840); *The North American Sylva* Vol. 2, pp. 6–8, Plate 44 (Nuttall 1846)	8–10 stamens per flower (Plate 44).	The names used by Pursh, Hooker, and Lindley are given as synonyms. *Crataegus rivularis* Nutt. ex Torr. & Gray of the Rocky Mountains is also described. "It was also observed by Douglas in the interior of Oregon, where we likewise met with it. It is, in all probability, the smoother, supposed variety of *C. punctata*, mentioned by Hooker in his Flora." (Nuttall 1846)

Table 1. continued

Name	Documentation	Evidence	Notes
***C. rivularis* Nutt.** ***C. douglasii* Lindl.**	"Pioneer Botanist William Cusick: His Dark and Silent World" (Love 2007) Cusick 1474, (HUH01612619! NDG022224! ORE46066!) collected 1887 on the Willamette, Oregon.	NDG022224 has black fruits with 15–20 stamens.	W.C. Cusick note in packet accompanying the HUH specimen reads, "*Crataegus rivularis*. I suppose this must be the prevailing form in Willamette. Shrub or small tree commonly of streambanks, of more upright growth, lighter colored and smoother bark than in E. Oregon *C. douglasii*; but from what I saw of it they are hardly distinct."
***C. rivularis* Nutt.** ***C. douglasii* Lindl.**	*Flora Franciscana* (Greene 1891)	*Crataegus rivularis* described as "thorns short, stout … calyx-lobes short, obtuse, often pubescent on the margin… Sierra and Plumas counties, and far to the northward and eastward," with *C. douglasii* contrasted as "thorns 1 in. long … calyx-teeth lanceolate, nearly as long as the tube, pubescent … In the northern counties; perhaps not within our limits."	The first species corresponds to the entities studied here with about 20 stamens per flower, whereas the second matches the current concept of *C. douglasii*. Greene described the genus as having 5–20 stamens per flower, but the species descriptions do not include stamen numbers.
***C. gaylussacia* A. Heller**	Heller (1903) NY00435881, Heller 6052 and isotypes distributed by Heller (e.g., NY00435882, NY00435883).	"…thorns stout, scattered, 1 cm long; … fruit … surmounted by five short, obtuse calyx lobes; …" Stamen number per flower not reported. Type collected from Sebastopol, Sonoma Co. CA.	"Heretofore this distinct species has passed for *C. rivularies* [sic], Nutt., collected originally by Nuttall in the Rocky Mountains of Montana, the type of which is preserved in the herbarium of Columbia University, New York City, and is quite different from our California plant." Heller specimens examined here (Appendix 1) average 14–17 stamens per flower.
***C. douglasii* var. *suksdorfii* Sarg.**	Correspondence between W.N. Suksdorf and C.S. Sargent, 1904–1907; Sargent (1907a). WSU has Suksdorf's draft of his October1905 letter to Sargent re the specimens of forms D, X, Y, and Z (R.M. Love transcription). In addition to this type material at HUH, Suksdorf distributed duplicates and new collections from the 'type' trees widely (Appendix 1).	Extensive tabulation of shoot, thorn, leaf, flower, and fruit characters by Suksdorf in letter to Sargent dated October 1905 (draft in Suksdorf papers at University of Washington; transcribed and translated from the German by B. Schulz, M. Schoeffler, and H. Wittman).	Four morphotypes designated by Suksdorf (D, X, Y, and Z): D, with 20 stamens per flower, WNS4419 (Falcon Valley); WNS4034, WNS5026, WNS5031, WNS5040 (all Bingen). Described by Sargent as *C. douglasii* var. *suksdorfii* without designation of a type (Table 2). X, Y, and Z, all with approximately 10 stamens per flower and referred by Sargent to *C. douglasii* var. *douglasii* on the basis of having examined Lindley's (1835) illustration of *C. douglasii* as well as specimens.

Table 1. continued

Name	Documentation	Evidence	Notes
***C. suksdorfii* (Sarg.) Kruschke**	Kruschke (1965)		Kruschke misspelled Suksdorf's name and neglected to designate a type for the new species (Voss 1965). Recent authors nevertheless agree with Kruschke's change (Brunsfeld & Johnson 1990; Dickinson et al. 1996; Dickinson & Love 1997; Phipps & O'Kennon 2002).
***C. gaylussacia* A. Heller**	Phipps (2015)		Citing the priority of Heller's name, Phipps did not distinguish the different cytotypes with 20 stamens per flower.

of $x = 17$ determined by Moffett (1931), as against that of $x = 16$ (Longley 1924), but not before the difference in geographic focus of the sampling for each of these earlier studies led El-Gazzar (1980) to describe North American hawthorns as $x = 16$ *C.* subg. *Americanae*, distinct from $x = 17$ European *C.* subg. *Crataegus*.

While apomixis in Rosaceae is well known (Hojsgaard & Pullaiah 2022), gametophytic apomixis was not actually demonstrated in *Crataegus* until the work of Muniyamma (Muniyamma & Phipps 1979a; Muniyamma & Phipps 1984), followed by that of Ptak (1986, 1989), on triploids and tetraploids in *C.* subg. *Americanae* and *C.* subg. *Crataegus*. Subsequent work (Muniyamma & Phipps 1985; also Ptak 1986) demonstrated that diploids produce mainly reduced, sexual megagametophytes. Controlled pollinations combined with cytological analyses of *C.* subg. *Americanae, C.* subg. *Crataegus*, and *C.* subg. *Sanguineae* taxa showed that polyploids are self-fertile and pseudogamous (pollination is required for endosperm development, even if embryos develop parthenogenetically), whereas diploids appear to exhibit the gametophytic self-incompatibility found in other Rosaceae (Dickinson et al. 1996; Dickinson et al. 2007; Dickinson & Phipps 1986; Hauck et al. 2006; Lewis 1947; Love & Feigen 1978; Vašková & Kolarčik 2019). Flow cytometry dramatically increased the numbers of taxa for which ploidy level data are available, and has made it possible to infer the events leading to the formation of individual seeds, rather than predicting seed formation events from observations of megagametophyte development (Kolarčik et al. 2022; Kolarčik et al. 2018; Lo et al. 2013; Matzk et al. 2000; Talent & Dickinson 2007a; Talent & Dickinson 2007b; Talent & Dickinson 2007c; Vašková & Kolarčik 2019). In *C.* subg. *Sanguineae*, two sections (sects. *Douglasianae* and *Salignae* T.A. Dickinson & Ufimov) have been described as agamic complexes comprising both diploids and polyploids based on flow cytometric methods (Dickinson et al. 2008; Talent & Dickinson 2005; Talent & Dickinson 2007b) ground-truthed in part by the earlier cytological observations (Dickinson et al. 1996), morphological variation (Dickinson et al. 2008), and molecular evidence for the occurrence of hybridization and allopolyploidy as well as autopolyploidy (Liston et al. 2021; Lo et al. 2009b; Lo et al. 2010; Zarrei et al. 2014).

Biogeography.—The geographic distributions of the taxa in *C.* ser. *Douglasianae* provides an example of geographic parthenogenesis, that is, the much wider distribution of apomictic polyploids, compared to their diploid, sexual relatives, with the apomicts occupying more challenging environments (drier, colder) than those occupied by diploids, and having expanded into previously glaciated areas (Dickinson et al. 2021 and references therein; see below).

Morphological variation and taxonomic revision.—In the case of the black-fruited hawthorns of western North America modern data acquisition methods and analyses have provided support for infrageneric classifications, but this support has not yet been translated into taxonomic decisions about individual species that are also supported by non-molecular evidence. Here we seek to remedy this by answering with mainly non-molecular data the question of what Suksdorf's hawthorn is, as follows: (1) how many distinct 20-stamen black-fruited entities are present in western North America? The abundance of Suksdorf's specimens, hence morphological comparison here between historical and modern specimens, greatly helps us in making this decision. (2) How should these entities be recognized taxonomically (cf. Soltis et al. 2007)? Is the *Flora North America* treatment of all these entities as *C. gaylussacia* (Phipps 2015) the best solution? And (3) what do the answers to these questions say regarding the species concepts appropriate for use in *Crataegus* and, more generally in other, comparable agamic complexes? In what follows, data on molecular variation will be adduced where relevant in support of conclusions drawn from variation in breeding system, morphology, and ploidy level. In a companion paper we address parallel questions as they apply to Douglas hawthorn, *C. douglasii*, and to the morphologically similar taxa that have been segregated from it.

MATERIALS AND METHODS

Our principal sample ($N = 247$; Appendix 1) comprises, for the most part, specimens in the Green Plant Herbarium (TRT) at the Royal Ontario Museum (ROM) collected in the course of fieldwork in western North America by the first author and collaborators and, as a result of the transfer of his *Crataegus* research collection to TRT, by J.B. Phipps and his co-workers. We refer to western North America as our area of concern on

purpose, as we do not wish to have to explain a non-standard expansion of the (from our Canadian perspective, inaccurate) term, "Pacific Northwest." The specimens and records on which our study is based belong to *C.* ser. *Douglasianae*, and come from southern Alaska, British Columbia, Washington, Idaho, Montana, Oregon, and California north of the Bay Area. In addition to material at TRT, abundant type material of *C. douglasii* var. *suksdorfii* Sarg. is found elsewhere because of the way in which W.N. Suksdorf distributed duplicate specimens of the five trees from which he collected the specimens sent to Sargent at Harvard in 1905 (isosyntypes; Table 2; cf. Dickinson & Love 1997; Sargent 1907a). Suksdorf subsequently also distributed specimens from these trees to many other herbaria. Taken together, the multiple specimens available for each of Suksdorf's numbers cited in Sargent's protologue mean that descriptors unavailable in specimens examined by Sargent prior to his 1907 publication may be found in one or more of the duplicates that Suksdorf subsequently collected and later distributed (Table 2). In like manner, there are also several specimens distributed by A.A. Heller as isotypes of his *C. gaylussacia* (Appendices 1, 3; Heller 1903). These type and other specimens of biogeographic or historical importance for understanding the taxonomy of western North American *C.* ser. *Douglasianae* (including the duplicates of the syntypes collected by Suksdorf after 1907) have been included in the loans received from the herbaria indicated in Tables 1 and 2. In what follows we will refer to the black-fruited, 20-stamen entities of western North America as either *C. gaylussacia* s.str. of Marin and Sonoma counties in California, or *C. suksdorfii* sensu lato. Comparison is made with 10-stamen *C. douglasii* (including some of its segregate species) because sometimes *C. douglasii* is not distinguished from *C. suksdorfii* sensu lato, and because *C. douglasii* appears to be the link between diploid and some polyploid cytotypes of *C. suksdorfii* sensu lato (Lo et al. 2009b). Many specimens examined here were also used in an earlier study of western North American black-fruited hawthorns that included both *C.* sect. *Douglasianae* and sect. *Salignae* (Dickinson et al. 2008).

The *Crataegus* specimens studied here and in earlier work have been georeferenced, as described elsewhere (Dickinson et al. 2021). The geographic distribution of the *Douglasianae* cytotypes and species is thus generally well documented, notably in the context of geographic parthenogenesis (maps in Christensen et al. 2014; Coughlan et al. 2017a; Coughlan et al. 2014; Dickinson et al. 2008; Dickinson et al. 2021—see DOI 10.5281/zenodo.5567918; Lo et al. 2009b; Lo et al. 2013). Patterns of allopatry and sympatry, and morphological differentiation, have also been tabulated (Table 6 in Dickinson et al. 2021). These recent comparisons also include *Crataegus chrysocarpa* Ashe and *C. macracantha* Lodd. ex Loudon in *C.* subg. *Americanae* (Dickinson et al. 2021; Liston et al. 2021), as these two species belonging to *C.* subg. *Americanae* represent likely parents of the *Douglasianae* allopolyploids (Zarrei et al. 2014). Geographic coordinates for specimen records are documented in Appendices 1 and 2. Many of the specimens used here also provided data, or served as vouchers, for earlier work that employed data from cytological or flow cytometric determinations of ploidy level (Coughlan et al. 2014; Dickinson et al. 1996; Dickinson et al. 2008; McGoey et al. 2014; Talent & Dickinson 2005; Talent & Dickinson 2007a; Talent & Dickinson 2007b; Talent & Dickinson 2007c). Some of these studies also documented DNA sequence variation in chloroplast and nuclear loci (Liston et al. 2021; Lo et al. 2009b; Lo et al. 2010; Lo et al. 2013; Zarrei et al. 2014; Zarrei et al. 2015), and these results are integrated into the discussion below.

A subsidiary sample corresponds to individuals studied by one of us in order to examine the relationships between *C. douglasii* microsatellite genotypes, niche breadth, range extent, and pollen fertility (as a proxy for fitness) (Appendices 2, 4; see Table 1 and Fig. 2 in Coughlan et al. 2017b; Han 2013; Han et al. 2013). For comparative purposes, this sample also includes representatives of *C. gaylussacia* and *C. suksdorfii* sensu lato, as well as members of *C.* subg. *Americanae*. In order to maximize group sizes, only five taxonomic groups were recognized in this sample: *C.* subg. *Americanae* (*C. chrysocarpa* and *C. macracantha*, $N = 9$ and 4, respectively), 150 *C. douglasii* ($N = 133$) and its segregates (*C. atrovirens* J.B. Phipps & O'Kennon, $N = 2$; *C. castlegarensis* J.B. Phipps & O'Kennon, $N = 7$; *C. okennonii* J.B. Phipps, $N = 4$; *C. phippsii* O'Kennon, $N = 3$; *C. shuswapensis* J.B. Phipps & O'Kennon, $N = 1$), *C. gaylussacia* ($N = 17$), allopolyploid *C. suksdorfii* sensu lato ($N = 16$), and diploid *C. suksdorfii* sensu lato ($N = 37$). The geographic distribution of *these* sampling sites is summarized here (Fig.

Table 2. Wilhelm Suksdorf specimens of *Crataegus douglasii* var. *suksdorfii* Sarg. in the Harvard University Herbaria (A) from trees mentioned in the protologue of Sargent (1907a); all from Washington, U.S.A. (Weber 1944). The holotype designated here and the syntypes all are labeled Crataegus Douglasii Lindl. and are annotated by C.S. Sargent, "var. Suksdorfii n. var. Sarg."

Specimens (collection number, HUH barcode number)	Date	Locality	Notes
W.N. Suksdorf 4034 (HUH00018058) HUH00018059	24 Apr 1905 01 Jul 1905	Bank of the Columbia River, Bingen, Klickitat Co.	Original material; syntype.
W.N. Suksdorf 4419 (HUH00018057)	**A.** 16 Jul 1905 **B.** 10 Aug 1905	Border of meadow, Falcon Valley, W. Klickitat Co.	Original material. **Holotype designated here** (Fig. 9).
W.N. Suksdorf 4419 (HUH00018056) W.N. Suksdorf 4419 (HUH00018055)	01 Aug 1907 07 Jun 1909	Falcon Valley	Not original material; not seen by Sargent prior to publication; not a syntype.
W.N. Suksdorf 5026 (HUH00018053)	21 Apr 1905; 25 Apr 1905	Bingen, Klickitat Co.	Original material; syntype.
W.N. Suksdorf 5026 (HUH00018054)	30 Jun 1905	Bingen, Klickitat Co.	Original material; syntype.
W.N. Suksdorf 5026 (HUH00018052)	08 July 1907	Bingen	Not original material; not seen by Sargent prior to publication; not a syntype.
W.N. Suksdorf 5031 (HUH00018048)	22 Apr 1905	Bingen, Klickitat Co.	Original material; syntype.
W.N. Suksdorf 5031 (HUH00018049)	01 Jul 1905		
W.N. Suksdorf 5040 (HUH00018050)	03 May1905	Border of bottom land, Bingen, W. Klickitat Co.	Original material; syntype.
W.N. Suksdorf 5040 (HUH00018051)	01 Jul 1905		

3; Table 3) using the R package *ggmap* (Kahle & Wickham 2013) and Google Maps. Because our other distribution data are already published, they are not documented further here except as noted, and are instead discussed below in concert with the other results on which our conclusions are based.

