WHAT IS DOUGLAS HAWTHORN?

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Abstract: The reproductive biology of hawthorns is critical for understanding their diversification. Only recently has substantially more been learned about northwestern hawthorn than was the case due to the pioneering phase of botanical exploration in the region. Self-incompatibility, self-fertility, and gametophytic apomixis all occur. In the Pacific Northwest cytotypes and morphotypes of black-fruited Douglas hawthorns (Crataegus section Douglasii) are distinguishable but are not perfectly concordant in their variation. Differences in floral development between morphotypes suggest how morphotype differentiation may have come about. This differentiation has been driven, not only in section Douglasii but repeatedly in almost all North American sections of the genus, by hybridization, polyploidization, and responses to various selective pressures on different aspects of reproduction. We review progress to date in synthesizing data on variation in reproductive biology and morphology in order to answer the question posed in the title. A minimum of three taxa should be recognized: C. douglasii Lindley, C. suksdorfii (Sargent) Kruschke, and C. rivularis Nuttall. In addition to exploring the possible hybrid origin of C. douglasii, the affinities of all three taxa with other black-fruited taxa in both Asia and North America need to be studied further.

Key words: Crataegus douglasii, meristic variation, systematics, evolution


INTRODUCTION

The simple answer to the question posed in our title is "Crataegus douglasii Lindley." However, any repeated examination of northwestern hawthorn leads to the questions, "which black-fruited hawthorn is C. douglasii, what are the others, and why all this confusion?" We believe that answers to these questions lie in the examination of Crataegus section Douglasii and its taxonomic history, the phenetic variation it exhibits, its breeding systems and chromosome number variation, and its floral development and floral biology. Here we review progress to date in each of these areas, in order to give the answer to the title question as it stands at present.

TAXONOMIC HISTORY

Black-fruited Crataegus section Douglasii occurs in the Pacific Northwest and Rocky Mountains. The first collection of these plants was made by Lewis and Clark in April 1806, along the Columbia River at the start of their return journey eastward (Meehan, 1898; Sargent, 1902, fn. p. 35). However, although labelled as "Deep purple Haw," Lewis and Clark's specimen was ascribed to the scarlet-fruited C. glandulosa Wild. (synonym C. sanguinea Pallas, Mespilus rotundifolia Ehrh.) by F.T. Pursh in his Flora Americana septentrionalis (Pursh, 1814).

David Douglas was the first botanist to draw concerted horticultural and scientific attention to North American black-fruited hawthorns, by means of collections made in the course of his first collecting trip to the Pacific Northwest for the Horticultural Society of London. In April 1825, a few weeks after disembarking from the Hudson's Bay Company ship William and Ann, he and his friend the ship's doctor, John Scouler, collected hawthorns in the vicinity of Fort Vancouver (Douglas' number 129, "Crataegus sp.;", Douglas, 1914). Douglas' diary indicates that he collected hawthorns along the Columbia River (not the Colorado River, as noted by Sargent 1892, and repeated by Kruschke 1965) not only near the coast but also in the interior. On 13 April 1826 he was near the confluence of the Columbia and Spokane Rivers, packing up seeds to be carried back to England, when he recorded that

...
Douglas's and Scedler's specimen (Figure 1) were described as C. punctata along with W. J. Hooker (Hooiker, 1833), who cited "Douglas. MSS. 2628, Herb. Hort. Soc. Lond." as the authority for this name (Hooker, 1832). Hooker observed that Douglas's collections comprised two varieties, "... one has a flat seed in every part, the other has the peccules, calyces, and under-side of the leaves downy." In the meantime, the Hawthorn seeds collected by Douglas were grown out by the Horticultural Society. In 1834 Douglas was in the Hawaiian Islands and died as a result of an untimely and mysterious accident. He was honored posthumously the following year by J. Lindley, (1835) who cited "Douglas, MSS apud. Herb. Hort. Soc. "Society. In 1834 Douglas was in the Hawaiian Islands, and travelled to the Pacific Northwest overland with the Wyeth Party. His C. douglasii, described based on material cultivated by the Horticultural Society (Lindley, 1835; 1838) (Figure 2). Lindley's specimen was the basis for C. douglasii Scedler, a group of black-fruited Hawthorns distinguished by their relatively unlobed leaves in the subgenus classification published by J. Loudon in his Arboretum et Fruticetum Britannicum (1838).