Morphological and genetic data analyses.—The morphological data explored here using uni- and multivariate methods represent a subset of a panel of descriptors employed earlier (Table 2 in Dickinson et al. 2008; Dickinson et al. 2021). These descriptors are employed here in a sample that includes, for the first time, the type material of *C. douglasii* var. *suksdorfii* Sarg. (Sargent 1907a), *C. gaylussacia* A.Heller (Heller 1903), and subsequent collections from the same trees. One of these descriptors used previously (Dickinson & Phipps 1985; density of marginal teeth adjacent the leaf apex; see below and Appendix 3) was analyzed by itself in order to contrast diploid and possibly autopolyploid cytotypes with the allopolyploid cytotypes of *C. suksdorfii* sensu lato. The descriptors employed here were tested for normality with and without transformations (logarithmic, square root) using Ryan and Joiner's normal probability plot correlation statistic (Ryan & Joiner 1974 (updated 1990)). Critical values for this statistic were calculated according to Ryan and Joiner using a purpose-written function in R (R Core Team 2021).

Following earlier practice (Dickinson et al. 2021; Vander Kloet & Dickinson 1999), we purposely chose to analyze a limited number of ratio-scale descriptors in order to use variables coming as close as possible to meeting the assumptions of discriminant or canonical variates analysis (CVA), namely normality and homoscedasticity. In this way, with fewer variables (four, plus four dummy variables representing the five groups in the 20-stamen subsample only) relative to the number of specimens from which data were collected (136), there is a greater chance that the sample results are predictive of features of the parent populations (Gittins 1985). In the taxonomic descriptions given below the ranges given for quantitative descriptors represent the second and third quartiles of the data (mean values obtained from measurements of up to 10–20 structures per specimen), that is, the central 50 percent of the observations. Extreme values, when given parenthetically, are the observed maxima and minima of the descriptors in question. In this approach, we follow

TABLE 3. Differences in taxon dispersions for the four thorn and leaf dimensions (Fig. 1; all except THND log-transformed) between black-fruited *Crataegus taxa*, from ANOVA of multivariate distances from specimen to taxon median vector (taxon dispersions as the average of these distances for each taxon; given below taxon name; R package *vegan* function **betadisper**). Significance levels from Tukey's HSD test (ns, not significant; *, $p < 0.05$, ***, $p < 0.001$) are reported for testing H0: pairwise equality of taxon dispersions. Table entries are the absolute values of the rounded off differences between the taxon dispersions and their significance level.

	diploid *C. suksdorfii* s.l. (*N* = 36) **0.3095**	**allopolyploid *C. suksdorfii* s.l. (*N* = 77)** **0.2891**	***C. gaylussacia* (*N* = 23)** **0.2316**
***C. suksdorfii* s.l.**	0.0204 ns		
C. gaylussacia	0.0779 *	0.0575 ns	
allopolyploid			
***C. douglasii* (*N* = 110)**			
0.2228	0.0867 ***	0.0664 ***	0.0089 ns

in a simplified way (because of our varying and sometimes small sample sizes) the suggestions of Jardine and Sibson (1970) for employing quantitative data in taxonomic studies.

The microsatellite data of Coughlan et al. (2017a; 2017b) have been re-analyzed here as presence/absence data for 233 individuals and 581 alleles (Table 3) using GenoDive (Meirmans 2020; Analysis of Molecular Variance, AMOVA). Of these 236 individuals (Table 3), 114 were shared with the morphometrics sample of 246 individuals (Appendix 1).

R functions were used to summarize morphological and genetic data analytically and graphically, notably by means of box plots and normal probability plots (R functions **boxplot** and **qqnorm,** respectively), principal components analysis (PCA; R function **prcomp**), and functions in the *adegenet* (Jombart 2015; Jombart & Ahmed 2011; Jombart & Collins 2015), *ape* (Paradis et al. 2004), *candisc* (Friendly & Fox 2017) and *vegan* (Oksanen et al. 2022) packages implementing variously principal coordinates analysis (PCoA; function **pcoa**) and CVA (functions **candisc, betadisper** for morphological data, and **dapc** for microsatellite data). Dimensionality of the data and hence significance of the ordination axes were evaluated according to the proportion of the total sample variance for which they accounted, using the broken-stick criterion (Frontier 1976; Legendre & Legendre 1998) calculated with a purpose-written function in R. Where axes failed to meet the broken-stick criterion, comparison was made with the equipartition of the sample variance between the ordination axes. Statistical evaluation of the group structure in our sample involved testing both the null hypothesis of equal group dispersions using a multivariate analog of Levene's test (R function **betadisper;** Anderson 2006; Levene 1960; Oksanen et al. 2022; Van Valen 1978), and that of equal group mean vectors (CVA; R function **candisc**).

Pollen stainability.—Direct examination of ploidy level in type specimens using flow cytometry of seed tissue is impractical, owing to the uncertainty surrounding the success of flow cytometry with seeds more than a century old, the limited numbers of fruits available for the destructive sampling needed to obtain seeds (often only one, or none at all, may be found in a fruit), to say nothing of concerns about any destructive sampling at all involving type specimens. Alternative sources of data from which ploidy level can inferred might include stomate size, but that is not informative in this case (Fig. 9 in McGoey et al. 2014). We resorted instead to pollen stainability (Appendix 4), since diploid *Crataegus* (and many tetraploids) have highly stainable pollen, whereas triploids tend to have pollen that is less well stained by dyes taken up by the microgametophyte cytoplasm and nuclei and only the cell walls are stained (Alexander 1969; Han 2013; Han et al. 2013). Details of our use of Alexander's stain, together with glycerine jelly and a hematocytometer (to also quantify numbers of pollen grains produced), are given elsewhere (Dickinson & Phipps 1986). For some of the samples an Infinity 1 digital camera and Infinity Analyze 5.0.3 software (both from Lumenera Corporation, Ottawa ON) were used to capture microscopic images of pollen grains in the hematocytometer. Doubly and singly stained pollen grains in these images were then counted using the public domain Java image processing program

ImageJ 1.4.6 combined with the cell counter plugin (Abràmoff et al. 2004; Han 2013; Han et al. 2013). Beta regression (function **betareg** in the R package *betareg*; Cribari-Neto & Zeileis 2010) was used to compare proportions of doubly stained pollen grains in *Crataegus suksdorfii* sensu lato cytotypes.

Flow cytometry.—Flow cytometric determinations of nuclear DNA content were made to estimate ploidy level in leaf, embryo, and endosperm tissue as described earlier (Appendices 1, 2; Talent and Dickinson 2005; 2007b; Lo et al. 2013; Coughlan et al. 2014; Coughlan et al. 2017b; see also Supplementary Data Table S4 in Dickinson et al. 2021). Flow cytometric seed scans (FCSS) to determine breeding system in some cases were carried out on individuals from populations from which embryological evidence had been obtained earlier (Dickinson et al. 1996; Talent & Dickinson 2007a; Talent & Dickinson 2007b; Talent & Dickinson 2007c).

Data availability.—Most of the voucher specimens for the data collected above (Appendices 1–4) are deposited in the Green Plant Herbarium (TRT) of the Royal Ontario Museum (ROM). Images of most of these specimens are accessible online, and links to these images are embedded in the records for each voucher in the TRT specimen database. This database itself is accessible online via the Canadensys Explorer portal (Canadensys 2020) and GBIF (GBIF: The Global Biodiversity Information Facility 2021). Links and locality data are also given in the Appendices here and are mapped on Zenodo (DOI 10.5281/zenodo.5567918; Dickinson et al. 2021 Fig. 1, 9). Microsatellite data have been deposited as described by Coughlan et al. (2017; see also Fig. 2 and Appendix 2). In addition, the data appendices for this paper (Appendices 1–4), images of the type material referred to below (holotype, paratypes, and exemplars of *C. suksdorfii sensu stricto and C. ×cogswellii*), together with exemplars of the other species treated here (*C. chrysocarpa*, *C. macracantha*, *C. douglasii and its segregates*, *C. gaylussacia*), and copies of Han (2013) and Han et al. (2013) are accessible online in MorphoBank Project P832 (Dickinson & Han 2023; http://morphobank.org/permalink/?P832, and its folios cited below).

RESULTS

***Morphological variation in* Crataegus *ser.* Douglasianae.**—The dominant pattern of variation found in *C.* ser. *Douglasianae* as a whole is the stamen number bimodality seen not only here along PC1 (Fig. 1A; Dickinson et al. 1996; Dickinson et al. 2008; Dickinson et al. 2021; Evans & Dickinson 1996) but also in all other groups of North American *Crataegus* that have been studied in detail (Dickinson & Phipps 1985; Phipps 1997; Phipps 2015). The ratio scale descriptors, of thorns (length, width) and leaf shape (lengths above and below the widest point, X and Z respectively, scaled by maximum leaf width, Y, cf. Dickinson et al. 2008; Marshall 1978) were normally distributed, at least after logarithmic transformation (thorn length, scaled leaf lengths). While variation in the thorn dimensions also correlates with stamen number variation (Fig. 1A), as do other descriptors (re calyx lobe shape and margination see Table 2, and Fig. 7, 8c, and 8d, all in Dickinson et al. 2008), the variation in the leaf dimensions does not, and instead determines the second PC axis here (Fig. 1A). Variation in ploidy level is similarly correlated with variation between stamen-number entities; ploidy level also varies within the 20-stamen group (Fig. 1B). Inclusion of Heller and Suksdorf type material in the multivariate analyses, as well as specimens collected by David Douglas, links our results to the concepts of these authors' taxa (Fig. 1C). Availability of data from type specimens supports differentiating *C. gaylussacia* and *C. suksdorfii* sensu lato (Fig. 1C, D). These analyses are also part of the basis for choosing a holotype for a restricted concept of *C. suksdorfii* (Fig. 1C, D). Material of *C. douglasii* examined here includes a limited number of specimens identified as belonging to its segregate species (Fig. 1C; Appendix 1, 3), but detailed analyses of these taxa will follow in a separate paper.

Comparison of taxon dispersions for the morphological descriptors (Table 3) demonstrated departure from homoscedasticity related, at least in part, to large differences in sample sizes (Table 3). Diploid, presumptively sexual *C. suksdorfii* sensu lato had the greatest dispersion, while dispersions of the *C. douglasii* and *C. gaylussacia* polyploid presumptive apomicts were both small (Table 3). Dispersion of allopolyploid, apomictic *C. suksdorfii* sensu lato was intermediate between these extremes. In the CVA (Fig. 1D), despite the absence of

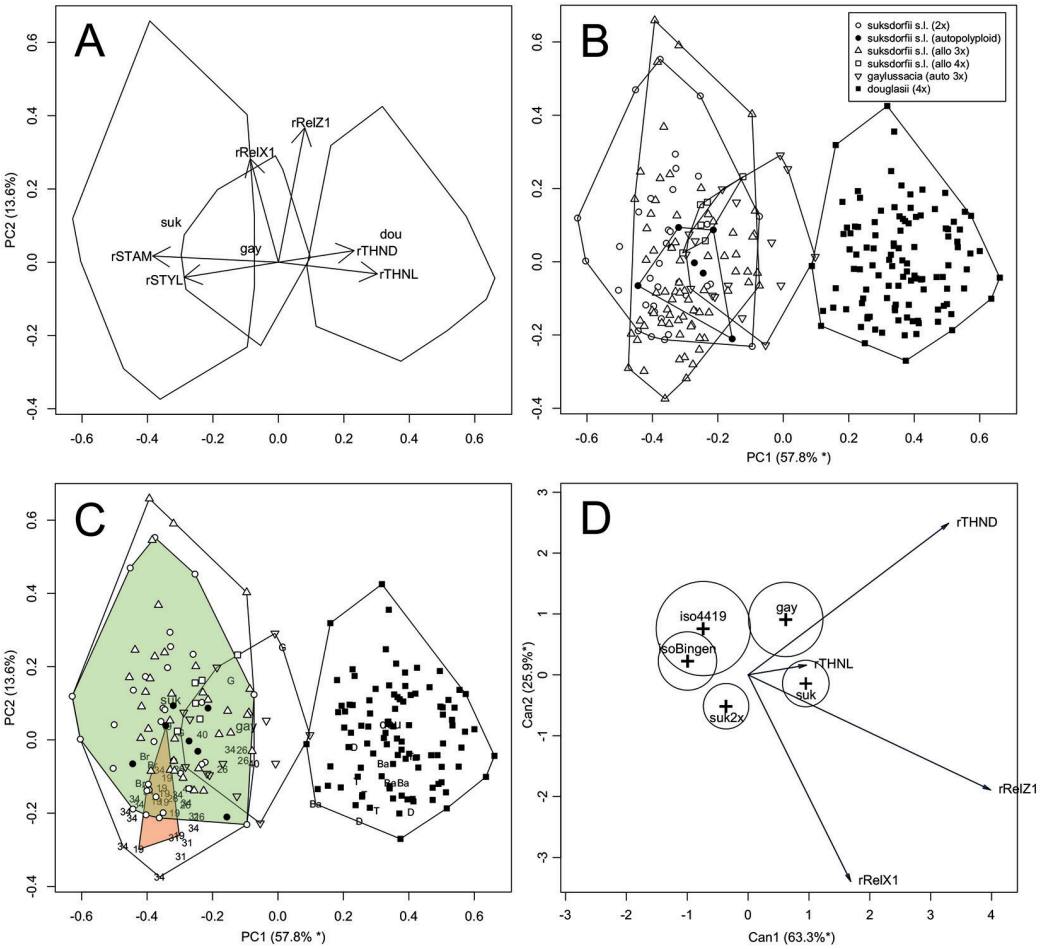

Fig. 1. Principal Components (PCA; A–C) and Canonical Discriminant (CA; D) Analyses of a *Crataegus* morphology dataset (*N* = 246; Appendix 1) with six descriptors (used earlier in Dickinson et al. 2008) transformed by ranging to a (0,1) interval: THNL, Thorn length (mm); THND, Thorn diameter at base (mm); relX, Leaf blade length above the widest point divided by leaf width at the widest point; relZ, Leaf blade length below the widest point divided by leaf width at the widest point; STAM, Number of stamens per flower (fruit); STYL, Number of styles per flower (fruit). A. PCA biplot showing the component-descriptor correlations as vectors. Convex hulls enclose points representing specimens of *C. suksdorfii* sensu lato (suk) with 20 stamens per flower, specimens of *C. gaylussacia* (gay) with 20 stamens per flower from Marin and Sonoma counties in California, and specimens of *C. douglasii* (dou) with 10 stamens per flower (Appendix 1). B. Cytotype differentiation of the sample as given in the inset key. Convex hulls enclose points representing specimens of the different cytotypes. C. Positions of type specimens included in the sample: *C. suksdorfii* sensu stricto, *W.N. Suksdorf numbers 4034, 4419, 5026, 5031,* and *5040* (holotype and isosyntypes); Br, *C. punctata brevispina* collected by David Douglas; G, *C. gaylussacia*; D, *C. douglasii* specimens and specimens grown from seed collected by David Douglas; Ba, *C. douglasii* forma *badia*; and T, *C. tennowana* (the latter two synonymized with *C. douglasii*. In C, the convex hulls enclose points representing specimens of *C. gaylussacia*, *C. douglasii*, and the diploid and polyploid components of *C. suksdorfii* sensu lato. Specimens representing *W.N. Suksdorf 4419*, the holotype of *C. suksdorfii* proposed below, are also enclosed within a convex hull. D. Canonical Discriminant Analysis of five 20-stamen groups of specimens in our sample: gay, *C. gaylussacia*; iso4419, *W.N. Suksorf 4419*, *C. suksdorfii* sensu lato isosyntype collected in 1905 in 'Falcon Valley,' Klickitat Co. WA (Love 1998); isoBingen, W.N. Suksorf isosyntypes (*4034, 5026, 5031, 5040*) collected in 1905 along the Columbia River in Bingen WA; suk, allopolyploid *C. suksdorfii* sensu lato; and suk2x, diploid *C. suksdorfii* sensu lato. Asterisks indicate that the ordination axis corresponds to a significant eigenvalue according to the broken-stick criterion (PCA) or other criterion (likelihood ratio for canonical axes; Friendly & Fox 2017); axes not associated with eigenvalues judged to be significant in these ways should be compared with the equidistribution among all axes of the total sample variance.

the contrast in stamen and style numbers per flower (Fig. 1A), four of the five taxon centroids are distinct (Wilks' statistic approximate $F_{12, 632.63} = 23.75$, $p << 0.001$).

Distinctiveness of* Crataegus gaylussacia.—Crataegus gaylussacia*, as described by Heller (1903), differs from other western North America hawthorns with black fruit and 20 stamens per flower in having short thorns that are wider at the base than those of diploid and allopolyploid members of *C. suksdorfii* sensu lato (Fig. 1A, D; Fig. 2A, B). Short shoot leaf petioles are also substantially shorter than in *C. suksdorfii* sensu lato (Fig. 2C). In addition to flow cytometric determinations of triploidy in *C. gaylussacia* (Appendix 1; Coughlan et al. 2017b; Dickinson et al. 2021), we also have two comparisons of embryo and endosperm ploidy levels that indicate the breeding system in these plants. In both cases the endosperm ploidy level is three times that of the triploid embryo (Appendix 1), suggesting the fertilization of two unreduced, triploid central cell nuclei by a single, unreduced triploid sperm nucleus (N. Talent per. comm. 2011).

We also carried out a reanalysis of the microsatellite data obtained from a portion of our sample that was analyzed earlier (Table 1 and Fig. 2 in Coughlan et al. 2017b; Appendix 2). Here we simply looked at the extent to which these allele presence/absence data differentiate the 20-stamen entities studied here from *C. douglasii* and from each other. Discriminant analysis (R package *adegenet*, function **dapc**) of scores on the first 50 principal component axes for these data (accounting for approximately 80% of the sample variance; DAPC) demonstrated the overlap of the 20-stamen diploid *C. suksdorfii* sensu lato and *C. gaylussacia* samples, and their differentiation from the sample of 10-stamen *C. douglasii* on the first discriminant function (Fig. 4). Similar results were obtained earlier when analyzing Bruvo distances for a sample comprising only diploid *C. suksdorfii* sensu lato, *C. gaylusaccia*, and *C. douglasii* (not shown). The second discriminant function corresponded to the contrast between the *C.* subg. *Americanae* individuals (10 stamen *C. chrysocarpa* and *C. macracantha*) and the sample of 20-stamen allopolyploid *C. suksdorfii* sensu lato. Neither of these discriminant functions accounted for significant proportions of the total variance according to Frontier's broken-stick criterion (df1, 50%; df2, 26%; corresponding broken-stick values 52% and 27%), corresponding to the considerable overlap between the five samples (Fig. 4). Nevertheless, AMOVA of the original genotype data using the *rho* analogue of FST (Meirmans 2020; Ronfort et al. 1998) for these five groups indicated significant differentiation ($rho = 0.039$, $p = 0.001$, d.f. = 4, 228). These authors note that use of *rho* does not depend on knowledge of either ploidy level or breeding system and so is suitable for the comparison here of allopolyploids, autotriploids, and diploids. Significant DAPC results were also obtained when analyzing the differentiation of just the three 20-stamen black-fruited entities (AMOVA: $rho = 0.015$, $p = 0.001$, d.f. = 2, 67). In this case, however, the first discriminant function differentiating the diploids and autotriploids from the allopolyploids was significant (df1, 88%; corresponding broken-stick value 75%).

***What then is* Crataegus suksdorfii *(Sarg.) Kruschke*?—**We note that neither Sargent, nor Kruschke when he raised Sargent's variety to a species, designated a holotype for this taxon at either level (Kruschke 1965; Sargent 1907a; Voss 1965; Voss 1966). How then should the name *Crataegus suksdorfii* be applied and typified, if *C. gaylussacia* is to be restricted in its application? What is the significance of the variation in ploidy level seen outside *C. gaylussacia* sensu stricto (Marin and Sonoma counties) in the 20-stamen black-fruited hawthorns of western North America (Talent & Dickinson 2005; Dickinson et al. 2008)? Fortunately, Sargent's taxon, *C. douglasii* var. *suksdorfii*, was based on material from five different trees at two locations in Klickitat County, Washington (Love 1998; Weber 1944). These specimens were sent him by Wilhelm Suksdorf (Dickinson & Love 1997; Sargent 1907a). Suksdorf collected from these trees repeatedly, and included additional specimens from them in sets of material that he distributed to several herbaria in the United States (Table 2). As a result, our morphological analysis (Figs. 1–2; Fig. 5) includes seven syntypes, 21 isotypes, and eight duplicates (i.e., collected in 1907 or later) of Sargent's *C. douglasii* var. *suksdorfii* (Appendices 1, 3, 4; HUH material tabulated in Table 2; more such specimens undoubtedly exist in other herbaria). In order to associate Sargent's name with one cytotype, and provide a new name for the other, we infer the ploidy level of the individuals from which Suksdorf collected his specimens.

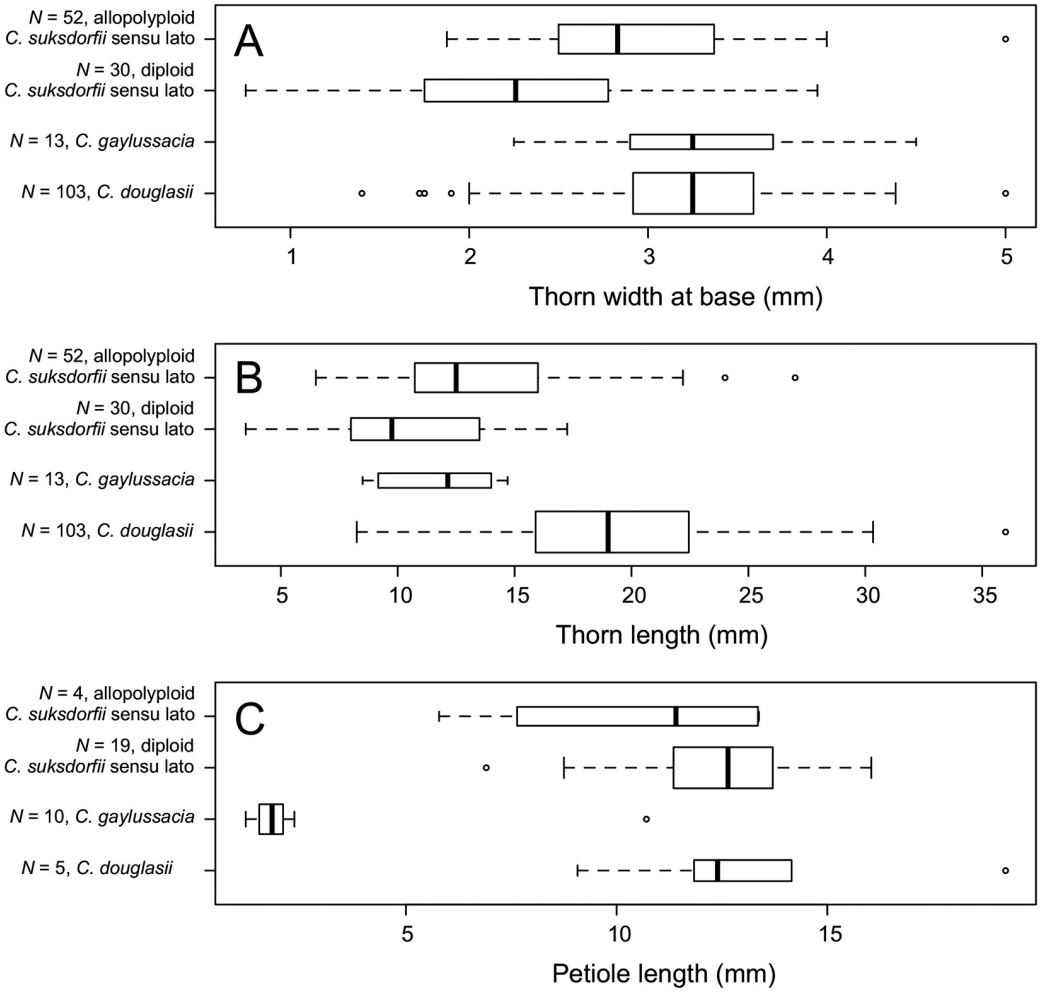

Fig. 2. Boxplots contrasting thorn and petiole dimensions between *Crataegus gaylussacia* and *Crataegus suksdorfii* sensu lato (and *C. douglasii;* compare Fig. 1; Appendix 1). A, width of thorn at its base in mm. B, length of thorn in mm; C, petiole length in mm; note difference in scales between A, B, and C. Data are mean dimensions for samples of five thorns per each of 198 specimens, or a similar number of petioles for 38 specimens.

At the macroscopic level, diploids in *C. suksdorfii* sensu lato overlap most of the allopolyploids and some *C. gaylussacia* in the plane of PC1 and PC2 (these account for 71% of the sample variance; Fig. 1B). However, the diploids and allopolyploids differ in the density of marginal teeth adjacent to the leaf apex (Fig. 5; Table 2 in Dickinson et al. 2008). Tooth density in the type material of *C. douglasii* var. *suksdorfii* resembles that seen in a geographically wide sample of allopolyploids (9–12 teeth per cm), and differs from that seen in diploids and autopolyploids (6–9 teeth per cm; Fig. 5; Appendix 3). We also need to corroborate this result with a direct estimate of the ploidy level of the individuals from which Suksdorf collected his specimens. At the microscopic level, neither stomate size nor density vary in a useful way between diploid and polyploid *C. suksdorfii* sensu lato (McGoey et al. 2014). Pollen size likewise does not predict ploidy level (T.A. Dickinson unpubl. data). Pollen fertility (stainability), however, does vary with ploidy level (Dickinson & Phipps 1986): while diploids and (to a significantly lesser extent) tetraploids are generally pollen-fertile, triploids are not (Fig. 6; Appendix 1, Table 4). Pollen stainability of Suksdorf's specimens is in the range 54–67% (Fig. 6; Table 4).

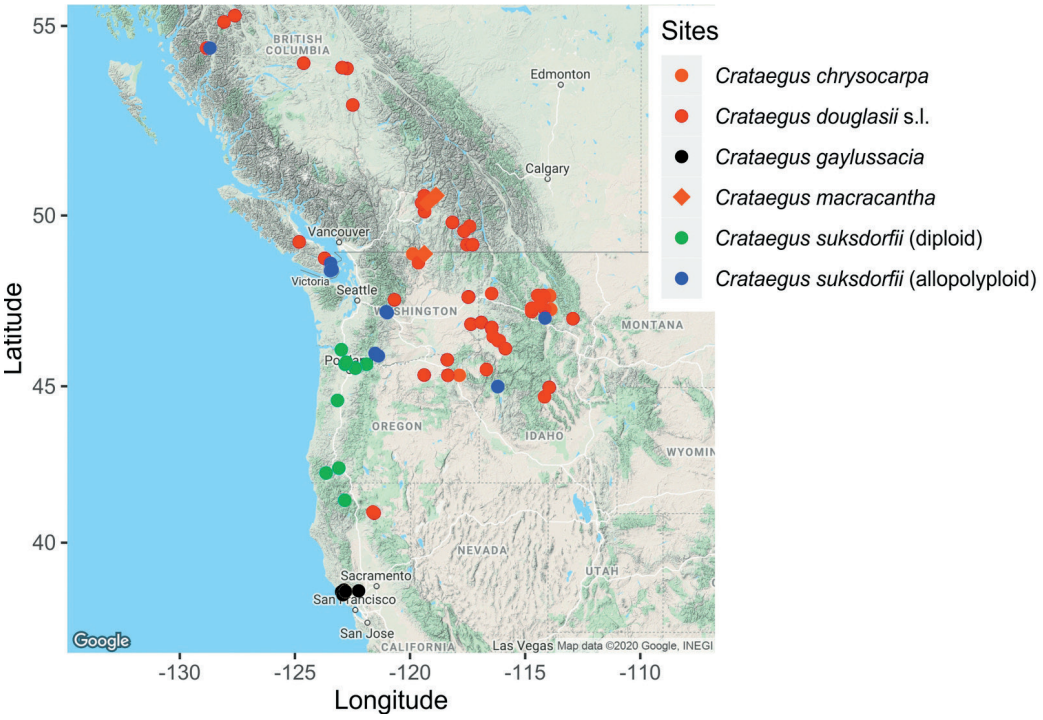

Fig. 3. Map of western North America showing the locations at which 233 *Crataegus* individuals were sampled for DNA extraction and amplification microsatellite loci (Appendix 2; Coughlan et al. 2017b; Han 2013; Han et al. 2013). Taxa sampled at each site indicated by symbol shape and color. Figure produced using R package *ggmap* (Kahle & Wickham 2013) and Google Maps (Map data © Google).

Sargent's description of *C. douglasii* var. *suksdorfii* (Sargent 1907a) cites four specimens collected by Suksdorf along the Columbia River at Bingen, Washington, while a fifth was collected at Suksdorf's farm in "Falcon Valley" (a name coined by Suksdorf himself for his farm located in the NE corner of Section 12, T5N R11E; Table 2; Weber 1944), 26 km north of the river, and 550 m higher. We have chosen the higher elevation fruiting specimen as the holotype for *C. douglasii* var. *suksdorfii* Sarg., and hence for *C. suksdorfii* (Sarg.) Kruschke, because the specimen is typical, and this elevation better resembles the elevations at which most allopolyploid *C. suksdorfii* sensu lato are found, east of the Cascades in Oregon, Idaho, Washington, Montana, and British Columbia (Coughlan et al. 2017b; Dickinson et al. 1996; Dickinson et al. 2021; Lo et al. 2013; Talent & Dickinson 2005). The northernmost stations for the allopolyploids do include sea level sites in southernmost Alaska, British Columbia, and northwestern Washington, but these are up to 1,000 km (and 7–10 degrees) north of the type locality. In what follows, we provide a new name for the diploids in *C. suksdorfii* sensu lato.

***Distinctiveness of diploid* C. suksdorfii *sensu lato*.—**Diploid *C. suksdorfii* sensu lato have the narrowest thorns in *C. suksdorfii* sensu lato (Fig. 2A). Leaves of diploid *C. suksdorfii* sensu lato (and autotriploid *C. gaylussacia*) have fewer marginal teeth adjacent the apex than do those of allopolyploid *C. suksdorfii* sensu lato (Fig. 5). Diploid *C. suksdorfii* sensu lato are highly pollen fertile, unlike most autopolyploids and triploids (Fig. 6) and regularly form seed sexually, unlike polyploid hawthorns in general (Coughlan et al. 2014; Coughlan et al. 2017b; see also Supplementary Data Table S4 in Dickinson et al. 2021; Lo et al. 2013; Talent & Dickinson 2007a–c). Microsatellite data suggest that these contrasts are associated also with genetic differentiation (Fig. 4; Coughlan et al. 2017b; Lo et al. 2009b).

DISCUSSION

We argue that there are three distinct 20-stamen black-fruited entities present in western North America. The taxonomic treatment that follows recognizes these three entities as distinct species, recircumscribing two well-established ones that are in common use, and adding one new name. Finally, we discuss the species concepts that are appropriate for recognizing the role of hybridization and apomixis in the diversification in western North America black-fruited hawthorns. Just as recent, comprehensive taxonomic work on North American hawthorns (Phipps 2015) represented taxonomic hypotheses open to testing with new data, our treatment here is both a test of Phipps' taxonomic hypothesis regarding the black-fruited hawthorns of western North America and a new hypothesis that can be evaluated in the future with more extensive sampling and larger datasets, notably for flow cytometric evaluations of ploidy level and breeding system, and for molecular data with which to document more thoroughly the reticulate evolution that has occurred in the group.

TABLE 4. Beta regression (function *betareg* in the R package **betareg**; Cribari-Neto & Zeileis 2010) on cytotype of the proportion of *Crataegus suksdorfii* sensu lato pollen grains doubly stained with Alexander's stain (Fig. 6). Coefficients for cytotype levels are relative to the pollen stainability of diploids (intercept; $N = 8$; CA, OR; Appendix 4). Coefficients (and their standard errors) are given for both the regression model for the mean and that for the precision ("similar to the inverse of a variance in a linear regression model or the dispersion in a GLM"; Cribari-Neto & Zeileis 2010). Individuals labelled "allopolyploid" are those found east of the Cascades (ID, WA) for which ploidy level data were unavailable but are presumed to be triploid or tetraploid (Appendix 4).