Thomas Nuttall was the next botanist to encounter C. douglasii, in the year of Douglas' death, when he traveled to the Pacific Northwest overland with the Wyeth expedition. He described and illustrated what we know as C. douglasii as C. sanguinea Palis (Torrey and Gray, 1840), writing that when other supplies of fresh fruit or vegetables had been exhausted, "... the ripe berries produced by the Hawthorns were collected with avidity" (Nuttall, 1865). His C. rivulata (Figure 3), from the Rocky Mountains, was first published by Torrey and Gray (1840). In his own description (Nuttall, 1865), he speculated that Douglas may also have observed this plant, "in the interior of Oregon," going on to suggest that it represents "... all in probability, the smoother, supposed variety of C. punctata, mentioned by Hooker in his Floras."

Other black-fruited western Hawthorns were described around the turn of the century, including C. sanguinea var. brevispina, as described by C. douglasii as C. sanguinea Palis (Torrey and Gray, 1840), writing that when other supplies of fresh fruit or vegetables had been exhausted, "... the ripe berries produced by the Hawthorns were collected with avidity" (Nuttall, 1865). His C. rivulata (Figure 3), from the Rocky Mountains, was first published by Torrey and Gray (1840). In his own description (Nuttall, 1865), he speculated that Douglas may also have observed this plant, "in the interior of Oregon," going on to suggest that it represents "... all in probability, the smoother, supposed variety of C. punctata, mentioned by Hooker in his Floras."

Ernest J. Palmer began his work on C. douglasii under Sargent's tutelage, and in his earlier work on the genus (Palmer, 1935; 1932) he apparently accepted the idea that differences in stamen and style length were of the same species level. After Sargent's death in 1932 Palmer's work on the genus led him to synonymize many of Sargent's species. Among these, C. brevicaulis was synonymized with C. douglasii in the case of section Crus-Galii in his "Illustrated Flora of the northeastern United States and adjacent Canada" (Palmer, 1946). Subsequently, however, Palmer apparently reconsidered this approach, and in his revisited edition of both Missouri and northeastern C. douglasii (Palmer, 1963a; Palmer, 1960) he combined a great many entities with different stamen numbers as conspecific varieties or forms.

Working in Wisconsin during the 1950s and 1960s, Emil P. Krauschke was much more emphatic in the opinion that 20- and 30-stamen Hawthorns could not belong to the same species (Krauschke, 1965). Accordingly, Krauschke raised C. douglasii var. siskiyouensis to species rank, although without typifying it. In Ontario, Phillips and Muqyammya (1980) documented 10 series in which some species have approximately 20 stamens per flower while the others have approximately 10 stamens per flower. In some cases the stamen number characters are clearly distinct, based on correlated variation in a number of other characters, as described elsewhere (Rickett, 1946; Rickert, 1957; Dickinsson and Phipps, 1985; Dickinson and Campell, 1991). In most of the morphotypes, black-fruited species occupying a substantially wider range of moisture conditions than var. douglasii. Thus, at
some relatively mesic sites on the eastern slopes of the Cascades in Washington, or in Idaho and western Montana, both forms are present. At drier sites, like most of those at which black-fruited hawthorns are found in eastern Oregon and Washington, only var. douglasii occurs.

The disjunct distribution of eastern C. douglasii was noted by Fernald (1935) and has been discussed by Marquis and Voss (1984), Brunsfeld & Johnson (1990), and Dickinson et al. (in press). Marquis (1994) suggested that the distributions of woody species with fleshy fruits that have populations in the Great Lakes basin disjunct from larger ones in western North America (e.g., Opisopanax hirtellus, Vaccinium membranaceum, Rubus parviflorus) are difficult to explain by eastward post-glacial dispersal, given the presence of Lake Agassiz, subsequently the increasing aridity of the Great Plains, and the lack of east-west animal migration patterns. On the other hand, however, eastward routes could have involved the shorelines of periglacial Lakes Agassiz and Barlow-Ojibway 9–11 k y ago (Marquis and Voss, 1981; McAndrews, Liu, Manville, Press and Vincent, 1987; Breziliev and Whetstone, 1993).

MORPHOLOGY AND REPRODUCTIVE BIOLOGY

The discovery that Crataegus section Douglasii comprises morphotypes with flowers whose modal numbers of stamens are either approximately 20 or approximately 10 per flower mirrors what has been found in most other groups of North American—but not Eurasian—hawthorns (Christensen, 1992; Brunsfeld and Johnson, 1994; and compare observations by Eggelston, 1908a and Schneider, 1906). Differentiation with respect to floral architecture in section Douglasii (Dickinson et al., in press) may be accompanied by variation in leaf and stem morphology (Figure 1–6; Brunsfeld, 1993); this variation is currently being documented across the range of the section. Variation in breeding system and chromosome number is frequent in the Maloideae (Campbell et al., 1992) and there are several parallel differences in reproductive and vegetative morphology (Dickinson, 1986; Dickinson and Phipps, 1986), but only up to a point (Dickinson et al., in press). Gametophytic apomixis, polyplody, and self-compatibility have been demonstrated in C. douglasii var. douglasii, while diploidy and self-incompatibility have been shown to occur in C. douglasii var. suksdoljii (Taylor and Mulligan, 1968; Love and Feigen, 1978; Brunsfeld and Johnson, 1990). However, gametophytic apomixis and polyplody also occur in var. suksdoljii (Dickinson et al., in press). Unlike Amelanchier (C. S. Campbell, unpublished data), it still remains to be shown with what frequency sexually and sexually produced offspring occur in seed famillies of hawthorns in which gametophytic apomixis occurs. No data whatsoever are available concerning the relative success of sexually and asexually produced Maloid individuals.

FLORAL DEVELOPMENT

New information on the repeated variation in stamen number observed in North American hawthorns comes from an examination of floral development in section Douglasii by Evans (Evans and Dickinson, 1996). In summary, Evans demonstrated that the differences in stamen number between C. douglasii var. douglasii (both eastern and western) and suksdoljii, and C. rivularis, were due to the failure to initiate, in the 10-stamen taxa, two additional whorls of stamens that are formed in the 20-stamen ones. Departures from perfectly pinnate arrangements of either 10 or 20 stamens per flower were associated with distortions of the floral apex that reduced the space available for the initiation of stamen primordia.

PHYLOGENY

A preliminary attempt at reconstructing phylogenetic relationships between North American and Eurasian black-fruited hawthorns was made, in order to organize the data available and to explore alternative hypotheses. A suite of seven characters (Table 1) was scored for eight taxa (Table 2), based on information from herbarium specimens and the literature (see citations in Table 2). Two of the eight taxa are artificial, and represent similar black- (Nigrae-Penlagynae) or red-fruited (Sangaminae-Crataegus) series from different sections (Table 2). These were created in order to reduce the number of taxa, given the limited number of characters available, and because the component entities differed little from each other (i.e., not at all with respect to the character-states employed; Table 2). Phylogenies were inferred with PHYLIP 3.5 (Felsenstein, 1993). Program PENNY was used to find all shortest trees under the constraint that section Douglasii is monophyletic (by using character weights); Felsenstein, (1993) and without this constraint. The constrained analysis yielded five trees of 16 steps, and the unconstrained analysis 23 trees of 13 steps. Program CONSENSUS was used to summarize these trees at strict (five trees) or majority-rule (23 trees) unrooted consensus trees (Figure 7–8). MacClade (Maddison and Maddison, 1992) was used to draw trees and to trace character-state changes on them. When the Douglasii taxa were not constrained to form a monophyletic group (Figure 8) there was consistently a clade made up of the four 20-stamen taxa other than section Crat­
galli. Re-rooting this tree at the red-fruited Sangaminae-Cra­taegus had the effect of making that taxon paraphyletic with the remaining three 20-stamen black-fruited taxa (Figure 7). The same effect was achieved by re-rooting the constrained tree (Figure 8). Cladistic relationships between sections Crat­
galli and the three western 10-stamen taxa (douglasii, piperi, rivularis) were more varied. The propensity for an associa­tion between the latter three could be taken as support for the hypothesis that the two black-fruited ones originated in crosse...
between C. douglasii var. suksdorfii and C. pieri (see below). Only one more character-state change is required by the five trees in which the C. douglasii var. suksdorfii and C. pieri have expanded the concept of var. Douglasii! So WHAT IS C. DOUGLASII? Careful examination of the literature and of the specimens available to 19th and early 20th century workers suggests the following points. (1) As pointed out by Hooker (1832), Douglas' states were scored based on measurements of only a small number of specimens; more rigorous sampling is essential for differentiation that exists between \( C. \) douglasii and \( C. \) gaylussacia. (2) How they are controlled during development (e.g., calyx lobe margination, leaf lobing) or because they represent size changes (thorn length). In this preliminary analysis, character-states were scored based on measurements of only a small number of specimens; more rigorous sampling is essential for a definitive analysis (Stevena, 1991, 1996). Stamen number was not used, in part so to observe its behavior as a dependent variable, and in part because it appears to be highly correlated with style number. Ploidy level was not used since it varies within the taxa considered, rather than between them. Further work is required to understand evolving characters, develop new ones (e.g., from molecular data), and so increase the number of taxa that can be considered.

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