	Mean	Precision
(Intercept)	2.250***	3.591***
	(0.197)	(0.504)
allopolyploid	-1.384***	-1.006
$N = 12$	(0.258)	(0.641)
allo4x (MT)	-1.325***	-1.203
$N = 5$	(0.348)	(0.793)
auto3x (OR)	-1.810***	-1.211
$N = 9$	(0.279)	(0.677)

Log-likelihood = 30.379, N = 34
*** = p < 0.001; ** = p < 0.01; * = p < 0.05

Digital images of type specimens are increasingly being made available online and open-access, although the usability of the images may vary with respect to resolution and ease with which an image may be examined in detail online. Some sites offer only a single image size, while others may provide two views of an entire specimen, one that fills the available screen window, and another at maximum resolution. Specimens held in the ROM Green Plant Herbarium (TRT) are examples of the latter when viewed on their University of Toronto repository (accessible by searching on either the Canadensys or the GBIF website; see also the Data Appendices). Accessed using the MorphoBank project associated with this publication (Dickinson & Han 2023), the images of the type specimens described below can be downloaded or zoomed continuously online to any desired magnification. As Borges et al. (2020) note, specimen images like these lend themselves not only to qualitative comparisons but also to digital measurements using tools like ImageJ (Abràmoff et al. 2004), always assuming that the parts of interest are fully visible in the image.

***Distinctiveness of* Crataegus gaylussacia *A. Heller.*—**As noted above, the bimodal distribution of stamen (and style) numbers per flower seen in *C.* ser. *Douglasianae* (Fig. 1) is nothing new (Brunsfeld & Johnson 1990; Dickinson et al. 1996; Dickinson et al. 2008; Dickinson & Love 1997; Phipps 2015; Sargent 1907a). What is new is that we now have a better idea of the biogeographic (Fig. 3; Coughlan et al. 2017b; Coughlan et al. 2014; Fig. 1 and 9 in Dickinson et al. 2021), morphological (Fig. 1A), and cytological (Fig. 1B) heterogeneity of the species complex that has been called *C. gaylussacia* by Phipps (2015), or that can be referred to instead as *C. gaylussacia* sensu stricto, and *C. suksdorfii* sensu lato. Type material was included in loans obtained for this project, but the relevance of *C. gaylussacia* did not become clear until new field collections were obtained, starting in 2010, that provided material for flow cytometric ploidy level, pollen fertility, and molecular analyses.

Crataegus gaylussacia has a limited distribution in California (Marin and Sonoma counties) that does not overlap with the distributions of either diploid or allopolyploid *C. suksdorfii* sensu lato (Fig. 9 in Dickinson et al. et al. 2021). Ecologically, Coughlan et al. (Coughlan 2012; 2017b; their Fig. 1e, 2b) have shown that the sites occupied by *C. gaylussacia* are quite different (soils more acidic and coarser) from those where the other *Douglasianae* are found. Similarly, the climate niche occupied by *C. gaylussacia* appears distinct from (more

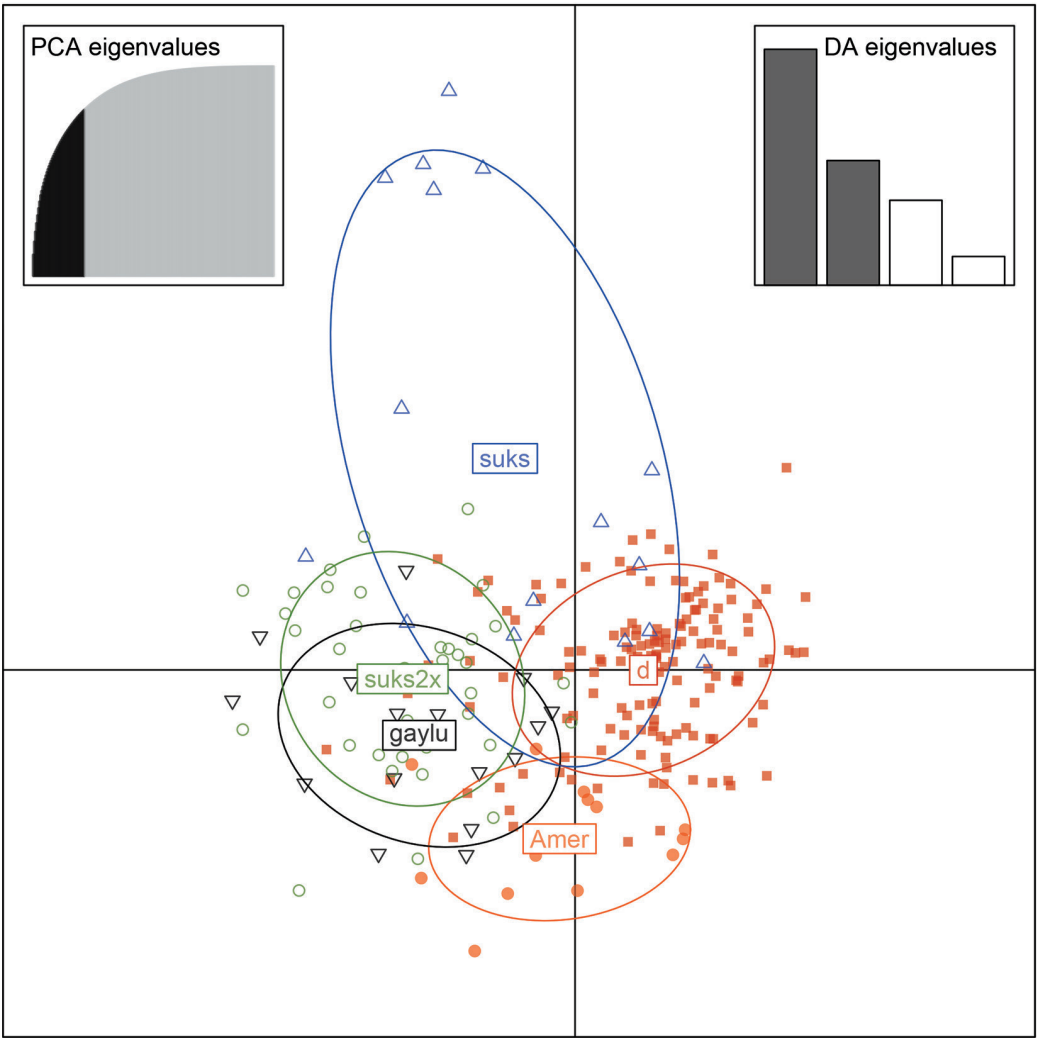

Fig. 4. Discriminant Analysis of Principal Components for a sample of 233 *Crataegus* of western North America (Appendix 2; see Fig. 2 in Coughlan et al. 2017b) and presence/absence data for 301 microsatellite loci represented by their scores on the first 50 principal components (PC), shown in the plane of the first two discriminant axes for five taxonomic groups. Open symbols, 20-stamen entities autotriploid *C. gaylussacia* (gaylu; triangles), allopolyploid *C. suksdorfii* sensu stricto (suks; squares), and diploid *C. rhodamae-loveae sp. nov.* (suks2x; circles). Filled squares (d), 10-stamen tetraploid (and pentaploid) *C. douglasii* (and its segregates; see text for details). Filled circles (Amer), 10-stamen red-fruited tetraploid members of *C.* subg. *Americanae* (*C. chrysocarpa* and *C. macracantha*); all other individuals are black-fruited members of *C.* subg. *Sanguineae*. Text labels indicate taxon centroids; inertia ellipses summarize the scatter of points for each ellipse (R package *adegenet*, function dapc; Jombart & Collins 2015). Left inset, scree plot showing that approximately 80% of the total sample variance is accounted for by the eigenvalues corresponding to the first 50 PC axes. Right inset, bar plot showing the relative proportions of the sample variance accounted by the four discriminant axes; the first two (shaded) account for 50% and 26% of the sample variance respectively; the corresponding critical values from the broken-stick distribution are 52% and 27% (Frontier 1976; Legendre & Legendre 1998).

seasonally dry than) those of *C. douglasii* and *C. suksdorfii* sensu lato (Fig. 1e–g in Coughlan et al. 2017b; Fig. 7C, F–I and Fig. 8 in Dickinson et al. 2021; Fig. 7 in McGoey et al. 2014). McGoey et al. also showed that stomatal densities in *C. gaylussacia* are higher than in either diploid *C. suksdorfii* sensu lato or *C. douglasii* (Fig. 5A in McGoey et al. 2014). Populations of *C. gaylussacia* sensu stricto in California appear to comprise apomictic autotriploids (N. Talent, pers. comm. 2011; Coughlan et al. 2017b; Coughlan et al. 2014; Zarrei et al. 2014). In addition, autotriploid *C. gaylussacia* shares with diploid, but not allopolyploid, *C. suksdorfii* sensu lato a single nucleotide polymorphism in the plastid *matK* DNA barcode (Table 3 in Zarrei et al. 2015). Based on data from 14 plastid loci, *C. gaylussacia* shares its chloroplast genome with *C. suksdorfii* sensu lato, *C.* × *cogswellii*, *C. douglasii*, and some, but not all of, the *C. douglasii* segregate taxa that have been described (Fig. 1 in Zarrei et al. 2015).

Elsewhere (Christensen et al. 2014; Coughlan et al. 2017b; Coughlan et al. 2014; Dickinson et al. 2021) we have distinguished *C. gaylussacia* from the other western North American black-fruited hawthorn with 20 stamens per flower that are referred to here as *C. suksdorfii* sensu lato. We reiterate this point now: *C. gaylussacia* should be restricted to presumptively apomictic autopolyploids of limited geographic distribution (Fig. 3), occurring uniquely on sites with abundant soil moisture for only part of the year (many California specimens from sites identified as marshes) and more acidic soils (Coughlan et al. 2017b), and associated with some degree of morphological differentiation (Fig. 1D, 2). Finally, reanalyses of the microsatellite data of Coughlan et al. (Coughlan et al. 2017b) and Han (Han 2013; Han et al. 2013) support differentiating autotriploid *C. gaylussacia* from allopolyploid, but not from diploid, *C. suksdorfii* sensu lato (Fig. 4). We thus align ourselves here with arguments made by Soltis et al. (2007) in support of recognizing autopolyploids as species (see below).

***What is* Crataegus suksdorfii *(Sarg.) Kruschke*?—**The principal stimulus for the first author's interest in western North American black-fruited hawthorns was the suggestion in the literature that, unlike most other North American hawthorn species complexes, diploid and presumptively ancestral *C. suksdorfii* sensu lato were already known from the Queen Charlotte Islands of British Columbia (today, Haida Gwaii; Taylor & Mulligan 1968). However, early chromosome counts for *C. suksdorfii* sensu lato were exclusively polyploid (Oregon triploids and tetraploids; Dickinson et al. 1996), apart from a single diploid count in Idaho (Brunsfeld & Johnson 1990). All of these latter counts came from sites above 4,000 feet elevation. Subsequent flow cytometric analyses of population samples from Idaho, Montana, Oregon, and Washington corroborated the occurrence of triploids and tetraploids east of the Cascades, and demonstrated that diploid *C. suksdorfii* sensu lato is found only west of the Cascades, in northern California, Oregon, and southwestern Washington (Lo et al. 2013; Talent & Dickinson 2005). Parallel analyses of microsatellite, chloroplast, and nuclear loci showed differentiation between diploid and presumptively autopolyploid *C. suksdorfii* sensu lato on the one hand, and tetraploid *C. douglasii* and presumptively allopolyploid *C. suksdorfii* sensu lato on the other (Coughlan et al. 2017b; Dickinson et al. 2021; Lo et al. 2009b; Lo et al. 2010; Zarrei et al. 2014). These studies included triploid observations from individuals and populations studied previously that strongly suggest earlier diploid chromosome counts from Haida Gwaii (Taylor & Mulligan 1968) and Idaho (Brunsfeld & Johnson 1990) were in error. In the material they examined, Taylor and Mulligan (1968) observed irregularities during the first meiotic division, including univalents (at metaphase) and laggards (in anaphase and telophase), much as seen in Washington *C. suksdorfii* (Klickitat Co.) and Ontario *C. douglasii* (Grey Co.; Fig. 3e–g in Dickinson et al. 1996).

The available molecular evidence thus supports a hybrid origin for some, but not all, polyploid components of *C. suksdorfii* sensu lato (Lo et al. 2009b; Lo et al. 2010; Lo et al. 2013; Zarrei et al. 2014). Pollen stainability data have given us a means to link our recent collections to the specimens examined by Sargent in describing *C. douglasii* var. *suksdorfii*, which in turn helps us identify *C. suksdorfii* sensu stricto with the allotriploid and allotetraploid individuals (Lo et al. 2009b; Lo et al. 2010; Zarrei et al. 2014) with poor pollen stainability that are found east of the Cascades, in the northern Rocky Mountains, and north into formerly glaciated areas of British Columbia (Fig. 6; Dickinson 2021). We note that in other Malinae, correlations between ploidy level and pollen stainability have been less clear, as in *Sorbus* sensu lato (Rich 2009). Our

results that contrast the poor pollen stainability of most triploids with that of diploids and tetraploids (Fig. 6) could be related to the way in which, following suggestions in Berlyn and Miksche (1976), our method used glycerine jelly to prevent the differential movement of filled and empty pollen grains (empty grains may migrate to the periphery of a preparation; Dickinson & Phipps 1986).

***Recognition of diploid* C. suksdorfii *sensu lato as a new species.*—**Naming diploid *C. suksdorfii* sensu lato as a species distinct from the earlier named autotriploid *C. gaylussacia* represents a twist on the more common question of whether to recognize an autopolyploid variant of a named diploid species. Majeský et al. (2017) cite several genera where apomictic autopolyploids are not recognized taxonomically as distinct from their diploid progenitors. These authors then go on to posit allopolyploidy as the first criterion for recognition of a polyploid apomict as a new species, and for treating autopolyploid apomicts as conspecific with the diploid. However, Majeský et al. do not mention arguments made by Soltis et al. (2007) supporting species status for autopolyploids based on contrasts in geographic distribution and morphology, and evidence of reproductive isolation, in comparison with their diploid progenitor that, together suggest the two cytotypes represent distinct evolutionary trajectories. Judd et al. (2007) in fact described *Tolmiea diplomenziesii* in just this way, as the allopatric, cryptic, diploid progenitor of autotetraploid *T. men*ziesii.

Based on current knowledge, diploid *C. suksdorfii* sensu lato is distinct morphologically (Fig. 5), ecologically (Coughlan et al. 2017b; Dickinson et al. 2021), biogeographically (Fig. 3; Dickinson et al. 2021), and genetically (Fig. 4; Coughlan et al. 2017b; Fig. 9a in Dickinson et al. 2008; Lo et al. 2009b; Lo et al. 2010; Love & Feigen 1978; Zarrei et al. 2014). In addition to data from microsatellites, the single nucleotide polymorphism in the plastid *matK* DNA barcode and sequence data from two chloroplast intergenic spacers (*psbA-trnH* and *trnH-rpl2*; Lo et al. 2010), and two unlinked nuclear loci (*PEPC* and *PISTILLATA*; Lo et al. 2010) distinguish this diploid taxon from its allopolyploid derivatives. These self-fertile, pseudogamously apomictic, allopolyploid derivatives in *C. suksdorfii* sensu stricto (and *C. douglasii*) thus represent markedly divergent evolutionary trajectories from that of ancestral, sexual, and self-incompatible diploid *C. suksdorfii* sensu lato. We suggest these differences argue against referring to the three 20-stamen entities considered here as merely three chromosome races of *C. gaylussacia*. Treatment as varieties of the still earlier described *C. douglasii* (Holmgren 1997) seems equally unwarranted. Such a simplification might seem desirable from the perspective of preparing guides for natural resource managers or amateur naturalists but it denies a more detailed biological reality that may be important for biodiversity conservation, especially in the light of climate change. It's also important to note that we seek to recognize the single sexual, diploid entity that is likely ancestral to the other two. This is different from naming multiple apomictic, allopolyploid genotypes arising from crosses and backcrosses between diploids and polyploids (i.e., forming triploids, and B_{II} and B_{III} tetraploid hybrids; Dickinson 2018) as appears to have happened with *C. douglasii* (Zarrei et al. 2015) and probably also other *Crataegus* species complexes. The taxonomic treatment below distinguishes the diploid, ancestral entity from allopolyploid *C. suksdorfii* sensu stricto and autotriploid *C.gaylussacia*, as *Crataegus rhodamae-loveae* sp. nov.

***The occurrence of autopolyploids in* Crataegus rhodamae-loveae *sp. nov.*—**In addition to autotriploid *C. gaylussacia*, our sample of *C. suksdorfii* sensu lato also includes autopolyploids. Each of two local populations at high elevations on the western slopes of the Cascades in Oregon (in Douglas and Lane counties; Appendix 1) includes individuals shown to be apomictic and (or) autotriploids or autotetraploids on the basis of cytological or flow cytometric data, together with data from microsatellites, chloroplast DNA, two nuclear loci (*PEPC*, *PISTILLATA*), and ITS2 (Dickinson et al. 1996; Dickinson et al. 2008; Lo et al. 2009b; Lo et al. 2010; Lo et al. 2013; Zarrei et al. 2014). In addition to these individuals, Zarrei et al. (2014) identified two other triploid individuals, from Idaho, that showed only the diploid ribotype H, unlike other presumptively allotriploid ones with two or three ribotypes. These latter two individuals could represent ribotype sampling error, as there are no molecular data comparable to those supporting the autopolyploidy of the high elevation Oregon samples. We include the high elevation Oregon autopolyploids in *C. rhodamae-loveae* as they appear to be minimally differentiated morphologically (Fig. 1B, Fig. 5) and genetically (Fig. 9a in Dickinson et al.

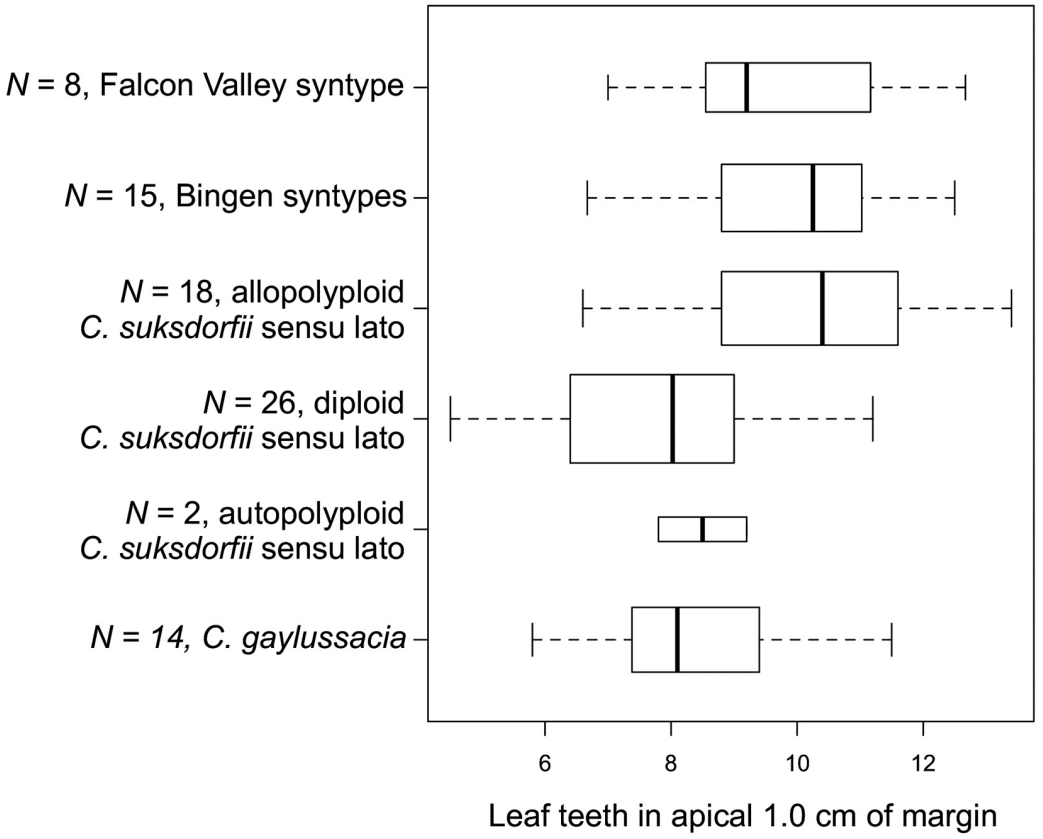

Fig. 5. Boxplots contrasting the density of leaf teeth between diploid and autopolyploid, and allopolyploid, *Crataegus suksdorfii* sensu lato. Data from isosyntypes (Bingen, Falcon Valley) of *C. douglasii* var. *suksdorfii* Sarg. demonstrate their similarity to the allopolyploids (Appendix 3). The isosyntypes were collected by W.N. Suksdorf at Bingen, Washington along the Columbia River (WNS4034, 5026, 5031, and 5040), and at his farm in "Falcon Valley" (WNS4419). Data are mean densities for five leaves for each of the numbers of specimens shown.

2008) from, and are in geographic proximity to, the diploids. Little else is known about autopolyploids in *Crataegus*, but there is evidence from other Rosaceae (Dickinson 2018), including *Malus* (Considine et al. 2012) that autopolyploids can arise at low frequencies from crosses between diploids in which rare failures of meiosis produce unreduced gametes. Saltatory formation of autotriploids followed by backcrosses to diploids can in turn produce tetraploids in which self-sterility may break down and production of unreduced gametes may be perpetuated.

Species concepts appropriate for western North American black-fruited hawthorns.—In suggesting answers to the questions posed at the outset, we have been guided by the idea that taxonomy shapes thinking about species evolution, so that infrageneric and subfamilial phylogenies and classifications should circumscribe ("lump") the units that need to be considered together (Ufimov & Dickinson 2020). At the species level, however, splitting may be needed in order to distinguish contrasting evolutionary trajectories and their potential fates (Robuchon et al. 2019). Ideally, future attempts to marshal distributional and morphological data in evaluating discontinuities between entities will employ the "gaps in morphology across geography" approach suggested by Zapata and Jiménez (see application by Vásquez-Cruz et al. 2017; Zapata & Jiménez 2012). For now, however, non-statistical approaches suffice, and the issue is really about evaluating what is being recognized at the species level.

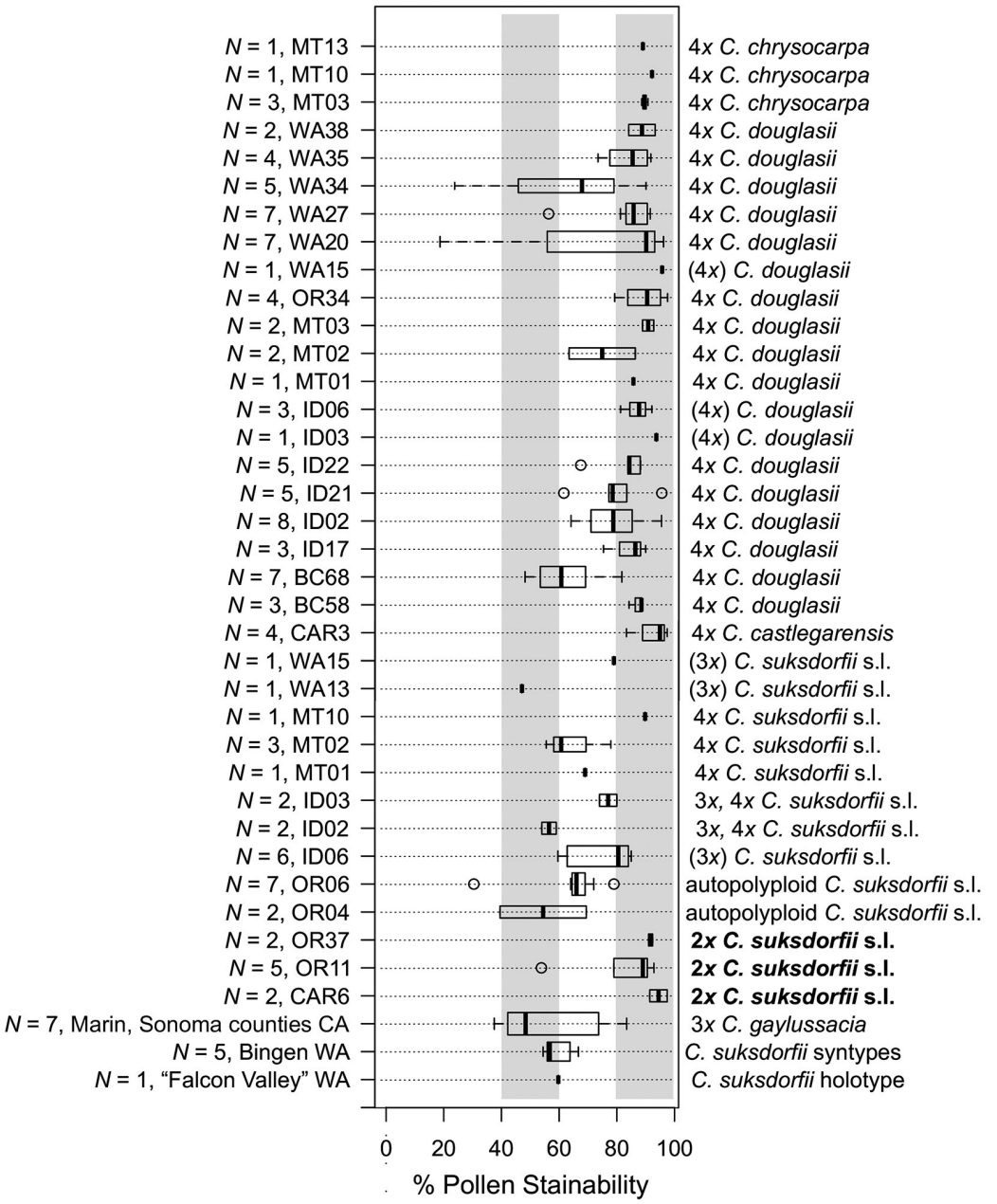

Fig. 6. **Boxplots contrasting pollen fertility in relation to ploidy level and taxon in *Crataegus* subg. *Americanae* and *Sanguineae* (Appendix 4). Fertility indicated by uptake of all components of Alexander's stain (Malachite Green, Acid Fuchsin, Orange G; Alexander 1969; see text for details) versus staining of pollen walls only by Malachite Green. Data are percentage fully stained grains per specimen in the sites and taxa indicated. Data for the "Falcon Valley" WA holotype individual of *C. suksdorfii* comes from *W.N. Suksdorf 4419*, 7 Jun 1909 (WS142845, which is the same collection as HUH00018055, Table 2; compare Fig. 9).**

Up to now one of us has been concerned to argue against naming apomictic entities as if they were directly comparable to species comprising interbreeding (or potentially interbreeding) individuals, much as seen in diploid, self-incompatible, sexually reproducing hawthorns (Dickinson 1998; Dickinson 1999; Dickinson 2018). This perspective stemmed from reflecting on the early 20th century history of North American *Crataegus* taxonomy (Dickinson 1983; Dickinson 1999), and from comparing multivariate morphological variation in local population (topodeme) samples of diploid, self-sterile sexuals (more variable) and triploid or tetraploid self-fertile, pseudogamous apomicts (less variable; Dickinson 1986; Dickinson et al. 2007; Dickinson & Phipps 1985; Dickinson & Phipps 1986). These concerns, however, are more relevant to the systematics of the *C. douglasii* complex (work in progress) and will be detailed elsewhere and in the context of suggestions from Majeský et al. (2017). In the case of the three 20-stamen *Douglasianae* species advocated for here, the contrasts between them seem apparent and can be seen as reflecting use of, for example, an Ecological Species concept (Van Valen 1976) or an Evolutionary Species Concept (Simpson 1961).

Crataegus resembles *Amelanchier*, another genus in the Malinae, in which apomixis, hybridization, and polyploidy have resulted in similar taxonomic complexity. In North American *Amelanchier* three kinds of species have been identified: sexual diploids that are readily interpreted as species by most species concepts (a minimum of 12 diploid species and a variety, worldwide; nine diploid taxa in North America); some widespread, morphologically distinctive allotetraploid apomicts (e.g., *A. cusickii*), and many apomictic allopolyploid microspecies of limited geographic distribution (Burgess et al. 2015; Burgess et al. 2014; Cushman et al. 2017). Autopolyploids have not been found. Hybridization links these different species types into species complexes that may be more identifiable as such than identifiable to a particular species, if at all (Cushman et al. 2017). In *Crataegus,* in addition to diploid species, we also see examples of widespread allopolyploids such as *C. douglasii* and *C. suksdorfii* sensu stricto. We will argue elsewhere that some of the allopolyploid, apomictic species described as segregates from *C. douglasii* are microspecies and can be treated as parts of wider species complexes comparable to those in *Amelanchier.*

Ecological differentiation and hybridization in western North American black-fruited hawthorns.— Striking differences in climatic and edaphic niches are seen between the taxa in western North American *C.* ser. *Douglasianae* (Coughlan et al. 2017b; Dickinson et al. 2021). These are correlated with the breeding system and ploidy level variation discussed above and, as mentioned already, with the areal extents of the distributions of the species involved, such that the apomictic allotetraploids can be said to exhibit geographic parthenogenesis. An explanatory hypothesis shared with one of us by the late S.J. Brunsfeld is that substantially greater ecological amplitude was introduced into *C.* sect. *Douglasianae* by hybridization with members of *C.* subg. *Americanae* (Dickinson & Love 1997). Four of seven binary phenetic characters supported this hypothesis in a cladistic analysis of eight *Crataegus* OTUs (Fig. 7 in Dickinson & Love 1997). We now have molecular data (Liston et al. 2021; Zarrei et al. 2014) supporting this hypothesis. Lack of conflict between trees based on chloroplast loci and ones based on nuclear loci suggests that hybridization was pollen-mediated (Liston et al. 2021; see Fig. 6 in Zarrei et al. 2014), involving pollen transfer from *Americanae* polyploids to ancestral diploid *C. suksdorfii* sensu lato (Liston et al. 2021). Initially this would have given rise to ancestral, triploid *C. douglasii*, and to tetraploid *C. douglasii* following backcrossing to the diploid (gene flow (1) in Fig. 7). Allopolyploid *C. suksdorfii* sensu stricto resulted from crosses between *C. douglasii* and diploid *C. suksdorfii* sensu lato (gene flow (2) in Fig. 7; Lo et al. 2009b; Lo et al. 2010). Two modern species in *C.* subg. *Americanae*, *C. chrysocarpa* (*C.* ser. *Coccineae* (Loudon) Rehder) and *C. macracantha* (*C.* ser. *Macracanthae* (Loudon) Rehder), have nearly transcontinental ranges extending into almost complete sympatry with allopolyploid, but not diploid, *Douglasianae*. *Crataegus chrysocarpa* is in fact the most cold-hardy North American hawthorn species (Phipps 2015). Hybridization with these tetraploid *Americanae* would have introduced the 10-stamen trait and an enhanced capacity for gametophytic apomixis into the *Douglasianae* as well (the same scenario would apply to Rocky Mountain sect. *Salignae*; Dickinson et al. 2021).

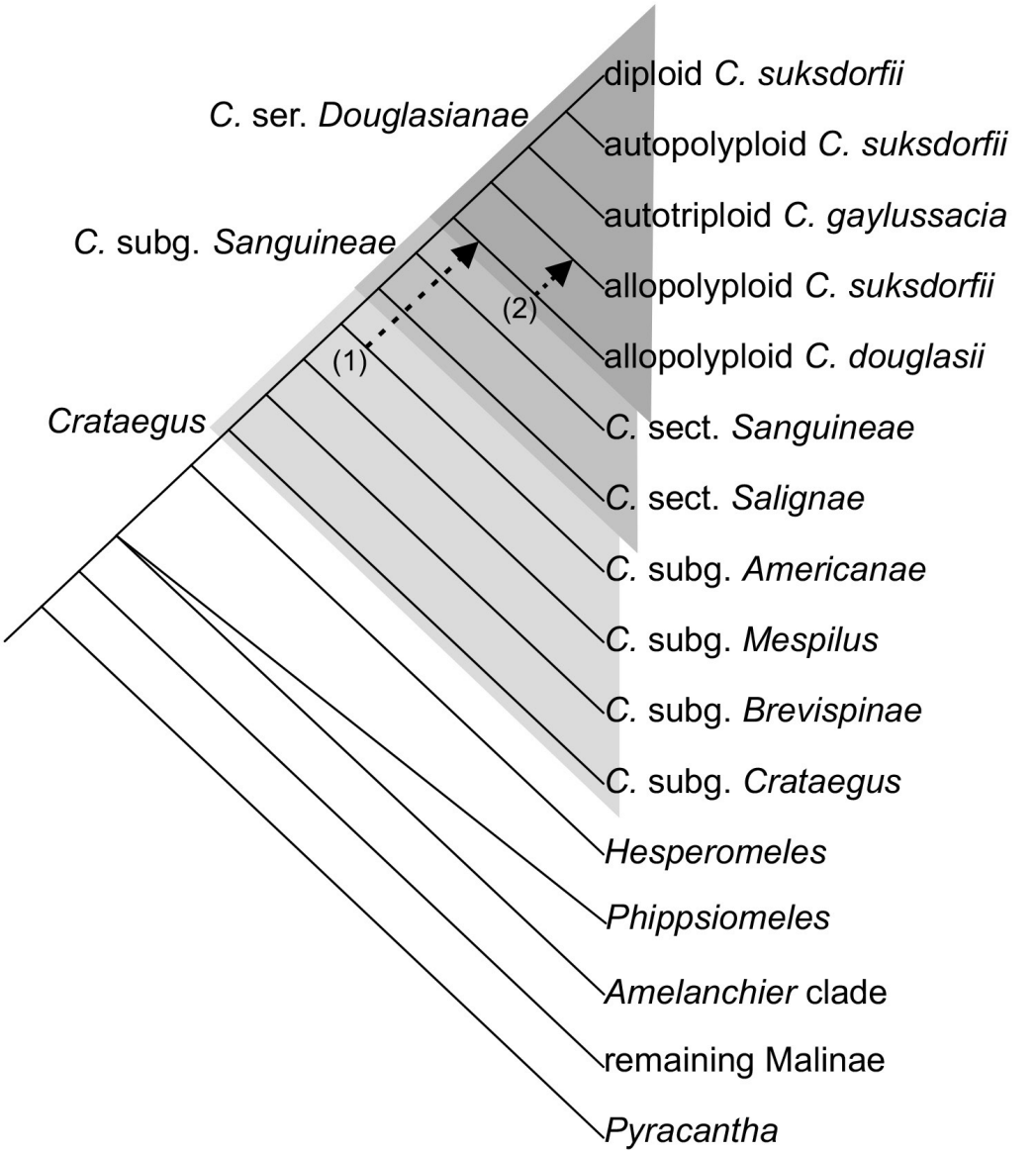

Fig. 7. Reticulation diagram depicting Rosaceae subtribe Malinae, subgenera in *Crataegus* L., sections in *C.* subg. *Sanguineae*, and taxa within *C.* ser. *Douglasianae* discussed here. Relationships are based on whole plastome phylogenies published in Liu et al. (2020) and Ufimov and Dickinson (2020; Liston et al. 2021), and on inferences about reticulation based on these and other studies (Coughlan et al. 2017b; Lo et al. 2009b; Lo et al. 2010; Zarrei et al. 2014). Dashed arrows indicate gene flow: (1) via reduced 2*x* pollen from tetraploid *C.* subg. *Americanae*; onto stigmas of (ancestral) diploid *C. rhodamae-loveae* sp. nov., and a triploid bridge, to give rise to tetraploid *C. douglasii*; and (2) via reduced 2*x* pollen from tetraploid *C. douglasii* onto stigmas of (ancestral) diploid *C. rhodamae-loveae* sp. nov., to give rise to allotriploid *C. suksdorfii* (and, by backcrossing to the diploid parent, allotetraploids). The position of *Phippsiomeles* B.B.Liu & J.Wen follows Liu et al. (2019) and additional information from R. Schmickl and R. Ufimov (personal communication 2023). Tree drawn using the R package *Tree Tools* (Smith 2019).

TAXONOMIC TREATMENT OF THE WESTERN NORTH AMERICAN 20-STAMEN BLACK-FRUITED HAWTHORNS IN *CRATAEGUS* SER. *DOUGLASIANAE* (ROSACEAE SUBTRIBE MALINAE)

Crataegus sect. Douglasianae Rehder ex C.K. Schneid.
Crataegus ser. Douglasianae Rehder

TYPE: *Crataegus douglasii* Lindl. Edwards's Bot. Reg. 21:t. 1810. 1835.

Description.—Shrubs or small trees up to 10 m tall. Shoots dimorphic, sympodial, vigorous branches (long shoots) often with indeterminate growth during a growing season (thus with both preformed and neoformed leaves) and internodes 2–5 (or more) cm, bearing axillary shoots of determinate growth (short shoots; preformed leaves only) with internodes short (less than 2 cm) or absent. Buds ovoid, reddish brown, shiny, (1–)2–3(–4) mm long. Short shoots frequently developing as thorns, by reduction or suppression of leaf development, sclerification of the axis, and formation of a sharp tip, 5–30(40) mm long, more or less straight, 1.5–4 mm in diameter at the base. Young shoots of the current year orange or brown, glabrous or sparsely pubescent, mature shoots of the previous year vary from reddish brown to red purple, older branches gray or copper-colored. Leaves of flowering and short shoots (microphylls–) notophylls, alternate, simple, blades varying from lanceolate and oblanceolate to more or less elliptic or rhombic-elliptic, 1.5 to 2.5 times as long as wide, up to 10 cm long, glabrous or pubescent at maturity, unlobed or sparsely lobed, sinuses shallow. Venation pinnate, with major secondary veins craspedodromous or semicraspedodromous (Dickinson & Yan 2021). Short shoot leaves exhibit heteroblastic variation in shape from the shoot base to the tip (Dickinson & Phipps 1984). Stipules usually caducous, but sometimes persistent on long shoots. Inflorescences terminal, overwintering in bud, almost always on short shoots, bracteate, usually comprising two or more axillary dichasial cymes (the lowermost axillated by a foliage leaf, upper ones by bracts) in addition to the terminal one, thus 10–20 flowered. Pedicels, peduncles and hypanthia glabrous or pubescent. Flowers perfect, regular, epigynous, calyx lobes 5, entire or sparsely toothed, 2.0–3.5 mm long, petals 5 free, stamens 10–20 free, undehisced anthers pink or cream-colored (*C. douglasii*) at anthesis, styles 4–5, and ovules 2 per locule, superposed. Fruits polypyrenous drupes, purple to black, ellipsoidal to suborbicular (diameters of dry fruits 6–10 mm). Pyrenes single-seeded, the same number as the styles and locules, their radial surfaces pitted or grooved.

Crataegus ser. *Douglasianae* is distinguished by its fruit color from the red-, orange-, and yellow-fruited members of *C.* sect. *Sanguineae* (*C.* ser. *Sanguineae* (Zabel ex C.K. Schneid.) Rehder and ser. *Altaicae* J.B. Phipps; not *C.* ser. *Nigrae* (Loudon) Russanov). It differs from black-fruited *C.* ser. *Nigrae* and *C.* sect. *Salignae* in thorn diameter, leaf shape, and geographic distribution.

Distribution.—Western North America (southernmost Alaska, British Columbia, Cypress Hills of Alberta and Saskatchewan, Washington, Idaho, western Montana, Oregon, western Wyoming, northern California), with disjunct occurrences (*C. douglasii*) in the upper Great Lakes basin (Ontario, Minnesota, Wisconsin, Michigan).

Remarks.—See Ufimov and Dickinson (2020) for notes on spelling of the section and series names, and a key to the sections in *C.* subg. *Sanguineae*. Other modern descriptions are given elsewhere (Phipps 2015; Phipps & O'Kennon 2002). Microsatellite, plastome, and nuclear loci sequence data are available as noted here and elsewhere (Coughlan et al. 2017a; Coughlan 2012; Coughlan et al. 2017b; Liston et al. 2021; Liu et al. 2019; Lo 2008; Lo et al. 2009a; Lo et al. 2007; Lo et al. 2009b; Lo et al. 2010).

Ploidy level.—*x* = 17 (Gladkova 1968; Muniyamma & Phipps 1979b), 2*n* = 2*x*, 3*x*, 4*x*, 5*x* depending on species.

KEY TO WESTERN NORTH AMERICAN *CRATAEGUS* SER. *DOUGLASIANAE* WITH CONSISTENTLY (15–)20 STAMENS PER FLOWER (OR FRUIT).

1. Short shoot leaves densely toothed, 8–12 teeth per cm adjacent to leaf apex (pollen-infertile allotriploids and allotetraploids; British Columbia, Idaho, Montana, Oregon and Washington east of the Cascade Range). _____ **C. suksdorfii** (Sarg.) Kruschke sensu stricto.

1. Short shoot leaves more coarsely toothed, 6–9 teeth per cm adjacent to leaf apex.
   2. Thorns 2.5–4 mm in diameter at base; petioles 1–2.5 mm (pollen infertile autotriploids; Marin and Sonoma counties, California). _____ **C. gaylussacia** A. Heller.
   2. Thorns 1.5–3 mm in diameter at base; petioles 11–14 mm (mostly pollen-fertile diploids; northern California, Oregon, southwestern Washington, west of the Cascade Range). _____ **C. rhodamae-loveae** sp. nov.

Crataegus ×suksdorfii (Sarg.) Kruschke, Milwaukee Public Mus. Publ. Bot. 3:163. 1965 (as *sucksdorfii*) (**Fig. 8A**). TYPE: U.S.A. WASHINGTON. Klickitat Co.: "Falcon Valley," 10 Aug 1905, *W.N. Suksdorf 4419* (HOLOTYPE designated here: HUH00018057!, Fig. 9B; Table 2; ISOTYPES: HUH!, WS!, WTU! Note.—Holotype not designated by Kruschke.

≡ *Crataegus douglasii* Lindl. var. *suksdorfii* Sarg. Bot. Gaz. 44:65. Jul 1907; SYNTYPES: *W.N. Suksdorf 4034* (CAS!, HUH!, ID!, MO!, ORE!, OSC!, WS!, WTU!); *5026*, (DAO!, HUH!, WS!); 5031, (HUH!, WS!); *5040*, (HUH!, WS!), all from Bingen, Washington, U.S.A (Table 2). Holotype not designated; *W.N. Suksdorf 4419* incorrectly cited as "4919" by Sargent.

= *Crataegus punctata* Jacq. var. *brevispina* Douglas ex Hook. (K!) (Fig. 10).

Description.—Trees or shrubs to 7(–12) m, bark orange-brown on young twigs, becoming gray with age, smooth, but on trunks and large branches flaking irregularly. Thorns 7.5–14 mm long, more or less straight, 2.5–3.5 mm in diameter at the base. Leaves (microphylls–) notophylls, unlobed (occasionally pinnately lobed), singly to doubly serrate, 9–11 teeth per cm adjacent leaf apex, leaf base angles acute, bases cuneate or decurrent, apex angles obtuse to acute, apices mostly convex or straight, surfaces pubescent, glabrescent, or glabrous, petioles 7–13 mm long. Flowers with calyx lobes 1–2 mm long, not toothed, stamens 15–20, free, undehisced anthers pink at anthesis, 4–5 styles. Dried fruits 4–7 mm in diameter, purple-black at maturity, with persistent calyx lobes. For exemplars, see https://morphobank.org/permalink/?F1091.

Distribution.—As circumscribed below, western North America (southernmost Alaska, British Columbia, Oregon and Washington east of the Cascades, Idaho, western Montana.

Remarks.—We denote this taxon as a nothospecies because molecular evidence indicates that it is an allopolyploid intersubgeneric hybrid, formed as a result of a series of crosses and backcrosses involving fertilizations of unreduced gametes in one or more members of *C.* subg. *Americanae* and ancestral, diploid *C. suksdorfii* sensu lato (*C.* subg. *Sanguineae*) (Fig. 7; Liston et al. 2021; Lo et al. 2009b; Lo et al. 2010; Zarrei et al. 2014). In this connection, we note that the feature linking the type material to the wider sample of allopolyploid *C. suksdorfii* sensu lato available to us is the reduced stainability of pollen, contrasted with the greater stainability of pollen from diploids and tetraploids (Fig. 6). The original material for Sargent's description of his new variety named in honor of the collector, W.N. Suksdorf, comprises specimens from five trees, four along the banks of the Columbia River in Bingen, Washington, and the fifth from Suksdorf's farm, collected from "Border of meadow, Falcon Valley, W. Klickitat Co," approximately 10 km southeast of Glenwood and 535 m above Bingen (Township 5N Range 11E Section 12, east half of the northeast quarter; Love 1998; Weber 1942; Weber 1944). These five trees are the only materials of this taxon cited in Sargent's protologue. There is no reference to a type in the paper or on the labels of the specimens cited, unusual even in light of Sargent's idiosyncratic use of type designations (Macklin et al. 2000). Accordingly, we designate the Falcon Valley specimen, W.N. Suksdorf's number 4419 (HUH00018057; Fig. 9), collected 10 August 1905 (the right hand gathering of the two on the sheet) as the holotype for *C. suksdorfii* (Sarg.) Kruschke because overall, it is the specimen most typical of allopolyploid *C. suksdorfii* sensu lato. This collecting site is close to, and at an elevation (560 m above sea level; ASL) comparable to (i.e., >100 m ASL), that of most of the other locations at which we have found allotriploid and allotetraploid individuals of this species (Fig. 3; Dickinson et al. 2021). Sea level or near sea level occurrences of this taxon are found at northern coastal sites in Alaska, British Columbia, and Washington (e.g., Hyder, Haida Gwaii, San Juan Is.; Appendix 1). A holotype is needed because Kruschke's change in rank was not validly published, as he failed to realize that after 1 January 1958 for his change in

rank to be validly published he needed to designate a single specimen as the type of the new name (Phipps 2008; Shenzhen Code Article 8.1, 8.2, and 40.1; Voss 1965). We nevertheless retain Kruschke as the authority for the change in status as Phipps has done in other cases (Phipps 2008).

Ploidy level.—Allopolyploids, 2n = 51 and 68, based on flow cytometric determinations of nuclear DNA content (N. Talent unpubl. data; Coughlan et al. 2014; Lo et al. 2013), and analyses of nuclear and plastome DNA sequences (Liston et al. 2021; Lo et al. 2009b; Lo et al. 2010; Zarrei et al. 2014).

Similar species.—*Crataegus shuswapensis* J.B. Phipps & O'Kennon may have 15–18 stamens per flower but typically has flowers with 10 stamens; leaves are rhombic and broader and more markedly lobed than is typical in *C.* ×*suksdorfii*. *Crataegus shuswapensis* is known only from south-central British Columbia (Phipps & O'Kennon 2002; for exemplars, see https://morphobank.org/permalink/?F1098).

Crataegus gaylussacia A. Heller, Bull. S. Calif. Acad. Sci. 2:69. 1903 (**Fig. 8B**). TYPE: U.S.A. CALIFORNIA. Sonoma Co.: Lagoon at Sebastopol, 20 Aug 1900, *A.A. Heller 6052* (HOLOTYPE: NYBG00435881 (photo 00435881.jpg, http://sweetgum.nybg.org/science/vh/specimen-details/?irn=660541); ISOTYPES: HUH!, JEPS!, RM!, US!).

Crataegus gaylussacia has the following heterotypic synonyms sensu J.B. Phipps (2013, 2015): *Crataegus douglasii* var. *suksdorfii* Sarg. Bot. Gaz. 44:65. 1907, *C. punctata* var. *brevispina* Douglas ex Hook., Fl. Bor.-Amer. (Hooker) 1(4):201. 1832, *C. suksdorfii* (Sarg.) Kruschke, Milwaukee Public Mus. Publ. Bot. 3:163 (1965).

Description.—Trees or shrubs to 7(–10) m, bark orange-brown on young twigs, becoming gray with age, smooth, but on trunks and large branches flaking irregularly. Thorns 9–14(–17) mm long, more or less straight, 3–4 mm in diameter at the base. Leaves microphylls, unlobed (occasionally pinnately lobed), singly to doubly serrate, 7–10 teeth per cm adjacent leaf apex, leaf base angles acute, bases cuneate or decurrent, apex angles acute, apices mostly convex or straight, surfaces pubescent, glabrescent, or glabrous, petioles 1–2(–5) mm long. Flowers with calyx lobes 1–2 mm long, not toothed, stamens 15–20, free, undehisced anthers pink at anthesis, 4–5 styles. Dried fruits 4–5 mm in diameter, purple-black at maturity, with persistent calyx lobes (often regardless of the number of pyrenes a fruit may contain only a single seed). For exemplars, see https://morphobank.org/permalink/?F1093.

Distribution.—Apparently restricted to Marin and Sonoma counties in California (Fig. 3; 20–130 m ASL; California interior chaparral and woodlands ecoregion, NA1202).

Remarks.—In contrast to the recent *Jepson Manual* and *Flora North America* treatments (Phipps 2013; Phipps 2015) the name *Crataegus gaylussacia* is here restricted to the California autotriploids because of their unique combination of cytotype, ecology (Coughlan 2012; Coughlan et al. 2017b), morphology (Fig. 1, 2), and macrosatellite genotype (Fig. 5). Heller (1903) observed that, prior to being recognized as a new species, the Sonoma County plants were referred to *C. rivularis* Nutt., a taxon now known to differ markedly from *C. gaylussacia* in leaf shape, thorn size, and stamen number per flower (Dickinson et al. 2008; Phipps 1999; Phipps 2015). Greene, in his *Flora Franciscana* (1891), followed Brewer and Watson (1880) in noting that *C. gaylussacia* (as his *C. rivularis*) occurred in Sierra and Plumas counties, between Modoc Co. and Alpine Co. Greene contrasted *C. douglasii* as having longer thorns than *C. gaylussacia* (as *C. rivularis*), and suggested that *C. douglasii* might not occur within the limits of his flora ("middle California"). The stamen number data from an Alpine Co. specimen (*D.W. Taylor 5115,* 9-Sep-1975 (UC1561066! headwaters of Forestdale Creek) suggests that more collecting in the Sierra Nevada, from Kern Co. north, with careful attention to variation in stamen numbers per flower, would repay the effort. Similarly, new collections from California north of the San Francisco Bay area and west of the Central Valley. Parallel collections of leaf tissue on desiccating silica gel could provide material for flow cytometric and molecular studies that could further illuminate the distributions of *C. gaylussacia* and *C. douglasii*, to say nothing of the correct application of these names in accounts of the California flora.

Ploidy level.—Autotriploids, 2n = 51, based on flow cytometric determinations of nuclear DNA content (N. Talent unpubl. data; Coughlan et al. 2014) and analyses of ITS2 ribotype diversity (Zarrei et al. 2014).

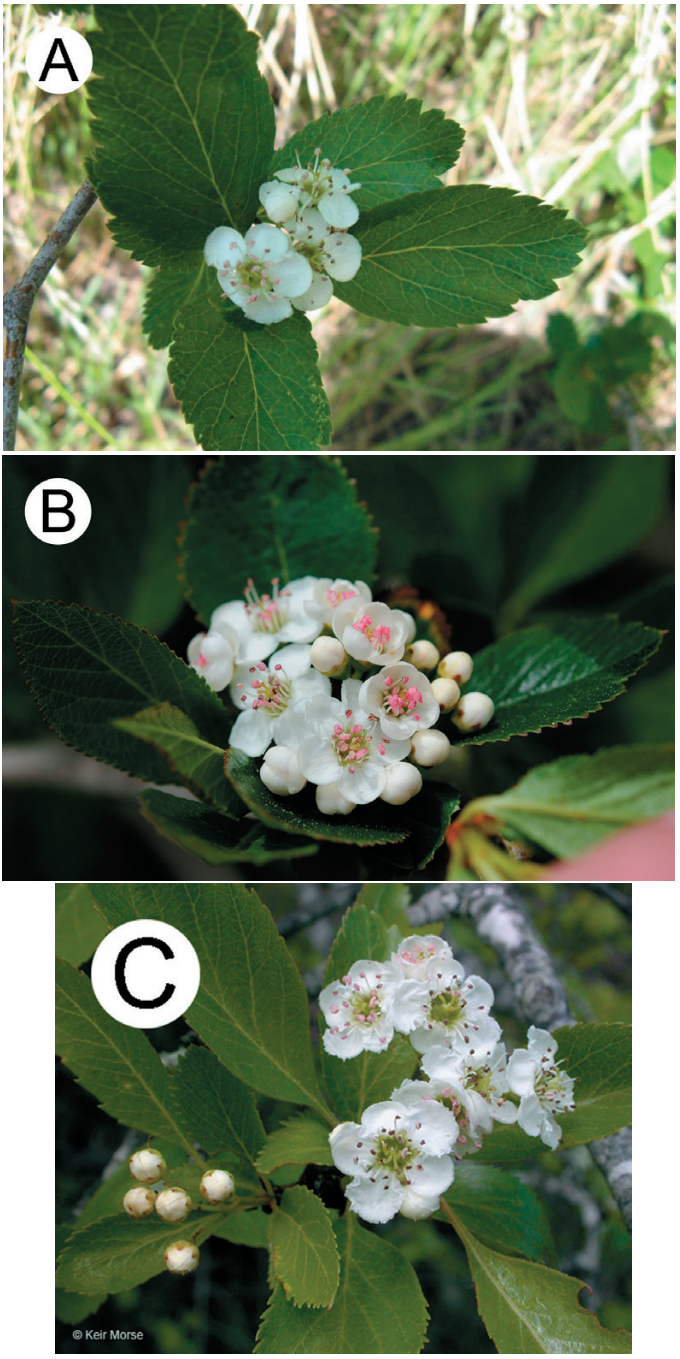

Fig. 8. Western North American 20-Stamen Black-Fruited Hawthorns (*Crataegus* Section *Douglasianae*). **A.** *Crataegus* ×*suksdorfii* (Sarg.) Kruschke; TRT00014409, *Heckel, M. & Talent N. NT565*, 15 May 2010, triploid, Castlegar, British Columbia. Photo: N. Talent; used with permission. **B.** *Crataegus gaylussacia* A. Heller; TRT00002016, *Shiller, J., Tusha, J., Dickinson, T.A. & Heckel, M. PORE-509-1*, 26 Apr 2010, triploid, Point Reyes National Seashore, California. Collected under National Park Service permit PORE-2010-SCI-0010. Photo: T.A. Dickinson. **C.** *Crataegus rhodamae-loveae* sp. nov. Photo © Keir Morse 2008, Deer Creek Center, Selma, Oregon; used with permission (https://calphotos.berkeley.edu/cgi/img_query?enlarge=0000+0000+0208+0944).

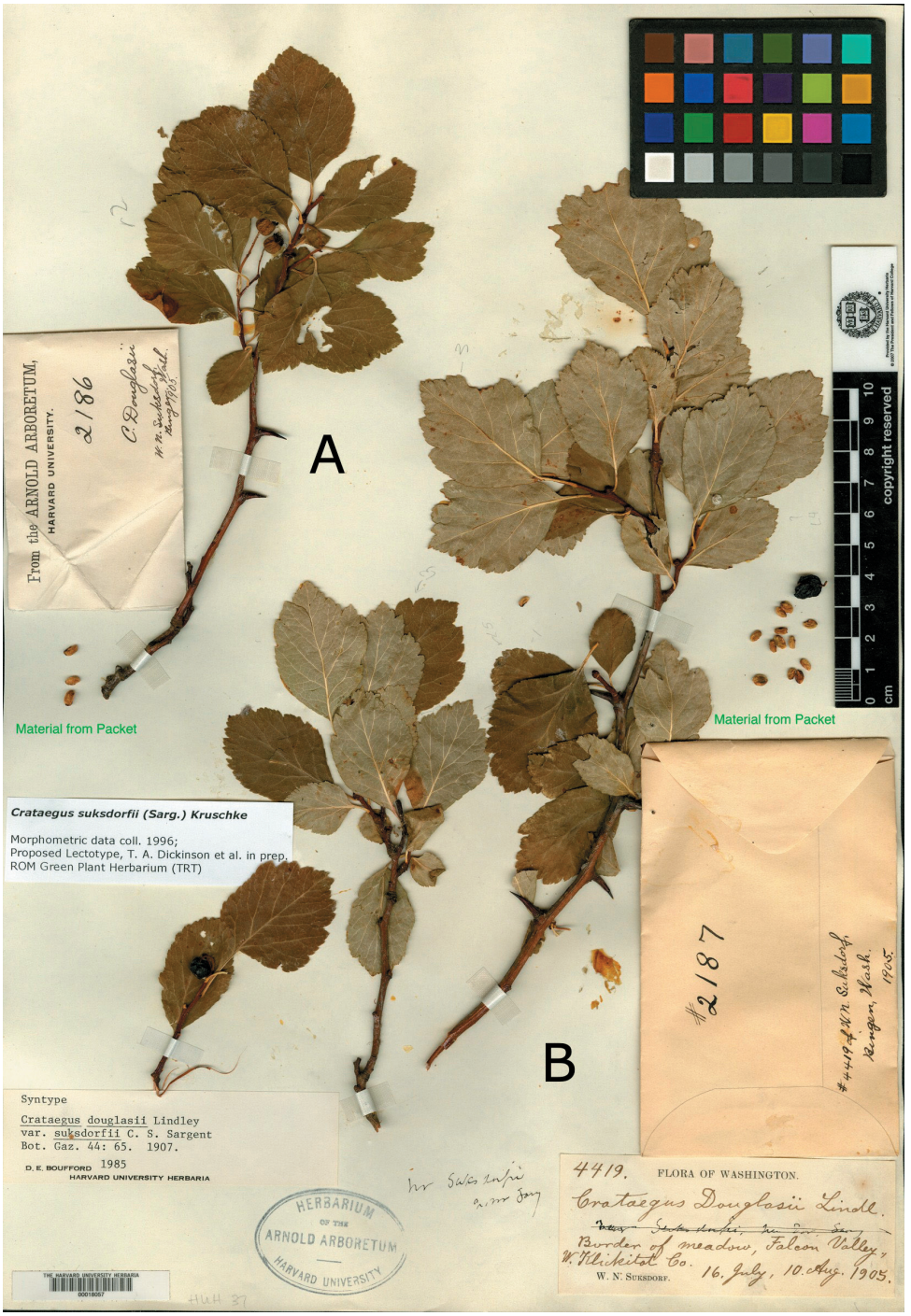

Fig. 9. Holotype designated here of *Crataegus suksdorfii* (Sarg.) Kruschke, *W.N. Suksdorf 4419*, 10 Aug 1905, Falcon Valley, Klickitat Co., Oregon (B; A00018057, the three fragments at the lower right side of the sheet with black fruit). Image courtesy of the Herbarium of the Arnold Arboretum of Harvard University, Cambridge, Massachusetts, USA. Sixty percent of 375 pollen grains from another specimen of this tree (*W.N. Suksdorf 4419*, 7 Jun 1909; WS142845) were found to be doubly-stained when treated with Alexander's stain (Fig. 6).

Crataegus rhodamae-loveae T.A. Dickinson, **sp. nov. (Figs. 8C, 10, 11, 12)**. TYPE: U.S.A. OREGON. Jackson Co.: N side of Lampman Road above Rogue River, ca. 80 m NE of the junction with Highway 99, Aug 2011, *J.C. Coughlan, H. Moothoo, & C. Shaw JC039* (HOLOTYPE: TRT00020284!).

= *Crataegus suksdorfii* (Sarg.) Kruschke sensu lato in part; = *C. gaylussacia* sensu J.B. Phipps (2013, 2015) in part.
= *Crataegus brevispina* Douglas ex Steud., Nomencl. Bot. (Steudel), ed. 2, 1:432. 1840, nom. inval.
= *Crataegus punctata* var. *brevispina* Douglas ex Hook., Fl. Bor.-Amer. (Hooker) 1(4):201 (1832). (**Fig. 10**).

Diagnosis.—Differing from the two other members of *Crataegus* ser. *Douglasianae* with approximately 20 stamens per flower, *C. gaylussacia* A. Heller and *C.* ×*suksdorfii* (Sarg.) Kruschke, in being predominantly a sexual, pollen-fertile diploid (2*n* = 34) rather than an apomictic polyploid; thorns shorter and narrower, 7–12 mm long, 1.5–2.5 mm wide at base; leaf marginal teeth coarser, 6–9 per 1.0 cm adjacent leaf apex, than those of *C.* ×*suksdorfii*; leaves variable in shape, but overall long-elliptic, often longer below the widest point (obovate; 0.7–1.0 × width) than in the other species discussed here. Found west of the Cascades in Oregon and adjacent California and Washington, mostly at lower elevations (10–1,000 m ASL) than *C.* ×*suksdorfii*, allopatric with the other species discussed here; also autopolyploids (2*n* = 51, 68) on the western slopes of the Cascades in Oregon (1,200–1,350 m ASL).

Description.—Trees or shrubs to 7 (–12) m, bark orange-brown on young twigs, becoming gray with age, smooth, but on trunks and large branches flaking irregularly. Thorns 7–12 mm long, straight, 1.5–2.5 mm in diameter at the base. Leaves (microphylls–) notophylls, unlobed (occasionally pinnately lobed), singly to doubly serrate, 6–9 teeth per cm adjacent leaf apexsurfaces pubescent, glabrescent, or glabrous, petioles 11–14 mm long. Flowers with calyx lobes 1–2 mm long, not toothed, stamens 15–20, free, undehisced anthers pink at anthesis, 4–5 styles. Dried fruits 4–7 mm in diameter, purple-black at maturity, with persistent calyx lobes. For images of the type material see https://morphobank.org/permalink/?F1092.

Distribution.—Populations of diploid *Crataegus rhodamae-loveae* are found west of the Cascades summit (Fig. 3; Fig. 1 and 9 in Dickinson et al. 2021), at elevations less than 100 m ASL, apart from ones in Rogue River drainage in Jackson and Josephine Counties, Oregon (300 - 400 m ASL), and those in northwestern California (to 1,000 m ASL). Autopolyploids are found in Oregon at elevations 1,000–1,250 m ASL. These locations correspond to the following ecoregions (Anonymous 2010; Griffith et al. 2016; Thorson et al. 2003): Willamette Valley (Oregon, Washington), Cascades (California, Oregon, Washington), Eastern Cascades Slopes and Foothills (California), and Klamath Mountains (California, Oregon).

Remarks.—Both *Crataegus rhodamae-loveae* and *C. douglasii* were collected by David Douglas on his first trip to the Pacific Northwest, 1825–1827, as is shown by his three sheets of specimens at Kew. In writing up Douglas' collections in the Flora boreali-americana, W.J. Hooker (1832) observed, "Two varieties are in Mr. Douglas's collection from the North-West coast; both, indeed, with short thorns; one is glabrous in every part, the other has the peduncles, calyces, and under-side of the leaves downy." The type of *C. douglasii* (K000442061) is from a tree grown from at the Horticultural Society of London from seeds collected by Douglas in 1826, near the confluence of the Spokane and Columbia rivers (Douglas 1914). Flowers and pedicels on this specimen are glabrous. Maceration of three anthers in Alexander's stain showed virtually all pollen grains to be doubly stained, hence fertile (compare Fig. 6). A second sheet has one specimen (K000442063) labelled "Columbia [John] Scouler," and four more attributed to David Douglas. There are two labels, *Crataegus punctata*, and *Crataegus punctata* var. *brevispina*, corresponding to the entry in W.J. Hooker's Flora boreali-americana Volume 1, Part 4 (Hooker 1832). The first label is associated with three specimens (K000442064, K000442065, K000442066) that have flowers with approximately 10 stamens per flower. The *Crataegus punctata* var. *brevispina* label is next to the fourth specimen (K000442062) and both it and the Scouler specimen have about 20 stamens per flower. This fourth specimen has pubescent pedicels and pollen grains from anthers macerated in Alexander's stain were also almost entirely double stained. The third sheet (K000370425) bears four leafy inflorescences collected by Douglas in 1825 "near the confluence of the Columbia" and is labelled as *Crataegus sanguinea* var. *douglasii* Torr. & A. Gray. All four have flowers with pubescent pedicels and hypanthia, and (15–)20 stamens per flower. Twenty-five pollen grains from anthers of

Fig. 10. ***Crataegus rhodamae-loveae*** **sp. nov.; one of four similar small flowering short shoots collected by David Douglas in April 1825, "near the confluence of the Columbia" (Appendix 1; K000370425); represents the pubescent entity ignored by Lindley (who, in any case, was describing the species grown in the garden of the Horticultural Society). Hypanthium long pubescent, calyx lobes with entire margins, short (< 2 mm). Twenty-five pollen grains from this specimen (piece 3, at the bottom right of K000370425, were found to be doubly-stained when treated with Alexander's stain (Fig. 6); no empty grains were seen. Image © The Board of Trustees of the Royal Botanic Gardens, Kew. Reproduced with the consent of the Royal Botanic Gardens, Kew.**

one specimen (Fig. 10) were all doubly stained, with no sign of any empty grains. The pubescent pedicels were an early indication that specimens collected in Columbia County, Oregon, and Clark County, Washington, by Peter Zika in 2003 with around 20 stamens per flower were different from other *C. suksdorfii* sensu lato material studied up until then. These and other specimens from the same and nearby sites were the first *C. suksdorfii* sensu lato individuals shown to be diploids (Talent & Dickinson 2005). Subsequent collections from elsewhere in the diploid range showed that the correlation between diploidy and pubescence was not constant. However, this does suggest that the pollen-fertile 20-stamen *C. suksdorfii* sensu lato specimens collected by David Douglas probably came from forays he made in the vicinity of Fort Vancouver after his arrival there in early April 1825, and so are likely to represent the first specimens of *Crataegus rhodamae-loveae*.

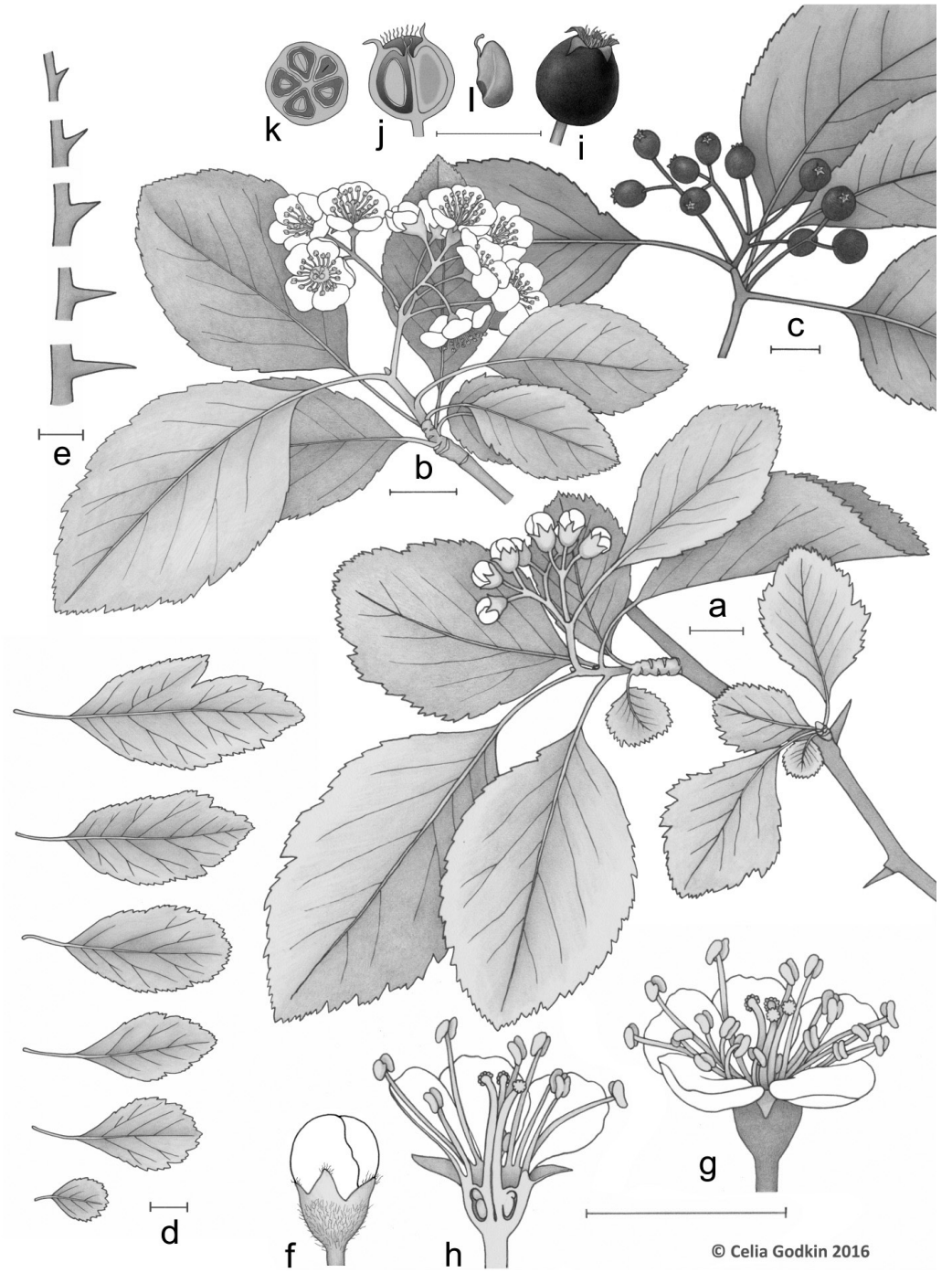

Fig. 11. *Crataegus rhodamae-loveae* sp. nov. (a) pre-anthesis flowering branch; (b) anthesis; (c) fruiting branch; (d) short shoot leaf spectrum; (e) variation in thorn size; (f) flower, pre-anthesis (Kew 000370425); (g) flower at anthesis; (h) median longisection of flower at anthesis; (i) mature fruit; (j) median longisection of mature fruit; (k) median transverse section of mature fruit; (l) individual pyrene. Scale bars = 1.0 cm.

Fig. 12. Holotype of *Crataegus rhodamae-loveae* sp. nov.: U.S.A. Oregon. Jackson Co.: N side of Lampman Road above Rogue River, approx. 80 m NE of the junction with Highway 99, Aug 2011, *J.C. Coughlan, H. Moothoo & C. Shaw JC039* (TRT00020284).

Etymology.—Diploid *C. suksdorfii* sensu lato is named as a new species in honor of Oregon botanist and historian of Pacific Northwest botany, Rhoda M. Love (1932–2022; pp. 19–20 in Meyers et al. 2015). Rhoda Love was the first to study North American hawthorn reproductive biology by means of pollination experiments, introduced the first author to the Oregon flora, and became a valued mentor and colleague. In naming this species we explicitly disagree with Guedes et al. (2023) that eponyms should be avoided. Rather, eponyms can reflect the involvement of the honoree with the plant being named. Such names are an important way for taxonomists to recognize the contributions of others to their work and to the study and preservation of plants and their habitats. This represents an important social dimension of taxonomy that should weigh against possible adverse cultural and political uses of eponyms.

Ploidy level.—Diploids, 2n = 34; also autopolyploids, 2n = 51 and 68, based on chromosome counts (Dickinson et al. 1996) and flow cytometric determinations of nuclear DNA content (N. Talent unpubl. data; Coughlan et al. 2014; Lo et al. 2013; Talent & Dickinson 2005), and analyses of nuclear and plastome DNA sequences (Lo et al. 2009b; Lo et al. 2010; Zarrei et al. 2014).

Hybrid.—*Crataegus* ×*cogswellii* K.I.Chr. & T.A. Dickinson (= ♀ *Crataegus rhodamae-loveae* (diploid *C. suksdorfii*) × ♂ *C. monogyna*) PhytoKeys 36:19 (2014). Individuals with pinnately lobed leaves may represent *monogyna* introgression. For exemplars, see https://morphobank.org/permalink/?F1097.

Conservation Status.—Introgression from sympatric *C. monogyna* could erode the genetic integrity of *Crataegus rhodamae-loveae*.

Paratypes: U.S.A. CALIFORNIA. Siskiyou Co.: T41N R9W S3 N side of Fay Lane, 28 Jul 2006, *T.A. Dickinson & E.Y.Y. Lo 2006-19* (TRT00001569); Fay Lane, 28 Jul 2006, *T.A. Dickinson & E.Y.Y. Lo 2006-20* (TRT00020296); T41N R9W S3 N side of Fay Lane, 28 Jul 2006, *T.A. Dickinson & E.Y.Y. Lo 2006-22* (TRT00001563). **OREGON. Columbia Co.:** Sauvie I, just N of Columbia-Multnomah county line, 20 Aug 2011, *J. Coughlan, H. Moothoo, & C. Shaw, JC119* (TRT00020235); Sauvie I, just N of Columbia-Multnomah county line, 18 May 2011, *J. Coughlan, M. Zarrei, & C. Shaw JC114* (TRT00020171); Diblee Pt., 20 May 2011, *J. Coughlan, M. Zarrei, & C. Shaw JC136* (TRT00020242); Sauvie I, just N of Columbia-Multnomah county line, 2 May 2010, *J. Shiller, J. Tusha, T.A. Dickinson, & M. Heckel 2010-13* (TRT00002011); T7N R2W S6, Diblee Pt., 18 Sep 2003, *P.F. Zika 19064* (TRT00001689). **Douglas Co.:** Upper Elk Meadow, 26 May 1987, *R.M. Love 8766* (TRT00001668); Upper Elk Meadow, 29 Jun 2003, *R.M. Love C-2003-39* (TRT00001669). **Hood River Co.:** Cascade Locks, 20 Aug 2011, *J. Coughlan, H. Moothoo, & C. Shaw JC092* (TRT00020154). **Josephine Co.:** Deer Creek Centre, Deer Creek, at confluence of Squaw Creek, 12 May 2011, *J. Coughlan M. Zarrei, & C. Shaw JC045* (TRT00020323). **Lane Co.:** Patterson Mt. Prairie, 9 Jun 2004, *E.Y.Y. Lo, T.A. Dickinson, S. Nguyen, & R.M. Love EL65* (TRT00001760); Patterson Mt. Prairie, 9 Jun 2004, *E.Y.Y. Lo, T.A. Dickinson, S. Nguyen, & R.M. Love EL52* (TRT00001656). **Linn Co.:** Corvallis, KOA Campground, Aug 2011, *J. Coughlan, H. Moothoo, & C. Shaw JC060* (TRT00020147); Cogswell-Foster Reserve, 10 Jun 2004, *E.Y.Y. Lo, T.A. Dickinson, & S. Nguyen EL68* (TRT00001724). **Multnomah Co.:** 1.5 km NE of Troutdale, 20 Aug 2011, *J. Coughlan, H. Moothoo, & C. Shaw JC098* (TRT00020160); 1.5 km NE of Troutdale, 20 Aug 2011, *J. Coughlan, H. Moothoo, & C. Shaw JC099* (TRT00020162); 1.5 km NE of Troutdale, 20 Aug 2011, *J. Coughlan, H. Moothoo, & C. Shaw JC102* (TRT00020164); 1.5 km NE of Troutdale, 20 Aug 2011, *J. Coughlan, H. Moothoo, & C. Shaw JC103* (TRT00020166); 1.5 km NE of Troutdale, 20 Aug 2011, *J. Coughlan, H. Moothoo, & C. Shaw JC104* (TRT00020372). **OREGON or WASHINGTON:** near the confluence of the Columbia, 30 Apr 1825, *D. Douglas, s.n.* (K000370425); near Ft. Vancouver, 30 Apr 1825, *D. Douglas s.n.* (K000442062); near Ft. Vancouver, 30 Apr 1825, *D. Douglas s.n.* (K000442064). **WASHINGTON. Clark Co.:** T4N R1W S13, ca. 1.5 air mi NNW of Ridgefield, 15 Jun 2003, *P. Zika 18485* (TRT00001805); T4N R1E S5, 4 air mi NE of Ridgefield, 15 Jun 2003, *P. Zika 18486* (TRT00001808).

Appendix 1. Vouchers for morphometric data.

Appendix 2. Vouchers for microsatellite data.

Appendix 3. Vouchers for data on the density of leaf marginal teeth were collected.

Appendix 4. Vouchers for pollen stainability data.

These appendices will be made available as part of MorphoBank Project P832.

ACKNOWLEDGMENTS

We are deeply indebted to the herbaria that lent specimens for this study and (or) made specimen data available online (Appendix 1). We are especially grateful for the permissions received to dissect flowers and remove pollen. Likewise, the research described here would not have been possible without the gift to the ROM of the J.B. Phipps *Crataegus* research collection by the University of Western Ontario (now Western University). Specimens collected by and given to the Phipps collection and to the ROM Green Plant Herbarium

(TRT) by Rhoda M. Love and Peter Zika have been especially important for our research over the years. T.A.D. is indebted to landowners for permission to collect *Crataegus* species on their properties. We acknowledge the Cunningham Marsh Preservation Committee, Point Reyes National Seashore, Siskiyou Field Institute, D. Smith, W. Earle, M. Graham, B. Jensen, G. Cooley, R. Thompson, J. Herrick, R. & M. Johnson, A. Anderson, T. Steen, G. Powell, R. & J. Pojar, C. Delong, B. Rogers, H. Massicotte, L. Tackaberry and J. Lee for information concerning and access to collection sites. We thank J. Pojar (BC Forest Service) and M. Stensvold (USDA Forest Service, Sitka AK) for information on *Crataegus* occurrences in Alaska. Many of the collections could not have been made without the help of field guidance from R. Dotterer, R.M. Love, J.B. Phipps, and the late Steve Brunsfeld. We also thank the collectors listed in Appendix 1 for their assistance in the field, notably J.M. Coughlan and M. Zarrei. We thank N. Talent for her collection, photos, specimen identifications, and flow cytometry expertise, and K. Brown, K. Buck, T. Harding, R. Martin, C. Ng, L. Podvoiskaia, for specimen curation, data collection, and laboratory assistance. The late Barbara Schulz undertook to translate W.N. Suksdorff's manuscript draft of the data table he sent to C.S. Sargent. Jen Shiller and J. Tusha took part in a University of Toronto 399 Research Excursion Program that collected specimens and yielded data on pollen production and stainability. Deborah Metsger managed the move of the Phipps collection to the ROM and its accessioning into TRT. Brenna Wells maintains the herbarium database from which specimen data in Appendices 1–4 were drawn. TRT staff and volunteers processed and helped curate specimens. T.A.D. is indebted to Celia Godkin for the illustration of *Crataegus rhodamae-loveae* (Fig. 11), and to R. Schmickl (Prague) and R. Ufimov (Vienna) for discussions of *Crataegus* phylogeny. Photographic images of plants and type specimens were kindly provided by the Harvard University Herbaria, the Hunt Institute for Botanical Documentation (Carrie Roy), the Herbaria of the Royal Botanic Garden, Kew (S. Zmarzty), and K. Morse. This research was funded by the Royal Ontario Museum (ROM) Future Fund, the Department of Museum Volunteers, and the Governors of the Royal Ontario Museum, and by the ROM/ROMCA (Royal Ontario Museum Curatorial Association) Special Research Fund, 2014–2019; Discovery Grant A3430 (re-applied for at 3–5 year intervals), from the Natural Sciences and Engineering Research Council of Canada (NSERCC), 1987–2015; and NSERCC Strategic Project Grant (381073), 2010–2012, joint with Prof. S. Stefanović (University of Toronto–Mississauga), Paul Shipley (University of British Columbia–Okanagan), S. Proctor (University of Alberta) and the Naturally Grown Herb and Spice Growers Co-operative (HerbPro; Edgewood BC, J. Lee, President); P. Brown (British Columbia Institute of Technology) materially assisted us in obtaining this grant. Funding from the Canada Foundation for Innovation, NSERCC, and the Université de Montréal provided the Canadensys infrastructure and equipment that made possible imaging the TRT specimens and deployment of the specimen data and images via the Canadensys and GBIF portals. We are indebted to the Robarts Library of the University of Toronto, and Sian Meikle and Nancy Fong, for making possible the online availability of these TRT *Crataegus* specimen images (Appendices 1–4). Fieldwork and data collection by Shiller and Tusha in 2010 were supported by a grant from the University of Toronto Faculty of Arts and Science. S.H.'s participation was funded in part by her 2012 NSERCC Undergraduate Student Research Award. Several of the student assistants acknowledged above were co-funded by the University of Toronto Work Study program; all of the University of Toronto and NSERCC funding was facilitated by the Department of Ecology and Evolution (and its predecessor, the Department of Botany). Finally, helpful, supportive reviews of the manuscript from Gerry Allen and Ron Lance are gratefully acknowledged.

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